RANGELAND ECOPHYSIOLOGY

Jenesio I. Kinyamario
University of Nairobi, School of Biological Sciences, Nairobi, Kenya

Victor R. Squires
University of Adelaide, Australia

Keywords: C_3, C_4, photosynthesis, water use efficiency, nitrogen, productivity, rangeland management, crassulacean acid metabolism (CAM), physiological processes, CO_2 fixation, Leaf area index (LAI), photosynthetically active radiation (PAR)

Contents

1. Implications of plant physiological processes for rangeland ecosystems
1.1. Plant Level Interactions
1.2. Management Implications:
2. Photosynthesis
2.1. C_3, C_4 Pathways in Photosynthesis
2.2. Crassulacean Acid Metabolism (CAM)
3. Geographical and ecological distribution of different photosynthetic pathway plants
4. Comparative analysis of photosynthetic pathways
4.1. CO_2 Compensation Point
4.2. Light Saturation
4.3. Light Compensation Point
4.4. Temperature Optima
4.5. Water Use Efficiency
4.6. Nitrogen Use Efficiency
4.7. Photorespiration
5. Photosynthetic capacity, quantum yield, and productivity
6. Implications for Rangeland Management
6.1. Herbivory
6.2. Carbohydrate Reserves
6.3. Drought and Overgrazing Combine to Cause Much Stress
6. 4. Climate Change
6.5. Invasive Species
6.6. Fires
7. Conclusions
Glossary
Bibliography
Biographical Sketches

Summary

Plants fix radiant energy through fixation of carbon into biomass that is consumed by animals. Therefore, the rates of carbon fixation and factors that determine these rates will determine the number of grazers a rangeland can be able to optimally carry (carrying capacity). Environmental factors that determine bioproductivity rates are

basically those that determine rates of CO_2 fixation through the process of photosynthesis and respiration. Other factors include grazing pressure (defoliation, trampling, nutrient cycling) precipitation, light, temperature, wind, soil parameters, and inter-specific and intra-specific plant competition.

Photosynthesis is the driving force of plant growth and animal production and is dependent on the area and efficiency of green plant tissue. Photosynthesis is a photochemical process by which plants fix carbon dioxide by use of solar radiation into organic acids and ultimately to sugars. There are two parts to photosynthesis: The ***light reaction*** happens in the thylakoid membrane of the chloroplast and converts light energy to chemical energy and the ***dark reaction*** takes place in the stroma within the chloroplast, and converts CO_2 to sugar.

Plants with higher photosynthetic capacity end up with higher CO_2 carbon gains and hence in dry matter accumulation (***productivity***). Productivity is dependent on the assimilatory capacity of the plant, the length of the growing season and the effects of environmental factors such as precipitation, temperature, radiation, soil fertility, etc.
The dilemma for rangeland managers is to optimize photosynthesis on the one hand and still achieve efficient harvesting of the product on the other. Management of rangelands requires that managers understand the defoliation resistance mechanisms within grass plants.

1. Implications Of Plant Physiology For Rangeland Ecosystems

Rangelands are important grazing ecosystems comprising of assemblages of plants and herbivores (see *Rangeland communities: structure, function, and classification*) and the physiological processes that go on within them are not well understood by the ranchers or herders who use them. Plants fix radiant energy through fixation of carbon into biomass that is consumed by animals. Therefore, the rates of carbon fixation and factors that determine these rates will determine the number of grazers a rangeland can be able to optimally carry (carrying capacity). Environmental factors that determine bioproductivity rates are basically those that determine rates of CO_2 fixation through the process of photosynthesis (see below) and respiration. Other factors include grazing pressure (defoliation, trampling, nutrient cycling) precipitation, light, temperature, wind, soil parameters, and inter-specific and intra-specific plant competition.

1.1. Plant Level Interactions

Plants interact at several levels; individual and close neighbors. At the individual level this interaction is among different leaves at different leaf layers that may induce leaf shading. This is determined by the leaf area index (LAI) of the plant. Close neighbors have the strongest interactions towards each other. It has been demonstrated that as radiant energy passes through a dense sward, it gets diminished exponentially towards the lower sward levels near the ground surface depending on the LAI of the sward. This is both in quality and quantity, called light attenuation and follows the Beer-Lambert law. Therefore leaves in the top of the canopy will receive more energy and of better quality than the lower canopy levels leaves. The radiant energy useful in photosynthesis is in the spectral range of 380 – 710 nm (called photosynthetically active radiation (PAR) often referred as 400 – 700 nm, PAR).

The canopy photosynthesis of crops and natural communities will be determined largely by the product of their average PAR and their LAI. Therefore the gross productivity of the community will be equal to the integrated value of canopy photosynthesis throughout the growing season. There is a linear relationship between canopy photosynthesis and light interception whereby early in the growing season or after defoliation by herbivory, light interception is closely related to the available LAI and crop growth and dry matter production will be proportional to the rate of light absorption (Monteith, 1981). This is attributable to the rapid increase in canopy photosynthesis as a result of increasing leaf area index until the eventual canopy closure later occurs. After canopy closure, there is no longer linear relationship between light interception and available leaf area that will strictly follow Beer-Lambert extinction law due to mutual shading although this may not limit overall stand productivity.

$$I_z = I_o \exp^{-k\, LAI}$$

where, I_z = light received at a given canopy depth; I_o = incident light received at top of plant canopy; k = extinction coefficient specific to the plant community, LAI = cumulative leaf area index above the level at which I_z is estimated, the cumulative LAI .

More photosynthesis will tend to occur in the top canopy layers and diminish with the depth of the canopy. Due to shading photosynthetic activity of grasses were shown to reduce by about 50% in the middle canopy leaves and about 70% in bottom canopy leaves of a grassland range in Kenya.

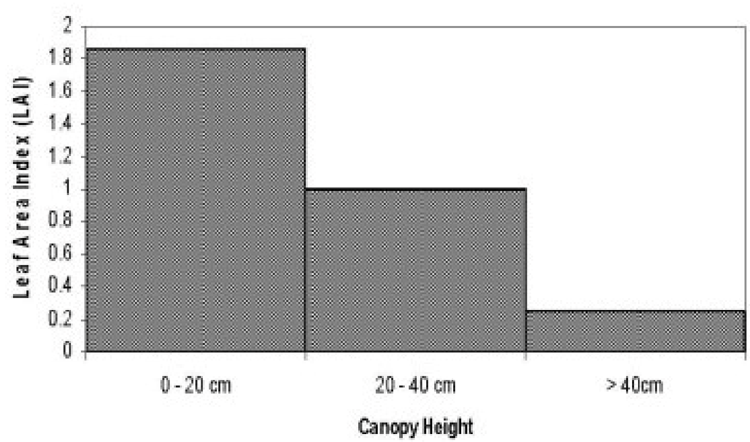

Figure 1. Distribution of leaf area index (LAI) in relation to height above ground within a grassland canopy in the Nairobi National Park, Kenya (Data: J.I. Kinyamario unpublished)

Competition among and between different individuals for various environmental requirements will determine the kind of community that results in a particular rangeland ecosystem. Competition for light is usually experienced in any typical plant community but is less of a problem in semi arid rangelands where the nearest neighbor distance is usually much wider.

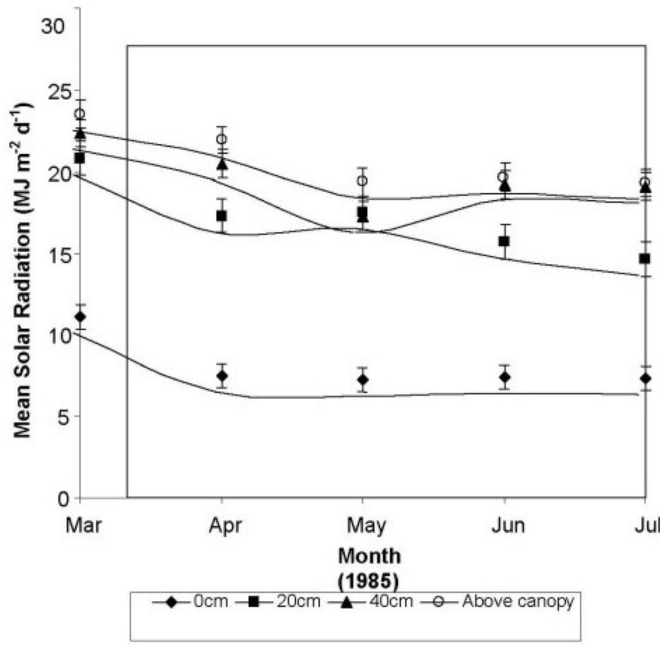

Figure 2. Mean solar energy (MJ m^{-2} d^{-1}) received at various canopy levels in various months of the growing season (1985) at grassland sward in the Nairobi National Park (Data: J.I. Kinyamario unpublished)

1.2. Management Implications:

1. Plant type selection (C_3 vs C_4, species and cultivars) affects seasonal production profile
2. Defoliation intensity (number of animals for how long) affects light capturing capacity (of the plant)

2. Photosynthesis

Photosynthesis is the driving force of plant growth and animal production and is dependent on the area and efficiency of green plant tissue. Photosynthesis is a photochemical process by which plants fix carbon dioxide by use of solar radiation into organic acids and ultimately to sugars.

The sugar contains the stored energy and serves as the raw material from which other compounds are made. It occurs in the presence of water, solar energy and plant chlorophyll molecules that must trap the solar energy to allow the process to take place. This process, which takes place inside chloroplasts, involves important and specific enzymes. The process of photosynthesis can be simplified as follows:

$$CO_2 + 2H_2O \xrightarrow[\text{Chlorophyll}]{\text{Solar Energy}} (CH_2O)_n + H_2O + O_2$$

Photosynthesis follows a rather well understood pathway among plants. During the process, the water molecule is split into protons and electrons are released that drive the process.

There are two parts to photosynthesis: The ***light reaction*** happens in the thylakoid membrane of the chloroplast and converts light energy to chemical energy. This chemical reaction must, therefore, take place in the light. Chlorophyll and several other pigments such as beta-carotene are organized in clusters in the thylakoid membrane and are involved in the light reaction. Each of these differently-colored pigments can absorb a slightly different color of light and pass its energy to the central chlorophyll molecule to do photosynthesis. The central part of the chemical structure of a chlorophyll molecule is a porphyrin ring, which consists of several fused rings of carbon and nitrogen with a magnesium ion in the centre. The ***dark reaction*** takes place in the stroma within the chloroplast, and converts CO_2 to sugar. This reaction doesn't directly need light in order to occur, but it does need the products of the light reaction (ATP and another chemical called NADPH). The dark reaction involves the ***Calvin cycle*** in which CO_2 and energy from ATP are used to form sugar. Actually, notice that the first product of photosynthesis is a three-carbon compound called glyceraldehyde 3-phosphate. Almost immediately, two of these join to form a glucose molecule.

The energy generated in the form of ATP during phosphorylation is used together with the reducing power ($NADPH_2$) gained during the reaction to reduce CO_2 to carbohydrates with a higher energy value. This process takes place in the stroma of chloroplasts. Some plants are known to fix carbon dioxide resulting into either three or four carbon stable products. Hence, plants are divided into two major groups in terms of these pathways, namely C_3 or C_4 plants.

-
-
-

Bibliography

[C4 photosynthesis is an adaptation that enhances plant carbon gain in warm climates with high light and relatively low atmospheric CO2 concentration, the complex interactions between C4 anatomy and biochemistry appear to have evolved over thirty times independently within the angiosperms].

Briske, D.D. and J.R. Hendrickson. 1998. Does selective defoliation mediate competitive interactions in a semiarid savanna? A demographic field evaluation. *Journal of Vegetation Science* 9:611-622[Discusses the development of effective responses by plants to the impact of grazing. Morphological and physiological traits, including crop architecture are involved].

Briske, D.D., and J.H. Richards. 1995**.** Plant response to defoliation: a physiological, morphological, and demographic evaluation. pp. 635-710. In D.J. Bedunah and R.E. Sosebee (eds.). *Wildland plants: physiological ecology and developmental morphology. Society for Range Management*, Denver, CO. [Several plant traits, including the location and availability of meristems, architectural attributes influencing palatability and residual leaf area following defoliation have proved especially important to our understanding of grazing resistance in plants].

Briske, D.D., and J.H. Richards. 1995**.** Plant response to defoliation: a physiological, morphological, and demographic evaluation. pp. 635-710. In D.J. Bedunah and R.E. Sosebee (eds.). *Wildland plants: physiological ecology and developmental morphology.* Society for Range Management, Denver, CO. [Several plant traits, including the location and availability of meristems, architectural attributes influencing palatability and residual leaf area following defoliation have proved especially important to our understanding of grazing resistance in plants].

Ehleringer JR, Cerling TE, Dearling D (eds). 2005. A history of atmospheric CO_2 and its effects on plants, animals and ecosystems. Berlin, Germany: Springer-Verlag, New York. [Extensive research in geology, atmospheric science, and paleontology provides a detailed history of CO2 in the atmosphere and an understanding of factors that have influenced changes in the past].

Ehleringer JR, Cerling TE, Helliker BR. 1997. C_4 photosynthesis, atmospheric CO_2 and climate. Oecologia 112: 285–299. [The objectives of this synthesis are (1) to review the factors that influence the ecological, geographical, and palaeoecological distributions of plants possessing C_4 photosynthesis and (2) to propose a hypothesis/model to explain both the distribution of C_4 plants with respect to temperature and CO_2 and why C_4 photosynthesis is relatively uncommon in dicotyledonous plants, especially in comparison with its widespread distribution in monocotyledonous species].

Giussani LM, Cota-Sánchez JH, Zuloaga FO, Kellogg EA. 2001. A molecular phylogeny of the grass subfamily Panicoideae (Poaceae) shows multiple origins of C4 photosynthesis. American Journal of Botany 88: 1993–2012. DNA sequence data from the chloroplast gene *ndhF* were analyzed to estimate the phylogeny of the subfamily Panicoideae, with emphasis on the tribe Paniceae. The phosphoenol pyruvate carboxykinase (PCK) subtype of C4 photosynthesis has evolved only once, as has the NAD-malic enzyme (ME) subtype; all other origins are NADP-ME.

Hassan, S. N., Rusch, G. M., Hytteborn, H., Skarpe, C.,and Kikula, I. 2007. Effects of fire on sward structure and grazing in western Serengeti, Tanzania. *African Journal of Ecology* 46, 174–185.[In Serengeti fire is used as a management tool to improve the forage quality for large herbivores. However, little is known of the effects of fire on grazing resources particularly sward structure, its influence on herbivore forage patch selection and utilization to the relative amount of phytomass consumed in burnt and nonburnt patches].

Hattersley PW. 1983. The distribution of C_3 and C_4 grasses in Australia in relation to climate. *Oecologia* 57: 113–128. [It has been shown that C_3 and C_4 species can differ in anatomical, biochemical and physiological and ecological aspects. There is relationship between the distribution of C4 species and climatic patterns]

Hibberd JM, Quick WP. 2002. Characteristics of C_4 photosynthesis in stems and petioles of C_3 flowering plants. *Nature* 415: 451–454.[Tobacco, a typical C_3 plant, shows characteristics of C_4 photosynthesis in cells of stems and petioles that surround the xylem and phloem, and that these cells are supplied with carbon for photosynthesis from the vascular system and not from stomata. These photosynthetic cells possess high activities of enzymes characteristic of C_4 photosynthesis, which allow the decarboxylation of four-carbon organic acids from the xylem]

Hodgkinson,K.C., Ludlow, M.M., Mott.J.J. and Baruch, Z.1989. Comparative responses of savanna grasses *Cenhrus ciliaris* and *Themeda triandra* to defoliation. *Oecologia* 79:45-52 [Discusses the plant adaptation to stress of defoliation and resistance to grazing].

Keeley JE, Rundel PW. 2003. Evolution of CAM and C_4 carbon concentrating mechanisms. *International Journal of Plant Sciences.* 164: S55–S77. [Mechanisms for concentrating carbon around the Rubisco enzyme, which drives the carbon-reducing steps in photosynthesis, are widespread in plants; in vascular plants they are known as crassulacean acid metabolism (CAM) and C_4 photosynthesis. The proximal selective factor driving the evolution of this CO_2-concentrating pathway is low daytime CO_2. In terrestrials the ultimate selective factor is water stress that has selected for increased water use efficiency.

This biochemical pathway is most commonly associated with a specialized leaf anatomy known as Kranz anatomy. The ultimate selective factor driving the evolution of this pathway is excessively high photorespiration that inhibits normal C_3 photosynthesis under high light and high temperature in both terrestrial and aquatic habitats. This knowledge is used to illuminate the role of atmospheric CO_2 in the modern carbon cycle and in the evolution of plants and animals].

Kinyamario, J.I. and S.K. Imbamba. Dry Savanna, Kenya. In, Primary Productivity of Grass Ecosystems of the Tropics and Sub-tropics (S.P**.** Long, M.B. Jones and M. Roberts, Edts.). **-** 1992 *Chapman and Hall, London, pp 123 -140* [A study was carried out on net primary productivity of four contrasting tropical grasslands and showed that these ecosystems are far more productive than earlier suggested, when full account is taken of losses of plant organs above and below-ground. These conclusions have wider implications in prediction of global carbon cycling by grassland ecosystems].

Kinyamario, J.I., M.J.Trlica and T.J.Njoka. Influence of tree shade on plant water status, gas exchange and water use efficiency on Panicum maximum Jacq. and Themeda triandra Forssk. in a Kenyan savanna**. –** 1995 *African Journal of Ecology, 33: 114 -123.* [A study of net CO_2 assimilation rate and water vapor exchange of *Panicum maximum* that grows predominantly beneath savanna tree canopies, and *Themeda triandra* that grows primarily in adjacent open grassland sites, was carried out on both sites in Nairobi National Park. *Panicum maximum* exhibited less water stress, had lower stomatal conductance and transpiration, and had higher water use efficiency than *T. triandra* under tree canopies].

Leegood RC. 2002. C4 photosynthesis: principles of CO2 concentration and prospects for its introduction into C3 plants. *Journal of Experimental Botany* 53: 581–590. [The aim of this review is to discuss the properties of this CO_2-concentrating mechanism, and thus to indicate the minimum requirements of any genetically-engineered system. In particular, the Kranz leaf anatomy of C_4 photosynthesis and the division of the C_4-cycle between two cell types involves intercellular co-operation that requires modifications in regulation and transport to make C_4 photosynthesis work. Some examples of these modifications are discussed.

Monson RK. 1989a. On the evolutionary pathways resulting in C4 photosynthesis and crassulacean acid metabolism (CAM). *Advances in Ecological Research* 19: 57–101.

Monteith JL 1981. Climate variation and growth of crops. *Quarterly Journal Royal Meteorological Society* 107:749–774 [A classic paper that sets out principles governing germination and growth of plants. Seed germination and early plant growth are complex procedures dependent on the interaction of soil temperature and soil moisture as well as photoperiod. Germination begins when an imbibed seed is exposed to temperatures above the base temperature].

Sage RF. 2002b. C_4 photosynthesis in terrestrial plants does not require Kranz anatomy. *Trends in Plant Science* 7: 283–285. [C_4 photosynthesis without Kranz anatomy (single-cell C_4 photosynthesis) occurs in only 0.003% of known species of C_4 flowering plants. Using light microscopy, the anatomy of aquatic, floating and terrestrial leaves from eight of the nine species in the tribe was examined to assess the pattern of evolution of C_4 photosynthesis and Kranz anatomy among these vernal pool grasses. These findings support previously proposed hypotheses suggesting that Orcuttieae are derived from a terrestrial ancestor and are now becoming more specialized to an aquatic environment].

Biographical Sketches

Dr. Jenesio I. Kinyamario is an Associate Professor with the School of Biological Sciences, University of Nairobi, in Kenya. He received a BSc (Biology) from University of Nairobi, an MSc (Range Sciences) from Texas A&M University and a PhD (Plant Ecology) at University of Nairobi. His research focuses on bioproductivity and ecophysiology of African tropical grasslands. He has also worked with scientists at NREL and Department Forest, Rangeland & Watershed Stewardship (Rangeland Ecology) at Colorado State University to understand pastoral systems in East Africa.

Dr Victor Squires is an Australian who as a young man studied animal husbandry and later Botany/Ecology. He has a PhD in Rangeland Science from Utah State University**.** He is a former Dean of the Faculty of Natural Resources at the University of Adelaide and was the Foundation Director of the National Key Center for Dryland Agriculture and Land Use Systems. Since retirement from the University, Dr Squires was a Visiting Fellow at the East West Center in Hawaii and is currently an Adjunct Professor in the University of Arizona, Tucson. He has been a consultant to World Bank, various

UN agencies and the Asian Development Bank. He was GEF Advisor on a World Bank pastoral development project in NW China in 2006-2007. He is author of over 100 papers in refereed journals and numerous invited chapters and author/editor of 6 books. He was awarded the 2008 International Award and Gold Medal for International Science and Technology Cooperation by the Government of China.