

CHAPTER 1

Background

In a forest different species of trees, shrubs and herbs grow together mutually, share solar radiation for photosynthesis and absorb soil moisture and nutrients from the soil horizon with their efficient root systems distributed at different soil profiles depending on the species. They grow together and maintain their dynamic growth if not disturbed by environmental stresses, such as cyclones, illegal logging, over-grazing by animals, expansion of agriculture other human activities and so on. The plants absorb soil moisture and nutrients for their growth and development. The mature leaves finally fall to the ground, mix with the soil and thereby recycle nutrients. Adverse climatic conditions, high temperatures, global warming, cyclones, water and cold stress affect the growth of the trees and shrubs in the forests prevailing in different regions of the world. Some species have a capacity of adaptation to these environmental stresses, others are susceptible and fail to survive. Forests give us timber, fire wood, medicinal plants, other products for our livelihood and forage for animals. There exists a great diversity in the leaf canopy and crown architecture, branching patterns, leaf morphology and floral structure. Forests

provide different types of soft and hard woods for the wood and paper industries depending on the structural organisation of wood. Different species flower in different seasons, produce fruits and disperse seeds for germination, regeneration of seedlings and maintaining their life cycles. Forests save our lives by absorbing and reducing the carbon dioxide load liberated in the lower horizon of the atmosphere through the process of photosynthesis, liberating oxygen for our respiration and storing carbon in the wood, important for the wood industry. Most of them are perennial, few are annual. Different species flower at different times of the year depending on their photoperiod requirement. They flower, produce fruits and finally disperse seeds on the ground which germinate and emerge on the advent of favorable weather, thereby maintaining the life cycle. It is necessary to understand the dynamic activities of the species present in a forest varying widely in different climatic zones of the world, in arid, semiarid, temperate or alpine zones. The authors have original findings of these activities.

A knowledge of the autoecology and ecophysiology of the trees in a forest is an essential pre-requisite to understand

the growth of trees required for efficient forest management by forest managers and rangers. They should know the phenology (flowering, fruiting, seed dispersal) and the effects of environments on the growth and development of each species and globally for taking effective measures for maintaining forest health. We present here up to date literature on various aspects of autoecology and ecophysiology from tropical, temperate, arid-semiarid and a few alpine forests globally. We present here our research advances on various aspects of autoecology and ecophysiology of semiarid Tamaulipan thorns which may serve as a model to study the autoecology of trees in other regions. In addition, we provide an extensive review on various aspects of autoecology globally.

1.1 A definition of autoecology

Autoecology involves all aspects of the dynamism of populations and the physiological traits of trees, their light requirements and also their life history pattern and physiological and morphological characters (Fetcher et al., 1994).

1.2 A definition of ecophysiology

Ecophysiology (from Greek οἶκος, *oikos*, “house(hold)”; φύσις, *physis*, “nature, origin”; and -λογία, *-logia*, “discussion”), environmental physiology or physiological ecology is a biological discipline that studies the adaptation of an organism’s physiology to environmental conditions. It is closely

related to comparative physiology and evolutionary physiology. See: *ecophysiology of tree growth* on Wikipedia, the free online encyclopedia.

Ecophysiology of tree growth can be defined in terms of an increase in the size of an individual or a stand. Growth is usually expressed as a change in size per unit of time and area. The growth of trees is influenced by several physiological traits and environmental conditions of the forest ecosystem. This also deals with various functional, physiological and biophysical aspects of woody trees to plant productivity. There is a great necessity to determine the variability of physiological functions among tree species and their adaptation to the environment.

1.3 Environment

Forest environment plays an important role in the growth of a tree. Environment can be classified as climatic, edaphic, physiographic and biotic. The climatic factors prevailing in different semiarid, tropical and temperate regions affect the growth and adaptation of trees. The climatic factors related to atmospheric conditions are solar radiation, light, air composition, wind, temperature, precipitation, relative humidity and intensity of light. These climatic factors determine the distribution of vegetation.

We want to mention here a brief account of climate change and its effect on forests. A change in climate due to an increase of carbon dioxide concentration has a direct impact on the productivity of forests. Climate determines the distribution of vegetation in a forest ecosystem. There exists

a good relation of the climate with the conservation and development of forest. It is essential for foresters to have good understanding of the climate changes and its impact on forest productivity and to take the necessary measures to protect it.

We are very much concerned about how human activities such as the burning of fossil fuels, conversion of forests to agricultural lands and other illegal activities cause a significant increase of carbon dioxide and other green house gases (GHG) in the atmosphere. On the other hand, both forests and human uses of forest products contribute to a gradual increase of GHG in the atmosphere. Fortunately the trees and forests with their ability to absorb CO₂ and carbon have an opportunity to mitigate climate change. GHG cause the retention of heat in the lower atmosphere due to absorption of light and its reflection by clouds and other gases.

The earth receives radiant energy from solar radiation for its utilisation by the plants for photosynthesis and by humans for other activities. Short-wave solar energy (visible) received from the sun passes through the atmosphere, thereby warming the earth's surface. Long-wave thermal radiation is absorbed by a number of GHG. These GHG accumulate in small amounts in the lower layer of the atmosphere and reflect long-wave thermal radiation in all directions. Some of the radiation is directed towards the earth's surface. The amount of GHG in the atmosphere influences global temperature.

Green house gases present in the earth's surface are water vapour (H₂O), carbon dioxide (CO₂), nitrous oxide (NO₂), ozone (O₃), carbon monoxide (CO) and chlorofluorocarbons (CFC). The concentrations

of these gases have changed in the earth over geological time scales. The increase of agriculture, animal husbandry, grazing and an increase in human population has indirectly increased the levels of these GHG, enhancing global warming, thereby threatening the security of human life, animals and so on. Over and above this, an incessant logging of trees for timber has a direct impact in the increase of GHG. Constant emissions of carbon dioxide and its accumulation in the lower profile of the atmosphere enhances contamination, but thanks to the forest ecosystem of trees and shrubs, even the lower organisms capture carbon dioxide and utilise it in the process of photosynthesis and the accumulation of carbon in wood and biomass, thereby reducing the carbon dioxide load and at the same time liberating oxygen necessary for the respiration of living organisms. Now we can present a brief account on the effects of environmental components on forest growth and productivity.

1.4 Solar radiation

Solar radiation is the main source of energy for our life and all living organisms. It provides light, temperature and energy for growth and development. Although a large part of radiation is absorbed by the atmosphere, a small part reaches the earth's surface and is captured by leaves through chlorophylls and converted into chemical energy by the process of photosynthesis. This energy is stored in the grains and fruits serving as a source of energy for us. Not all solar radiation fully reaches the earth's surface. A large part of the ultraviolet rays (wavelength 0.12–0.40 µm) are absorbed

by oxygen, nitrogen and ozone present in the atmosphere. The visible portion of solar radiation (wave length 0.40–0.71 μm) is called visible light.

1.5 Solar radiation and vegetation

Solar radiation supplies heat, illumination and chemicals and produces electrical effects on the earth's surface. Solar radiation contributes with light and temperature for the growth of the ecosystem: a proper temperature range is necessary for various physiological activities, viz. transpiration, photosynthesis and respiration. For proper growth of plants a suitable range of temperature is very essential. An optimum air temperature is necessary for the germination of seeds. Higher air temperature increases microbial activity on the soil surface, leading to a rapid decomposition of organic matter, release of nutrients and formation of humus. Temperature affects the activities of enzymes. Plants are adapted to different regions, such as arid, temperate and alpine climates, thereby temperature requirements vary in the different regions.

1.6 Light requirement of tree species

Plants require light for photosynthesis and growth. The species require abundant light for their optimum growth and development. Shade plants are capable of growing under shade. These plants require shade at least in the early stages for optimum growth and development. Shade-tolerant plants possess a range of adaptations to

help them to survive and alter the quantity and quality of light typical of shade environments. Shade leaves and shade-tolerant species have a higher photosynthetic efficiency per unit of leaf area under low-light conditions than sun leaves and intolerant species. Under high light conditions, the reverse is true. This is because shade leaves of intolerant species lose photosynthetic efficiency when they are suddenly exposed to high light intensities. Excess light incident on a leaf can cause photoinhibition and photodestruction. Plants adapted to high light environments have a range of adaptations to avoid or dissipate the excess light energy, as well as mechanisms that reduce the amount of injury caused.

1.7 Photomorphogenesis and photoperiodism

Light intensity is an important component in influencing the temperature of plant organs (energy budget). Light directly affects tree growth through its intensity, quality and duration.

1.8 Photosynthesis

Photosynthetic activity contributes greatly to the production of biomass. This is also influenced by the intensity of leaves and canopy orientation. It is expected that trees with an open leaf canopy are more efficient in photosynthesis than those with a closed canopy. The rate of photosynthesis is influenced by both plant and environmental factors. Light quality is of interest in relation to considerations of the merits of uneven- versus even-aged stands. Light

plays an important role for the natural regeneration and maximum production of high quality wood.

1.9 Temperature

Temperature is a very important factor for photosynthesis. Both air and soil temperature influence plant growth and thus affect forest vegetation. The proper temperature range is necessary for various physiological activities. Each plant species requires an optimum temperature for plant growth. A temperature lower than the optimum required for each species affects its growth. Some species are well adapted to a xeric habitat, some to temperate and others to alpine zones. With an increase in temperature plant growth increases up to its optimum temperature. The low temperatures prevailing in winter affect seed germination.

1.10 Water relations

Water is one of the most important factors influencing the distribution, growth and development of vegetation and is essential for all vital processes such as photosynthesis. It forms the essential constituents of cell sap and cell vacuoles. It works as a medium for the absorption of plant nutrients and plant metabolism. It is necessary for the germination of seeds; and it is necessary for all plant movement. A plant cell requires about 90% water to maintain its vital activity. A substantial decrease in water in the cell causes plasmolysis, thereby inhibiting all metabolic activities. Water potential plays an important role to maintain

a pressure gradient in the plant cells required for the transport of water from one to another. Water is absorbed by roots and is transported upwards through xylem vessels to the leaves and other organs to help in metabolic activities. Excess water is lost through transpiration via the stomatas, thereby maintaining a water balance in the plant cells. Water deficiency causes a lowering in plant water potential, while an excess of water due to flooding affects respiration and plant growth. The sequential process of water absorption, its translocation and loss by the transpirational flux is discussed in brief below.

Water is absorbed by roots and then is transported through the mostly dead xylem tissue from the soil to the leaves and finally transpired to the atmosphere. The loss of water through transpiration creates a vacuum pressure in the leaf mesophyll due to which water in the xylem is under negative pressure and creates cohesive forces in xylem vessels between water molecules to maintain the water columns intact. Roots absorb water from soils owing to the difference of water potential between the soil and cells. There is always a gradient of water potential from the peripheral cortical cells to the interior cells, finally reaching the endodermis, due to water entering the xylem vessels. Once it reaches the xylem vessels, water moves up by a suction force called the ascent of sap. The adjacent phloem tissue is under positive pressure that is maintained osmotically with assimilated sugars and dissolved minerals. Variability in soil and atmospheric conditions influences the interaction between the pressures and structural properties, determining the tissue resistivity against embolism

formation under high negative pressures in xylem tissue that threatens the integrity of xylem transport. Only a small amount is consumed in the process of photosynthesis. The main effect of water on photosynthesis is indirect, through the hydration of protoplasm and stomatal closure.

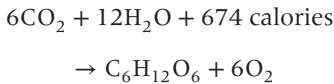
The deficiency of water called water stress affects the growth and development of plants. Each species requires an optimum amount of water below which the growth of this species is reduced. The species adapted to drought is called drought-resistant. Drought-resistant plants have several morphological, anatomical and biochemical mechanisms of resistance, similar to species tolerant to low temperatures. The density of trichomes, leaf surfaces with a waxy coating, thick cuticles, compact palisade cells and a few biochemical components, such as proline, sugars and ABA are related to drought resistance. In the semiarid tropics, several species are tolerant to drought, others not so much. We need to identify them in a forest.

1.11 Plant nutrients

The photosynthetic efficiency of leaves depends on the soil nutrient supplies. A good amount of nutrient improves the photosynthetic capacity of trees. Photosynthesis involves physicochemical processes that occur in the presence of light energy and enzymatic processes that occur in dark reactions. It involves mainly two processes: Photosystem I, during which radiant energy is absorbed by chloroplasts, leading to the photolysis of water. The chemical process during which CO_2

is fixed occurs in dark reactions. This is influenced by the quantity of CO_2 fixed by each gram of foliage and indirectly by the increased size of individual leaves and the total size of crown and root system. An increase in leaf area contributes to a high photosynthetic capacity. The photochemical process starts when the chloroplasts capture radiant energy and transfer the energy to a chemical process during the dark phase. Two types of chlorophylls are involved in this process: chlorophyll *a* and chlorophyll *b*. The chloroplasts are composed of stacks of thylakoids (like coins) and stroma between the chloroplasts. The photochemical process occurs in the thylakoids while the chemical reaction combining the CO_2 with H_2O occurs in the stroma. The light energy absorbed by chlorophyll in the photochemical reaction is transmitted to the dark reaction in the absence of light for the chemical combination of CO_2 and H^+ liberated during the photolysis of water to form the first product of photosynthesis, phosphoglyceraldehyde. Then glucose-1-phosphate, a three-carbon compound, enters the phosphate pentose pathway (Calvin Cycle) and phosphate, a high energy compound, helps in the transfer of energy from one compound to another. The Calvin Cycle ultimately forms glucose, the final product; and the phosphate is liberated to function again in the transfer of energy. Thereby 674 calories of radiant energy absorbed by the chlorophyll pigments are stored in the glucose; and the glucose in turn is stored as a carbohydrate in insoluble starch. The photosynthates and glucose are transmitted and finally stored in plant biomass and wood as sources of energy liberated during

the process of respiration for various metabolic processes in the plant.



1.12 Role of nutrients in plant life

Several nutrients take part in the growth and development of plants, such as carbon, oxygen and hydrogen from the air or from water. Although plants absorb more than 40 elements during their growth, not all of them are essential for growth and development.

Elements which have been proved to be essential for the growth and development of plants are called essential elements. The nutrients which are required in larger proportion are called major nutrients, for example carbon (C), hydrogen (H), nitrogen (N), calcium (Ca), phosphorus (P), magnesium (Mg), potassium (K), oxygen (O) and sulfur (S). Those required in smaller amounts are called minor nutrients, for example iron (Fe), zinc (Zn), chlorine (Cl), copper (Cu), molybdenum (Mo), boron (B) and manganese (Mn). Deficiency in these micronutrients affects plant growth.

Nitrogen (N) is the most common nutrient that limits forest growth. It forms the skeleton of protein and help in enzyme action. Phosphorus (P) is for energy transformation. Sulphur acts as a milder substitute for oxygen although it is required to form two aminoacids: methionine and cysteine. Potassium (K) activates many enzymes. Calcium (Ca)

connects organic molecules. Magnesium (Mg) is present at the center of chlorophyll. Iron (Fe) is a key element for respiration and photosynthesis processes. Manganese (Mn) plays a significant role during respiration and photolysis of water. Copper (Cu) is involved in oxidation–reduction reactions.

The photosynthetic efficiency of foliage depends decisively on soil nutrient supplies. By improving the nutrient status of a site we also improve the photosynthetic capacity of trees. The effect is both direct (quantity of CO_2 fixed by each gram of foliage) and indirect by increasing the size of individual leaves, total size of crown and root system.

1.13 Plant factors

In plants, net photosynthesis is dependent on leaf age position within crown. The fully expanded leaves in a conifer are the most efficient of all age classes owing to varying rates of respiration and insect or disease damage. The upper crown leaves are the most productive, exposed directly to sunlight. The leaves present in the lowest whorls contribute little to net photosynthesis as most of the leaves do not receive direct sunlight. Variation in photosynthesis occurs between crown classes and species (Gholz et al., 1979). We have developed a hypothesis that trees with an open canopy have a great capacity of capturing solar radiation and photosynthesising, compared to those with close, overlapping leaves. Few of these trees with an open canopy have the capacity to capture 50% carbon, as discussed later. Plants with an open canopy have highly

branched stems while those with a close canopy possess a stout basal stem, yet to be confirmed. Leaf surface structures containing high stomatal frequency, trichome density, silica contents, wax contents and so on could be related to the adaptation of trees to xeric and biotic environments, as discussed later.

1.14 Respiration

Respiration is the process by which energy fixed by photosynthesis in plants is made available for metabolic processes. This energy is stored in wood as potential energy which is released by combustion. The implications are obvious. Per unit area, having fewer but larger diameter trees is better than keeping more but smaller diameter trees from the standpoint of wood production.

1.15 Phenology and ecology

Variations in tree phenology are good indicators of the plant species' response to climate change. In a tropical region, Borchert (1980) investigated the phenology and ecophysiology of a tropical tree: *Erythrina poeppigiana* O. F. Cook. Under the climatic conditions of San Jose in Costa Rica, leaf fall, flowering and shoot emergence of *E. poeppigiana* were markedly asynchronous among trees of the same population, suggesting strong endogenous control of the tree's development. During one year, trees showed two cycles of leaf shedding and shoot emergence. The endogenous periodicity of leaf shedding appeared to be primarily the result of leaf senescence. During the dry season, leaf senescence and hence

leaf shedding were enhanced owing to tree severe water deficits. As a consequence of leaf shedding, water stress was reduced and shoot emergence started under continued drought. The degree of water stress, causing stem shrinkage, was affected by tree size, soil moisture availability and seasonal changes in evapotranspiration. The phenology of *Erythrina* along an altitudinal gradient of increasing atmospheric water stress showed a transition from an evergreen to a deciduous habit. With increasing drought, consecutive developmental stages tended to be more separate in time and more synchronised.

1.16 Effect of drought stress

Drought stress greatly affects the growth of trees, frequently causing fires during summer. Bréda et al. (2006) made a review of the physiological responses, adaptation processes and long-term consequences under a drought event that occurred in temperate Western Europe during 2003. They emphasised the need to understand the key processes that may allow trees and stands to overcome such severe water shortages. They reviewed the impact of drought on exchanges at soil-root and canopy-atmosphere. They quantified and modelled CO₂ flux, the decline in transpiration, water uptake and in net carbon assimilation due to stomatal closure. Estimates of soil water deficit gave a quantitative index of soil water shortage. They reported the irreversible damage imposed on water transfer within trees and particularly within xylem and also the inter-specific variability of these properties among a wide range of tree species. There occurred inter-specific diversity of hydraulic and

stomatal responses and a large diversity in traits potentially related to drought tolerance. The potential involvement of hydraulic dysfunctions or of deficits in carbon storage under long-term decline of tree growth and development and for the onset of tree dieback was emphasised. Bréda et al., 2006 reported that the starch content in stem tissues recorded at the end of summer 2003 was used to predict crown conditions of oak trees. Similarly, Bréda et al. (2006) made a review of ecophysiological responses, adaptation processes of temperate forest trees and stands under severe drought and long-term consequences that occurred in Western Europe during 2003. They highlighted the need to understand the key processes that may allow trees and stands to overcome such severe water shortages. They reviewed the current knowledge available about such processes. They explained the impact of drought on exchanges at soil–root and canopy–atmosphere interfaces and illustrated this with examples from water and CO₂ flux measurements following spring: low starch contents were correlated with large twig and branch decline in the tree crowns.

1.17 Ecological plasticity

Man's broad diffusion and active management of the sweet chestnut in past centuries established the species at the limits of its potential ecological range in many European mountain areas. It is hypothesised that the chestnut tree has considerable plasticity, enabling the species to adapt to very different sites and conditions. In order to test this hypothesis, Pezzatti et al. (2009) applied

the pipe-model approach, postulating the constancy of the leaf area/sapwood area (LA/SA) relationship for single portions of a tree. They analysed the variation of the LA/SA coefficient among chestnut trees subjected to different sites conditions (e.g. convex vs concave sites) in order to gain an insight into the plasticity of the species. The results established that the sweet chestnut is able to greatly vary the allocation of resources with respect to environmental conditions. In particular, the LA/SA coefficient was high when trees were growing in sites with a good water supply.

1.18 Productivity

The productivity of a tree is influenced by various climatic conditions, solar energy, temperature, pigments contributing to the productivity of biomass, dry matter and timber production, radiation, temperature and energy budget. Among them the following factors are important.

- 1 Carbon utilisation
- 2 Utilisation and cycling of mineral elements
- 3 Water relations.

In a forest ecosystem, individual species compete for the capture of solar radiation by plant pigments, chlorophyll and other pigments by the process of photosynthesis, thereby leading to carbon fixation (carbon sequestration) and dry matter production. Several physico-chemical and biochemical process occur in this vital process. Solar energy passes through the atmosphere, finally reaches the plant cover and is distributed at different profiles of leaf canopy, vertically, horizontally, then captured by leaves for the process of CO₂ assimilation during the process

of photosynthesis; this finally leads to the production of dry matter. The leaves exposed directly to solar energy have a greater capacity for photosynthesis than those inside the plant cover. It is expected that the photosynthetic capacity of leaves present at different profiles of the tree varies widely. Variation in the contents of plant pigments and leaf canopy cover is expected to cause variation in carbon sequestration among different plant species. Therefore, there is a necessity to make comparative studies in the pigment contents and carbon fixation capacity.

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