21

Nutrient Supply and Cycling

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Case Study: A Fragile Crust

Soils in the Colorado Plateau in western North America are covered by a **biological crust** (or *cryptobiotic* crust)—a mixture of hundreds of species of cyanobacteria, lichens, and mosses.

Similar crusts are found in other arid and semi-arid regions.

Figure 21.1 Biological Crust on the Colorado Plateau

ECOLOGY, Figure 21.1

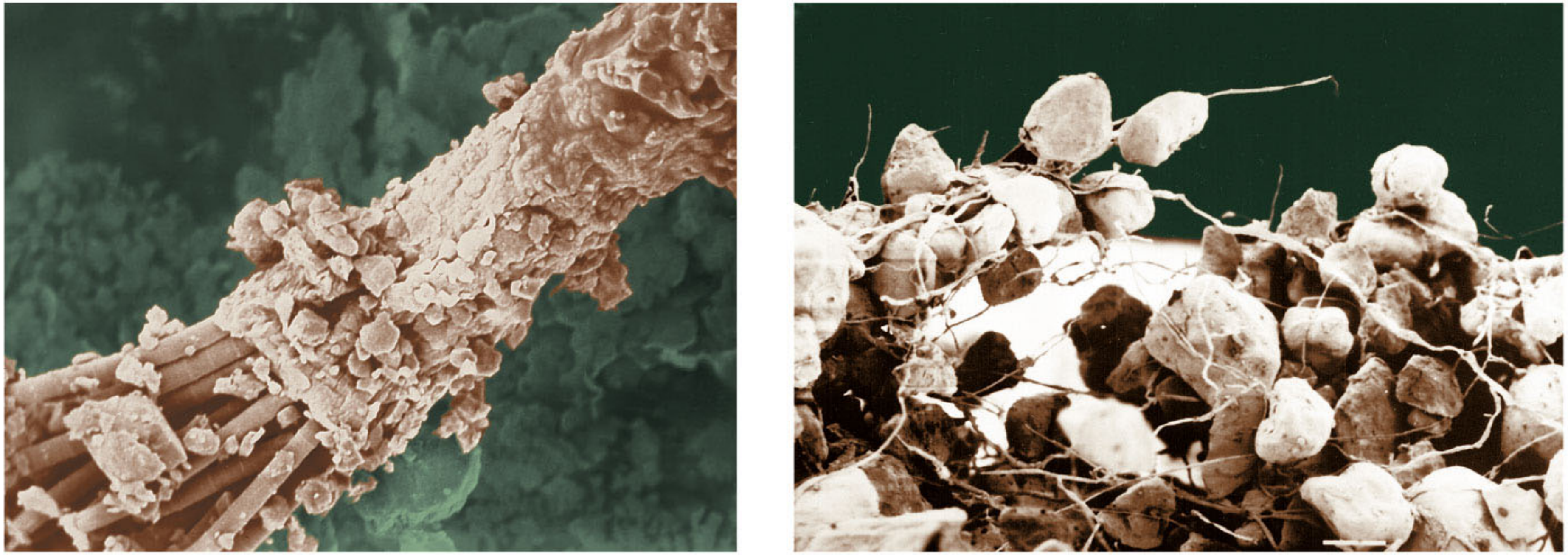
Case Study: A Fragile Crust

The crusty nature is due to filamentous cyanobacteria, which create a sheath of mucilaginous material as they move through the soil after a rain.

When the soil dries, the cyanobacteria move to deeper layers, and the sheath material binds the soil particles together.

Figure 21.2 Cyanobacterial Sheaths Bind Soil into Crusts

(A) (B)



Case Study: A Fragile Crust

Colorado Plateau soils are exposed to harsh conditions.

Temperatures range from –20°C in winter to 70°C in summer.

Evapotranspiration is high; drying and sparse vegetation allow winds to carry away fine particles.

Precipitation often comes as brief, intense thunderstorms.

Case Study: A Fragile Crust

Biological crusts anchor the soil in place in the face of high winds and torrential rains.

Livestock grazing on the Colorado Plateau has resulted in trampling of the biological crust, and overgrazing.

Recently, off-road and all-terrain vehicles use has increased, along with motorcycles, mountain bikes, and hikers.

Case Study: A Fragile Crust

A minority of users drive vehicles off designated roads and across soils covered with biological crusts.

A large part of the landscape has been disturbed to some degree during the past 150 years, and the rate of disturbance is increasing.

Case Study: A Fragile Crust

Recovery of biological crusts following disturbance is slow.

Decades are required for reestablishment of cyanobacteria and up to centuries for recolonization by lichens and mosses.

What are the implications for loss of biological crusts in arid ecosystems?

Introduction

All organisms require specific chemical elements for metabolism and growth.

Organisms absorb these elements from the environment or get them in their food.

The ultimate source of mineral nutrients is the Earth’s crust.

Biogeochemistry is the study of the physical, chemical, and biological factors that influence the movements and transformations of elements.

Understanding biogeochemistry is important in determining the availability of **nutrients**—chemical elements required for metabolism and growth.

Introduction

Nutrients must be present in certain forms to be available for uptake.

The rate at which physical and chemical transformations occur determines the supply of nutrients.

Biogeochemistry is an integrative discipline with contributions from soil science, hydrology, atmospheric science, and ecology.

Nutrient Requirements and Sources

Concept 21.1: Nutrients enter ecosystems through the chemical breakdown of minerals in rocks or through fixation of gases in the atmosphere.

All organisms share similarities in their nutrient requirements.

Amounts and specific nutrients needed vary according to the organism’s mode of energy acquisition, mobility, and thermal physiology.

Nutrient Requirements and Sources

Example: Mobile animals have higher metabolic rates than plants, and higher requirements for nutrients such as nitrogen (N) and phosphorus (P).

TABLE 21.1

Elemental Composition (as Percentage of Dry Mass) of a Plant and an Animal

Element (symbol)	Plant (corn, *Zea mays*)	Animal (human, *Homo sapiens*)
Oxygen (O)	44.43	14.62
Carbon (C)	43.57	55.99
Hydrogen (H)	6.24	7.46
Nitrogen (N)	1.46	9.33
Silicon (Si)	1.17	0.005
Potassium (K)	0.92	1.09
Calcium (Ca)	0.23	4.67
Phosphorus (P)	0.20	3.11
Magnesium (Mg)	0.18	0.16
Sulfur (S)	0.17	0.78
Chlorine (Cl)	0.14	0.47
Iron (Fe)	0.08	0.012
Manganese (Mn)	0.04	—
Sodium (Na)	—	0.47
Zinc (Zn)	—	0.01
Rubidium (Rb)	—	0.005

Source: Epstein and Bloom 2005.

Note: Dashes indicate a neglible amount of an element.

Carbon is a component of structural compounds in plant cells and tissues; nitrogen is largely tied up in enzymes.

C:N ratios reflect biochemistry: Animals have lower C:N ratios (e.g., 6 for humans); plants have C:N ratios of 10–40.

Herbivores must consume more food than carnivores to get enough nutrients such as N.

Nutrient Requirements and Sources

All plants require a core set of nutrients.

Some species have specific requirements. Some C_4 and CAM plants require sodium. (All animals require it.)

Some plants that host N-fixing bacteria require cobalt.

Some plants growing in selenium-rich soil require it as a nutrient, but it is toxic to most plants.

TABLE 21.2

Plant Nutrients and Their Principal Functions

Nutrients	Principal functions
Carbon, hydrogen, oxygen	Components of organic molecules
Nitrogen	Component of amino acids, proteins, chlorophyll, nucleic acids
Phosphorus	Component of ATP, NADP, nucleic acids, phospholipids
Potassium	Ionic/osmotic balance, pH regulation, regulation of guard cell turgor
Calcium	Cell wall strengthening and functioning, ionic balance, membrane permeability
Magnesium	Component of chlorophyll, enzyme activation
Sulfur	Component of amino acids, proteins
Iron	Component of proteins (e.g., heme groups), oxidation–reduction reactions
Copper	Component of enzymes
Manganese	Component of enzymes, activation of enzymes
Zinc	Component of enzymes, activation of enzymes, component of ribosomes, maintenance of membrane integrity
Nickel	Component of enzymes
Molybdenum	Component of enzymes
Boron	Cell wall synthesis, membrane function
Chlorine	Photosynthesis (water splitting), ionic and electrochemical balance

Sources: Salisbury and Ross 1992; Marschner 1995.

Nutrient Requirements and Sources

Plants and microorganisms take up nutrients in simple, soluble forms from the environment.

Animals mostly get nutrients in food in the form of complex molecules. Some of these are broken down and new molecules are synthesized. Other molecules are absorbed intact, such as some amino acids.

Nutrient Requirements and Sources

All nutrients are ultimately derived from abiotic sources: Minerals in rocks and gases in the atmosphere.

Nutrients may be cycled within an ecosystem, repeatedly passing through organisms and the soil or water.

Nutrient Requirements and Sources

Minerals—solid substances with characteristic chemical properties.

Rocks are collections of different minerals.

Elements are released from rock minerals by **weathering**.

Mechanical weathering—the physical breakdown of rocks.

Expansion and contraction from freeze–thaw and drying–rewetting cycles break rocks into smaller pieces.

Plant roots and gravity (e.g., landslides) also contribute.

Mechanical weathering exposes minerals to the processes of **chemical weathering**—chemical reactions release soluble forms of the mineral elements.

Weathering is one of the processes that result in soil formation.

Soil is a mix of mineral particles, solid organic matter (primarily decomposing plant matter), water containing dissolved organic matter, minerals, and gases (the *soil solution*), and organisms.

Soil properties influence the availability of nutrients to plants.

Texture—determined by particle size. The coarsest soil particles are **sand**.

Clays are the smallest particles (< 2 μm). They have a semicrystalline structure and weak negative charges on the surface that can hold onto cations and exchange them with the soil solution.

Clay particles can be a reservoir for some nutrient ions such as Ca^{2+}, K^{+}, and Mg^{2+}.

Cation exchange capacity—the ability of a soil to hold and exchange these ions, related to amount and types of clay particles present.

Texture also influences soil water-holding capacity.

Soils with a high proportion of sand have large spaces between the particles, and do not hold water well. Water drains through quickly.

Parent material—the rock or mineral material that was broken down by weathering to form a soil.

Parent material may be the underlying bedrock, or sediment deposited by glaciers (**till**), deposited by wind (**loess**), or by water.

Chemistry and structure of the parent material determines rate of weathering, and amount and type of minerals released; thus it influences soil characteristics such as fertility.

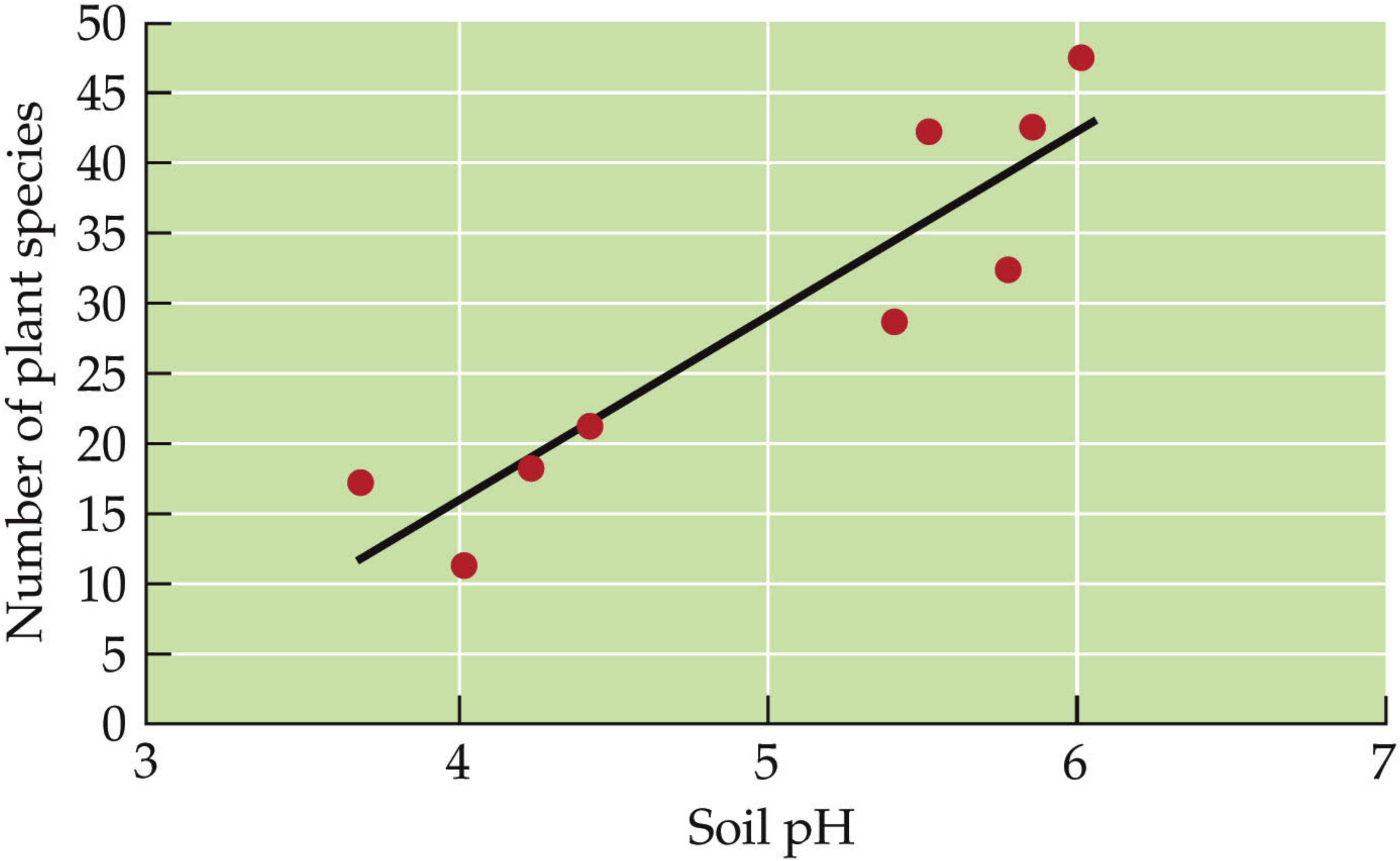
Example: Soils derived from limestone have high levels of Ca^{2+}, K^{+}, and Mg^{2+}.

Nutrient Requirements and Sources

The parent material exerts an influence on abundance, growth, and diversity of plants in an ecosystem.

Gough et al. (2000) showed that variation in parent material pH was correlated with plant species richness in Arctic ecosystems.

Figure 21.3 Plant Species Richness Decreases with Increasing Soil Acidity



ECOLOGY, Figure 21.3

Nutrient Requirements and Sources

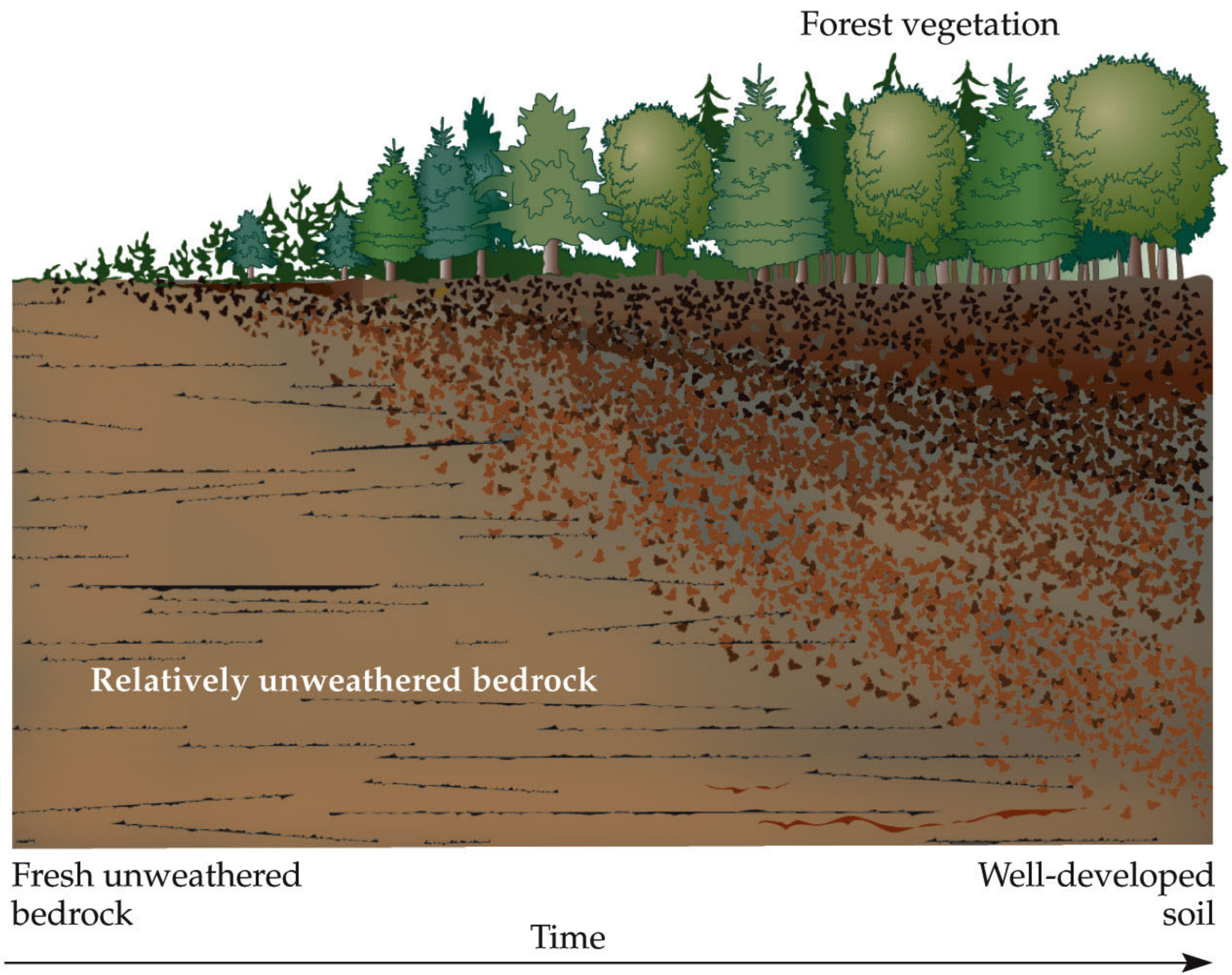
The parent material had variable amounts of calcium-rich glacial loess, which influenced soil pH.

Soil acidity negatively impacts nutrient availability, and inhibits plant establishment.

Over time, soil formation involves weathering, accumulation of organic matter, and chemical alteration and *leaching* of dissolved organic matter and fine mineral particles from upper to lower layers.

These processes result in the formation of layers or **horizons**, distinguished by color, texture, and permeability.

Figure 21.4 Development of Soil Horizons



ECOLOGY, Figure 21.4

Nutrient Requirements and Sources

The processes involved in soil development occur fastest in warm, wet conditions.

Tropical forest soils have experienced high rates of weathering and leaching for a long time, and are nutrient-poor. Most of the nutrients in these ecosystems are in the living tree biomass.

Nutrient Requirements and Sources

When tropical forests are cleared and burned, those nutrients are lost in smoke and ash and soil erosion.

These ecosystems can take centuries to return to their previous state.

Nutrient Requirements and Sources

Organisms, especially plants, bacteria, and fungi, contribute organic matter to soils.

This organic matter is an important reservoir of nutrients such as N and P.

Organisms can also affect weathering rates through the release of CO_2 and organic acids.

Nutrient Requirements and Sources

The atmosphere is the ultimate source of carbon and nitrogen for ecosystems.

These nutrients must be transformed or *fixed* by organisms.

Carbon is taken up as CO_2 by autotrophs through photosynthesis, and fixed into organic compounds.

The atmosphere is 78% nitrogen, as N_2.

This form can not be used by most organisms because of the energy required to break the triple bond.

Nitrogen fixation—the process of converting N_2 into a biologically useful form.

Biological fixation uses the enzyme **nitrogenase**, which only occurs in certain bacteria.

Some of the N-fixing bacteria are free-living, others are symbionts.

Symbiotic relationships include legume plants and bacteria in the family Rhizobiaceae.

The plants provide the bacteria with a habitat in special root structures called nodules, and supply them with carbon compounds as an energy source.

The plants get fixed nitrogen in return.

Figure 21.5 Legumes Form Nitrogen-Fixing Nodules

(A)

(B)

Other symbioses:

- Alders and *Frankia* (actinorhizal associations).
- Water fern *Azolla* and cyanobacteria.
- Lichens that include fungal and N-fixing cyanobacterial symbionts.
- Termites with N-fixing bacteria in their guts.

Nutrient Requirements and Sources

Humans fix atmospheric nitrogen when they manufacture synthetic fertilizers using the Haber–Bosch process:

Ammonia is made from atmospheric nitrogen under high pressure using an iron catalyst.

Nutrient Requirements and Sources

Nitrogen fixation requires a lot of energy.

Up to 25% of the photosynthetic energy fixed by plants is required to support the N-fixing bacteria.

Thus, there is a trade-off to the symbiosis. Allocation of energy to N-fixation rather than to growth lowers the ability of the plants to compete for resources other than nitrogen.

Nutrient Requirements and Sources

The atmosphere also contains fine dust and suspended solid, liquid, and gaseous particles known as **aerosols**.

This particulate matter falls to Earth by gravity or with precipitation—**atmospheric deposition**. It is an important source of nutrients for some ecosystems.

Nutrient Requirements and Sources

Aerosols containing cations from sea spray may be an important source of nutrients in coastal areas.

Dust originating in the Sahara Desert is an important input of iron into the Atlantic Ocean and phosphorus into the Amazon Basin.

Nutrient Requirements and Sources

Ecosystems have also been negatively impacted by atmospheric deposition of pollutants from agricultural and industrial processes.

Acid rain has been associated with declines in forest ecosystems in the eastern U.S. and Europe.

Concept 21.2: Chemical and biological transformations in ecosystems alter the chemical form and supply of nutrients.

Foremost among the nutrient transformations is the decomposition of organic matter, which releases nutrients back into the ecosystem.

Nutrient Transformations

Detritus includes dead plants, animals, and microorganisms, and egested waste products.

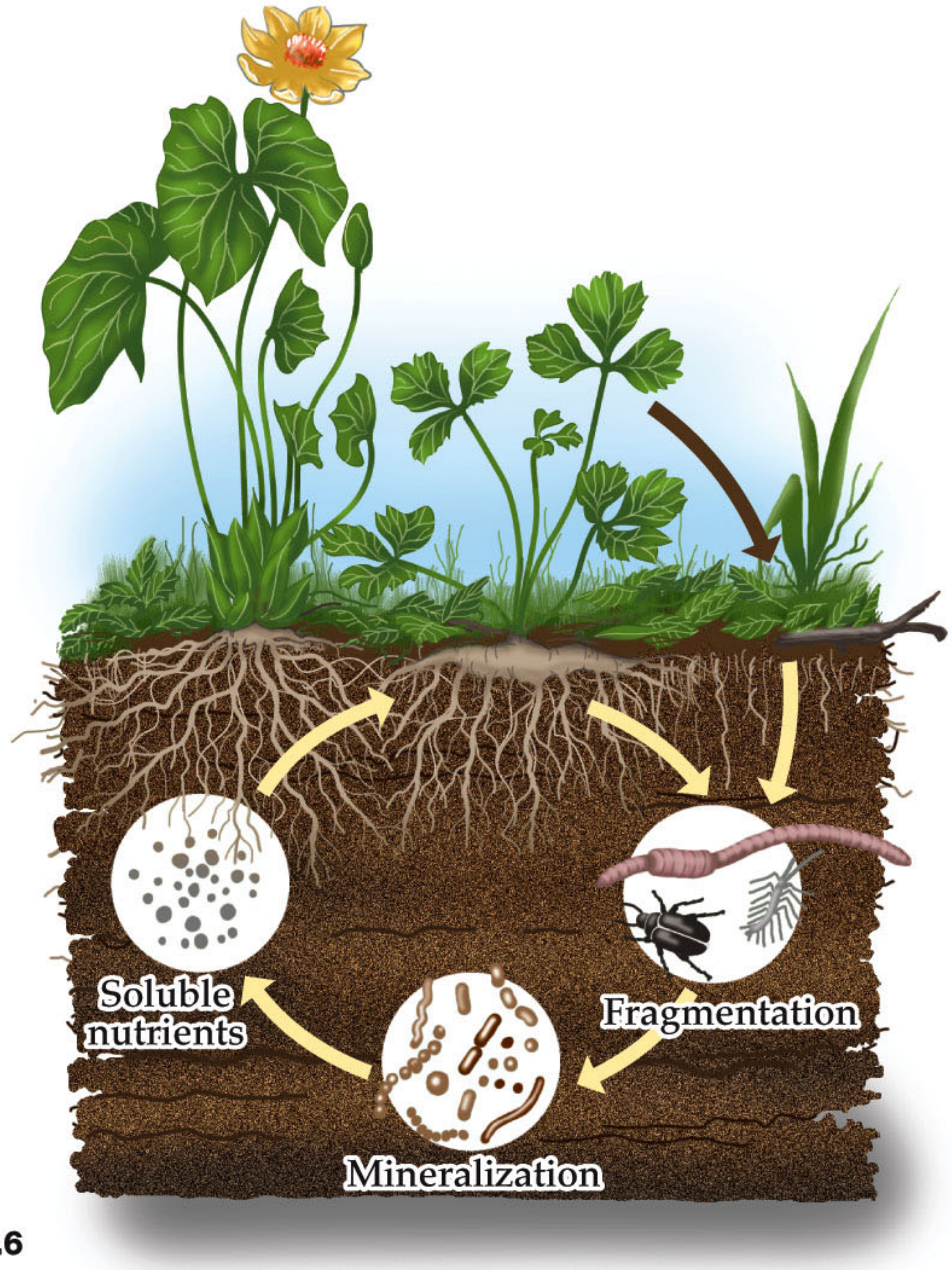
Nutrients in detritus, especially N and P, are made available by **decomposition**—the process by which detritivores break down detritus to obtain energy and nutrients.

Decomposition releases nutrients as simple, soluble organic and inorganic compounds that can be taken up by other organisms.

Fresh, undecomposed organic matter on the soil surface is known as **litter.**

As animals such as earthworms, termites, and nematodes consume the litter, they break it up into progressively finer particles.

Figure 21.6 Decomposition



ECOLOGY, Figure 21.6

Nutrient Transformations

Chemical conversion of organic matter into inorganic nutrients is called remineralization.

Heterotrophic microorganisms release enzymes that break down organic macromolecules.

Abiotic and biotic controls on decomposition and mineralization determine nutrient availability to autotrophs.

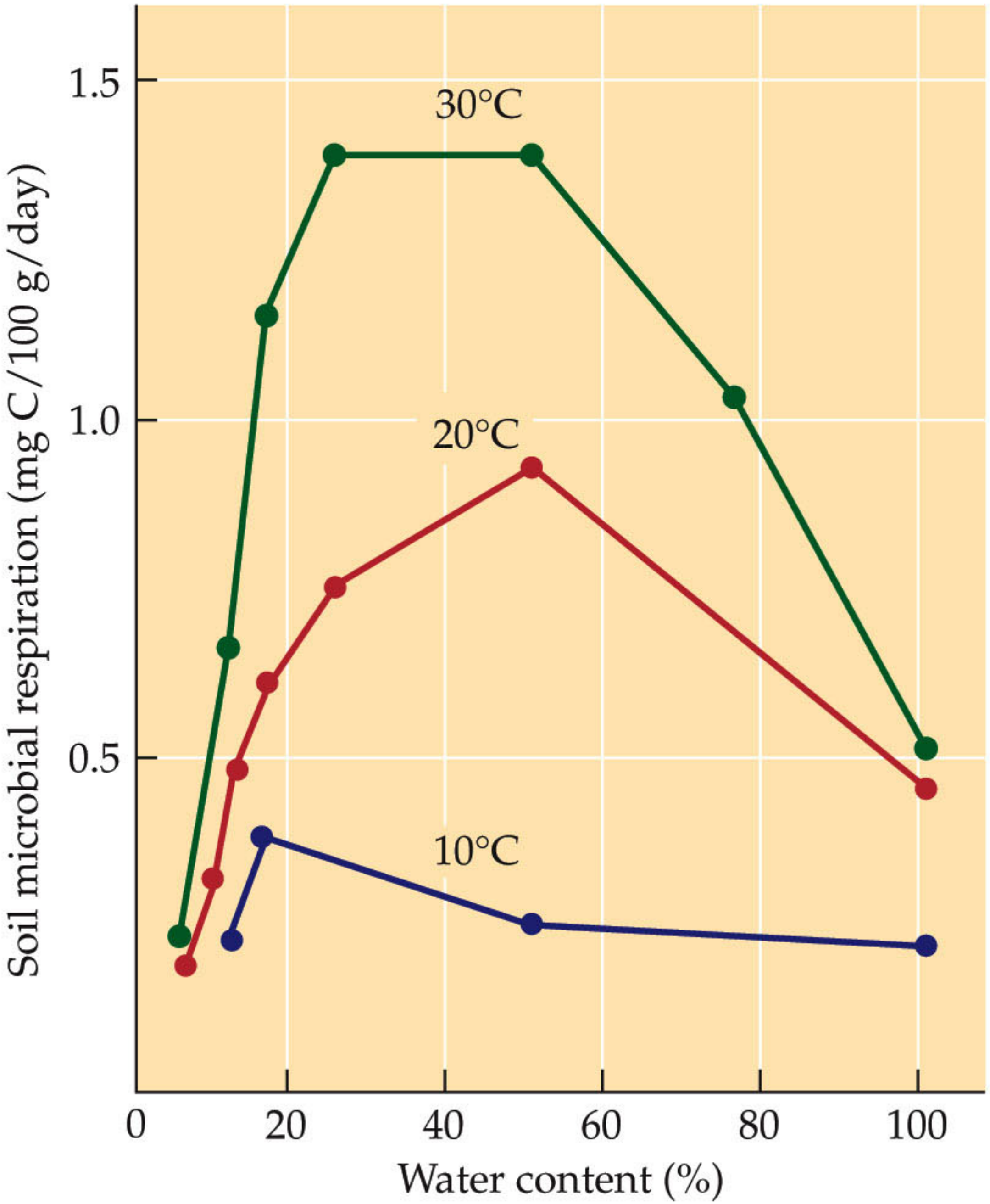
Nutrient Transformations

Decomposition and remineralization rates are faster in warm, moist conditions.

Soil moisture influences the availability of water and oxygen to microorganisms.

Wet soils have low O_2 concentrations, which inhibits detritivores.

Figure 21.7 Climate Controls the Activity of Decomposers



ECOLOGY, Figure 21.7

Nutrient Transformations

The amount of nutrients released during decomposition depends on the nutrient requirements of the decomposer organisms, and the amount of energy the organic matter contains.

Organic matter with high C:N will result in a low net release of nutrients.

Nutrient Transformations

Heterotrophic microorganisms require C:N at a 10:1 ratio.

About 60% of carbon they take up is lost in respiration.

The optimal organic matter C:N for microbial growth is 25:1. After the 60% loss of C, the C:N ratio is 10:1.

Nutrient Transformations

If C:N of organic matter > 25:1, all the N would be taken up and used by the microorganisms.

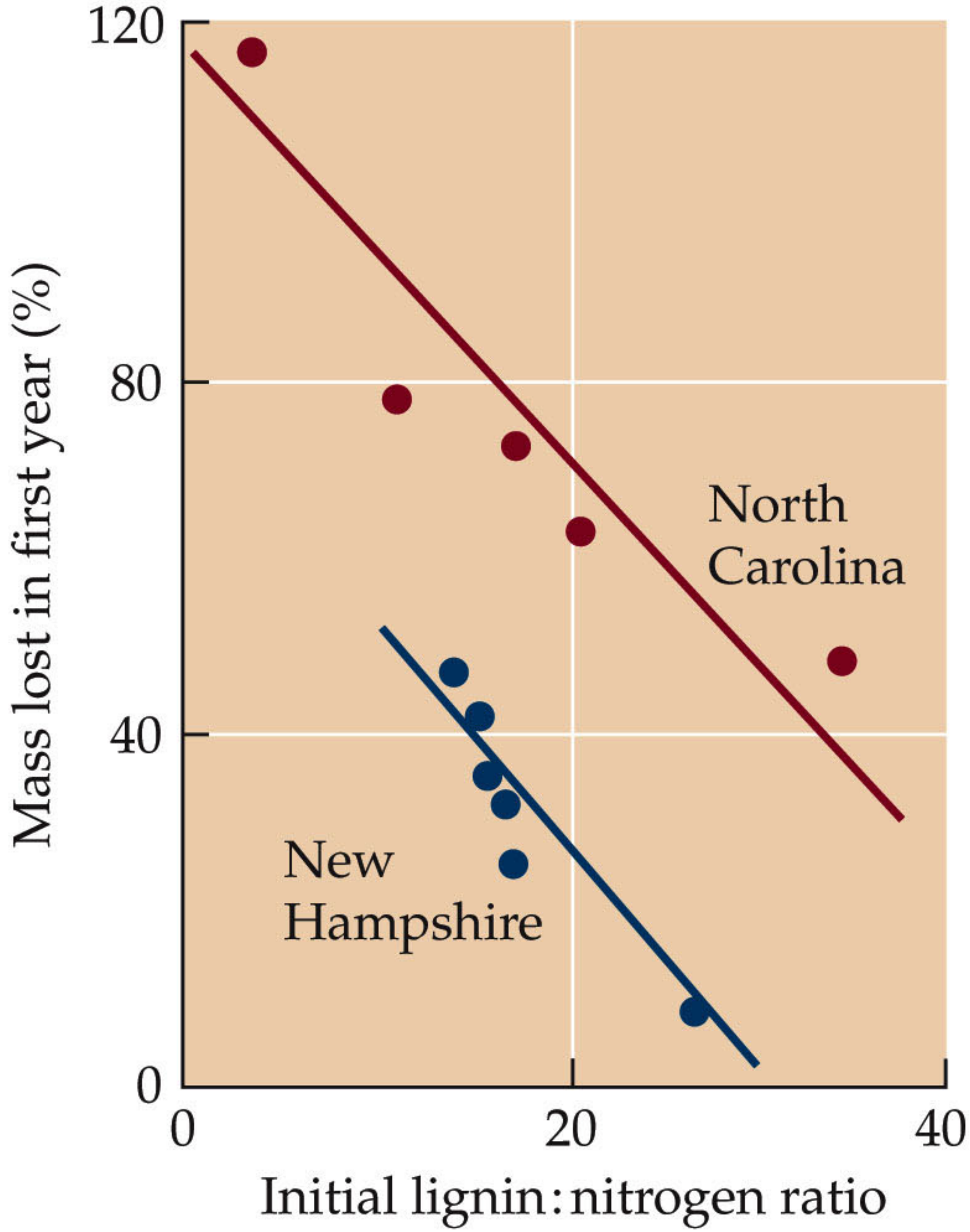
If organic matter C:N < 25:1, some N will be released into the soil.

Carbon chemistry determines how rapidly organic matter can be decomposed.

Lignin is a carbon compound that strengthens plant cell walls, and is difficult for soil microorganisms to degrade. It decomposes very slowly.

The amount of lignin in cell walls varies with plant species.

Figure 21.8 Lignin Decreases the Rate of Decomposition



ECOLOGY, Figure 21.8

Nutrient Transformations

Plant litter may contain secondary compounds.

High concentrations can lower nutrient release during decomposition, by inhibiting the microorganisms; or by stimulating their growth, leading to greater microbial uptake of nutrients.

Nutrient Transformations

Plants can influence decomposition rates in the soil by altering the chemistry or amount of litter.

Lower decomposition rates lowers soil fertility.

For plants with slow growth rates, this may reduce competition from faster growing plants.

Nitrogen transformations:

Nitrification—NH_3 and NH_4^+ are converted to NO_3^- by chemoautotrophic bacteria, in aerobic conditions.

Denitrification—some bacteria use NO_3^- as an electron acceptor, converting it into N_2 and N_2O, in anoxic conditions.

Soil fertility has traditionally been estimated from the concentration of inorganic forms of nitrogen (NO_3^- and NH_4^+).

But studies in Arctic and alpine ecosystems showed that rates of inorganic N supply were lower than what plants were actually taking up.

In these systems, plants were using organic forms of nitrogen.

Work in marine ecosystems had shown that phytoplankton could take up amino acids from water; and mycorrhizae had been shown to take up organic N from the soil and supply it to plants.

Nutrient Transformations

Some plants, particularly sedges, can take up organic N without mycorrhizae.

The mineralization step in decomposition may not be as necessary for nitrogen supply in plants as has been commonly thought.

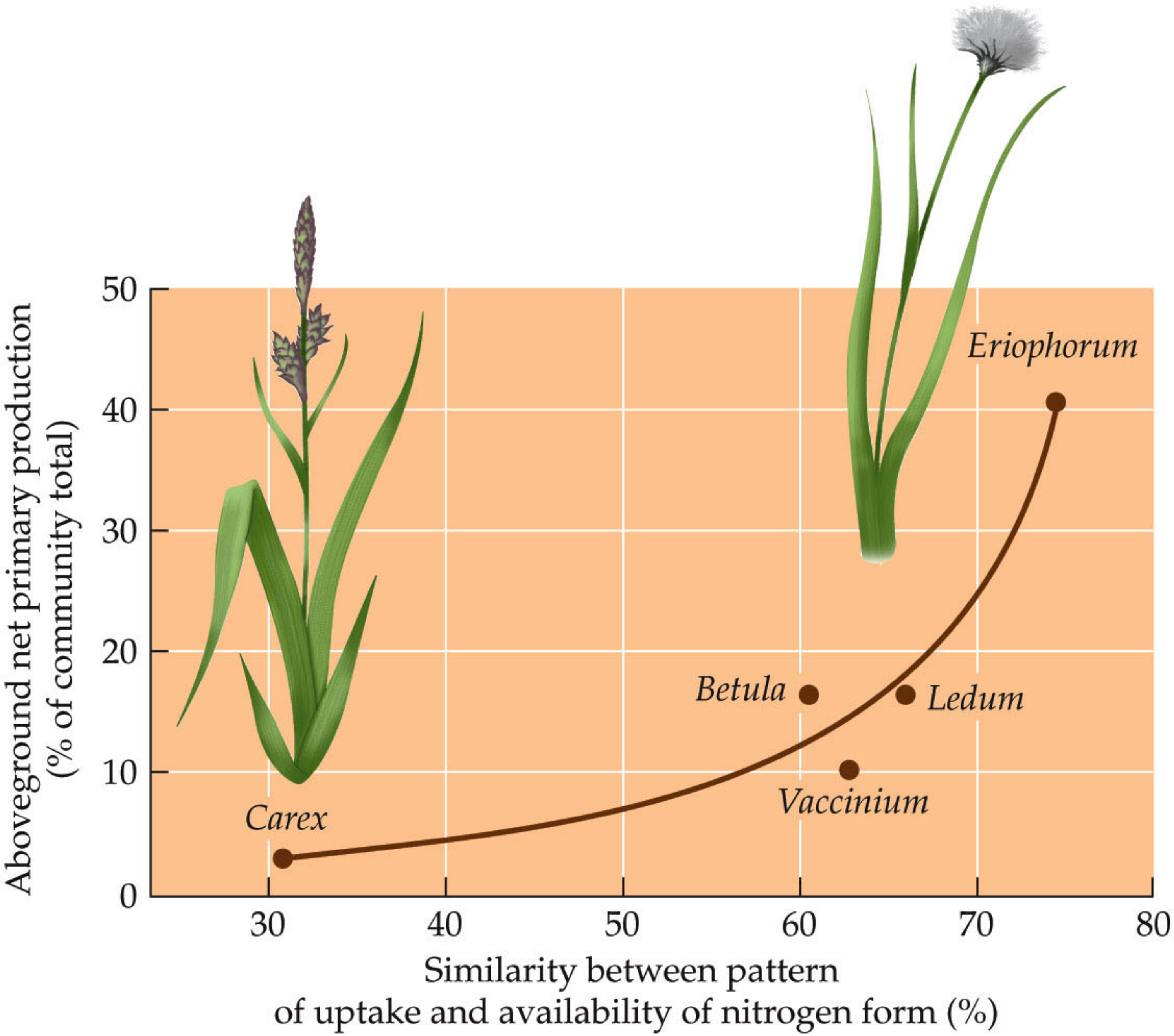
Plants in some Arctic and alpine communities may avoid competition by preferential uptake of specific forms of nitrogen.

In a study in northern Alaska, McKane et al. (2002) measured uptake of different N forms by several plants species. The species did show preferential uptake.

The use of different forms of N by these tundra plants is a rare example of resource partitioning in plants.

They also found that dominance was related to the similarity between a species’ preferred form of nitrogen and the availability of that form in the soil.

Figure 21.9 Community Dominance and Nitrogen Uptake



ECOLOGY, Figure 21.9

Nutrient Transformations

Plants can recycle some nutrients internally.

Before leaf fall, nutrients and nonstructural compounds are broken down to smaller forms, moved to the stem and other parts of the plant and stored.

Nutrient Transformations

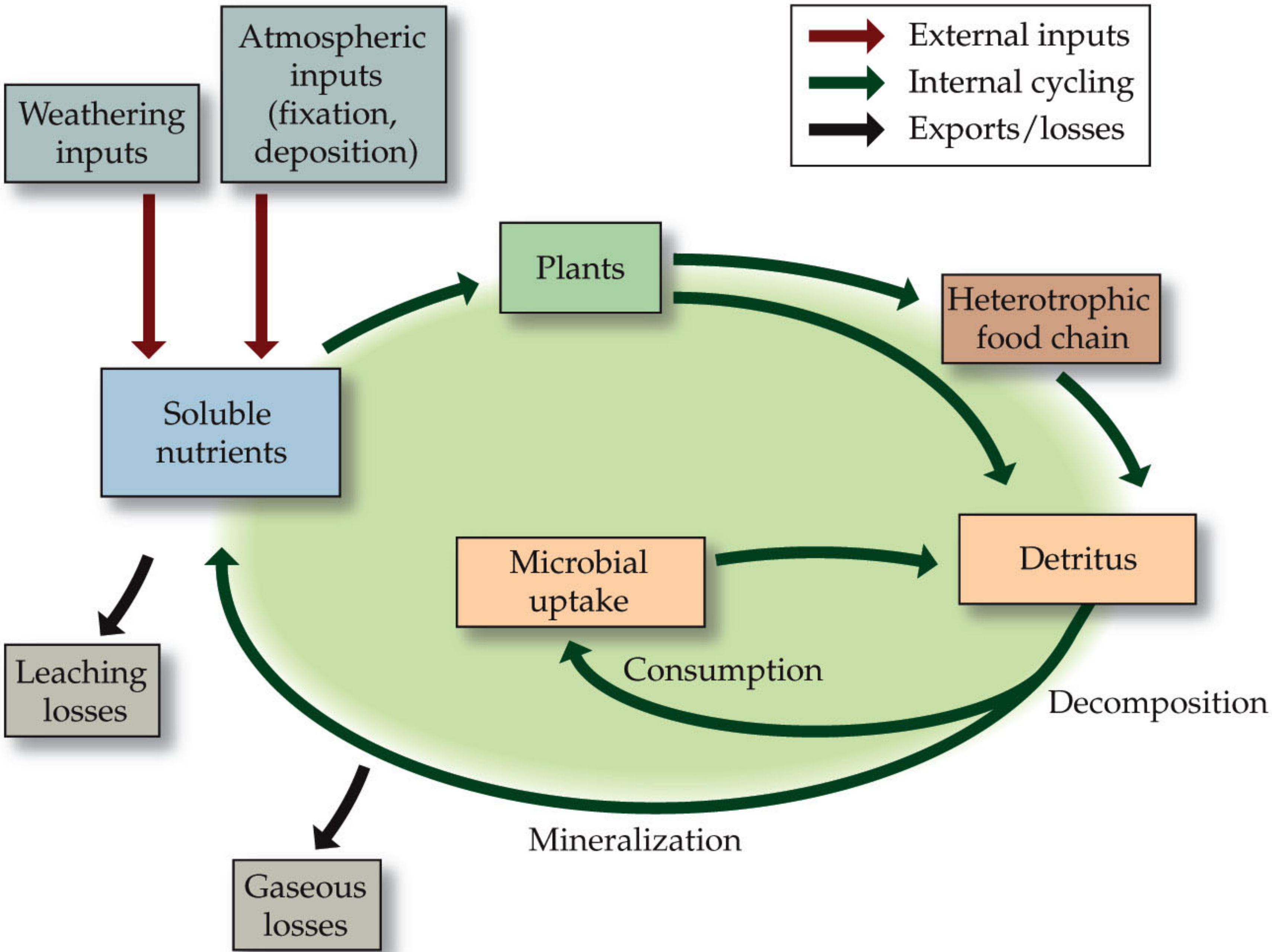
Chlorophyll molecules in deciduous leaves are broken down to recover N and other nutrients, while other pigments (carotenoids, xanthophylls, anthocyanins) remain to produce spectacular autumn colors.

Plants may resorb as much as 60–70% of the N and 40–50% of the P in their leaves before they fall.

Concept 21.3: Nutrients cycle repeatedly through the components of ecosystems.

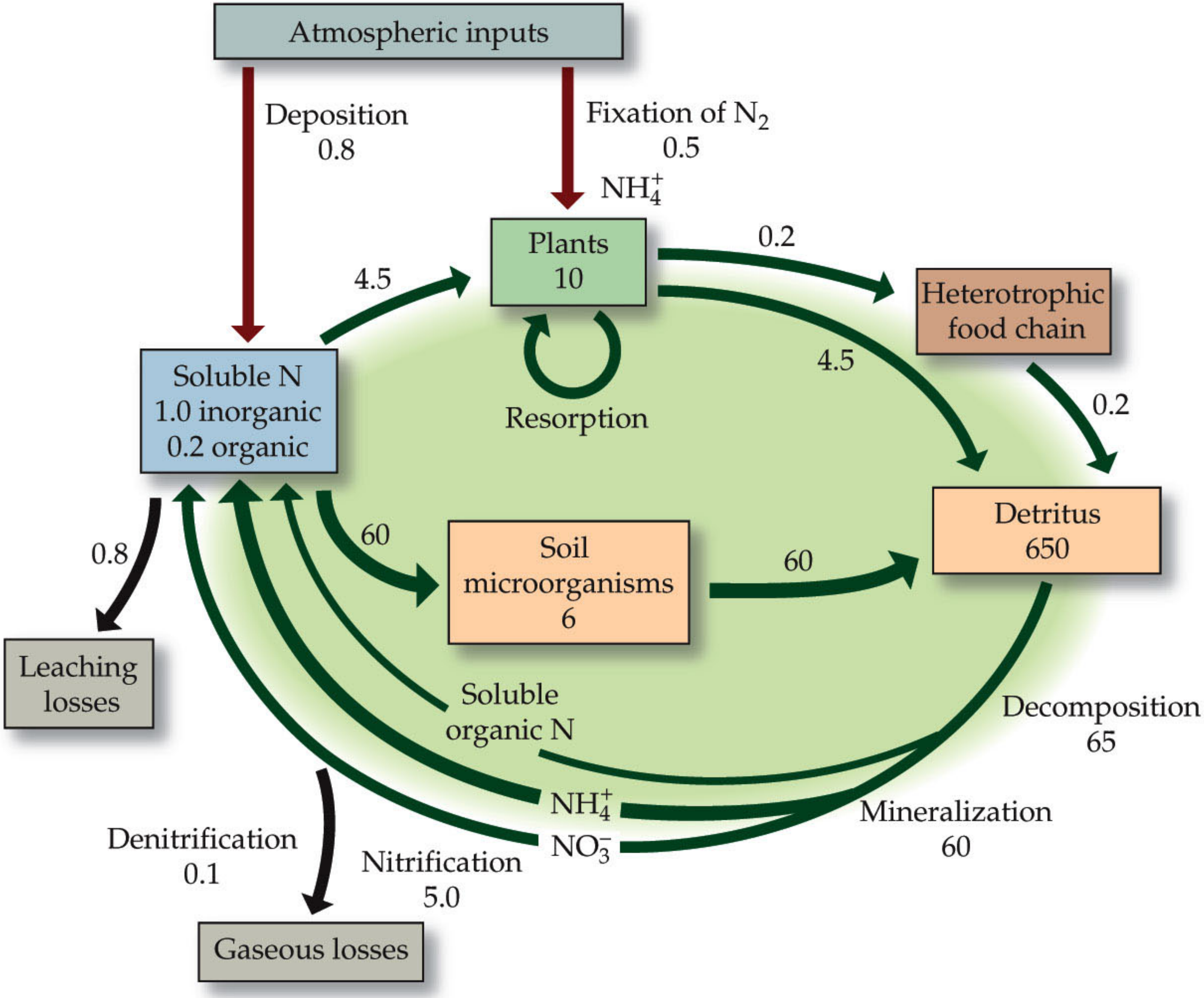
Nutrient cycling—the movement of nutrients within ecosystems, as they undergo biological, chemical, and physical transformations.

Figure 21.10 Nutrient Cycles



ECOLOGY, Figure 21.10

Figure 21.11 Nitrogen Cycle for an Alpine Ecosystem, Niwot Ridge, Colorado



ECOLOGY, Figure 21.11

Nutrient Cycles and Losses

The rate of nutrient cycling depends on the nature of the element, and the location of the cycle.

Example: In the open ocean photic zone, N and P may cycle over a period of hours to days, while zinc may cycle over geologic time scales.

Nutrient Cycles and Losses

Nutrient cycling rates are also influenced by climate, as temperature and moisture affect metabolic rates of the organisms involved in nutrient transformations.

Rates of nutrient cycling can be quantified by estimating:

Pools—the total amount of a nutrient in a component of the ecosystem.

Mean residence time (**turnover rate**)—amount of time on average that a molecule spends in the pool.

Mean residence time = total pool of element/rate of input.

A comparison of mean residence times for organic matter and nutrients indicates that nutrient pools in the soils of tropical forests are much smaller than those in boreal forests.

Turnover rates of N and P are more than 100 times faster in tropical forest soils than in boreal forest soils.

TABLE 21.3

Turnover Rates of Soil Organic Matter and Nutrients in Forest and Shrubland Ecosystems

		Mean residence time (years)				
Ecosystem type	**Soil organic matter**	**N**	**P**	**K**	**Ca**	**Mg**
Boreal forest	353	230	324	94	149	455
Temperate coniferous forest	17	18	15	2	6	13
Temperate deciduous forest	4	5	6	1	3	3
Chaparral	4	4	4	1	5	3
Tropical rainforest	0.4	2	2	1	1.5	1

Source: Schlesinger 1997.

The influence of climate on rates of decomposition is greater than its influence on primary productivity.

Permafrost in boreal soils keeps soil cool and rates of biological activity low. It also blocks percolation of water, creating wet, anoxic conditions.

Litter from conifer trees has secondary compounds that slow rates of decomposition.

Nutrient Cycles and Losses

Retention of nutrients in an ecosystem is related to uptake into biological and physical pools and to the stability of the nutrient forms.

Example: NO_3^- is more easily leached from soils than a protein.

Nutrient Cycles and Losses

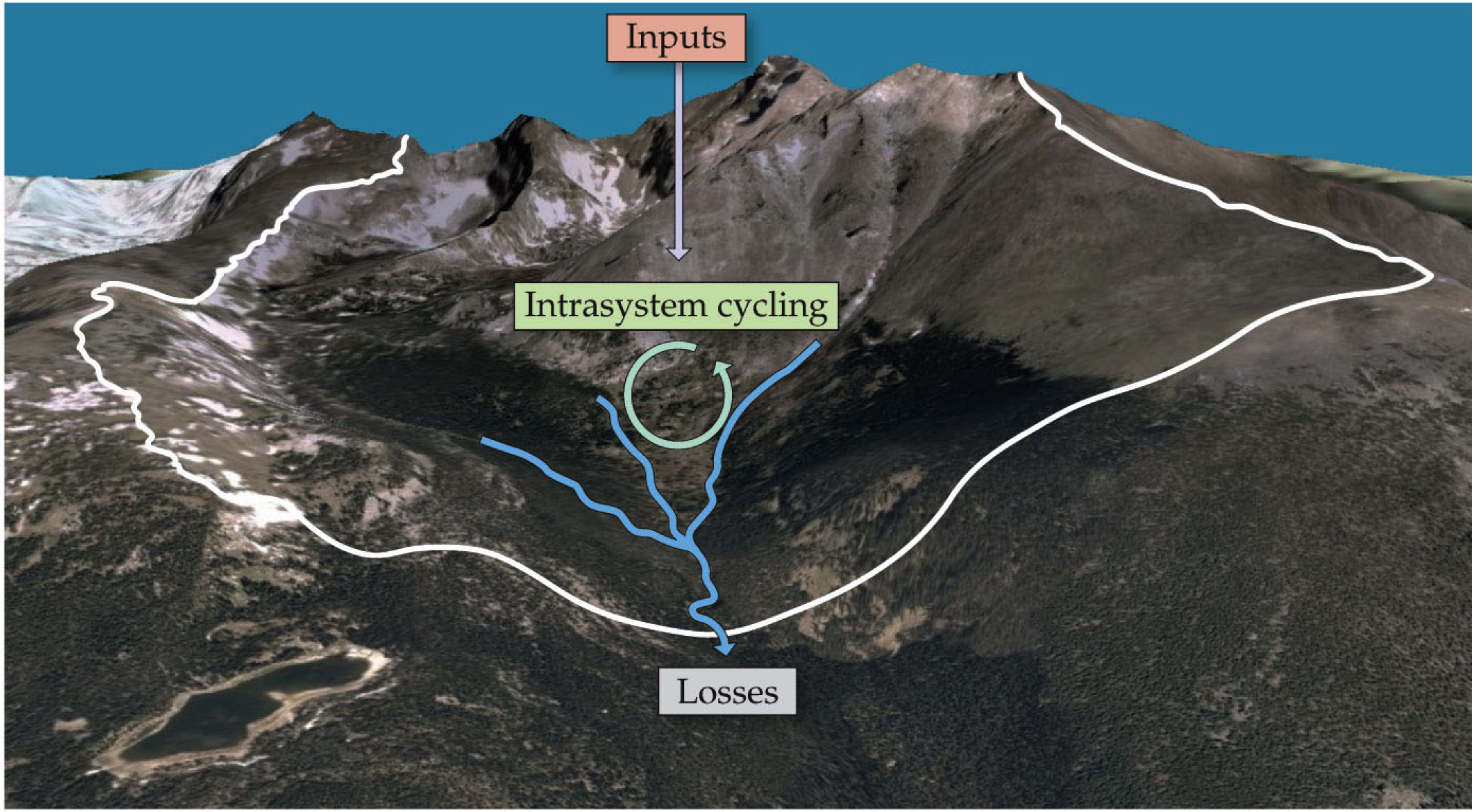
Nutrients are lost from an ecosystem when they leach out of the root zone, and into groundwater and streams.

They can also be lost as gases, or converted into chemical forms that cannot be used by organisms.

In order to determine nutrient inputs and losses, we must define ecosystem boundaries.

For terrestrial ecosystems, a single drainage basin is often used, called a **catchment** or **watershed**—the terrestrial area that is drained by a single stream.

Figure 21.12 Catchments Are Common Units of Ecosystem Study



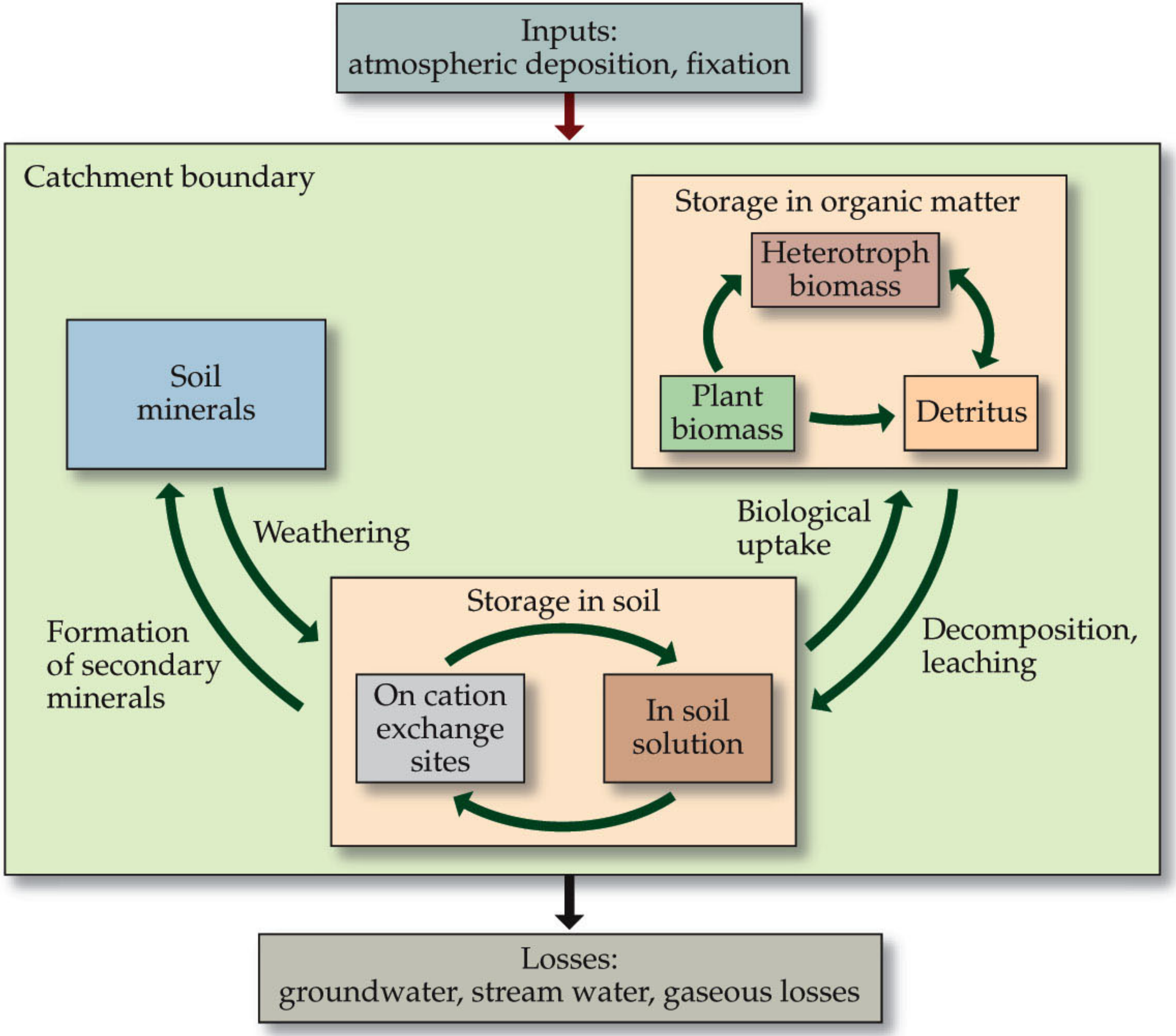
Nutrient Cycles and Losses

Nutrient inputs into a catchment include atmospheric deposition and nitrogen fixation.

Nutrients that enter may be stored in the soil or taken up by organisms.

They are transferred between ecosystem components by herbivory and predation, decomposition, and weathering processes.

Figure 21.13 Biogeochemistry of a Catchment



ECOLOGY, Figure 21.13

Nutrient Cycles and Losses

Nutrient losses are assumed to be primarily in stream water, quantified by measuring dissolved and particulate matter in stream water.

But nutrients can also be lost to the atmosphere.

Nutrient Cycles and Losses

Catchment studies have been done at the Hubbard Brook Experimental Forest in New Hampshire since 1963.

This research has provided information about the roles of organisms and soils in nutrient retention, how ecosystems respond to disturbances such as logging and fire, and long-term trends in nutrient flows associated with acid rain and climate change.

Nutrient Cycles and Losses

Vitousek (1977) used a catchment approach to study the effect of disturbance on nutrient retention.

He proposed that nutrient retention would be related to forest growth rates.

Nutrient Cycles and Losses

He predicted that high rates of primary production during intermediate successional stages would result in highest retention of nutrients, and nutrients most limiting to primary production would be retained more tightly than nonlimiting nutrients.

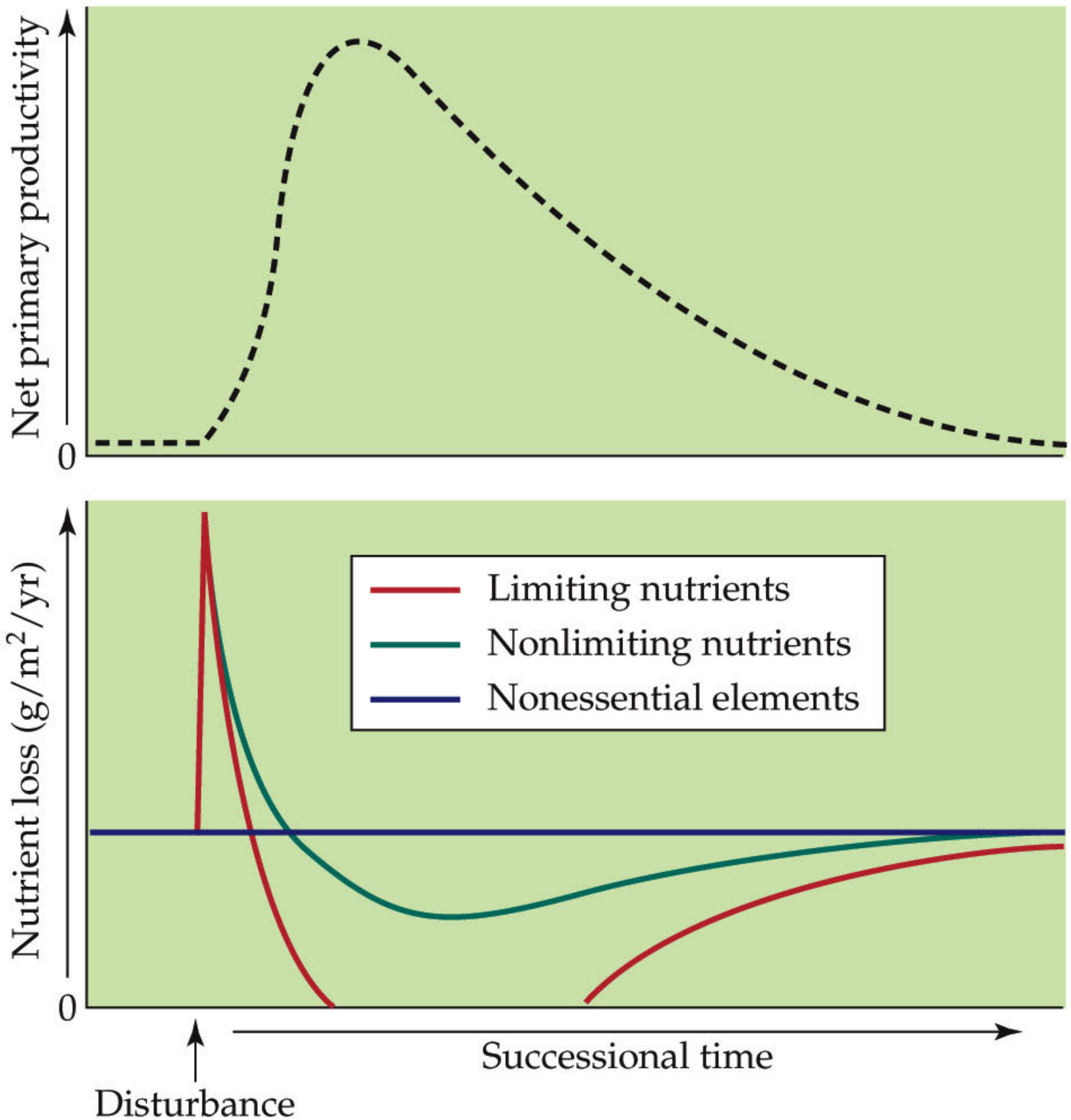
Nutrient Cycles and Losses

Vitousek studied multiple watersheds at different stages of succession.

Losses of N (a limiting nutrient) as nitrate in stream water from forests at intermediate successional stages were much less than those from old-growth forests

Losses of nonlimiting nutrients, such as K, Mg, and Ca, showed less sensitivity to forest successional stage.

Figure 21.14 Retention of Nutrients Is Highest at Intermediate Stages of Forest Succession (Part 1)



ECOLOGY, Figure 21.14 (Part 1)

Figure 21.14 Retention of Nutrients Is Highest at Intermediate Stages of Forest Succession (Part 2)

Mean Growing Season Streamwater Concentrations (μeq/liter)

	Old-growth	Successional	Ratio of concentrations
NO_3^-	53 (5)	8 (1.3)	6.63
K^+	13 (1)	7 (0.5)	1.81
Mg^{++}	40 (4.9)	24 (1.6)	1.67
Ca^{++}	56 (4.5)	36 (2.5)	1.56
Cl^-	15 (0.3)	13 (0.3)	1.15
Na^+	29 (2.6)	28 (0.9)	1.04
SO_4^{--}	119 (4.6)	123 (6.5)	0.97
Si	75 (7)	86 (5)	0.87

Note: Standard error in parentheses.

In early primary succession, there is little organic matter in the soil, so there is little N from decomposition.

N availability should be an important limit on primary production and community composition in early stages.

As the pool of N in soil organic matter increases, its limitation of primary production should decrease.

Phosphorus originates from weathering of the mineral apatite.

As the supply of P from weathering is exhausted over time, decomposition becomes increasingly important.

Soluble P may combine with iron, calcium, or aluminum to form insoluble compounds that are unavailable as nutrients—**occlusion**.

Nutrient Cycles and Losses

P in occluded forms increases, and P becomes more limiting in later successional stages.

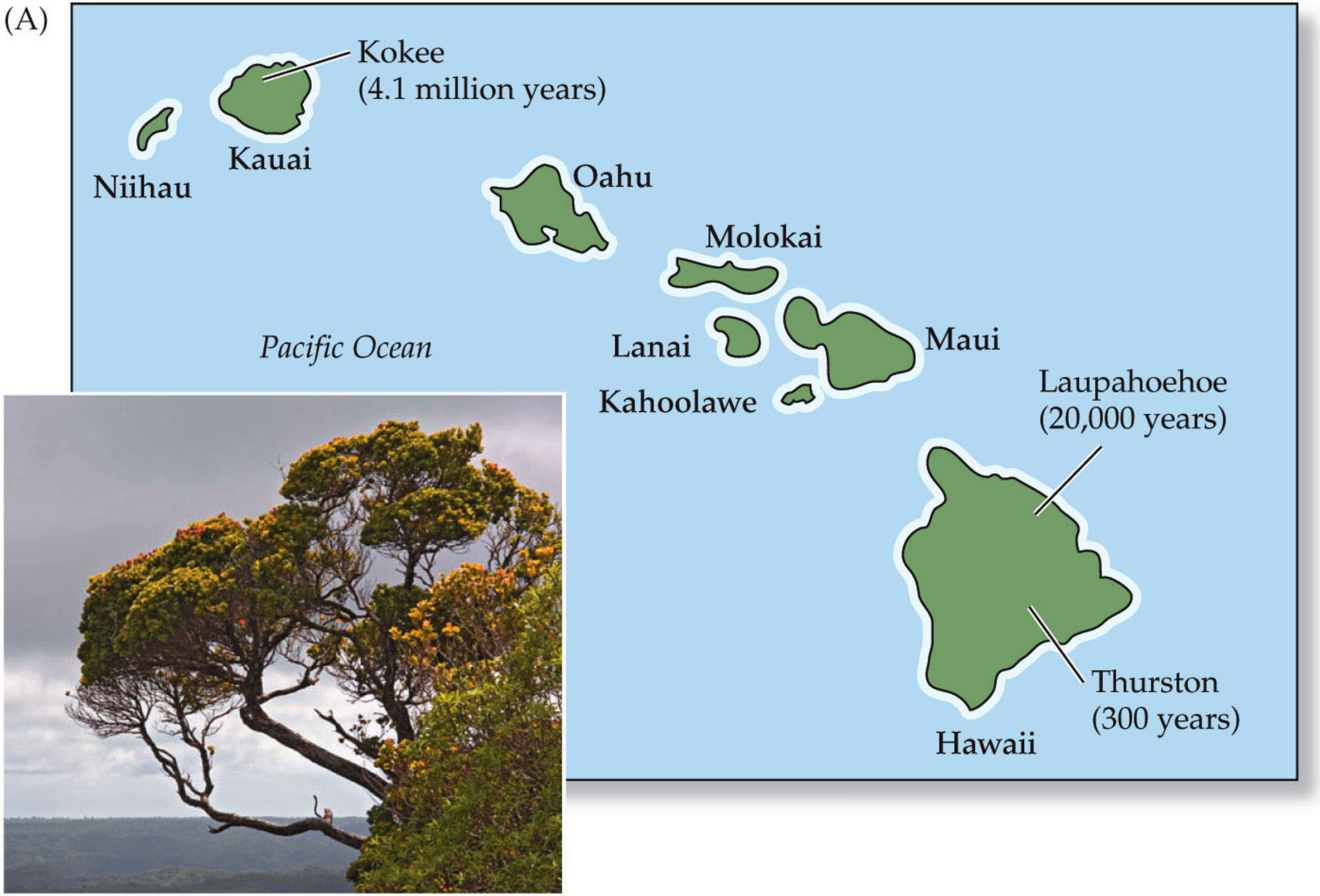
N should be limiting early in succession, N and P should both be limiting at intermediate stages of succession, and P should be limiting late in succession.

Vitousek et al. tested this in the Hawaiian Islands.

Movement of the Pacific tectonic plate has given rise to this chain of volcanic islands, resulting in the oldest islands in the northwestern part of the chain, the youngest in the southwest.

The islands thus have ecosystems of varying ages.

(A)

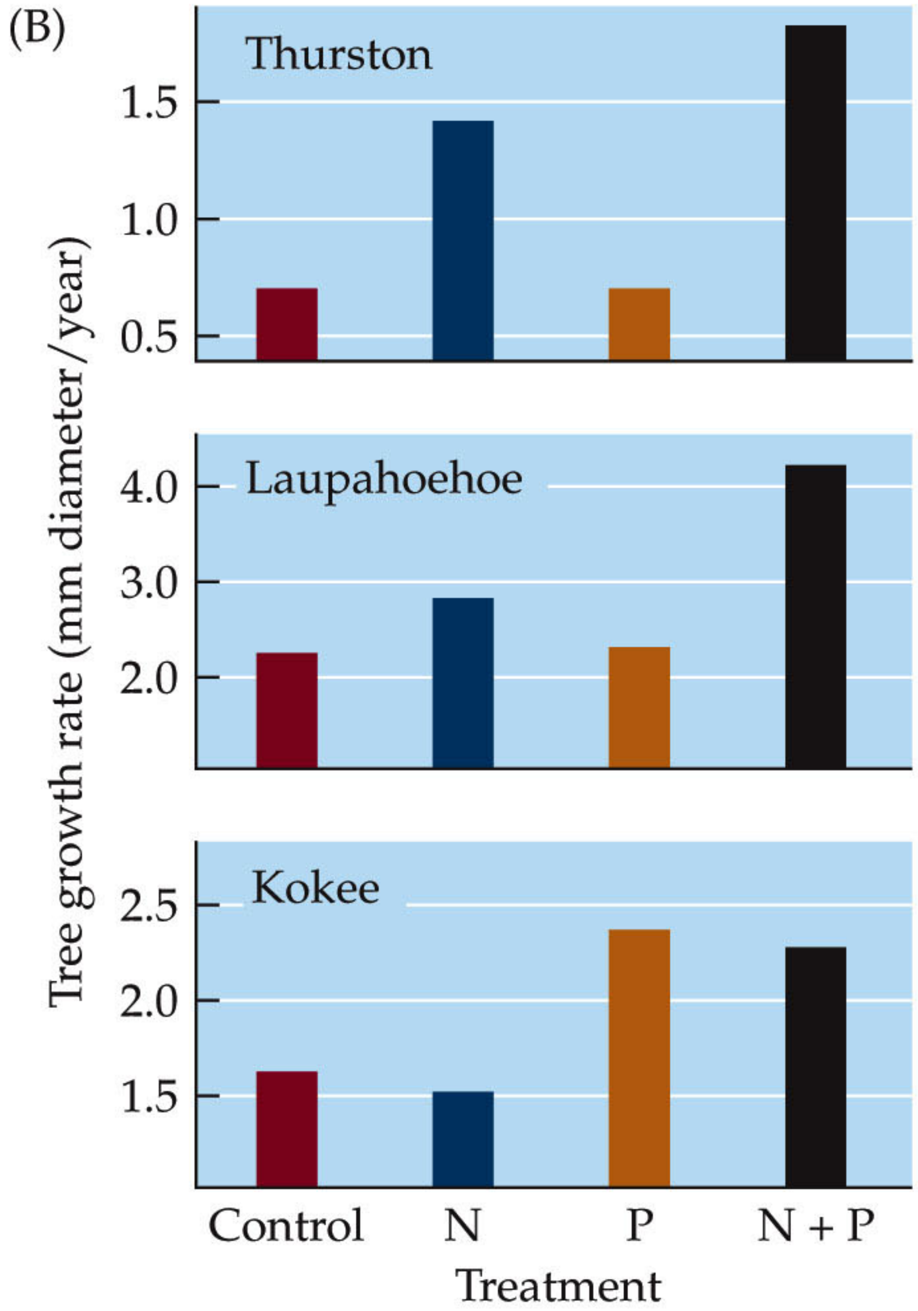

Kokee
(4.1 million years)
Niihau
Kauai
Oahu
Molokai
Lanai
Maui
Kahoolawe
Pacific Ocean
Laupahoehoe
(20,000 years)
Thurston
(300 years)
Hawaii

Vitousek et al. added N, P, or N + P to plots in three ecosystems of different ages and measured the effects on the growth of the dominant tree, Ohi’a.

N was most limiting to tree growth in the youngest ecosystem, while P was most important in the oldest ecosystem.

N + P increased tree growth in the intermediate-aged ecosystem.

Figure 21.15 B Nutrient Limitation of Primary Production Changes with Ecosystem Development



ECOLOGY, Figure 21.15 (Part 2)

Soils in temperate, high-latitude, and high-elevation zones are often subjected to major disturbances (e.g., large-scale glaciation, landslides) and are less likely to reach ages at which P becomes limiting.

Concept 21.4: Freshwater and marine ecosystems receive nutrient inputs from terrestrial ecosystems.

Nutrients lost from terrestrial ecosystems often end up in streams, lakes, and oceans.

Nutrients in Aquatic Ecosystems

Organic matter and dissolved nutrients from terrestrial ecosystems are the primary nutrient source for rivers and streams.

Biogeochemical processing in moving stream water can be significant.

N exports from major rivers are correlated with N inputs to rivers by anthropogenic pollution.

But export rates are lower than input rates due to processing in the rivers, especially denitrification and biological uptake.

These processes are enhanced when benthic detritus is high.

Figure 21.16 Rivers Are Important Modifiers of Nitrogen Exports (Part 1)

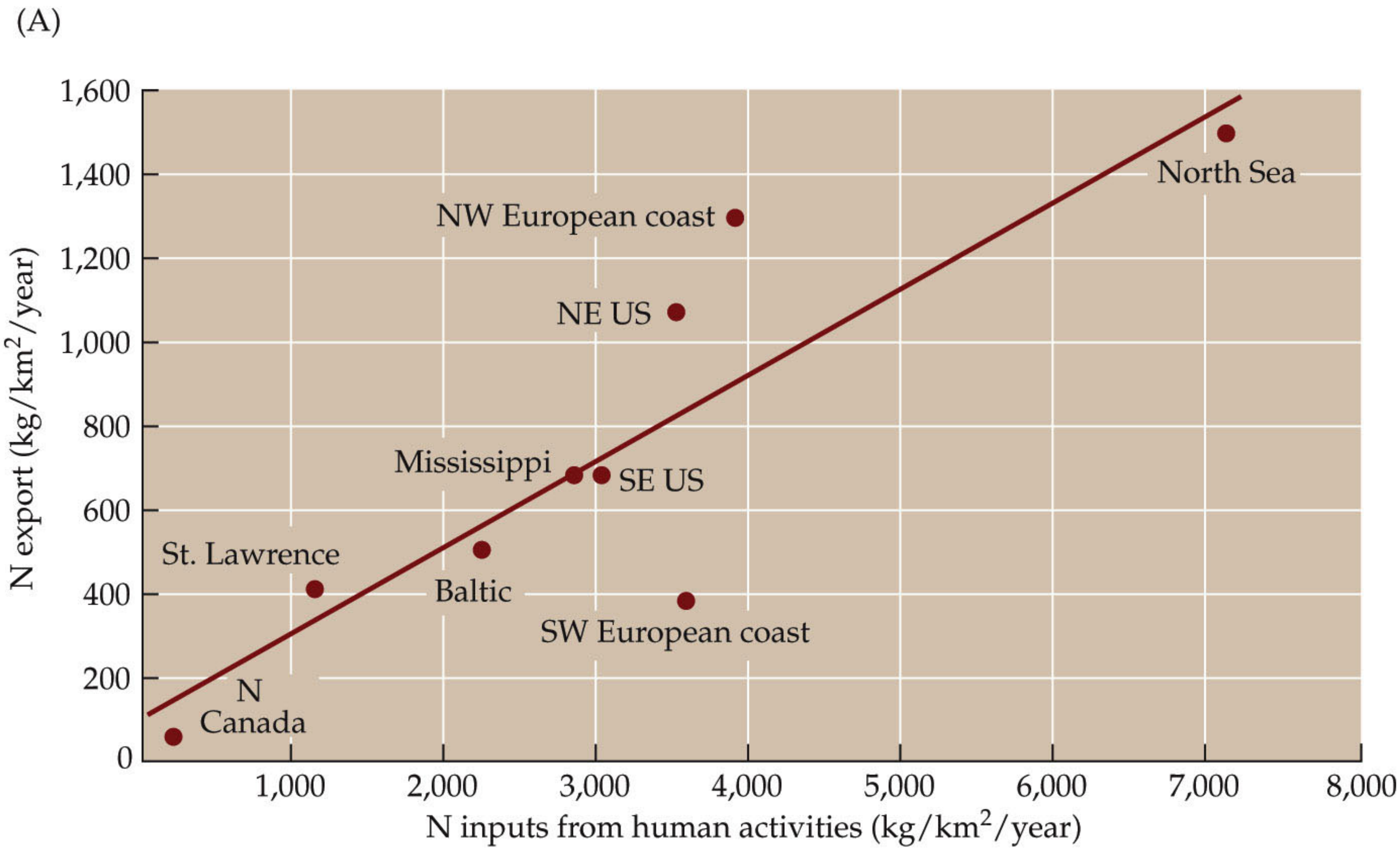


Figure 21.16 Rivers Are Important Modifiers of Nitrogen Exports (Part 2)

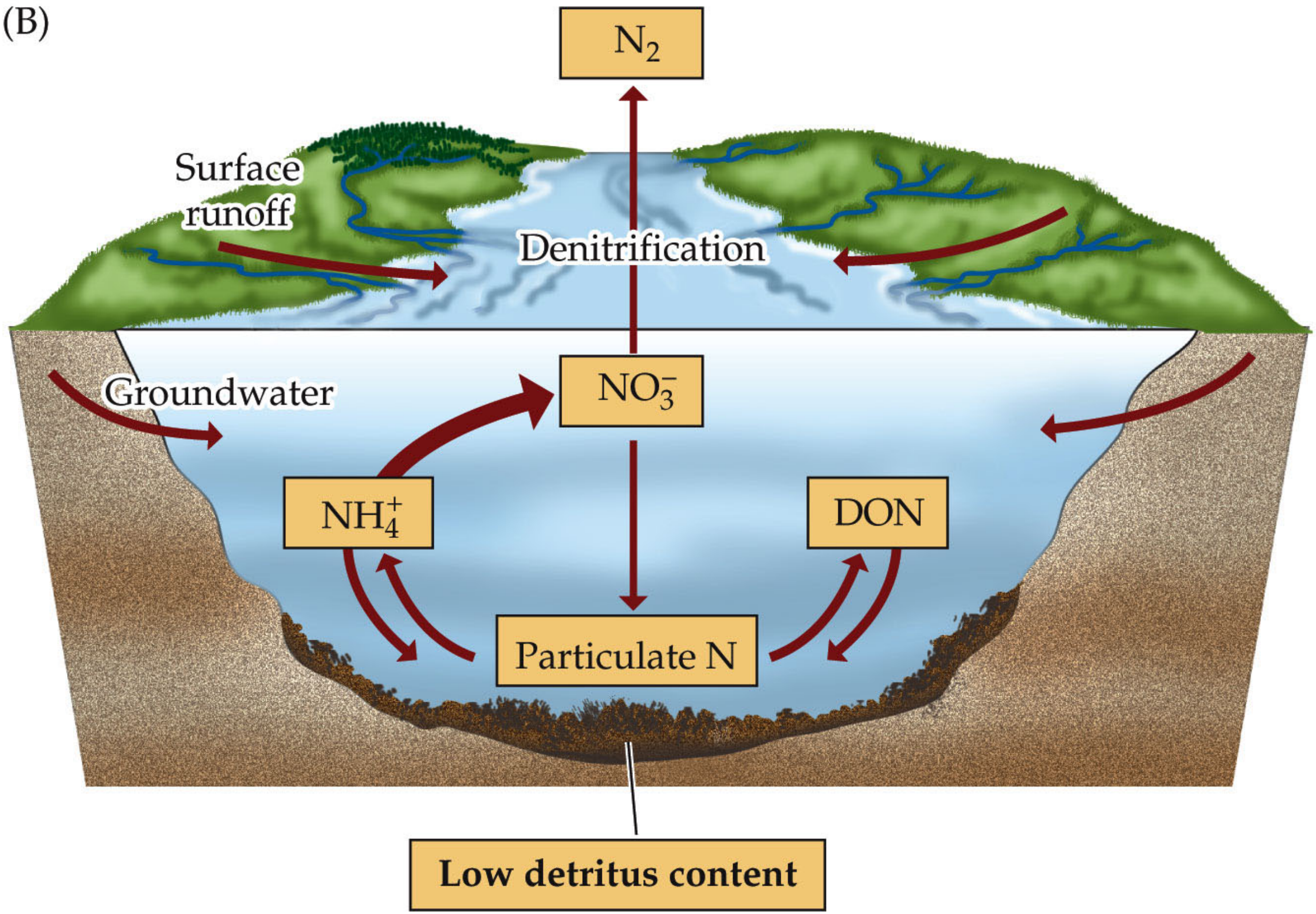
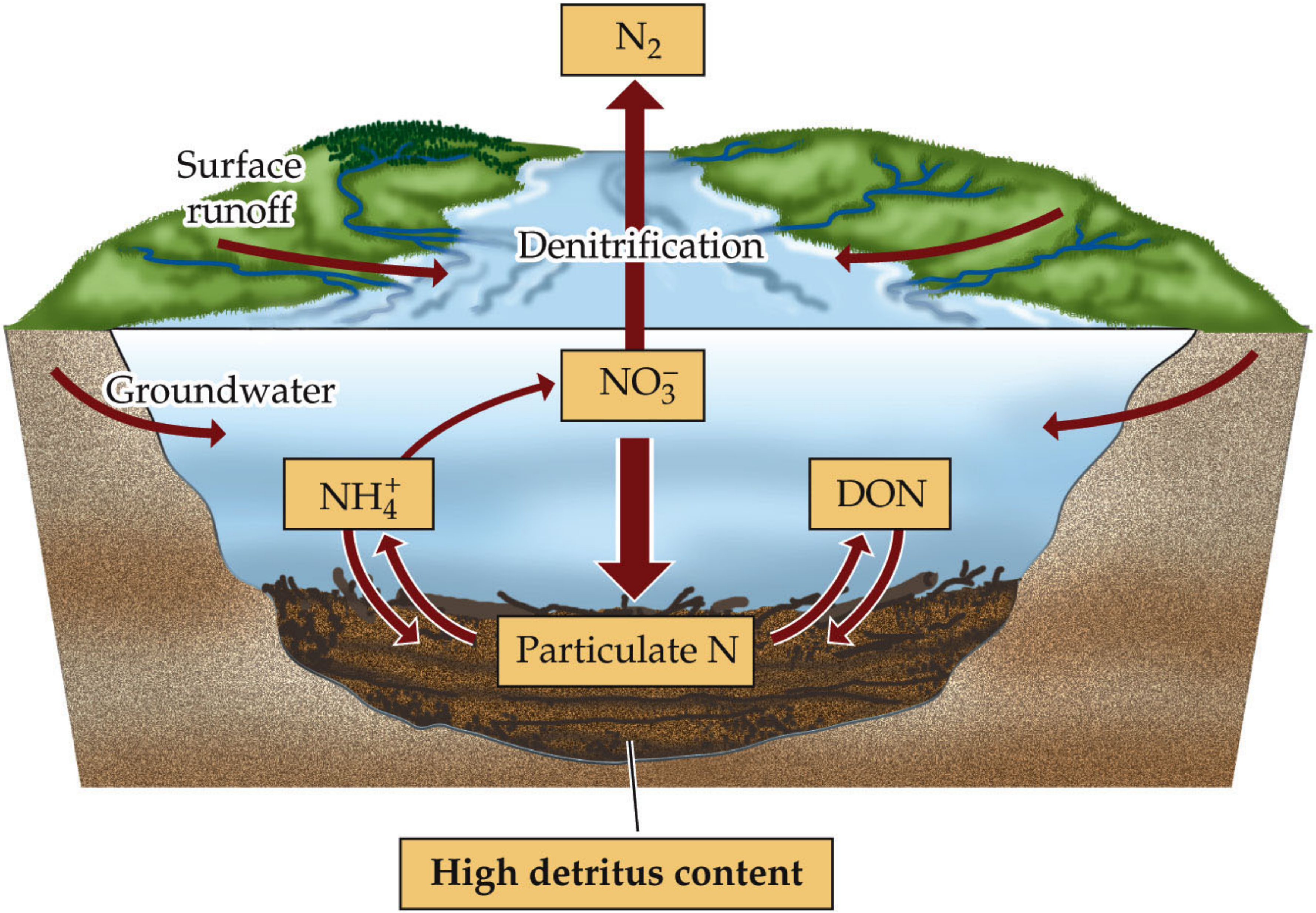


Figure 21.16 Rivers Are Important Modifiers of Nitrogen Exports (Part 3)



ECOLOGY, Figure 21.16 (Part 3)

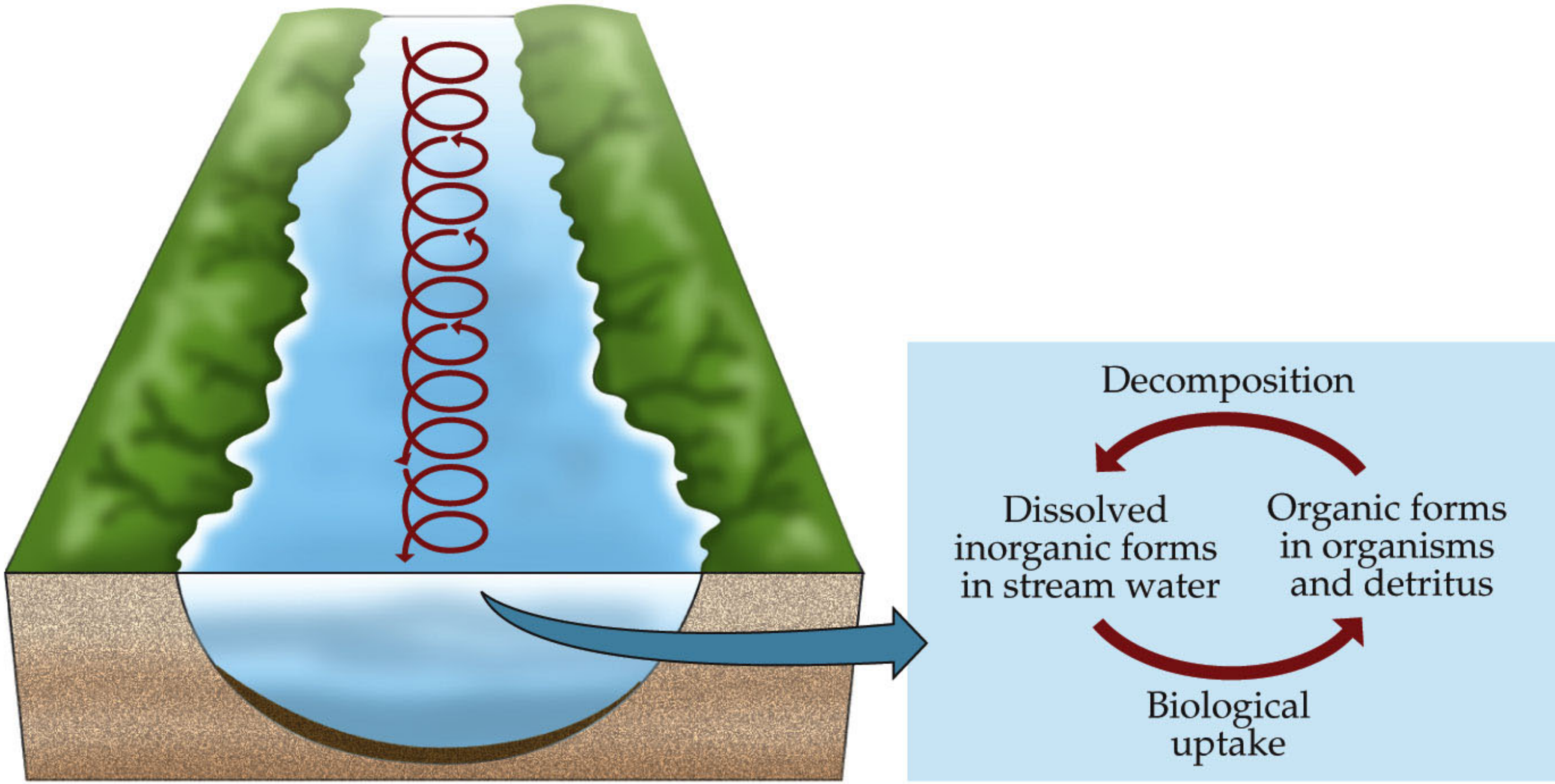
Nutrients in Aquatic Ecosystems

Nutrients in streams can be recycled repeatedly as water flows downstream.

Nutrients are transferred between dissolved inorganic forms, organisms, and detritus.

The repeated uptake and release of nutrients in association with the movement of water is called nutrient "spiraling."

Figure 21.17 Nutrient Spiraling in Stream and River Ecosystems



Nutrients in Aquatic Ecosystems

The time required for a full turn of the spiral depends on amount of biological activity, water velocity, and form of the nutrient.

Retention of N and P increases downstream due to increasing spiral lengths.

Lakes receive nutrient inputs from stream water, atmospheric deposition, and terrestrial litter.

P is usually the limiting nutrient in lakes, but N may be limiting in some lakes.

Nutrient transfer between trophic levels is very efficient. Detritus is decomposed in the water column and sediments, providing internal nutrient input.

Nutrients in Aquatic Ecosystems

In the photic zone, some cyanobacteria fix N, which is favored when ratios of dissolved N to P are low ($N:P < 10$).

Nutrients are progressively lost as detritus is deposited in the lake sediments. Anoxic conditions reduce decomposition. In the reducing environment, some elements change form (e.g., Fe^{3+} to Fe^{2+}).

Low oxygen in the sediments also promotes denitrification, and bacteria may reduce sulfate (SO_4^{2-}) to hydrogen sulfide (H_2S).

Lake mixing brings dissolved nutrients from the bottom water to the surface layers, along with detritus that may be decomposed by bacteria.

Nutrients in Aquatic Ecosystems

Lakes are classified according to nutrient status:

Oligotrophic—nutrient-poor, low primary productivity.

Eutrophic—nutrient-rich, high primary productivity.

Mesotrophic—intermediate nutrient levels.

Nutrients in Aquatic Ecosystems

Natural processes, plus lake size and shape, determine nutrient status.

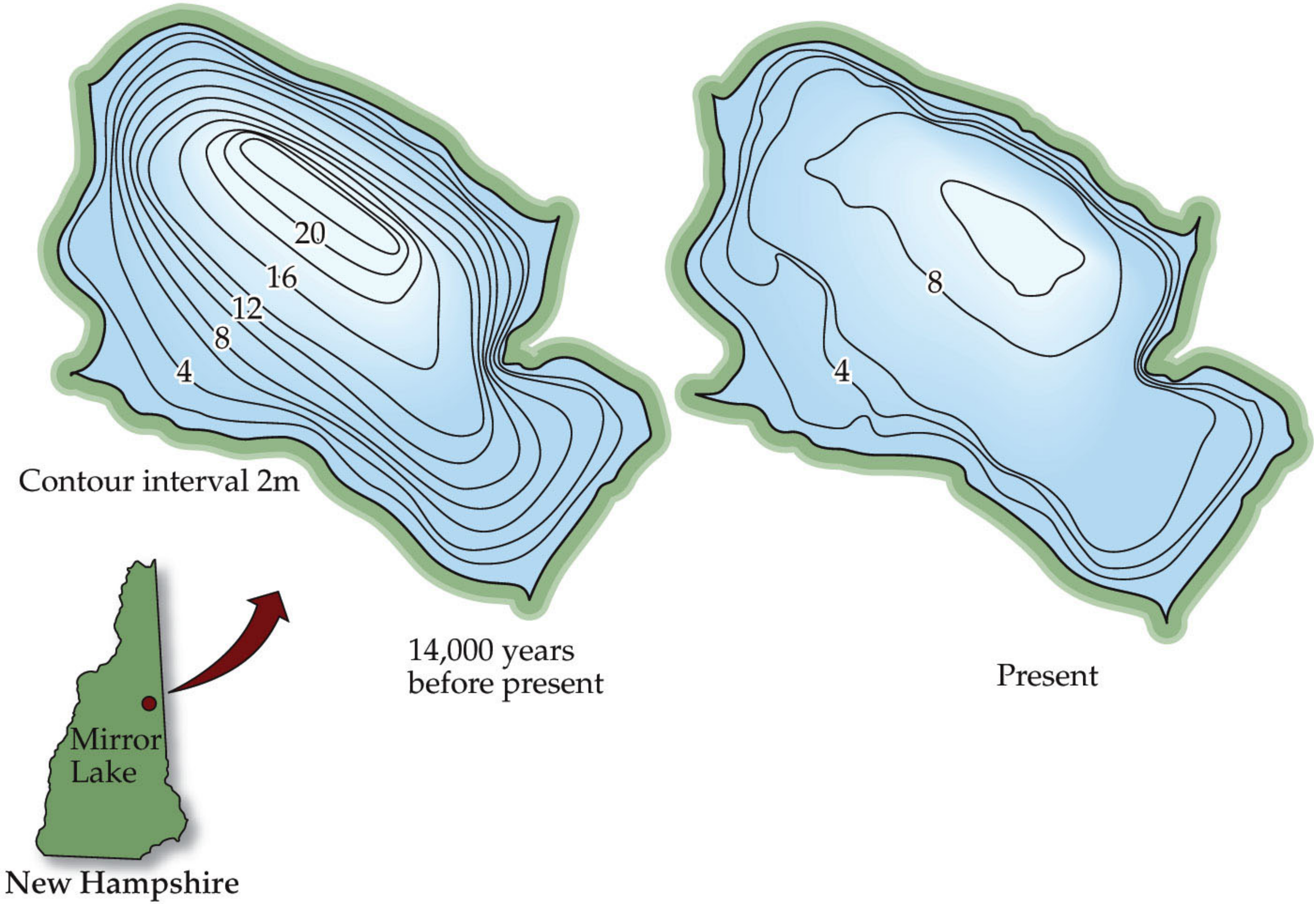
High mountain lakes are typically oligotrophic due to short growing season and low temperatures, and they tend to be deep with small surface areas.

Shallow lakes in the tropics or low elevations tend to be eutrophic.

Over time, the nutrient status of a lake may shift from oligotrophic to eutrophic, called **eutrophication**.

Sediments accumulate over time, and the lake becomes more shallow. Summer water temperatures increase, decomposition increases, and the lake becomes more productive.

Figure 21.18 Lake Sediments and Depth



ECOLOGY, Figure 21.18

Nutrients in Aquatic Ecosystems

Human activities accelerate the process of eutrophication by inputs of sewage, detergents, agricultural fertilizers, and industrial wastes.

Water clarity in Lake Tahoe has declined because of N and P inputs from neighboring communities.

Nutrients in Aquatic Ecosystems

Water clarity is dependent on phytoplankton density, and is measured using a Secchi disk—a black and white disk lowered into the water.

The maximum depth at which the disk can be seen is the *depth of clarity*.

In Lake Tahoe, this depth has decreased by 10 m in 30 years.

Anthropogenic eutrophication can be reversed by controlling nutrient inputs.

In Lake Washington, Seattle, treated sewage with high P concentrations resulted in eutrophication in the 1960s and 1970s. Phytoplankton densities and blooms of cyanobacteria increased.

Based on the advice of W.T. Edmondson, Seattle began a program to divert the treated sewage from the lake to Puget Sound.

Water clarity increased, and by 1975, the lake was declared to be recovered.

Figure 21.19 Lake Washington: Reversal of Fortune (Part 1)

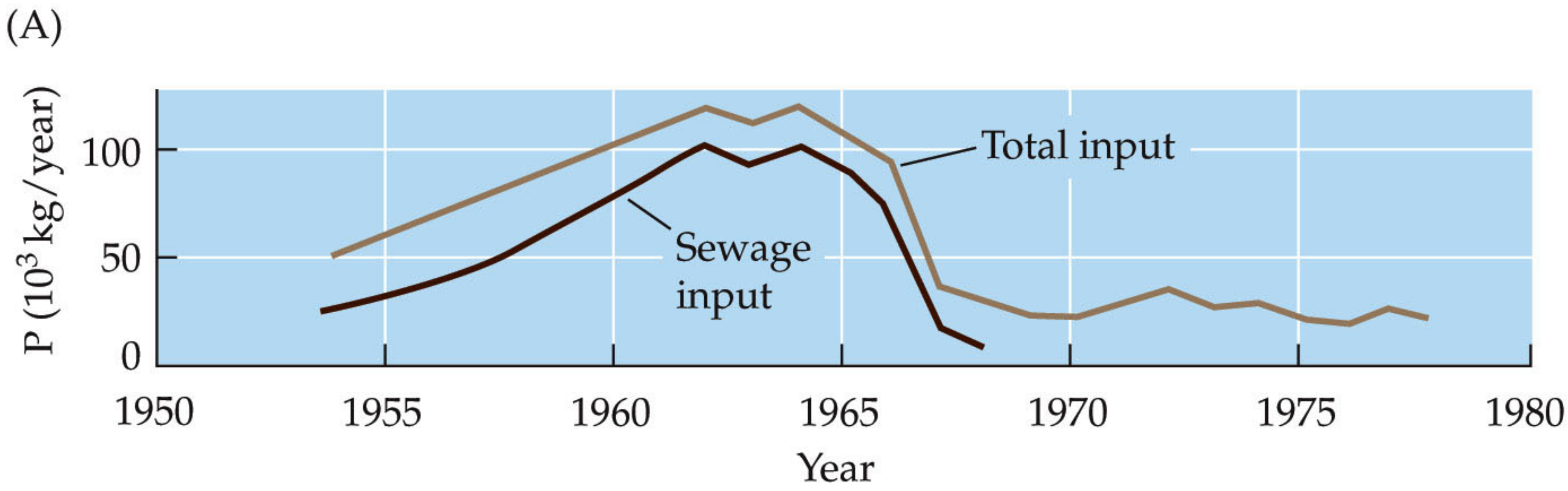
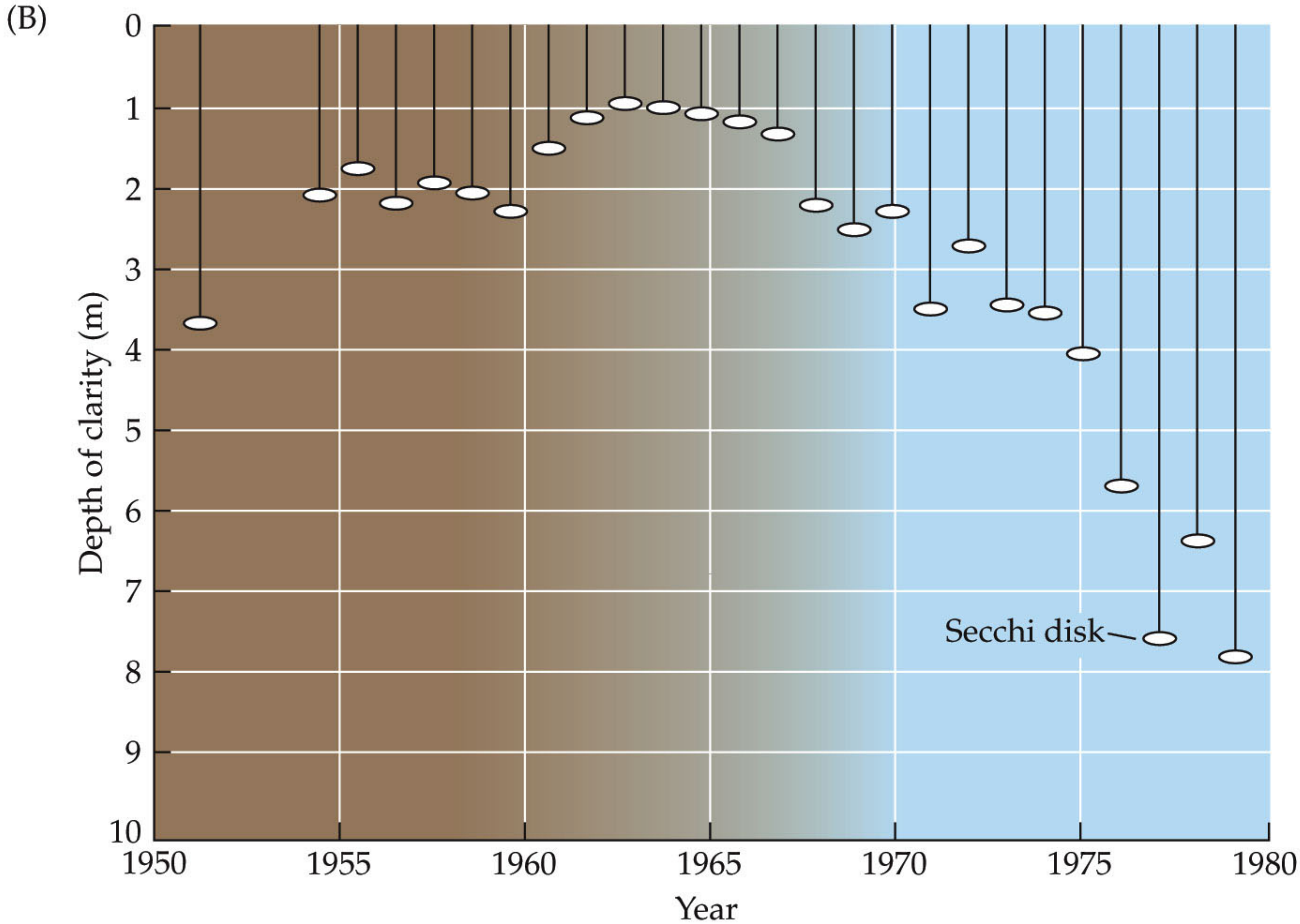


Figure 21.19 Lake Washington: Reversal of Fortune (Part 2)



ECOLOGY, Figure 21.19 (Part 2)

Nutrients in Aquatic Ecosystems

In estuaries, where rivers meet sea water, the chemical form of nutrients can change.

Changes in pH and water chemistry can release some P bound to soil particles.

The velocity of the river water also decreases, and sediments settle out, providing detritus and nutrients.

Nutrients in Aquatic Ecosystems

Estuaries often have salt marshes that trap both river and ocean sediments, and have high nutrients.

Nutrients in Aquatic Ecosystems

Productivity in the open ocean can be limited by N, P, Fe, and Si.

N sources include river input, atmospheric deposition, internal cycling.

N-fixing by cyanobacteria may be limited by molybdenum, part of the nitrogenase enzyme.

Nutrients in Aquatic Ecosystems

P, Fe, and Si enter the marine system in dissolved and particulate form from rivers, and atmospheric deposition of dust.

Human activities, including large-scale desertification and deforestation, are increasing these inputs.

Nutrients in Aquatic Ecosystems

Deep sediments accumulate in the oceans.

Sulfate reduction and denitrification are important processes in these anoxic sediments, and some decomposition and mineralization of organic matter occurs.

Nutrients in Aquatic Ecosystems

Zones of upwelling bring deep, nutrient-rich waters to the surface.

These zones of upwelling are highly productive and are important areas for commercial fisheries.

Case Study Revisited: A Fragile Crust

Loss of the biological crust affects nutrient processes.

The crusts prevent soil erosion by binding soil particles together. Activity of the organisms in the crust may also influence nutrient inputs, and desert productivity.

Case Study Revisited: A Fragile Crust

Neff et al. (2005) studied the effects of cattle grazing on the Colorado Plateau, using plots that had never been grazed, and plots that had been closed to grazing in 1974.

Biological crust was present at all sites, but had clearly been damaged by the grazing.

Case Study Revisited: A Fragile Crust

Dust from atmospheric deposition was estimated by the magnetic properties of the soils.

Dust from distant areas has more iron oxides than the native soil, and gives a stronger magnetic signal.

The dust is a source of nutrients, and loss of the dust is a measure of erosion.

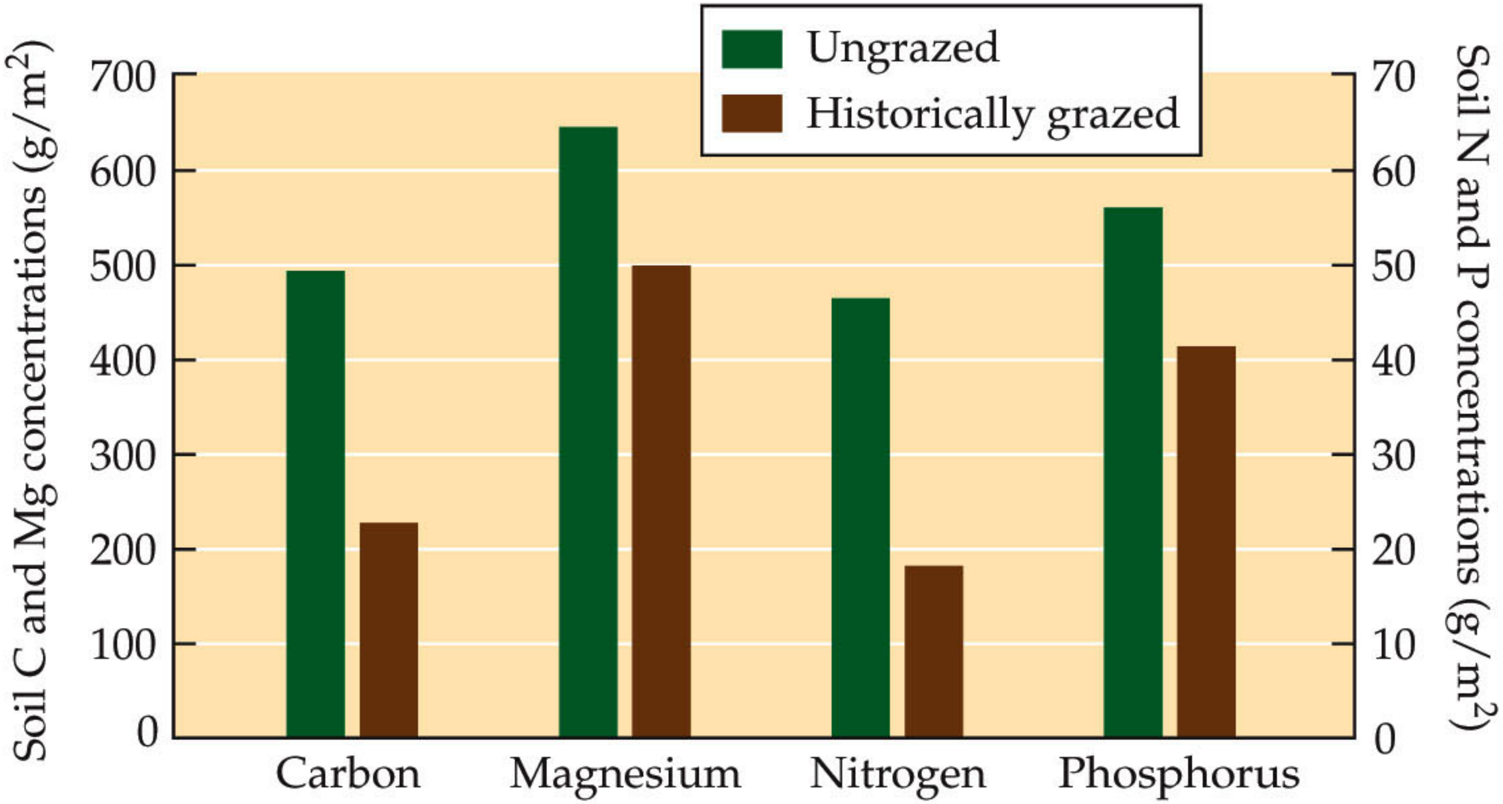
Case Study Revisited: A Fragile Crust

Soils in grazed plots had less Mg and P than in ungrazed plots.

The well developed crust in ungrazed plots had lower erosion rates and better retention of dust.

The crusts may also contribute to soil water retention, and to chemical weathering by altering pH.

Figure 21.20 Loss of Biological Crusts Results in Smaller Nutrient Pools



Case Study Revisited: A Fragile Crust

Soils in grazed plots had 60%–70% less C and N.

Although the crust had begun to recover, losses during the grazing period were high.

Cyanobacteria in crusts fix significant amounts of N.

Case Study Revisited: A Fragile Crust

The dark surface of the crust absorbs more solar radiation, and crust-covered soils retain more water.

This promotes decomposition and remineralization.

Connections in Nature: Nutrients, Disturbance, and Invasive Species

By increasing nutrient supplies and stabilizing soils, biological crusts enhance primary production.

Plants growing in association with crusts have higher growth rates and contain more nutrients.

Plant cover increases, and there is a lower germination and survival rate for invasive plant species.

Connections in Nature: Nutrients, Disturbance, and Invasive Species

Prior to Euro-American settlement, the Colorado Plateau area was not heavily grazed by native animals.

Aridity and long-term development of biological crusts may have given the soils of the Colorado Plateau an especially low tolerance for heavy grazing.

Connections in Nature: Nutrients, Disturbance, and Invasive Species

Soil disturbance and loss of biological crust has been conducive to the spread of non-native species, notably cheatgrass.

Cheatgrass is a spring annual that sets seed, dies, and dries out by early summer, increasing the amount of dry, combustible vegetation during the summer.

Connections in Nature: Nutrients, Disturbance, and Invasive Species

Cheatgrass has increased fire frequency to intervals of about 3–5 years, compared with natural fire frequencies of 60–100 years.

Native grasses and shrubs can not recover from these frequent fires, and cheatgrass increases in dominance.

Figure 21.21 Scourge of the Intermountain West

Connections in Nature: Nutrients, Disturbance, and Invasive Species

Cheatgrass lowers rates of nitrogen cycling by producing litter with a higher C:N ratio relative to native species.

The combination of increased fire frequency, increased competition, and less nutrient cycling has led to decreases in native species diversity in many areas.