Biometeorology, ESPM 129

Lectures 2 Characterizing the Vegetation Canopy, Part I: Structure and Function

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This set of lectures will discuss:

2.1 Structure and Function, Overview

2.2 Leaf area index
      i. Observations
      ii. Theoretical Limits
      iii. Variation with time: season, decade, century
      iv. Variation with space: height, horizontal, globe
      v. Measurement methods
      vi. Predicting leaf area index, nutrition, functionality and water balance
      vii.   Predicting leaf area from allometry

L2.1. Structure and Function

'Form Follows Function', Louis Henri Sullivan (1856-1924), architect

'Form follows function—that has been misunderstood. Form and function should be one, joined in a spiritual union', Frank Lloyd Wright (1869-1959), protégé' of Louis Henri Sullivan and architect

      On walking through the woods, one of the first impressions one draws is that a forest is a structurally complex entity. If one is walking through a temperate hardwood or tropical forest, one observes trees of multiple stature, age and species. Stopping and looking upward into the canopy crown, one sees that many leaves are sunlit leaves, their inclination angles are rather erect, they are rather thick and they tend to be arranged in clumps (Parker, 1995). At eye-level, tree trunks, understory vines, saplings and shrubs immediately come to view. Understory leaves are relatively thin and tend to be oriented horizontally, to absorb as much light as possible, in the sun-dappled shade. Looking downward one sees

fresh and decomposing litter, soil, rocks, fallen logs, seedlings, herbs and shrubs.

Figure 1 A walk through the woods. Armstrong Redwoods State Preserve, Guerneville, CA. Ian McCully, photo.

Walking through forests in seasonally dry climates, like the ponderosa pine ecosystem of the western United States or oak woodland ecosystems in Mediterranean climates, one observes a stand with fewer tree species, than a temperate or tropical forest. The architecture of forest canopies in xeric environments is more complex due to periodic fires and seasonal drought. Structurally, the forest canopy is a patch-work of dense and clumped young trees, open spaces, tall and solitary old trees and a mat of shrubs and herbs in and around gaps.

Unseen by the naked eye is functional complexity. As stomata open to allow CO_2 to diffuse into the mesophyll, water is lost, as photosynthesis, respiration, stomatal conductance and transpiration operate in concert with one another. Biophysics, competition and natural selection act as governors on the ultimate rates of photosynthesis and transpiration that a leaf can achieve; these processes interact to constrain leaf morphology, photosynthetic capacity, stomatal conductance, leaf water potential, root-shoot allocation and resource acquisition (e.g. nutrients and soil moisture).

Structural and functional complexity of a forest is not static. On visiting a forest many times over a year, one will observe both gradual and

dramatic transitions in structure and function. During the winter, the forest may be leafless or dormant and respiring. With the occurrence of spring comes a flush of growth. Rapid changes in biological activity and structure occur as leaves expand, nodes elongate, roots grow and reproductive organs emerge. Coincidently, photosynthetic capacity of leaves changes rapidly during this period, as chloroplast with nitrogen-rich RUBP are constructed. During the summer, gradual changes in canopy structure, maximum stomatal conductance and physiological capacity occur as leaves age, experience water deficits, acclimate, are eaten or drop due to prolonged drought. With the approach of autumn, the face of the landscape changes yet again. Leaves re-translocate nitrogen back to stems, their photosynthetic capacity diminishes, they senesce and they drop from the trees.

Understanding complexity in canopy structure and function are key to quantifying carbon dioxide and water vapor exchange of forest stands, information that is used in models that predict and diagnose weather, climate, biogeochemical cycling and forest dynamics. This is because many structural and functional properties of plant canopies alter: 1) wind and turbulence within and above the canopy, **by exerting drag**; 2) the **interception and scattering of photons** throughout the canopy; 3) the **heat load** on leaves and the soil; 4) the **physiological resistances** to water and CO_2 transfer and 5) the **biochemical capacity** to consume or respire carbon dioxide.

Any study on canopy microclimate or mass and energy exchange is essentially worthless, unless it is accompanied with information on canopy architecture, plant structure and function. Such a folly would be equivalent to trying to study demographics of a city without knowing the population. For example, how could you estimate the water use of San Francisco without knowing the number of people, houses and toilets in the city?

In this lecture we focus on the physical attributes of plant canopies and how they relate to biometeorological variables and processes.

L2.2 Physical Attributes of Plant Canopies

Reviews on the topic of canopy structure define several specific terms (Parker, 1995). **Physiognomy** is concerned with the shape of crowns. **Architecture** describes growth patterns and forms of stems. **Organization** relates to the statistical distribution of canopy components in time and space and texture refers to the crown units of the overstory. In a broad sense, I define a **plant canopy** as an amalgam of herbs, shrubs, plants and underlying soil that exists on a landscape.

Important attributes of a plant canopy that relate to mass and energy exchange, canopy microclimate and ecosystem physiology and functioning include:

1) **leaf area index** of the canopy (the amount of leaf area per ground area);
2) **shape** and **size** of leaves (needles vs planar, projected vs surface area of needles and shoot to total needle area);
3) **vertical distribution** of leaf area;
4) **spatial distribution** of leaves (are they dispersed in a random, clumped or regular fashion?)
5) **seasonal** variation of leaf area (is the canopy evergreen or deciduous?)
6) **leaf angle distribution** (are leaves erect, planophile, spherical?; are they azimuthally symmetric or asymmetric?)
7) **canopy height** (short and aerodynamically smooth vs tall and aerodynamically rough)
8) **crown volume** and **shape** (vertical and horizontal dimensions; conical, ellipsoidal, spherical)
9) **plant species** (species number, functional types)
10) **stem density** (stems per hectare);
11) **spatial distribution** of plants (random, clumped, rows, regular);
12) **photosynthetic pathway** (C_3, C_4, CAM);
13) **plant habit** (deciduous/evergreen; woody/herb, annual/perennial)
14) **age structure** (disturbed/undisturbed, plantation, native, agriculture, even aged, mixed aged)
15) **exposure/acclimation** (sunlit/shaded, thickness, clumping, angle);
16) **woody biomass** area index (silhouette woody biomass per unit area);
17**) rooting** depth, root architecture (fibrous, tap), accessible water and nutrient volume
18**) history** and type of **disturbance** (recent fires, logging, plowing, re-planting)

Different attributes of a plant canopy influence the state of the atmosphere and components of mass and energy exchange in various ways.

Leaf size, shape and orientation affect:

1) the properties of the **leaf boundary layer**;
2) the **reflectance** and **transmittance** of light;
3) leaf's **energy balance**;
4) **Umbra** and **penumbra** (full or partial shade);
5) Leaf or needle **clumping**;

Figure 2. Blue oak leaves (*Quercus douglasii*).

The thickness of the leaf boundary layer affects the rate diffusion of trace gas to and from the leaf.   The interception of light depends on leaf orientation, relative to the sun, and how clumped the leaves or needles may be. If a leaf is big enough to block the solar disk, as viewed by another leaf, full shade is cast. Otherwise the inferior leaf is exposed to partial or penumbral shade. The optical properties of leaves affect how much intercepted radiation is available for evaporating water, photosynthesis and heating a leaf. The temperature of a leaf governs kinetic rates of many important biochemical processes like photosynthesis, respiration, plus the production of secondary compounds like isoprene.

Growth form and geometry of a canopy or group of plants affects mass and energy exchange by how it traps photons, exerts drag and alters physiological functioning. Tall plant stands are **aerodynamically rougher**, so turbulent mixing and transport is more efficient. Tall plant stands also trap photons more efficiently, so they are optically **darker**. This means they absorb more solar energy and hence have more energy available to evaporate water and heat the air. **Tall plants**, on the other hand, exert a **stronger resistance** to water transport through their xylem. So taller plants may impose stronger physiological restraints on mass and energy exchange than may shorter plants.

The structure of a plant canopy is not static with time. It can vary over the course of a year and over the course of the plant's lifespan. **Evergreeness** and **deciduousnes**s are two examples of seasonal behavior by plants. Evergreen shed older leaves after new leaves unfold, so there is an annual cycling of foliage. On a shoot of a conifer, for example, many years of needles will coexist. Their photosynthetic capacity diminishes with age. We also know that the photosynthetic capacity of co-occurring deciduous and evergreen plants of the same genus (e.g. *Quercus*) can differ by a factor of two, with greater capacity being associated with the deciduous species.

Evergreen type often occurs in habitats where carbon assimilation is restricted by unfavorable conditions, as in the boreal forest. But it can also occur in tropical regions where there is essential little seasonality, hence no reason to become dormant and drop leaves. Conifers also reside on soils with lower nutrient availability (Sprugel, 1989).

The deciduous type leaf is more productive and its dominance on the landscape is more common when nutrients and water is plentiful. The seasonal pattern of having or

dropping leaves has dire impact on mass and energy exchange. The rates of sensible heat and the reflectivity of a forest differ markedly if it has leaves or not.

Plant function, as identified by its photosynthetic pathway will affect its stomatal conductance and the partitioning of energy into evaporating water and generating heat. It will also affect the efficiency of photosynthesis.

A quantitative understanding about how plant functional and structural attributes affect the canopy microclimate and mass and energy exchange can be gained by examining the **Conservation of Mass** equation. A simplified version of the conservation of mass can be used to demonstrate that the net flux density (moles m^{-2} s^{-1}) of carbon dioxide or water vapor between a forest and the atmosphere (F) can be estimated by integrating the source-sink strength with respect to height (S(z)):

$$F = \sum_{0}^{h} S(z)\Delta z \quad (1$$

This assumption is valid as long as the forest is horizontally homogeneous and the environmental conditions are not varying.

Conceptually, the **source-sink strength** of vegetation is proportional to **leaf area density** ($a(z)$) and the differences between the **scalar concentration** in the atmosphere (C_a) adjacent to leaves and that inside the leaves (C_i). It is inversely proportional to the sum of the **aerodynamic** (r_a) and **stomatal resistances** (r_s):

$$\frac{\partial F}{\partial z} = S(z) = -a(z)\frac{(C(z) - C_i)}{r_a + r_s} \quad (2$$

For CO_2, the daytime sink strength in a layer of canopy is determined by the balance between a biochemical and physiologically-limited demand of leaves and the diffusional-limited supply from the atmosphere and through the leaf boundary layer (Farquhar et al., 1980).

Using Equation 1 as a framework, one can identify how physical and functional attributes of single leaves, individual plants and plant stands impact carbon, water and energy exchange through their impact on **boundary layer** (G_a) and **surface conductances** (G_s), **physiological sink capacity** (C_i) and **photon transport** through leaf mesophyll and canopy foliage (*P(0)*, the probability of beam penetration) (Table 1).

As this course develops over the course of this semester we focus on much of the material presented in this table in greater detail. The next section of this lecture will focus exclusively on leaf area index, its variations in time and space and how to measure it. We will cover other attributes of plant canopies in succeeding lectures.

L2.1 Leaf Area Index

Leaf area is one of the most important biometeorological variables to be characterized. It is an inventory of the population of leaves that are absorbing light and momemtum and are exchange heat, moisture, CO_2 and trace gases with the atmosphere. From a micrometeorological perspective an increase in leaf area index increases light interception and the source/sink strength for heat, water and CO_2 exchange. It can also start a negative feedback loop by increasing drag on wind, decreasing wind velocity that acts to reduce mass and energy exchange (Albertson et al., 2001). Lower wind velocity in the canopy will also act to accentuate profiles of temperature, humidity and CO2 in the vegetation, which in turn will have feedbacks with physiological resistances linked to the stomata.

In general, **Leaf Area Index** is the amount of one-sided leaf area per unit area of ground. But for conifers, that have cylindrical needles, one may consider either the projected area of the needles or the **hemi-surface area** of the needles (Chen and Black, 1992).
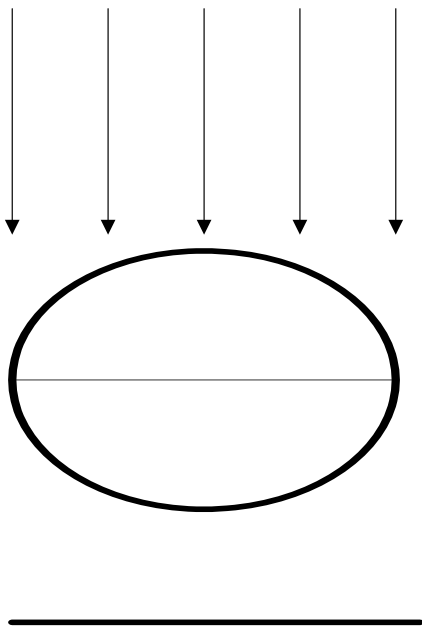
Figure 3 Projected area of a hemicircle onto a flat surface. Notice the surface area of the hemi-circle is greater than its projected area.

Different plant functional types will possess a different amount and range of leaf area, leaf biomass and leaf area density. To give the reader, appreciation for the range and ranking of values we draw information from a network of long term ecological and biometeorology studies.

Table 1 Global survey of leaf area index of landscape classes. (Asner et al., 2003)

Functional type	Mean LAI	Std Dev
Polar desert/alpine tundra	3.85	2.37
Moist tundra	.82	.47

Boreal forest woodland	3.11	2.28
Temperate savanna	1.37	.83
Temperate evergreen broadleaved forest	5.4	2.32
Temperate mixed forest	5.26	2.88
Temperate conifer forest	6.91	5.85
Temperate deciduous forest	5.3	1.96
Temperate wetland	6.66	2.41
Cropland Temperate	4.36	3.71
Plantation Temperate	9.19	4.51
Tall medium grassland	2.03	5.79
Short grassland	2.53	.32
Arid shrubland	1.88	.74
Mediterranean shrubland	1.71	.76
Tropical wetland	4.95	.28
Tropical savanna	1.81	1.81
Tropical evergreen rain forest	5.23	2.61
Tropical deciduous forest	4.67	3.08
Tropical pasture	2.85	2.62
Crop tropical	3.65	2.14
Plantation tropical	9.91	4.31

Based on a brief literature survey we see that a range of values exist for forests, crops, grasslands and other plant types. We also notice a confined range of values. We see no canopies with leaf area indices exceeding 10, let alone reaching 20. Nor do we see plant stands with very low fractional values, except after a major disturbance like fire, harvesting or plowing. This leads us to ask:

How much leaf area can a plant canopy sustain?

From a light harvesting perspective, there tends to be an upper limit of leaf area that a canopy can sustain. Jarvis and Leverenz (1983) used Beer's Law to derive a simple equation for estimating leaf area index. Beer's Law predicts light transmission through a turbid medium, in terms of the relative light transmission (I/I_o), as an exponential function of leaf area index (L) and a proportionality constant (k); k reflects the geometric influence associated with the angle between leaves and the sun:

$$I / I_0 = \exp(-kL)$$

On the basis of this relation one can calculate the amount of canopy that will develop enough leaf area to intercept over 95% of incident sunlight, a value large enough to sustain enough photosynthesis to offset respiratory costs. If a canopy intercepts 95% of incident sunlight, then only 5% is transmitted through the vegetation, a value that relates to I/I_0. Algebraic re-arrangement of Beer's law produce

$$L = -\ln(0.05) / k$$

Results from applying this equation are listed in Table 1. For planar leaves, we may assume the light extinction coefficient, k, equals 0.5. In this case, the theoretical limit for leaf area index is about 6. In practice this value will vary with the leaf angle distribution and clumping (topics covered in later lectures). Conifers possess clumped shoots, thereby they are able to maintain higher leaf area indices than broadleaved plant stands.

Table 2 List of leaf area index, measured and computed (adapted from Jarvis and Leverenz, 1983).

Species	L	K	$L_{95\%}$
Pinus resinosa	2.6	0.40	7.5
Pinus radiate	8.3	0.51	5.9
Pinus sylvestris	2.8	0.62	4.8
Picea sitchensis	9.8	0.53	5.7
Picea abies	8.4	0.28	10.7
Psuedotsuga menziesii	11	0.48	6.2
Eucalpytus maculata	2.8	0.57	5.3
Liriondendron tulipifera	6.0	0.29	10.3
Fagus crenata	7.0	0.65	4.6
Quercus robur	5.0	0.39	7.7
Populus tremula	3.8	0.39	7.7

So far we have noted a wide range of leaf area indices for different ecosystems. If we are to predict fluxes of mass and energy between the biosphere and atmosphere, predict weather and climate, radiation attenuation, or interpret the radiation reflected from the land, as detected by satellites, we'd like to know a ball-park value of leaf area index *a priori*. The key question to ask is:

What factors cause leaf area index to differ among ecosystems?

Correlative and biogeographical analyses suggests that leaf area index is strongly tied to site water balance and nutrient status (Scheffer et al., 2005; Woodward, 1987).
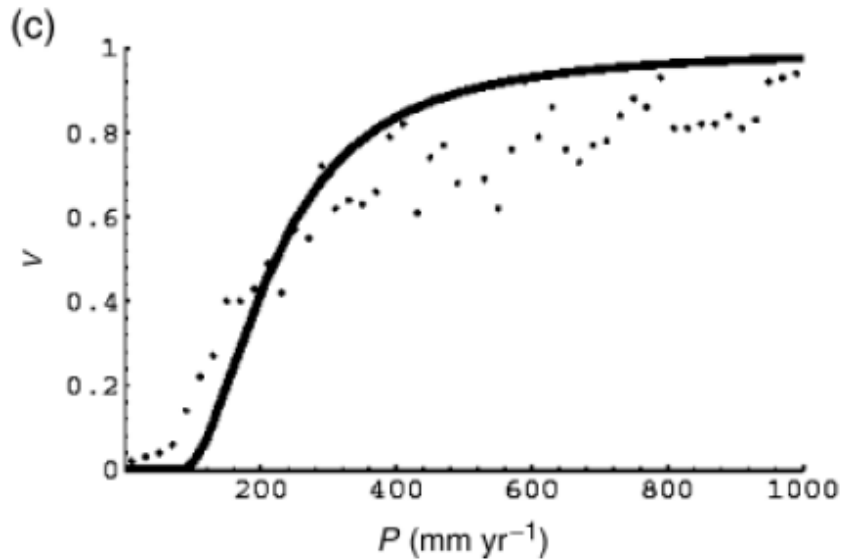
Figure 4 Relation between fraction of vegetative cover, V, and annual precipitation, P (Scheffer et al., 2005)

The data presented Figure 3 support this notion. They indicate that a strong relation exists between leaf area index, precipitation and potential evaporation (a measure of the net water balance) and leaf nitrogen content (a measure of nutrition and photosynthetic capacity). The independent axis is based on a dimensionless quantity, and is an example of applying engineering scaling theory to ecology and biometeorology applications. Note that this relationship says nothing about how leaf area may vary within a habitat. But its mechanism is attributed to a series of connected facts: 1) light interception and canopy coverage scale with primary productivity (Monteith, 1977); 2) primary productivity scales with evaporation (Sinclair et al., 1984); and 3) the amount of water evaporated by a landscape is limited by available rainfall and net radiation (Budyko, 1974; Priestley and Taylor, 1972).
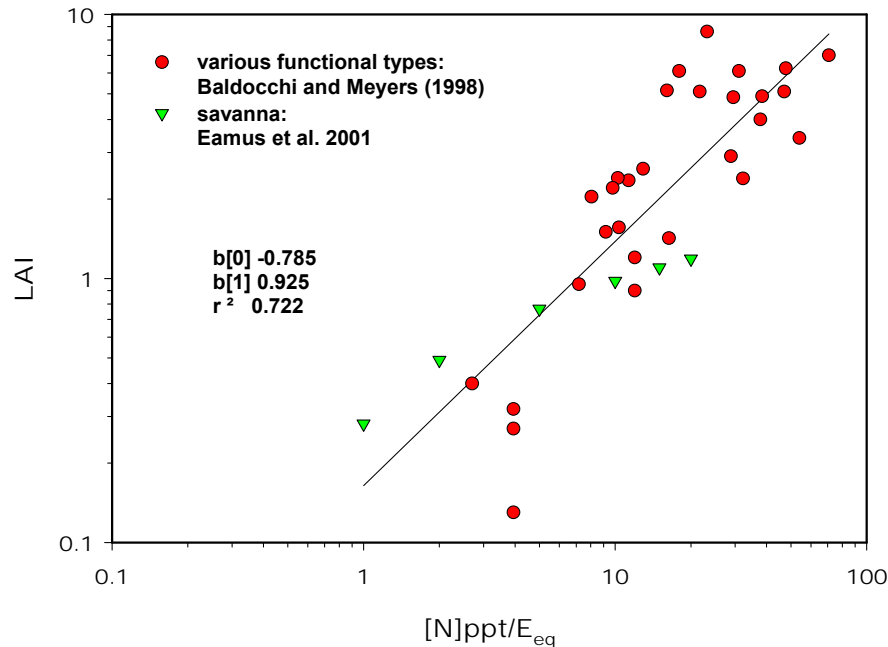
Figure 5 Correlation among leaf area index and climate and biogeochemical factors (precipitation,

leaf nitrogen content and evaporation) (Baldocchi and Meyers, 1998; Eamus and Prior, 2001).

Additional sources of variation include age, disturbance history, soil texture and genetic material.   Nor does this relation deal with effects of complex terrain, accessibility to ground water and the runoff of precipitation. Nevertheless, independent data, obtain across a transect of Australian savanna (Eamus and Prior, 2001), supports the ideas presented in this simple figure and for conditions at the drier end of the plant-climate continuum.   Leaf nitrogen improves the coefficient of determination (r^2) because it is a subtle marker of drought effects. As water is needed to provide nutrients, too much rain leaches N. Consequently, plants in dry climates produce thick leaves with high N.

L2.2 Temporal Variations in Leaf Area Index

Within a given plant functional type, leaf area will vary with time and space. The major scales of temporal variation are associated with the seasons and decades. The major spatial source in leaf area is in the vertical and horizontal dimensions.

a. Seasonal Variations

Herbaceous and woody vegetation all experience significant seasonal changes in leaf area. Annual grasses, herbs and crops must grow from a seed. Their seasonal development of leaf area is initially slow, experiences an exponential growth phase, a plateau and a reduction, as leaves senescence and drop. Consequently, a crop growing in the temperate zone of North America may not reach maximum leaf area index (and full

canopy closure, LAI > ~3) until midsummer (e.g. day 210) (Figure 4). In other words, this soybean crop only forms a closed canopy for about 40 days of the year. This is an important fact to recognize because it demonstrates that crops, because they are grown from seed, are inefficient solar collectors for much of the growing season. Ultimately this limits their potential to convert sunlight into biomass that can be converted to energy.
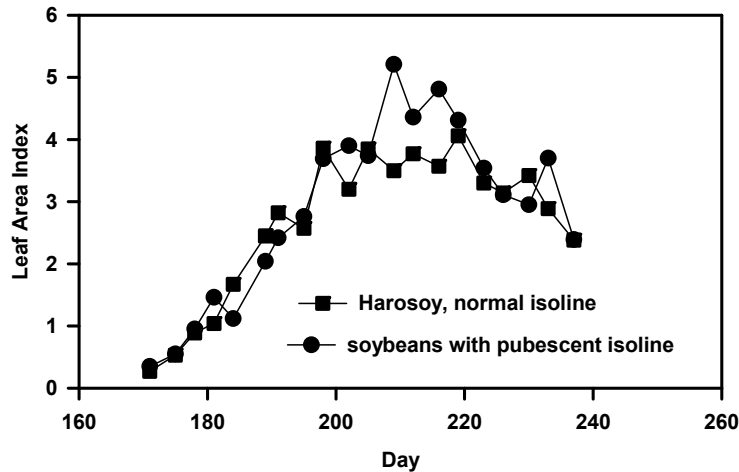

Figure 6 Seasonal variation of leaf area index of soybeans, growing near Mead, NE in 1979. data of D. Baldocchi.

Perennial vegetation, such as deciduous forests, experiences a different time course than crops. During the winter dormant period only stems and twigs are exposed. Leaf expansion can be rapid in spring, as leaves growth draws on reserves laid down the previous fall. In Oak Ridge, TN full canopy and maximum leaf area will occur by about day 140. As one progresses northward to New England, maximal leaf area will occur about a month later. But this date is still much sooner than the date of peak LAI experienced by crops. In the autumn (> day 300), many leaves are present, but they are senescent and are physiologically inactive. By comparing data in Figures 4 and 5 we observe that canopy coverage over cropland is quite sparse for a long portion of the growing season, as compared to forests growing in a similar temperate zone.
The forest attains full leaf coverage for over 150 days of the growing season, compared to 40 or so days by the crop.
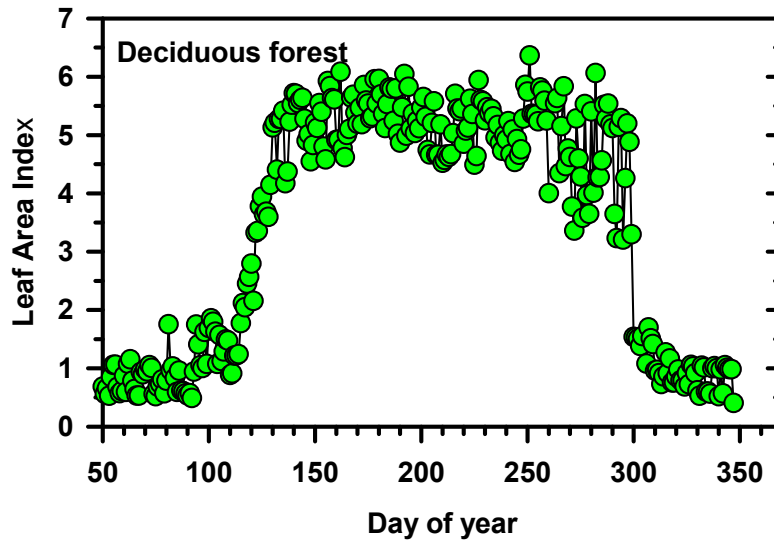
Figure 7 Seasonal change in leaf area index of a temperate broadleaf forest (Wilson and Baldocchi, 2000). Inferred from light transmission measurements.

With most canopies it is difficult to measure leaf area as frequently as desired. Indirect assessments of leaf area index can be acquired by relating leaf area index to albedo or reflective vegetation indices. A few years ago NASA launched the TERRA satellite and it is now being used as a tool to assess seasonal trends in leaf area index using the MODIS sensor (Figure 6).
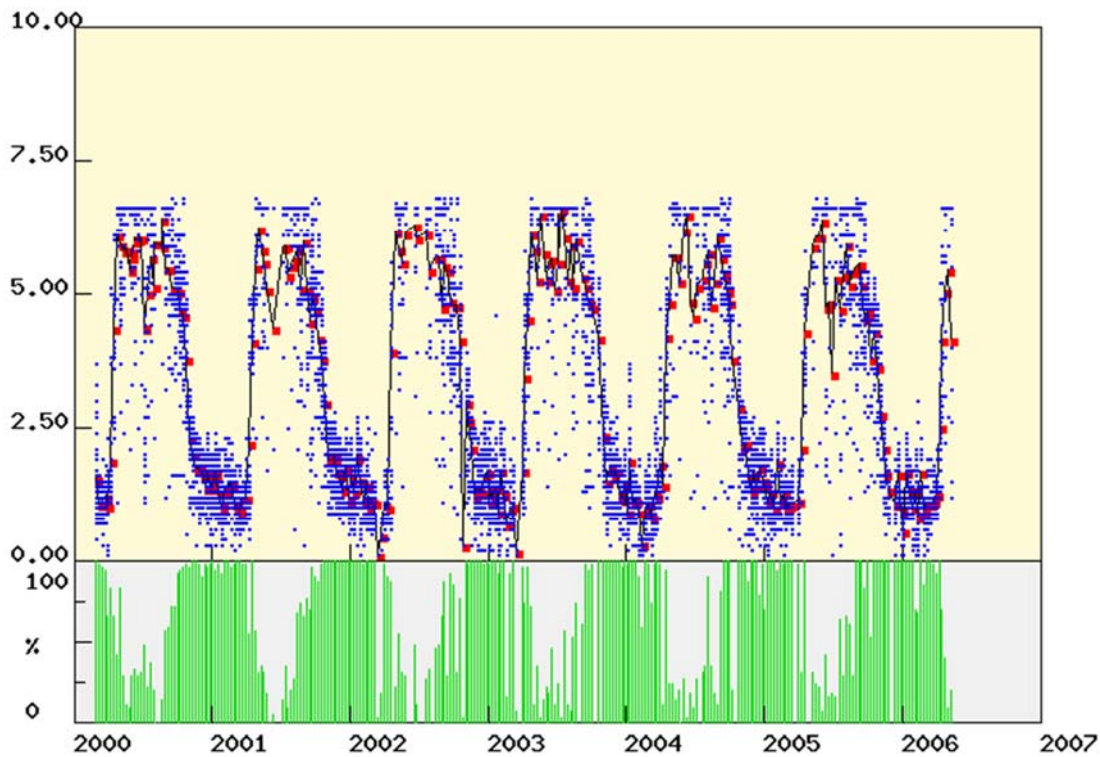
Figure 8 Seasonal variation in fraction of Leaf Area Index. These calculations were derived from MODIS sensor on the TERRA satellite. Data are available from the FLUXNET web site.

When assessing leaf area index of native vegetation with remote sensing, it is important to distinguish live from dead leaf matter, which is a major problem with perennial grasslands.

L2.3 Spatial Variations in Leaf Area Index

If we divide the canopy into multiple layers we will observe different amounts of leaf area in different layers. The amount of leaf area per unit volume is the **leaf area density**. The total **leaf area index** of a plant stand, then, is simply the integral, or summation, of the leaf area density (*a(z)*) of successive layers:

$$L = \int_0^h a(z)dz \approx \sum a(z)\Delta z$$

a. Vertical

Forests experience pronounced vertical zonation in leaf area. Ecologists define six levels within a forest ((Parker et al., 1989) (Figure 7). The **emergent layer**, the **outer canopy**, the **overstory**, the **middle story**, the under story and the **ground layer**. These layers are defined as follows:

1. Emergent layer: an irregular zone of extremely tall trees, rising above the mean canopy.

2. Outer canopy: surface of canopy in direct contact with the atmosphere. It is an undulating surface, with walls and canyons of plant material that form gaps.

3. Overstory: the layer consisting of dominant and co-dominant trees.

4. Middle story: a transitional area, where tree crowns are partly illuminated and suppressed.

5. Understory (subcanopy). woody plants reside in shaded areas. They tend to be fully suppressed. Growth is resumed when a nearby tree falls and produces a gap in the forest.

6. Ground layer: this layer is at the bottom of the forest and contains seedlings, herbs, and litter.
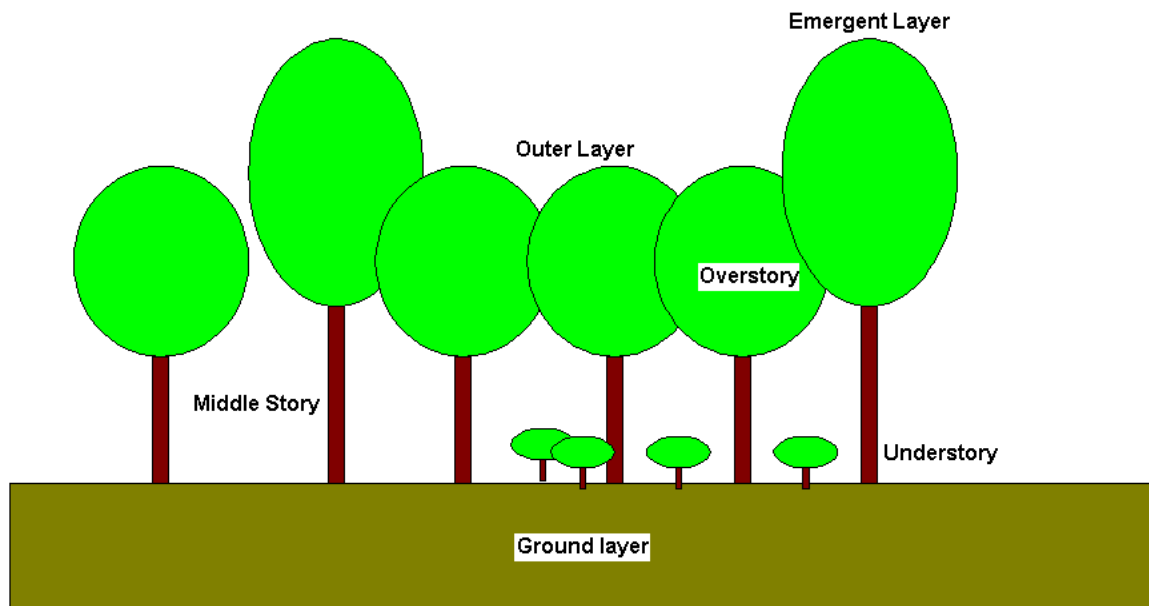
Figure 9 Schematic view of forest layers (adapted from Parker, 1995).

More recently, Parker and Brown (2000), working on an old growth Douglas fir forest defined three zones, on the basis of light transmission and variance. They defined the upper bright zone, a mild transition zone and a lower dim zone.

An example of the vertical variation of leaf area density of a 50 year old temperate deciduous forest is shown in Figure 8 (Hutchison et al., 1986). In this case, about 75% of the leaf area occurs in the upper 25% of the canopy. We will see in later lectures how the

distribution of leaf area affects wind, light, temperature and other microclimatic variables in a canopy.
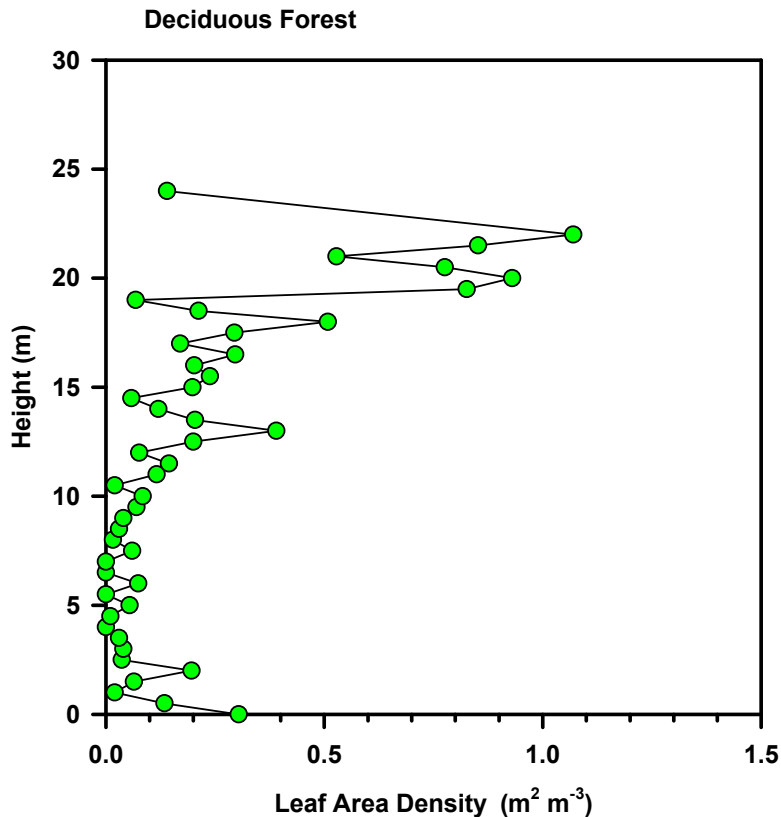
Deciduous Forest

Figure 10 Leaf area profile, temperate broadleaved forest, Hutchison et al. (1986)

The previous figure gives us a static view of the leaf area profile in a forest; wide application of such a figure forces one to suffer from scientific error on the basis of too little data. As more and more data have become published in the literature we learned that the vertical structure of a forest is not static in time or space (Aber, 1979; Parker and Brown, 2000). The vertical variation of a forest will vary by species, functional type and as a forest matures, on decadal to century time scales. For example, in a mixed species forest, different species will have different vertical profiles, too. (Figure 9). These results are very important as we are now able to invoke ecological rules to help us prescribe leaf area profiles in forests.
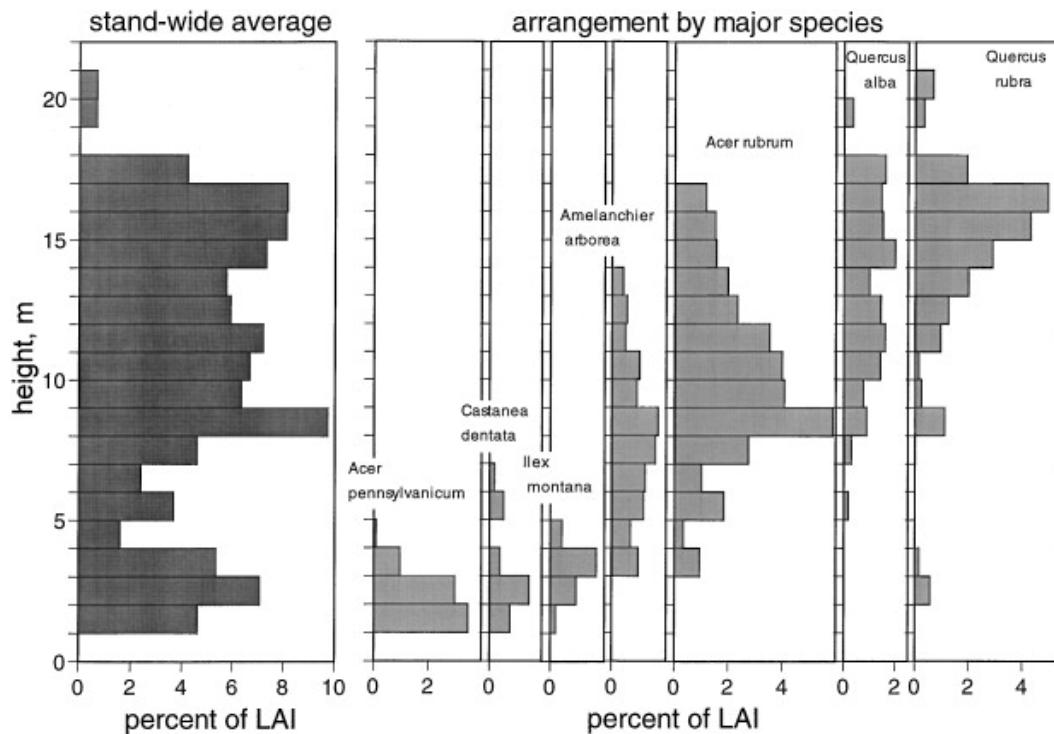
Figure 11 Profile of leaf area in an eastern deciduous forest. Parker GG**, Brown MJ (2000)**

Perennial vegetation, such as forests, experience four stages of development (Sprugel, 1985). So one can expect the forest to maintain a different leaf area indices and LAI profiles as it progresses through its life cycle (Aber, 1979). The sequence of development of a hardwood forest is noted in the following (Figure 10):

1. **Stand reinitiation**. 1-10 years. Herbs and shrubs dominate site (species A dominates)

After disturbance seeds, spores and rhizomes are available to germinate and grow quickly. Light conditions have improved and there is less competition for water and nutrients. With disturbances such as floods, volcanoes and landslides there is new substrate.

Animals and insects and birds are important for re-introducing new genetic material.

A young forest is a short stand with a vertical distribution of leaf area that can be approximated with a Gaussian distribution.

2. **Stem exclusion stage** (aggradation phase).

Woody species start to monopolize a plot. Invasion of other trees and shrub seedlings stops. Presences of herbs and grasses is reduced or absent. physiognomic and species diversity is low (species B dominates).

Self thinning is quite severe with time and may reach 90%. Stem thinning follows a –3/2 law with time.

Leaf area of the stand reaches its maximum during the stem exclusion period.

Upper limit of leaf area tends to correspond with about 90% interception of sunlight., which for hardwoods is on the order of 5 to 6.

3. **Under-story re-initiation stage** (aggradation phase continues). Dominant woody species start to lose dominance of the site. Understory becomes reestablished. Includes shade tolerant herbs and may have shade tolerant seedlings.

Trees approach maximum height, growth slows. Gaps are created by mortality and allow shade tolerant understory to be established.

A forest of intermediate age is a much taller stand. It possesses a disproportionate amount of leaf area near the top of the stand and possesses little leaf area in the understory.

4. **Old growth stage**. If no disturbance, first generation trees die. More tolerant trees replace them and grow in gaps are areas of degenerated canopy. (species b, c and d dominate). Little if any height growth occurs. Diameter growth continues, on the other hand. Tree species and structural diversity is maximal. The leaf area index profile is 'bottom heavy'.
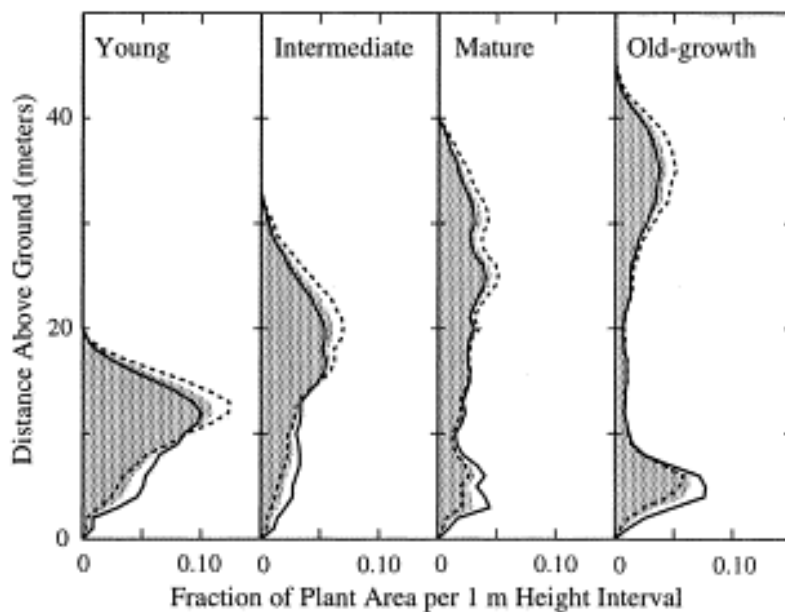

Figure 12 Variation of leaf area index profile with stand age, after (Harding et al., 2001)

b. Horizontal Variation

The horizontal distribution of plants and leaf area canopy can be homogeneous or heterogeneous. Within the homogenous class are closed stands, which may possess foliage that is distributed in a random or uniform manner.   A 'big-leaf' or plane parallel turbid medium is a common abstraction of horizontally homogeneous canopies.

Heterogeneous stands can have vegetation that is spatially arrayed in clumped (oak/grass savanna) or regular (as row crops, vineyards) patterns. Once we define the location of a plant, its canopy can take a variety of shapes. Foliage envelopes are often defined as discrete arrays of plants (cones, ellipses, cubes, cylinders) or rectangular or triangular hedges. Heterogeneous stands may form closed canopies, as does a tropical forest or an open stand, such as an oak/grass savanna.
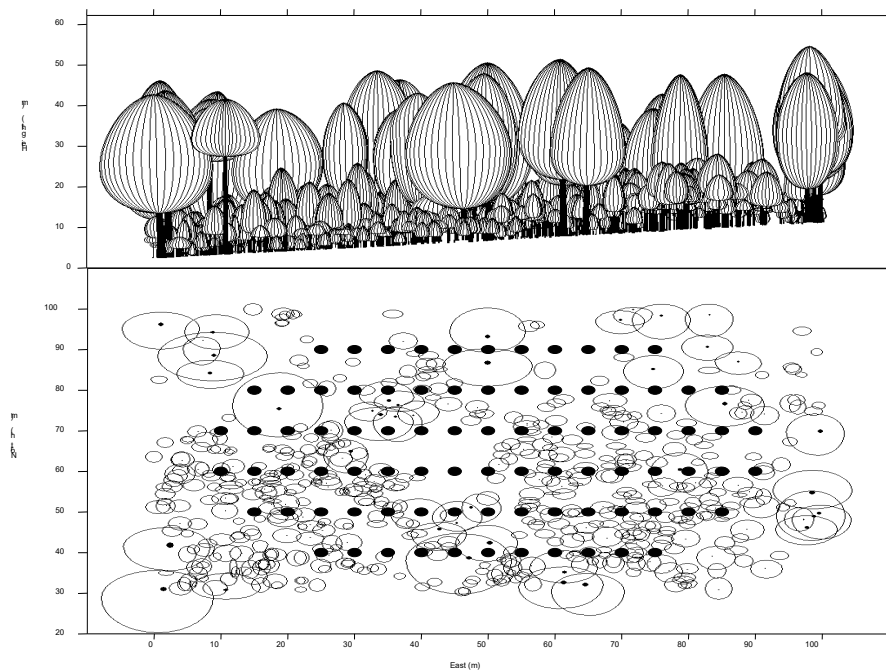

Figure 13 Spatial distribution of a ponderosa pine stand. (Law et al., 2001).

Within a foliage envelope leaves may possess random or clumped groupings. In the case of conifers needles are perched on shoots. Hence, a detailed analysis of leaf area index produces a wide distribution of estimates based on whether one is in the crown or gaps.

There is freeware software on the internet for visualizing forest stands. One example is Stand Visualization System
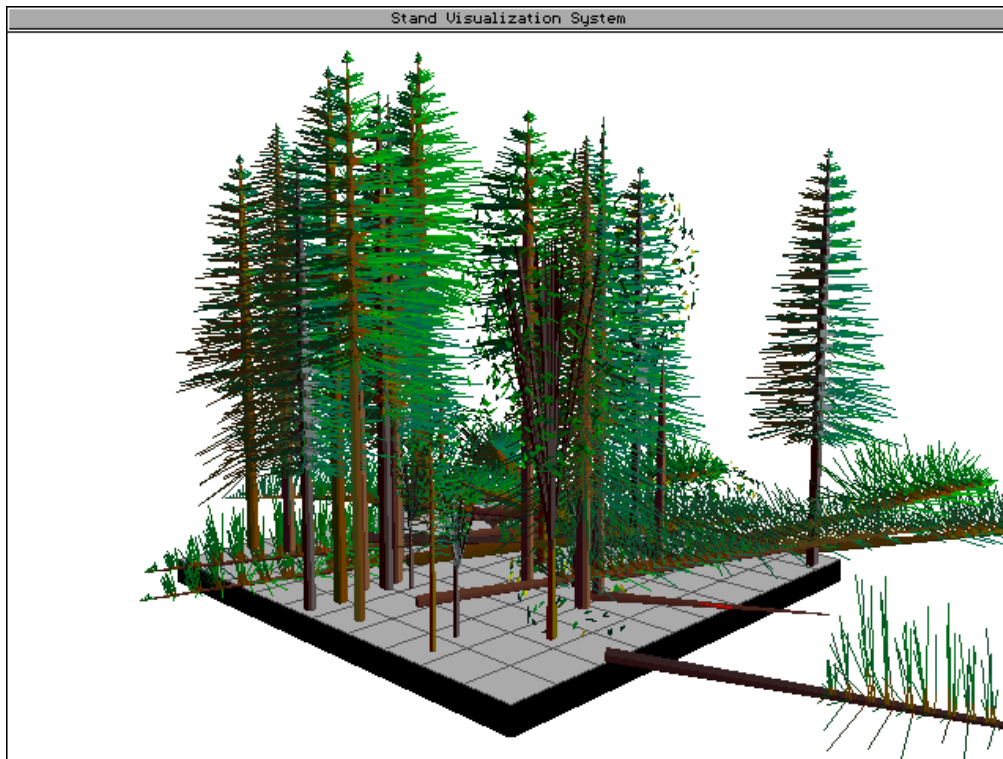
Biometeorology, ESPM 129

http://forsys.cfr.washington.edu/svs.html

Figure 14 http://forsys.cfr.washington.edu/bitmaps/cover.gif

And new developments of LIDAR allow us to image our canopies in equisite 3 dimensional resolution.
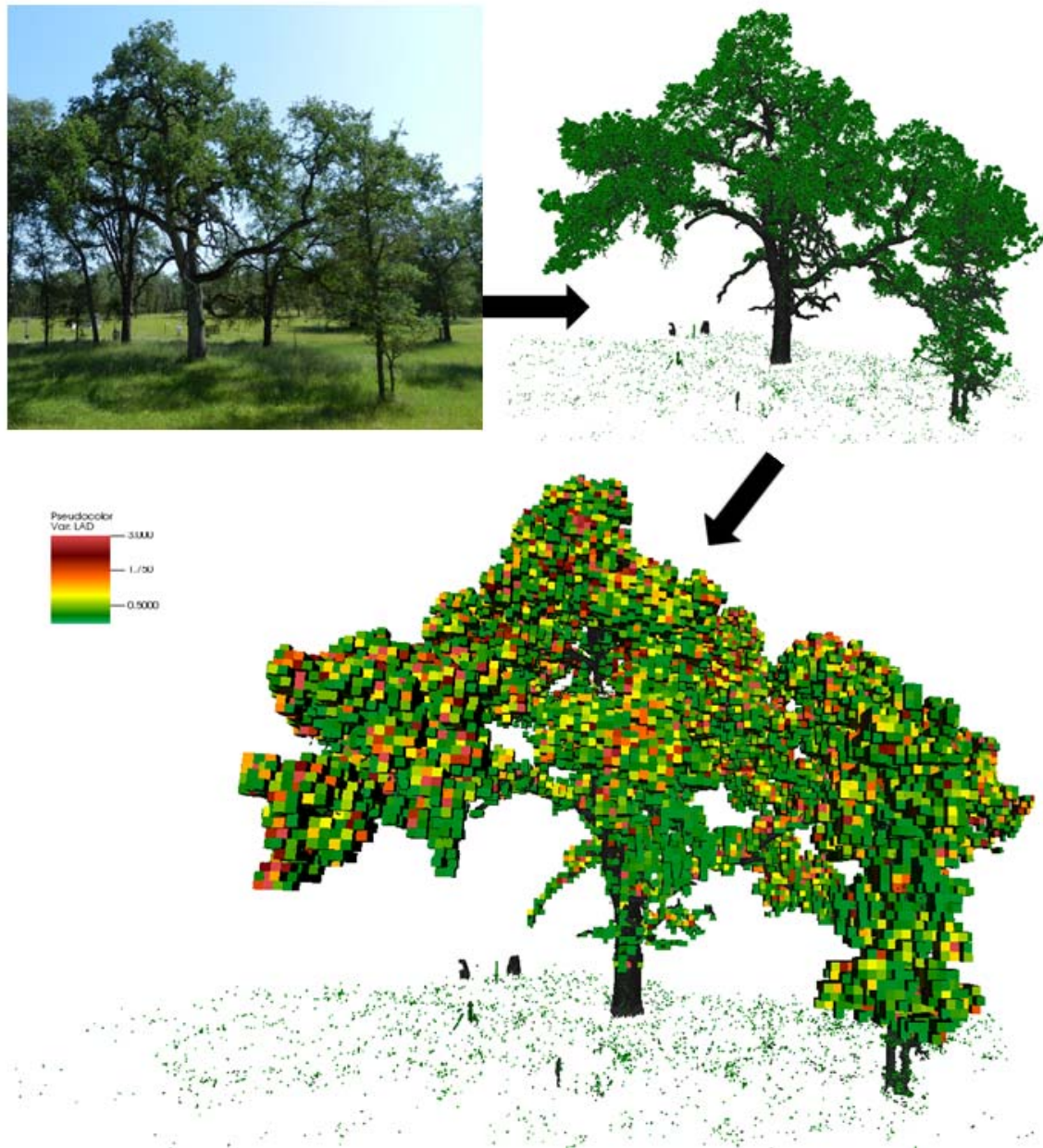
Figure 15 Beland et al. unpublished

L3.4 Leaf Area Index and Growth Measurement Methods

Direct and **indirect** methods are used to assess leaf area index (Chen, 1996; Jonckheere et al., 2004). Direct methods are labor intensive, and in the case of tall trees, may be impractical. They involve manually sampling of leaves. The method is destructive and time consuming. One must also consider a proper sampling strategy to ensure a statistically representative number of leaves and plants. Four sampling methods, used most often, are the stratified clip method, the dispersed individual plant method, point quadrat method and litter fall collection method.

a Direct methods

Several direct and indirect methods exist for determining leaf area index.

The **Stratified Clip Method** is a simple a direct method for evaluating leaf area. The first step is to delimit a rectangular (or circular) area of known dimension. Horizontal layers are successively clipped. For small crops, samples 0.5 by 0.5 m to 1 by 1 m are typical. The area of leaves are measured directly with an automatic planimeter, a very labor intensive task. Often investigators will develop relations between leaf weight and leaf area from a subsample. Then, estimate the leaf area on the basis of the total weight of the sample. This short cut can be subject to error, as specific leaf weight varies with height and species. One also needs to determine how many samples are required to provide a robust estimate of the population mean. The number of samples will increase with the heterogeneity of the stand.

A second method is the **Dispersed** individual plant method. This method involves detailed measurements on individual plants. It is most often used in forestry, where it is simpler to fell tall trees, than to measure vertical profiles of vegetation. Foresters also apply regression statistics to samples to develop allometric relations, from which leaf area, or some other structural parameter, can be assessed by a simply measured surrogate such as diameter at breast height.

The **point quadrat** method involves the passing of metal probes through the canopy, much like the transmission of a ray of light. The leaf area of the canopy can be related to the number of contacts that a probe makes with the foliage.

The **litter fall method** places bushel baskets of know area under a forest. Leaves are collected and their leaf area is measured. Caution should be exercised using a weight/area ratio to determine leaf area from bulk weight measurements. The ratio of leaf weight to area varies with depth in the canopy.

Allometric Scaling Laws

Many ecologist develop and use allometric relations to evaluate leaf area index (Gower et al., 1999; Whittaker and Woodwell, 1967) since it is very laborious and time consuming to harvest a large number of trees. To obtain a statistically representative sample they often measure such indices as diameter at breast height and relate that to leaf area index. One common function is the logarithmic relation between diameter of breast height or basal area (the independent variable) and leaf area index.

$$\log(y) = A + B\log(x)$$

This equation can produce a power law relation between mass per dry weight, M, or plant area, A, and stem diameter, D.

$$M = aD^b$$

$$A = cD^e$$

Whittaker and Woodwell (1967) developed a regression of leaf area index on basal area (as well as for bark area) for forests growing in New York and the Smoky Mountains. They reported that values of a A ranged from 2.93 to 3.8 and B ranged from 1.52. An example of the relation between leaf area index and sapwood area is shown in figure 13.
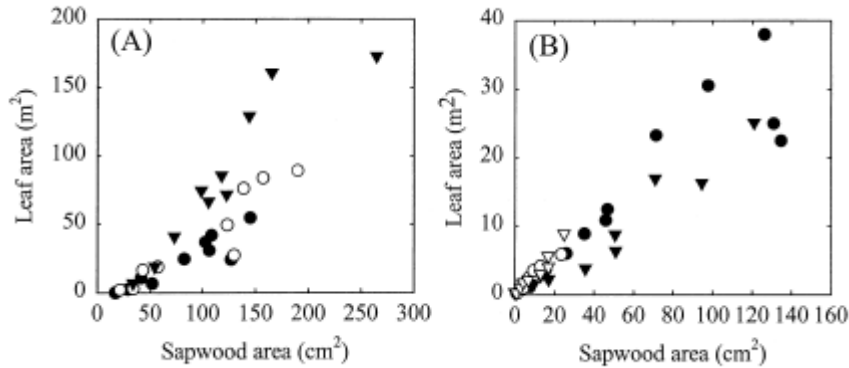

Figure 16 Leaf area index versus sapwood area for a spectrum of trees. Data from Gower et al., 1999

Gower et al. (1999) report strong correlations between leaf area index and sapwood area for several tree species, as well as diameter at breast height. But they conclude that site specific allometric relations need to be developed for accurate estimates of leaf area index.
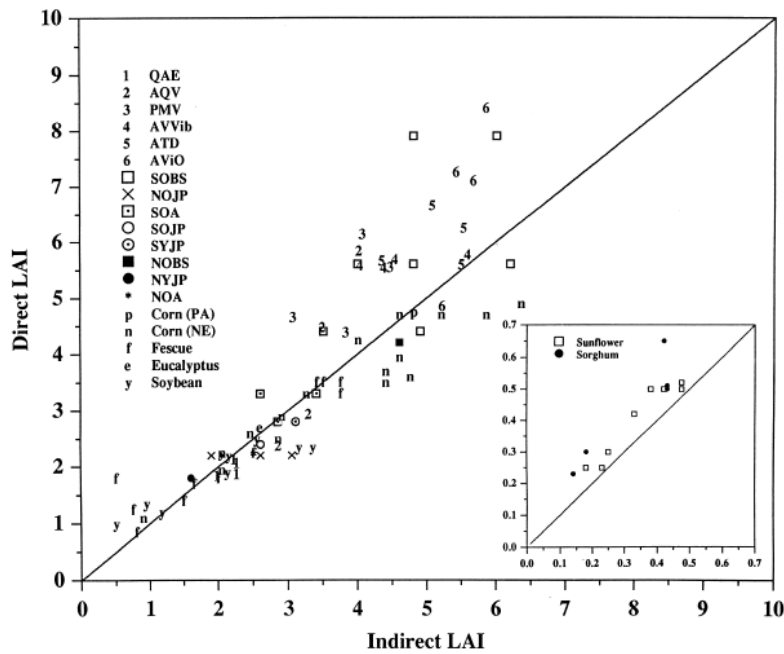
Figure 17 Test of estimates of leaf area index based on 'direct' allometric methods and 'indirect' light transmission methods. Gower et al, 1999

More recently, a group of scientist led by West (Enquist et al., 2003; West et al., 1999) have re-evaluated scaling theory and reassert that the allometric relations follow certain power laws. By comparing their theory with data they show that that these power laws are valid for over 20 orders of magnitude.   For example, cross sections of tree trunks and aeorta scale with mass to the ¾ power, as does metabolic rates (B) of organisms. The mechanisms for such scaling derive from 3 points:

1. Living things are sustained by transport of materials (water, nutrients) through networks of paths.
2. For the network to function, it must be space filling throughout the volume
3. the final branch is scale invariant
4. the energy required to transport material must be minimized.

From first principles we can draw insight into the exponents of power law between area (A) and volume (V), and with assumptions on density convert these to mass.

$$A \sim l^2 \therefore l \sim A^{1/2}$$
$$V \sim l^3 \therefore l \sim V^{1/3}$$
$$A \sim V^{2/3}$$
$$\rho \sim M/V \sim g/l^3$$

Annual rate of growth, G, scales as a ¾ power of body mass, M, for over 20 orders of magnitude ($G \sim M^{3/4}$). Plant body length scales as ¼ power of mass. And photosynthetic body mass, M_p scales with ¾ power of non-photosynthetic body mass, M_n ($M_p \sim M_n^{3/4}$). Together they find that growth rate is directly proportional to photosynthetic body mass, M_p. ($G \sim M_p$).

b. Indirect Methods

Indirect methods of estimating leaf area index are based on light transmission or reflectance theories (Chason et al., 1991; Chen, 1996; Chen et al., 1997; Jonckheere et al., 2004; Lang, 1987). This can be done by interpreting light and dark spots on hemispherical photographs or by employing quantum sensors that either traverse through a canopy or measure the sky brightness. The theory on radiative transfer will be discussed in more detail, but here we introduce the methods of indirectly assessing leaf area in brief, for completeness.
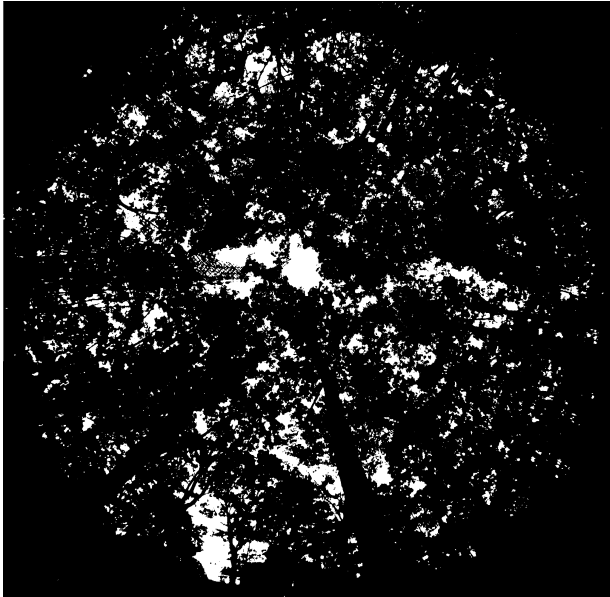

Figure 18 Hemispherical photograph of a deciduous, temperate broadleaved forest near Oak Ridge, TN.

Hemispherical measurements from hemispheric photos (Jonckheere et al., 2004; van Gardingen et al., 1999) or sensors (eg, LAI-2000) assume that leaf area index, L, is a function of the natural log of beam transmission, T, integrated over the hemisphere.

$$L = -2\int_0^{\pi/2} \ln(T(\theta)\cos(\theta)\sin(\theta)d\theta$$

The concept of using beam penetration to estimate leaf area index was pioneered by Lang (1987), who realized that the contact number (K) can be represented by the product of the

leaf area index and the direction cosine function G. In turn this product is a function of the cosine of the zenith angle and the natural log of the light transmission fraction.

$$K(\theta) = LG(\theta) = -\cos\theta \ln(T(\theta))$$

Lang showed that the contact number is a linear function of zenith angle, θ

$$K(\theta) = a + b\theta$$

And he had the insight that the value for G is converges to about 0.5 when the sun zenith angle is at **one radian**, no matter what the leaf inclination angle distribution was.
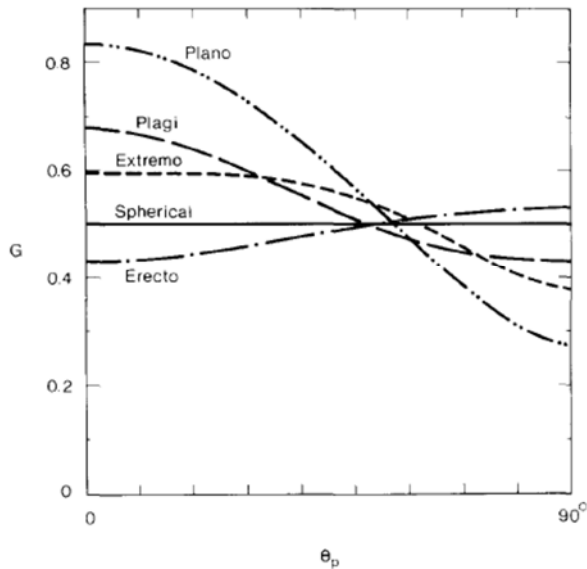

Figure 19 from Lang 1987. G function as a function of the solar zenith angle

Consequently, one can evaluate leaf area index with the measurements shown in Figure 16 and the following equation that is derived from the intercept (a) and slope (b)
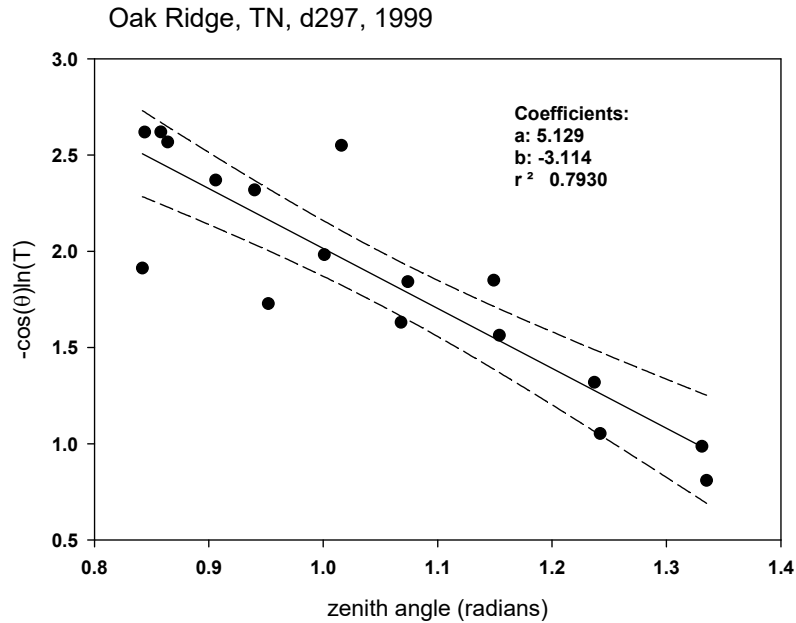
$$LAI = 2(a + b)$$

Oak Ridge, TN, d297, 1999

Figure 20 Relation between contact number and zenith angle, data of Baldocchi, Chason and Huston.

This approach is valid unless there is clumping of foliage (Chason et al., 1991; Chen, 1996). A comprehensive survey of comparing direct vs indirect measures of LAI is presented in Gower et al., 1999. Overall methods compare within 30%. The notable difference is that indirect methods saturate and plateau at leaf area indices of 5 to 6, which can correspond with direct measures as large as 9. In other words, indirect methods are unreliable if the canopy LAI exceeds 6.

Sparse canopies

Hemispherical photos of sparse canopies, tend to be ringed on the outer edge of the photo. So it is difficult to assess probability of gap with accuracy and precision (Ryu et al., 2010).

With the revolution of cheap and high resolution digital cameras, there is a new potential to assess gap fraction with a network of upward looking digital cameras (Ryu et al in press).

Using the upward looking digital cameras, we have been able to capture the phenology of an oak woodland well
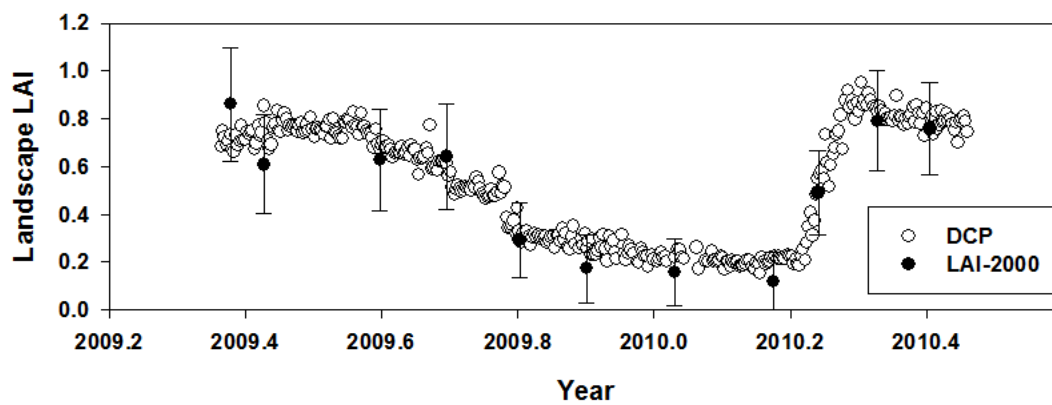
Spatial Distribution of Leaves and Shoots, Clumping Factors

We have spoken of very high leaf area indices being sustained by conifers. Leverenz and Hinckley (1990) contend that conifer shoots are able to utilize shade better than flat

leaves. They report a positive and linear correlation between the maximum leaf area and R, the ratio between the shoot silhouette area and the area of all the needles after they have been plucked from the shoot and are aligned on a flat plane. Values of R approaching on are indicative of a flat leaf or zero mutual shading by the needles. Their results support a hypothesis that shade adaptation by shoots affects their productivity more than the morphology of shoots.
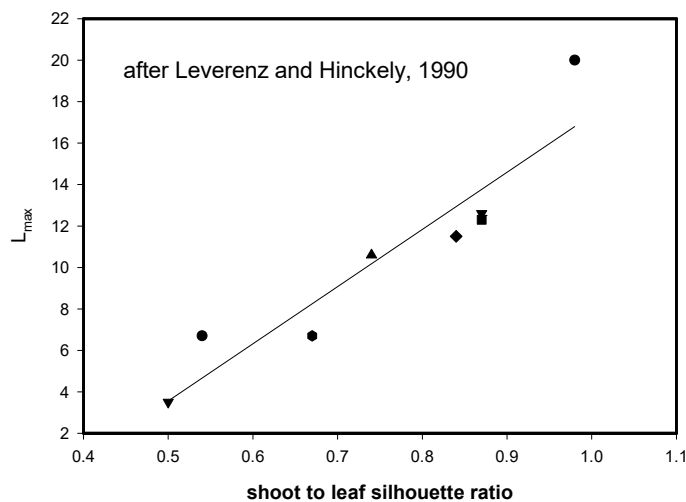

Figure 21 Comparison of maximum leaf area index the ratio between the projected shoot and needle area.

Estimates of projected effective and actual leaf area are interrelated to one another with the application of shoot and crown clumping factors.

From light transmission theory the effective leaf area index that intercepts photons is related to the hemisurface leaf area index through corrections for element and crown clumping:

$$L_e \sim L_{hc} \times \Omega_E / \gamma_E$$

The half-total surface area per m^2 ground corrected for clumping at the needle and shoot scales and wood interception is:

$$L_{hc} \sim L_e \times \gamma_E/\Omega_E$$

Where: γ_E is the needle-to-shoot area ratio for foliage clumping within shoot; Ω_E is the element clumping index that quantifies the effect of foliage clumping at scales larger than the shoot. This approach assumes that woody materials have a spatial distribution similar to foliage, and may result in a small error in the LAI estimates (Chen et al., 1997).

Measurements of woody biomass are rare. Yet, such information is needed to assess bole respiration, energy interception during the leafless dormant stage of deciduous forests. The plant surface area of bark ranges between 0.3 to 0.6 m^2 per meter of land (Hutchison et al., 1986; Whittaker and Woodwell, 1967).

There is also some controversy about the role of woody biomass. There is often a low probability that photons will intercept wood before leaves (Kucharic and Norman).

Table 3 A contemporary survey of canopy attributes was recently published by Gower et al., (1999), Law et al. (2001), Chen et al. 2005.

species	Ω	γ	L
Sugar maple	.95	1	7.1
Oak	.88	1	4.2
Hemlock	.94		5.4
Aspen	.64	1	3.3
Jack pine	.45	1.2-1.4	2.2
Black spruce	.38	1.3-1.4	5.6
Douglas fir		1.77	
Scots pine		1.75	
Red pine		2.08	6.1
Ponderosa pine	0.83	1.29	1.6
Broadleaf evergreen	0.63		
Broadleaf deciduous closed	0.69		
Needleleaf evergreen	0.62		
Needleleaf deciduous	0.68		

Chen et al (2005) just published a global survey and map of clumping factors, as shown in the figure below
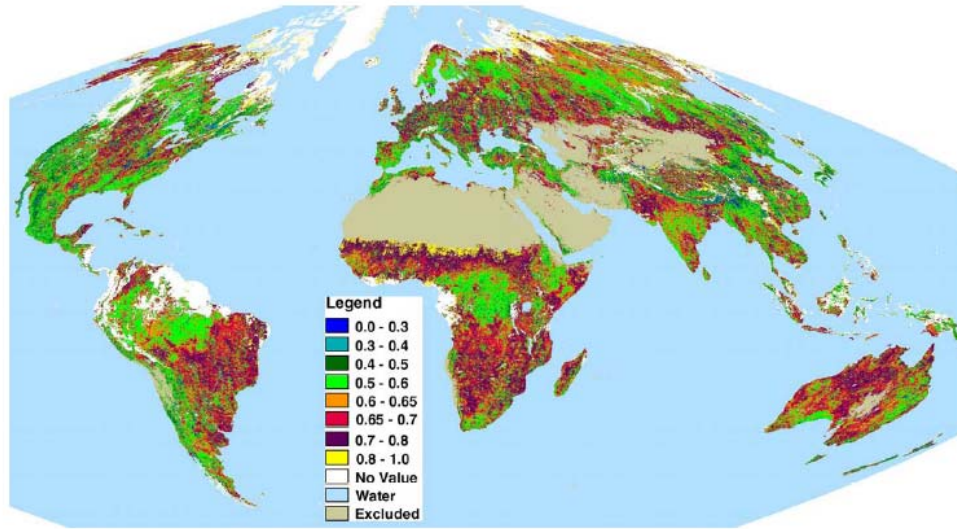
Biometeorology, ESPM 129

Fig. 6. Global vegetation clumping index map derived from POLDER 1 data using the normalized difference between interpolated hotspot and darkspot NIR reflectance and applied to vegetated land cover. Vegetation clumping increases with decreasing values of the index.

Detecting LAI From Space

Radiation sensed by satellites can provide global scale models need information on leaf area. Such information is very important due to the dynamic nature of ecosystems and their spatial extent; it is virtually impossible to send out teams into the field to assess leaf area directly. Modern scientists are estimating leaf area for sensors perched on satellites, such as LANDSAT, AVHRR, SPOT and the recently launched TERRA (MODIS/Land) http://modis-land.gsfc.nasa.gov//.

$$NDVI = \frac{I_{NIR} - I_{VIS}}{I_{NIR} + I_{VIS}}$$

The Normalized Difference Vegetation Index are a function of upwelling radiances (I) in the near infrared (nir) and visible wave bands, where the nir is associated with 800 nm wavelength radiation and the visible is linked to radiation near the 600 nm waveband.

NDVI can also be expressed in terms of reflectances

$$NDVI = \frac{\rho_{NIR} - \rho_{VIS}}{\rho_{NIR} + \rho_{VIS}}$$

NDVI ranges between zero and one. Sensor has restricted field of view (2-15 degrees) and is nadir viewing, from directly overhead.

Simple Ratio is another remote sensing index. The simple ratio is a function of near infrared radiation under field condition.

$$SR = \frac{I_{NIR}}{I_{VIS}}$$

$$SR = \frac{\rho_{NIR}}{\rho_{VIS}}$$

I_{vis}: (0.4 to 0.7 μm); I_{nir}: (0.7 to 1.1 μm)

Sellers (1987) developed theory showing how the Simple Ratio can be used to evaluate leaf area.

$$\frac{\partial(SR)}{\partial L} = \frac{1}{\rho_{vis}}(\rho_{vis}\frac{\partial\rho_{nir}}{\partial L} - \rho_{nir}\frac{\partial\rho_{vis}}{\partial L})$$

$$\frac{\partial(SR)}{\partial L} \sim \frac{\partial\rho_{nir}}{\partial L} \sim \exp(aL)$$

Since the sensitivity of SR is an exponential function of leaf area index, the index saturates as leaf area index increases, hence the method does not evaluate canopies with high leaf area well.
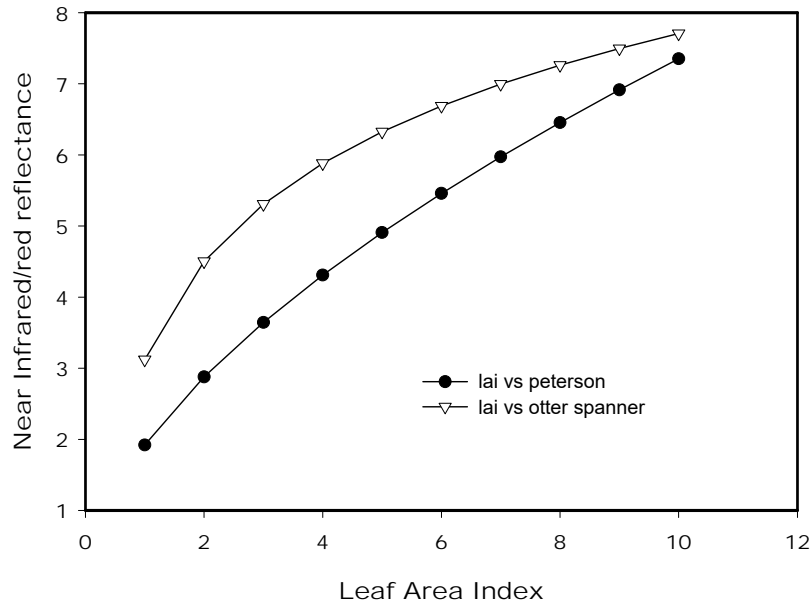
Figure 22 spectral reflectance index and leaf area index across a spectrum of leaf area indices. Data are from the OTTER project and reports by Peterson et al and Spanner et al.

Indices such as NDVI and SR were developed for the past generation of satellites, e.g. LANDSAT. Due to the coarse spectral resolution of these sensors, the indices are sensitive to contamination by the reflection of non-vegetated background material. On the other hand it is worth to continue computing these indices due to the historical length of their record, as such information gives us an unprecedented ability to monitor land use change.

With the launching of the TERRA satellite, with high spectral resolution, new and better indices have been developed, such as EVI, the enhanced vegetation index and its predecessor, SAVI (http://tbrs.arizona.edu/projects/evi.htm). The advantage of applying EVI is its ability to decouple confounding influences the canopy background and the atmosphere. Mathematically it is defined as:

$$EVI = G \frac{\rho_{nir} - \rho_{red}}{\rho_{nir} + C_1 \rho_{red} - C_2 \rho_{blue} + B}$$

G is a gain factor, C_1 and C_2 are atmospheric correction factors for the transmission of red and blue sunlight and B is the background brightness factor. Values adopted by NASA in their application of the EVI algorithm are: B=1, $C_1 = 6$, $C_2 = 7.5$, and G = 2.5.

Figure 19 shows a global map of EVI that is being generated routinely by the MODIS project.
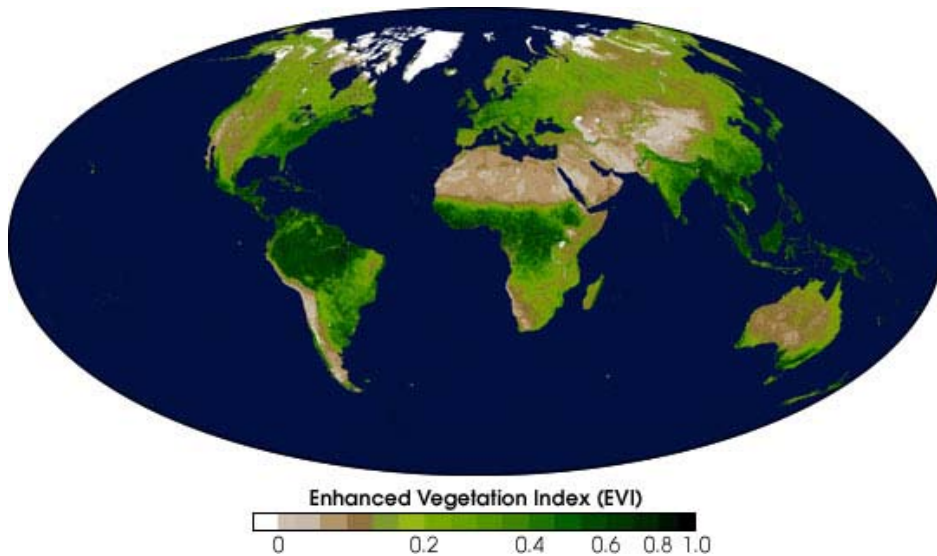

Figure 23 Global map of EVI. http://tbrs.arizona.edu:8080/modis/gm_index.htm

Remote sensing products are now being used to evaluate leaf area index at global and regional scales. Below we show a global map.
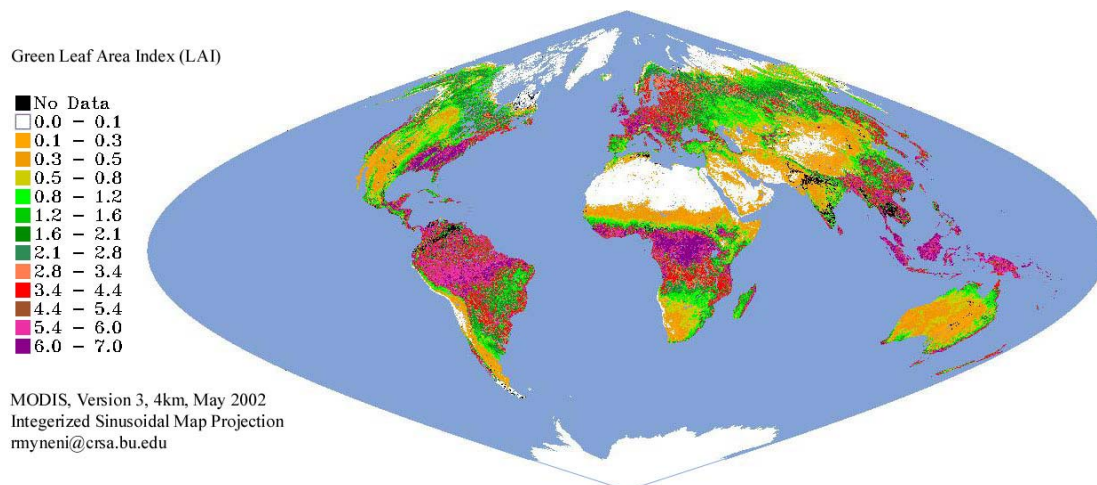

Figure 24 Global map of estimated leaf area index, May 2002. Lab of Ranga Myneni, Boston University.

Higher resolution AVHRR data can also be used to generate regional scale models of leaf area index.
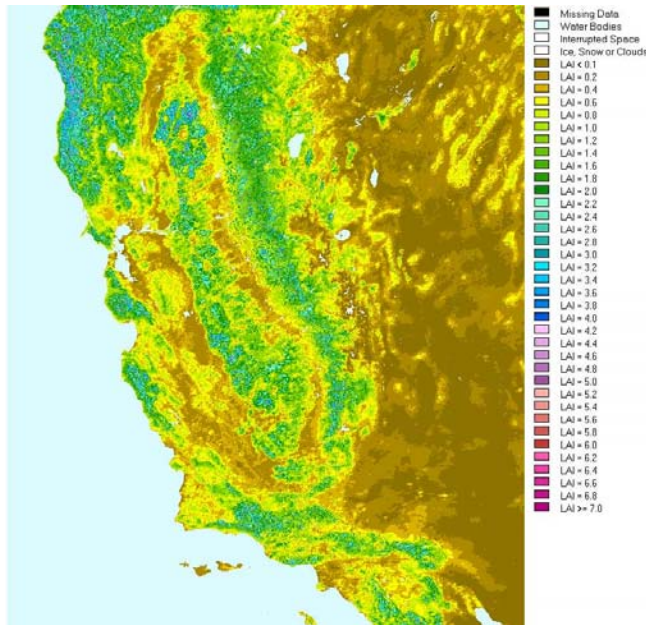

Figure 25 Summer maximum LAI in California. Computations by Ned Nikolov, 1 km resolution and corrected for clumping. Data are based on AVHRR data on the NOAA satellite (Nikolov and Zeller, 2006).

3.5 Other Measures of Stand Character

Information on growth is important for it informs us on how leaf area index, height and other plant features are changing with time. Several terms are used to describe the current status of plants and growth:

1. leaf fresh weight;
2. leaf water content (fresh-dry)/fresh;
3. specific leaf dry weight: mass dry/surface area;
4. Specific leaf area (SLA) is the ratio of leaf area to leaf mass. This is an index of leaf structure.   The inverse of SLA is specific leaf weight. The term has been criticized as being a misnomer as specific refers to 'per unit mass.;
5. Relative growth rate, RGR, R_w. Instantaneous rate of growth relative to the living plant biomass.

$$RGR = \frac{dW}{dt}\frac{1}{W} = \frac{d(\ln W)}{dt}$$

W is the total plant weight (g), time is time in days. Theoretically, W is living plant weight, so errors occur, in interpretation, when dead matter is used.

When growth is exponential, RGR is constant through the interval.

$$m(t) = m(t_0)\,exp(rgr(t - t_0))$$

The function concept of relative growth rate idea links back to Blackmun who used economic theory to examine plant growth. He assumed their growth rate was constant. In reality, RGR changes with ontogeny, it increases with time in the initial stages of life and decreases in the senescing stages (see Poorter and Garnier, 1999).

The da Vinci rule, cross sectional area of a trunk is equal to the sum of the cross section area of the branches at the next level (Enquist, 2002). Nice project to test with student data.

Summary

- Leaf area index is one of the most important biometeorological variables to assess, as it is a measure of the population of the plants and leaves that are interacting with the environment; this can occur by intercepting photons, being a source of water, heat or CO_2 or being a sink for CO_2 and pollutants.

- There are theoretical limits to how much leaf area a landscape can sustain. Assuming no limiting factors, then the amount of leaf area to intercept 95% of incoming sunlight sets the limit, which can vary between 3 and 10 depending on leaf angle orientation and clumping.

- Climatic factors that cause variations in leaf area index among ecosystems include precipitation, evaporation and leaf nutrient content.

- Leaf area index is not static with time. It changes markedly in deciduous plants as they transcend from dormancy to full leaf and leaf fall. Subtle changes in leaf area occur in evergreens as they drop and add leaves.

- Vertical profiles of leaf area need to be assessed to employ multi-layer models. Distribution of leaf area varies with stand age of forests.

- Methods to assess leaf area index are direct and indirect. Indirect methods depend on light transmission or reflection theory and can be assessed with hand held instruments or satellites peering down from space.

Data/Resources

New data on LAI are available on-line from the Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A.
http://www.daac.ornl.gov/VEGETATION/lai_des.html

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