19

Production

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- Primary Production
- Environmental Controls on NPP
- Global Patterns of NPP
- Secondary Production

- *Case Study Revisited*
- *Connections in Nature*: Energy-Driven Succession and Evolution in Hydrothermal Vent Communities

Case Study: Life in the Deep Blue Sea, How Can It Be?

The deep sea was once thought to have few forms of life because of the darkness (no photosynthesis), and tremendous pressures.

But in 1977, a whole new kind of community was discovered in the deep sea.

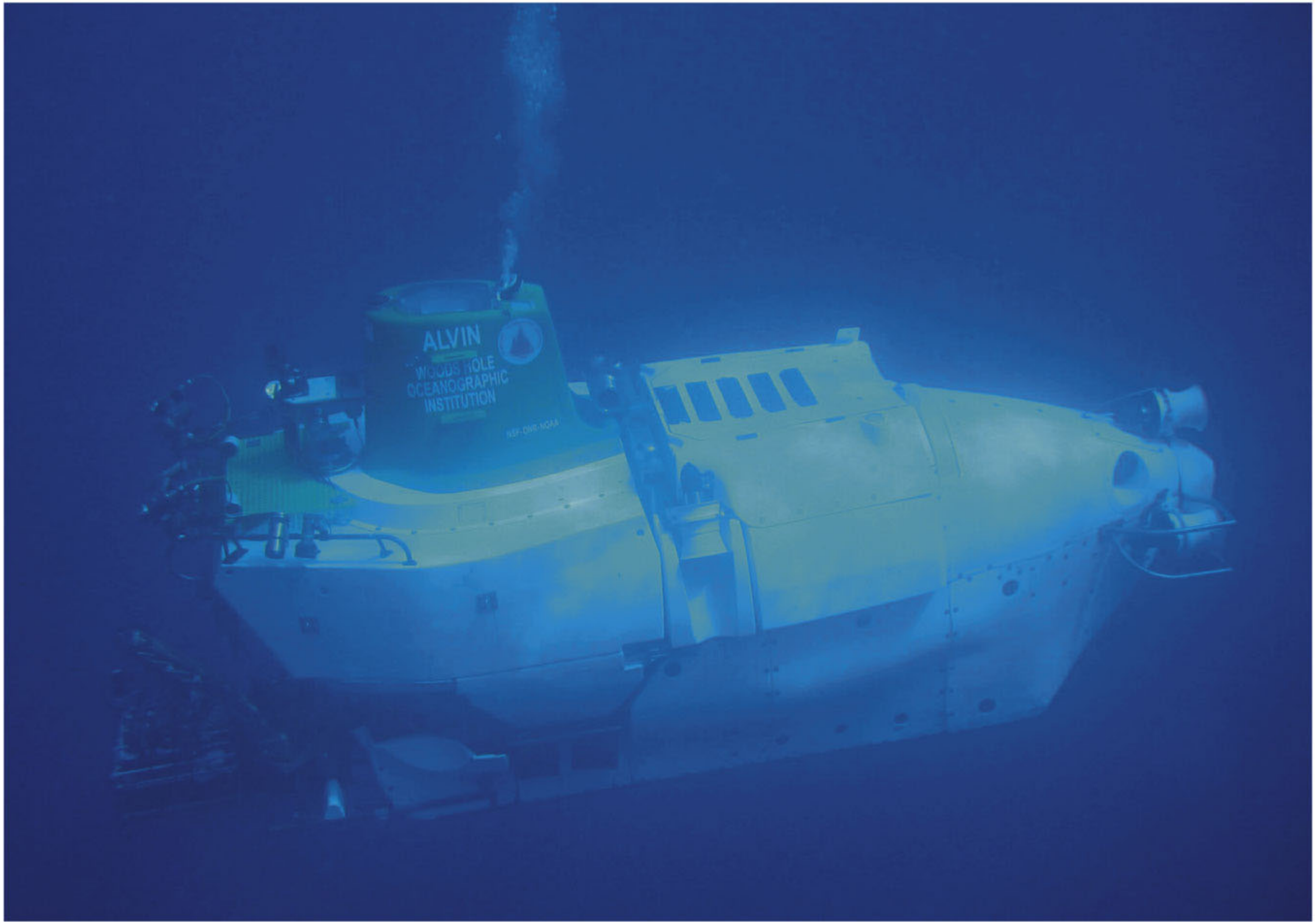
Case Study: Life in the Deep Blue Sea, How Can It Be?

Researchers using the submersible *Alvin* were searching the mid-ocean ridges for hot springs.

The ridges are the site of sea-floor spreading and are volcanically active.

Geologists hypothesized that heat from Earth’s crust would be released there by hot springs.

Figure 19.1 *Alvin* in Action

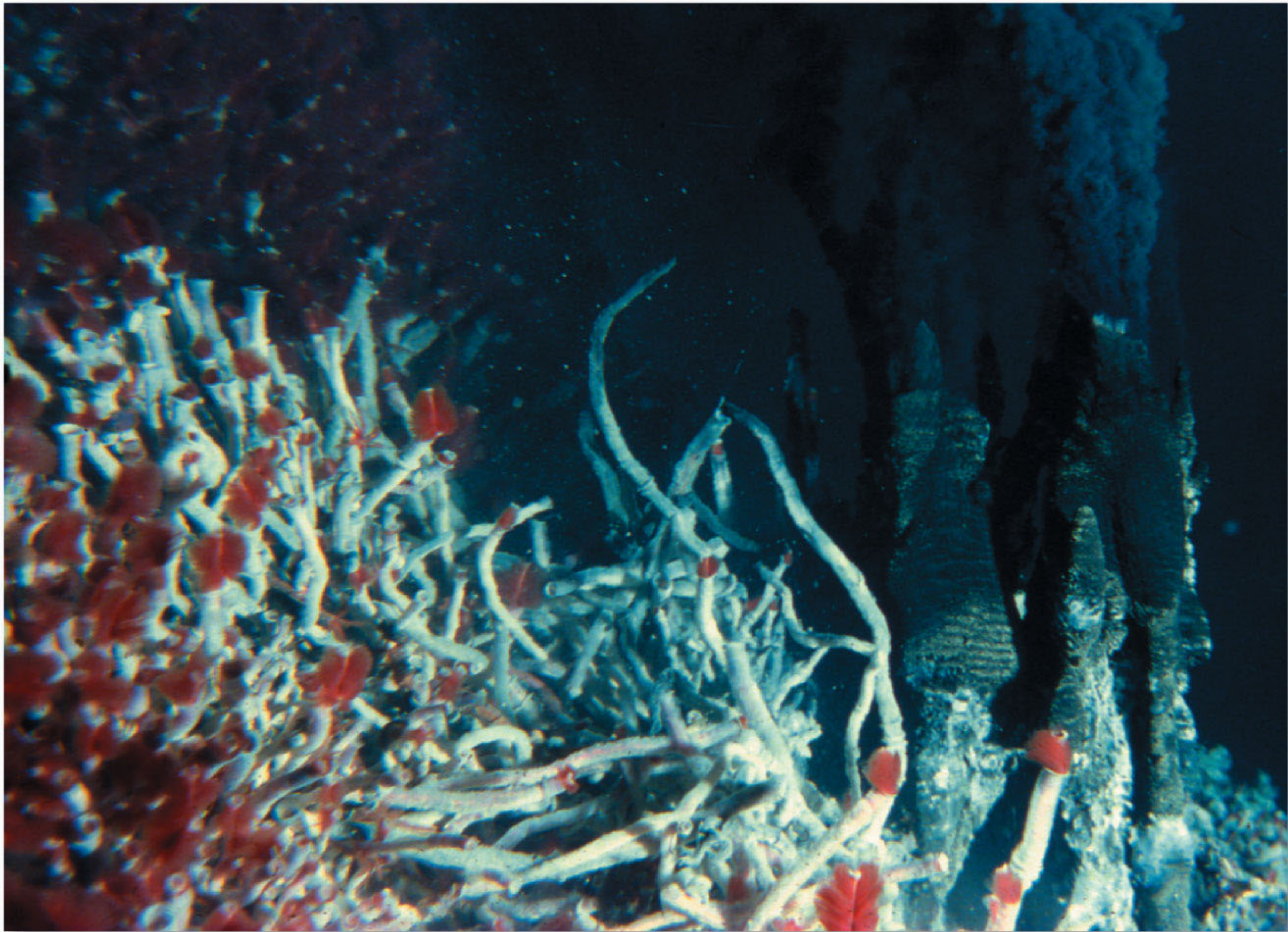


Case Study: Life in the Deep Blue Sea, How Can It Be?

Hot springs, or hydrothermal vents, were indeed found, along with an amazing community of living organisms—tube worms (*Riftia*), giant clams, shrimps, crabs, and polychaete worms.

Where did these organisms get energy? Photosynthesis was out, and the rate at which dead organisms from the upper zones accumulate on the bottom is very low.

Figure 19.2 Life around a Hydrothermal Vent



Case Study: Life in the Deep Blue Sea, How Can It Be?

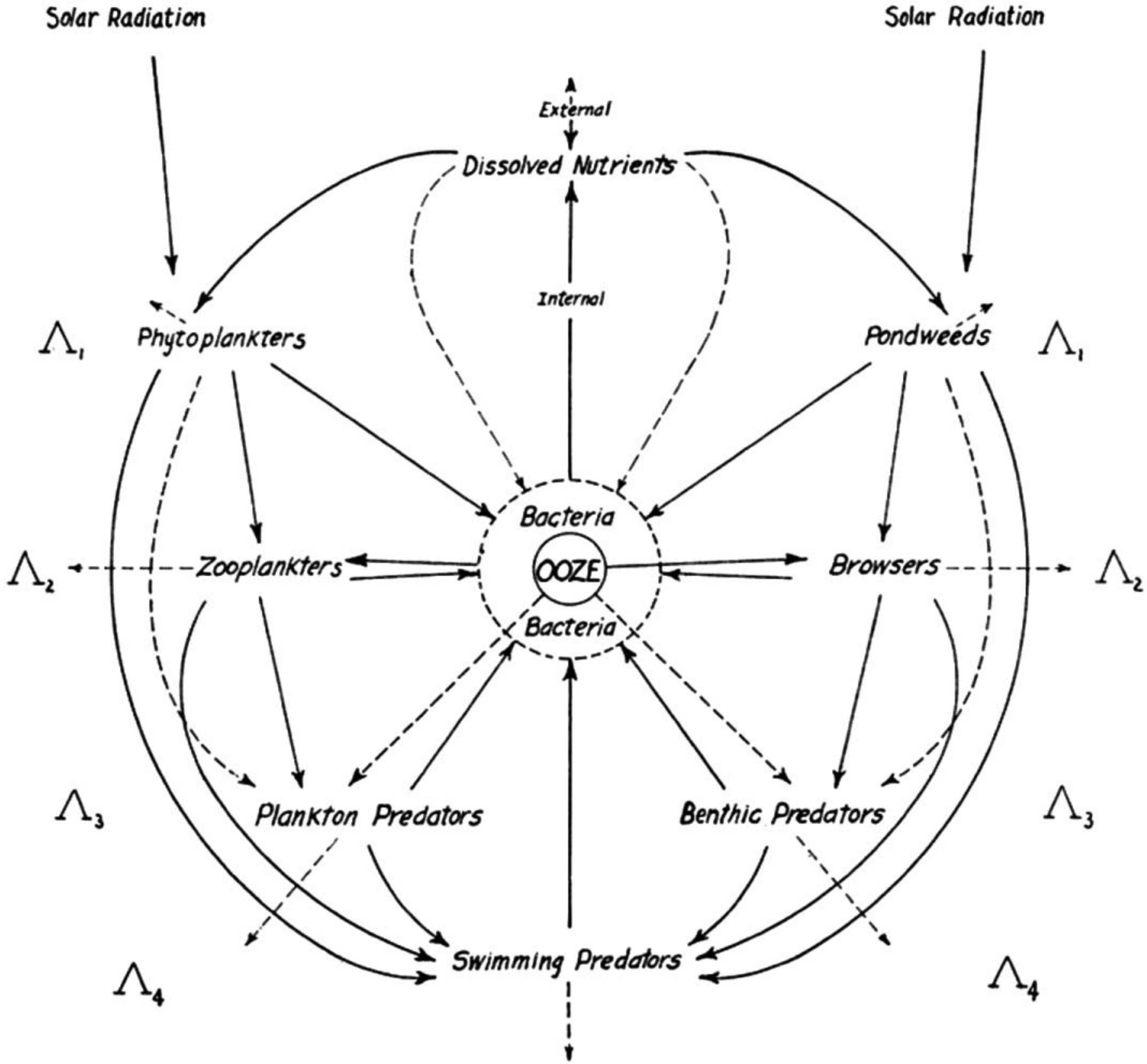
In addition, the water coming out of the vents was extremely hot, and contained minerals that would be toxic to most organisms.

How do these communities survive?

Introduction

In 1942, a groundbreaking paper on energy transfers in a bog ecosystem was published, one of the first in the area of ecosystem science.

Instead of putting the organisms into taxonomic categories, Lindeman grouped them into functional categories, based primarily on how they obtained their energy.


Solar Radiation
Solar Radiation
External
Dissolved Nutrients
Internal
Phytoplankters
Pondweeds
Λ_1
Λ_1
Zooplankters
Bacteria
OOZE
Bacteria
Browsers
Λ_2
Λ_2
Λ_3
Λ_3
Plankton Predators
Benthic Predators
Swimming Predators
Λ_4
Λ_4

Introduction

The term **ecosystem** was first used by A. G. Tansley (1935) to refer to all of the components of an ecological system, biotic and abiotic, that influence the flow of energy and elements.

The ecosystem concept is a powerful tool for integrating ecology with other disciplines such as geochemistry, hydrology, and atmospheric science.

Concept 19.1: Energy in ecosystems originates with primary production by autotrophs.

Primary production is the chemical energy generated by autotrophs, derived from fixation of CO_2 in photosynthesis and chemosynthesis.

Primary production is the source of energy for all organisms, from bacteria to humans.

Primary Production

Energy assimilated by autotrophs is stored as carbon compounds in plant tissues; carbon is the currency used for the measurement of primary production.

Primary productivity is the rate of primary production.

Primary Production

Gross primary production (**GPP**)—total amount of carbon fixed by autotrophs in an ecosystem.

GPP depends on the influence of climate on photosynthetic rate and the **leaf area index** (**LAI**)—leaf area per unit of ground area.

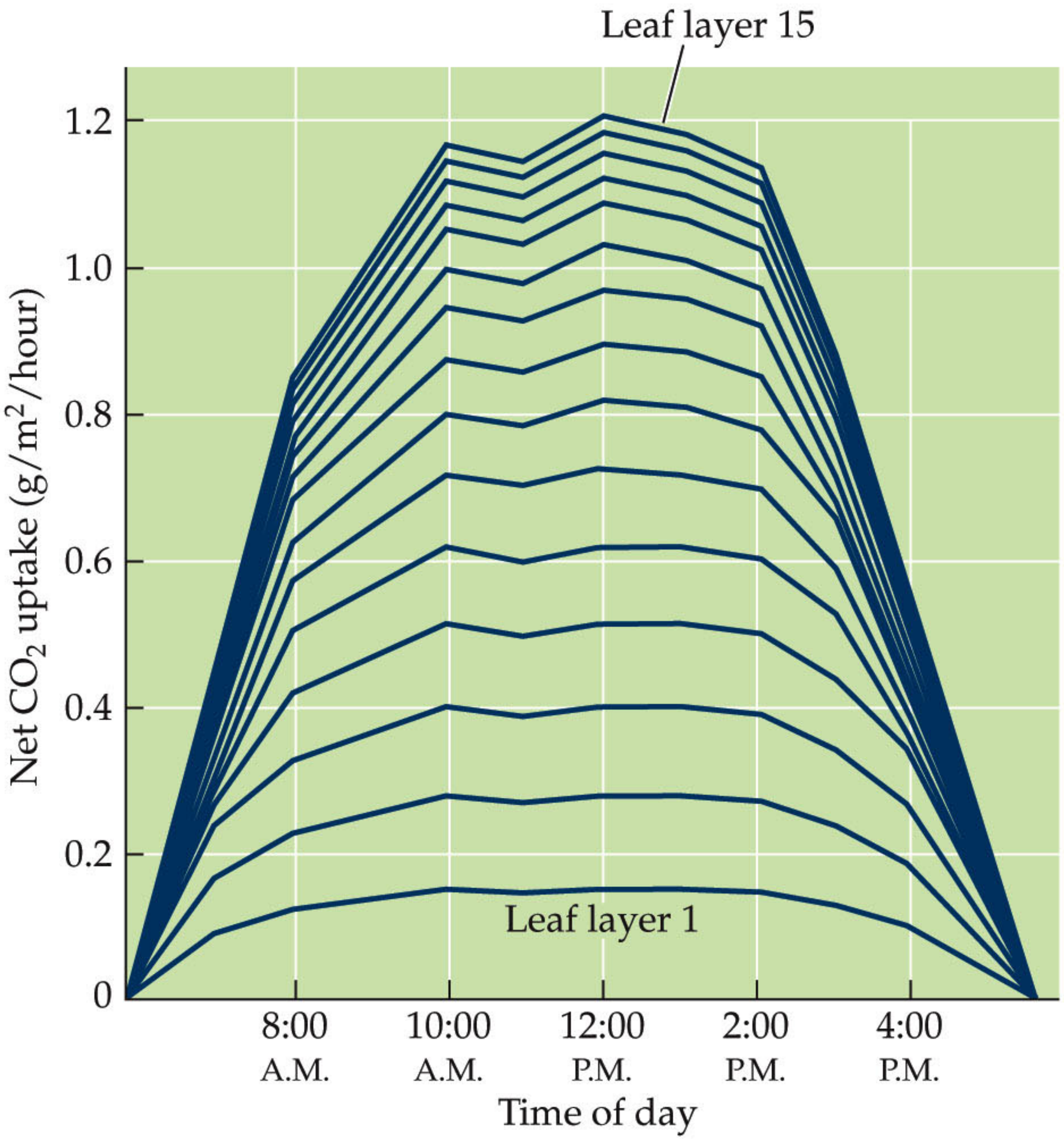
LAI varies among biomes:

- Less than 0.1 in Arctic tundra (less than 10% of the ground surface has leaf cover).
- 12 in boreal and tropical forests (on average, there are 12 layers of leaves between the canopy and the ground).

Because of shading, the incremental gain in photosynthesis for each added leaf layer decreases.

Eventually, the respiratory costs associated with adding leaf layers outweigh the photosynthetic benefits.

Figure 19.4 Diminishing Returns for Added Leaf Layers (Part 1)



ECOLOGY, Figure 19.4 (Part 1)

Figure 19.4 Diminishing Returns for Added Leaf Layers (Part 2)

Primary Production

Plants use about half of the carbon fixed in photosynthesis for cellular respiration to support biosynthesis and cellular maintenance.

All living plant tissues lose carbon via respiration, but not all tissues acquire carbon via photosynthesis (e.g., woody stems).

Net primary production (**NPP**):

NPP = GPP – respiration

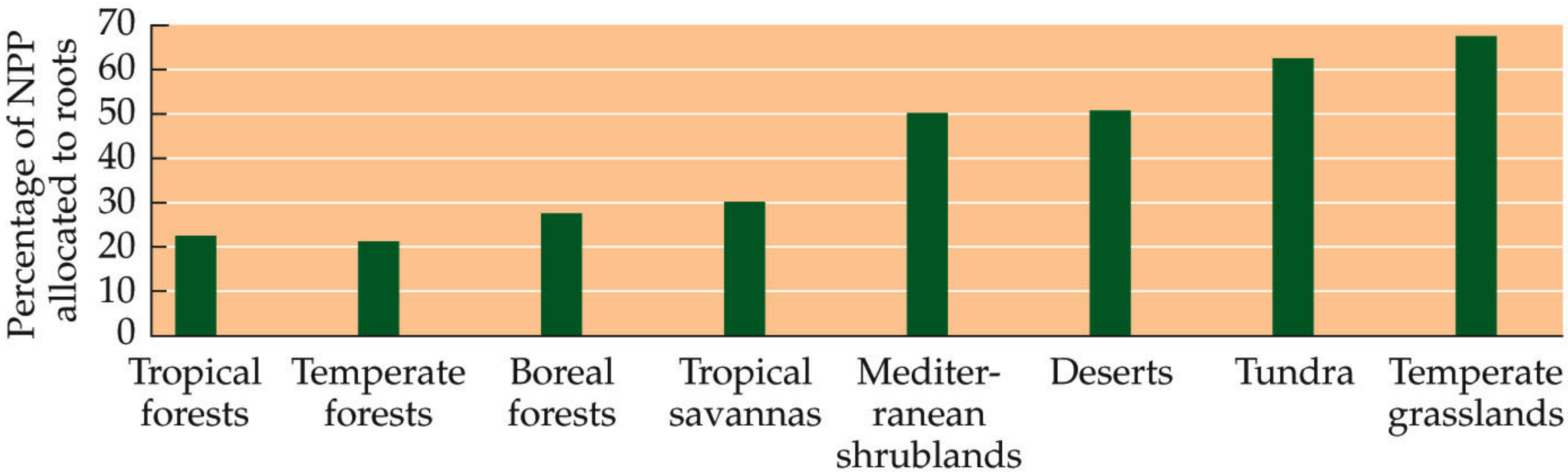
- NPP represents the biomass gained by the plant.
- NPP is the energy left over for plant growth and consumption by detritivores and herbivores.
- NPP represents storage of carbon in ecosystems.

Plants can respond to environmental conditions by allocating carbon to the growth of different tissues.

Allocation of NPP to growth of leaves, stems, and roots is balanced so that plants can maintain supplies of water, nutrients, and carbon.

Example: Grassland plants allocate more NPP to roots because soil nutrients and water are scarce.

Figure 19.5 Allocation of NPP to Roots



Allocation of NPP to storage products such as starch provides insurance against losses of tissues to herbivores, disturbances such as fire, and climatic events such as frost.

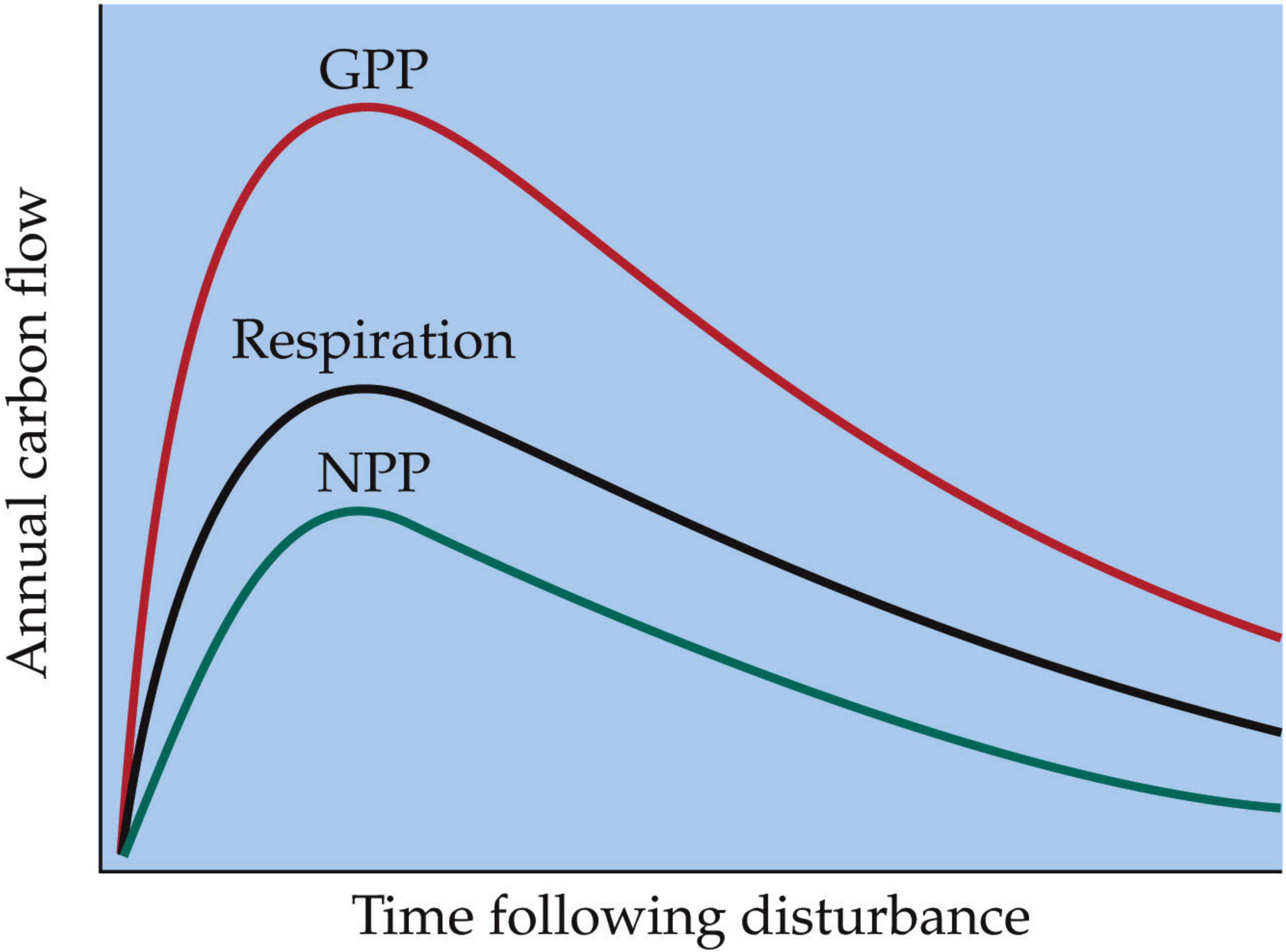
Substantial amounts of NPP (up to 20%) may be allocated to defensive secondary compounds.

Primary Production

As ecosystems develop during succession, NPP changes as LAI, ratio of photosynthetic to nonphotosynthetic tissue, and plant species composition all change.

The highest NPP is usually in the intermediate successional stages, when photosynthetic tissues, plant diversity, and nutrient supply tends to be highest.

Figure 19.6 NPP Changes during Forest Succession



ECOLOGY, Figure 19.6

Primary Production

Although NPP may decrease in later successional stages, old-growth ecosystems have large pools of stored carbon and nutrients and provide habitat for late successional animal species.

Primary Production

It is important to be able to measure NPP.

- NPP is the ultimate source of energy for all organisms in an ecosystem.
- Variation in NPP is an indication of ecosystem health—changes in primary productivity can be symptomatic of stress.
- NPP is associated with the global carbon cycle.

In terrestrial ecosystems, NPP can be estimated by measuring the increase in plant biomass in experimental plots, and scaling up to the whole ecosystem.

Harvest techniques provide reasonable estimates of aboveground NPP, particularly if corrections are made for losses to herbivory and mortality.

Measuring belowground NPP is more difficult.

- Roots *turn over* more quickly than shoots; that is, more roots are “born” and die during the growing season.
- Roots may exude a significant amount of carbon into the soil, or transfer carbon to mycorrhizal or bacterial symbionts.

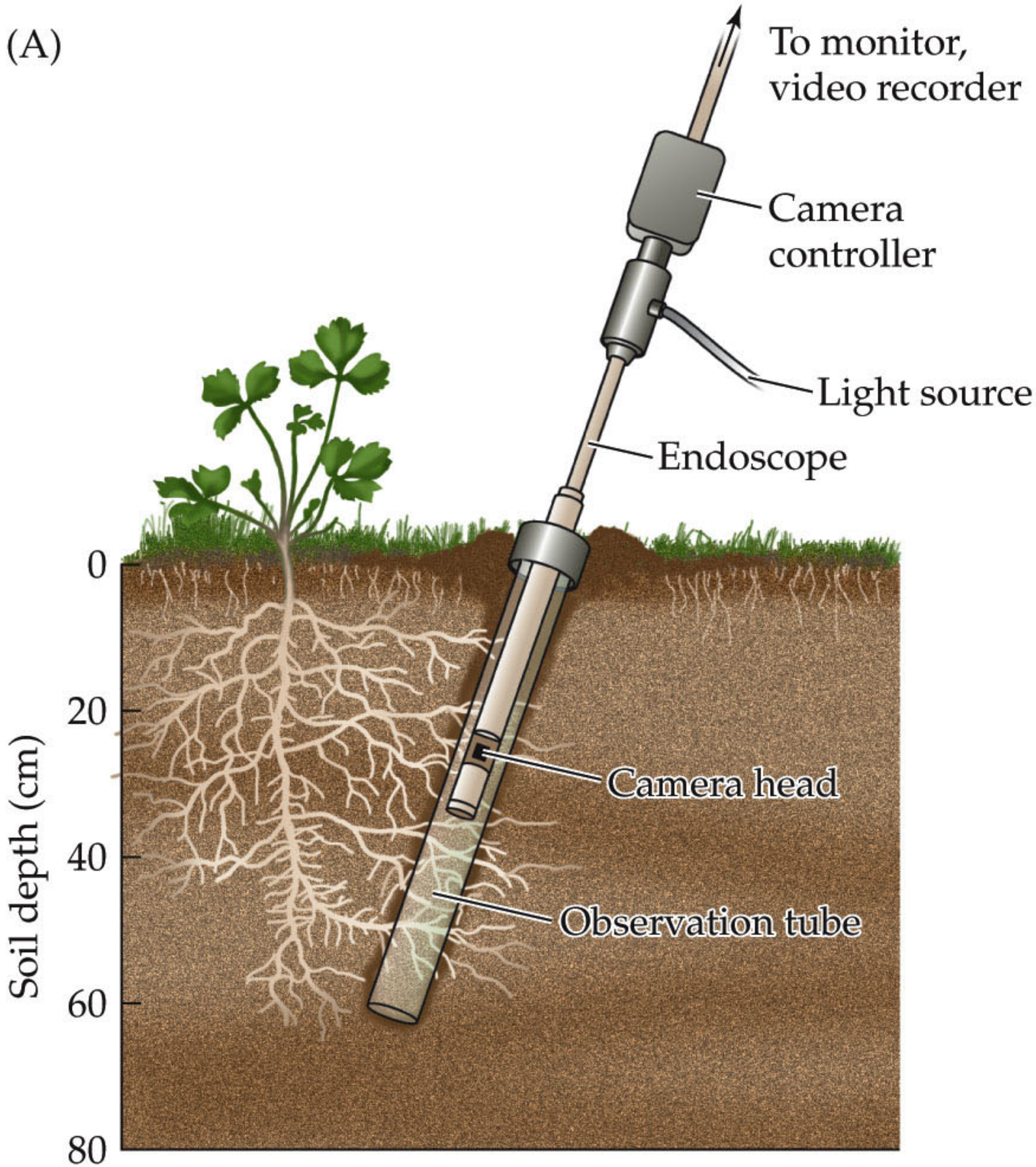
Harvests for measuring root biomass must be more frequent, and additional correction factors must be used.

Biomass can be estimated from aboveground measurements and algorithms that relate above- and belowground biomass.

Minirhizotrons are underground viewing tubes outfitted with video cameras.

They have led to significant advances in the understanding of belowground production processes.

Figure 19.7 A Tool for Viewing Belowground Dynamics (Part 1)



ECOLOGY, Figure 19.7 (Part 1)

(B)

Harvest techniques are impractical for large or biologically diverse ecosystems.

Chlorophyll concentrations can provide a proxy for GPP and NPP. They can be estimated using remote sensing methods that rely on reflection of solar radiation.

Chlorophyll absorbs visible solar radiation in blue and red wavelengths and has a characteristic “spectral signature.”

Plants also have higher reflectance in the infrared wavelengths than do bare soil or water.

Indices for estimating NPP from reflection of several different wavelengths have been developed.

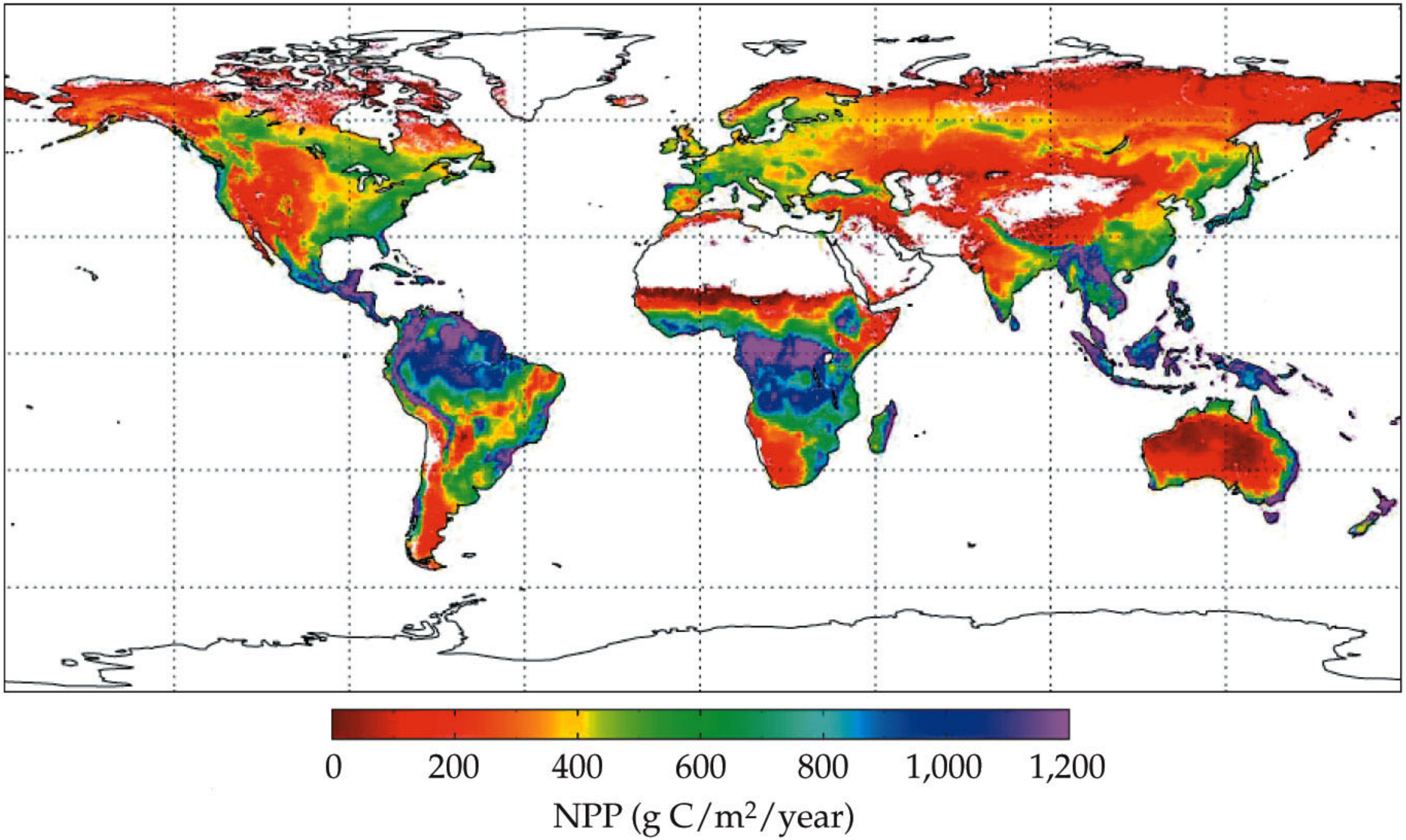
Primary Production

NDVI (normalized difference vegetation index) uses the difference between visible light and near-infrared reflectance to estimate the absorption of light by chlorophyll.

This is then used to estimate CO_2 uptake.

NDVI is measured using satellite sensors.

Figure 19.8 Remote Sensing of Terrestrial NPP



NPP can be estimated from GPP and respiration measurements.

This involves measuring change in CO_2 concentration in a closed chamber.

Sometimes whole stands of plants are enclosed in a chamber or tent and exchange of CO_2 with the atmosphere in the tent is measured.

Sources of CO_2 added to the tent atmosphere are respiration by plants and heterotrophs, including soil microorganisms.

Uptake of CO_2 is by photosynthesis.

The net change in CO_2 concentration inside the tent is a balance of GPP uptake and total respiration—**net ecosystem production** or **net ecosystem exchange** (**NEE**).

Heterotrophic respiration must be subtracted to obtain NPP.

NEE can also be estimated by measuring CO_2 at various heights in a plant canopy and the atmosphere above, called eddy correlation or eddy covariance.

A gradient of CO_2 develops because of photosynthesis and respiration.

During the day, CO_2 decreases in the canopy with photosynthesis. At night, CO_2 is higher in the canopy.

Instruments are mounted on towers to take continuous CO_2 measurements.

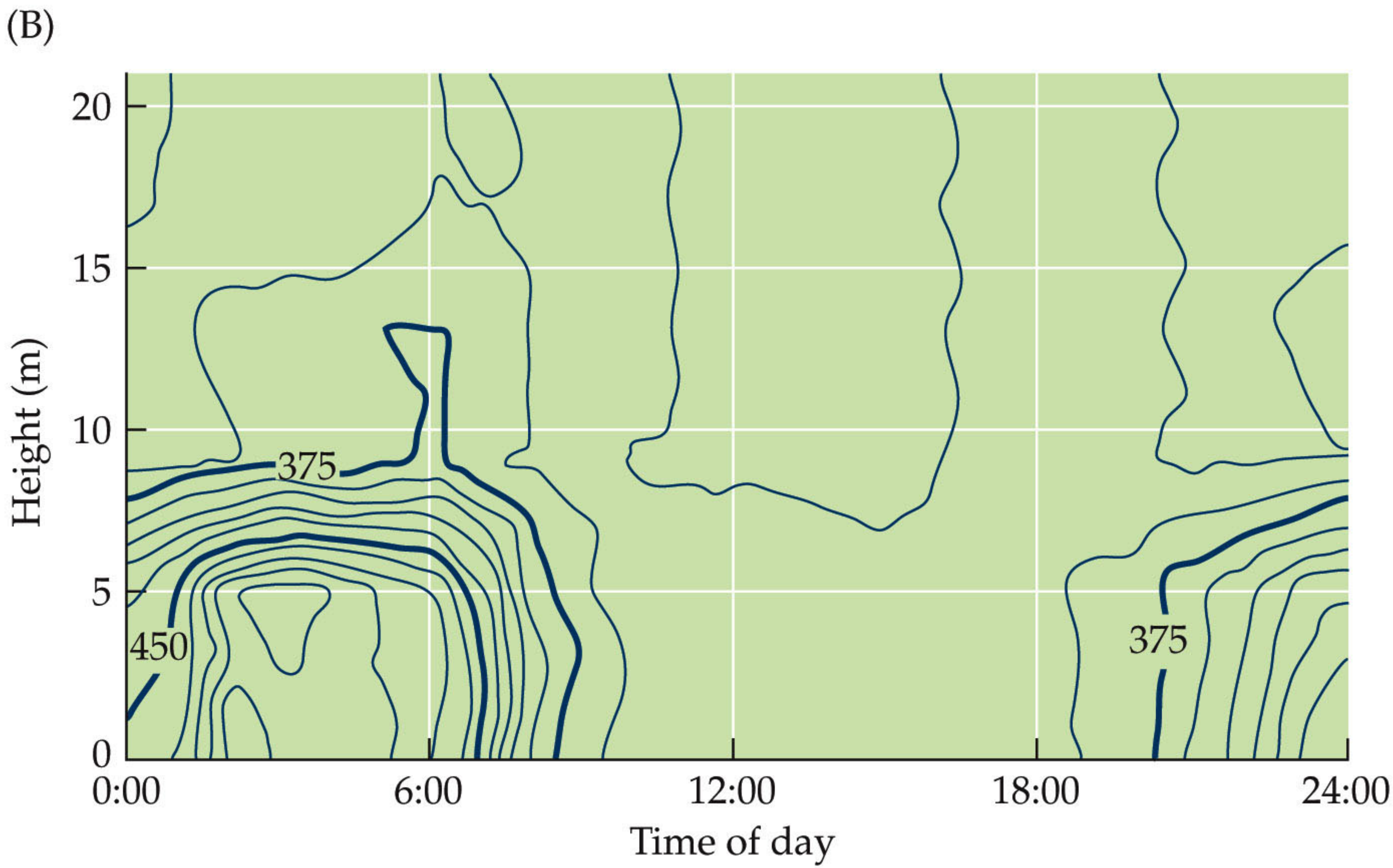
NEE can be estimated for up to several square kilometers of the surrounding area.

A network of these sites has been established in the Americas to increase our understanding of carbon and climate.

Figure 19.9 Eddy Covariance Estimates of NPP (Part 1)

(A)

ECOLOGY, Figure 19.9 (Part 1)


(B)
Height (m)
20
15
10
5
0
375
450
375
0:00
6:00
12:00
18:00
24:00
Time of day

Primary Production

Phytoplankton do most of the photosynthesis in aquatic habitats.

Phytoplankton turn over much more rapidly than terrestrial plants, so biomass at any given time is low compared with NPP; harvest techniques are not used.

Primary Production

Photosynthesis and respiration are measured in water samples collected and incubated at the site with light (for photosynthesis) and without light (for respiration).

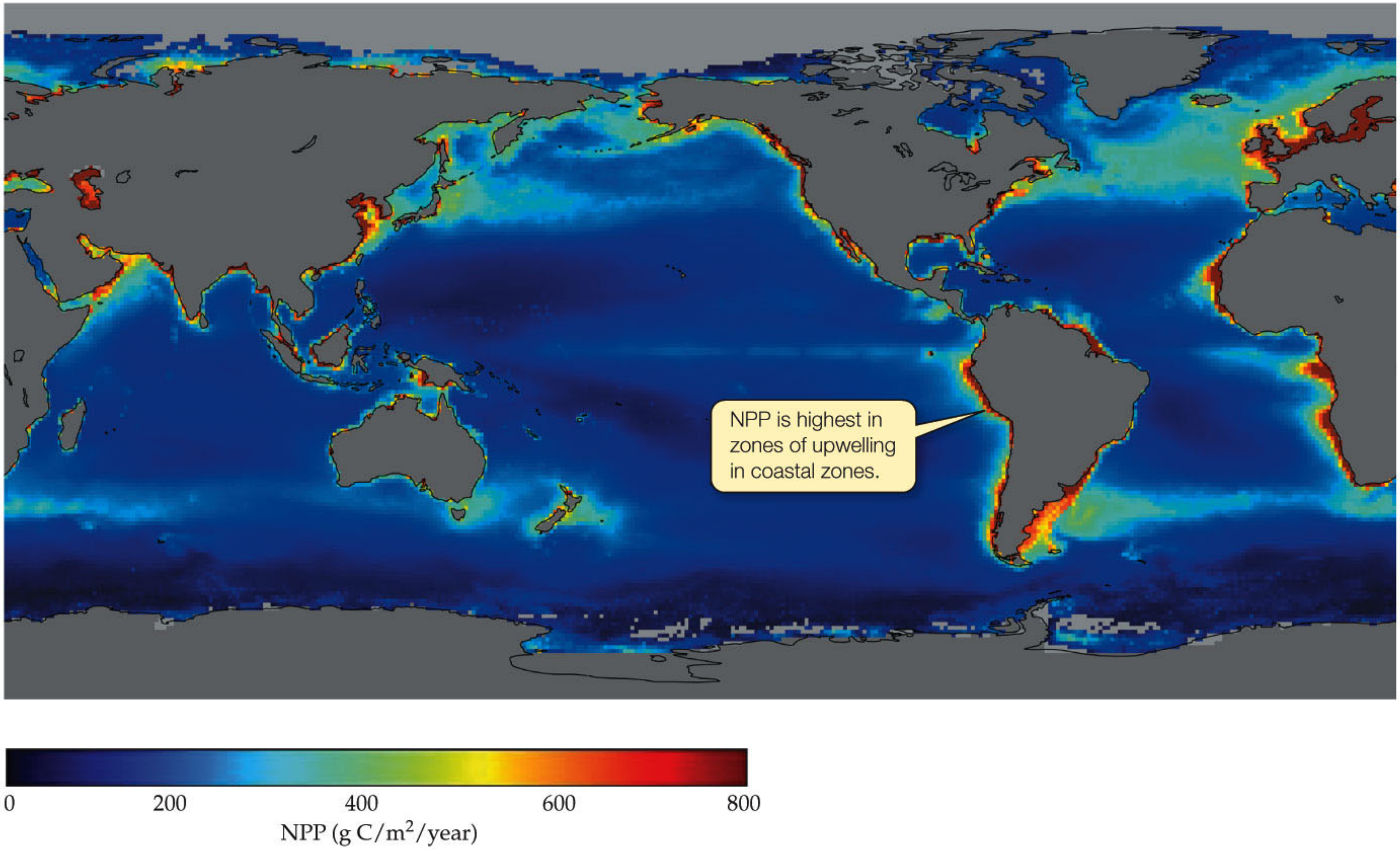
The difference in the rates is equal to NPP.

Primary Production

Remote sensing of chlorophyll concentrations in the ocean using satellite sensors provides good estimates of marine NPP.

Indices are used to indicate how much light is being absorbed by chlorophyll, which is then related to NPP.

Figure 19.10 Remote Sensing of Marine NPP



Environmental Controls on NPP

Concept 19.2: Net primary productivity is constrained by both physical and biotic environmental factors.

NPP varies substantially over space and time.

NPP is correlated with climate (temperature and precipitation) on a global scale.

Figure 19.11 Global Patterns of Terrestrial NPP Are Correlated with Climate (Part 1)

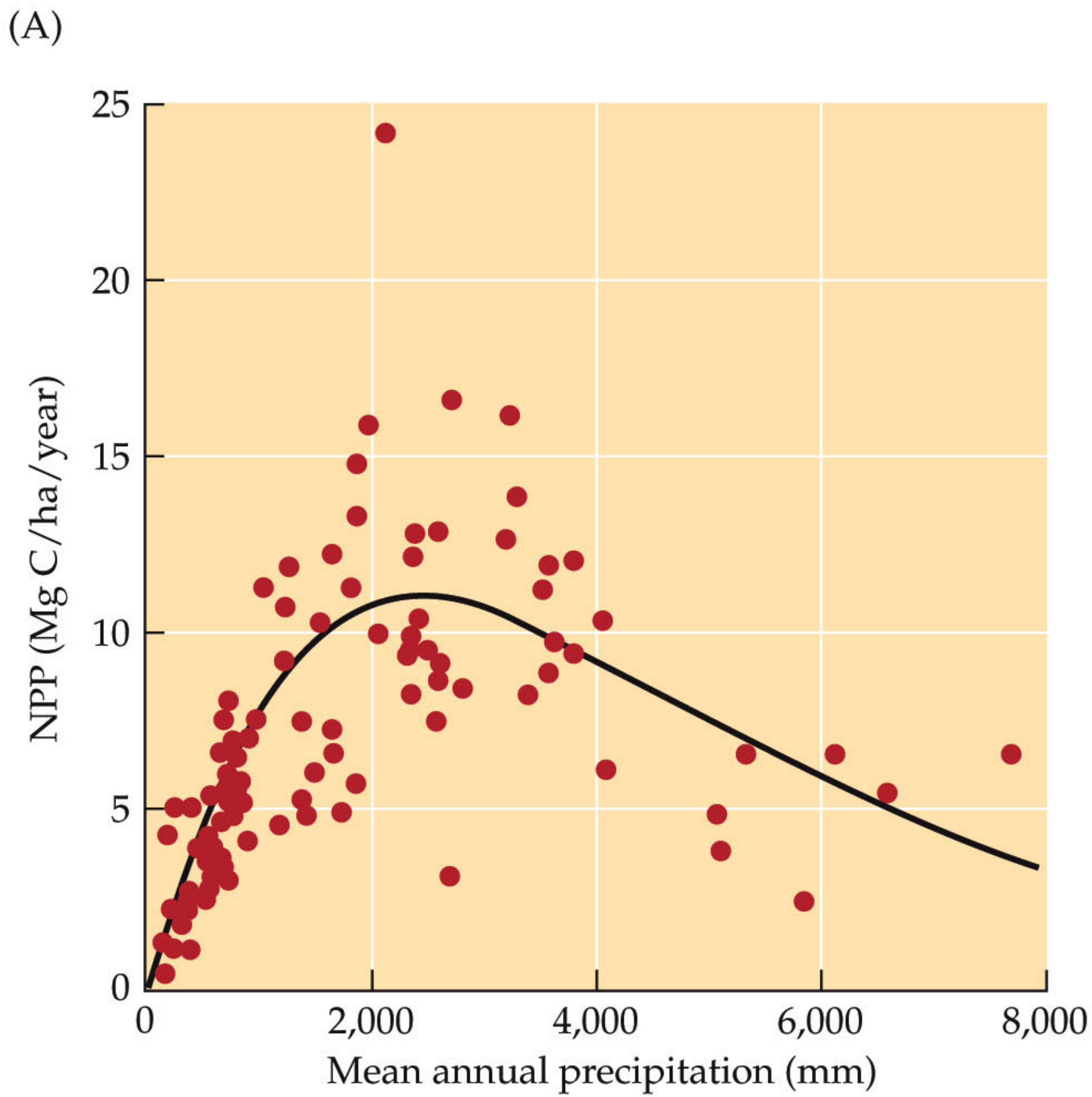
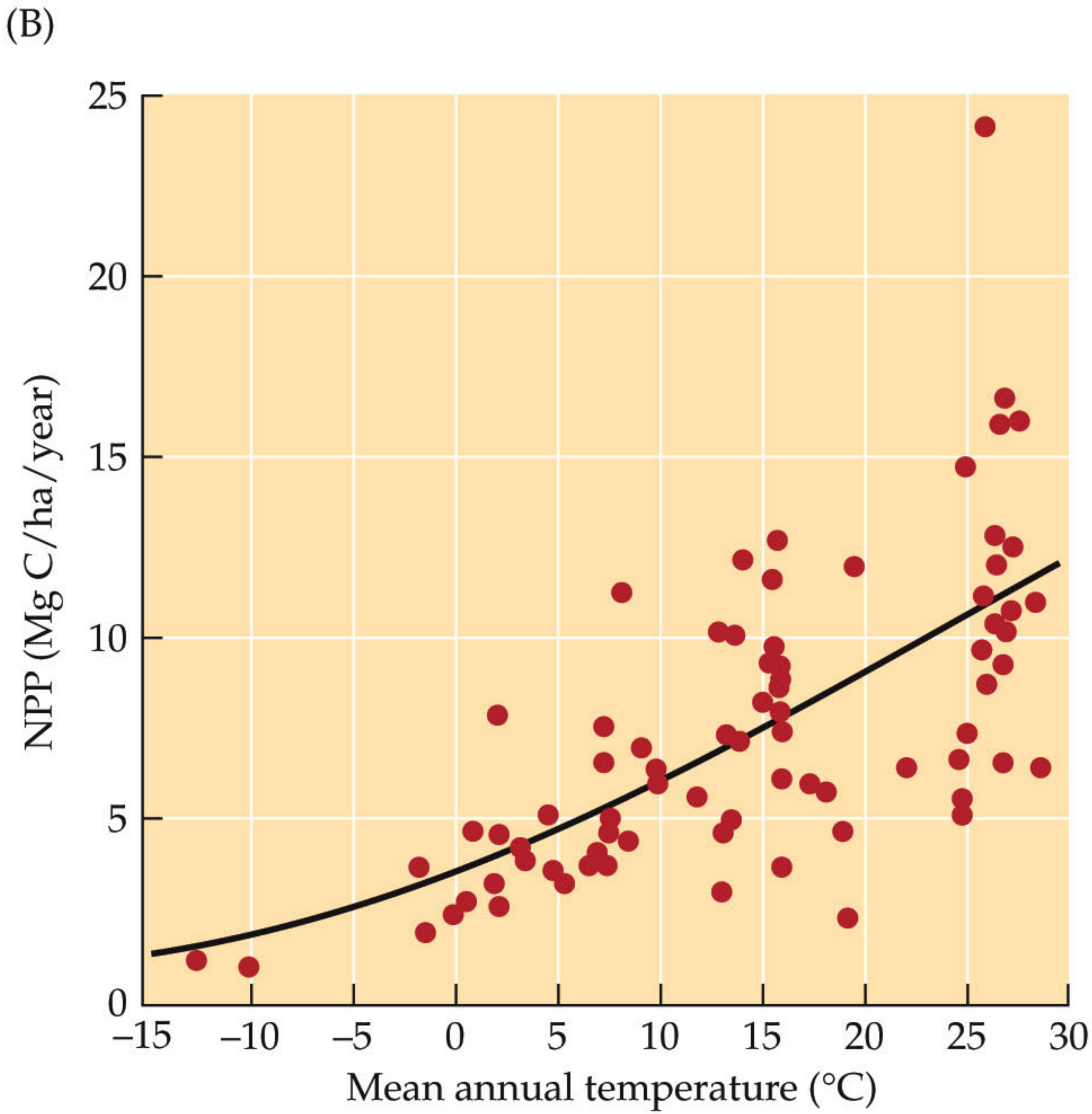


Figure 19.11 Global Patterns of Terrestrial NPP Are Correlated with Climate (Part 2)



ECOLOGY, Figure 19.11 (Part 2)

Environmental Controls on NPP

Water availability influences photosynthesis via the opening and closing of stomates, and temperature influences the enzymes that facilitate photosynthesis.

At very high precipitation, NPP may decrease because of greater cloud cover and lower sunlight, leaching of nutrients from soils, and soil saturation, which results in anoxic conditions.

Environmental Controls on NPP

Climate influence on NPP can also be indirect, mediated by factors such as nutrient availability.

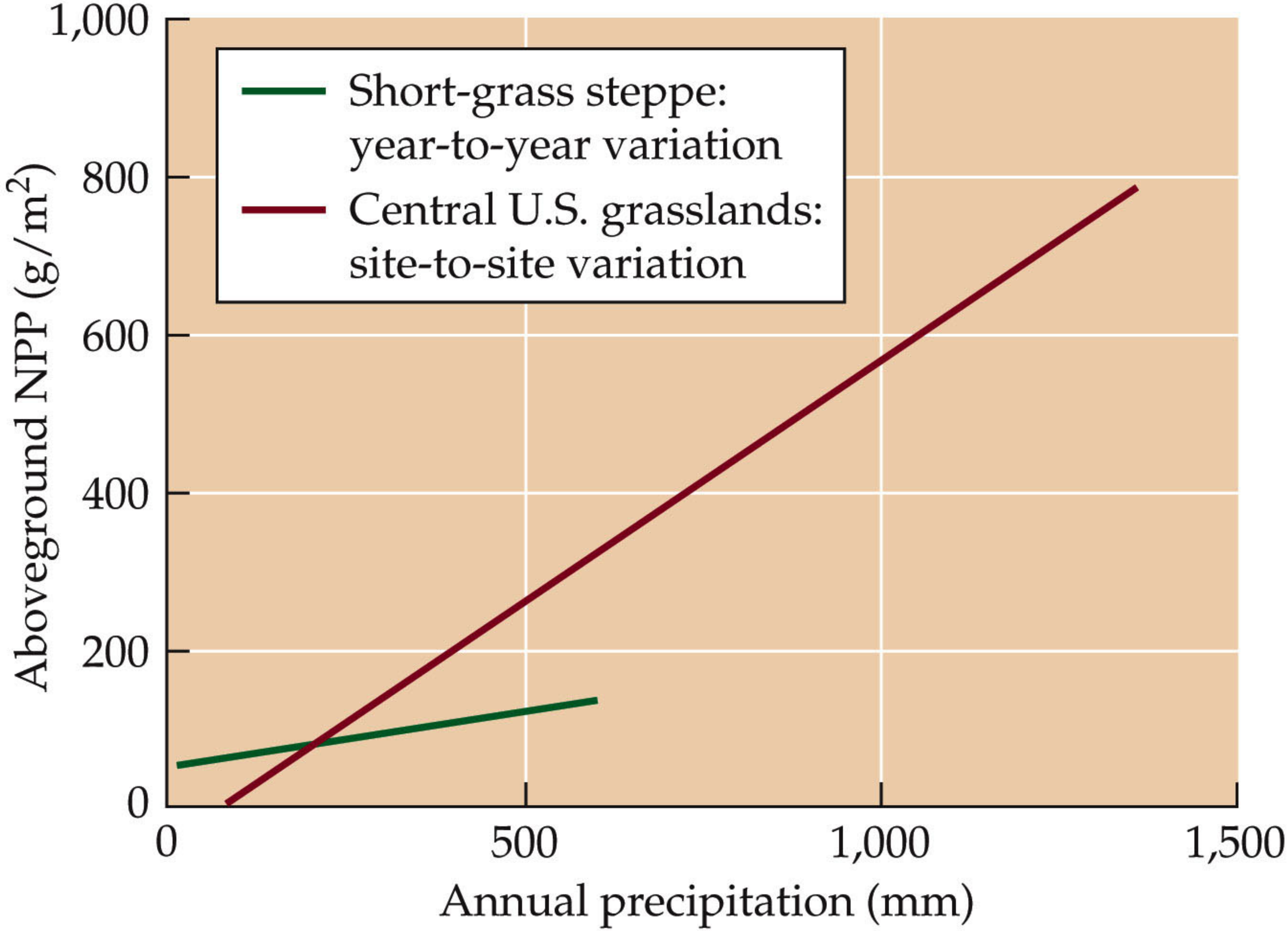
NPP in a short-grass steppe ecosystem changed in response to year-to-year variation in precipitation (Lauenroth and Sala 1992).

Environmental Controls on NPP

They also looked at the relationship between NPP and precipitation across several grassland ecosystems in the central U.S.

NPP variation with precipitation was greater over the range of sites, than it was from year to year at one site.

Figure 19.12 The Sensitivity of NPP to Changes in Precipitation Varies among Grassland Ecosystems



The difference was attributed to variation in species composition across the sites.

Different grass species have different growth responses to water availability.

They also suggested there was a time lag in the response of the short-grass steppe to increased precipitation.

Environmental Controls on NPP

The results of several experiments indicate that nutrients, particularly nitrogen, control NPP in terrestrial ecosystems.

In a fertilization experiment in two alpine communities—dry and wet meadows—N, P, and N+P were added to different plots (Bowman et al. 1993).

Environmental Controls on NPP

In the dry meadow, N limited NPP.

In the wet meadow, both N and P limited NPP.

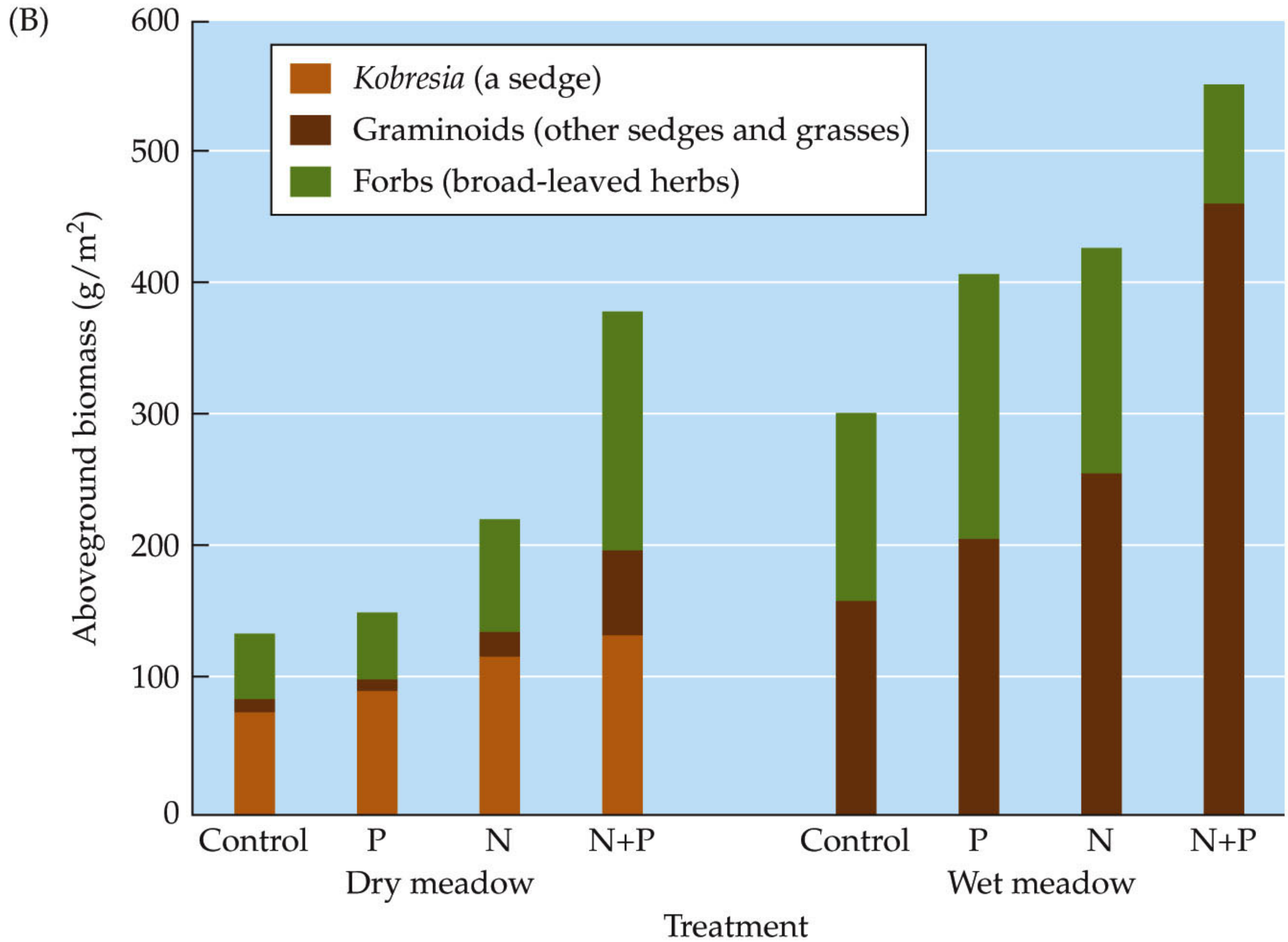
Another experiment showed that the addition of water to the dry meadow did not increase NPP.

Soil moisture affects nutrient supply through its effects on decomposition and movement of nutrients in the soil.

Figure 19.13 Nutrient Availability Influences NPP in Alpine Communities (Part 1)

(A)

Figure 19.13 Nutrient Availability Influences NPP in Alpine Communities (Part 2)



Environmental Controls on NPP

Increase in NPP was not uniform across all plant types.

Change in NPP in the dry meadow resulted from change in species composition. The dominant plant biomass did not increase as much as others.

In the wet meadow, the dominant’s biomass increased more than the others.

Environmental Controls on NPP

Plants from resource-poor communities show less response to fertilization than plants from resource-rich communities.

They have different capacities to use resources.

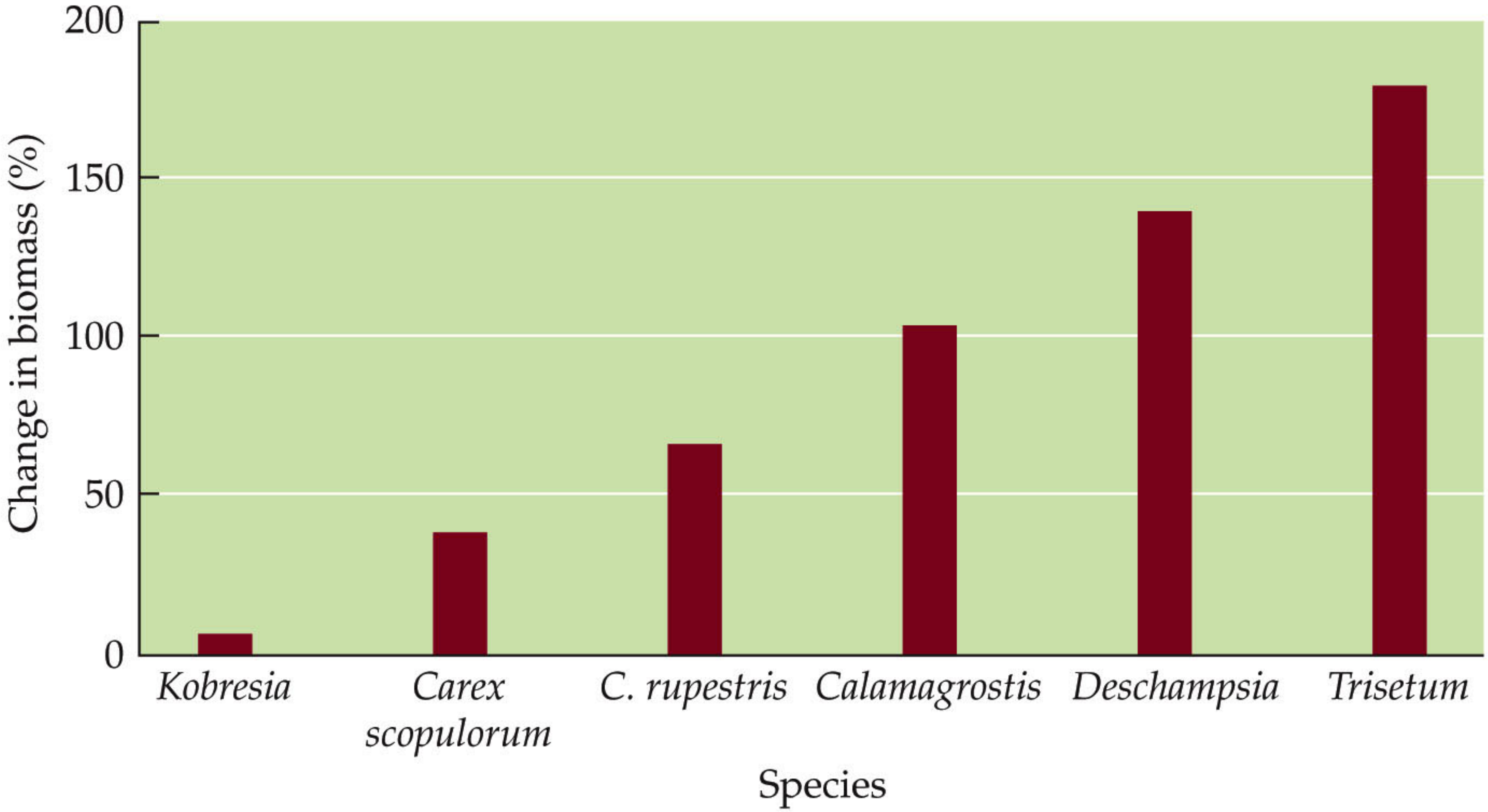
Plants of resource-poor communities tend to have low intrinsic growth rates, which lowers their resource requirements.

Environmental Controls on NPP

Plants of resource-rich communities tend to have higher growth rates, which make them better able to compete for resources, particularly light.

When nutrient-poor communities are fertilized, there is often a change in species composition; indicating the importance of species composition in NPP rates.

Figure 19.14 Growth Responses of Alpine Plants to Added Nitrogen



ECOLOGY, Figure 19.14

Environmental Controls on NPP

NPP in lake ecosystems is often limited by phosphorus availability.

Many lake experiments use enclosures called “limnocorrals”—clear containers with open tops to which nutrients can be added.

NPP is measured by change in chlorophyll concentrations or number of phytoplankton cells.


DISTURB

Environmental Controls on NPP

Whole-lake fertilization experiments have also been done at the Experimental Lakes Area in Ontario.

Declining water quality in the 1960s motivated David Schindler to do experiments to determine whether inputs of nutrients in wastewater were causing the dramatic increases in the growth of phytoplankton.

Environmental Controls on NPP

Nitrogen, carbon, and phosphorus were added to all or half of several lakes.

Results showed that P was the limiting nutrient.

P addition resulted in massive increases in cyanobacteria.

Figure 19.16 Response of a Lake to Phosphorus Fertilization

ECOLOGY, Figure 19.16

Environmental Controls on NPP

In rivers and streams, NPP is often low. The majority of the energy is derived from terrestrial organic matter.

Water flow limits phytoplankton growth; most NPP is from macrophytes and attached algae.

The *river continuum concept* describes the increasing importance of in-stream NPP as the river flows downstream.

Environmental Controls on NPP

Suspended sediment in rivers can limit light penetration; thus water clarity often controls NPP.

Nutrients, particularly nitrogen and phosphorus, can also limit NPP in streams and rivers.

Environmental Controls on NPP

Limiting nutrients vary in marine ecosystems.

Estuaries are usually nutrient-rich; variation in NPP is correlated with N inputs from rivers.

N from agricultural and industrial practices can result in blooms of algae and “dead zones.”

Environmental Controls on NPP

Dead zones are areas of low oxygen, and high fish and zooplankton mortality.

The bacterial decomposition of algae from the blooms depletes the dissolved oxygen in the water.

Environmental Controls on NPP

In the open ocean, NPP is mainly from phytoplankton.

Picoplankton (cells < 1 μm) contribute as much as 50% of the total marine NPP.

Floating seaweeds such as *Sargassum* also contribute to NPP.

Environmental Controls on NPP

In coastal areas, kelp forests may have leaf area indices and rates of NPP as high as those of tropical forests.

“Meadows” of seagrasses such as eelgrass (genus *Zostera*) are also important nearshore zones.

Environmental Controls on NPP

In the open ocean, NPP is mostly limited by nitrogen.

But NPP in the equatorial Pacific Ocean appears to be limited by iron (Martin et al. 1994).

Environmental Controls on NPP

Because windblown dust from Asia is a source of iron, it could be important in the global climate system through its influence on marine NPP, and thus on atmospheric CO_2 concentrations.

During glacial periods, large parts of the earth could have contributed dust (and iron) that fertilized the oceans.

The concomitant increase in CO_2 uptake by marine phytoplankton could have reduced atmospheric CO_2 concentrations, setting up a positive feedback that cooled the climate even more.

This led to the suggestion that fertilizing the oceans with iron could reduce global warming.

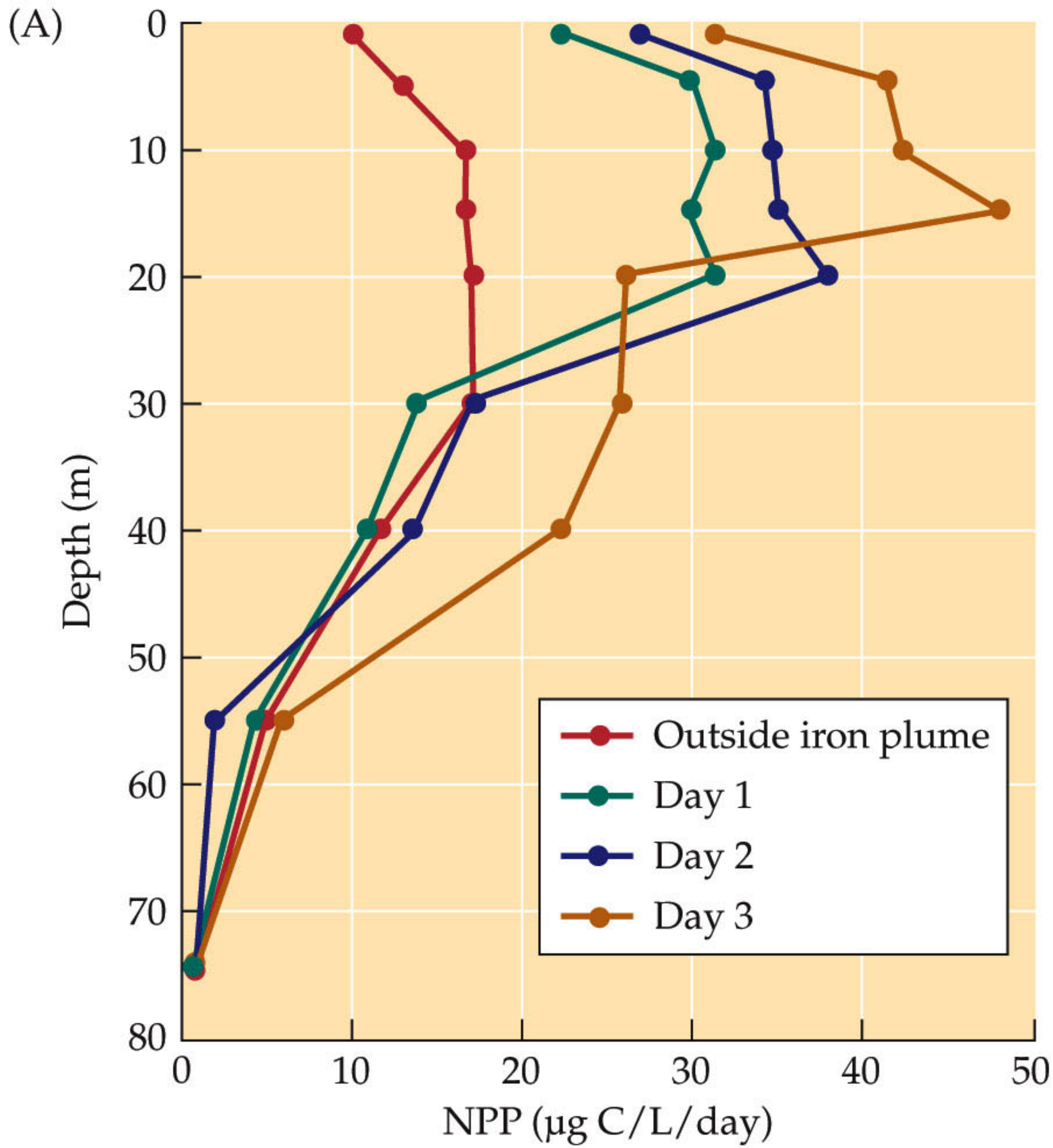
Environmental Controls on NPP

Martin is famously quoted as having said "Give me half a tanker-load of iron, and I'll give you an Ice Age."

Large-scale experiments with iron sulfate additions were done in 1993, called IronEx I.

A 64 km^2 area was fertilized with 445 kg of iron, which resulted in a doubling of phytoplankton biomass and a fourfold increase in NPP.

Figure 19.17 Effect of Iron Fertilization on Marine NPP (Part 1)



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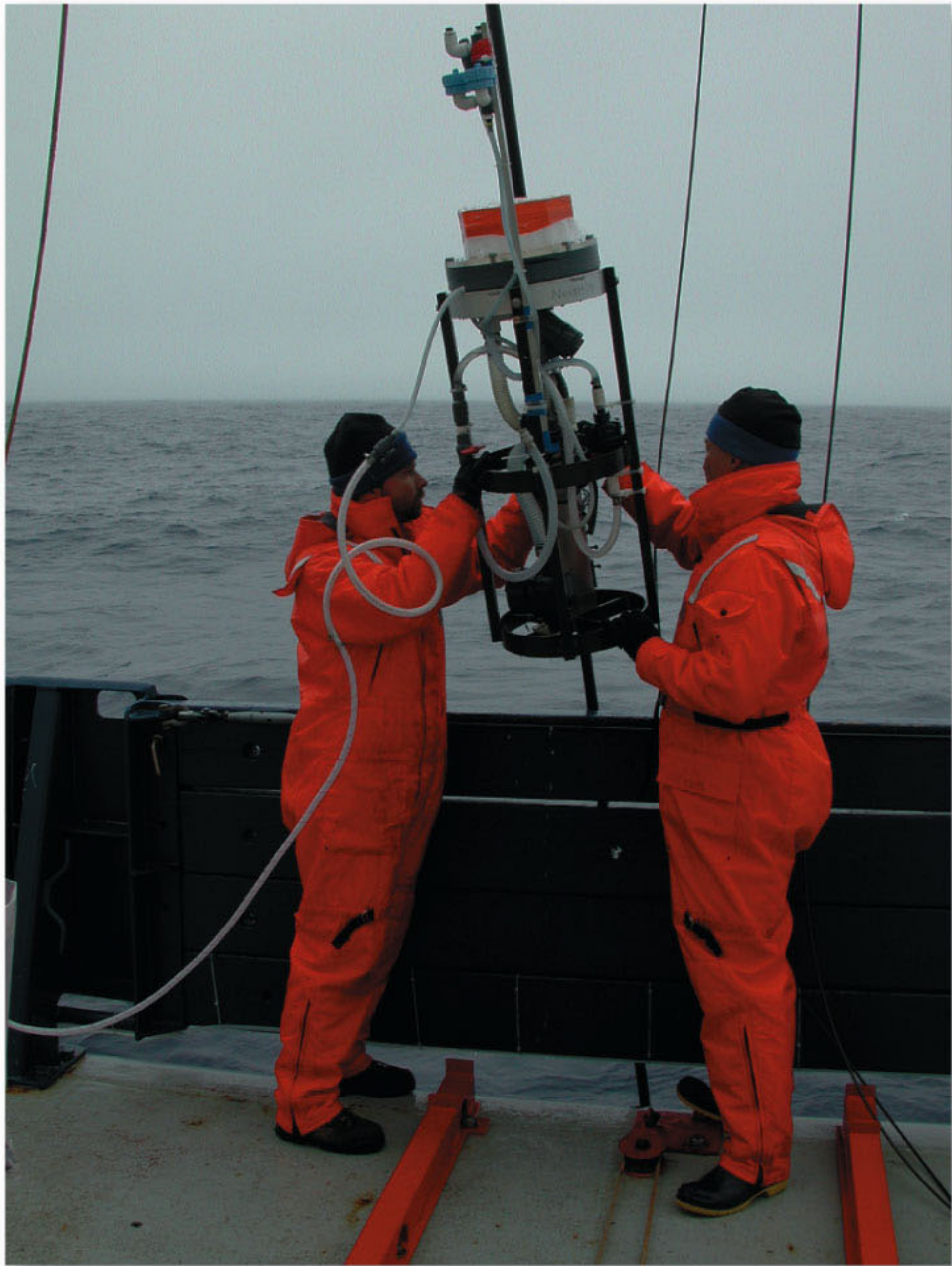


ECOLOGY, Figure 19.17 (Part 2)

Environmental Controls on NPP

This and other experiments support the iron limitation hypothesis.

But large-scale fertilization of the oceans is unlikely to be a solution to the increasing CO_2 in the atmosphere.

Some of the CO_2 taken up by phytoplankton is returned to the atmosphere via respiration of zooplankton and bacteria.

Environmental Controls on NPP

Also, iron is lost relatively quickly from the surface photic zone, sinking to deeper layers where it is unavailable to support phytoplankton growth.

Concept 19.3: Global patterns of net primary production reflect climatic controls and biome types.

Remote sensing and eddy covariance techniques have improved our ability to estimate global patterns of NPP.

Global NPP has been estimated to be 105 petagrams (1 Pg = 10^{15} g) of carbon per year.

54% of this carbon is taken up by terrestrial ecosystems, 46% by primary producers in the oceans.

The average rate of NPP for the land surface (426 g C/m^2/year) is higher than for oceans (140 g C/m^2/year).

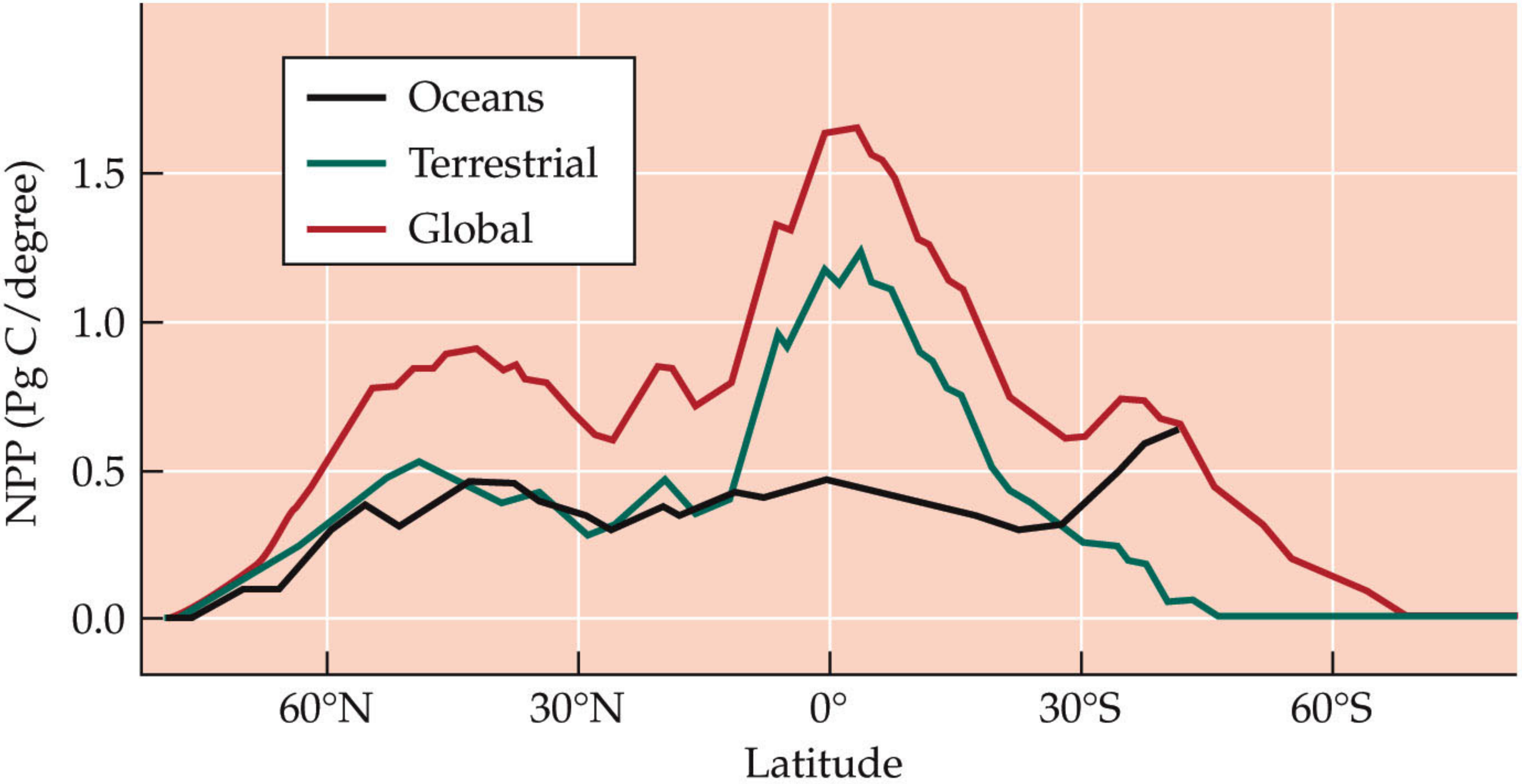
Global Patterns of NPP

Highest rates of NPP on land are found in the tropics.

This pattern results from latitudinal variation in climate and length of the growing season.

Tropical zones have long growing seasons and high precipitation, promoting high rates of NPP.

Figure 19.18 Latitudinal Variation in NPP



Global Patterns of NPP

NPP decreases in arid regions at about 25° N and S.

High latitudes have short growing seasons; low temperatures constrain nutrient supply by lowering decomposition rates, which in turn limits NPP.

Global Patterns of NPP

Oceanic NPP peaks at mid-latitudes, where zones of upwelling are found.

Upwellings bring nutrient-rich deep water to the surface.

Global Patterns of NPP

NPP varies among biomes.

Tropical forests and savannas contribute about 60% of terrestrial NPP (30% of global NPP).

Coastal zones account for 20% of oceanic NPP, or about 10% of total global NPP.

The open ocean accounts for the majority of oceanic NPP, and about 40% of total global NPP.

TABLE 19.1

Variation in NPP among Terrestrial Biomes

Biome	NPP (Pg/year)	Terrestrial NPP (%)
Tropical forest	17.8	32
Broad-leaved deciduous forest	1.5	3
Broad-leaved and needle-leaved forest	3.1	5
Needle-leaved evergreen forest	3.1	5
Needle-leaved deciduous forest	1.8	3
Savanna	16.8	30
Grassland	2.4	4
Shrubland	1.0	2
Tundra	0.8	1
Desert	0.5	1
Crops	8.0	14

Source: Field et al. 1998.

Global Patterns of NPP

Variation in NPP among terrestrial biomes is associated mostly with differences in leaf area index and length of growing season.

Variation in NPP among aquatic ecosystems is primarily related to variation in inputs of nutrients.

Secondary Production

Concept 19.4: Secondary production is generated through the consumption of organic matter by heterotrophs.

Secondary production—energy derived from consumption of organic compounds that were produced by other organisms.

Secondary Production

Heterotrophs are classified according to the type of food they eat.

Herbivores consume plants and algae; carnivores consume other live animals; detritivores consume dead organic matter (detritus).

Omnivores consume both plants and animals.

Determining what organisms eat is not always simple.

One method compares the isotopic composition of an organism to its potential food sources.

Concentrations of naturally occurring stable isotopes of carbon (^{13}C), nitrogen (^{15}N), and sulfur (^{34}S) differ among potential food items.

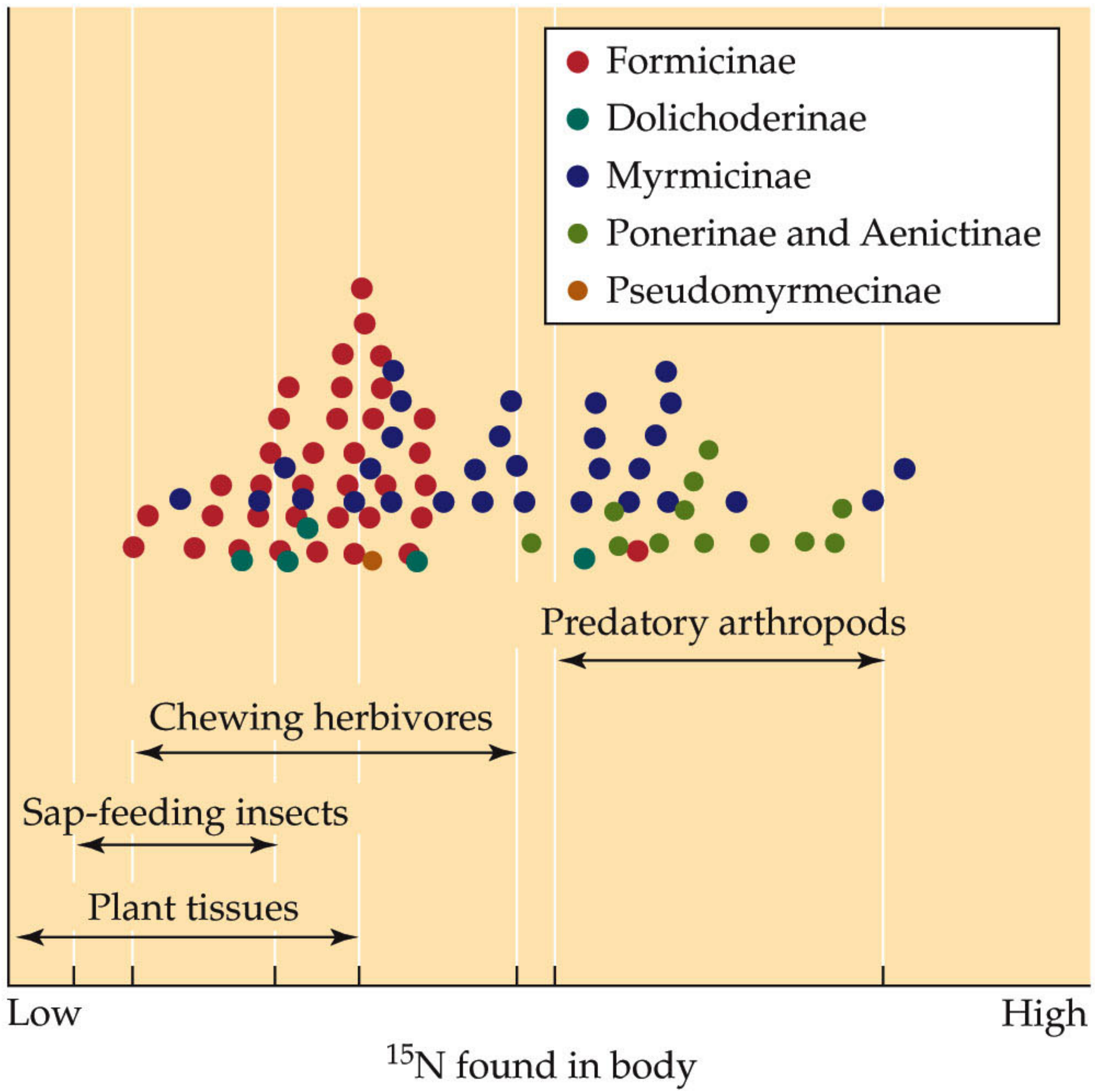
Secondary Production

To address the question of why ants in tropical rainforest canopies are so abundant relative to the abundance of suitable prey, Davidson et al. (2002) hypothesized that the ants must be obtaining most of their food directly or indirectly from plant sources.

They measured the ^{15}N composition of plants, sap-feeding insects, herbivores, and predatory arthropods.

^{15}N values of the ants indicated that most of their nitrogen, and thus their diet, came from sap exuded by sap-feeding insects.

Figure 19.19 Nitrogen Isotopic Composition of Ants and Their Diets



Secondary Production

Some organic matter consumed by heterotrophs is incorporated into biomass, some is used in respiration, some is egested in urine and feces.

Net secondary production =
ingestion – respiration – egestion

Secondary Production

Net secondary production depends on the "quality" of the heterotroph's food (digestibility and nutrient content), and physiology.

Animals with high respiration rates (e.g., endotherms) have less energy left over to allocate to growth.

Secondary Production

Net secondary production in most ecosystems is a small fraction of NPP. The fraction is greater in aquatic ecosystems than terrestrial.

Most is associated with detritivores, primarily bacterial and fungi.

In chemosynthesis, some bacteria use chemicals such as hydrogen sulfide (H_2S, and HS^- and S^{2-}), as electron donors to take up CO_2 and convert it to carbohydrates:

$$S^{2-} + CO_2 + O_2 + H_2O \rightarrow SO_4^{2-} + (CH_2O)_n$$

The bacteria are called chemoautotrophs.

Case Study Revisited: Life in the Deep Blue Sea, How Can It Be?

Several lines of evidence suggested that chemoautotrophs were the major source of energy for the hydrothermal vent ecosystems:

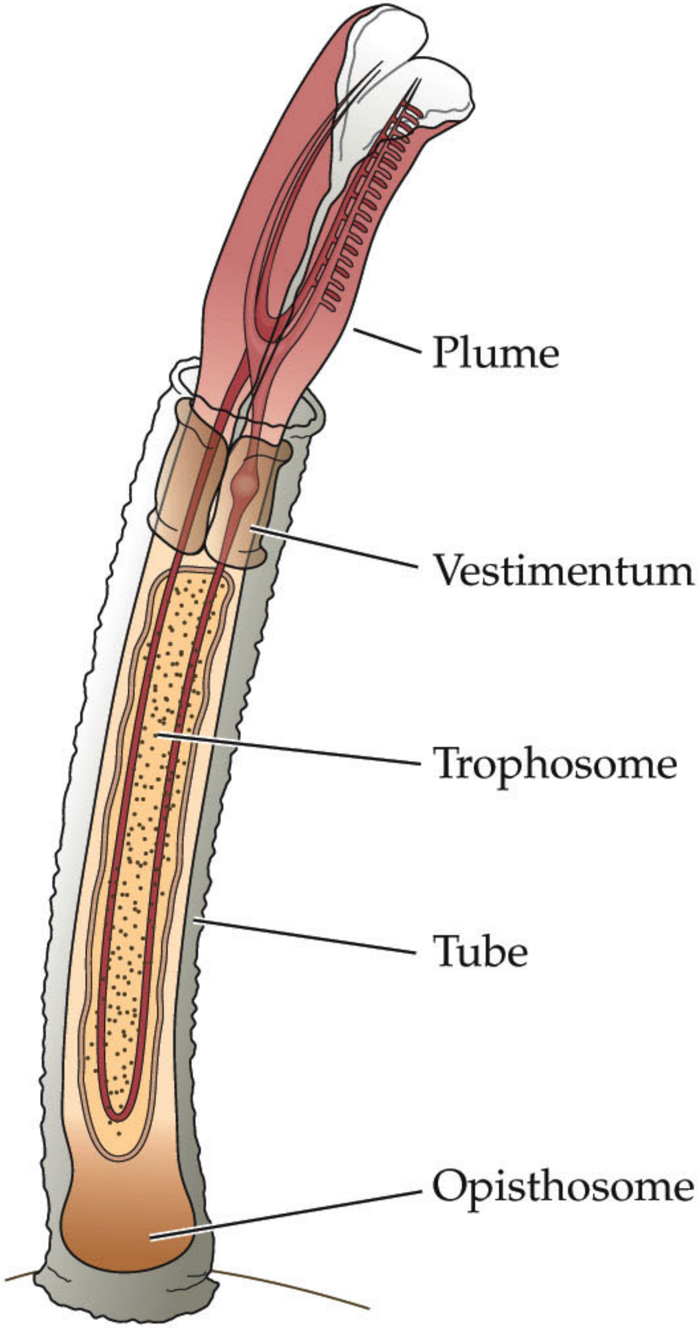
- Ratios of $^{13}C/^{12}C$ in the vent invertebrates were different from those of phytoplankton in the photic zone. This indicated their food source was not detritus from the upper ocean.

Case Study Revisited: Life in the Deep Blue Sea, How Can It Be?

- Tube worms from the vents (*Riftia*) were found to lack mouths and digestive systems.

They have trophosomes, specialized tissue that contains symbiotic bacteria, elemental sulfur, enzymes associated with the Calvin cycle, and enzymes involved in sulfur metabolism.

Figure 19.20 *Riftia* Anatomy



ECOLOGY, Figure 19.20

Case Study Revisited: Life in the Deep Blue Sea, How Can It Be?

Clams and other organisms in the vent communities also housed symbiotic bacteria.

The tube worms and clams get carbohydrates from the chemoautotrophic bacteria.

The bacteria also detoxify sulfides in the water, which would normally inhibit aerobic respiration.

Case Study Revisited: Life in the Deep Blue Sea, How Can It Be?

The invertebrates supply the bacteria with CO_2, O_2, and sulfides at higher rates than they could get if they were free-living.

The symbiosis is therefore a mutualism, and results in higher productivity than if the organisms lived separately.

Connections in Nature: Energy-Driven Succession and Evolution in Hydrothermal Vent Communities

Hydrothermal vent ecosystems last about 20 to 200 years.

The hot spring eventually stops emitting water and sulfides, and the community collapses.

Rates of colonization and development of vent communities are higher when they are closer to other existing vent communities.

Connections in Nature: Energy-Driven Succession and Evolution in Hydrothermal Vent Communities

Colonization begins with chemoautotrophic bacteria, sometimes in very high densities.

Tube worms are often the first invertebrates to arrive.

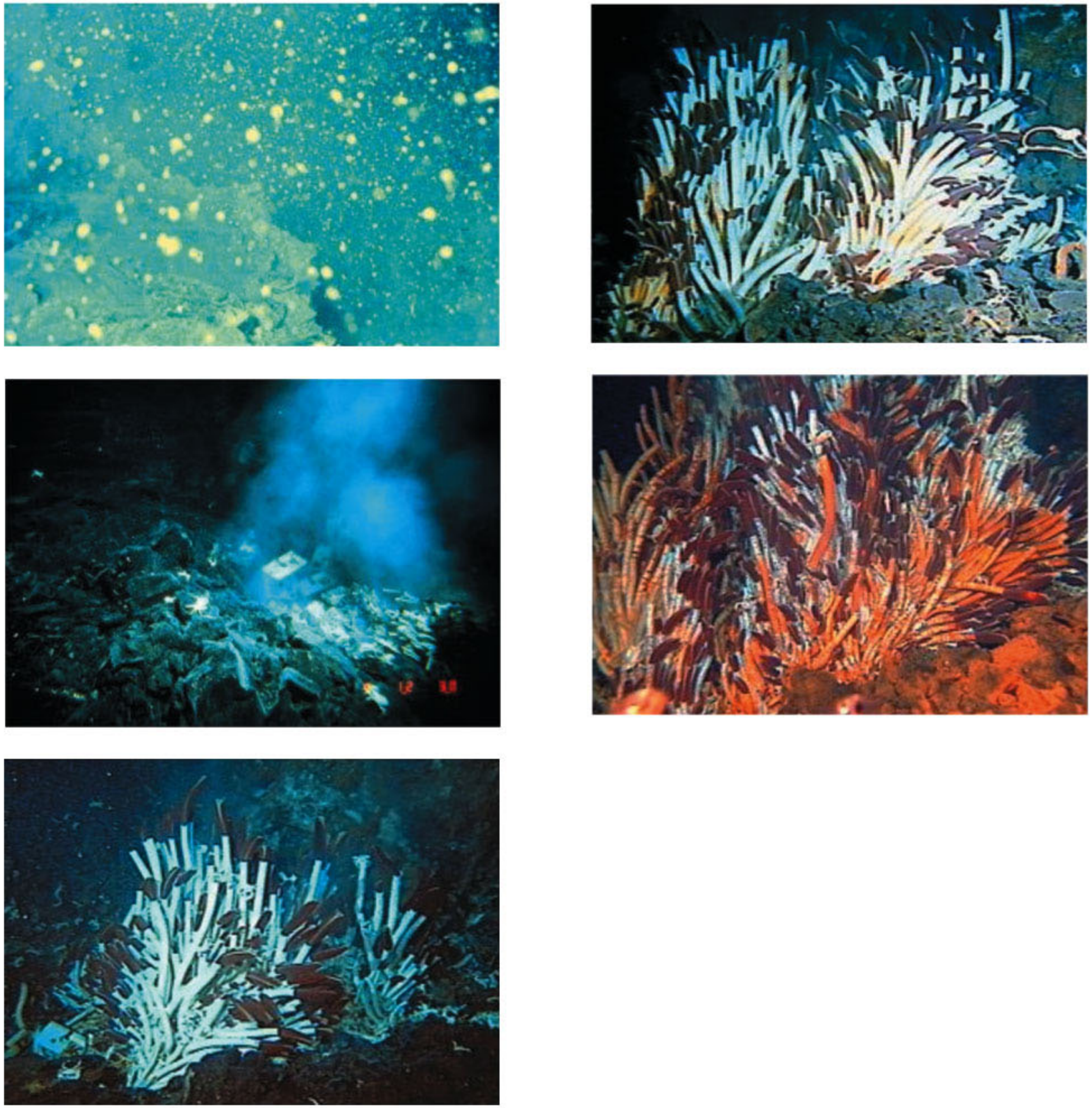
Clams and other mollusks are thought to be better competitors and over time they increase in abundance at the expense of the tube worms.

Connections in Nature: Energy-Driven Succession and Evolution in Hydrothermal Vent Communities

Scavengers and carnivores, such as crabs and lobsters, are found at low densities in the developing community.

When the vent stops flowing, worm and bivalve populations decline; and scavengers increase until the energy available in the form of detritus is gone.

Figure 19.21 Succession in Hydrothermal Vent Communities



Connections in Nature: Energy-Driven Succession and Evolution in Hydrothermal Vent Communities

The pattern of succession in these communities is subject to the same random factors found in other habitats: The order of arrival of organisms can influence the long-term dynamics of the community.

Connections in Nature: Energy-Driven Succession and Evolution in Hydrothermal Vent Communities

Phylogenetic relationships between vent organisms and their non-vent relatives show deep evolutionary divergence.

About 500 vent species have been described, 90% are endemic.

Connections in Nature: Energy-Driven Succession and Evolution in Hydrothermal Vent Communities

Phylogenetics can also be used to explore coevolution in the invertebrates and their bacterial symbionts.

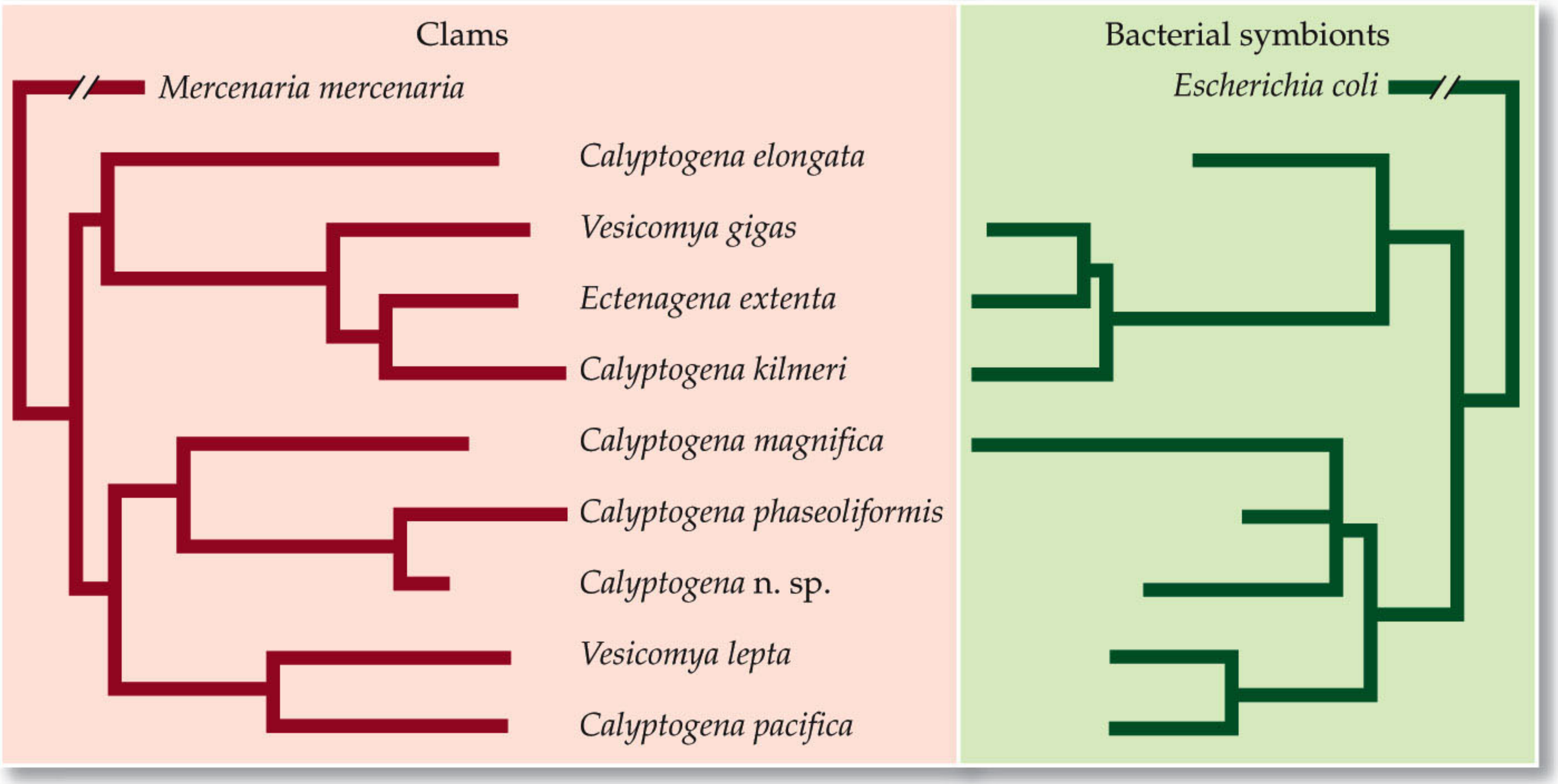
Clams in the family Vesicomyidae transfer bacteria to their offspring in the cytoplasm of their eggs.

Peek et al. (1998) collected eight species of clams in three genera.

They used ribosomal DNA to construct phylogenetic trees.

The trees showed remarkable congruence, providing strong evidence that speciation in the clams and their bacterial symbionts has occurred synchronously.

Figure 19.22 Coevolution of Vent Clams and Their Symbiotic Bacteria



It has been suggested that life on Earth originated in hydrothermal vents.

The reducing environment of the vents is conducive to abiotic synthesis of amino acids.

There are vents with lower temperatures at shallow depths where amino acid genesis could (and does) occur.