

## **Lecture 5 Characterizing the Vegetation, Part IV: Plant Functional Types, Biogeography**

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### **This lecture will discuss:**

1. the concept of plant functional types, as related to canopy mass and energy exchange, and their attributes
2. overview of biogeography models that are being coupled to climate and biogeochemistry models
3. the geographic distribution of plants, plant functional types and leaf area, as determined by climate, land surface classifications

### **L5.1 Introduction**

Many biometeorological field studies are diagnostic. They measure the weather over or within a vegetated canopy for a specific duration and they attempt to interpret the response using statistics or mathematical models. To interpret measurements of weather, climate or mass and energy exchange correctly we need information on canopy structure and architecture (e.g. canopy height, leaf area index, leaf area profile, leaf angle distribution). If we expect to understand how the climate or mass and energy fluxes may vary in time and space, a prognostic exercise, we will need to **predict** how vegetation will vary in **time** and **space** and respond to climatic perturbations.

The goal of this lecture is to discuss **climate factors** that affect the **distribution** and the **status** of **vegetation**.

At first look, the task of understanding links between climate and vegetation can be daunting, as there are millions of plant species on Earth. As a biometeorologist, several questions come to the forefront.

1. *Do certain types of plant inhabit certain climate zones?*
2. *Must we be concerned about the physical attributes of every species in a landscape, region or continent to assess the microclimate and mass and energy exchange?*
3. *Can general rules be applied that describe the attributes of plant canopies for the sake of computing mass and energy exchange?*

### L5.1 Bioclimatology, Plants and Climate

Knowledge about links between **climate** and **vegetation** has existed for centuries. Eighteenth century scientists such as Linnaeus and 19<sup>th</sup> Century explorer/scientists such as von Humboldt and Koeppen were instrumental in cataloging associations between plant types and climate. In the past century, ecologists and biogeographers have made formal advances in using correlation between vegetation structure, soils and climate to classify ecosystems (Holdridge, 1947; Hopkins, 1938; Jenny, 1994; Thornthwaite, 1948). Early scientists were interested in why vegetation occupied certain habitats and how that was affected by soil and climate. In contrast, modern ecologists ask questions about species richness, abundance, patterns.

Tansley and Frederic Clements were ecologists (active in the 1930s) who have had much influence on modern thought about ecosystem structure. Both advocated that plant communities were **integrative** with numerous **emergent properties**, and acted as a supra organism. In contrast, other scientists, such as H. Gleason, considered ecosystems to be a random assemblage of adapted species. Modern ecological theories on community structure and dynamics fall in the school of Gleason, while Biometeorologists tend to fall into the holistic camp of Clements, for practical reasons. (it is noteworthy that this approach was the philosophy behind the design of the International Biosphere Program, 1964-1974) by ecologists.

Basic concepts of biogeography are of growing importance to biometeorology as we endeavor in the future to interact more with scientists who model the climate and dynamic aspects of vegetation and ecosystems. If one expects to model the long-term climate correctly, one will need a representative simulation of the underlying vegetation. And as climate changes, we need to know how vegetation will respond to such changes, on short physiological and long time scales that allow ecosystem migration and re-equilibration.

How plants are distributed across the globe is affected by how they capture and use resources. **Climate** factors affecting physiology and plant distribution, most, include **available sunlight, water availability, low temperate and high temperature** extremes. The global distribution of limiting factors on net photosynthesis are shown in Figure 1.

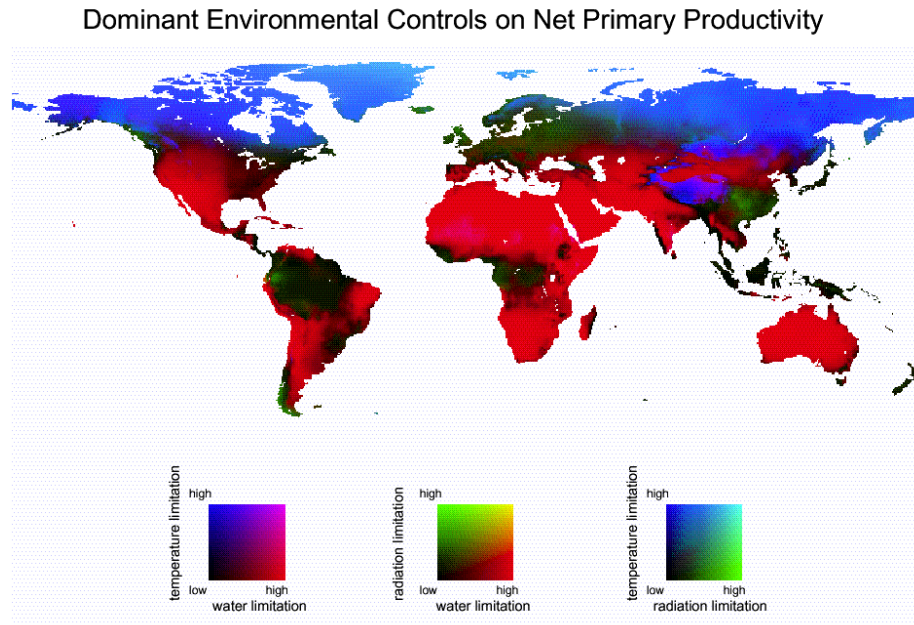


Figure 1 (Churkina, Running, 1998)

In the following section we discuss each factor one by one.

### *Light*

From first principles one can draw correlations between certain climate variables and plants. Available **sunlight** drives **photosynthesis**. Typically, 1.4 g dry matter is produced for 1MJ of intercepted sunlight (2.5% efficiency). To a first approximation, areas with high light availability have the potential to develop more biomass than will habitats with low light. This is mostly true as long as there is enough water.

By knowing what the solar constant is, the transmissivity of sunlight through the atmosphere and the surface of land area occupied by plants we can combine this information to compute the upper bound of net primary production by the global ecosystem.

The upper bound for global gross primary productivity can be estimated as a product of

- Solar Constant,  $S^*$  ( $1356 \text{ W m}^{-2}$ )
  - Ave on Earth  $S^*/3.1415$
- Transmission of sunlight through the atmosphere ( $1-0.17=0.83$ )
- Conversion of shortwave to visible sunlight (0.5)
- Conversion of visible light from energy to photon flux density in moles of quanta ( $4.6/10^6$ )
  - Mean photosynthetic photon flux density,  $Q_p$  ( $\text{mole m}^{-2} \text{ s}^{-1}$ )
- Fraction of absorbed  $Q_p$ , minus reflection and transmission ( $1-0.1=0.9$ )

- Photosynthetic efficiency,  $\alpha$  (0.02 mole C/mole quanta)
- Arable Land area ( $\sim 100 * 10^{12} \text{ m}^2$ )
- Length of daylight (12 hours \* 60 minutes \* 60 seconds = 43200 s/d)
- Length of growing season (150 days)
- Gram of carbon per mole (12 g/mole)

$$\text{GPP} = 1356 * 0.83 * 0.5 * 4.6 * 0.9 * 0.02 * 100 * 10^{12} * 43200 * 150 * 12 / 3.1415 = 115 * 10^{15} \text{ gC y}^{-1}$$

For reference, current estimates of Global GPP are on the order of  $120 * 10^{15} \text{ gC y}^{-1}$

### *Water*

**Water** is needed to expand and hydrate cells and to transfer nutrients. Clearly, there is a consequential body of literature showing a link between leaf area index and the site water balance. In temperate zones, 380 mm of water in the form of precipitation establishes the lower limit for existence of open woodland; interestingly in the past year we have conducted a water balance of an oak savanna field site that borders the great grassland of the Central Valley of California. It used 380 mm of water, while a nearby open grassland uses 300 mm of water per year! Higher amounts of precipitation are need for open forest (500 mm) and for closed forest (640 mm) (Woodward, 1987). In boreal zones, the thresholds of available water are different. In Alaska, 180 mm is needed to establish an open forest. This lower threshold is indicates that **available water** rather than **total precipitation** is more important, as evaporation is lower in cooler climates. At the interface between the boreal forest and temperate grasslands, it has been found that aspen occur where evaporation exceeds precipitation and conifers inhabit areas where precipitation exceeds evaporation (Hogg, 1994; Hogg, 1997). This idea has been expanded on in recent work by Stephenson (1990).

A graphical description of the relation between plant types, evaporation and water deficits can be attributed to work by Stephenson (1990), Figure 2. In this analysis **water deficits are** defined in terms of the difference between actual and potential evaporation. It is revealed that forests and tundra exist where the water deficit is less than 400 mm per year. In contrast, grasslands can exist where water deficits are higher ( $> 300$  mm per year). **Grasslands** require **more** water than **shrublands**. The key attribute and success of the analysis of Stephenson (1990) is that he assessed actual evaporation and water deficits, rather than using similar and more traditional measures such as temperature, precipitation and potential evaporation (e.g. Thornthwaite, Holdridge), which are seen in classic analyses of biogeography.

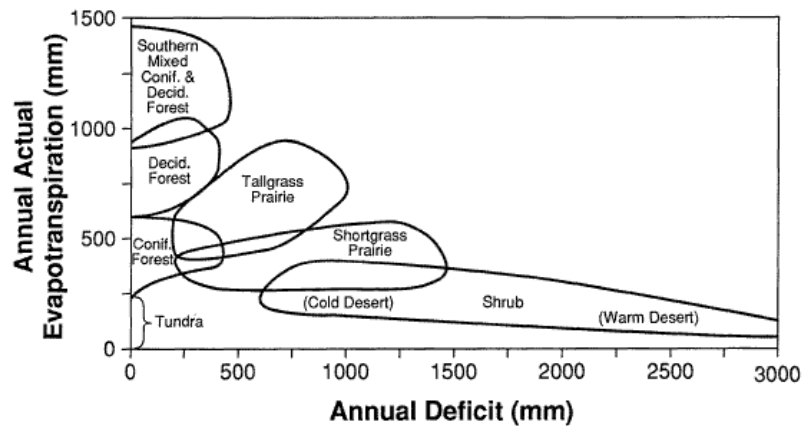


FIG. 2. The distribution of the major North American plant formations relative to annual AET and D (from Stephenson, 1990).

**Figure 2 Relation with plant functional types and water balance in North America (adapted from Stephenson, 1990)**

Assuming that water and light are the resources that most often limit plant growth, corollaries can be generated that arise from these interactions (Smith, Huston, 1989):

1. ***Plants that grow rapidly under conditions with sufficient soil moisture are unable to survive under dry conditions.*** Conversely, plants adapted to dry conditions, do not grow rapidly when ample soil moisture is available. In the Bay Area, gardeners do not recommend watering native oaks during the dry summer season, as it will kill them.
2. ***Tolerance to low light and soil moisture is interdependent and inversely correlated.*** Adaptations that allow plants to grow in low light do not allow it to survive dry conditions.
3. ***Plants that can photosynthesize at high rates and grow rapidly under high light are unable to survive at low light (they are shade intolerant).***
4. Conversely, ***shade tolerant plants have low growth rates and photosynthetic potentials, even under high light conditions.*** Shade **intolerant** plants possess high light compensation and saturation points and tend to live for shorter periods and shorter structure than shade tolerant plants.

#### *Cold Temperature Limitations*

Only certain plants can survive in cold temperature, as is noted by the low diversity of the boreal forest. Conifers have **tracheids** with bordered pits, so they can withstand freezing of xylem.

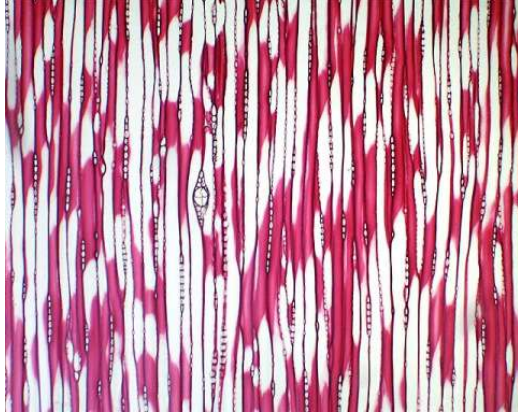


Figure 3 [http://botit.botany.wisc.edu/images/130/Wood/Pinus/Pinus\\_Wood\\_-\\_tangential\\_section/Tangential\\_section\\_MC.html](http://botit.botany.wisc.edu/images/130/Wood/Pinus/Pinus_Wood_-_tangential_section/Tangential_section_MC.html)

This isolates embolism and cavitations from one another. Cold and frozen soils (permafrost) can limit the zone that roots can explore. This can have two effects. In one case it may limit the available water available to the plant. In a second case, a perched water table can be formed, causing the below ground environment to be anaerobic.

#### *Extreme Temperature Limitations*

Desert plants adapt many strategies to exist in the hot dry climate of deserts. Mechanisms include **acclimation**, **adaptation** and **avoidance**. Leaves can be highly reflective, to limit radiation loads. Leaves can be very small to be effective in transferring heat. Plants can use the CAM photosynthesis pathway (like ice plant and cacti), which open stomata at night, when evaporation demand is lower. Cactus, can **store water**. Annual grasses in the Mediterranean climates avoid drought by completing their life cycle very quickly when water is available then enduring the heat spell as **seeds**. Or shrubs and trees can withstand extreme temperatures by developing small leaves, by being drought deciduous (California Buckeye), by going dormant or by developing deep root systems that can tap extraneous sources of water.

Different strategies of resource use allows plants to fill different ecological roles under different resource conditions, e.g. certain plants may be early successional species in one habitat and late in another. Cost/benefit theory, as developed by Mooney, Givnish, Chapin, Bloom and others, indicates that there are trade offs between **tolerance to low resource availability and maximum potential growth rate**. This trade off has been reported for light, soil water and nutrient supplies. It forms a dichotomy between competitive plants (those with high growth rates, but a low tolerance for stress) versus stress tolerant plants (which maintain low rates of growth, but have high tolerance).

Differential root-shoot allocation is one way by which plants adapt to the constraints of available energy and soil moisture, and optimize their ability to gain or acquire these resources. When nutrients and soil moisture is plentiful, plants allocate little resources to roots. Instead, they invest most of their resources to above ground parts to capture light. In contrast, when soil moisture and nutrients are scarce, plants invest more in roots. The

co-existence of trees and grass in the oak savanna of California is a classic example of two plant forms exploiting different niches.

At whole plant scale, **acclimation** involves a balance between benefits of higher photosynthetic capacity per unit leaf area versus the cost of supporting higher capacity (Sims, Pearcy, 1994). Shade plants have a higher leaf area to mass ratio, so they can capture light more effectively (their leaves also tend to be oriented parallel to the ground, too). Less root allocation is required by shade plants to maintain a favorable water balance, because stomatal conductance and evaporation is less.

In the previous lecture, we saw that other attributes of plants vary with resources, too. As light energy diminishes, the ratio between leaf area and leaf weight increases. In addition, plants found under dry conditions have low leaf area and small stature. Significant amounts of solar radiation are available at the ground. Woody plants in arid zones tend to be shade intolerant. They increase in size, as moisture becomes more available. Finally, there is more genetic diversity under wetter conditions because more light use strategies are available.

## L5.2 Plant Functional Types

**Do Species Matter?** This question is being asked more and more as we worry about biodiversity and the irrevocable destruction of tropical rain forests. The answer to this question depends upon what process one is referring. A plant anatomist or botanist is concerned about the intricate detail of plants, such as details of leafing patterns, venation of leaves, how and why leaf shapes may vary in different environments. In these situation **Species do matter**.

Whether increasing species diversity is important or not is another key question. A more succinct question is:

*does the functioning of an ecosystem depend upon the identity of the species, the number of species, the functional roles these species possess or the functional roles that are represented in the system?*

One study (e.g. (Tilman et al., 2001) revealed that **functional composition and diversity** explained differences net primary productivity, plant nitrogen and light interception rather than **species diversity**; they conclude that the impact of all species is not equal.

Recently, Kleidon and Mooney (2000) examined the role of biodiversity with a global process model. They were able to model species diversity from climate using a 'generic' plant. Features of import included 'good growing days', which acts as a species sieve.

In contrast, questions asked by a biometeorologist involve mass and energy exchange between the biosphere and atmosphere. In many situations information on plant physiological capacity and canopy structure are adequate. This point is reinforced with

the scaling analysis of Allen et al. (2002) who show that the energy flux of a population per unit area ( $B_i$ ) is invariant with mass of the system ( $M$ ):

$$B_T = N_i B_i \propto M_i^{-3/4} M_i^{3/4} = M^0$$

because the metabolic rate of individuals,  $B_i$  scale with the  $3/4$  power of body size and the number density of the populations scales with the  $-3/4$  power of body size. When temperature is considered then the energy flux is proportional to temperature. This additional information does allow them to predict that species diversity increases with environmental temperature.

Another case where information on species is important to a biometeorologist involves the emission of volatile biogenic hydrocarbons from forests. The emission of isoprene and monoterpenes is species specific.

And in a recent analysis I conducted using data from the Fluxnet web page I found that there was a negative correlation between evaporation and species number for temperate deciduous forests. Introducing additional species may reduce potential evaporation by spreading out nitrogen across species and limiting the integrative stomatal conductance. For example, multi-specied forests introduce species with *ring porous* and *diffuse porous* wood, which have different abilities to conduct water through their xylem.

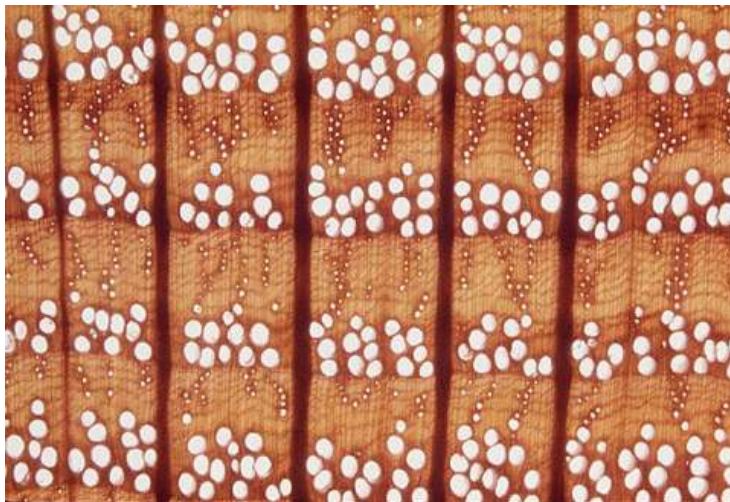


Figure 4 Ring porous wood, eg Quercus, Ulmus.

[http://botit.botany.wisc.edu/images/130/Wood/Ring\\_Porous\\_Wood\\_MC\\_.html](http://botit.botany.wisc.edu/images/130/Wood/Ring_Porous_Wood_MC_.html)

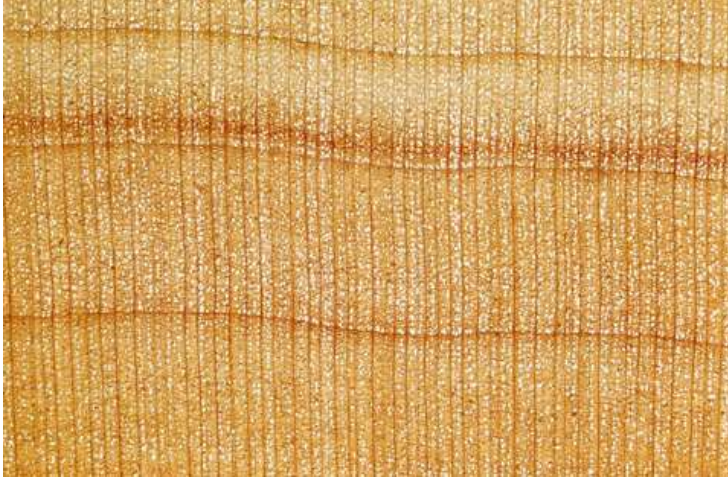


Figure 5 Diffuse porous wood, eg *Acer*, *Populus*, *Salix*, *Betula*,  
[http://botit.botany.wisc.edu/images/130/Wood/Diffuse\\_Porous\\_Wood\\_MC\\_.html](http://botit.botany.wisc.edu/images/130/Wood/Diffuse_Porous_Wood_MC_.html)

Such differences can lead to ranking of evaporation rates across the deciduous biome, with mixed species forests achieving lower rates of evaporation.

- Prince Albert, Sask: Blanken, Black
- Oak Ridge, TN: Baldocchi, Wilson, Falge
- ▲ Borden, Ont; Lee, Fuentes
- ▼ Pellston, MI; Curtis
- ◆ Harvard Forest, MA; Wofsy, Barford, Goulden
- Hesse, France; Granier

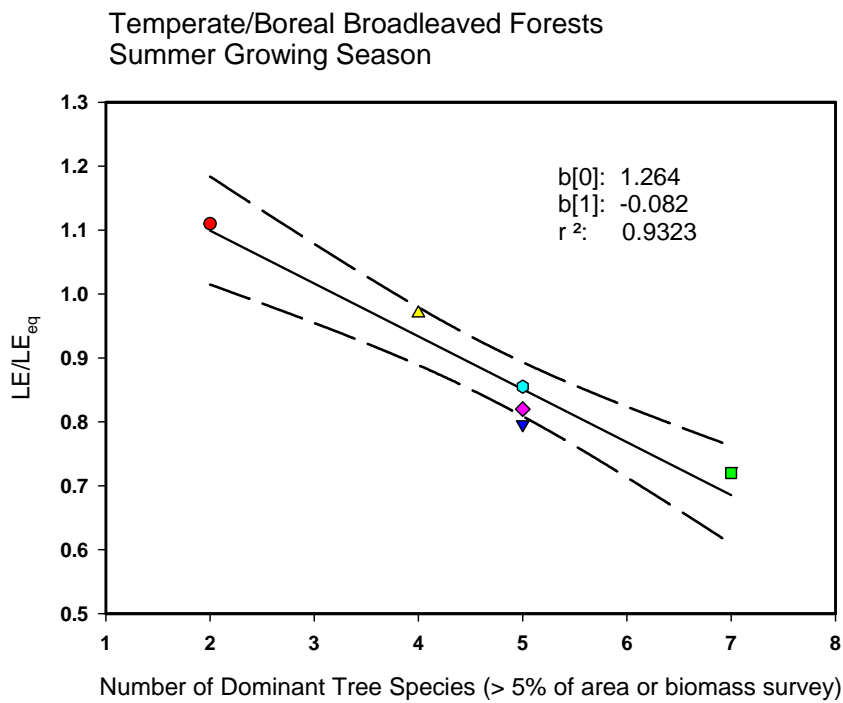


Figure 6 after D. Baldocchi. 2003.

We cannot, from a practical standpoint, worry about the attributes of every species on Earth, when develop biometeorological models for climate, weather and ecological applications. Our alternative is to use information on **plant functional type**.

Grouping plants by functional groups has origins as far back at Theophrastus (circa 300 BC). The modern call for this action started in the late 1960s and early 1970s by scientists such as Root, Cummins and Botkin. Acceptance of the concept of functional types comes from a wide range of evidence, as has been reported in several synthesis articles by card-carrying ecologists (Cornelissen *et al.*, 2003; Reich *et al.*, 1997; Smith, Huston, 1989).

As of 1997, a book on **Functional Groups** (Smith *et al.*, 1997) stated that there was no clear definition for this term. Though there is convergence to thinking that functional groups describe are a biotic group of an ecosystem that perform the same function.

**Species** are a group that use the same resources and can inter-breed. This idea can be expanded to groups of species that share resources or respond to mechanisms in a similar manner. A **functional group** is a:

*"... a grouping of organisms that respond in a similar way to a syndrome of environmental forcings (Gitay and Noble, 1997)*

Important attributes for classifying a functional type include (Smith *et al.*, 1997):

1. physiognomy,
2. desiccation features,
3. life span,
4. pollination,
5. seed dispersal,
6. photosynthetic pathway,
7. shade tolerance,
8. fire tolerance,
9. nutrient stress tolerance

The basis of this approach stems from the simple fact that plants must conform to the laws of physics. They need to acquire energy to perform work. They must acquire substrate material to grow.

A functional linkage between carbon, water and nitrogen budgets is manifested through their mutual interdependency. Plants are autotrophs (self-feeders), so they must photosynthesize to sustain their metabolism. Their **photosynthetic capacity** scales with a **leaf's nitrogen** content because the chief photosynthetic enzyme, RUBISCO, is a nitrogen rich compound (Field, 1991; Field, Mooney, 1986). An outcome of the link between photosynthesis and leaf nitrogen content is a dependency of several photosynthetic model parameters on one another. Furthermore, rates of **dark respiration**

and **water use** are constrained by rates of **photosynthesis**. Plants cannot respire more carbon than they have assimilated, otherwise they would be dead. With respect to water use, stomata are the gatekeepers for the diffusion of water and carbon dioxide in and out of leaves. Since **stomatal conductance** is closely linked to **photosynthesis** it is also correlated with **leaf nitrogen content** (Field, 1991; Kelliher *et al.*, 1995; Schulze *et al.*, 1994). An obvious functional division that is related to C-N-H<sub>2</sub>O links is along photosynthetic pathway, eg the C<sub>3</sub>, C<sub>4</sub> and CAM photosynthetic pathways.

Since we are concerned with energy and substrate acquisition by plants we adopt an alternative definition:

*a set of biological entities that possess common functional or structural attributes (Valentini et al., 1999).*

From this definition we further define a land-atmosphere functional unit as:

*a patch of landscape whose exchange mass and energy with the atmosphere shows a coordinated and specific response to environmental factors*

Empirical rationale for adopting Functional Grouping was demonstrated by Valentini *et al.* (1998), using principal component analysis. They showed that 86% of the variance of among ecosystem and biometeorological properties such as canopy resistance, Bowen ratio, leaf area index and photosynthetic capacity could be achieved by grouping over 20 diverse canopy types into 3 functional groups.

Though the vegetation of the earth is diverse, it can possess rather uniform physiognomical appearance and structure in zones of the world, even though the species, genera and families may have evolved differently (Schulze, 1982). Often, plant evolution **converges** with respect to **function** and **architecture** for analogous climates (Reich *et al.*, 1999; Schulze *et al.*, 1996). This occurs because certain plant attributes are better able to survive and out-compete competitors, in a given habitat, wherever on the globe that habitat may be. Consequently, we observe that boreal forests possess certain similar properties, be they in Siberia, Canada or Finland. The same generality may be implied for Mediterranean ecosystems growing in Chile or California.

Ecologists have examined **leaf longevity** from the perspective of maximizing carbon gain (Kikuzawa, 1995; Chabot and Hicks, 1982). Mathematically, the longevity is a function of photosynthesis, construction costs and the time when photosynthesis becomes zero. For the purpose of conducting biometeorological research, it is often convenient to divide plants into several distinct and workable categories:

- 1) annual and perennial herbs;
- 2) shrubs
- 3) trees.

The herbaceous class includes annuals, biennials and deciduous and evergreen perennial herbs.

**Annuals** survive harsh weather (cold or dry periods) as **seeds**; the annual grasslands of California are a prime example of this axiom. Annuals occur in all climate regions of the world, in open habitats and early successional situations. They are successful in semi-arid and arid regions. Because their life cycle must be completed in one year, they are not very successful in arctic and alpine locales. Perennial herbs include biennials (parsley) or desert succulents.

Woody plants have secondary growth and conversion of structural tissue into non-living (and non-respiring) biomass but is functional, as it can storage and conduct water. Woody plants are grouped by **leaf longevity** (evergreen/deciduous), rather than shapes, eg shrub/tree. Ironically, evergreen plants do not save much energy by retaining leaves for multiple years (Sprugel, 1989). Evergreen trees are able develop ‘deeper canopies’, ones with twice as much leaf area as broad leaved trees. But even in this regard it is not obvious as to what the advantages of a deeper canopy are as over 95% of incident light is intercepted with leaf areas exceeding five. Sprugel (1989) summarizes the physiognomy of evergreen/deciduous and broad and needleleaf trees.

**Table 1**

Type	Growth habitat
Evergreen needle leaf	Gymnosperm, conifers present in cool and temperate zones, rocky and nutrient poor sites, can be early successional species
Evergreen broad leaved	Inhabit marine climates and tropics; they do not tolerate frost well.
Deciduous needle leaf	Exist in marginal habitats, near timberline and continental extremes, eg <i>Larix</i> in Siberia.
Deciduous broadleaves	Angiosperms, dominant characteristics of lowland temperate forests, inhabit montane and boreal zones

With regards to evergreen and deciduous oaks growing side by side on the California coastal range, there are trade offs between length of growing season and photosynthetic capacity. Deciduous oaks have a photosynthetic capacity that is double that of their evergreen cousins (Hollinger, 1992; Mooney, Dunn, 1970).

Many scientists have explored the idea of functional groups. Below we outline a few of the ideas from some leading scientists in the field.

*Woodward’s Concepts of Functional Groups*

In defining functional groups, Woodward (1987) starts with a perspective that adopts an initially broad categorization, He uses **temperature** as a dividing principle. Temperature can be used to delineate maximum and minimum temperature, which define heat and cold

tolerant plants and establishes the temperature range of plant survival. Furthermore, temperature is correlated with available energy, so it can be used to classify functional groups associated with resource capture. Information on temperature can also be used to assess shade and sun tolerances

**Table 2** *Temperature limits of plant establishment (after Woodward 1987)*

minimum temperature for survival	temperature range
evergreen broadleaf (chilling sensitive)	10 C
evergreen broadleaf (frost sensitive)	0C
evergreen broadleaf survival limit	-15
deciduous broadleaf survival limit	-40 C
evergreen boreal conifer	<< -40 C
deciduous boreal conifer (larch)	< -70 C

**Table 3**

temperature optimum for photosynthesis	
18	arctic tundra
16	boreal
21	cool temperate
26	Warm temperate
28	subtropical and tropical

**Table 4**

temperature threshold for leaf growth	
< 2.5 C	arctic tundra
2.5 to 5 C	Boreal
5 to 7 C	cool temperate
10 to 15 C	subtropical and tropical

**Table 5**

temperature threshold for hydraulic conductivity	
< 3 C	arctic tundra and boreal
5 to 7 C	temperate

8 to 13 C	subtropical and tropical
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*Walker’s Concepts of Functional Groups*

Brian Walker recently summarized a list of plant attributes that should be considered with studying environmental change. This list is very relevant to our study of biometeorology.

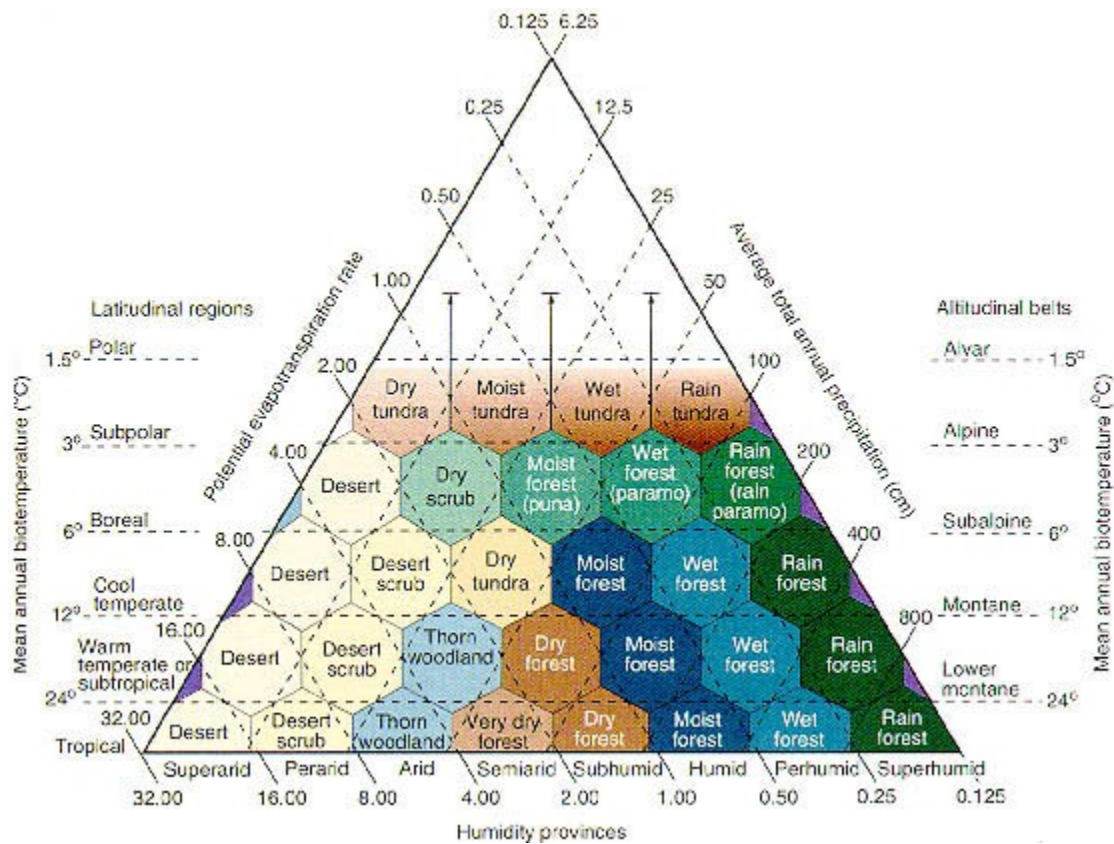
**Table 6**

<b>environmental variable</b>	<b>plant response</b>	<b>plant attribute</b>
CO <sub>2</sub>	photosynthetic pathway, water use efficiency	C <sub>3</sub> /C <sub>4</sub> / CAM pathway
maximum temperature	heat resistance, water access, albedo	Plastic threshold effect, root depth, color
minimum temperature	frost resistance	Plastic threshold effect
mean temperature	growth, competition	Broad optimum temperature
water, total	growth, competition	Size
water, seasonal	phenology	phenology
water,depth	root depth	Growth, competition
water, drought frequency	drought resistance	Lower threshold
Fire	resistance, seed regeneration	
available nutrients	growth, competition	optimal level, threshold

**L5.3 Plant Classification Schemes**

To perform biometeorological tasks, such as computing fluxes of mass and energy, we will need information on the attributes of the underlying surface. Hence, it is of utmost importance to know how to divide the biosphere into representative classes and to know how and where those classes are distributed across the globe.

Holdridge (1947) developed one of the first quantitative plant climate classifications. He defined "life zones" based on annual temperature and precipitation. The broad forcing factors are temperature and water budget. With this approach he categorized 20 major ecosystems that describe biome/vegetation types.



**Figure 7 Holdridge plant, climate classification scheme,**  
<http://www.cieer.org/geirs/viewer/holdridge.jpg>

Holdridge defined boundaries between major vegetation units according to 1) mean annual biotemperature; 2) total annual precipitation, and 3) the ratio of mean annual potential evapotranspiration to mean total annual precipitation.

He attempted to derive bioclimatic indicators that could be derived from conventional and simple climate measurements. One factor was **biotemperature**, the mean daily temperature above zero C, divided by the days of the year (365). This variable gives a better indicator of heat during the growing season. The demand for water is evaluated by an estimate of **potential evaporation**. In this case the simple, and temperature dependent Thornthwaite method, is used since potential evaporation is rarely measured. The third bioclimatic variable is **annual precipitation**.

This classification was derived from a scientist working in the tropics, so it has a tropical bias and does not consider seasonality. More modern classification scheme attempt to remedy this over site by incorporating information on structure and function, seasonality and soil characteristics. The early plant climate classification schemes did not have thorough climate data bases available.

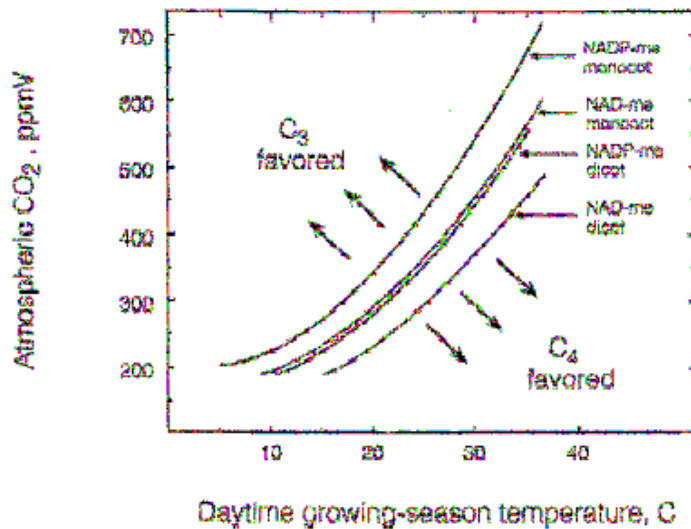
At the far extreme of complexity is the approach of Box (1981). Box defines climate limitations on plant species types, rather than vegetation formations. This method introduces more subdivisions and basis the classification on physiognomic and morphology. Box uses 8 bioclimatic indices.

**Table 7 Bioclimate variables of Box (1981)**

mean temperature of the warmest month
mean temperature of the coldest month
range between Tmax and Tmin
mean annual precipitation
moisture index (ppt-PET)
mean total precipitation of the wettest month
mean total precipitation of the driest month
mean total precipitation of the warmest month

*Case: Why aren't C<sub>4</sub> plants dominant in dry and sunny California?*

Whether C<sub>3</sub> or C<sub>4</sub> grasses exist in a region depends on, among other factors, the temperature of the growing season. California is hot and warm. Based on ecophysiological principles one may expect many C<sub>4</sub> grasses to live here. To the contrary, Californian grasslands are annual grasslands that use the C<sub>3</sub> pathway. Due to the Mediterranean climate rains fall in the winter and spring, when temperatures are cool and below a threshold for the existence of C<sub>4</sub> plants (Ehleringer *et al.*, 1997). Paleocology studies also revealed that C<sub>4</sub> plants were able to out compete C<sub>3</sub> grasses during the Holocene period (and ice ages). During this period, CO<sub>2</sub> levels were low, so photorespiratory costs for C<sub>3</sub> plants were high relative to C<sub>4</sub> plants, which don't experience photorespiration.



**Fig. 2** Modeled crossover temperatures of the quantum yield for CO<sub>2</sub> uptake for monocots and dicots as a function of atmospheric CO<sub>2</sub> concentrations. The boundary conditions for both monocots and dicots are NADP-me C<sub>4</sub> plants (upper boundaries) and NAD-me C<sub>4</sub> plants (lower boundaries). The crossover temperature is defined as the temperature (for a particular atmospheric CO<sub>2</sub> concentration) at which the quantum yields for CO<sub>2</sub> uptake are equivalent for both the C<sub>3</sub> and the C<sub>4</sub> plant. Data are based on average values from Table 4

Figure 8 Adapted from Ehleringer et al. 1997.

## Summary

- Functional types are a way of incorporating distinct properties of plants towards understanding plant-atmosphere exchange without worrying about the effects of each species, as some species contribute more than others.
- Functional properties of interest include photosynthetic pathway, rooting depth, leaf longevity, physiognomy, desiccation features, shade tolerance, fire tolerance, nutrient stress tolerance
- Plant Biogeography concerns us with the geographical distribution of plants. Plant functional types are distributed according to site water balance, rainfall, extreme low and high temperatures.
- Functional convergence produces different species in different parts of world to adopt similar structural and functional features in similar climates.
- Site water balance (precipitation minus evaporation) has a strong influence on the plant functional type that inhabits a region.

## Web Resources

USGS Climate-Vegetation Atlas of North America

<http://climchange.cr.usgs.gov/info/veg-clim/>

## References

- Allen AP, Brown JH, Gillooly JF (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* **297**, 1545-1548.
- Churkina G, Running S (1998) Contrasting Climatic Controls on the Estimated Productivity of Global Terrestrial Biomes. *Ecosystems* **1**, 206-215.
- Cornelissen JHC, Lavore S, Garnier E, *et al.* (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**, 335-380.
- Ehleringer J, Cerling T, Helliker B (1997) C4 photosynthesis, atmospheric CO<sub>2</sub>, and climate. *Oecologia* **112**.
- Field CB (1991) Ecological scaling of carbon gain to stress and resource availability. In: *Response of Plants to Multiple Stressors*, pp. 35-65. Academic Press.
- Field CB, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: *On the economy of plant form and function* (ed. Givnish TJ), pp. 25-55. Cambridge University Press.
- Hogg EH (1994) Climate and the Southern Limit of the Western Canadian Boreal Forest. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **24**, 1835-1845.
- Hogg EH (1997) Temporal scaling of moisture and the forest-grassland boundary in western Canada. *Agricultural and Forest Meteorology* **84**, 115-122.
- Holdridge LR (1947) Determination of world plant formations from simple climatic data. *Science* **105**, 367-368.
- Hollinger DY (1992) Leaf and Simulated Whole-Canopy Photosynthesis in 2 Cooccurring Tree Species. *Ecology* **73**, 1-14.
- Hopkins AD (1938) Bioclimatics: a science of life and climate relations, p. 187. US Dept of Agriculture, Washington, DC.
- Jenny H (1994) *Factors of Soil Formation: A System of Quantitative Pedology* Dover Press.
- Kelliher FM, Leuning R, Raupach MR, Schulze E-D (1995) Maximum conductances for evaporation from global vegetation types. *Agricultural and Forest Meteorology* **73**, 1-16.
- Kleidon A, Mooney HA (2000) A global distribution of biodiversity inferred from climatic constraints: results from a process-based modelling study doi:10.1046/j.1365-2486.2000.00332.x. *Global Change Biology* **6**, 507-523.
- Mooney H, Dunn EL (1970) Photosynthetic systems of Mediterranean climate shrubs and trees of California and Chile. *American Naturalist* **104**.
- Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: Global convergence in plant functioning. *PNAS* **94**, 13730-13734.

- Schulze E-D, Kelliher FM, Korner C, Lloyd J, Leuning R (1994) Relationships Among Maximum Stomatal Conductance, Ecosystem Surface Conductance, Carbon Assimilation Rate, and Plant Nitrogen Nutrition: A Global Ecology Scaling Exercise. *Annu. Rev. Ecol. Syst.* **25**, 629-660.
- Sims DA, Pearcy RW (1994) Scaling Sun and Shade Photosynthetic Acclimation of *Alocasia-Macrorrhiza* to Whole-Plant Performance .1. Carbon Balance and Allocation at Different Daily Photon Flux Densities. *Plant Cell and Environment* **17**, 881-887.
- Smith T, Huston M (1989) A theory of the spatial and temporal dynamics of plant communities. *Plant Ecology* **83**, 49-69.
- Smith TM, Shugart HH, Woodward FI (1997) *Plant Functional Types: their relevance to ecosystem properties and global change* Cambridge University Press.
- Sprugel DG (1989) The Relationship of Evergreenness, Crown Architecture, and Leaf Size. *American Naturalist* **133**, 465-479.
- Stephenson NL (1990) Climatic Control of Vegetation Distribution: The Role of the Water Balance. *American Naturalist* **135**, 649-670.
- Thorntwaite CW (1948) An Approach toward a Rational Classification of Climate. *Geophysical Review* **38**, 55.
- Tilman D, Reich PB, Knops J, *et al.* (2001) Diversity and Productivity in a Long-Term Grassland Experiment. *Science* **294**, 843-845.
- Valentini R, Baldocchi DD, Tenhunen JD (1999) Ecological controls on land surface interactions. In: *Integrating hydrology, ecosystem dynamics and biogeochemistry in complex landscapes*. (eds. Tenhunen JD, Kabat P).
- Woodward FI (1987) *Climate and Plant Distribution* Cambridge University Press.