Direct and Indirect Estimation of Leaf Area Index, f_{APAR}, and Net Primary Production of Terrestrial Ecosystems

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A primary objective of the Earth Observing System (EOS) is to develop and validate algorithms to estimate leaf area index (L)*, fraction of absorbed photosynthetically active radiation* (f_{APAR})*, and net primary production (NPP) from remotely sensed products. These three products are important because they relate to or are components of the metabolism of the biosphere and can be determined for terrestrial ecosystems from satellite-borne sensors. The importance of these products in the EOS program necessitates the need to use standard methods to obtain accurate ground truth estimates of* L*,* f_{APAR}*, and NPP that are correlated to satellite-derived estimates. The objective of this article is to review direct and indirect methods used to estimate* L*,* f_{APAR}*, and NPP in terrestrial ecosystems. Direct estimates of* L*, biomass, and NPP can be obtained by harvesting individual plants, developing allometric equations, and applying these equations to all individuals in the stand. Using non-site-specific allometric equations to estimate* L *and foliage production can cause large errors because carbon allocation to foliage is influenced by numerous environmental and ecological factors. All of the optical instruments that indirectly estimate* L *actually estimate "effective" leaf area index* (L_E) *and underestimate* L *when foliage in the canopy is nonrandomly distributed (i.e., clumped). We discuss several methods, ranging from simple to complex in terms of data needs, that can be used to correct estimates of* L *when foliage is clumped. Direct estimates of above-ground and below-ground net primary production* (NPP_A *and* NPP_B*, respectively) are laborious, expensive and can only be carried out for small plots, yet there is a great need to obtain global estimates of NPP. Process models, driven by remotely sensed input parameters, are useful tools to examine the influence of global change on the metabolism of terrestrial ecosystems, but an incomplete understanding of carbon allocation continues to hamper development of more accurate NPP models. We summarize carbon allocation patterns for major terrestrial biomes and discuss emerging allocation patterns that can be incorporated into global NPP models. One common process model, light use efficiency or epsilon model, uses remotely sensed* f_{APAR}*, light use efficiency (LUE) and carbon allocation coefficients, and other meteorological data to estimates NPP. Such models require reliable estimates of LUE. We summarize the literature and provide LUE coefficients for the major biomes, being careful to correct for inconsistencies in radiation, dry matter and carbon allocation units.* ©*Elsevier Science Inc., 1999*

INTRODUCTION

Humans have affected and continue to affect the Earth. For example, large areas have undergone land use change (e.g., deforestation, desertification), the chemical composition of gases in the atmosphere has been altered, surface water and aquifers have been contaminated, and atmospheric deposition of nitrogen and sulfur have begun to change the biogeochemical cycles in terrestrial and aquatic ecosystems. These changes are well documented (IPCC, 1995), but their effects on the sustainability of life are not fully understood. Mission to Planet Earth (MTPE), a NASA-initiated program that uses space-, ground-, and aircraft-based measurement systems, was founded to improve the understanding of the fundamental processes that define the Earth system

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(Asrar and Greenstone, 1995). The processes include hydrologic, biogeochemical, atmospheric, ecological, and geophysical phenomena, all of which influence the composition, structure, and function of terrestrial ecosystems. An essential program of MTPE is the Earth Observing System (EOS)—a comprehensive science-driven Earth system research program. EOS is designed to provide long-term high quality remotely sensed data for a large percentage of the surface of the Earth with a high spatial and spectral resolution. Remote sensing uses radiance data obtained from air- or satellite-borne sensors to indirectly measure key characteristics of the biosphere. Accurate use of processed radiance data requires scientists to first develop algorithms or models that relate the land surface or atmospheric characteristics to the radiance data. Therefore, the success of EOS is highly dependent upon accurate "ground-truth" or direct measurements. A second requirement is that the ground measurements are made using consistent or uniform methods to ensure data compatibility. The latter issue is a concern when small data sets, from individual studies, are combined to determine if regional or global relationships exist (Goward and Dye, 1997).

The objectives of this article are to review current direct and indirect methods used to measure leaf area index (*L*), fraction absorbed photosynthetic active radiation (f_{APAR}), and net primary production (NPP) of terrestrial ecosystems. Where possible, we compare different indirect approaches of estimating *L* to direct estimates. Leaf area index is selected because of its important influence on the exchange of energy, water vapor, and carbon dioxide between terrestrial ecosystems and the atmosphere (Bonan, 1993). The importance of *L* is clear because most ecosystem process models that simulate carbon and hydrologic cycles require *L* as an input variable. Net primary production is a useful indicator of the metabolism of the ecosystem and is an important component of net ecosystem exchange or net ecosystem productivity. Unfortunately, few studies measure fine root and mycorrhiza net primary production (NPP_{FR})—a significant component of NPP. In this article we summarize root:total net primary production ratios to determine if general allocation rules can be used in global NPP models. NPP can be indirectly estimated by measuring the seasonal or annual incident photosynthetically active radiation that is intercepted or absorbed by the canopy and assuming a light use efficiency (LUE) value. This indirect approach has a sound physiological basis (Landsberg et al., 1997; Haxeltine and Prentice, 1996) and is the basis for numerous global NPP models because f_{APAR} can be remotely sensed (Goward and Dye, 1995). However, this approach requires accurate estimates of LUE—a coefficient describing the conversion of light to organic matter by plants. In doing so, care must be taken to ensure that standard units of radiation and organic matter are used.

MEASURING LEAF AREA INDEX

A number of direct and indirect methods have been used to estimate *L*. Direct measurement approaches include area harvest, application of allometric equations to stand diameter data, and leaf litterfall. Numerous commercially available instruments, such as Decagon ceptometer, Li-Cor LAI-2000, DEMON and TRAC, are used to indirectly estimate *L* (Fassnacht et al., 1994; Chen et al., 1997); all of the instruments measure light transmittance and assume foliage is randomly distributed in the canopy. Below we review the more common direct and indirect approaches used to estimate *L*.

DIRECT MEASUREMENTS OF *L*

Area harvest involves the periodic destructive sampling of vegetation in plots during the growing season. The plots should be located randomly in a single community or stratified if more than one community is to be studied. The harvested foliage tissue is subsampled for specific leaf area (SLA, the ratio of fresh leaf area to dry foliage mass) determination, and the remaining foliage mass is dried to a constant mass. Plant tissue samples should be dried at 60–70°C; higher temperatures should be avoided because they may volatilize compounds. If more than one species is present, separate estimates of leaf biomass and SLA should be obtained for each species because they differ among species (Landsberg and Gower, 1997). When sampling the foliage in the canopy, vertical stratification is required to account for the decrease of foliage:branch mass and SLA deeper in the canopy. Also some attempt should be made to characterize the SLA for each age-cohort of foliage because SLA can differ by twofold from new to old foliage (Landsberg and Gower, 1997).

The area harvest approach is more appropriate for short-stature ecosystems (e.g., grasslands, agriculture crops, tundra) than for forests because this approach is very laborious when done for an area of sufficient size to adequately characterize the spatial heterogeneity. Alternatively, leaf area can be estimated from allometric relationships applied to each tree surveyed in randomly located plots in the community of interest. Allometry is the relationship between the mass or area of a part (e.g., leaf mass or area), or all of an organism, and an independent variable. The dependent variable is indirectly estimated because it is difficult, and often laborious, to measure. The independent variable commonly used to estimate leaf mass or area is stem diameter or sapwood cross sectional area. Direct measurement of biomass and area of plant parts using allometry involves harvesting plants that encompass the size range encountered in the survey plots, measuring the fresh mass of each component and subsampling each tissue for water content. The dry mass of each tissue on a tree is calculated as the product of the total wet mass of each tissue × the dry: wet mass of each tissue. An example of the detailed description of the field methods used to destructively harvest trees to determine the mass and area of the biomass components is provided by Gower et al. (1992) and Gower et al. (1997).

A mathematical relationship is fit to the data, generally of the form in Eq. (1),

$$M_D \quad or \quad A = aD^b, \tag{1}$$

where M_D or A is dry mass or area, respectively, of a plant part, D is stem diameter, usually at breast height (i.e., D_{BH}), and a and b are regression coefficients. D is usually measured at breast height (1.37 m) for trees or at the soil surface for small plants (e.g., shrubs, seedlings). The relationship depicted in Eq. (1) follows a power or exponential form and assumes a uniform variance (i.e., homoscedasiticity) of the dependent variable over the range of the independent variable. Often researchers describe the allometric relationship using Eq. (2),

$$log\ M_D \quad or \quad log\ A = a + b(log\ D), \tag{2}$$

where log is the natural or $base_{10}$ logarithmic transformation. Equation (2) is preferred over Eq. (1) for two reasons. First, the assumption of homoscedasiticity is often violated: the variance of the dependent variable often increases as D increases. The double logarithmic transformation model in Eq. (2) consistently corrects for this problem compared to other models (e.g., $A=a+bD$, or $A=a+b(\log D)$ models (Appendix). Either the natural or $base_{10}$ logarithmic transformation can be used; both will yield the same b coefficient (i.e., slope) although the a coefficient (Y intercept) will differ. From a practical standpoint, the $base_{10}$ transformation better lends itself to graphical presentations. A second advantage of using Eq. (2) is that it facilitates the statistical comparison of two or more allometric equations because the comparison of two or more allometric equations is more difficult for curvilinear than linear relations. The predicted value derived from Eq. (2) has a small downward bias because of the logarithmic transformation. All allometric equations should be corrected for logarithmic bias using Eq. (3) (see Sprugel, 1983):

$$CF = exp((2.303 * (MSE^{0.5}))^2/2), \tag{3}$$

where CF=correction factor that the dependent variable should be multiplied by, and MSE=$\log_{10}$ transformed regression mean square error.

Allometric equations relating foliage mass to stem diameter (D) or sapwood cross sectional area (A_S) at breast height (1.37 m) can be used to directly estimate L if specific leaf area (SLA) is known, where SLA is the ratio of fresh foliage surface area to unit dry foliage mass. Specific leaf area is an important physiological characteristic because it is positively correlated to maximum photosynthetic rate and percent leaf nitrogen concentration—key determinants of productivity (Reich et al., 1995). Specific leaf area is also an important parameter in ecosystem process models because it provides the coefficient to convert foliage mass to leaf area (Landsberg and Gower, 1997). Unfortunately, there is no consistent basis for defining SLA; the lack of a standard definition has caused great confusion in the literature and hampered synthesis activities. Specific leaf area values reported in the literature are expressed on a projected, single-sided, total, and one-half the total surface area basis. The inconsistent definition of SLA can in part be attributed to the poor theoretical understanding of radiation interception by nonflat leaves such as conifer shoots (Chen and Black, 1992). Often scientists provide insufficient description of how SLA was measured for other scientists to convert SLA to a common basis for comparison or model parametrization. For example, if needles are shaped like cylinders (some pines), then a conversion factor of π (3.1416) should be used to convert projected leaf area to total leaf area (Grace, 1987). However, if needles have a square cross section (e.g., black spruce, *Picea mariana*), the conversion from projected area to surface area depends on how the leaf was projected. Unless extreme care is exercised in documenting how projected-area measurements are made, the data may be unreproducible by others and become the source of large errors (e.g., the diagonal of a square is 40% larger than one side and with the slight twist typical of many needles the orientation may be unknown). To avoid further confusion, we recommend that scientists report SLA on the basis of half the total needle surface area—we refer to this quantity as hemisurface area (HSA). A quick, and accurate method for estimating total leaf surface area is summarized by Chen et al. (1997). One half the total leaf area is the appropriate parameter for radiation transfer models and is useful when comparing different leaf shapes. For flat leaves, HSA is the same as projected leaf area.

Developing site-specific allometric equations is laborious; therefore scientists commonly use existing allometric equations. Numerous publications present allometric relationships between leaf area and stem diameter (e.g., Gholz et al., 1979; Gower et al., 1998). Using general allometric equations to estimate L for a specific stand can result in moderate to large errors because numerous abiotic and biotic factors influence the allometry coefficients (Fig. 1A). Grier et al. (1984) calculated foliage biomass for five Douglas-fir (*Pseudostuga menziesii*) stands using site-specific and generalized regression equations and found the generalized equations produced errors ranging from −8% to +93%. The large differences in foliage mass translate to similar differences in L.

An understanding of the factors that influence leaf mass or area allometric equations can be used to help select an appropriate allometric equation, when more

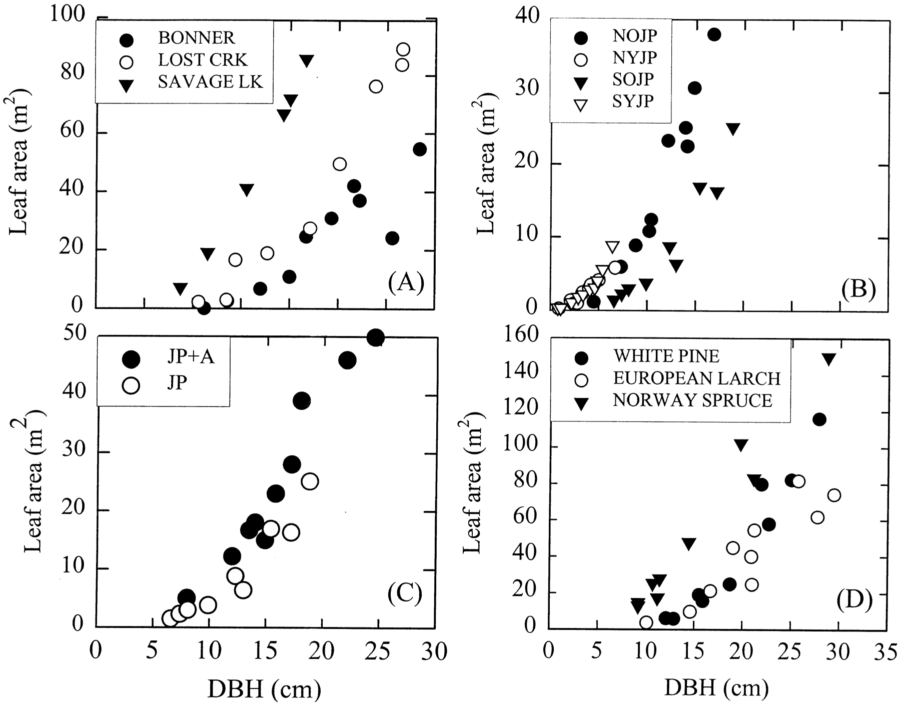

Figure 1. Relationship between leaf area and stem diameter for select tree species illustrating the influence of a) environment, b) tree size, c) nitrogen availability, and d) leaf longevity. a) Comparison of leaf area allometric equations for three western larch stands in contrasting climates (Kloeppel, 1998). b) Comparison of leaf area allometric equations for young and old jack pine trees (Gower et al., 1997). c) Comparison of leaf area allometric equations for jack pine trees grown with and without a nitrogen fixing green alder understory (Vogel and Gower, 1998). d) Comparison of leaf area allometric equations for three conifers with different leaf longevities grown in adjacent plots (Gower et al., 1993b). For each example (a–d), the slope and/or the intercept coefficient(s) differ significantly ($p<0.05$).

than one equation exists. One factor that strongly influences the allometric coefficients is tree size. Estimating the leaf area of trees that have diameters that exceed the diameter range for the trees for which the equation were developed results in moderate to large over-estimates of leaf area (Fig. 1B). This same pattern has been reported for temperate forest tree species (Grier and Milne, 1981; Marshall and Waring, 1986). Nutrient availability also influences the allometric coefficients. For example, boreal jack pine (*Pinus banksiana*) trees growing with a nitrogen-fixing green alder (*Alnus creneta*) understory support a greater leaf area than trees without the N-fixing alder (Fig. 1C). Other scientists have also shown that fertilization influences the allometry of new foliage mass or area (Brix and Mitchell, 1983; Grier et al., 1984; Gholz et al., 1991; Gower et al., 1992). The influence of nutrient availability on leaf area allometry is suppressed if water availability is more limiting (Gower et al., 1993a). Leaf area allometric equations differ among plant species as well (Fig. 1D). For a similar diameter, trees with a greater leaf longevity support a greater leaf area (Gower et al., 1993b). Also, shade-tolerant species support a greater leaf area than shade intolerant species (Grier and Logan, 1977; Chapman and Gower, 1991). We conclude that site-specific allometric equations should be developed when accurate estimates of L are needed (i.e., EOS validation program). Scientists should use caution in selecting the allometric equation used to estimate L if site-specific allometric equations cannot be developed. The two most important criteria to consider when selecting allometric equations are correctly matching the plant species and size.

A slight variation of the allometric equation is the pipe model, which correlates the cross-sectional area of a stem or branch that is responsible for water transport (i.e., sapwood) to foliage mass (Shinozaki et al., 1964a,b). More recently, leaf area is used in place of foliage mass because transpiration is correlated to foliage surface area, not foliage mass. The form of the pipe model is usually linear. The physiological basis of the relationship between leaf area and cross-sectional sapwood area implies that the pipe model may alleviate the need for site-specific allometric equations. For example, Waring et al. (1982) reported that the ratio of projected leaf area:sapwood cross-sectional area differs very little (0.15–0.18) for lodgepole pine (*Pinus contorta*) in three contrasting environments. However, Figures 2a and 2b illustrate that the pipe model is influenced by the same environmental and ecological factors that affect the allometric coefficients in Eq. (2). The patterns shown in Figures 2a and 2b are representative of the results from other studies (Waring et al., 1984; Brix and Mitchell, 1983; Whitehead et al., 1984; Gower et al., 1993b; Mencuccini and Grace, 1995).

We do not attempt to review field methods to characterize the detailed canopy architecture (i.e., branch and needle angles, etc.) of plant communities. Such measurements are several to tenfold times more time consuming than determining biomass and area of plant parts and few data are available. Pertinent articles related to this topic include Lang (1990) and Fournier et al. (1996).

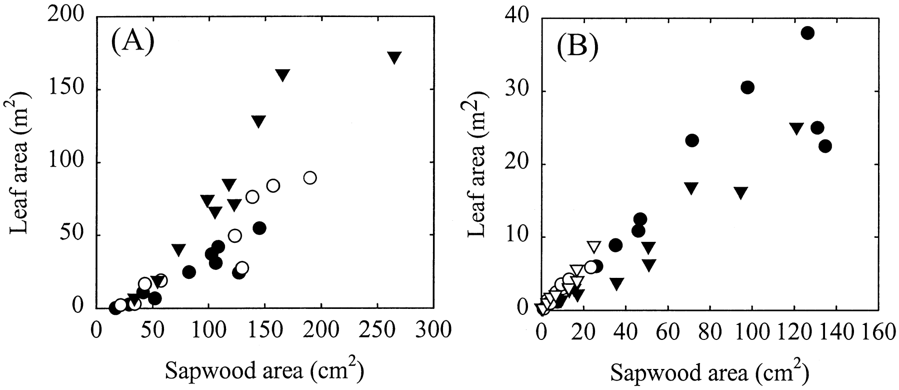

Figure 2. Leaf area sapwood allometric relationships for a) jack pine and b) western larch trees. Sources of data are S. T. Gower (unpublished data) and Kloeppel (1998).

ESTIMATING LEAF AREA INDEX USING INDIRECT MEASUREMENTS OF CANOPY GAP FRACTION

Recently, much emphasis has been placed on using indirect optical measurement techniques, particularly suited to measuring the canopy gap fraction, to estimate L of vegetation canopies. Several optical instruments that measure the canopy gap fraction from beneath, or within, plant canopies, over a range of zenith angles are now commercially available (Welles, 1990; Welles and Cohen, 1996). In this section we discuss the fundamental theory used to estimate L and highlight the strengths, weaknesses, and potential pitfalls of estimating L from multiangular canopy gap fraction measurements. We conclude with a comparison of direct and indirect measurements for canopies of forest and agriculture crops and discuss sample size requirement.

THEORY

For canopies that exhibit a random distribution of foliage elements (i.e., leaves, needles, stems, branches, shoots), L can be derived from the probability that a beam of direct radiation will pass unobstructed through a canopy. The penetration of direct beam radiation through any canopy is influenced by all of the canopy elements. The position, angle distribution, and the spatial relationships of the elements influence the extinction of solar radiation as it passes through a canopy (Norman and Jarvis, 1974; Welles, 1990; Chen and Black, 1992; Smith et al., 1993). The underlying strategy is to use a model based on L and leaf angle distribution to describe radiation attenuation through a canopy (Welles and Cohen, 1996). Actual measurements of the photosynthetically active radiation (PAR), usually made beneath or within a plant canopy, are used to invert the radiation model to estimate L. Foliage orientation (i.e., spherical leaf angle distribution) can be estimated indirectly for canopies that have leaves distributed approximately randomly; but, for more complex canopies, foliage orientation is usually designated because these data are often lacking and are exceedingly difficult to measure in forest ecosystems (Kucharik, 1997). In a perfect world, all canopies would behave exactly like the radiation model; but, in reality, many variations of canopy architecture exist. Thus, the success of the indirect approach to estimating L is correlated to how accurately the simplified radiation model mimics the true canopy architecture (Welles and Cohen, 1996).

The probability (P) of a light ray missing all foliage elements while passing through a canopy at some angle can be described by the Beer-Lambert Law [Eq. (4)]:

$$P(\theta)=exp[-K(\theta)\Omega\theta L/cos(\theta)], \qquad (4)$$

where $K(\theta)$ is a canopy extinction coefficient, defined as the fraction of leaf area that is projected onto a plane perpendicular to the beam direction (θ). $\Omega\theta$ is a nonrandomness factor, and all the leaves are assumed to be symmetrically distributed in azimuth. Values of $\Omega(\theta)$ are greater than 1.0 for regular foliage dispersions, equal to 1.0 for a random distribution, and less than 1.0 for clumped canopies (Nilson, 1971). Nonrandom distributions of foliage, or foliage clumping, can occur at the leaf, branch, and individual tree levels. For a given L, radiation transmission is greater through a canopy with nonrandomly (i.e., clumped) than randomly distributed foliage. The clumping index that is derived from canopy gap-size data is commonly referred to as the "element clumping index" (denoted by the symbol $\Omega_e(\theta)$) because it pertains to the clumping of foliage at scales larger than the defined element size in the canopy. For conifers the chosen elements are shoots and for broad-leaved deciduous canopies the standard element is the leaf.

MEASURING THE CANOPY GAP FRACTION

Generally, $K(\theta)$ is unknown, and multiple angle measurements of gap fraction are required to derive $K(\theta)$ and the product $L[\Omega(\theta)]$ simultaneously. The canopy gap or sky fraction can be measured over a range of zenith angles using a variety of optical instrumentation, some of which are commercially available (i.e., LAI-2000 Plant Canopy Analyzer , DEMON, Ceptometer, hemispherical photography, multi-band vegetation imager (MVI) [for more information on these instruments, see Welles (1990) and Welles and Cohen (1996)]. The Ceptometer and DEMON require numerous measurements at different zenith angles, while the other instruments obtain multiple measurements of $K(\theta)$ at different θ simultaneously. Measurements of $f_{\mathrm{gap}}(\theta)$ at various values of θ have been used successfully to estimate the composite value L [$\Omega(\theta)$] (Lang et al., 1985; Welles, 1990; Chen and Cihlar, 1995; Chen et al., 1997; Kucharik et al., 1997). To obtain an independent estimate of L using Eq. (4), an estimate of $\Omega(\theta)$ is required because commercially available instruments calculate L as the product of L times $\Omega(\theta)$. This composite value is defined as the "effective L" [$L_e(\theta)$] (Chen and Cihlar, 1995). Usually, an assumption of randomness [$\Omega(\theta)=1$] is used to derive values of L in many canopy studies using optical measurements of the canopy gap or sky fraction since information about $\Omega(\theta)$ is not used in the instrument software algorithms that calculate L. Estimates of L derived from optical instruments can suffer from two sources of error: 1) nonrandom distribution of foliage in the canopy and 2) radiation interception by wood elements. Below we evaluate the importance of each of these sources of error and offer approaches to correct the problem.

The assumption of random distribution of foliage in a canopy may be valid for many closed canopy deciduous forests, pastures, grasslands, and agriculture crops, but it is invalid for open-canopy forests: boreal coniferous and aspen forests (Kucharik et al., 1997; Chen et al., 1997) and open-canopy temperate conifer forests (Lang et al., 1985; Gholz et al., 1991; Gower and Norman, 1991; Fassnacht et al., 1994; Chen et al., 1997). Assuming a random distribution of foliage can produce errors in excess of 100% (Fassnacht et al., 1994). One obvious difficulty with using Eq. (4) to derive estimates of L is obtaining an appropriate value for $\Omega(\theta)$. Chen and Cihlar (1995) used indirect measurements of the canopy gap-size distribution, based on sunfleck measurements, to develop a powerful and robust set of equations that estimate $\Omega(\theta)$.

The canopy gap-size distribution and gap fraction (or sunfleck fraction—which is the gap fraction at a solar zenith angle) are not identical. Gap size is the actual dimension of gaps between individual elements, ranging from a fraction of a centimeter to several meters in coniferous canopies (Kucharik, 1997; Kucharik et al., 1997). Gap fraction is the percentage of background area viewed from above (ground or understory), below (sky and clouds), or within a canopy. Both gap fraction and gap-size distribution depend on the angle from which the canopy is viewed. Chen (1996) and Chen et al. (1997) demonstrate that gap-size information can be related to a value of $\Omega_e(\theta)$ (Chen and Cihlar, 1995; Kucharik et al., 1997).

Table 1. Element Clumping Factors $\Omega_e(0)$ and L Estimates, Measured toward the Canopy Zenith Using the Multiband Vegetation Imager (MVI), and Within-Shoot Clumping Factors (γ_e), and Crown Depth to Diameter Ratio (D) for Several Forest Ecosystems

Species	$\Omega_e(0)$[a]	γ_e	L	D
Sugar maple (WI)	0.95	1.0	7.1	1.0
Oak (NC)	0.88	1.0	4.2	1.0
Hemlock (WI)	0.94	—	5.4	
Aspen[b]	0.64	1.0	3.3	1.5–2.0
Jack pine[c]	0.45	1.2–1.4[g]	2.2	3–4
Black spruce[b]	0.38	1.3–1.4[g]	5.6	5–6
Douglas-fir[d]	—	1.77	—	
Scots pine[e]	—	1.75	—	
Jack pine[f]	—	1.3	2.6	
Red pine[f]	—	2.08	6.1	

[a] Measurements made with MVI (Kucharik, 1997; Kucharik et al., 1997).
[b] Measurements made at BOREAS Southern Study Area (SSA).
[c] Measurements made at BOREAS Northern Study Area (NSA).
[d] Smith et al. (1993).
[e] Stenberg et al. (1994).
[f] Chen and Cihlar (1995).
[g] Range reported for BOREAS IFC 1-3 1994 (Chen et al., 1997).

The two instruments that have been used to quantify values of $\Omega_e(\theta)$, the TRAC (Tracing Radiation and Architecture of Canopies; Chen et al., 1997) and the MVI (Multiband Vegetation Imager; Kucharik et al., 1997) are sufficiently complex that most scientists are not likely to use them routinely. Both of these instruments are generally unable to capture within-shoot clumping (needles clumped on conifer shoots) because these gaps are usually less than a few millimeters, below the resolution of the TRAC and MVI. Thus, the needle area within a shoot is not accurately measured as part of the gap-size distribution, thereby requiring an additional correction factor to correct for needle packing on shoots. The within-shoot clumping factor is based on a ratio of the shoot silhouette area to total needle hemi-surface area (γ_e), or some variation thereof (Oker-Blom and Smolander, 1988; Fassnacht et al., 1994; Stenberg et al., 1994; Chen and Cihlar, 1995; Chen et al., 1997). Chen et al. (1997) correct values of $\Omega_e(\theta)$ using an equation given by $\Omega(\theta)=\Omega_e(\theta)/\gamma_e$. A more general equation relating gap fraction to L is given by

$$f_{gap}(\theta)=exp[-K(\theta)\ L\ \Omega_e(\theta)/\gamma_e\ cos(\theta)]. \qquad (5)$$

Values of γ_e, or its equivalent, have been measured for a variety of species, and generally fall in the range of 1.2–2.1 (Table 1). The $\Omega_e(\theta)$ that is estimated using the TRAC instrument (Chen et al., 1997) or MVI (Kucharik et al., 1997) includes clumping at scales larger than the average element size; thus values of γ_e are essential to obtaining accurate estimates of L using clumping factors obtained with these instruments. Broad-leaved deciduous canopies have no within-leaf clumping of foliage (i.e., $\gamma_e=1.0$). All values of γ_e must be estimated independently of $\Omega_e(\theta)$. Nilson (1971) first described a clumping index without any specification of angular dependence. Using the MVI and a Monte Carlo model, Kucharik et al. (1997) found that canopy nonrandomness factors $[\Omega_e(\theta)]$ based on gap-size distribution data exhibit a strong dependence on zenith angle in some plant canopies.

Values of $\Omega_e(0)$ (clumping factor measured toward the canopy zenith) measured by the MVI are reported in Table 1 for several forest species. Kucharik et al. (1997; 1998a) found that the lowest clumping factors for forest canopies occurred at view angles toward the canopy zenith. As the view through the canopy approaches 90°, the canopy gap-size distribution approaches a random distribution. The values of $\Omega_e(\theta)$ reported for some of BOREAS sites using the TRAC (Chen et al., 1997) and MVI (Kucharik et al., 1997) differ, presumably because theTRAC measures sunfleck size distributions for sun angles between 30° and 60°, while MVI measures sunfleck size distribution toward the canopy zenith.

Measuring the canopy gap-size distribution is difficult; therefore, a simplified approach for estimating $\Omega_e(\theta)$ is desirable. Kucharik et al. (1998a) used a Monte Carlo model to develop relationships between easily measured canopy architecture characteristics and $\omega_e(\theta)$ for a variety of canopy types. Using values of crown diameter, tree density, crown porosity, and crown depth, they derived a relationship between canopy clumping factors and zenith angle. The simple empirical approach to estimating clumping factors avoids the laborious measurements of the canopy gap-size distribution as a function of angle, which can only be made with specialized instruments. Moreover, it is conceivable that this clumping factor may be calculated from remotely sensed data. $\Omega_e(0)$ can be approximated from the ratio of the crown depth (base of live crown to top of canopy) to crown diameter (measured at the widest extent) using Eq. (6), which is a simplified approach developed by Kucharik et al. (1998a):

$$\Omega_e(\theta)=\Omega_e(0)/\{\Omega_e(0)+[1-\Omega_e(0)]\ \exp[-2.2(\theta)^p]\}, \quad (6)$$

where $p=3.80-0.46D$ and θ is given in radians (Kucharik et al., 1998a). If values of $D>6.1$ (tall, polelike trees), $p = 1.0$; and, if $D<1.0$, $p=3.34$. Generally, $\Omega_e(\theta)$ approaches a value of 1.0 as θ nears 90°. The value of D in Eq. (6) controls how rapidly the value of $\Omega_e(\theta)$ approaches its near maximum value. Generally, narrow conical canopies, such as those of black spruce, have a more pronounced change in $\Omega_e(\theta)$ with angle than spherically shaped crowns (i.e., aspen) (Kucharik et al., 1998a). This characteristic is important to quantifying the transmission of radiation at angles off the zenith.

CORRECTING INDIRECT *L* ESTIMATES FOR BRANCH AND STEM AREA

The value of L that is derived from simple gap fraction measurements is really a plant area index, because all tissue, including stems and branches, intercept light and contribute to the measured gap fraction value. Consequently, values of $L_e(\theta)$ $\{L\ [\Omega(\theta)]\}$ obtained from the inversion of Eq. (5) should not be substituted for values of L. Some debate has taken place on whether the canopy total woody area values should be subtracted from L estimates derived with optical instrumentation (Deblonde et al., 1994; Chen et al., 1997). Tree stems and branches may or may not contribute significantly to the interception of light in canopies, depending on the forest species and stage of leaf-out, senescence, or defoliation due to disease.

Table 2 summarizes the contribution of woody area to the total plant area index for a variety of forest species with a wide range in L. Generally, woody material, on a hemisurface area basis, comprises from 5% to 35 % of the total plant area in these forests (Table 2). If the total woody area of the canopy were subtracted from the L estimate derived from Eq. (5), an assumption is implied that stems and branches are positioned randomly with respect to other foliage in the canopy. However, if leaves or shoots preferentially mask branches in the canopy, then a distinct correlation exists between branch and leaf (shoot) location, and a smaller adjustment should be made to correct indirect foliage estimates to leaf area index than suggested by the wood: total area values in Table 2. Branches are often assumed to intercept a small fraction of incoming radiation in healthy forest canopies with a minimal amount of dead branch material (Lang et al., 1991; Fassnacht et al., 1994; Fournier et al., 1996; Kucharik et al., 1998b). Kucharik et al. (1998b) used the MVI to quantify the amount of branch area that influenced gap fraction measurements; they found that only 5% of the branches influenced the indirect L $[L_e(\theta)]$ in aspen stands and 10% of the branches influenced the indirect L $[L_e(\theta)]$ in jack pine and black spruce stands. Kucharik et al. (1998b) suggest that branches may be neglected in indirect estimates of L for fully leaved canopies because they tend to be preferentially covered up by leaves, and minor corrections can be done for lower stems. Other corrections may be required for partially defoliate canopies or for species that retain a large number of dead branches on the lower stem (Kucharik et al., 1998b).

In natural forests, stems can be considered to have a location that is random with respect to other crowns in the canopy. Because stems do not have a specific spatial relationship to other foliage, their contribution to values of L derived from gap fraction measurements could be significant. However, Kucharik et al. (1998b) assert that stems do not affect MVI measurements of L.

COMPARISON OF DIRECT AND INDIRECT ESTIMATES OF *L*

An obvious goal of using indirect techniques and approaches to estimate L is to be able to compare favorably

Table 2. Estimates of Total Plant Area Index (PAI), Leaf Area Index (LAI), Woody Area Index, (WAI), and Woody to Total Plant Area Ratio (All Area Estimates Reported on a Hemi-surface Area Basis)

Species	*PAI* *(m^2/m^2)*	*LAI* *(m^2/m^2)*	*WAI* *(m^2/m^2)*	*WAI:PAI*
Sitka spruce[1]	10.4	8.0	2.4	0.23
Red pine[2,3]	6.56	6.13	0.44	0.07
Jack pine[2,3]	2.92	2.60	0.32	0.11
Black spruce[4a,5a]	6.36	5.6	0.76	0.12
Jack pine, old[4a,5]	3.63	2.4	1.23	0.34
Jack pine, young[4a,5a]	2.96	2.8	0.16	0.05
Aspen[5a,5a]	4.16	3.3	0.86	0.21
Black spruce[4b,5b]	5.06	4.8	0.86	0.17
Jack pine, old[4a,5b]	2.93	2.2	0.73	0.25
Jack pine, young[4b,5b]	1.85	1.8	0.05	0.03
Aspen[4b,5b]	2.82	2.2	0.62	0.22
Douglas-fir[7]	8.50	7.80	0.70	0.08
Oak–hickory[8]	5.49	4.89	0.60	0.11

[1] Norman and Jarvis (1974).
[2] Deblonde et al. (1994).
[2] Chen and Cihlar (1995).
[4] Chen et al. (1997).
[5] Gower et al. (1997).
[6] Chen and Black (1991).
[7] Chason et al. (1991).
[a] Denotes measurements at BOREAS SSA sites.
[b] Denotes measurements at BOREAS NSA site.

with direct, destructive measurements, which are usually assumed to be more accurate and are typically the standard for comparison. Figure 3 compares direct and indirect estimates of L, corrected for foliage clumping and woody tissue, for a wide variety of ecosystems, including agricultural crops such as corn, fescue, soybean, sunflower, and sorghum and deciduous and coniferous forest species. Overall, direct and indirect estimates of L compare to within 25–30% for most canopies. We note that indirect estimates of L plateau around 5–6, while direct estimates reach 9. The likely cause is gap fraction saturation as L approaches 5–6. Optical measurements of L of 6 versus 9 must measure a difference in gap fractions of 5% versus 1%. Therefore, direct measurement is the only reliable approach for canopies with a $L>6$.

MEASURING ABSORBED PHOTOSYNTHETIC ACTIVE RADIATION (APAR) AND FRACTION APAR (f_{APAR})

The direct measurement of APAR in the field can be challenging, especially in heterogeneous canopies such as forests. Usually f_{APAR} is measured directly with a method that spatially averages; then continuous measurements of incident PAR are used to get long-term APAR estimates. Unfortunately, f_{APAR} often is measured instantaneously with clear or cloudy skies and the values can be unrepresentative of daily averages. Instantaneous measurements of f_{APAR} should be done under overcast conditions to obtain the most consistent values of APAR. In forests, adequate spatial sampling is exceedingly difficult to obtain. Sometimes LAI is measured and f_{APAR} calculated, assuming a random canopy model is suitable. As discussed earlier, clumping usually must be considered in forests to calculate f_{APAR} from LAI. Daily APAR frequently is estimated for a canopy from a measurement of LAI. If APAR is estimated from the transmittance of diffuse PAR for a uniform overcast sky, based on a random canopy model, the daily f_{APAR} under clear conditions will be within 15% of the overcast f_{APAR} for $0.5<\mathrm{LAI}<8$ and $0°<\text{latitude}<60°$.

The quantity f_{APAR} is defined as the fraction of incident photosynthetically active radiation (PAR) that is absorbed by a canopy, which usually includes the overstory and sometimes the understory and ground cover (e.g., moss or f_{APAR} is calculated using Eq. (7),

$$f_{APAR}=[(PAR_{\downarrow AC}-PAR_{\uparrow AC})-(PAR_{\downarrow BC}-PAR_{\uparrow BC})]/PAR_{\downarrow AC}, \tag{7}$$

where $PAR_{\downarrow AC}$ and $PAR_{\uparrow AC}$ are incident (downward) and reflected (upward) PAR above the canopy, respectively, and $PAR_{\downarrow BC}$ and $PAR_{\uparrow BC}$ are the corresponding terms for below the canopy. Solving Eq. (7) for the fraction of incident:reflected PAR for above (ρ_{AC}) and below (ρ_{BC}) the canopy, the equation can be written as Eq. (8):

$$f_{ARAP}=[1-\rho_{AC}(t)]-[1-\rho_{BC}(t)](PAR\downarrow_{BC}/PAR\downarrow_{AC}) . \tag{8}$$

The term $PAR_{\downarrow BC}/PAR_{\downarrow AC}=1-f_{IPAR}$, where f_{IPAR} is the fraction of PAR intercepted by the canopy. Many studies of light interception in canopies use f_{IPAR} instead of f_{APAR} be-

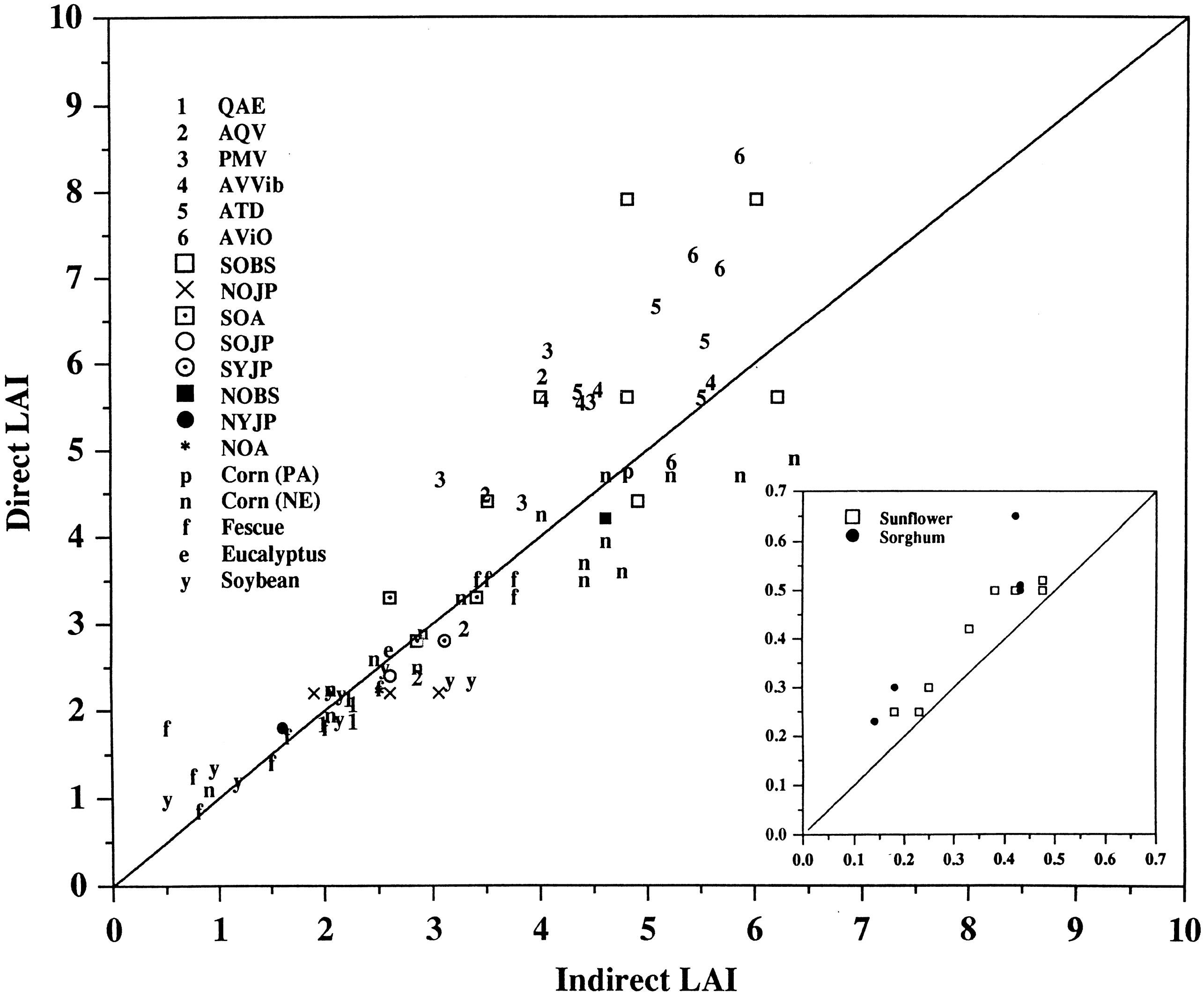

Figure 3. Direct and indirect estimates of *L* for forests and agricultural crops. Symbols and labels are defined as: QAE—jack pine, AQV—jack pine, PMV—mixed pine, AVVib—mixed northern hardwoods and pine, ATD—northern hardwoods, AviO—northern hardwoods in northern Wisconsin, USA (Fassnacht and Gower, 1997); BOREAS sites are SOBS—Southern study area (SSA) old black spruce, NOJP—Northern study area (NSA) old jack pine, SOA—SSA-old aspen, SOJP—SSA-old jack pine, SYJP—SSA-young jack pine, NOBS—NSA-old black spruce, NYJP—NSA-young jack pine, and NOA—NSA-old aspen (Chen et al., 1997; Gower et al., 1997). For agricultural crops and Eucalyptus, data are reproduced after Norman and Campbell (1989). PA denotes corn data from Pennsylvania, and NE is corn data from Nebraska.

cause it is easier to measure and almost the same value. The reflectivities are usually small and do not vary greatly among canopies; thus the major effort is to adequately characterize ($PAR_{\downarrow BC}/PAR_{\downarrow AC}$). The $PAR_{\downarrow BC}/PAR_{\downarrow AC}$ ratio is closely related to canopy gap fraction defined in Eq. (4) and therefore is influenced by sun zenith angle, the amount of diffuse radiation, and canopy clumping.

When *L* is estimated indirectly from gap fraction or radiation attenuation measurements, the number of measurements required to estimate *L* within a specified accuracy depends on the heterogeneity of the canopy. Using the Li-Cor LAI-2000 Plant Canopy Anaylzer (Li-Cor Inc., Lincoln, NE) in a variety of forest ecosystems in northern Wisconsin, Fassnacht (1996) found that 5 to 22 measurements were required to estimate the mean within +10% (Fig. 4), with more measurements required for forests with an open, heterogeneous canopy.

NET PRIMARY PRODUCTION (NPP): THEORY

Net primary production, the annual net production of biomass, comprises roughly 50% of net canopy photosynthesis (Landsberg and Gower, 1997) and is an important component of net ecosystem exchange. Given the importance of NPP, there is great need for process models that accurately estimate NPP. Estimates of NPP from process

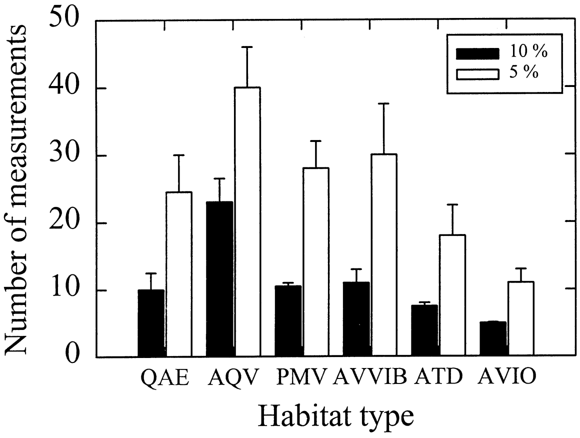

Figure 4. Comparison of the number of Li-Cor LAI-2000 measurements required to estimate the mean within a) 10% or b) 5% for six different forest types in northern Wisconsin, ranging from open-canopy needle-leaved pine forests (QAE and AQV), closed-canopy needle-leaved pine forests (PMV), closed-canopy mixed needle-leaved pine and broad-leaved deciduous (AV-Vib), to closed-canopy broad-leaved deciduous forests (ATD and AviO). Adapted from Fassnacht (1996).

models should be compared to field measurements of NPP, including all components (e.g., roots, understory, and ground cover), in diverse biomes to ensure the models accurately capture the influence of biophysical and ecological controls on NPP and carbon allocation. Confusion still surrounds both the definition of NPP and how to measure and calculate NPP. The conceptual definition of NPP is widely accepted [Eq. (9)]:

$$\text{NPP}=\text{GPP}-R_A, \tag{9}$$

where GPP is gross primary production and R_A is autotrophic respiration. However, GPP cannot be measured directly, and R_A is difficult to measure, especially in large stature or multi-species forests. Alternatively, NPP can be estimated using Eq. (10):

$$\text{NPP}=\sum P_i+H, \tag{10}$$

where P is the net production of dry biomass for each of the plant tissues (i). All plant tissues should be included: wood (or the stalk in the case of nonwoody plants), foliage, reproductive tissue, and roots including mycorrhizae. Consumption of organic matter by herbivores, or herbivory (H), between sampling periods will result in an underestimate of NPP unless the loss is quantified. Herbivory is generally less than 10% of NPP in forests, except during insect outbreaks when insects can consume 50% of NPP (Schowalter et al., 1986). The production of volatile carbon-based compounds and exudates are usually excluded because the limited data available suggest they comprise a small fraction of the NPP budget (generally <10%), but root exudates may be important for some herbaceous vegetation types (Clarkson, 1985).

ABOVE-GROUND NET PRIMARY PRODUCTION (NPP$_A$): MEASUREMENT

Equation (10) is appropriate to calculate NPP for any ecosystem, although the approach differs depending upon the structure, spatial heterogeneity, etc. Two common approaches to estimating NPP$_A$ are: area harvest and allometry. Area harvest entails periodic destructive sampling during the growing season of all above-ground live tissue in randomly located plots. The harvested organic matter is dried (or subsampled and dried) and statistically significant increments, or production, of organic matter are summed to estimate NPP$_A$. This approach is most appropriate for short-stature ecosystems such as grasslands, agricultural crops, tundra, etc. The area harvest approach is inappropriate for almost all forests because the annual production of organic matter is small relative to the spatial variability of standing organic matter. The alternative is to establish permanent plots in randomly selected locations of a representative stand, record the diameter and species of each tree or shrub in the plot, and estimate the annual production of organic matter for each component from annual radial increment data and allometric equations. The form of the allometric equations follows Eq. (2). The annual production of each tissue is calculated by measuring annual stem diameter increment for each tree in a fixed plot and applying the appropriate allometric equation to estimate the change in biomass for each tissue for one or more years.

Confusion surrounding the calculation of NPP can generally be traced back to two sources: the lack of allometric equations to estimate the production of some tissues, most notably foliage and fine roots, and the simultaneous production and shedding (e.g., mortality) of tissues. Allometric equations are often lacking for new foliage biomass (i.e., new foliage production). The alternative is to measure leaf litterfall and assume the foliage mass of the canopy is in steady state (i.e., new foliage production~leaf litterfall). Following this approach, scientists use Eq. (11):

$$\text{NPP}_A=B+D,$$

where B is biomass increment and D is detritus or litterfall production. Under no circumstances should new foliage production and leaf litterfall be included in the estimate of NPP. Using leaf litterfall to estimate foliage production for an aggrading evergreen forest may underestimate new foliage production because new foliage production exceeds leaf litterfall as the canopy biomass is accumulating. The assumption that foliage biomass of a forest canopy is at "steady state" should always be questioned, especially for ecosystems subject to droughts and windstorms (Linder et al., 1987; Grier, 1988).

Table 3. Summary of Methods and Calculations Used to Estimate Fine Root Net Primary Production (NPP_{FR})

Method	*Calculation Formula*	*Sample Reference*
Max–min	$^1NPP_{FR}=FR_{MAX}-FR_{MIN}$	Keyes and Grier (1981)
Sequential coring	$^1NPP_{FR}=\sum(FR_{MAX}-FR_{MIN})$	Gower et al. (1992)
Ingrowth cores	$^2NPP_{FR}=\sum(FR)$	Vogt and Persson (1991)
		Hendrich and Pregitzer (1993)
Minirhizotron	$^3NPP_{FR}=\sum(FR_L\times SRL)$	Steele et al. (1997)
		Nadelhoffer et al. (1985)
N budget	$^4NPP_{FR}=N_{AU}-\sum(N_{UF}+N_{US}+N_{UB})+\Delta N_{soil}$	Ruess et al. (1996)
		Raich and Nadelhoffer (1989)
C budget	$^5TRCA=S-D_A$	Gower et al. (1996)

[1] FR_{MAX} and FR_{MIN} are maximum and minimum fine root mass, respectively.

[2] FR is fine root mass.

[3] FR_L is fine root length and SRL is specific fine root length (mass per unit length).

[4] N_{AU} is apparent nitrogen uptake and is calculated as (N mineralization$+N$ atmospheric deposition$+$N fixation)$-$N leaching and denitrification and change in soil N content (ΔN_{soil}), and N_{UF}, N_{US}, and N_{UB} are annual nitrogen uptake by foliage, stem, and branches, respectively.

[5] TRCA is total root carbon allocation, S is annual soil surface CO_2 flux, and D_A is above-ground detritus production.

A more confusing and potentially larger source of error relates to tree mortality. There is confusion about when tree mortality should be added to NPP estimates, and the answer is dependent upon how the production of woody biomass was measured (Binkley and Arthur, 1993). Tree mortality should be added to annual biomass increment when biomass increment is calculated from repeated measures of stem diameters for two years (i.e., t and $t+n$, respectively), but should be excluded when radial increments cores from live trees at time t are used to back-calculate annual biomass increment at time $t-n$.

BELOW-GROUND NET PRIMARY PRODUCTION (NPP_B)

Despite the fact that NPP_B equals or exceeds NPP_A for many ecosystems, estimates for NPP_B are rare compared to NPP_A estimates. Even today some reported average biome values of NPP_B are based on only a few studies (Landsberg and Gower, 1997). The lack of NPP_B data is attributed to two factors: Estimating NPP_B remains difficult and controversial (Laurenroth et al., 1986, Vogt et al., 1986, Publicover and Vogt, 1993, Nadelhoffer and Raich, 1992, Steele et al., 1997), and all the methods used to estimate are laborious and costly. For brevity, we do not attempt to review the advantages and disadvantages of all the approaches, but refer interested readers to several current reviews (Vogt and Persson, 1991; Vogt et al., 1997; Fahey et al., 1998). Instead, we briefly review the various methods and provide some general comments on their use.

Below-ground NPP is comprised of two components: coarse and fine + mycorrhizae NPP. There is no consistent definition for diameter size class to distinguish between coarse and fine roots, but fine roots are generally considered to have diameters <2–3 mm. Although coarse root biomass far exceeds fine root biomass, fine root NPP often exceeds coarse root NPP. Coarse root biomass and NPP are estimated using allometric equations (see Santantonio et al., 1977) similar to Eq. (2). Historically, fine root net primary production (NPP_{FR}) was assumed to comprise a constant fraction of NPP_A and much of the literature today is still based on these data. Other approaches include: max–min live fine root biomass, sequential coring fine root biomass, ingrowth cores, minirhizotron, nitrogen mass balance, and soil carbon balance (Table 3). The soil carbon balance method differs from the other methods because this method provides an estimate of total carbon allocation below ground (i.e., the estimate does not distinguish between root net primary production and root respiration), unless an assumption is made about the contribution of root respiration to soil surface CO_2 flux). The maximum–minimum method undoubtedly underestimates fine root NPP because of simultaneous fine root production and turnover. The accuracy of the sequential coring approach continues to be debated, but is believed to provide realistic estimates of fine root NPP if used properly (Vogt et al., 1986). The minirhizotron approach is gaining popularity and has the potential to yield fine root phenology, production and mortality (Fahey et al., 1998). Ingrowth cores may work in some systems, but they were found to be unreliable in boreal forests (Steele et al., 1997).

ESTIMATING NPP FROM STAND TO GLOBE

Process models, driven by remotely sensed data, are useful tools for estimating NPP for areas larger than can be quantified using field-based measurements. Current NPP models do an adequate job of estimating NPP; however, an incomplete understanding of the influence of abiotic and biotic factors on carbon allocation limits further development of process models. It is questionable if global terrestrial NPP models will contain sufficient carbohydrate and nutrition physiology, key factors controlling carbon allocation in plants (Landsberg and Gower, 1997), to warrant a mechanistic approach to carbon allocation. The definition of "mechanistic" depends upon

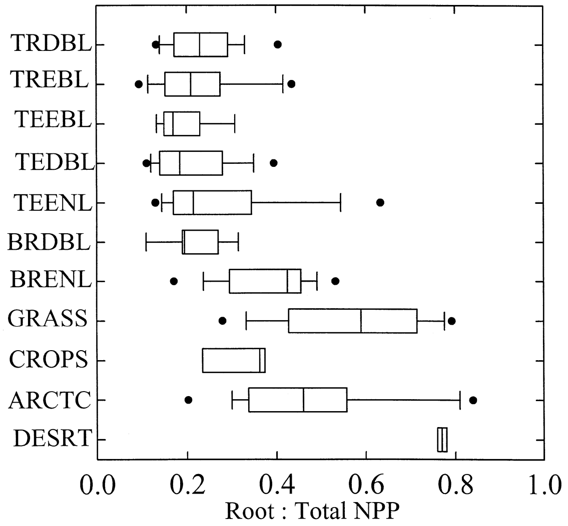

Figure 5. Below-ground: total net primary production ratios for tropical deciduous broad-leaved (TRDBL), tropical evergreen broad-leaved (TREBL), temperate deciduous broad-leaved (TEDBL), temperate evergreen needle-leaved (TEENL), boreal deciduous broad-leaved (BRDBL), boreal evergreen needle-leaved (BRENL), grassland and tropical savannas (GRASS), agricultural crops (CROPS), arctic tundra (ARCTC), and deserts (DESRT).

each scientist's perspective. For example, the use of the total root allocation model proposed by Raich and Nadelhoffer (1989) is a useful approach for estimating below-ground carbon allocation for world forests, but may be insufficient for developing a carbon budget for an aggrading forest (Gower et al., 1996). Total root allocation and fine root net primary production are positively correlated to total net primary production in forests (Nadelhoffer and Raich, 1992); however, it is unclear if these relationships hold for other biomes.

For the immediate future, scientists will be using average carbon allocation coefficients for major biomes and adjusting these ratios based on simple indices of water and nutrient availability (*sensu* Running and Gower, 1991). This approach requires average and maximum and minimum below-ground :total NPP ratios for major biomes. Figure 5 summarizes NPP_B:NPP ratios for major terrestrial biomes; we excluded NPP_B estimates that were obviously calculated as a ratio of NPP_A. Several general patterns are apparent. The fraction of NPP allocated to roots is greater for ecosystems dominated by nonwoody plants (e.g., deserts, grasslands and tropical savannas, and arctic tundra) than for forests. In general, a greater fraction of NPP is allocated to roots in evergreen conifer than deciduous broad-leaved in boreal and to a lesser extent temperate climates—a finding that is consistent with an earlier study (Vogt et al., 1986). Few estimates of NPP_B exist for tropical forests, making any conclusions tenuous; however, based on the data available, the fraction of NPP allocated to roots appears to be lower than early estimates. For a similar climate, numerous abiotic and biotic factors can cause variations in global carbon allocation relationships (i.e., affect the NPP_{FR}:NPP_A ratio). Greater nutrient and/or water availability decrease relative allocation of carbon to fine roots and increase allocation to aboveground tissues, especially foliage (Landsberg and Gower, 1997). For a similar forest biome, evergreen conifers tend to have a greater NPP_{FR}:NPP_A ratio than deciduous forests (Vogt et al., 1986; Gower et al., 1998). The effect of each of these factors on below-ground carbon allocation can be approximated using scalars, as done by Running and Gower (1991). A remaining large uncertainty is if NPP_B:NPP ratio changes in a consistent pattern during stand development (Gower et al., 1996); some crops certainly do this (e.g., Foth, 1962).

INDIRECTLY ESTIMATING NPP USING EPSILON MODELS

Monteith (1972) first illustrated the positive relationship between NPP and absorbed photosynthetically active radiation; this proportionality has since become known as the light use efficiency or epsilon (ε) model. Light use efficiency models are widely used to simulate NPP for terrestrial biomes (Heiman and Keeling, 1989; Running and Hunt, 1993; Ruimy et al., 1994; Potter et al., 1993; Field et al., 1995; Prince and Goward, 1995; Hunt et al., 1996; Liu et al., 1997). The basis for this model is that photosynthetic fixation of carbon by leaves is proportional to absorbed visible quanta (McCree, 1972), and, even though this light-assimilation relation is nonlinear for individual leaves, it is nearly linear for most canopies (Hesketh and Baker, 1967) because of the role of canopy architecture. The LUE model has two advantages: 1) The model is simple, and some evidence exists to suggest that maximum light use efficiency may be conservative within major vegetation classes, and 2) the fraction of photosynthetic active radiation absorbed by green leaves in a canopy (f_{APAR}) can be remotely sensed, as has been shown with both empirical (e.g., Daughtry et al., 1983; Steinmetz et al., 1990; Landsberg et al., 1997) and theoretical studies (Kumar and Monteith, 1981; Myneni et al., 1995a,b). Despite the increasing popularity of LUE models, this approach to simulating NPP from vegetation indices that are remotely sensed has several sources of uncertainty and inconsistencies. Sources of confusion include:

- incident solar radiation versus incident photosynthetically active radiation
- intercepted versus absorbed radiation
- interception of radiation by nonphotosynthetic plant parts
- respiration loss by nonphotosynthetic tissue
- length of the measurement period

Table 4. Modeled Fraction Absorbed Photosynthetic Active Radiation (f_{APAR}), Fraction Intercepted Photosynthetic Active Radiation (f_{IPAR}), Fraction Absorbed Solar Radiation (f_{ASR}), and Fraction Intercepted Solar Radiation (f_{ISR}) from Canopies of Varying LAI Averaged over a Clear, Midsummer Day in Kansas

LAI	f_{APAR}	f_{IPAR}	f_{ASR}	f_{ISR}	$\frac{\text{IPAR}}{\text{APAR}}$	$\frac{\text{ISR}}{\text{APAR}}$	$\frac{\text{ASR}}{\text{APAR}}$
0.5	0.29	0.29	0.18	0.21	1.00	1.55	1.29
1.0	0.49	0.50	0.31	0.37	1.01	1.62	1.33
2.0	0.72	0.74	0.47	0.59	1.02	1.75	1.41
4.0	0.89	0.93	0.64	0.81	1.04	1.96	1.53
8.0	0.95	0.99	0.73	0.96	1.04	2.15	1.65

[a] In the photosynthetic active radiation wavelengths leaf and soil reflectances are 0.065 and 0.10, respectively, and in the near-infrared wavelengths leaf and soil reflectances are 0.42 and 0.30, respectively. The leaf angle distribution is spherical and the daily integrated solar radiation is 29.4 MJ and incident photosynthetic active radiation is 13.8 MJ. ISR is intercepted solar radiation and ASR is absorbed solar radiation.

- inconsistencies among methods for estimating absorbed radiation including effects of nonrandom foliage distributions
- incomplete estimates of NPP because of measurement difficulties with below ground, simultaneous growth and death of tissues and differences between instantaneous biomass and NPP
- carbon fixed by photosynthesis versus biomass increment
- uniform versus functional group epsilon values
- differing efficiency of direct versus diffuse light by plants

Below, we address each of these issues and provide suggestions to correct uncertainties or highlight needed research to resolve the problem.

Empirical estimates of LUE should always be based on absorbed photosynthetically active radiation (APAR), not solar radiation (SR), because the near-infrared portion of the solar spectrum is not effective in sustaining photosynthesis (McCree, 1972). Some studies use intercepted solar radiation (ISR) or absorbed solar radiation (ASR), but near-infrared radiation is not involved in photosynthesis and is strongly scattered by the canopy. Furthermore, the pervasive scattering in the near-infrared requires the use of much more complicated models to estimate APAR from solar measurements. For consistent measurements of LUE, solarimeters should never be used inside of plant canopies. The solar radiation incident on canopies tends to contain a relatively constant fraction of PAR; varying from 42% to 55%, depending on location and sky conditions. Therefore, direct measurements of PAR above the canopy are preferred rather than assuming 50% of the solar is PAR. Based on a detailed radiation model for a generic canopy, it can be seen that factors to correct intercepted (ISR) or absorbed solar radiation (ASR) to APAR are large (20–30%) and are correlated to *L* (Table 4). The ratios on the right part of Table 4 can be used to convert various forms of radiation to APAR, and the fact that the conversion depends on LAI adds a complication that most researchers tend to neglect. Many studies provide insufficient data to convert ISR or ASR to APAR correctly. The relative increase in the ISR/APAR ratio by 30% is not negligible, and we encourage scientists not to use ISR in the future. Intercepted photosynthetic active radiation (IPAR) is also used to estimate LUE. Typically IPAR is within 4% of APAR (Table 4; Gallo and Daughtry, 1986; Russell et al, 1989); however, if LAI is very low (~0.2) and the soil is very reflective (PAR reflectance=0.5), then APAR may be 40% larger than IPAR for a random canopy because additional PAR reflected from the soil is absorbed by the leaves. Many researchers assume that f_{IPAR} and f_{ISR} are equal for full-cover canopies (LAI>2); however, data from radiation models do not support this assumption. For example, this assumption would produce a discrepancy of 20% at LAI=2 (Table 4). For canopies that are clumped, such as forests, f_{IPAR} and f_{ISR} do more closely approach each other than for random canopies, and for conifers assuming $f_{IPAR}=f_{IAR}$ is probably an excellent assumption over a wide range of LAI values.

Radiation intercepted by nonphotosynthetic plant parts is not related to NPP. Interception of radiation by branches is not likely to be a serious problem because most plants display leaves above branches preferentially as discussed earlier with reference to measurements in tree canopies. If ISR or ASR are used, distinguishing radiation absorbed by leaves from that absorbed by branches can be exceedingly complex, because of the scattering of near-infrared radiation by leaves and absorption by branches and stems—this is another reason to avoid using ISR and ASR. A major problem associated with PAR absorbed by nonphotosynthetic tissue is dead leaves. Clearly PAR absorbed by green leaves is the desired quantity for estimating canopy carbon fixation (Gallo et al., 1993). Fortunately, remote vegetation indices are most closely related to green f_{APAR} (Hall et al.,

Table 5. Examples of Phenological Variation in Light use Efficiency for Agriculture Crops[a]

Species	*Age*	*Location*	*Duration*	*LUE*	*S. LUE Reference*	*Comments*
Wheat	—	U.K.	14 day	3.1 g NPP_T/MJ_{APAR}	Gallager and Biscoe (1978)	Fertilized, NPP_B=root mass
Wheat	—	U.K.	14 days	2.8 g NPP_T/MJ_{APAR}	Gallager and Biscoe (1978)	No fertilizer, NPP_B=root mass
Wheat	—	U.K.	1 season	2.2 g NPP_T/MJ_{APAR}	Gallager and Biscoe (1978)	Fertilized, NPP_B=root mass
Barley	—	U.K.	14 days	3.0 g NPP_T/MJ_{APAR}	Gallager and Biscoe (1978)	NPP_B=root mass
Barley	—	U.K.	Season	2.2 g NPP_T/MJ_{APAR}	Gallager and Biscoe (1978)	NPP_B=root mass
Maize	70 days	Ontario, Canada	2 weeks	3.45 g NPP_A/MJ_{APAR}	Tollenaar and Bruulsema (1988)	Avg 2 years, 2 cultivars
Maize	85 days	Ontario, Canada	2 weeks	3.21 g NPP_A/MJ_{APAR}	Tollenaar and Bruulsema (1988)	Avg 2 years, 2 cultivars
Maize	100 days	Ontario, Canada	2 weeks	2.74 g NPP_A/MJ_{APAR}	Tollenaar and Bruulsema (1988)	Silking
Maize	115 days	Ontario, Canada	2 weeks	3.45 g NPP_A/MJ_{APAR}	Tollenaar and Bruulsema (1988)	Physical maturity
Maize	Tasseling	Pennsylvania	3 weeks	3.4 g NPP_A/MJ_{APAR}	Yao (1980)	2 cultivars
Soybean	0–40 days	Ottawa, Canada	Month	0.71 g NPP_A/MJ_{IPAR}	Rochette et al. (1995)	$0 \leq L \geq 1$
Soybean	0–40 days	Ottawa, Canada	Month	0.95 g NPP_T/MJ_{IPAR}	Rochette et al. (1995)	$0 \leq L \geq 1$
Soybean	0–40 days	Ottawa, Canada	Month	1.58 g NPP_T/MJ_{IPAR}	Rochette et al. (1995)	$0 \leq L \geq 1$ (CO_2 e.c. meas)
Soybean	41–48 days	Ottawa, Canada	≈ Weekly	1.37 g NPP_A/MJ_{IPAR}	Rochette et al. (1995)	$1 \leq L \geq 2$
Soybean	41–48 days	Ottawa, Canada	≈ Weekly	1.48 g NPP_T/MJ_{IPAR}	Rochette et al. (1995)	$1 \leq L \geq 2$
Soybean	41–48 days	Ottawa, Canada	≈ Weekly	1.58 g NPP_T/MJ_{IPAR}	Rochette et al. (1995)	$1 \leq L \geq 2$ (CO_2 e.c. meas)
Soybean	49–97 days	Ottawa, Canada	≈ Weekly	1.86 g NPP_A/MJ_{IPAR}	Rochette et al. (1995)	$L>2$
Soybean	49–97 days	Ottawa, Canada	≈ Weekly	2.0 g NPP_T/MJ_{IPAR}	Rochette et al. (1995)	$L>2$
Soybean	49–97 days	Ottawa, Canada	≈ Weekly	1.89 g NPP_T/MJ_{IPAR}	Rochette et al. (1995)	$L>2$ (CO_2 e.c. meas)
Soybean	Season	Ottawa, Canada	Season	1.67 g NPP_A/MJ_{IPAR}	Rochette et al. (1995)	
Soybean	Season	Ottawa, Canada	Season	1.86 g NPP_T/MJ_{IPAR}	Rochette et al. (1995)	
Soybean	Season	Ottawa, Canada	Season	1.86 g NPP_T/MJ_{IPAR}	Rochette et al. (1995)	(CO_2 e.c. meas.)

[a] No attempt was made to adjust values to a common unit because the comparisons are only for different time periods for each study.

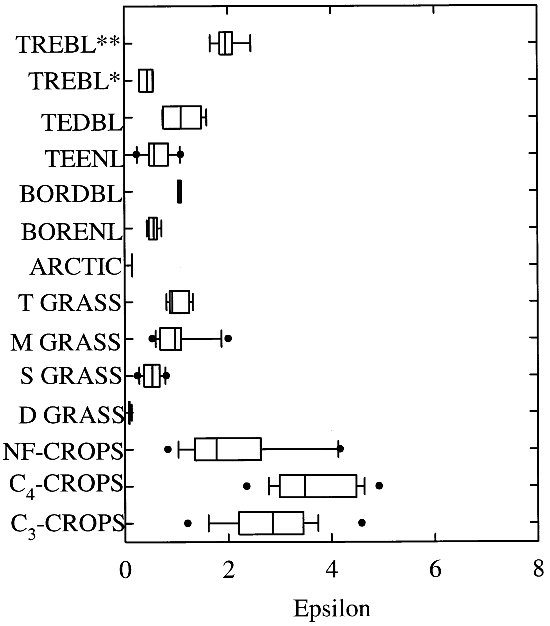

Figure 6. Calculated light use efficiency values for tropical deciduous broad-leaved (TRDBL), tropical evergreen broad-leaved where ** and * signify plantations and natural forest, respectively (TREBL), temperate deciduous broad-leaved (TEDBL), temperate evergreen needle-leaved (TEENL), boreal deciduous broad-leaved (BORDBL), boreal evergreen needle-leaved (BORENL), arctic tundra (ARCTIC), tallgrass prairie (T GRASS), mixed prairie (M GRASS), shortgrass prairie (S GRASS), desert (D GRASS), nitrogen-fixing crops (NF-CROPS), C4 crops (C_4-CROPS), and C3 crops (C_3-CROPS).

1990). In fact, the common reduction in LUE near the end of crop growing seasons may be related to PAR absorbed by dead leaves.

The influence of respiration on plant productivity is not adequately accommodated with a simple LUE approach, because respiration has a different dependence on temperature (and other factors) than LUE. Usually we assume that on a long-term basis correlations between radiation and temperature accommodate some of the effects of respiration in empirical estimates of LUE. Furthermore, climates associated with the major vegetation types are sufficiently consistent from month to month and year to year so that field estimates of LUE have general applicability. However, such assumptions may lead to possible failure of the estimates of maximum LUE under unusual conditions.

The measurement period with respect to the phenology of the plant can greatly influence LUE (Table 5). Hourly values of LUE can depend on the fraction of the radiation above the canopy that is direct beam versus sky diffuse radiation (Norman and Arkebauer, 1991). Also, daytime LUE values do not include the effect of nighttime plant respiration; which lowers the LUE value. Longer measurement periods average out short term effects and provide more stable values of LUE.

Excluding important components of forest production (e.g., understory, ground cover, and fine roots) is an important source of error in most estimates of LUE. Most estimates of LUE are based on aboveground components of the overstory layer (see the Appendix). Biomass allocation to NPP_B ranges from 20% to 75% of NPP in all terrestrial biomes (Fig. 5), and therefore cannot be ignored. Moreover, the fraction of total net primary production allocated to fine root production differs among plant functional groups (Fig. 5). In an attempt to resolve this serious problem, we used the average NPP_B:NPP ratios for each of the major biomes summarized in Figure 5 to derive LUE values. A related carbon allocation issue that can also introduce error in LUE estimates is varying biochemical composition, and its respective energy content, of the dry matter that is produced (Penning de Vries et al., 1974). For example, sunflower has a lower LUE than many other agricultural crops because of the high carbohydrate cost of the high oil content of the seeds (Flenet and Kiniry, 1995; Joel et al., 1997).

Several unique characteristics of boreal forests may explain the poor relationship between NDVI and "apparent" NPP (i.e., above-ground NPP for overstory only). First, leaf area index of boreal forests is small (Gower et al., 1997) and highly clumped (Chen et al., 1997; Kucharik et al., 1997), resulting in sufficient radiation reaching the forest floor to support a vigorous understory and ground cover vegetation. Remotely sensed vegetation indices, such as NDVI, are affected by all foliage bearing vegetation components (overstory, understory, and ground cover), yet NPP is often restricted to overstory.

Scientists use different assumptions about whether LUE differs among plant functional groups. Some models assume LUE does not differ among functional groups (Heiman and Keeling, 1989), other models assume LUE is constant for plant functional groups (Ruimy et al., 1994) and still other models incorporate the influence of environmental factors, such as water stress, temperature, and vapor pressure deficit, on LUE (Potter et al., 1993). There is a great need to determine if LUE differs among vegetation functional groups, but the noted inconsistencies described above must be addressed. The functional convergence hypothesis suggests that resource use efficiency (such as light use efficiency) is similar for ecosystems due to optimization driven by evolutionary adaptation (Field, 1991). Figure 6 summarizes LUE values for many of the major biomes recognized in global models. In general, LUE is greater for agricultural crops than trees, probably because the agricultural crops are well-watered and fertilized. Also, LUE is greater for deciduous than evergreen forests in boreal and temperate climates. Goetz and Prince (1996) also found that LUE was generally greater for aspen (0.92 gMJ^{-1} IPAR) than for black spruce (0.49 gMJ^{-1} IPAR).

The higher LUE under cloudy conditions arises because radiation is distributed more uniformly over all leaves in the canopy rather than saturating some leaves that are sunlit while others are in dark shade. While instantaneous LUE can vary by a factor of 2 for C_3 plants and a factor of 1.5 for C_4 plants (Norman and Arkebauer, 1991) as a function of the direct beam fraction, on a daily basis the variation is much less; being about a factor of 1.4 for C_3 plants and 1.2 for C_4 plants. Thus using typical or average beam fractions should provide LUE values usually within 20% of the actual daily values for C_3 plants and less uncertainty for C_4 plants.

CONCLUSIONS

- Applying site specific allometric equations to an adequate number of plots is the most desirable approach to obtaining ground truth estimates of leaf area index.
- Care must be exercised when selecting allometric equations from the literature to estimate *L*; tree size, species, and edaphic conditions all influence foliage allometric relations.
- To avoid further confusion, we recommend that future estimates of specific leaf area (SLA) be expressed as one-half total surface area, making conversion of *L* to one-half leaf area straightforward.
- Indirect optical estimates of *L* are commonly correlated to direct estimates of *L*, when optical estimates of *L* are corrected for nonrandom distribution of foliage at the shoot (conifer only) and tree-scale and for the contribution of wood to plant area index.
- Wood tissue comprises 3–34% of the plant area index in forests.
- Below-ground net primary production (NPP_B) is a significant fraction of total NPP (NPP). In general, i) a greater fraction of NPP is allocated to roots in nonwoody (e.g., deserts, grasslands and tropical savannas, and arctic tundra) versus forest biomes and ii) a greater fraction of NPP is allocated to roots in evergreen conifer than deciduous broad-leaved forests in boreal and temperate climates. Crops allocated a relatively small fraction of NPP to roots.

Table A1. List of Abbreviations Used Frequently in the Manuscript

ASR	absorbed solar radiation
APAR	absorbed photosynthetic active radiation
f_{APAR}	fraction absorbed photosynthetic active radiation
f_{IPAR}	fraction intercepted photosynthetic active radiation
f_{ISR}	fraction intercepted solar radiation
ISR	intercepted solar radiation
L	leaf area index, one half total surface area
L_E	leaf area index, effective
LUE	light use efficiency
NPP_A	net primary production, above-ground
NPP_B	net primary production, below-ground
NPP_{FR}	net primary production, fine roots+mycorrhizae
NPP_T	net primary production, total
PAR	photosynthetic active radiation

Table A2. Summary of Light Use Efficiency Values

Species	*Location*	*LUE*	*S LUE*	*Reference*	*Comments*
AGRICULTURE—C3					
Cotton	Texas	1.44 g NPP_A/MJ_{APAR}	1.87	Rosenthall and Gerik (1991)	3 cultivars, 2 yr
Johnson grass	Texas	2.3 g NPP_A/MJ_{IPAR}	2.85	Kiniry (1994)	Avg 2 years
Johnson grass/maize	Texas	2.9 g NPP_A/MJ_{IPAR}	3.59	Kiniry (1994)	Avg 2 years, intercropk—see maize
Winter wheat Trts	North Dakota	2.8–3.2 g NPP_A/MJ_{APAR}	1.33–3.71	Garcia et al. (1988)	Avg of 3 sites, 2 cultivar, 4 fert trts., 3 irr.
Winter wheat	U.K.	1.02 g NPP_T/MJ_{APAR}	1.02	Green (1987)	No fertilizer, NPP_B= root mass
	U.K.	1.45 g NPP_T/MJ_{APAR}	1.45	Green (1987)	Fertilized, NPP_B=root mass
Winter wheat	U.K.	2.2 g NPP_T/MJ_{APAR}	2.20	Gallager and Biscoe (1978)	Fertilized, $NPPP_B$=root mass
		2.0 g NPP_T/MJ_{APAR}	2.00	Gallager and Biscoe (1978)	No fertilizer, NPP_B=root mass
		2.2 g NPP_T/MJ_{APAR}	2.20	Gallager and Biscoe (1978)	Fertilized, NPP_B=root mass
Spring wheat	U.K.	2.0 g NPP_T/MJ_{APAR}	2.00	Gallager and Biscoe (1978)	
Wheat	Texas	2.8 g NPP_A/MJ_{IPAR}	3.47	Kiniry et al. (1989)	Mean of five values
Winter wheat	U.K.	2.2 g NPP_T/MJ_{APAR}	2.20	Gallager and Biscoe (1978)	NPP_B=root mass
		2.4 g NPP_T/MJ_{APAR}	2.40	Gallager and Biscoe (1978)	w/ & w/o fert, NPP_B=root mass
Barley	Scotland	3.37 g NPP_T/MJ_{APAR}	3.37	Russell and Ellis (1988)	NPP_B=root mass, vegetative period
Sugar beet	?	2.6 g NPP_T/MJ_{ISR}	5.20	Kumar and Monteith (1982)	
Sugar beet	U.K.	1.63 g NPP_T/MJ_{ISR}	3.26	Steven et al. (1983)	
Sunflower	Texas	3.1 g NPP_A/MJ_{IPAR}	3.84	Kiniry et al. (1989)	Avg of five trials, vegetative period
Rice	Philippines	2.7 g NPP_A/MJ_{IPAR}	3.34	Kiniry et al. (1989)	Avg of three trials, vegetative period
Potato	U.K.	1.76 g NPP_T/MJ_{ISR}	3.52	Allen and Scott (1980)	
AGRICULTURE—C4					
Maize	India	3.72 g NPP_A/MJ_{IPAR}	4.61	Sivikumar and Virmani (1984)	
Maize	Texas	3.5 g NPP_A/MJ_{IPAR}	4.33	Kiniry et al. (1989)	Vegetative period
Maize	Texas	3.6 g NPP_A/MJ_{IPAR}	4.46	Kiniry (1994)	Avg 2 years
Maize	Indiana	3.42 g NPP_A/MJ_{APAR}	4.45	Gallo et al. (1993)	FAPAR meas. at noon
Maize	Indiana	3.58 g NPP_A/MJ_{APAR}	4.65	Gallo et al. (1993)	FAPAR meas. at noon
Maize	Indiana	3.9 g NPP_A/MJ_{APAR}	5.07	Gallo et al. (1993)	FAPAR meas. at noon
Maize	Alberta, Canada	2.3 g NPP_A/MJ_{APAR}	2.99	Major et al. (1991)	Possible chilling injury
Millet	India	1.32 g NPP_A/MJ_{ISR}	3.43	Reddy and Willey (1981)	
Millet	India	1.7–1.96 g NPP_A/MJ_{ISR}	3.43–4.73	Squire et al. (1984a,b)	
Millet	Niger	1.34 g NPP_A/MJ_{ISR}	3.48	Azam-Ali et al. (1984)	Various planting densities, vegetative period
Millet	India	2.30 g NPP_A/MJ_{IPAR}	2.85	Marshall and Willey (1983)	Monoculture
		2.23 g NPP_A/MJ_{IPAR}	2.76	Marshall and Willey (1983)	Intercrop
Millet/groundnut	India	1.72 g NPP_A/MJ_{IPAR}	2.13	Marshall and Willey (1983)	Intercrop
Sorghum	India	2.81 g NPP_A/MJ_{IPAR}	3.48	Sivikumar and Virmani (1984)	
Sorghum	Texas	2.8 g NPP_A/MJ_{IPAR}	3.47	Kiniry et al. (1989)	
Sorghum	Texas	3.5 g NPP_A/MJ_{APAR}	4.55	Rosenthall et al. (1993)	2 cultivars, 4 densities
Sorghum	N.W. Australia	2.4 g NPP_A/MJ_{IPAR}	2.97	Muchow and Coates (1986)	3 sewing dates, 3 cultivars
AGRICULTURE—NITROGEN FIXERS					
Groundnut	India	0.95 g NPP_A/MJ_{IPAR}	1.18	Marshall and Willey (1983)	Monoculture
Groundnut	India	0.60 g NPP_A/MJ_{ISR}	1.56	Reddy and Willey (1981)	
Pigeon pea	India	1.04 g NPP_A/MJ_{IPAR}	1.29	Sivikumar and Vivmani (1984)	
Pigeon pea	West Indies	0.80 g NPP_T/MJ_{ISR}	1.60	Hughes et al. (1981)	Vegetative period
Cow pea	Nigeria	1.08 g NPP_A/MJ_{ISR}	2.81	Littleton et al. (1979)	50 days

(continued)

Table A2. (*continued*)

Species	*Location*	*LUE*	*S LUE*	*Reference*	*Comments*
Snap bean	Nairobi	0.85 g $\mathrm{NPP_T/MJ_{IPAR}}$	0.81	Coulson (1985)	
Field bean	U.K.	3.21 g $\mathrm{NPP_A/MJ_{APAR}}$	4.17	Green et al. (1987)	High moisture
Field bean	Reading, G.B.	4.1 g $\mathrm{NPP_T/MJ_{APAR}}$	4.10	Fasheun and Demuet (1981)	
Soybean	Ottawa, Canada	1.67 g $\mathrm{NPP_A/MJ_{IPAR}}$	2.07	Rochette et al. (1995)	
Soybean	Ottawa, Canada	1.86 g $\mathrm{NPP_T/MJ_{IPAR}}$	1.77	Rochette et al. (1995)	
Soybean	Ottawa, Canada	1.86 g $\mathrm{NPP_T/MJ_{IPAR}}$	1.77	Rochette et al. (1995)	(CO_2 e.c. meas.)
GRASSLANDS					
Desert	Jornada, NM	0.08, 0.13, 0.09 g $\mathrm{NPP_T/MJ_{APAR}}$	0.10	Sims et al. (1978a–c)	Control, 1970–72
Desert	Jornada, NM	0.07, 0.07, 0.08 g $\mathrm{NPP_T/MJ_{APAR}}$	0.07	Sims et al. (1978a–c)	Grazed, 1970–72
Short	Pantex, TX	0.24, 0.52, 0.77 g $\mathrm{NPP_T/MJ_{APAR}}$	0.51	Sims et al. (1978a–c)	Control, 1970–72
Short	Pantex, TX	0.29, 0.80, 0.76 g $\mathrm{NPP_T/MJ_{APAR}}$	0.62	Sims et al. (1978a–c)	Grazed, 1970–72
Short	Pawnee, CO	0.45, 0.54, 0.54 g $\mathrm{NPP_T/MJ_{APAR}}$	0.51	Sims et al. (1978a–c)	Control, 1970–72
Short	Pawnee, CO	0.43, 0.57, 0.31 g $\mathrm{NPP_T/MJ_{APAR}}$	0.44	Sims et al. (1978a–c)	Grazed, 1970–72
Northwest bunchgrass	ALE, WA	0.06, 0.06 g $\mathrm{NPP_T/MJ_{APAR}}$	0.06	Sims et al. (1978a–c)	Control, 1971–72
Northwest bunchgrass	ALE, WA	0.03, 0.05 g $\mathrm{NPP_T/MJ_{APAR}}$	0.04	Sims et al. (1978a–c)	Grazed, 1971–72
Mixed	Cottonwood, SD	0.77, 1.09, 0.66 g $\mathrm{NPP_T/MJ_{APAR}}$	0.84	Sims et al. (1978a–c)	Control, 1970–72
Mixed	Cottonwood, SD	0.68, 1.06, 0.53 g $\mathrm{NPP_T/MJ_{APAR}}$	0.79	Sims et al. (1978a–c)	Grazed, 1970–72
Mixed	Dickinson, ND	1.74 g $\mathrm{NPP_T/MJ_{APAR}}$	1.74	Sims et al. (1978a–c)	Control, 1970–72
Mixed	Dickinson, ND	2.00 g $\mathrm{NPP_T/MJ_{APAR}}$	2.00	Sims et al. (1978a–c)	Grazed, 1970–72
Mixed	Hays, KS	1.02 g $\mathrm{NPP_T/MJ_{APAR}}$	1.02	Sims et al. (1978a–c)	Control, 1970–72
Mixed	Hays, KS	0.93 g $\mathrm{NPP_T/MJ_{APAR}}$	0.93	Sims et al. (1978a–c)	Grazed, 1970–72
Tall	Osage, OK	0.89, 0.95, 0.80 $\mathrm{NPP_T/MJ_{APAR}}$	0.88	Sims et al. (1978a–c)	Control, 1970–72
Tall	Osage, OK	0.87, 1.25, 1.33 $\mathrm{NPP_T/MJ_{APAR}}$	1.15	Sims et al. (1978a–c)	Grazed, 1970–72
BOREAL EVERGREEN					
Jack pine (67)	BOREAS SSA	0.30 g $\mathrm{NPP_A/MJ_{IPAR}}$	0.56*	Gower et al., unpub. data	15 May–30 Sep
Jack pine (63)	BOREAS NSA	0.41 g $\mathrm{NPP_A/MJ_{IPAR}}$	0.75*	Gower et al., unpub. data	1 Jun–30 Sep
Black spruce (115)	BOREAS SSA	0.34 g $\mathrm{NPP_A/MJ_{IPAR}}$	0.62*	Gower et al., unpub. data	15 May–30 Sep
Black spruce (155)	BOREAS NSA	0.34 g $\mathrm{NPP_A/MJ_{IPAR}}$	0.62*	Gower et al., unpub. data	1 Jun–30 Sep
BOREAL DECIDUOUS					
Trembling aspen (67)	BOREAS SSA	0.90 g $\mathrm{NPP_A/MJ_{IPAR}}$	1.00*	Gower et al., unpub. data	15 May–30 Sep
Trembling aspen (53)	BOREAS NSA	0.89 g $\mathrm{NPP_A/MJ_{IPAR}}$	1.10*	Gower et al., unpub. data	1 June–30 Sep
TEMPERATE EVERGREEN					
Jack pine (52–61)	Wisconsin	0.41 g $\mathrm{NPP_A/MJ_{IPAR}}$	0.50	Gower et al., unpub. data	Low site quality, 1 May–30 Sep
Mixed pine (51–75)	Wisconsin	0.42 g $\mathrm{NPP_A/MJ_{IPAR}}$	0.51	Gower et al., unpub. data	Low site quality, 1 May–30 Sep
Mixed pines (58–90)	Wisconsin	0.48 g $\mathrm{NPP_A/MJ_{IPAR}}$	0.58	Gower et al., unpub. data	Med. site quality, 1 May–30 Sep
Red pine plantation (30)	Wisconsin	0.50 g $\mathrm{NPP_A/MJ_{IPAR}}$	0.60	Gower et al., unpub. data	1 May–30 Sep
Ponderosa pine (75)	Montana	0.20 g $\mathrm{NPP_A/MJ_{IPAR}}$	0.24	Gower et al., unpub. data	1 May–30 Sep
Slash pine (35)	Florida	0.40 g $\mathrm{NPP_A/MJ_{IPAR}}$	0.48	Gower et al., unpub. data	Infertile soil, season=1 yr
Douglas-fir/hemlock (45)	Oregon	0.90 g $\mathrm{NPP_A/MJ_{IPAR}}$	1.09	Gower et al., unpub. data	Fertile soil
Monterey pine (5)	New Zealand	0.75 g $\mathrm{NPP_A/MJ_{IPAR}}$	0.91	McMurtrie et al. (1994)	v. productive site, season= 1 yr
Monterey pine (25)	N.S.W. Australia	0.28 g $\mathrm{NPP_A/MJ_{IPAR}}$	0.34	McMurtrie et al. (1994)	High vpd, season=1 yr

(*continued*)

Table A2. (*continued*)

Species	*Location*	*LUE*	*S LUE*	*Reference*	*Comments*
Sitka spruce/red alder	Oregon	0.89 g NPP_A/MJ_{IPAR}	1.08	Runyon et al. (1994)	Environ. adjusted
		1.03 g NPP_A/MJ_{IPAR}			
Douglas-fir/white oak	Oregon	0.56 g NPP_A/MJ_{IPAR}	0.68	Runyon et al. (1994)	Environ. adjusted
		1.01 g NPP_A/MJ_{IPAR}			
Sitka spruce/hemlock	Oregon	0.56 g NPP_A/MJ_{IPAR}	0.68	Runyon et al. (1994)	Environ. adjusted
		0.61 g NPP_A/MJ_{IPAR}			
Douglas-fir/w. hemlock	Oregon	0.78 g NPP_A/MJ_{IPAR}	0.94	Runyon et al. (1994)	
		0.92 g NPP_A/MJ_{IPAR}			Fertilized
		0.89 g NPP_A/MJ_{IPAR}			Environ. adjusted
		1.14 g NPP_A/MJ_{IPAR}			Environ. adjusted, fertilized
Subalpine	Oregon	0.40 g NPP_A/MJ_{IPAR}	0.48	Runyon et al. (1994)	
		0.69 g NPP_A/MJ_{IPAR}			Environ. adjusted
Ponderosa pine	Oregon	0.19 g NPP_A/MJ_{IPAR}	0.23	Runyon et al. (1994)	
		0.62 g NPP_A/MJ_{IPAR}			Environ. adjusted
		0.58 g NPP_A/MJ_{IPAR}			Environ. adjusted, fertilized
TEMPERATE DECIDUOUS					
Northern hardwds (65–81)	Wisconsin	0.67 g NPP_A/MJ_{IPAR}	0.77	Gower et al., unpub. data	Low site quality, 1 May–30 Sep
Northern hardwds (67–79)	Wisconsin	0.64 g NPP_A/MJ_{IPAR}	0.74	Gower et al., unpub. data	Med. site quality, 1 May–30 Sep
Northern hardwds (59–71)	Wisconsin	0.65 g NPP_A/MJ_{IPAR}	0.75	Gower et al., unpub. data	High site quality, 1 May–30 Sep
Willow	U.K.	1.4 g NPP_A/MJ_{IPAR}	1.61	Cannell et al. (1987)	Container grown
		1.58 g NPP_T/MJ_{IPAR}	1.50	Cannell et al. (1987)	Container grown
Cottonwood	Scotland	1.50 g NPP_T/MJ_{IPAR}	1.43	Cannell et al. (1988)	Container grown
WOODLAND					
Juniper	Oregon	0.20 g NPP_A/MJ_{IPAR}	0.24	Runyon et al. (1994)	
TROPICAL EVERGREEN					
Tierra firme (0–1)	Colombia	0.37 g NPP_A/MJ_{APAR}	0.45	Saldarriaga and Luxmoore (1991)	Season=1 yr
Tierra firme (1–3)	Colombia	0.45 g NPP_A/MJ_{APAR}	0.55	Saldarriaga and Luxmoore (1991)	Season=1 yr
Tierra firme (3–10)	Colombia	0.46 g NPP_A/MJ_{APAR}	0.56	Saldarriaga and Luxmoore (1991)	Season=1 yr
Tierra firme (10–20)	Colombia	0.24 g NPP_A/MJ_{APAR}	0.29	Saldarriaga and Luxmoore (1991)	Season=1 yr
Tierra firme (20–200)	Colombia	0.24 g NPP_A/MJ_{APAR}	0.29	Saldarriaga and Luxmoore (1991)	Season=1 yr
Acacia auriculiformis	Hawaii	0.85 g NPP_A/MJ_{ISR}	2.07	Harrington and Fownes (1995)	Planted, 3 months
		0.87 g NPP_A/MJ_{ISR}	2.12	Harrington and Fownes (1995)	Coppiced, 3 months
Eucalyptus camaldulensis	Hawaii	0.80 g NPP_A/MJ_{ISR}	1.95	Harrington and Fownes (1995)	Planted, 3 months
		0.81 g NPP_A/MJ_{ISR}	1.98	Harrington and Fownes (1995)	Coppiced, 3 months
Gliricidia sepium	Hawaii	1.06 g NPP_A/MJ_{ISR}	2.59	Harrington and Fownes (1995)	Planted, 3 months
		0.65 g NPP_A/MJ_{ISR}	1.59	Harrington and Fownes (1995)	Coppiced, 3 months
Leucaena diversifolia	Hawaii	0.76 g NPP_A/MJ_{ISR}	1.85	Harrington and Fownes (1995)	Planted, 3 months
		0.35 g NPP_A/MJ_{ISR}	0.93	Harrington and Fownes (1995)	Coppiced, 3 months

[a] Data from original sources were converted to a standardized LUE (S LUE) of g total (above + below-ground) net primary production per MJ APAR using carbon allocation coefficients in Figure 5 and radiation conversion coefficients in Table 4. All data are for the growing season, unless noted in comments.

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