W. Larcher

Physiological Plant Ecology

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With 152 Figures

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Preface

Ecology is the science of the relationships between living organisms and their environment. It is concerned with the web of interactions involved in the circulation of matter and the flow of energy that makes possible life on earth, and with the adaptations of organisms to the conditions under which they survive. Given the multitude of diverse organisms, the plant ecologist focuses upon the plants, investigating the influence of environmental factors on the character of the vegetation and the behavior of the individual plant species.

Plant ecophysiology, a discipline within plant ecology, is concerned fundamentally with the physiology of plants as it is modified by fluctuating external influences. The aim of this book is to convey the conceptual framework upon which this discipline is based, to offer insights into the basic mechanisms and interactions within the system "plant and environment", and to present examples of current problems in this rapidly developing area. Among the topics discussed are the vital processes of plants, their metabolism and energy transformations as they are affected by environmental factors, and the ability of these organisms to adapt to such factors. It is assumed that the reader has a background in the fundamentals of plant physiology; the physiological bases of the phenomena of interest will be mentioned only to the extent necessary for an understanding of the ecological relationships. A real understanding of plant ecology requires familiarity with methodological problems and their solution; the texts by Šestak *et al.* (1971) on measurement of productivity parameters and Slavik (1974) on methods in the area of water relations are recommended.

Ecology is very much a modern field, but by no means a recent innovation. I have tried to portray this rich historical background in the choice of illustrations and tabular material; the results presented reflect the broadness of vision, the struggles and the successes of the pioneering experimental ecologists in the first half of this century, as well as the advances in knowledge made most recently.

For this English edition, the original German text has been revised, and in certain places expanded and corrected. Where possible, the German abbreviations have been replaced by those predominant in the English literature. Figures 3, 8 and 89 (formerly Fig. 90) have been extended, and three new figures have been added (Figs. 86, 145 and 152).

My first thanks are due to Dr. K. F. Springer; his publication of this English edition has made the textbook accessible to a wider circle of readers. I am grateful to the publisher of the original German edition, Roland Ulmer, for his cooperation. In particular, I thank Dr. Marguerite Biederman-Thorson for her thoughtful and sympathetic translation into English of the German text.

Above all, however, I should like to express my thanks to the pioneers of experimental ecology—Arthur Pisek, Otto Stocker, Heinrich Walter, and the late Bruno Huber. They inspired my enthusiasm for this difficult, but so attractive, field, and allowed me to benefit from their experience.

Innsbruck, September 1975 W. LARCHER

Abbreviations, Symbols and Conversion Factors

A	Area
Acc	Acceptor molecule
ADP	Adenosine diphosphate
ATP	Adenosine triphosphate
B	Plant biomass (also called phytomass, the mass of a stand of plants)
ΔB	Change in biomass (positive for a growing stand)
bar	Unit of pressure (1 bar = 1 megadyne per cm^2)
C	Concentration
C_a	Concentration of CO_2 and H_2O in the air outside a leaf
C_i	Concentration of CO_2 and H_2O in the intercellular system of a leaf
cal	Calorie, a unit of energy (1 cal = 4.1868 joule = $4.1868 \cdot 10^7$ erg)
D	Molecular diffusion coefficient
d	day as a unit of time
d	diameter
DL_{50}	Drought lethality (degree of dryness causing 50% injury)
DM	Dry matter
dm^2	Unit of area; for leaves, it refers to one (projected) surface
dm_2^2	Unit of leaf area referring to the entire surface (upper and lower)
E	Transpiration
E_c	Cuticular transpiration
E_s	Stomatal transpiration
ε_P	Efficiency of radiant energy conversion in terms of productivity of the vegetation
ε_F	Efficiency of radiant energy conversion in terms of photosynthesis
E_p	Evaporative power of the air; potential evaporation
erg	Unit of energy or work (1 erg = 1 dyn · cm)
Φ	Flux, mass flow
F	Photosynthesis
F_g	Rate of gross photosynthesis
F_n	Rate of net photosynthesis
g	Gram; unit of mass
G	Grazing (loss of dry matter to consumers)
GAP	Glyceraldehyde-3-phosphate
h	Hour; unit of time
ha	Hectare; unit of area (1 ha = 10^4 m^2)
$h\nu$	The energy of a light quantum
I	Irradiance; the radiation flux at a given level within a stand of plants or body of water
I_0	Maximum radiation flux; that incident upon a stand of plants or body of water
I_a	Long-wavelength radiation from the atmosphere
I_{abs}	Absorbed radiation
I_d	Direct solar radiation
I_g	Long-wavelength thermal radiation from ground and plants

I_t	Diffuse skylight and cloud-light
I_K	Compensation light intensity (at which $F = R$)
$\bar{I}_l$	Long-wavelength radiation balance
I_r	Reflected short-wavelength radiation
$\bar{I}_s$	Short-wavelength radiation balance
I_S	Light intensity at which photosynthesis is saturated
IR	Infrared radiation (> 750 nm)
J	Joule; unit of energy ($1\ J = 10^7$ erg)
k	Coefficient, conversion factor
k_F	Photosynthetic coefficient
k_M	Turnover factor for mineral nutrients in a stand of plants
k_P	Productivity coefficient
k_T	Reaction rate of biochemical processes at a given temperature
kcal	Kilocalorie ($1\ kcal = 10^3$ cal)
kg	Kilogram; unit of mass
kJ	Kilojoule ($1\ kJ = 10^3$ joule)
kLx	Kilolux ($1\ kLx = 10^3$ lux)
kW	Kilowatt ($1\ kW = 10^3$ watt)
l	Liter; unit of volume
L	Loss of organic dry matter as detritus
L_E	Water loss *via* evapotranspiration
L_I	Water loss *via* interception
L_O	Water loss *via* runoff and percolation
λ	Latent heat of vaporization of water
LAI	Leaf-area index
Lx	Lux; photometric unit of light intensity
m	Meter; unit of length
M_{abs}	Quantity of minerals absorbed
M_B	Mineral content of a stand of plants
M_G	Loss of minerals *via* grazing
M_i	Quantity of minerals incorporated
M_L	Loss of minerals as detritus
M_r	Minerals lost in inorganic form ("recretion")
mg	Milligram ($1\ mg = 10^{-3}\ g$)
min	Minute; unit of time
ml	Milliliter ($1\ ml = 10^{-3}\ l = 1\ cm^3$)
mm	Millimeter; unit of length ($1\ mm = 10^{-3}\ m$) and measure of precipitation (1 mm precipitation = 1 liter water $\cdot\ m^{-2}$ of ground)
µm	Micrometer ($1\ \mu m = 10^{-6}\ m$)
n	Number of particles
NAD^+	Nicotinamide-adenine-dinucleotide, reduced form: $NADH + H^+$ (simplified notation $NADH_2$); reduction system
$NADP^+$	Nicotinamide-adenine-dinucleotide-phosphate, reduced form: $NADPH + H^+$ ($NADPH_2$); reduction system
NAR	Net assimilation rate
nm	Nanometer ($1\ nm = 10^{-9}\ m$)
OxAc	Oxalacetate
P	Turgor pressure
P	Production (or productivity) of vegetation

P_g	Gross productivity
P_i	Inorganic phosphate
P_n	Net productivity
π	Osmotic pressure
PEP	Phosphoenol pyruvate
%	Percent (parts per hundred)
PGA	3-phosphoglyceric acid
pH	Negative logarithm of the hydrogen ion concentration
PhAR	Photosynthetically active radiation (400–700 nm)
ppm	Parts per million
Pr	Precipitation (total falling on a stand of plants)
Pr_n	Precipitation reaching the ground beneath a plant canopy
Ψ	Water potential
PWP	Permanent wilting percentage
Py	Pyruvate
Q	Energy flow
Q_E	Energy conversion associated with evaporation and condensation
Q_H	Energy conversion associated with convection
Q_I	Energy conversion associated with radiation from the sun and reradiation
Q_M	Energy conversion associated with metabolism
Q_P	Energy conversion in plant communities
Q_{Soil}	Energy conversion in the soil
Q_{10}	Temperature coefficient of biochemical and physiological process
r	Transport or diffusion resistance
r_a	Boundary (air) layer resistance
r_i	Diffusion resistances in the intercellular system
r_p	Diffusion resistances in protoplasm
r_s	Stomatal diffusion resistance
r_w	Diffusion resistances in the cell wall
r_x	Carboxylation (excitation) resistance
R	Gas constant ($R = 8.3\ \mathrm{J \cdot deg^{-1} \cdot mol^{-1}}$)
R	Respiration
R_d	Dark respiration
R_l	Respiration in the light
RH	Relative humidity
RuDP	Ribulose-1,5-diphosphate
RuP	Ribulose-5-phosphate
s	Second; unit of time
t	Time (point in time or duration)
t	Ton (Metric; $1\ \mathrm{t} = 10^3\ \mathrm{kg}$)
T	Temperature (all temperature data in °C)
T_a	Air temperature
T_l	Leaf temperature
τ	Matric pressure or potential
TL_{50}	Temperature-stress lethality (the temperature at which 50% of plants are killed by heat or cold)
torr	Unit of pressure ($1\ \mathrm{torr} = 1.33 \cdot 10^{-3}\ \mathrm{bar} \doteq$ a 1-mm column of Hg)
UV	Ultraviolet radiation (< 400 nm)
W	Watt; unit of power ($1\ \mathrm{W} = 1\ \mathrm{J \cdot s^{-1}}$)
W	Weight
W_{abs}	Quantity of water absorbed
W_{act}	Actual water content (when sample is taken)
W_{av}	Available water

W_d	Dry weight	WSD	Water saturation deficit
W_{FC}	Water content of soil at field capacity	yr	Year
		z	Relative height or depth
W_{PWP}	Water content of soil at permanent wilting percentage	∅	Diameter
		≐	Approximately equal to
W_f	Fresh weight	>	Larger than
W_s	Water content in saturated state	<	Smaller than

Equivalents

Radiation

$1\ \text{cal} \cdot \text{cm}^{-2} \cdot \text{min}^{-1} = 6.98 \cdot 10^5\ \text{erg} \cdot \text{cm}^{-2} \cdot \text{s}^{-1} = 6.98 \cdot 10^{-2}\ \text{W} \cdot \text{cm}^{-2}$
$1\ \text{erg} \cdot \text{cm}^{-2} \cdot \text{s}^{-1} = 1.43 \cdot 10^{-6}\ \text{cal} \cdot \text{cm}^{-2} \cdot \text{min}^{-1} = 10^{-7}\ \text{W} \cdot \text{cm}^{-2}$
$1\ \text{W} \cdot \text{cm}^{-2} = 10^7\ \text{erg} \cdot \text{cm}^{-2} \cdot \text{s}^{-1} = 14.3\ \text{cal} \cdot \text{cm}^{-2} \cdot \text{min}^{-1}$

$1\ \text{cal} \cdot \text{cm}^{-2} \cdot \text{min}^{-1} \doteq 60\ \text{kLx}$
$100\ \text{kLx} \doteq 1.5\ \text{cal} \cdot \text{cm}^{-2} \cdot \text{min}^{-1}$

Pressure

$1\ \text{bar} = 10^6\ \text{dyne} \cdot \text{cm}^{-2} = 1.019\ \text{atm (technical)}$
$1\ \text{atm (technical)} = 1\ \text{kg-weight} \cdot \text{cm}^{-2} \doteq 0.981\ \text{bar}$

Energy Consumption in the Evaporation of Water

Heat of vaporization at $0°\ C = 597\ \text{cal} \cdot g^{-1}\ H_2O$
at $10°\ C = 592\ \text{cal} \cdot g^{-1}$
at $20°\ C = 586\ \text{cal} \cdot g^{-1}$
at $30°\ C = 580\ \text{cal} \cdot g^{-1}$

Phytomass

$1\ \text{g DM} \cdot \text{m}^{-2} = 10^{-2}\ \text{t} \cdot \text{ha}^{-1}$
$1\ \text{t} \cdot \text{ha}^{-1} = 100\ \text{g} \cdot \text{m}^{-2}$
$1\ \text{g org. DM} \doteq 0.45\ \text{g C} \doteq 1.5\ \text{g } CO_2$
$1\ \text{g C} \doteq 2.2\ \text{g org. DM} \doteq 2.7\ \text{g } CO_2$
$1\ \text{g } CO_2 \doteq 0.67\ \text{g org. DM} \doteq 0.37\ \text{g C}$

Further aids to conversion can be found in the *Manuals of Methods* by Šestak *et al.* (1971) and Slavik (1974).

Contents

The Environment of Plants

Plants have colonized nearly all regions of the earth, including the oceans and inland waters; on land they can be found even in such inhospitable places as deserts and fields of ice. Far back in geological time, when the first land plants were evolving, they encountered a world of water, air and stone. That is, their environment consisted of the hydrosphere, atmosphere and lithosphere. Later, as the cover of vegetation gradually closed, and with the assistance of microorganisms and animals, there developed the most important substrate of plants: the soil—the pedosphere.

The Hydrosphere

The hydrosphere comprises the oceans of the world, which cover an impressive 71% of the earth's surface, as well as the inland waters and the groundwater. Great differences exist in the chemical compositions of these bodies of water (Fig. 1). Sea water, rich in Na^+, Mg^{2+}, Cl^- and SO_4^{2} and with an average salt content of 35 g · l^{-1}, differs fundamentally from fresh water, which usually contains more Ca^{2+} and HCO_3^-; but there are local differences as well, depending on the nature of the inflowing waters and the degree of mixing. Moreover, currents have an effect upon temperature gradients. Where there are no currents, the strong absorption of radiation in the upper levels of the water leads to a characteristic layering with respect to temperature and density; this has a marked influence upon nutrition, productivity and distribution of aquatic organisms (see p. 19).

The Atmosphere

The air enveloping the earth provides plants with carbon dioxide and oxygen. It also mediates the balance of water through the processes of rain, condensation and "evapotranspiration". Continual movement of the air ensures that its composition remains fairly constant—79% nitrogen (by volume), 21% oxygen and 0.03% carbon dioxide, water vapor and noble gases (Fig. 1). In addition the air contains gaseous, liquid and solid impurities; these are primarily sulfur dioxide, unstable nitrogen compounds, halogen compounds, dust and soot.

The part of the atmosphere with which plants come into contact is the troposphere, the weather zone of the earth's envelope of air. The nature of this zone varies over short distances and is characterized in several ways: (1) by the *weather* (short-term events such as showers, thunderstorms and gusts of wind), (2) by meteorological events of intermediate duration such as periods of rain or frost and (3) by the *climate* (the average state and ordinary long-term fluctuations in meteorological factors at a given place). Depending on the terrain and on the density, height and type of vegeta-

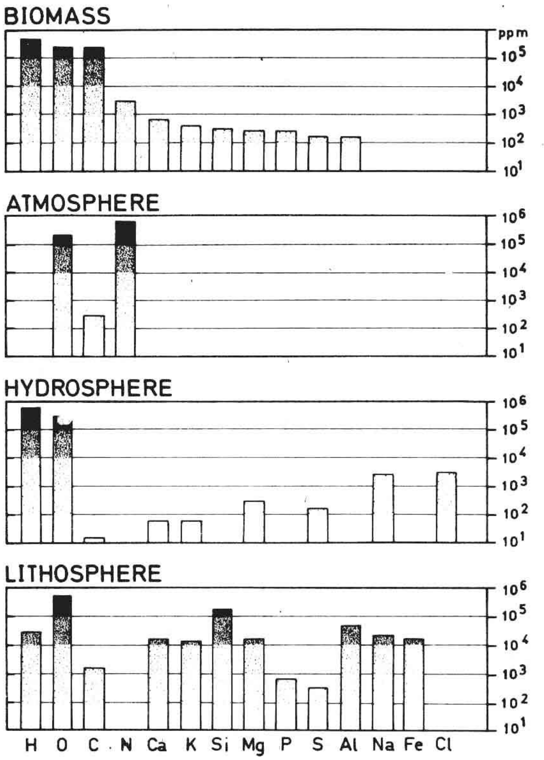

Fig. 1. Composition of the biomass, atmosphere, hydrosphere and lithosphere, in terms of the relative numbers of atoms (atoms per million atoms, not the proportion by weight) of the various chemical elements. The composition of living organisms is clearly distinct from that of the three components of their environment; they select from the available elements, according to their needs. The scale of the ordinate is logarithmic. For example, in the biomass H, O, C and N are present in the greatest proportions: $4.98 \cdot 10^5$ atoms per million (i. e., about 50% of all atoms) are hydrogen atoms; oxygen and carbon atoms each comprise $24.9 \cdot 10^5$ atoms per million (about 25%), and $2.7 \cdot 10^3$ (about 0.3%) are nitrogen atoms. (After Deevey, 1970)

tion, individual climatic regions of different sizes are formed. Within the large-scale "macroclimate" measured by the network of meteorological stations, one may distinguish "microclimates" that prevail in specific places such as certain slopes, narrow valleys and stands of vegetation; an "interface" climate–in the layer of air near the ground and the surface of leaves–may also be distinguished. Thus the parts of plants above ground are exposed to variability, in space and time, with respect to radiation, temperature, humidity, precipitation and air motion; any of these can from time to time represent a threat to the organism.

The Lithosphere and the Soil

The **earth's crust** is the inexhaustible storehouse for the variety of chemical elements of which organisms are composed (Fig. 1). The lithosphere exchanges matter with the hydrosphere, and also affects the composition of the atmosphere through volcanic action and the products of radioactive decay. Primarily, however, it is the basic material for the formation of the soil.

Soil is more than just superficially loosened lithosphere. It is the product of the transformation and mingling of mineral and organic substances. Soils are produced with the assistance of organisms and under the influence of environmental conditions. They are subject to continual change: soils grow, mature, and can age and perish. Physical and chemical weathering continuously frees mineral substances from the rocky substrate, and there is an unceasing decay of plant remains and dead organisms. These decay products, together with the excrement of soil animals, gradually turn into humus, which forms complexes with the mineral products of weathering. In natural soils a profile is established of more or less horizontal layers ("horizons"): between the strata of litter and humus, and the stratum where weathering of the parent rock occurs, there are transitional zones with varying proportions of humus. The types and thicknesses of the horizons in such a profile are characteristic of a given type of soil and reflect the influence of climate, plant cover, soil organisms, underlying rock and the activity of man. Pedology is the science of soil formation and composition, and of the classification of soil types. Knowledge of the fundamentals of this field is an absolute prerequisite to understanding plant ecology.

The solid particles in the ground stick together to form aggregates, leaving small open spaces. Together these form a system of pores penetrating the entire soil, filled partly with air and partly with water. Thus the soil is a three-phase system in which lithosphere (the solid phase), hydrosphere (fluids) and atmosphere (gases) are intermingled. It has an enormous capacity for uptake and storage, and is particularly suited for the buffering of physical and chemical influences. Below the top centimeters of soil the prevailing climate is more stable than that of the atmosphere; radiation is essentially unable to penetrate, there are no sharp gradients of temperature, and the processes of exchange are slow, occurring by diffusion. Therefore the soil is the most suitable habitat for many organisms. The roots—in many respects the most vulnerable organ system of the higher plants—are entirely adapted to life in the soil. A landscape without soil is a life-repelling "lunar" landscape. Only a few remarkable plants such as aerial algae, lichens and mosses can actually thrive on bare stone or sand.

The Biosphere

Atmosphere, hydrosphere and lithosphere existed before there was life on earth, but it is of course only through the appearance of living organisms that they became significant as an "environment". "Environment", as defined by A. F. Thienemann, is "the totality of external conditions affecting a living organism or a community (biocenosis) of organisms in its habitat (its biotope)". In this strict sense, only living beings have an environment. It comprises not only the influences exerted by the abiotic surroundings, but also those due to the other organisms present.

The part of the earth which supports life, called the biosphere, is the narrow band, about 100 m thick, above the earth and below the surface of the ocean, which is ordinarily inhabited by organisms. It is true that birds can fly as high as 2,000 m, and that there are bacteria on the floor of 10,000-m-deep marine trenches, but abundant life is limited to a much more restricted region near the surface of the earth. Trees stand no more than 70—100 m tall and sink their roots but a few tens of meters into the earth; in water the layer penetrated by light (and hence densely populated) ordinarily extends to a depth of 30 m, and at most to 100 m.

Among living organisms, the plants are of prime significance. They are capable of capturing and storing by photosynthesis the energy from outer space—that of sunlight—and in terms of mass they far exceed all other organisms; about 99% of the total mass of living beings (the biomass) on earth is accounted for by the plants (the phytomass). Because of this enormous mass, the plant cover is a stabilizing factor in the cycling of matter and has a crucial effect upon the climate.

The Ecosystem: Interplay of Biological and Environmental Factors

Communities of organisms and their abiotic surroundings interact in nature by many kinds of reciprocal relationships, both structural and functional. Circumscribed, more or less uniform sections of the biosphere delimit biogeocenoses, or ecosystems. The expression "biogeocenosis" was coined by V.N. Sukachev, and the term "ecosystem" is attributable to R. Woltereck and A.G. Tansley. H. Ellenberg defines the ecosystem as "a unitary system of interactions involving living organisms and their inorganic environment which is, to a certain degree, capable of self-regulation". In short,

$$\text{Ecosystem} = \text{community of organisms} + \text{environmental conditions}. \quad (1)$$

Each ecosystem has a certain spatial extent; together ecosystems form a diverse mosaic in the biosphere. A forest is an ecosystem, as is a meadow, a lake or an ocean. The principles by which all these ecosystems operate hold equally well for the biosphere as a whole, and as well for natural ecosystems as for artificial systems such as aquariums and self-contained manned spacecraft. Fig. 2 represents the typical structure of an ecosystem and the most important interactions both within it and between it and the external world.

The Components of an Ecosystem

Every independently functional ecosystem is composed of at least two biological components: the producers and the decomposers. Between these there may exist a whole chain of consumers.

Primary Producers are the autotrophic organisms, which effect the incorporation of inorganic elements in organic compounds and thus raise them to a higher energy level. The green plants and some bacteria utilize sunlight to form carbohydrates from carbon dioxide and water (photosynthesis), and these become the basis for further syntheses. Various microorganisms accomplish the same thing by using the energy freed by exergonic inorganic reactions (chemosynthesis).

Consumers (or phagotrophs) are the heterotrophic organisms that feed directly or indirectly upon the organic substances synthesized by the primary producers. The principal consumers are the herbivores and the plant parasites. The herbivores serve in turn as food for the carnivores, and both are attacked by animal parasites.

Decomposers (or saprotrophs) are those organisms that finally reduce plant and animal refuse to the level of its basic inorganic components. This group includes

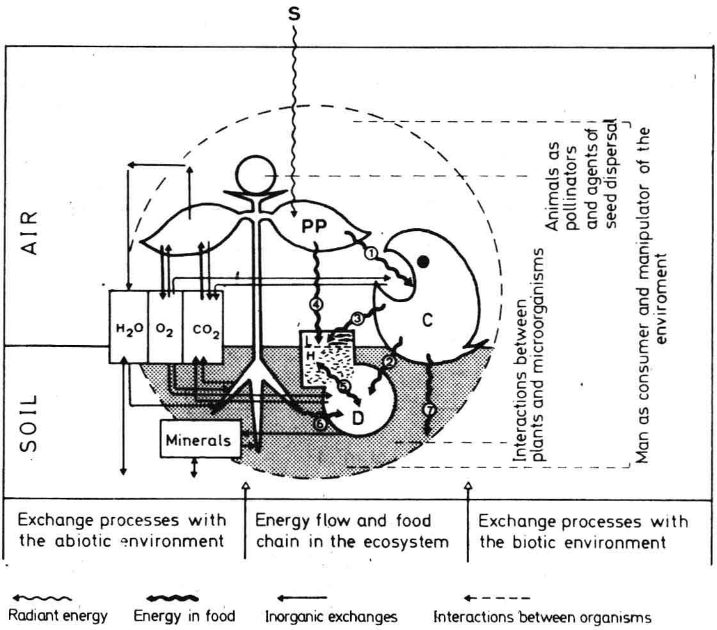

Fig. 2. The flow of energy and matter, and the cycling and exchange of substances, in a terrestrial ecosystem. *Components of the ecosystem: PP* primary producers; *C* consumers; *D* decomposers; *L* deposits of detritus (plant litter, bodies of animals); *H* humus. *Energy flow and the food chain; S* radiation from the sun; *1* consumption of plants as fodder and by parasites; *2* organic excretions from animals and microorganisms; *3* detritus consisting of animal cadavers and dead microorganisms; *4* detritus derived from the primary producers; *5* decomposition (humification and mineralization) of detritus; *6* organic excretions from the plants; *7* loss of organic waste from the ecosystem. *Inorganic transport of substances:* CO_2 to primary producers (photosynthesis) and from processes of breakdown in primary producers, consumers and decomposers (soil respiration), O_2 from primary producers (photosynthesis) to oxygen-consuming catabolic processes; H_2O from evaporative surfaces (from the ground and through organisms) into the atmosphere, as precipitation from the atmosphere into the soil, from the soil through consumption by organisms and loss by drainage; mineral substances from the soil into primary producers and back again *via* the food chain and the activity of decomposers (mineralization)

bacteria and some soil animals. The decomposers, like the herbivores and other consumers, can serve as food for other organisms. In such cases, they take on the role of *secondary producers*. Thus a single individual, depending on its position in the food chain, can play the role of secondary producer, consumer or decomposer.

Food Chains and Energy Flow in an Ecosystem

A "food chain" is defined as the sequence of stages through which stored energy in the form of food is passed from the primary producers to a number of organisms. As