Canopy Structure, and Leaf area, are fundamental features of the landscape. We can’t really understand the plant-atmosphere interactions without knowing how much vegetation is on the surface.
Plants are certain sizes in different regions for a variety of biophysical and ecological reasons. We will explore these.

'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

Quercus douglasii, 2 cm  
Acer macrophyllum, 30 cm

Biometeorological factors, conspiring with evolution and natural selection, conspire on determining the size of leaves for given environments. Hot dry zones tend to exhibit a proliferation of small leaves, which are effective in conducting heat away and maintaining a viable energy balance and surface temperature. Huge leaves tend to occur in darker reaches of a canopy and in wet humid climates, like the rain forests of the Pacific Northwest or the tropics.
Temporal and Spatial variations in Canopy Structure and Function modulate trace gas and energy fluxes

• by altering:
  1. wind and turbulence within and above the canopy
  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 CO₂ transfer and
  5. the biochemical capacity to synthesize or consume carbon

Reasons why and how structure and function affects biometeorological processes. Leaves intercept and reflect light, they absorb drag and alter turbulence and they provide sources and sinks for trace gases.
The Flux Density of mass ($F$) (moles m$^{-2}$ s$^{-1}$) or Energy (J m$^{-2}$ s$^{-1}$)

\[ F = \sum_{0}^{h} S(z) \Delta z \]

Theoretical reason why leaf area is important. The source and sink strengths of vegetation are proportional to the leaf area density, layer by layer.
Using Ohm’s Law, an analogy to electrical circuits and current flow, we see that the source sink strength, $S$, is directly proportional to the leaf area density of each layer, $a$. So we want to know how leaf area density varies with depth throughout a canopy.
We will investigate variations in leaf area index with time and space, understand its theoretical limits and ways to measure it.

| Characterizing the Vegetation Canopy:       |
| Leaf Area Index                            |
| • Leaf area index                          |
|   – Observations                           |
|   – Theoretical Limits                     |
|   – Predicting leaf area index,            |
|     • nutrition, functionality and waterbalance |
|     • from allometry                        |
|   – Variation with time:                   |
|     • season, decade, century              |
|   – Variation with space:                  |
|     • height, horizontal, globe            |
|   – Measurement methods                    |

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Definitions of leaf area index. Plant area index is the sum of leaf area and woody biomass silhouette indices.
Note that the hemispherical surface area index of a non-flat leaf, like a conifer needle, is greater than its projected index. We need information on projected area to study light interception. But the surface area is more important for studying processes like mass, heat and energy exchange.
Many groupings of ‘leaves’ experience clumping. The example is the area of a spruce shoot is different than the area of the individual needles. We need to study clumping to better understand light interception and its relation of leaf area index.

Actual vs projected shoot Area

\[
\overline{STAR} = \frac{1}{2\pi} \int_0^{2\pi} \int_0^{\%} \frac{A_{\text{silhouette}}(\phi, \gamma)}{A_{\text{needle}}} \sin \phi d\phi dy
\]
Comparison of maximum leaf area index the ratio between the projected shoot and needle area

after Leverenz and Hinckely, 1990
Cauchy’s theorem

the average silhouette of a convex solid
is $\frac{1}{4}$ of the surface area for any body shape.

For flat leaves, G, the ratio of the silhouette to plan area of a leaf,
is $\frac{1}{4}$ for total surface area and $\frac{1}{2}$ for the plan area

e.g. projected vs surface area of a sphere

$$\frac{A_p}{A} = \frac{\pi r^2}{4 \pi r^2} = \frac{1}{4}$$
Excellent survey on leaf area index among different plant functional groups. Inspect the table for the range of values (<1 to 10), canopies that are associated with high values, medium and low.

Also notice that leaf area index is more than one. In other words plant stands can sustain more meters of vegetated surfaces than a meter of ground area. Why is that? How can that happen? Theory helps us find the way.
Beer’s Law is fundamental in understanding the attenuation of light passing through a vegetative canopy. It also helps us understand the maximum value of leaf area index for a maximal amount of light attenuation.
Example of estimating leaf area index for condition when 95% of the light is attenuated by the canopy, or only 5% is transmitted through the foliage, to the ground.
From a light harvesting perspective a closed canopy occurs when leaf area index exceeds 3. Many upper limits are on the order of 5 to 6 for dense forests. Rarely are values higher, but clumping of foliage and unique leaf angle orientations can up the leaf area index sustained by dense canopies. Numbers greater than 10 are not to be trusted and are probably artifacts of sampling errors and upscaling.
How does leaf area index vary with climate and ecological zones? One needs water to sustain higher rates of transpiration and photosynthesis that are associated with dense stands. So as precipitation declines, so does the fraction of vegetative cover, and leaf area index. Note this figure shows a non-linear and saturating response. This curve is derived for subtropical regions. The water balance and critical points will vary in colder and warmer regions.

Scheffer et al. 2005
Another way to consider the role of water balance on LAI is to develop non-dimensional indices. We have found that LAI scales linearly on a log-log plot with the ratio between precipitation divided by equilibrium evaporation, multiplied by nutrition, in terms of nitrogen content of the leaves (mg/g).
Leaf area at specific locations can vary much with time or remain relatively invariant, as is the case of deciduous vs evergreen forests.
Crops experience much variation in LAI with time. The cropping cycle includes seeding and seedly stages, vegetative and canopy filling stages, reproductive and flowering, grain or fruit filling, maturation and senescence/harvest, followed by fallow.
Today we augment our measurements of LAI with images from digital cameras, giving us a nice calendar of crops stages. We have been fortunate to mentor many UCB summer students, who have helped us make these measurements.
It is hard to do clipping and sampling studies of tall complex forests. Hence we rely on light transmission measurements to infer leaf area index and its phenology. It is important to know when the growing season starts and ends, when maximum LAI is achieved, how LAI may decline during the growing season due to stresses like drought and insect herbivory and when autumn/fall occurs.
At individual forest sites the start of the growing season may vary by up to 30 days from year to year. On one hand an early growing season can be viewed as good if it extends the photosynthetic period. On the other hand, it may accelerate the depletion of the soil moisture pool and catalyze drought, as warm years tend to have early springs but are followed by dry summers.
Leaf area index density varies with depth in a canopy. Information on its distribution is needed to measure, interpret and model light transmission well. The distribution of leaf area index can vary by stand age and vegetation type.
Many different distributions are observed.

Spatial (Vertical) distribution of leaf area

- Top heavy distribution
- Bottom heavy distribution
- Even distribution
Example of different statistical distributions of leaf area index with height. Beta functions are one way to simulate these distributions.
Examples of leaf area index profiles for crops and forests

Meyers and Paw U, 1986, AgMet

Here is an example of LAI distributions for many crops and forests
Within a forest stand there are layers associated with different species due to their adaptations to shade and full sun.
Leaf area profiles of forests change with age and time since disturbance. Key phases are **Stand reinitiation.** 1-10 years. Herbs and shrubs dominate site (species A dominates)

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

**Under-story re-initiation stage** (aggradation phase continues)

**Old growth stage**
Direct and indirect methods exist to measure LAI. Direct are labor intensive and can suffer from biases in sampling insufficiently the natural heterogeneity of sparse canopies or accessing tall forests. Litter fall is one way to circumvent this limitations, but evergreen trees lose leaves year round, so collecting them can be troublesome.

Indirect methods rely on the probability of light beams passing through gaps or hitting leaves.
Leaf area can scale with easily measured metrics like diameter at breast height. These relations tend to follow log-log patterns. Allometric relations may need to be developed for specific stands and too often scientists fail to have the energy, time or inclination to fell trees and count all the leaves. Yet, once a relation exists, measurements of stem diameter are cheap, quick and easy.
Point quadrat method was developed in the 60s by Warren Wilson. Rods were inserted into a canopy and the number of contacts were counted. Then using probability theory and knowledge of leaf angles, leaf area index was deduced.
With hemispherical photographs one can measure gap fraction and infer leaf area index. The method was pioneered in the 70s, including my mentor, Boyd Hutchinson. The method is rapid, cheap and indirect, but there is art to detecting gaps and not be biased by light transmitted through leaves.
The other problem is with sparse canopies, like savannas. Most of the LAI is clumped in outer rings of the image. Alternatively zenith cameras may be useful in assessing gap fraction.
Cheap cameras on boards can be used to expand networks of cameras in the understory of forest.
Example of the phenology of LAI we can assess with a network of upward looking cameras.
LICOR 2000 is an instrument that measures gap fraction for 5 rings around the horizon.
Conceptually the product between leaf area index (L) and the G function, which represents the cosine between the angle of the sun and the angle normal to a leaf is equal to the cosine of the angle of the shaft of light and the fraction of light transmitted at that angle.

\[
L \cdot G(\theta) = -\cos \theta \cdot \ln(T(\theta)) = K(\theta)
\]

\[
G \sim 0.5 \text{ when the angle is 1 radian}
\]

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

Effective LAI (L G= K) is a function of the solar zenith angle (\(\theta\)) and the natural log of light transmission (T)
The trick to computing LAI with the LICOR method is knowing $G$, which is a function of view angle. But we know $G$ is approximately $0.5$ when the angle of light is at 1 radian. So we can solve for $L$ by plotting $\cos(\theta)$ times natural log of transmission vs zenith angle, fit a regression and solve for the slope and intercept. Evaluate the linear regression at one radian and solve for $a$ and $b$.
Tests of these comparisons between direct and indirect methods of LAI remain robust.
Yet, we find that certain natural forests possess clumped vegetation, so we have to consider clumping to deduce the correct LAI. This is an example of our work in Oak Ridge Tennessee, where we measured LAI with litterfall and compared it with measurements deduced by the LI-2000. Differences were due to clumping.
Here is results from our study in oak in California. Again we have to consider clumping.
Method Comparison in a Sparse, Heterogenous, Savanna Woodland

Effective LAI

LAI = f(clumping)

Ryu et al. 2010 AgForMat
For sparse canopies we have to consider gaps between clumps of vegetation, another degree of clumping.
# Global Survey of Leaf Clumping Factors, Satellite Remote Sensing

Table 1  
Average statistics calculated with the topographically corrected clumping index values over vegetated areas.

<table>
<thead>
<tr>
<th>Class</th>
<th>Class names</th>
<th>Mean</th>
<th>Stan. dev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Tree cover, broadleaf, evergreen</td>
<td>0.64</td>
<td>0.11</td>
</tr>
<tr>
<td>2</td>
<td>Tree cover, broadleaf, deciduous, closed</td>
<td>0.69</td>
<td>0.08</td>
</tr>
<tr>
<td>3</td>
<td>Tree cover, broadleaf, deciduous, open</td>
<td>0.72</td>
<td>0.06</td>
</tr>
<tr>
<td>4</td>
<td>Tree cover, needleleaf, evergreen</td>
<td>0.63</td>
<td>0.12</td>
</tr>
<tr>
<td>5</td>
<td>Tree cover, needleleaf, deciduous</td>
<td>0.78</td>
<td>0.07</td>
</tr>
<tr>
<td>6</td>
<td>Tree cover, mixed leaf type</td>
<td>0.72</td>
<td>0.11</td>
</tr>
<tr>
<td>7</td>
<td>Tree cover, regularly flooded, fresh water</td>
<td>0.67</td>
<td>0.15</td>
</tr>
<tr>
<td>8</td>
<td>Tree cover, regularly flooded, saline water</td>
<td>0.78</td>
<td>0.17</td>
</tr>
<tr>
<td>9</td>
<td>Mosaic: Tree cover/other natural vegetation</td>
<td>0.70</td>
<td>0.05</td>
</tr>
<tr>
<td>10</td>
<td>Tree cover, burnt</td>
<td>0.78</td>
<td>0.15</td>
</tr>
<tr>
<td>11</td>
<td>Shrub cover, closed-open, evergreen</td>
<td>0.77</td>
<td>0.17</td>
</tr>
<tr>
<td>12</td>
<td>Shrub cover, closed-open, deciduous</td>
<td>0.74</td>
<td>0.09</td>
</tr>
<tr>
<td>13</td>
<td>Herbaceous cover, closed-open</td>
<td>0.77</td>
<td>0.12</td>
</tr>
<tr>
<td>14</td>
<td>Sparse herbaceous or sparse shrub cover</td>
<td>0.78</td>
<td>0.16</td>
</tr>
<tr>
<td>15</td>
<td>Reg. flooded shrub and/or herbaceous cover</td>
<td>0.80</td>
<td>0.14</td>
</tr>
<tr>
<td>16</td>
<td>Cultivated and managed areas</td>
<td>0.78</td>
<td>0.11</td>
</tr>
<tr>
<td>17</td>
<td>Mosaic: cropland/tree cover/natural veg</td>
<td>0.77</td>
<td>0.12</td>
</tr>
<tr>
<td>18</td>
<td>Mosaic: cropland/shrub and/or grass cover</td>
<td>0.76</td>
<td>0.05</td>
</tr>
</tbody>
</table>

Pisek et al 2010

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Much excitement with new LIDAR sensors to measure canopy structure
From space we can infer LAI from normalized difference vegetation indices that measure reflectance in the visible and near infrared wave bands.
Examples of LAI deduced from space for a 1 km pixel grid
Maps of leaf area index can be produced globally and seasonally

Ranga Myneni, Univ Boston
Global maps of clumping indices have been derived
We used clumping factors and information on the fraction of absorbed visible light to estimate LAI globally.
Others have produced maps of LAI for California
Ned Nikolov, unpublished
Summary

- Leaf area index 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 CO2 or being a sink for CO2 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.

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Class Enrichment

• Go to the MODIS web site
• Download and plot annual trend of LAI for
  – conifer forest
  – deciduous forest
  – Tropical forest
  – Grassland
  – (follow data links)
• Discuss differences/similarities in trends and magnitudes

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