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Chapter 55

Ecosystems and Restoration Ecology

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What are the dynamics of energy and chemical nutrients in an ecosystem?

There is a one-way flow of energy through an ecosystem, whereas chemicals cycle within the ecosystem.



CONCEPT 55.1: Physical laws govern energy flow and chemical cycling in ecosystems

 Ecologists study the transformations of energy and matter in an ecosystem and map the movements of chemical elements

- An ecosystem includes all the living organisms in an area and the abiotic factors with which they interact
- An ecosystem can encompass a large area, such as a forest, lake, or island, or a microcosm, such as the space under a fallen log or a small desert spring



Energy Flow and Chemical Cycling

- Ecosystem dynamics involve two main processes: energy flow and chemical cycling
- Energy enters most ecosystems as sunlight, is converted to chemical energy by autotrophs, passed to heterotrophs as food, and dissipated as heat
- Energy cannot be recycled in ecosystems; a continuous influx of energy from an external source (the sun) is required

- Elements such as carbon and nitrogen are passed between biotic and abiotic components of an ecosystem
- Photosynthetic and chemosynthetic organisms take up inorganic chemicals and incorporate them into organic compounds
- The metabolism of organisms and breakdown by decomposers returns elements to inorganic form

Conservation of Energy

- Laws of physics and chemistry apply to ecosystems
- The first law of thermodynamics states that energy cannot be created or destroyed, only transferred or transformed
- Energy enters an ecosystem as solar radiation, is conserved, and is lost from organisms as heat

- The second law of thermodynamics states that every exchange of energy increases the entropy of the universe
- In an ecosystem, energy conversions are not completely efficient; some energy is always lost as heat

Conservation of Mass

- The law of conservation of mass states that matter cannot be created or destroyed
- Chemical elements are continually recycled within ecosystems
- Ecosystems are open systems, absorbing energy and mass and releasing heat and waste products
- If a nutrient's outputs from an ecosystem exceed its inputs, that nutrient will limit production

Energy, Mass, and Trophic Levels

- Primary producers are autotrophs that build organic molecules using either sunlight or inorganic compounds as energy sources
- Most are photosynthetic plants, algae, and prokaryotes, but some are chemosynthetic prokaryotes

- Heterotrophs are consumers that depend directly or indirectly on production by primary producers
- Herbivores are primary consumers; they eat primary producers
- Carnivores that eat herbivores are secondary consumers
- Carnivores that eat other carnivores are tertiary consumers

- Decomposers are heterotrophs that get their energy from detritus, nonliving organic matter
- Prokaryotes and fungi are the main decomposers
- Some secondary and tertiary consumers feed on decomposers

Figure 55.3



- Rod-shaped and spherical bacteria in compost (colorized SEM)
- Fungi decomposing a dead tree

- Decomposers convert organic matter from all trophic levels to inorganic compounds
- Excretion or death of decomposers returns inorganic molecules to the soil for absorption by producers



Animation: Energy Flow and Chemical Cycling

CONCEPT 55.2: Energy and other limiting factors control primary production in ecosystems

- In most ecosystems, primary production is the amount of light energy converted to chemical energy by autotrophs during a given time period
- In some ecosystems, chemoautotrophs are the primary producers

Ecosystem Energy Budgets

• The extent of photosynthetic production sets the "spending limit" for an ecosystem's energy budget

The Global Energy Budget

- The amount of solar radiation reaching Earth's surface limits production in most ecosystems
- About 50% of the incoming solar radiation is absorbed, scattered, or reflected by clouds and dust
- Of the fraction that hits photosynthetic surfaces, most is transmitted, reflected, or lost as heat
- About 1% of visible light striking photosynthetic organisms is converted to chemical energy

Gross and Net Production

- Total primary production is known as the ecosystem's gross primary production (GPP)
- GPP is measured as the conversion of energy from light (or chemicals) to the chemical energy of organic molecules per unit time

- Net primary production (NPP) is GPP minus energy used by autotrophs for respiration (R_a) NPP = GPP - R_a
- NPP averages about one-half GPP, and is expressed as
 - Energy per unit area per unit time $[J/(m^2 \cdot yr)]$, or
 - Biomass added per unit area per unit time [g/(m² · yr)]

- NPP is the amount of new biomass added in a given time period, not the total biomass of autotrophs
- Satellite data indicate that ecosystems vary greatly in NPP and contribution to the total NPP on Earth

- Tropical rain forests, estuaries, and coral reefs are among the most productive ecosystems per unit area
- Marine ecosystems are relatively unproductive per unit area but contribute much to global net primary production because of their size



- Net ecosystem production (NEP) is a measure of the total biomass accumulation of producers and consumers during a given period
- NEP is gross primary production minus the total respiration of all organisms (R_T) in an ecosystem

 $NEP = GPP - R_T$

- NEP is estimated by comparing the net flux of CO₂ and O₂ entering or leaving an ecosystem
- If more CO₂ enters than leaves, the system is storing carbon
- The release of O₂—a byproduct of photosynthesis—by a system is also an indication that it is storing CO₂

Primary Production in Aquatic Ecosystems

 In marine and freshwater ecosystems, both light and nutrients control primary production

Light Limitation

- Depth of light penetration affects primary production in the photic zone of an ocean or lake
- Light cannot be the main variable limiting primary production in the ocean, otherwise a latitudinal gradient of productivity would be expected

Nutrient Limitation

- Nutrients limit primary production in most oceans and lakes
- A limiting nutrient is the element that must be added for production to increase
- Nitrogen and phosphorous are the nutrients that most often limit marine production



Data from J. H. Ryther and W. M. Dunstan, Nitrogen, phosphorus, and eutrophication in the coastal marine environment, *Science* 171:1008–1013 (1971).

- Eutrophication is the process where primary production increases as an ecosystem changes from nutrient-poor to nutrient-rich
- Excess nitrogen runoff fertilizes phytoplankton, causing algal blooms and the occurrence of fatally low oxygen concentrations in marine "dead zones"

- Nitrogen and phosphorus are not the only nutrients that limit aquatic production
- Several areas in the ocean have low phytoplankton densities despite high nitrogen concentrations
 - For example, the micronutrient iron limits primary production in the Sargasso Sea

Table 55.1 Nutrient Enrichment Experiment for Sargasso Sea

Nutrients Added to Experimental Culture	Relative Uptake of ¹⁴ C by Cultures*
None (controls)	1.00
Nitrogen (N) + phosphorus (P) only	1.10
N + P + metals, excluding iron (Fe)	1.08
N + P + metals, including Fe	12.90
N + P + Fe	12.00

*14C uptake by cultures measures primary production.

Data from D. W. Menzel and J. H. Ryther, Nutrients limiting the production of phytoplankton in the Sargasso Sea, with special reference to iron, *Deep Sea Research* 7:276–281 (1961).

- In areas of upwelling, deep, nutrient-rich waters circulate to the ocean surface stimulating the growth of phytoplankton, the base of the marine food web
- Areas of upwelling host highly productive, diverse ecosystems and are prime fishing locations
- Nutrient inputs to lakes from sewage and fertilizer runoff promote the growth of primary producers
- When producers die, aerobic decomposers break them down and deplete the water of oxygen
- Large number of fish die due to insufficient oxygen

- In lakes, phosphorus limits cyanobacterial growth more often than nitrogen
- This has led to the use of phosphate-free detergents

Primary Production in Terrestrial Ecosystems

- In terrestrial ecosystems, temperature and moisture affect primary production on a large scale
- NPP increases with precipitation, temperature, and the amount of solar energy available



- Tropical rain forests, with warm, wet conditions are the most productive terrestrial ecosystems
- Low-productivity systems are generally hot and dry, like many deserts, or cold and dry, like arctic tundra
- Temperate forest and grassland ecosystems have moderate climates and intermediate productivity

- Nutrients also affect NPP in terrestrial ecosystems
 - For example, the introduction of foxes to islands near Alaska led to the conversion of grassland to less productive tundra
 - Foxes preyed upon and reduced populations of seabirds; this reduced the production of nutrient rich guano (bird waste)
 - Nutrient scarcity reduced growth of grasses and favored growth of tundra plants

Nutrient Limitations and Adaptations That Reduce Them

- Nitrogen is the most common limiting nutrient in terrestrial ecosystems
- Phosphorus can also be a limiting nutrient, especially in older soils
- Addition of nonlimiting nutrients will not stimulate production
- Adding a limiting nutrient will increase production, but only until some other nutrient becomes limiting

- Various adaptations have evolved in plants to increase uptake of limiting nutrients
 - Mutualisms between plants and nitrogen-fixing bacteria
 - Mycorrhizal associations between plants and fungi that supply limiting elements, such as phosphorus
 - Root hairs that increase surface area for absorption
 - Enzymes and other substances that increase nutrient availability when released into the soil

Effects of Climate Change on Production

- NPP increased in terrestrial ecosystems from 1982 to 1999, primarily due to decreased cloud cover over tropical forests
- Since 2000, gains in NPP have been erased due to major droughts in the southern hemisphere
- "Hotter droughts" have led to increased forest fires and bark beetle outbreaks



- Climate change can also affect whether an ecosystem stores or loses carbon over time
 - If NEP > 0, then an ecosystem stores carbon and acts as a carbon sink
 - If NEP < 0, then the ecosystem releases CO₂ and becomes a carbon source

- Climate change can cause an ecosystem to switch from a carbon sink to a carbon source
 - For example, in some arctic ecosystems, climate warming has increased the metabolic activities of soil microorganisms
 - The resulting uptick in CO₂ produced by cellular respiration now exceeds what is absorbed in photosynthesis

- A 2017 study found that with climate warming, large regions of tundra in Alaska now release more CO₂ than they absorb
- In 2013 and 2014, the entire state of Alaska released more CO₂ than it absorbed

CONCEPT 55.3: Energy transfer between trophic levels is typically only 10% efficient

 Secondary production of an ecosystem is the amount of chemical energy in food converted to new biomass during a given period of time

Production Efficiency

- About one-sixth of the energy in a leaf is used for secondary production in a feeding caterpillar
- The remaining energy is lost as heat during cellular respiration or passed in its feces
- Only energy stored as biomass in herbivores is available to secondary consumers



 An organism's production efficiency is the fraction of energy stored in assimilated food that is not used for respiration

Production = Net secondary production × 100% Assimilation of primary production

- Net secondary production is the amount of energy consumed and used for growth and reproduction
- Assimilation is the total energy consumed and used for growth, reproduction, and respiration

- Birds and mammals have low production efficiencies, about 1–3%, because they use a lot of energy maintaining a constant body temperature
- Ectothermic animals have higher production efficiencies
 - For example, fishes have efficiencies of about 10%
 - Insects and microorganisms have efficiencies averaging 40% or more

Trophic Efficiency and Ecological Pyramids

- Trophic efficiency is the percentage of production transferred from one trophic level to the next
- Energy locked in biomass that is not consumed by the next trophic level is not taken into account
- Trophic efficiency is, on average about 10%, with a range of 5% to 20%

- If multiplied through the food chain, approximately 0.1% of chemical energy fixed by photosynthesis reaches a tertiary consumer
- This is why most food chains are limited in length
- An energy pyramid represents the loss of energy with each transfer in a food chain



1,000,000 J of sunlight

- In a biomass pyramid, each tier represents the dry mass of all organisms in one trophic level
- Most biomass pyramids show a sharp decrease at successively higher trophic levels
- Some aquatic ecosystems have inverted biomass pyramids: Producers are consumed so quickly that they are outweighed by primary consumers



- Eating meat is an inefficient means of tapping photosynthetic production
- Agriculture could feed many more people using less land if we all fed as primary consumers

CONCEPT 55.4: Biological and geochemical processes cycle nutrients and water in ecosystems

- Although most ecosystems receive abundant solar energy, chemical elements are limited
- Life depends on recycling of essential chemical elements

Decomposition and Nutrient Cycling Rates

- Decomposers play a key role in the general pattern of chemical cycling
- Variation in decomposition rate causes the rate of nutrient cycling to vary greatly among ecosystems
- The rate of decomposition is controlled primarily by temperature and precipitation

Results



Data from J. A. Trofymow and the CIDET Working Group, *The Canadian Intersite Decomposition Experiment: Project and Site Establishment Report* (Information Report BC-X-378), Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre (1998) and T. R. Moore et al., Litter decomposition rates in Canadian forests, *Global Change Biology* 5:75–82 (1999).

- Areas with rapid decomposition can have relatively low levels of nutrients in the soil if they cycle rapidly
- In cold, wet ecosystems, such as peatlands, where decomposition is slow, large amounts of undecomposed organic matter are stored in the soil

- Decomposition is also slow in the anaerobic bottom sediments of aquatic ecosystems
- Because algae only take up nutrients from water, sediments can form a nutrient sink
- Productivity increases only when there is exchange between sediments and the surface, as occurs in upwelling

Biogeochemical Cycles

- Nutrient cycles are called biogeochemical cycles because they involve both biotic and abiotic components
- Gaseous carbon, oxygen, sulfur, and nitrogen occur in the atmosphere and cycle globally
- Heavier, less mobile elements include phosphorus, potassium, and calcium
- These elements cycle locally in terrestrial systems but more broadly when dissolved in aquatic systems

- The main reservoirs of elements are defined by two characteristics
 - Whether they consist of organic or inorganic materials
 - Whether these materials are available for direct use by organisms or unavailable



- There are four major factors to consider in the cycling of water, carbon, nitrogen, and phosphorus
 - Each chemical's biological importance
 - Forms available to life
 - Reservoirs
 - Key processes driving movement of each chemical through its cycle

Figure 55.14 Exploring water and nutrient cycling

The Water Cycle

- Water is essential to all organisms
- Liquid water is the primary physical phase in which water is used
- The oceans contain 97% of the biosphere's water;
 2% is in glaciers and polar ice caps, and 1% is in lakes, rivers, and groundwater
- Water moves by the processes of evaporation, transpiration, condensation, precipitation, and movement through surface and groundwater



The water cycle

The Carbon Cycle

- Carbon-based organic molecules are essential to all organisms
- Photosynthetic organisms convert CO₂ to organic molecules that are consumed by heterotrophs
- Carbon reservoirs include fossil fuels, soils and sediments, dissolved compounds in oceans, living biomass, the atmosphere, and sedimentary rocks
- CO₂ is taken up through photosynthesis and released through cellular respiration
- Volcanoes and the burning of fossil fuels and wood contribute significant amounts of CO₂ to the atmosphere



Animation: The Carbon Cycle



The Nitrogen Cycle

- Nitrogen, a component of amino acids, proteins, and nucleic acids, is often a limiting plant nutrient
- The atmosphere is the main nitrogen (N₂) reservoir
- N₂ must be converted to NH₄⁺ or NO₃⁻ for uptake by plants, via nitrogen fixation by bacteria
- Some bacteria can also use NO₂⁻
- Animals can only use organic nitrogen compounds

- Organic nitrogen is decomposed to NH₄⁺ by ammonification, and NH₄⁺ is decomposed to NO₃⁻ by nitrification
- Denitrification converts NO₃⁻ back to N₂





The nitrogen cycle



The nitrogen cycle

Animation: The Nitrogen Cycle

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The Phosphorus Cycle

- Phosphorus is a major constituent of nucleic acids, phospholipids, and ATP
- Phosphate (PO₄^{3–}) is the inorganic form of phosphorus used by plants
- Reservoirs include marine sedimentary rocks, soil, the oceans (dissolved compounds), and organisms
- Weathering of rocks releases phosphate into the soil, and it reaches aquatic systems through leaching



The phosphorus cycle

Case Study: Nutrient Cycling in the Hubbard Brook Experimental Forest

- The Hubbard Brook Experimental Forest has been used to study nutrient cycling in forest ecosystems since 1963
- The research team constructed a dam on the site to monitor loss of water and minerals
- They found that 60% of the precipitation exits through streams and 40% is lost by evapotranspiration



(a) Concrete dams and weirs enable monitoring of outflow

 In one experiment, a watershed was clear-cut to determine the effects of the loss of vegetation on drainage and nutrient cycling



(b) Clear-cut watershed

- Water and nutrient losses were significantly higher in the deforested site compared to the undisturbed (control) site
- These results showed that nutrient loss in a forest ecosystem is controlled mainly by plants



(c) Nitrate in runoff from watersheds

CONCEPT 55.5: Restoration ecologists return degraded ecosystems to a more natural state

- Given enough time, biological communities can recover from many types of disturbances
- Restoration ecology seeks to initiate or speed up the recovery of degraded ecosystems
- In some cases, the physical structure of the ecosystem must be restored before biological restoration can occur



(a) In 1991, before restoration



(b) In 2010, several years after restoration

- The long-term objective of restoration is to return an ecosystem as much as possible to its predisturbance state
- Two key strategies are employed in restoration: bioremediation and biological augmentation

Figure 55.17 Exploring restoration ecology worldwide

Kissimmee River, Florida

- Conversion of the Kissimmee River to a 90-km canal caused the surrounding wetlands to dry up, threatening fish and bird populations
- Filling part of the canal and reestablishing part of the river has helped restore the wetland ecosystem



Kissimmee River, Florida

Succulent Karoo, South Africa

- Overgrazing by livestock has damaged vast areas of land in this region
- Restoration efforts have included revegetating the land and employing sustainable resource management



Succulent Karoo, South Africa

Maungatautari, New Zealand

- Introduction of exotic mammals, including weasels, rats, and pigs, has threatened many native plant and animal species
- Restoration efforts include building fences around reserves to exclude introduced species

Figure 55.17_3



Maungatautari, New Zealand

Coastal Indonesia

- Destruction of coastal seaweed and seagrass beds has threatened a variety of fishes and shellfish
- Restoration efforts include constructing suitable seafloor habitat, transplanting and hand seeding seaweeds and seagrass

Figure 55.17_4



Coastal Indonesia

Bioremediation

- Bioremediation is the use of organisms—mainly prokaryotes, fungi, or plants—to detoxify polluted ecosystems
- The organisms can take up, and may metabolize, toxic molecules
 - For example, the bacterium Shewanella oneidensis metabolizes uranium to an insoluble form, less likely to leach into streams and groundwater



uranium-containing wastes

(b) Decrease of soluble uranium in groundwater due to microbial activity

Biological Augmentation

- Biological augmentation uses organisms to add essential materials to a degraded ecosystem
- For example,
 - nitrogen-fixing plants can increase the available nitrogen in soil
 - adding mycorrhizal fungi can help plants to access nutrients from soil

- Restoration of the physical structure and the plant community may not ensure recolonization by animals
- Ecologists may release animals at the site, establish wildlife corridors, or add features such as perches to encourage colonization

Ecosystems: A Review

- Populations are dynamic; they change in size through births, deaths, immigration, and emigration
- Individuals of different species interact in diverse ways, such as predation, herbivory, mutualism, and competition
- Organisms transfer energy and matter in ecosystems through trophic interactions that are impacted by abiotic factors such as temperature and light

MAKE CONNECTIONS: The Working Ecosystem



	NPP [g/(m² · yr)]	R _h [g/(m² ⋅ yr)]	NEP [g/(m² ⋅ yr)]
Before outbreak	440	408	
After outbreak	400	424	



A tree with dozens of "pitch tubes," indications of a damaging outbreak of mountain pine beetles (inset).
Data from the Study

Form of Energy	Amount [kcal/(m ² • yr)]
Solar radiation	600,000
Gross grass production	34,580
Net grass production	6,585
Gross insect production	305
Net insect production	81
Detritus leaving marsh	3,671

Data from J. M. Teal, Energy flow in the salt marsh ecosystem of Georgia, *Ecology* 43:614–624 (1962).

Figure 55.UN02_2







1,000,000 J of sunlight

