3. Theoretical Considerations

3.1 Climatic Influences on Plants

In principle, the boundaries of gene-ecological zones are determined by the discontinuous and often independent distributions of different environmental factors and parameters. Although each determinant factor can be qualified and quantified on an individual basis, their direct impact on biological systems is often influenced by, or inter-related with, other environmental factors. Organisms must contend with a host of selective pressures, the whole of which, over evolutionary time, are responsible for the adaptive features which we observe or predict in present plant populations. In the case of plants, many of these adaptive features relate in one way or another to a population's ability to photosynthesize and compete optimally in a given environment. Survivorship and success of plant populations depends greatly on their ability to make use of water and minerals, and these elements can vary in availability from one region to the next.

Figure 1 illustrates the manner in which differing temperature ranges and water regimes determine the structural features of plant species and physiognomic character of plant communities. Observable distinctions in tree morphology and community structures can be understood in terms of natural selection. Since most of the important timber species of Cambodia are tropical in nature, and occupy lowland environments that vary minimally in regard to temperature, their natural variability often relates to their response to different water regimes.

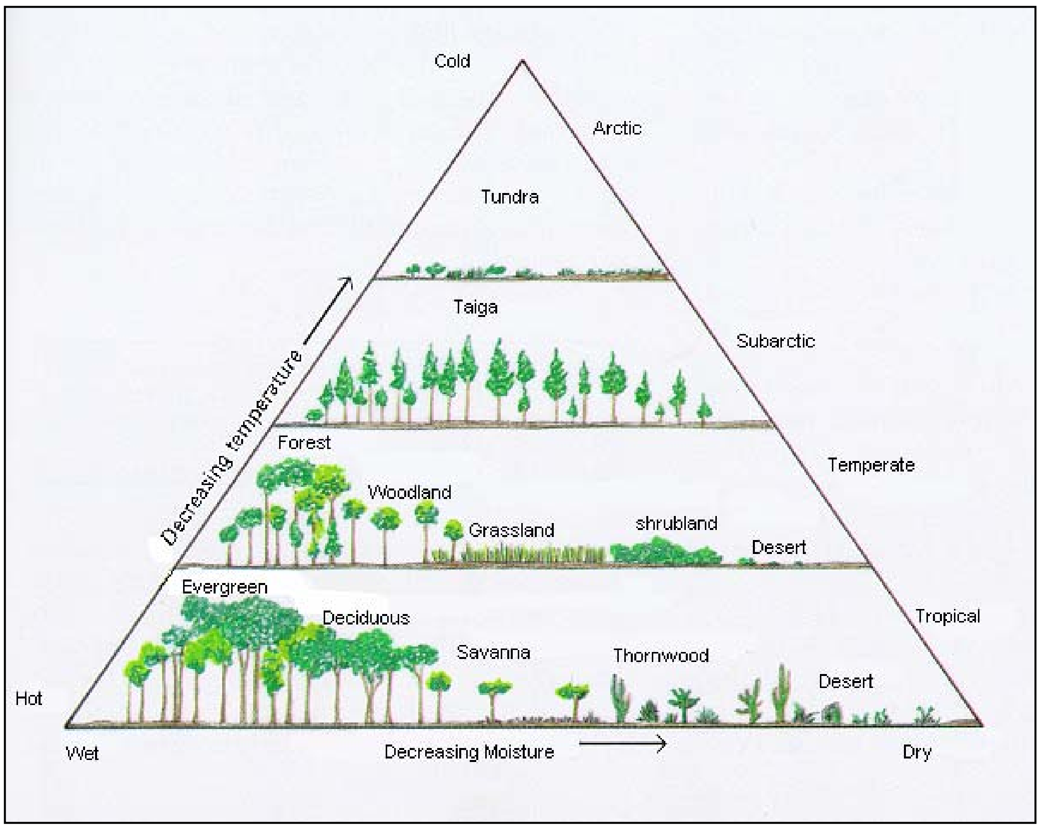


Figure 1. Influence of Water and Temperature Regimes on Vegetation
Source: Arms K. 1990

Generally speaking, the stature and productivity of tropical forests are determined by the availability of water. Plant communities that are tall (40-60 m), highly stratified, and evergreen, tend to occur in regions with a short dry season (< 2 months). Since water is always available in this environment, the limiting factor with which plants must compete is sunlight (hence large statures). As environments become drier, however, plants tend to be reduced in stature, and to produce small, deciduous leaves. These characteristics allow plants to reduce their surface areas, and hence transpiration rates (water loss) for prolonged periods of drought. As is often the case with adaptive features, there is a cost and benefit to either short or tall growth, the production of persistent or deciduous leaves, and the presentation of either large or small leaves.

Length and severity of dry seasons on a regional scale can also have considerable impacts on the timing of reproduction in plants and the behaviour of plant seeds and saplings. Plants that thrive in seasonally dry habitats tend to produce seeds that can withstand long and intense periods of drought, usually by means of long periods of dormancy. Moreover, their seedlings can be expected to be relatively hardy and pre-adapted to water stress. In contrast, plants that occur in evergreen forests tend to be heat intolerant, and generally produce seeds that are relatively short-lived. These plants tend to produce fast-germinating saplings that survive for extended periods of time in shaded understories, awaiting an opportunity for growth by the opening of light-gaps in the canopy.

In like manner, flowering phenology is also greatly affected by the length and intensity of rainy and dry seasons, as the movement of insect pollinators are substantially hindered by rainfall and cloud cover. Hence the flowering period of plant races in an evergreen forest may not be synchronized with flowering periods of neighboring populations in dry deciduous forest.

It is noteworthy that almost all of the priority species in the Cambodia Tree Seed Project (section 5) are native to 'Evergreen' and 'Deciduous' forest types. As a consequence, they tend to exhibit characteristics that are typical of plants that prefer high temperatures and significant quantities of water (Figure 1). We also encounter, however, forested savannahs (Figure 1) in regions of Cambodia that have low water retention (sandstones) and a long-lasting dry season, such as the lowland forests which lie East of the Mekong River (Map 11; section 5.1.8, the Lower Mekong Basis ecozone). And there are also 'thorn-wood forests' (Figure 1) which dominate the floodplains of Tonle Sap Lake (Map 11; section 5.1.3, the Tonle Sap Floodplain ecozone). Neither of these zones is particularly important, however, in the production of important timber trees (section 5).

Although the interactive influences of temperature and precipitation play a crucial principal role in determining the availability of water in woodlands, there are other mitigating factors that come into play. The availability of moisture is also regulated, for example, by topography, soil types, and in modern times, human influences on natural landscapes. All of these factors have a direct bearing on plant growth rates and forest productivity, since water is a basic ingredient of photosynthesis. Table 2 summarizes a variety of factors that have a direct impact on water availability and characteristics of plant communities.

Availability of water is also determined by temperatures, a factor that is important in regulating evapo-transpiration of individual plants and forests. The lower temperature limit for efficient photosynthesis is around 6^{o} C, whereas the upper limits depend greatly on the availability of water. As a general rule, the efficiency of photosynthesis begins to diminish when temperatures surpass 30^{o} C. It is notable that the lower temperature limits for photosynthesis do not exist in the tropical climates of Cambodia, and that the upper limits often prevail throughout the country for half the year. The coolest temperatures are to found, of course, in mountainous regions of Cambodia, and these conditions tend to correlate with an abundance of water.

Table 2. Factors Affecting Plant Growth

Climate	Site	Soil
• Temperature • rainfall • relation between precipitation and evapo-transpiration • wind velocity • air humidity • radiation	• slope • slope length • micro relief • external drainage • rocks and stones	• effective depth • texture • internal drainage • fertility • salinity • PH • Structure

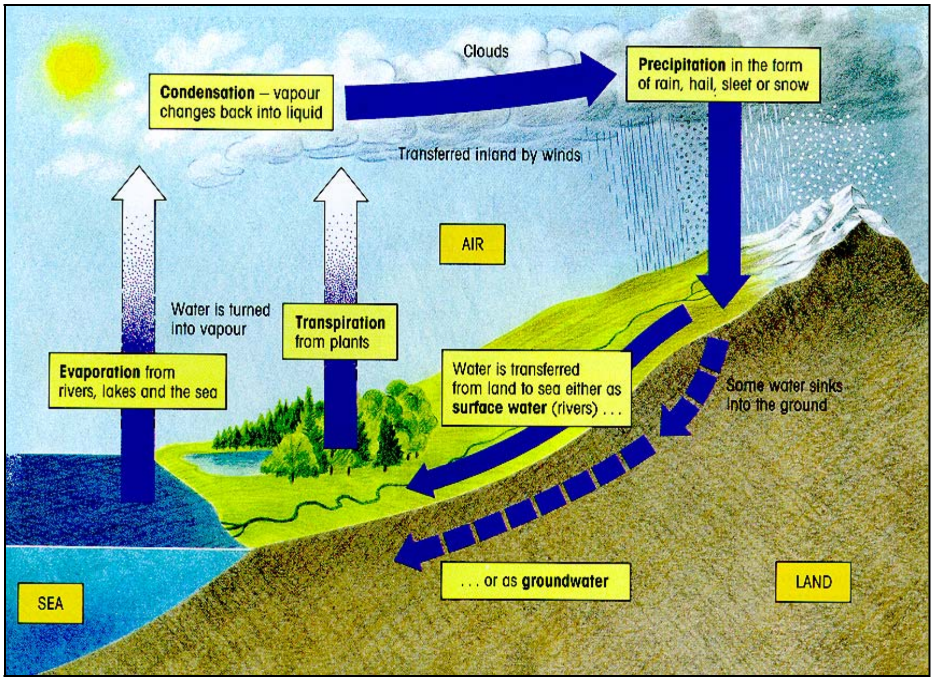
3.2 Topography

Due to the cooling effects of higher altitudes, and the condensation of water-saturated air in lowlands, topography is yet another important determinant factor of water availability. Mountainous terrain tends to receive larger amounts of annual precipitation in Cambodia, and for longer periods of time. Figure 2 illustrates the cyclical flow of water, and its complex interactions with the air and landforms.

As noted in Table 2, mountainous regions tend to be rocky, and therefore have soils that are less likely to retain water for plant communities. Furthermore, they are often defined by relatively steep slopes, which tend to drain the landscape of its water immediately after a rainfall. These same slopes can also affect evaporation rates of a forest, depending on the angle and pitch of slopes.

In contrast, the lack of relief can have the opposite of affect on water availability. Flatlands often receive precipitation that has fallen on nearby mountains, and then retain these waters in their shallow reliefs. This general scenario describes the physiography of Cambodia as whole, whose principal lowland forests are situated between the Dangrek and Central Annamite Mountains to the North and the Cardamom Mountains (*sensu lato*) to the South (Maps 2, 3).

Figure 2. The Water Cycle



(after Raven *et al*. 1993, from O'Brien, 2000)

3.3 Geology and Soil

The nature of soils and their underlying parent materials are equally important in determining the availability of both water and minerals. Alluvial sands, silts, and sandy soils are particularly common in floodplains, and these can serve to retain water in regions that experience a dry period during the year. As already noted, rocky soils and their underlying substrates are often incapable of retaining water and minerals. Consequently, they are often dry and infertile.

The fertility of soils is often determined by the nature of rock that characterizes a given region. The chemical characteristics of soil are often determined by the degree and manner in which regional rocks have decomposed over the geological course of time, and the character of rocks that serve as the parent material. Geological processes are influenced to varying degrees by climate, time, relief/topography, as well as biological processes that are determined by human and non-human organisms (animals/bacteria). All of these factors can have a direct or indirect bearing on a soil's acidity, colour, texture, structure, fertility, productive capacity, and permeability.

Soils are classified to a large extent by the size of their particles, from finest particles (clay) to coarse particles (silt, sand) to coarsest of particles (gravel). They are also influenced by the nature and content of their organic matter (humus). Soils are often formed by several distinctive horizons, each layer of which can be characterized in terms of their physical and chemical constitutions, or water-holding capacities.

They can also be characterized on the basis of their geological history and process of formation:

- sediments (e.g. sand, gravel)
- sedimentary rocks (e.g. sandstone, limestone)
- metamorphic rocks (e.g. schist, slate, quartzite)
- volcanic rocks (e.g. basalt)
- plutonic rocks (e.g. granite)

Table 3 summarizes the classification scheme of Driessen & Dudal (1989), which we cite in order to demonstrate their complexity, and the complicated processes that are involved in their formation.

Soils also have a direct impact on the adaptive features of plant species and communities. Soils that are comprised of inert, silicaceous sandstone or siltstone, for example, are often poor in water and mineral content due to leaching. Plant communities in these soils are often dominated by leguminous plants, owing to their symbiotic relationship with Nitrogen-fixing bacteria in their roots. Moreover, non-leguminous plants in sandy soils often require close associations with leguminous plants to obtain their needed allotments of nitrogen.

Various distinctive Cambodian plant communities have been defined specifically on the basis of their soil preferences types, as noted by Legris & Blanco (1972: p. 112; i.e., forests “terre rouge basaltiques”, “Terre Grise”, or limestone).

Table 3 – Soil Groupings of the FAO-UNESCO Systems (Driessen and Dudal, 1989)

Set	Dominant Identifiers	Main Soil Groupings
1	Organic soils	HISTOSOLS
2	Mineral soils in which soil formation is conditioned by **Human influences**	ANTHROSOLS
3	Mineral soils in which soil formation is conditioned by **Parent material** • soils developed in volcanic material • soils developed in residual and shifting sands • soils developed in expanding clays	 ANDOSOLS ARENOSOLS VERTISOLS
4	Mineral soils in which soil formation is conditioned by **Topography/Physiography** • soils in lowlands (wetlands) with level topography • soils in elevated regions with non-level topography	 FLUVISOLS GLEYSOLS LEPTOSOLS REGOSOLS
5	Mineral soils in which soil formation is conditioned by **limited Age**	CAMBISOLS
6	Mineral soils in which soil formation is conditioned by (**Climate and Vegetation**) in wet tropical and subtropical regions	PLINTHOSOLS FERRALSOLS NITISOLS ACRISOLS ALISOLS LIXISOLS
7	Mineral soils in which soil formation is conditioned by (**Climate and Vegetation**) in arid and semi-arid regions	SOLONCHAKS SOLONETZ GYPSISOLS CALCISOLS
8	Mineral soils in which soil formation is conditioned by (**Climate and Vegetation**) in steppes and steppic regions (prairies)	KASTANOZEMS CHERNOZEMS PHAEOZEMS GREYZEMS
9	Mineral soils in which soil formation is conditioned by (**Climate and Vegetation**) in subhumid forest and grassland regions	LUVISOLS PODZOLUVISOLS PLANOSOLS PODZOLS