5

Coping with Environmental Variation: Energy

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Case Study: Toolmaking Crows

Humans view toolmaking capacity as something that differentiates us from other animals.

But toolmaking in chimpanzees was observed for the first time in the 1920s.

Jane Goodall first observed a chimp in the wild make a tool to retrieve termites from a mound.

Figure 5.1 Nonhuman Tool Use

ECOLOGY, Figure 5.1

Case Study: Toolmaking Crows

Birds have also demonstrated toolmaking ability.

The first report was from the South Pacific where New Caledonian crows used tools to snag insects from decomposing trees (Hunt 1996).

The crows fashioned two different types of tools from plant materials.

Figure 5.2 Tools Manufactured by New Caledonian Crows

(A)

(B)

Case Study: Toolmaking Crows

Different individuals made the tools in the same way.

In a laboratory, the crows were able to make the same tools from wire.

Experiments showed that the tools increased food retrieval efficiency.

Consistency in the construction of the tools suggest that it is a skill learned socially within a population of animals.

Introduction

Energy is the most basic requirement for all organisms.

Without energy inputs, biological functioning ceases.

Organisms use many mechanisms to obtain energy.

Sources of Energy

Concept 5.1: Organisms obtain energy from sunlight, from inorganic chemical compounds, or through the consumption of organic compounds.

Energy exists in many forms in the environment.

- Sunlight is *radiant energy.*
- *Chemical energy* is stored in the bonds of food molecules.

Sources of Energy

- *Kinetic energy* associated with the movement of molecules is measured as temperature.

Kinetic energy determines the rate of activity and metabolic energy demand. Chemical and radiant energy are captured by organisms for growth and maintenance.

Sources of Energy

Autotrophs are organisms that assimilate energy from sunlight (*photosynthesis*), or from inorganic compounds (*chemosynthesis*).

The energy is converted into chemical energy stored in the carbon–carbon bonds of organic molecules.

Sources of Energy

Heterotrophs obtain their energy by consuming energy-rich organic compounds from other organisms.

This energy ultimately originated with organic compounds synthesized by autotrophs.

Some heterotrophs consume non-living organic matter.

Sources of Energy

Parasites and herbivores are heterotrophs that consume live hosts, but do not necessarily kill them.

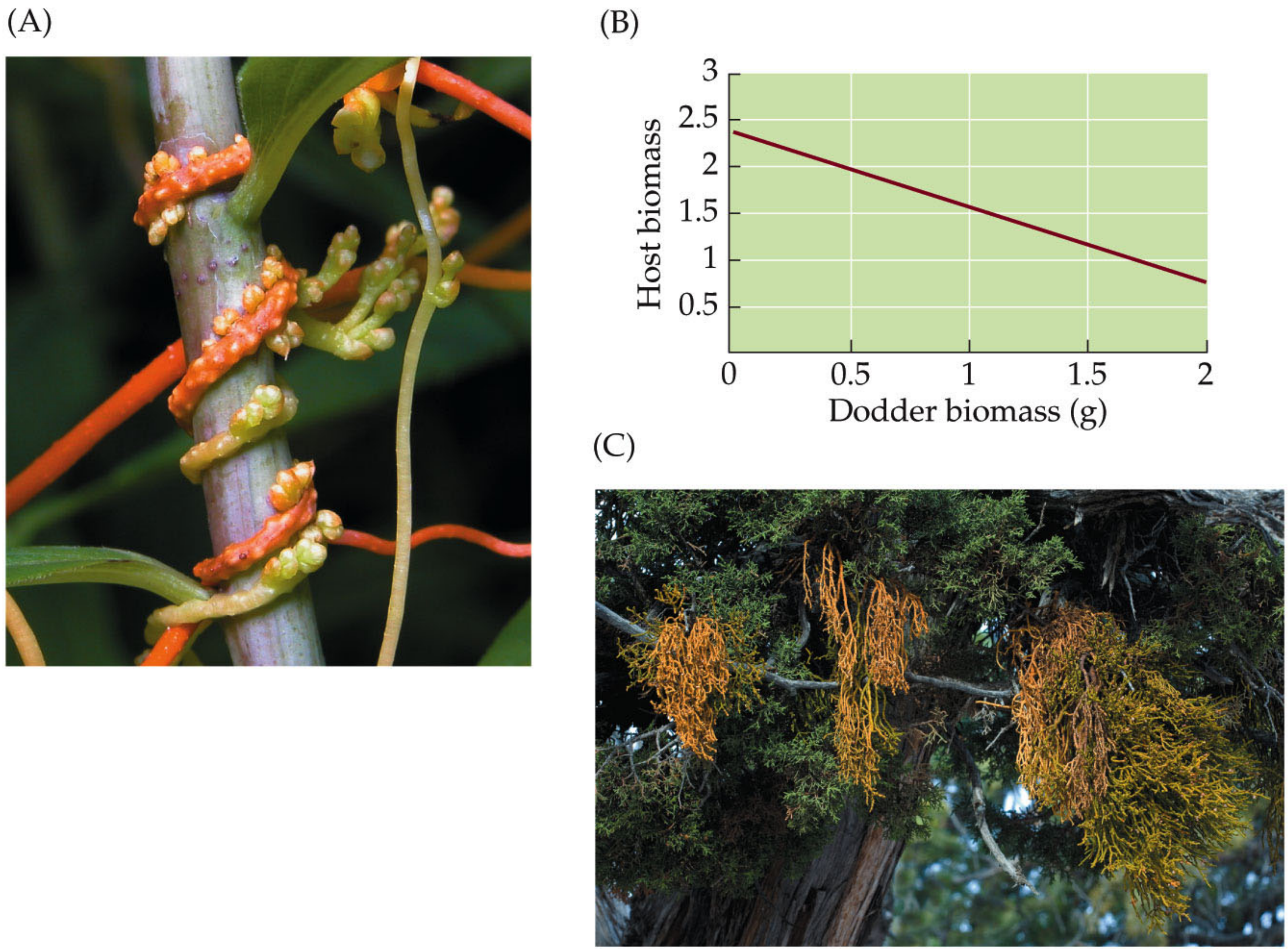
Predators are heterotrophs that capture and consume live prey animals.

Sources of Energy

Some plants are *holoparasites*. They have no photosynthetic pigments and obtain all their energy from other plants. Thus, they are heterotrophs.

Dodder is a holoparasite that is an agricultural pest and can significantly reduce biomass in the host plant.

Figure 5.3 Plant Parasites



ECOLOGY, Figure 5.3

Mistletoe is a *hemiparasite*—it is photosynthetic, but obtains nutrients, water, and some of its energy from the host plant.

Sources of Energy

Some animals can become photosynthetic by acquiring or consuming photosynthetic organisms, or living in a close relationship called *symbiosis*.

Sea slugs have functional chloroplasts that carry out photosynthesis. The chloroplasts are taken up from the algae that the slug eats.

Figure 5.4 Green Sea Slug

Concept 5.2: Radiant and chemical energy captured by autotrophs is converted into stored energy in carbon–carbon bonds.

Most autotrophs obtain energy through **photosynthesis**. Sunlight provides the energy to take up CO_2 and synthesize organic compounds.

Chemosynthesis (*chemolithotrophy*) is a process that uses energy from inorganic compounds to produce carbohydrates.

Chemosynthesis is important in bacteria involved in nutrient cycling, and in some ecosystems such as ocean vent communities.

Autotrophy

The earliest autotrophs were probably chemosynthetic bacteria or archaea.

The atmosphere was low in O_2 but rich in hydrogen, methane, and CO_2.

Many bacteria and archaea still use energy from inorganic compounds.

TABLE 5.1

Inorganic Substrates Used by Chemosynthetic Bacteria as Electron Donors for CO_2 Fixation

Substrate (chemical formula)	Type of bacteria
Ammonium (NH_4^+)	Nitrifying bacteria
Nitrite (NO_2^-)	Nitrifying bacteria
Hydrogen sulfide (H_2S/HS^-)	Sulfur bacteria (purple and green)
Sulfur (S)	Sulfur bacteria (purple and green)
Ferrous iron (Fe^{2+})	Iron bacteria
Hydrogen (H_2)	Hydrogen bacteria
Phosphite (HPO_3^{2-})	Phosphite bacteria

Source: After Madigan and Martinko 2005.

Autotrophy

In chemosynthesis, organisms get electrons by oxidizing the inorganic substrate.

The electrons are used to generate two high-energy compounds: **ATP** and **NADPH**.

Energy from ATP and NADPH is then used to take up, or “fix,” CO_2 and use the carbon to make carbohydrates.

Autotrophy

Alternatively, some bacteria can use the electrons from the inorganic substrate directly to fix CO_2.

The biochemical pathway used most commonly to fix CO_2 is the **Calvin cycle**, catalyzed by several enzymes.

It occurs in both chemosynthetic and photosynthetic organisms.

Important chemosynthesizers include the nitrifying bacteria (e.g., *Nitrosomonas*, *Nitrobacter*).

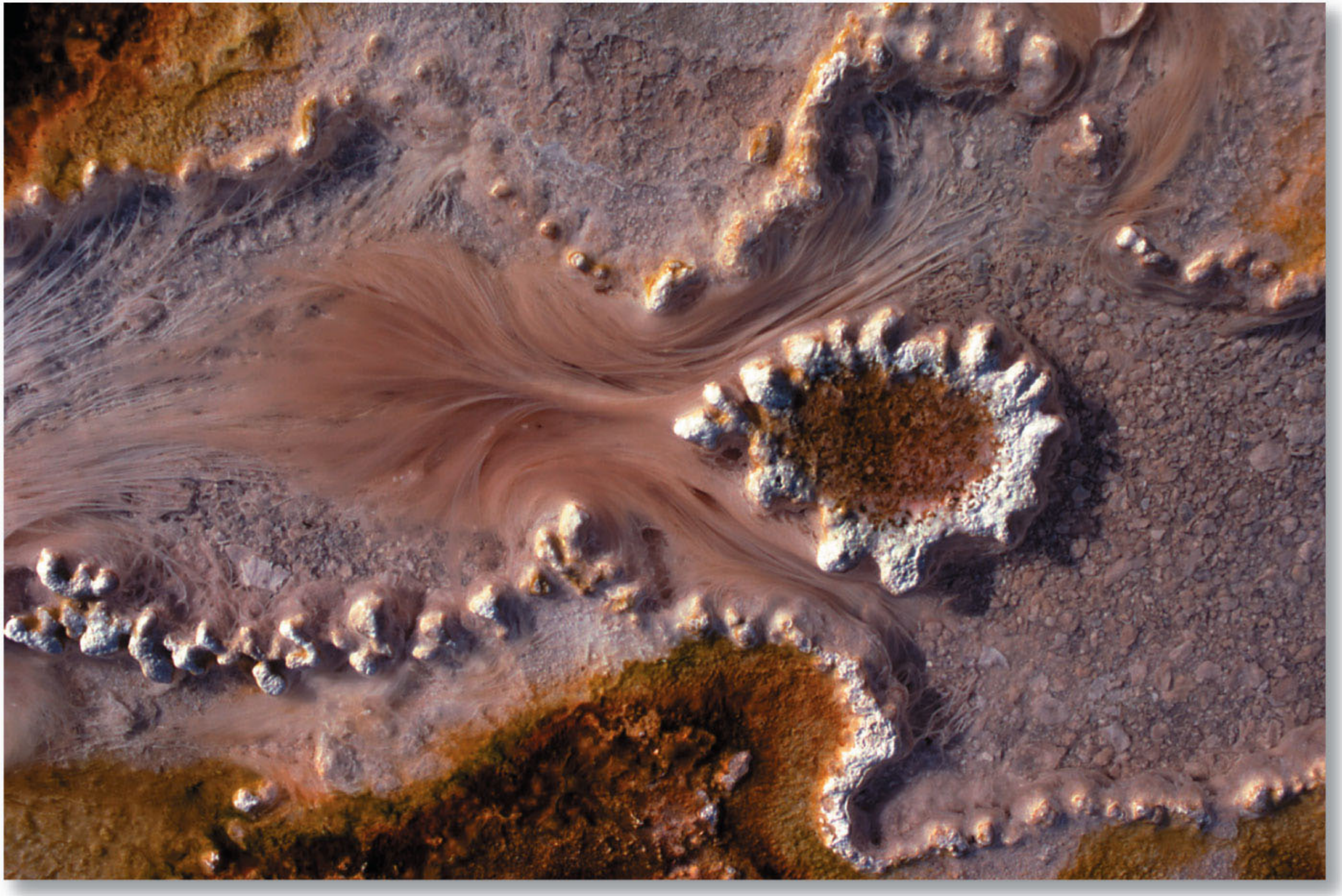
These bacteria convert ammonium (NH_4^+) to nitrite (NO_2^-), then oxidize it to nitrate (NO_3^-).

These conversions are an important component of the nitrogen cycle.

The sulfur bacteria occur in volcanic deposits, sulfur hot springs, and acid mine wastes.

Initially they use the higher-energy forms of sulfur, H_2S and HS^- (hydrogen sulfide), producing elemental S.

The bacteria then use elemental S as an electron source, producing SO_4^{2-} (sulfate).



ECOLOGY, Figure 5.5

Autotrophy

Most of the biologically available energy on Earth is derived from photosynthesis.

Photosynthetic organisms include some archaea, bacteria, and protists, and most algae and plants.

Autotrophy

Photosynthesis has two major steps:

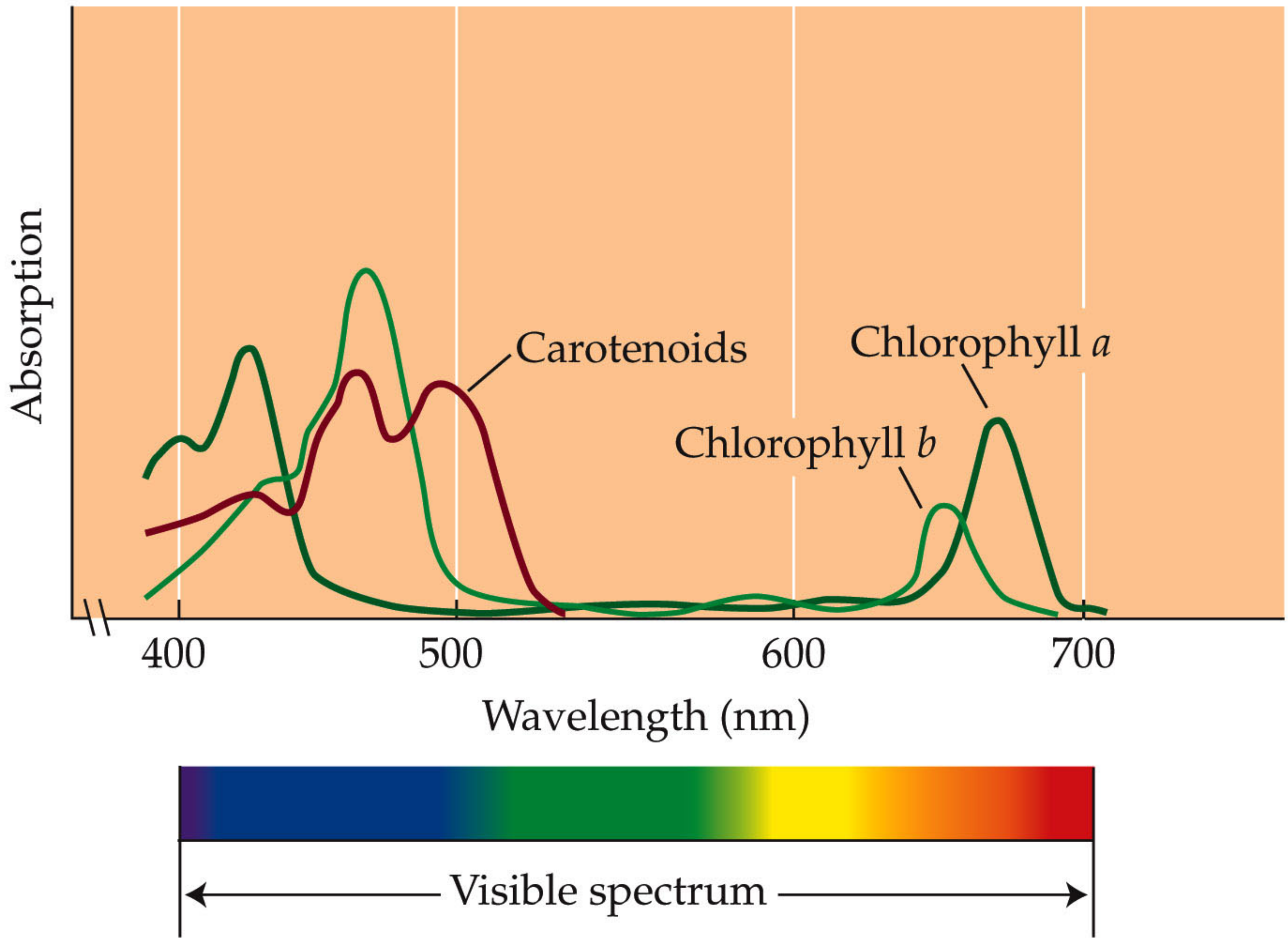
The “light reaction”—light is harvested and used to split water and provide electrons to make ATP and NADPH.

The “dark reaction”—CO_2 is fixed in the Calvin cycle, and carbohydrates are synthesized.

Light harvesting is accomplished by chlorophyll and accessory pigments.

Chlorophyll absorbs red and blue light and reflects green.

Accessory pigments include carotenoids. These pigments help harvest light energy, and also protect cells from intense solar radiation.


Absorption
Carotenoids
Chlorophyll *a*
Chlorophyll *b*
400
500
600
700
Wavelength (nm)
Visible spectrum

Autotrophy

The photosynthetic pigments and other molecules involved in the light reaction are embedded in a membrane.

In plants, the membrane is part of a specialized organelle called a chloroplast. In bacteria, pigments are embedded in the cell membrane.

Autotrophy

50 to 300 pigment molecules are grouped in antenna-like arrays.

The pigments absorb energy from discrete units of light, called photons.

The energy from sunlight is used to split water and provide electrons.

These electrons are passed on to molecular complexes on the membranes, where they are used to synthesize ATP and NADPH.

Autotrophy

The splitting of water generates O_2.

The evolution of photosynthesis was an important step in the development of the modern atmosphere with high O_2 levels.

This influences chemistry of the lithosphere, as well as the evolution of life.

Atmospheric O_2 led to formation of an ozone layer high in the atmosphere that shields organisms from high-energy ultraviolet radiation.

The evolution of aerobic respiration, in which O_2 is used as an electron acceptor, facilitated significant evolutionary advances.

Autotrophy

CO_2 diffuses across cell membranes or is taken up from the atmosphere through the stomates of vascular plants.

A key enzyme in the Calvin cycle is ribulose 1,5 bisphosphate carboxylase/oxygenase, or “rubisco.”

Rubisco is the most abundant enzyme on Earth.

Autotrophy

Rubisco catalyzes the uptake of CO_2 and synthesis of a three-carbon compound—phosphoglyceraldehyde, (PGA).

PGA is eventually converted into a six-carbon sugar.

The net reaction of photosynthesis is:

$$6CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 + 6O_2$$

Autotrophy

The rate of photosynthesis determines the supply of energy and substrates for biosynthesis, which in turn influences growth and reproduction.

Environmental controls on the photosynthetic rate are an important topic in physiological ecology.

Light is clearly important in determining photosynthetic rate.

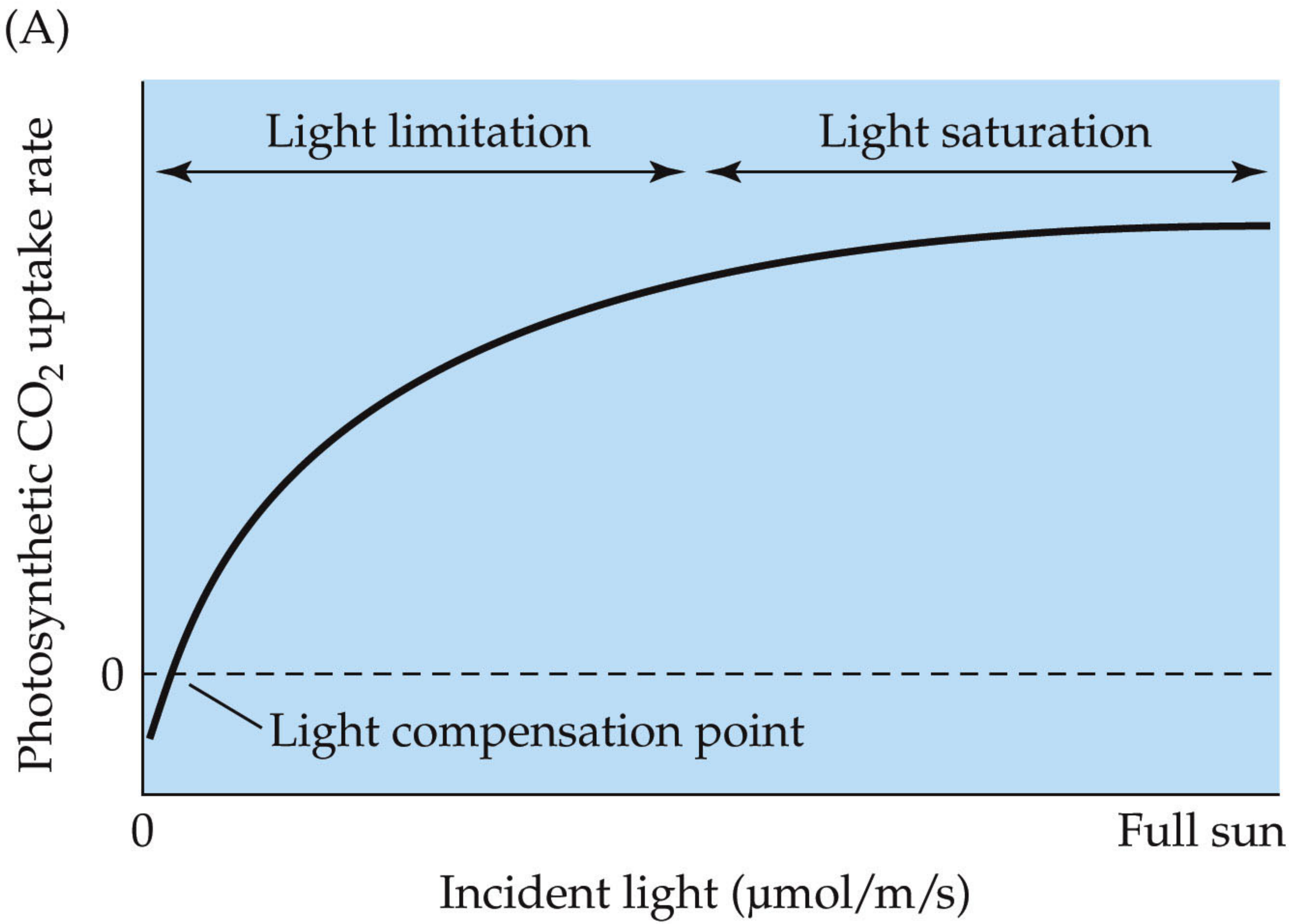
The relationship between light levels and photosynthetic rate can be shown by a *light response curve*.

Autotrophy

CO_2 uptake increases as light intensity increases until a *light saturation point* is reached.

The light level at which CO_2 uptake is balanced by CO_2 loss by respiration is the *light compensation point*.

Figure 5.7 A Plant Responses to Variations in Light Levels



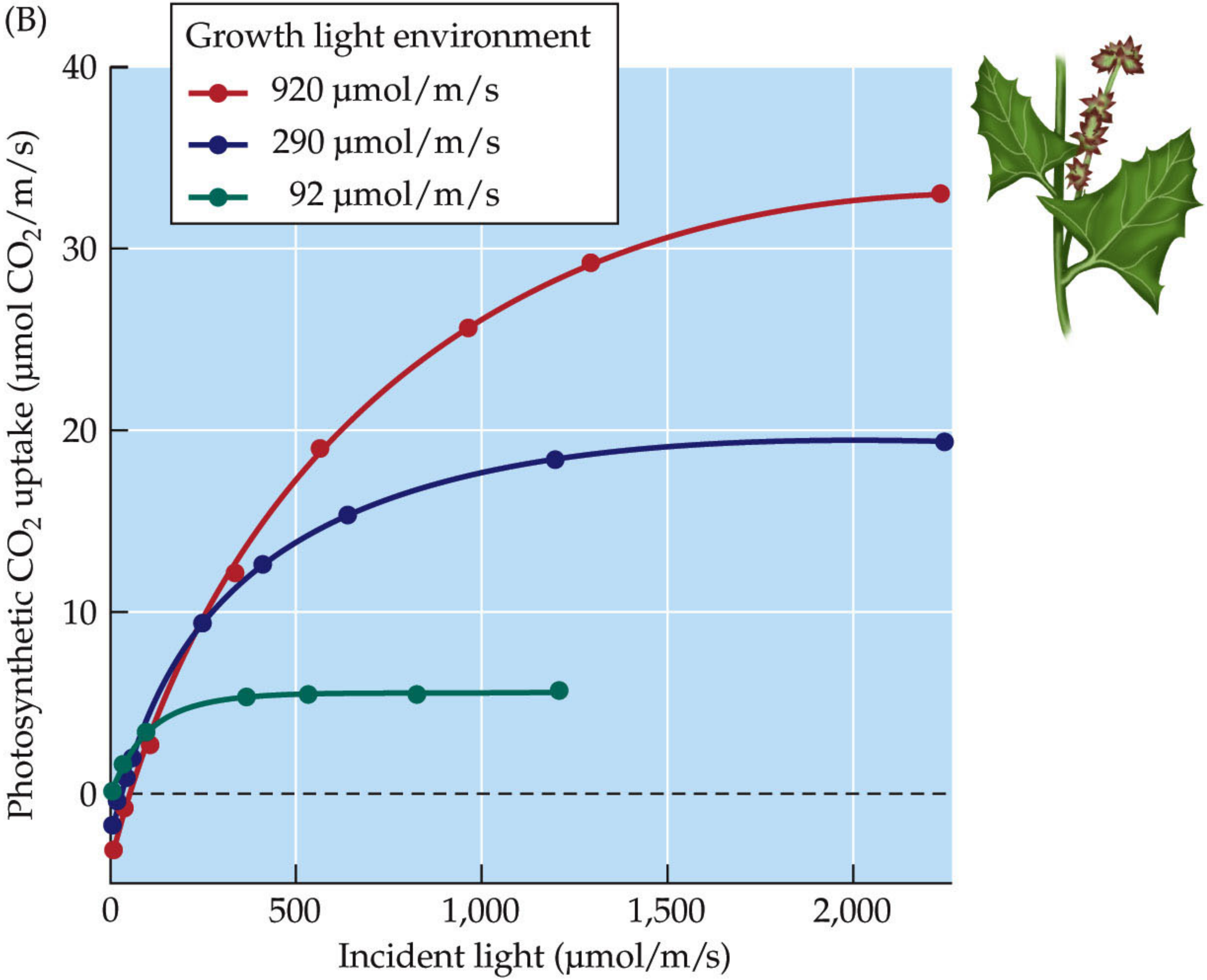
ECOLOGY, Figure 5.7 (Part 1)

How do plants cope with changing light intensities?

Bjorkman (1981) demonstrated that acclimatization to different light levels involves shifts in light response curves.

Plants grown in controlled conditions were able to adjust the light compensation point.

Figure 5.7 B Plant Responses to Variations in Light Levels



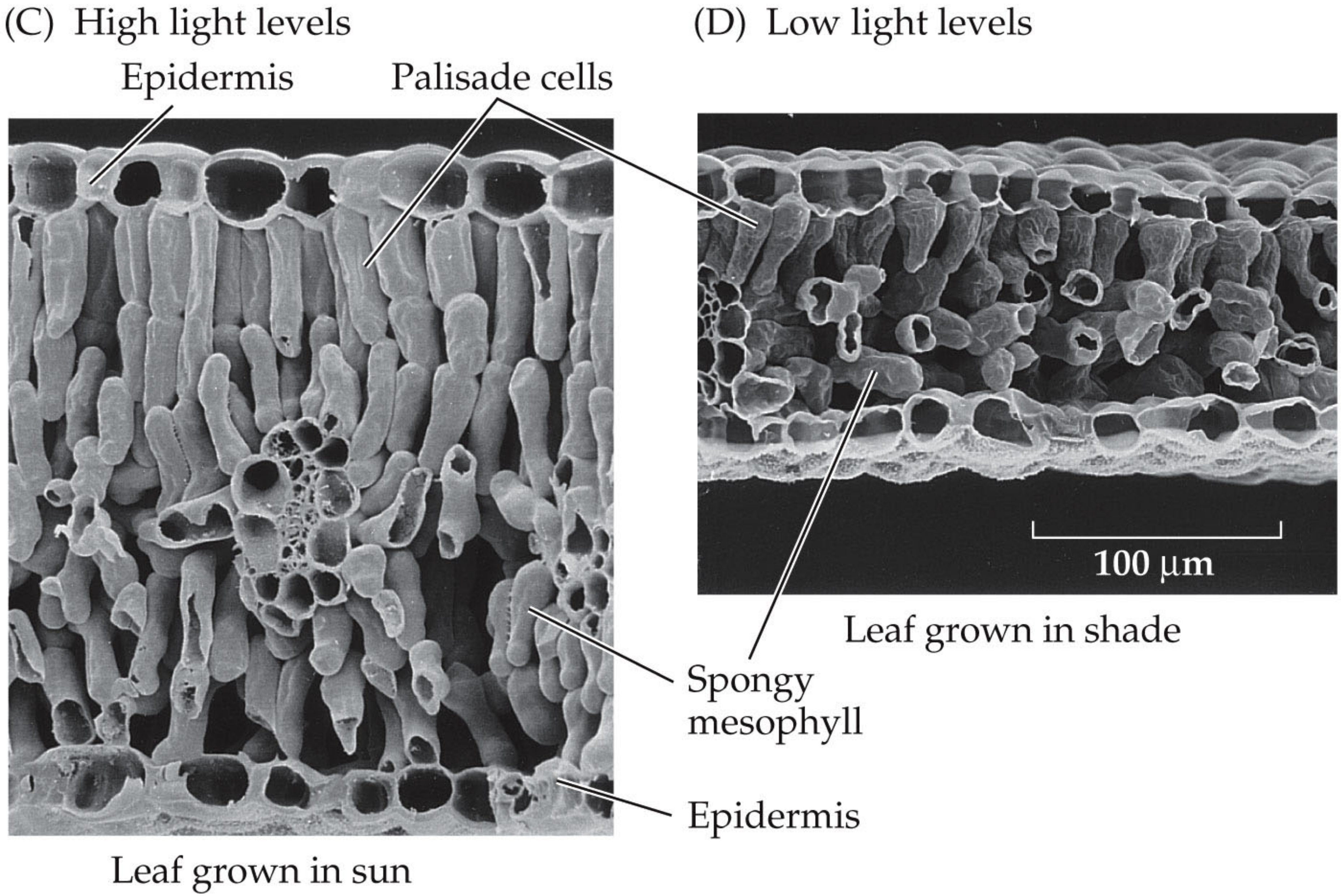
***ECOLOGY*, Figure 5.7 (Part 2)**

Autotrophy

Morphological changes are associated with this acclimatization.

Leaves grown at high light levels are thicker and have more chloroplasts than leaves grown in low light.

Figure 5.7 C Plant Responses to Variations in Light Levels



Autotrophy

Photosynthetic organisms may also alter the density of light-harvesting pigments and the amounts of photosynthetic enzymes.

Bacteria are especially well adapted to photosynthesis at low light levels; they can thrive in dimly lit environments such as relatively deep ocean water.

Water availability influences the supply of CO_2 for photosynthesis in terrestrial plants.

Low water potential causes the plant to close stomates, restricting CO_2 uptake.

This is a trade-off: Water conservation versus energy gain.

Keeping stomates open while tissues lose water can cause permanent impairments.

Closing stomates can increase chances of light damage to photosynthetic membranes because when the Calvin cycle is not operating, energy accumulates in the light-harvesting arrays.

Box 5.1 How Do Plants Cope with Too Much Light?

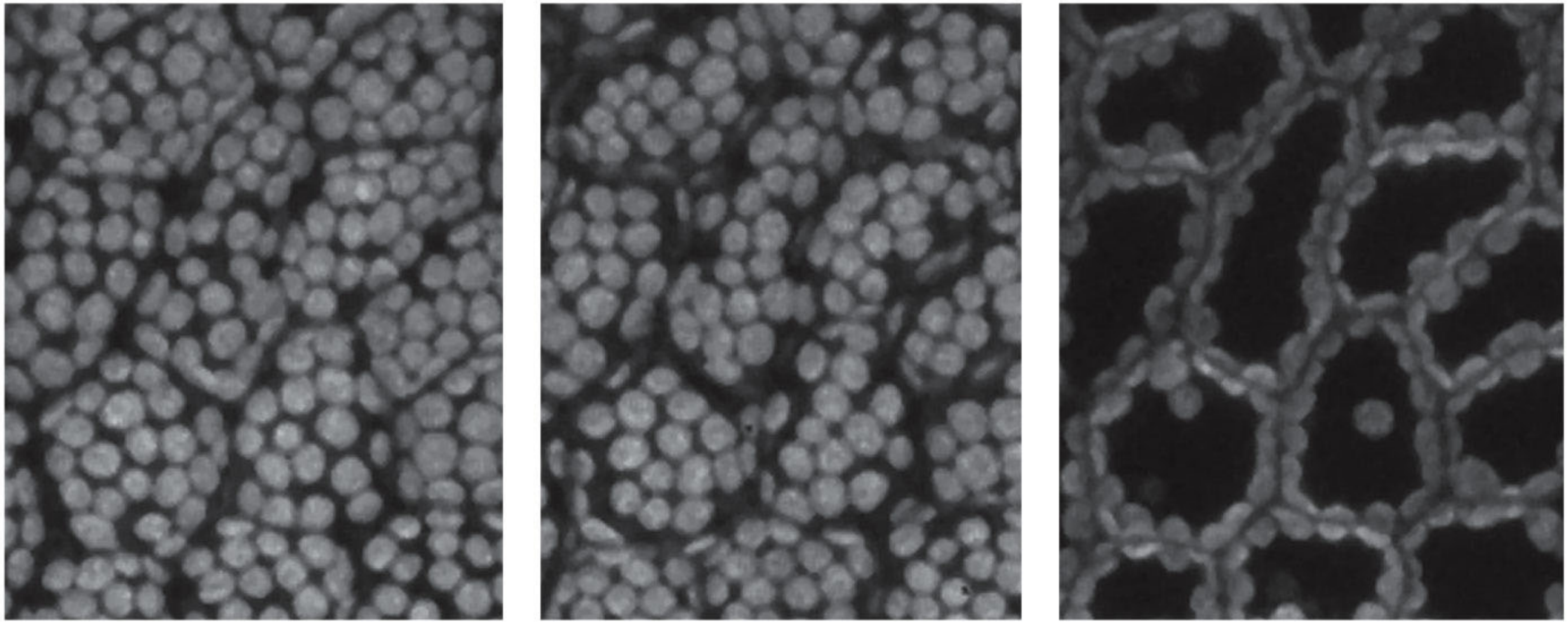
Photoinhibition: The excess energy generates toxic oxygen compounds that damage membranes.

Plants have evolved ways to dissipate this energy safely.

Some reduce exposure by moving leaves away from the sun, or curling leaves.

In some plants, the chloroplasts can migrate within a cell to promote self-shading.

(I) Darkness (II) Weak blue light (III) Strong blue light



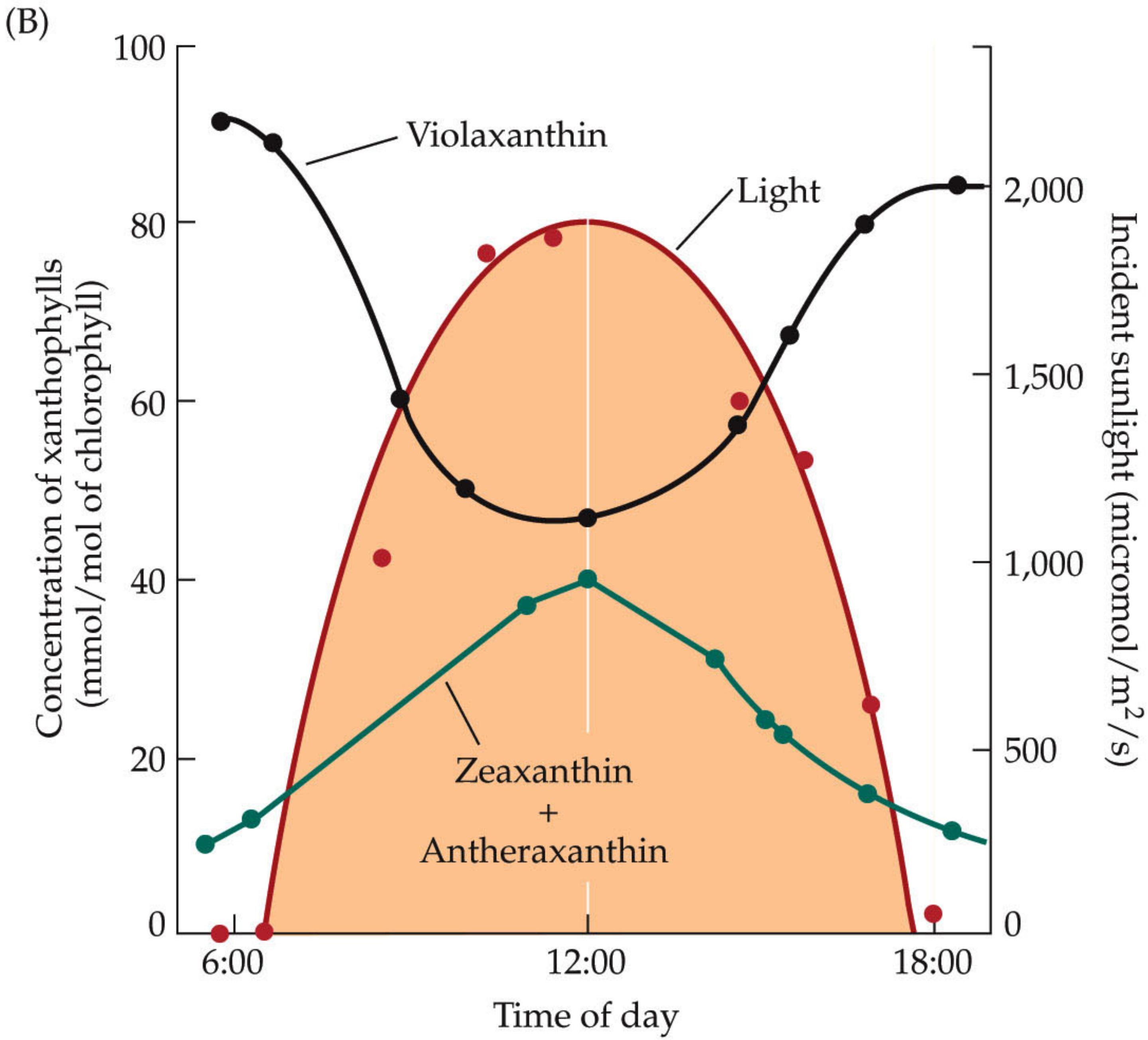
Box 5.1 How Do Plants Cope with Too Much Light?

Amounts of accessory pigments can be varied to dissipate light energy.

In the xanthopyll cycle, carotenoid pigments are converted from one form to another. Some forms are more efficient at dissipating the heat energy.

This cycle can take place over the course of a day.

Box 5.1, Figure B The Xanthophyll Cycle and Dissipation of Light Energy

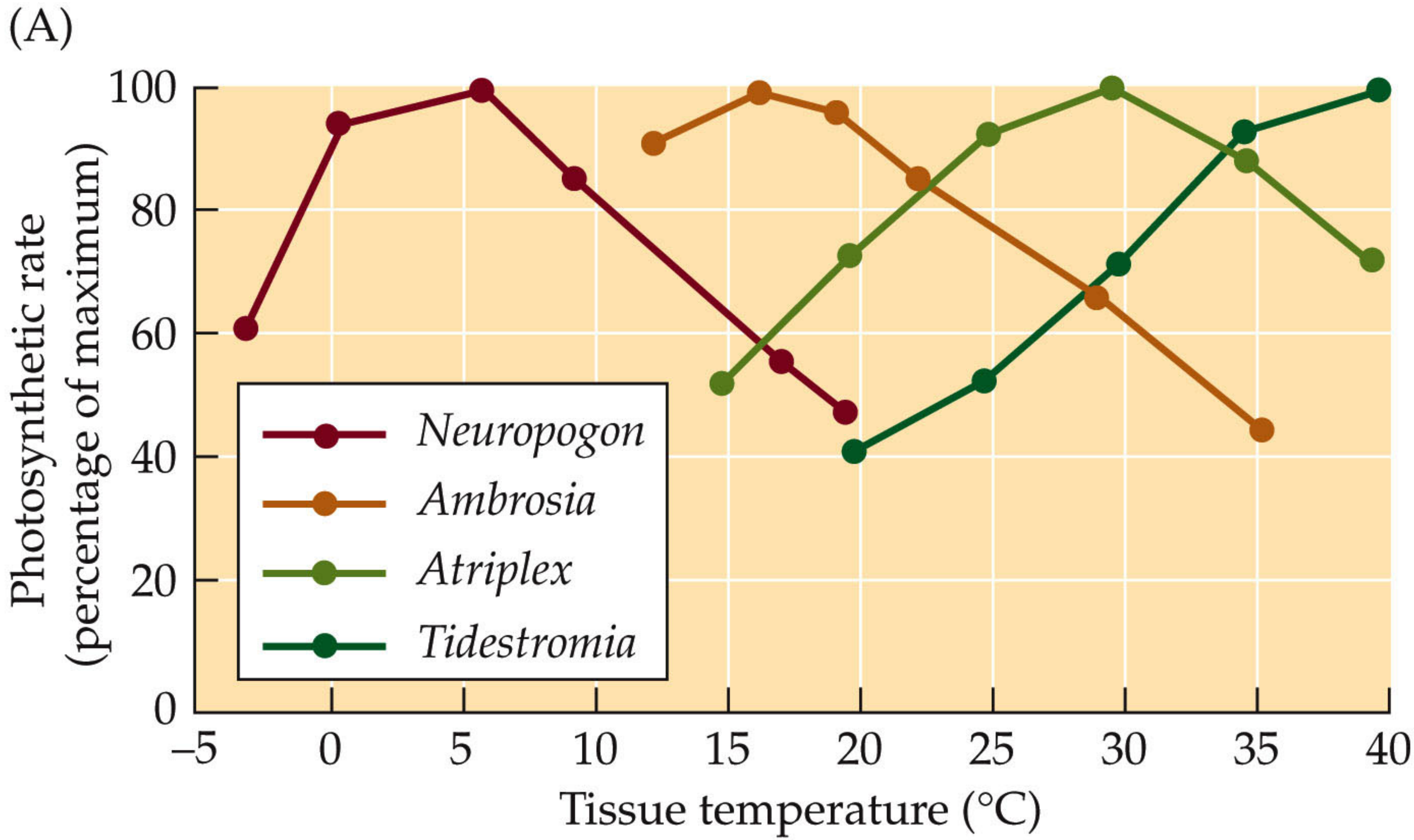


ECOLOGY, Box 5.1, Figure B

Acclimatization and adaptation to temperature variation involves the enzymes of the Calvin cycle and properties of the photosynthetic membranes.

Different forms of enzymes have specific ranges of optimal operating temperatures. Plants in different climates have different enzyme forms.

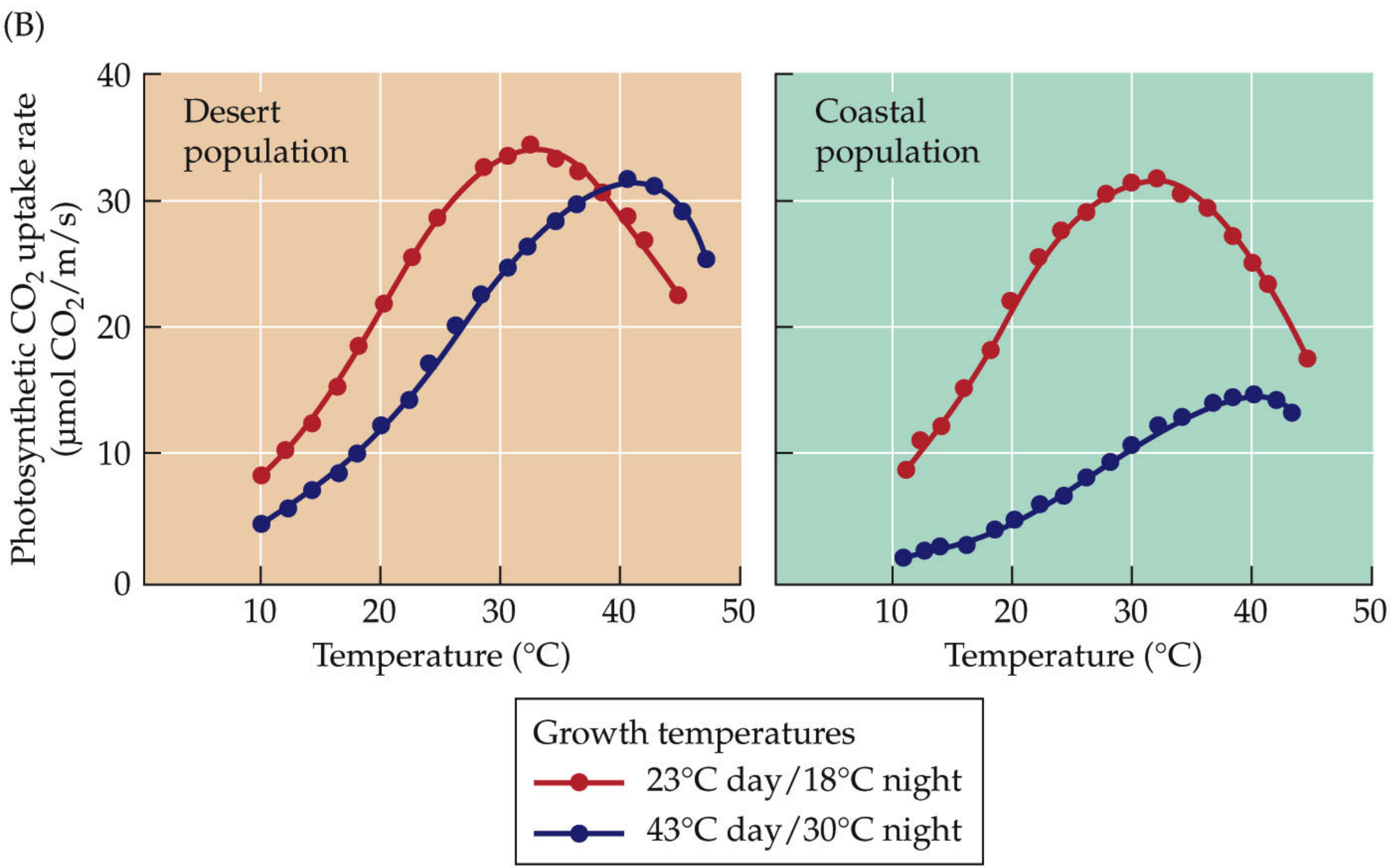
Figure 5.8 A Photosynthetic Responses to Temperature



Temperature also influences the fluidity of membranes.

Cold sensitivity in plants of tropical and subtropical biomes is associated with loss of membrane fluidity, which inhibits the functioning of the light-harvesting molecules.

Figure 5.8 B Photosynthetic Responses to Temperature



Autotrophy

Most of the nitrogen in plants is associated with rubisco and other photosynthetic enzymes.

Thus, higher amounts of nitrogen in the leaf are correlated with higher photosynthetic rates.

Autotrophy

Plants do not always allocate more nitrogen to leaves, however.

The supply of nitrogen is low relative to the demand for growth and metabolism.

Increasing nitrogen content of leaves increases the risk that herbivores will eat them, as plant-eating animals are also nitrogen-starved.

Concept 5.3: Environmental constraints resulted in the evolution of biochemical pathways that improve the efficiency of photosynthesis.

Plants that lack specialized biochemistry use the **C_3 photosynthetic pathway**.

Other metabolic processes can also decrease photosynthetic efficiency.

Rubisco can catalyze two competing reactions.

Carboxylase reaction: CO_2 is taken up, sugars are synthesized, and O_2 is released (photosynthesis).

Oxygenase reaction: O_2 is taken up, leading to breakdown of carbon compounds and release of CO_2 (**photorespiration**).

Photorespiration results in a net loss of energy.

The balance between the two reactions depends on temperature and the ratio of O_2 to CO_2 in the atmosphere.

As CO_2 concentration decreases relative to O_2 concentration, photorespiration increases.

Since photosynthesis evolved, atmospheric CO_2 concentration have varied.

As temperatures increase, the photorespiration rate also increases.

Energy loss due to photorespiration is particularly acute at times of high temperatures and low CO_2 concentrations.

Why hasn’t a new form of rubisco evolved so that photorespiration is minimized?

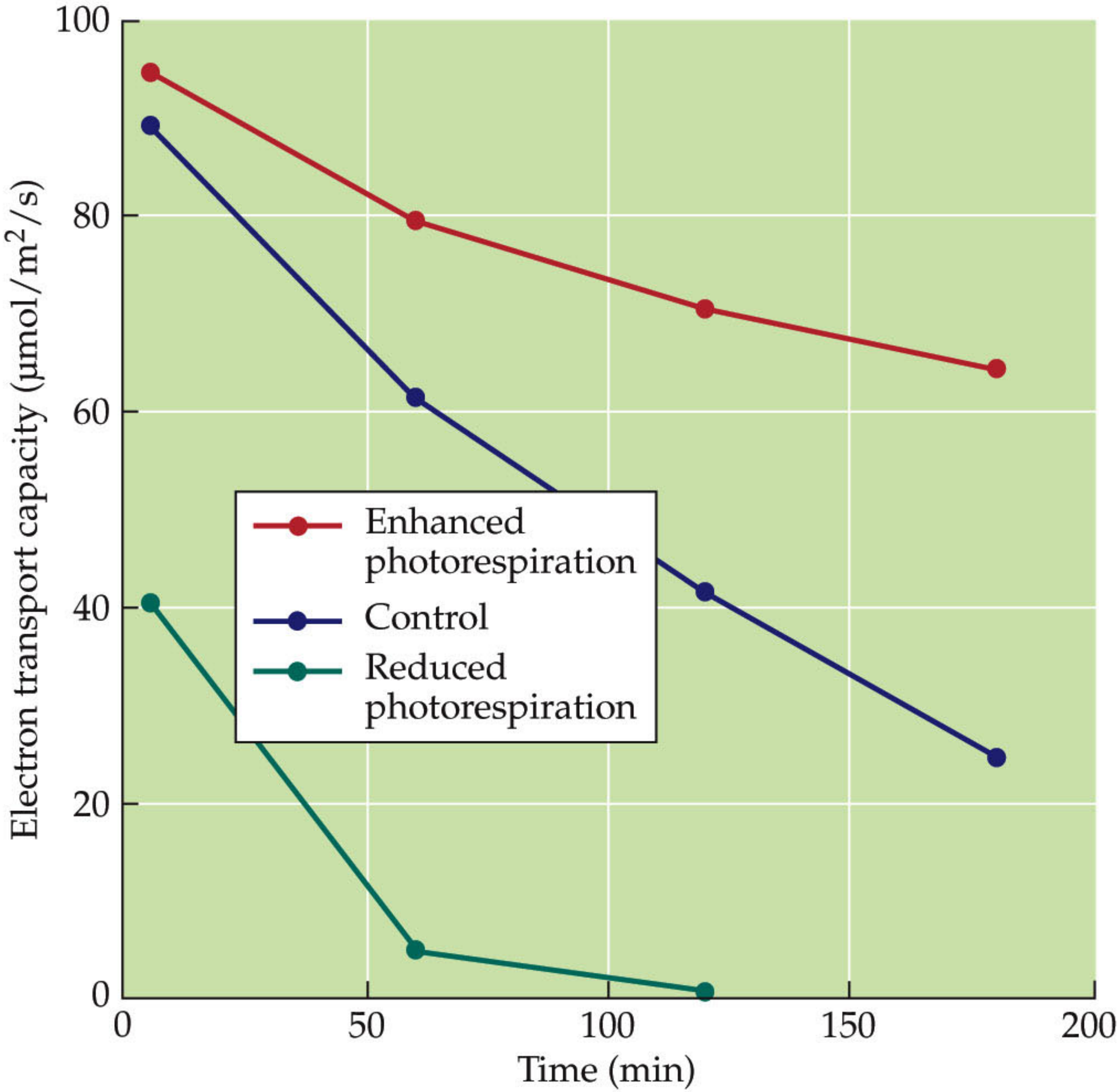
Evidence from experiments with *Arabidopsis thaliana* plants with a genetic mutation that knocks out photorespiration suggests that there is an advantage. These plants die under normal light and CO_2 conditions.

Photorespiration may protect plants from damage at high light levels.

Research using tobacco plants that had been altered to elevate or lower rates of photorespiration supports this idea (Kozaki and Takeba 1996).

Under high light intensity and low CO_2 concentrations, plants with higher rates of photorespiration showed less damage than control plants.

Figure 5.9 Does Photorespiration Protect Plants from Damage by Intense Light?



But in some conditions, photorespiration is not advantageous.

If atmospheric CO_2 is low and temperatures high, photosynthetic energy gain may not keep pace with photorespiratory energy loss.

Such conditions existed 7 million years ago, at about the time when C_4 photosynthesis first appeared.

The **C_4 photosynthetic pathway** reduces photorespiration.

It evolved independently several times in different species in 18 families.

Many grass species use this pathway, including corn, sugarcane, and sorghum.

Figure 5.10 Examples of Plants with the C_4 Photosynthetic Pathway

Corn (*Zea mays*), an important crop species

Rose moss (*Portulaca grandiflora*), a C_4 forb native to Uruguay

Globe amaranth (*Gomphrena globosa*), a C_4 forb native to Central and South America

C_4 photosynthesis involves biochemical and morphological specialization.

The supply of CO_2 to the Calvin cycle is increased, which lowers O_2 uptake by rubisco.

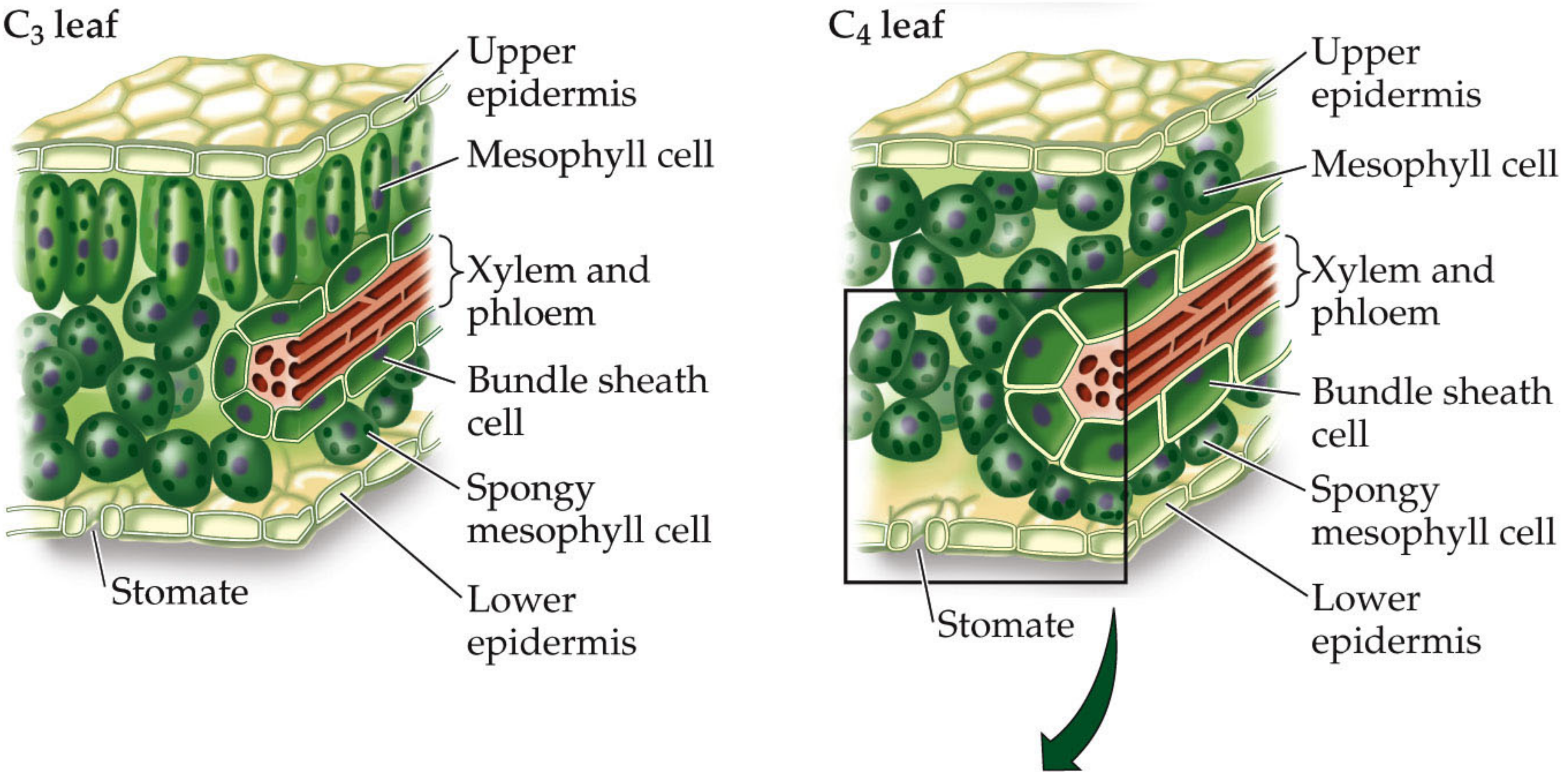
CO_2 is initially taken up by phosphoenol pyruvate carboxylase (PEPcase), which has greater affinity for CO_2, and does not take up O_2.

PEPcase fixes CO_2 in the mesophyll tissue.

A four-carbon compound is synthesized and transported to the bundle sheath cells where the Calvin cycle occurs.

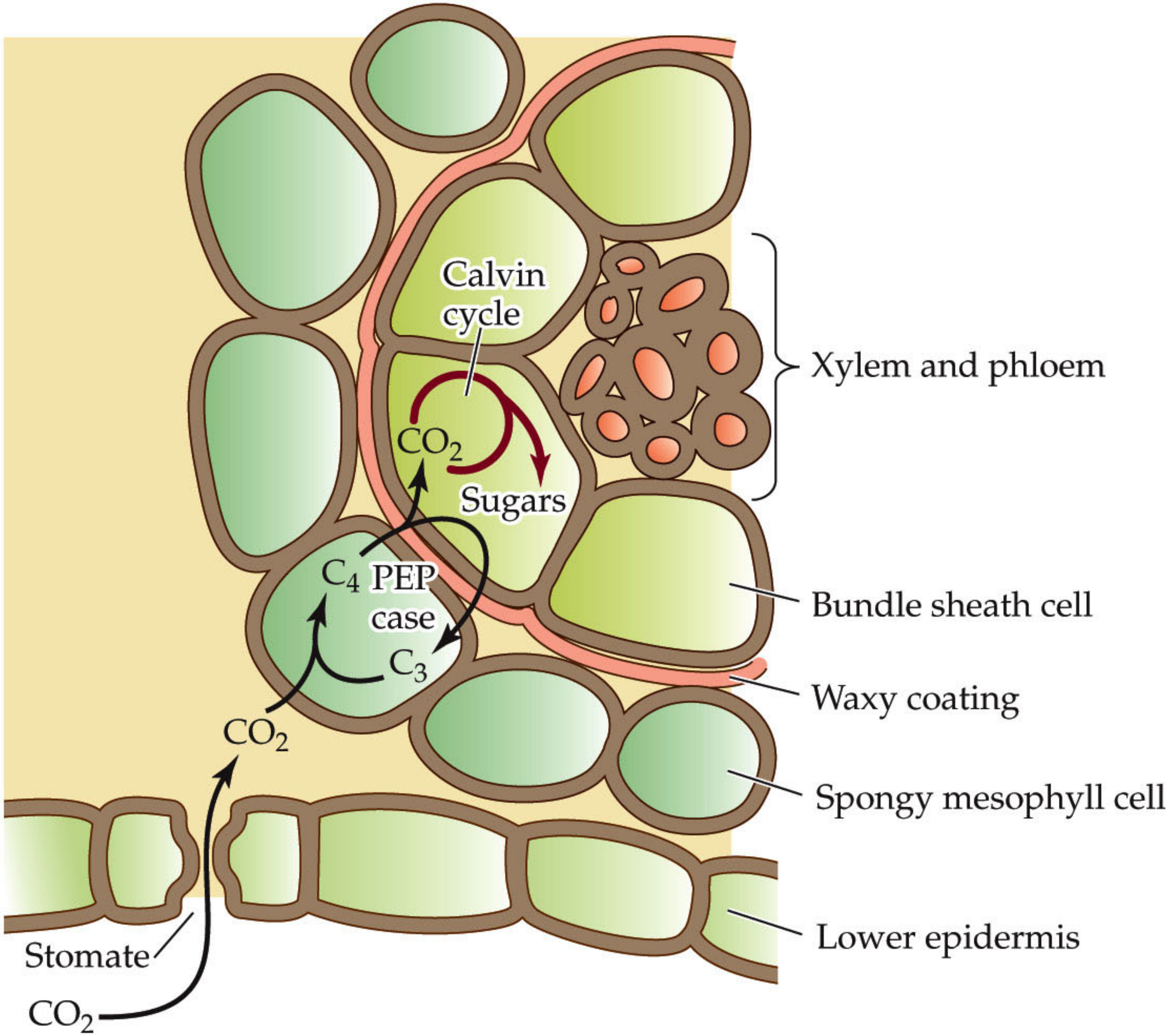
This compound is broken down to supply CO_2 to the Calvin cycle.

Figure 5.11 Morphological Specialization in C_4 Plants (Part 1)



ECOLOGY, **Figure 5.11 (Part 1)**

Figure 5.11 Morphological Specialization in C_4 Plants (Part 2)



ECOLOGY, **Figure 5.11 (Part 2)**

CO_2 concentrations in the bundle sheath cells are much greater than external CO_2.

Additional ATP is required for the C_4 pathway, but greater photosynthetic efficiency makes up for it.

C_4 plants can photosynthesize at higher rates than C_3 plants in conditions that promote photorespiration.

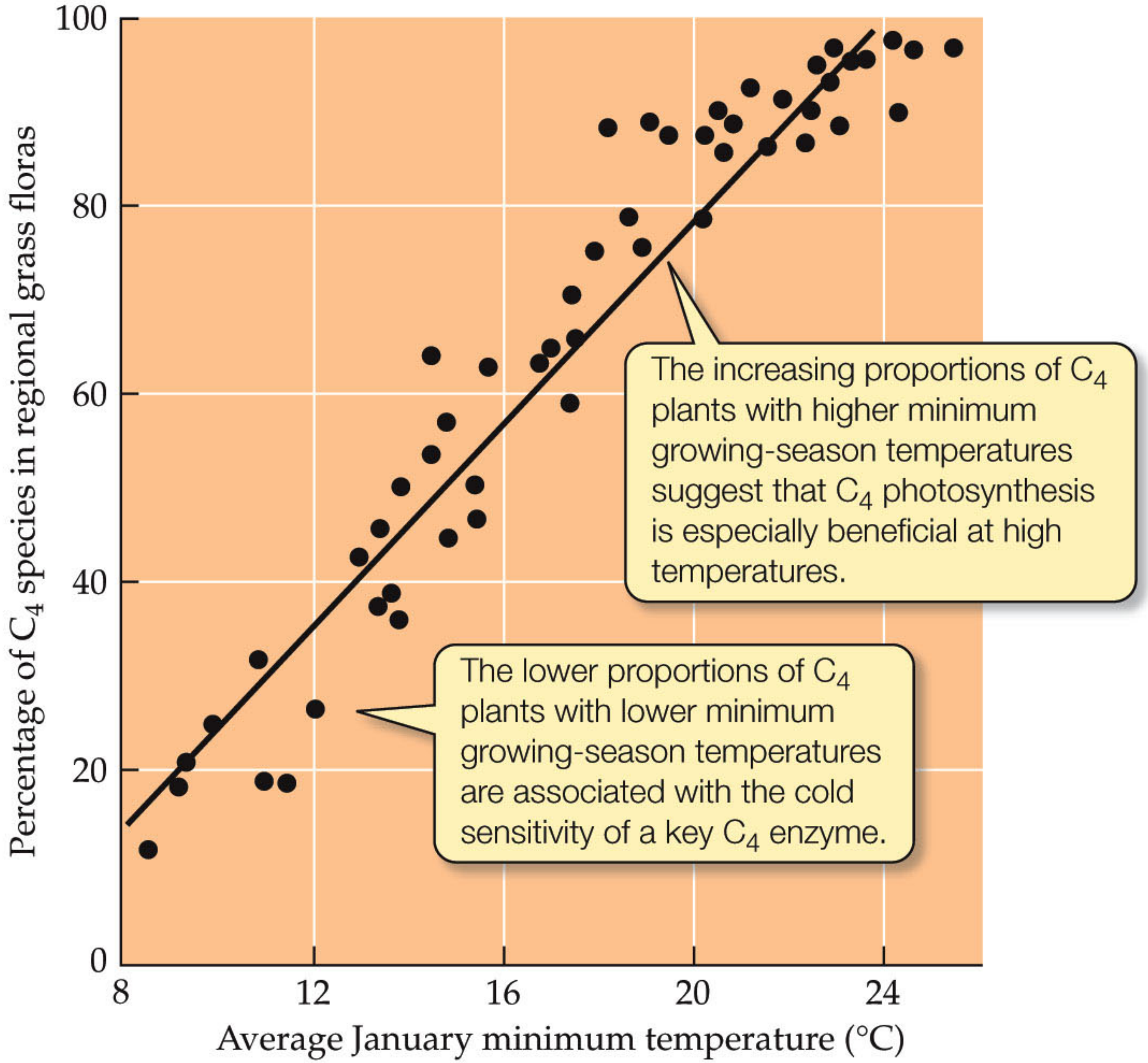
C_4 plants also have lower transpiration rates because PEPcase can take up CO_2 under the lower CO_2 that exist when stomates are not fully open.

Photosynthetic Pathways

Assuming that photosynthetic rates determine ecological success, climatic patterns can predict regions where C_4 plants will dominate.

There is a close correlation between growing-season temperature and the proportion of C_3 and C_4 species in the community.

Figure 5.12 C_4 Plant Abundance and Growing-Season Temperature



***ECOLOGY*, Figure 5.12**

As atmospheric CO_2 concentrations continue to increase, photorespiration rates are likely to decrease, and the advantages of C_4 over C_3 photosynthesis may be diminished.

This may lead to changes in the proportions of C_3 and C_4 plants.

Some plants have a unique photosynthetic pathway that minimizes water loss—**crassulacean acid metabolism** (**CAM**).

This pathway occurs in over 10,000 plant species belonging to 33 families.

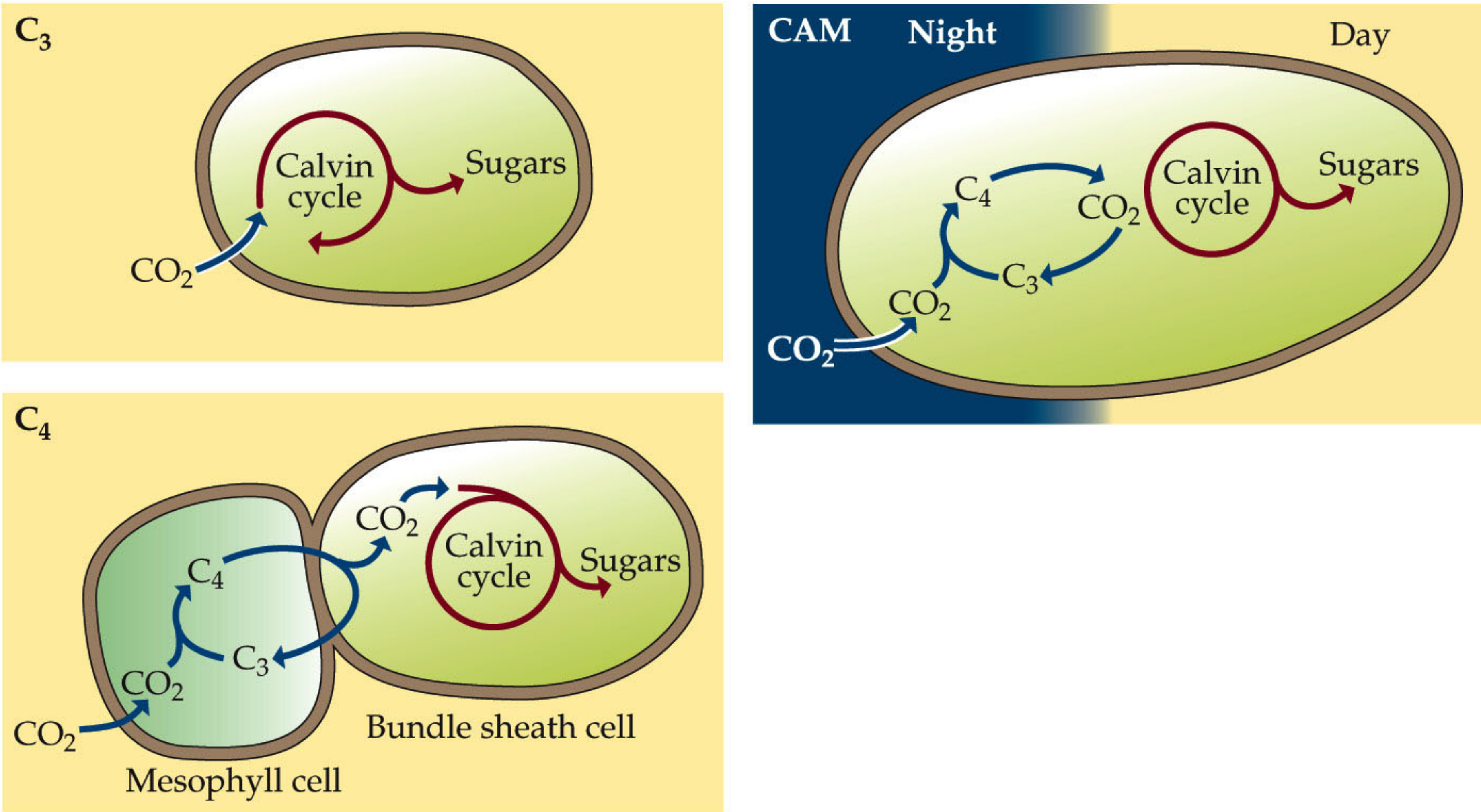
Photosynthetic Pathways

In CAM, CO_2 uptake and the Calvin cycle are separated temporally.

CAM plants open their stomates at night when air temperatures are cooler and humidity higher.

The plants loose less water than if stomates are open during the day.

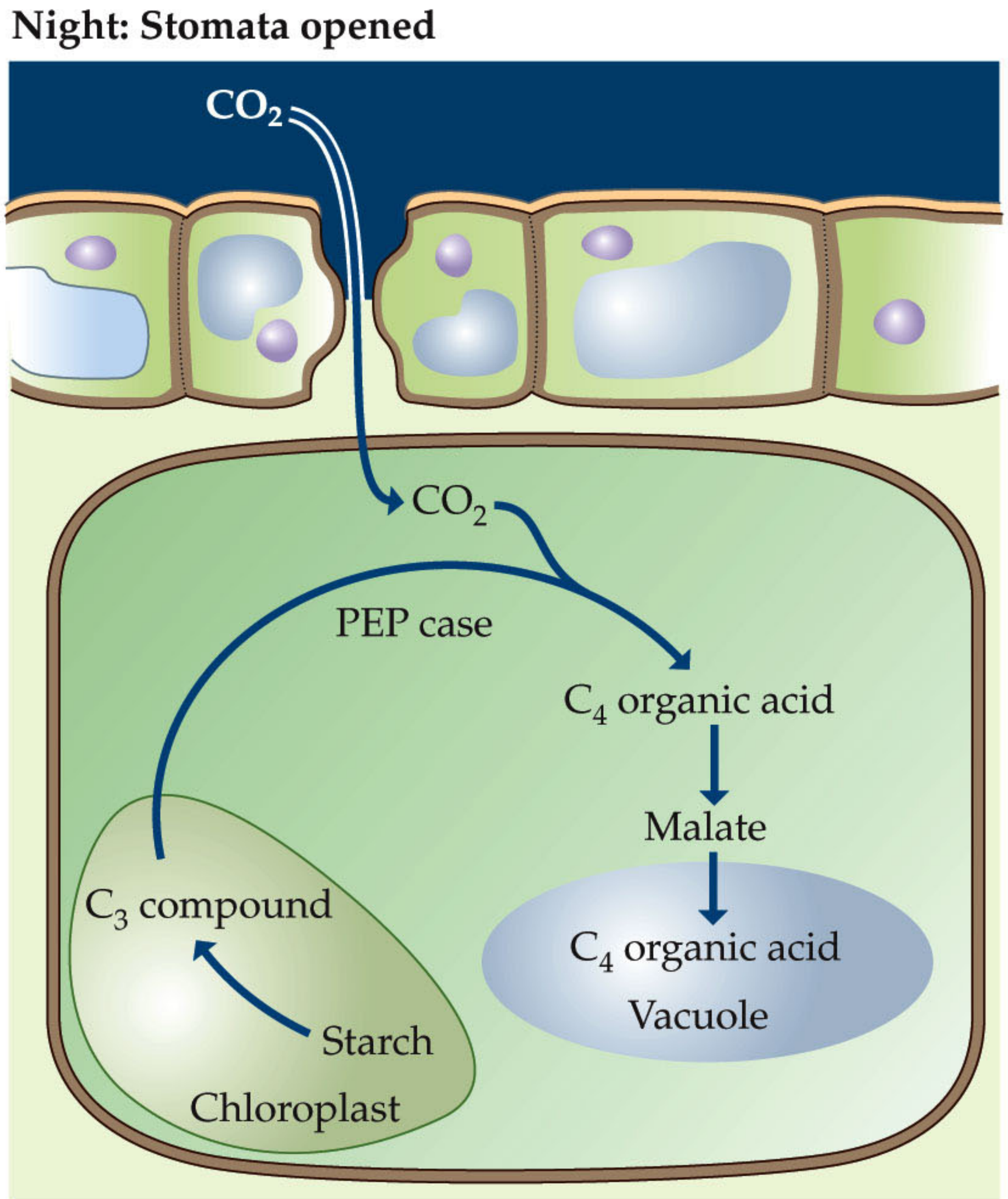
Figure 5.13 C_3 versus C_4 versus CAM Photosynthesis



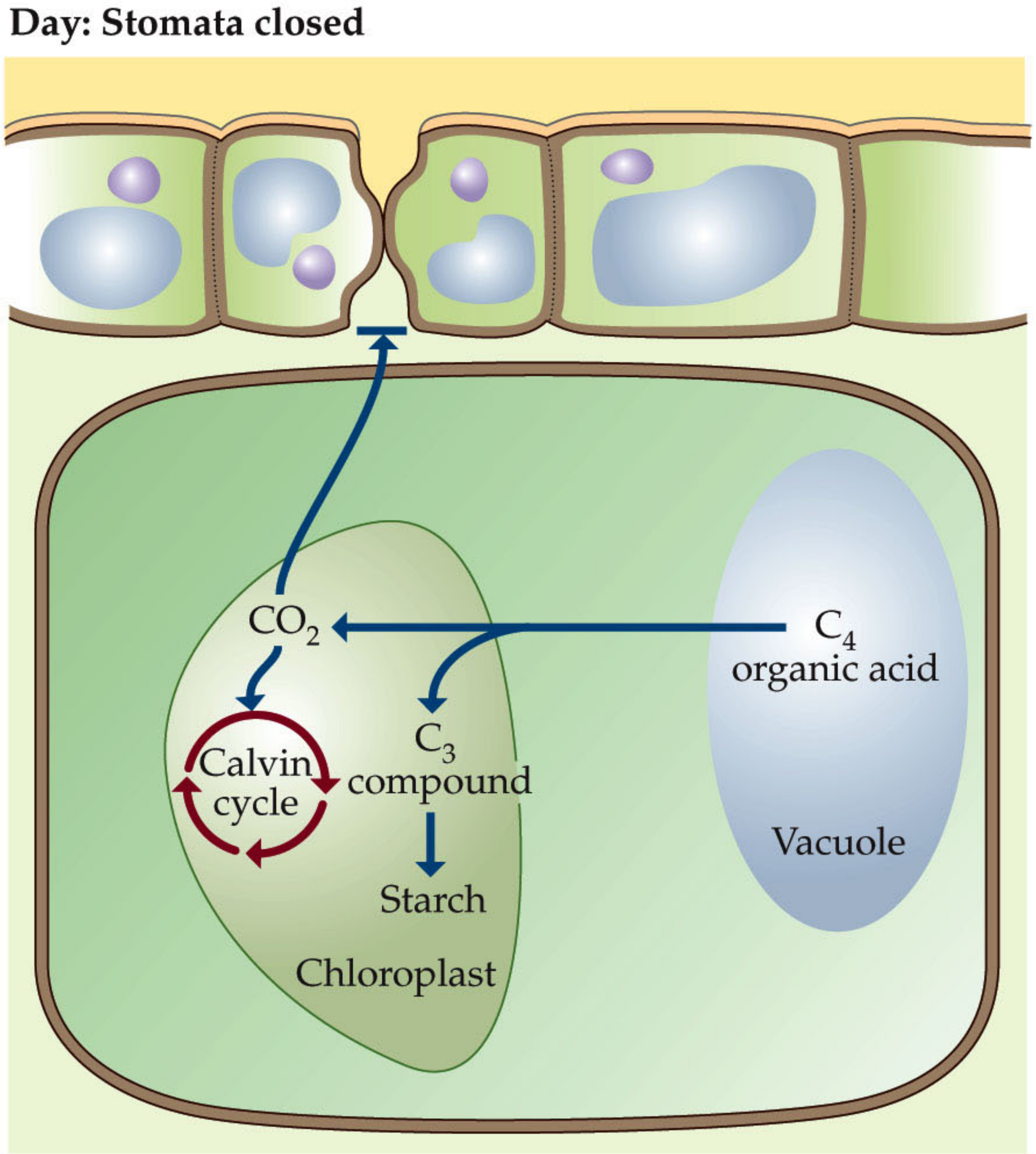
At night, CAM plants take up CO_2 using PEPcase and incorporate it into a four-carbon acid, which is stored in vacuoles.

During the day, the organic acid is broken down and CO_2 is released to the Calvin cycle. The CO_2 concentrations are high, reducing photorespiration and increasing photosynthetic efficiency.

Figure 5.14 CAM Photosynthesis (Part 1)



ECOLOGY, **Figure 5.14 (Part 1)**



ECOLOGY, Figure 5.14 (Part 2)

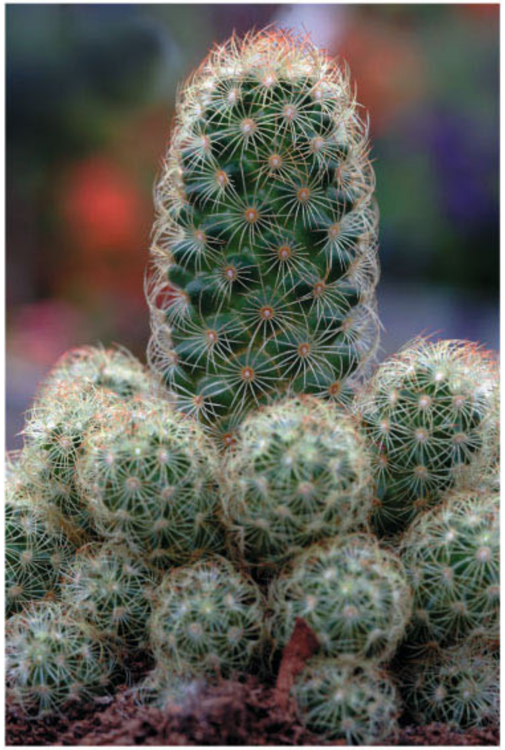
CAM plants are often succulent, with thick, fleshy leaves or stems. This enhances their nighttime acid storage capacity.

They are often associated with arid environments.

Some occur in the humid tropics—mostly epiphytes that grow on tree branches and have less access to water.

Figure 5.15 Examples of Plants with CAM Photosynthesis

Crassula tabularis, a stem succulent plant native to the desert of Namibia



Golden star cactus (*Mammillaria elongata*), native to Mexico

Pineapple (*Anana comosus*), a bromeliad native to Central and South American tropical forests

CAM is also found in some aquatic plants such as quillwort (*Isoetes*).

The rate of CO_2 diffusion into water is slow, and CAM may facilitate CO_2 uptake at low CO_2 concentrations in aquatic environments.

Some plants can switch between C_3 and CAM—**facultative CAM**.

When water is abundant, they use the C_4 pathway, which allows more carbon gain.

If conditions become arid or saline, they switch to CAM. It is irreversible in some species but not others.

Concept 5.4: Heterotrophs have evolved mechanisms to acquire and assimilate energy efficiently from a variety of organic sources.

The first organisms on Earth were probably heterotrophs that consumed amino acids and sugars that formed spontaneously in the early atmosphere.

Since that time, heterotrophs have evolved a wide range of methods for energy acquisition.

Heterotrophy

Heterotrophs consume energy-rich organic compounds (food) from their environment and convert them into usable chemical energy (ATP), by glycolysis.

The energy gain depends on the chemistry of the food.

Heterotrophy

The effort invested in finding and obtaining the food also influences how much benefit the heterotroph gets from consuming it.

Example: Microorganisms that feed on soil detritus invest little energy to find food, but the detritus has low energy content.

Heterotrophy

Living food organisms are more rare, and they may have defense mechanisms.

Example: A cheetah hunting a gazelle invests substantial energy in finding, chasing, capturing, and killing its prey, but it obtains an energy-rich meal.

Heterotrophy

Food chemistry depends on the type of organism it derives from.

Plant, fungal, and bacterial cells have more structural components, such as cell walls, that are not easily digested.

Animal cells are generally more energy-rich.

Heterotrophy

Most food consists of complex compounds that must be transformed into simpler compounds before they can be used as energy sources.

Proteins, carbohydrates, and fats are broken down into their component amino acids, simple sugars, and fatty acids.

Heterotrophy

Fats have more energy than carbohydrates per unit mass, and carbohydrates have more energy than amino acids.

Amino acids also provide nitrogen.

Heterotrophy

Some activities require specific energy-containing compounds.

Insect flight requires a lot of energy. Some insects have fat storage bodies for lipids to initiate flight.

Humans require carbohydrates for brain activity. Low blood sugar can lead to poor cognitive ability.

Heterotrophy

Heterotrophs range in size from archaea and bacteria (0.5 μm) to blue whales (up to 25 m).

Feeding methods and the complexity of food absorption are accordingly very diverse among heterotrophs.

Heterotrophy

Archaea, bacteria, and fungi excrete enzymes into the environment to break down organic matter; they digest their food outside their bodies.

Hetertrophic bacteria species have adapted to a wide variety of organic energy sources, and produce a wide variety of enzymes to break them down.

Heterotrophy

This ability of bacteria is exploited in *bioremediation*—fuels, pesticides, sewage, and other toxic wastes are cleaned up by using microorganisms that can break down the chemicals.

Heterotrophy

Multicellular organisms have evolved specialized tissues and organs for absorption, digestion, transport, and excretion.

Animals have tremendous diversity in morphological and physiological feeding adaptations, which reflect the diversity of the foods they consume.

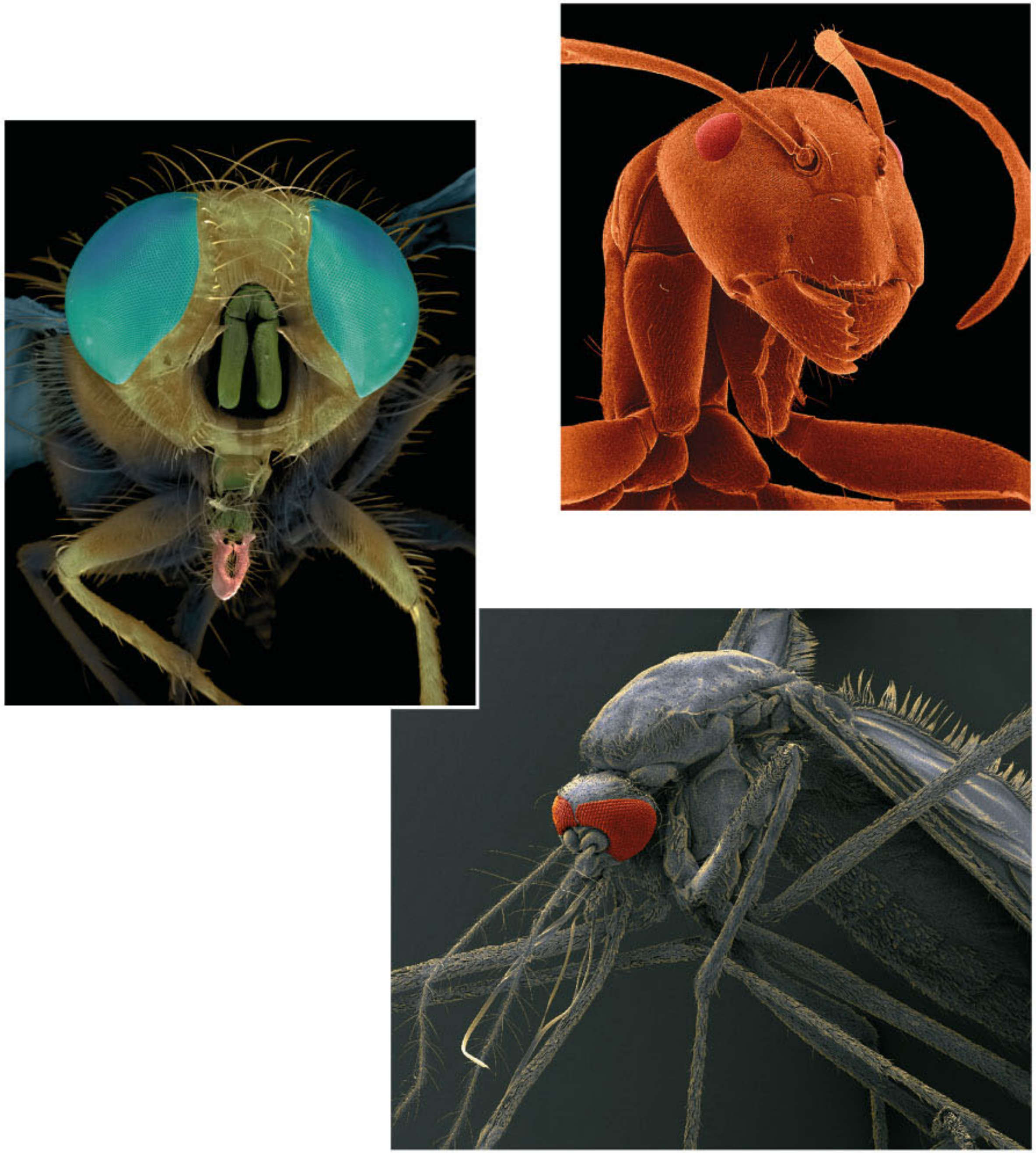
Heterotrophy

All insects have the same basic set of mouthparts.

Several paired appendages are used to seize, handle, and consume food.

Variation in these mouthparts reflects feeding specializations.

Figure 5.16 Variations on a Theme: Insect Mouthparts



Heterotrophy

Birds also have variation in mouthparts (bills) which they use to capture, manipulate, and consume their prey.

Variation in bill morphology reflects adaptations that help to optimize food acquisition and minimize competition among groups of birds.

Figure 5.17 Variations on a Theme: Bird Bills

ECOLOGY, **Figure 5.17**

Heterotrophy

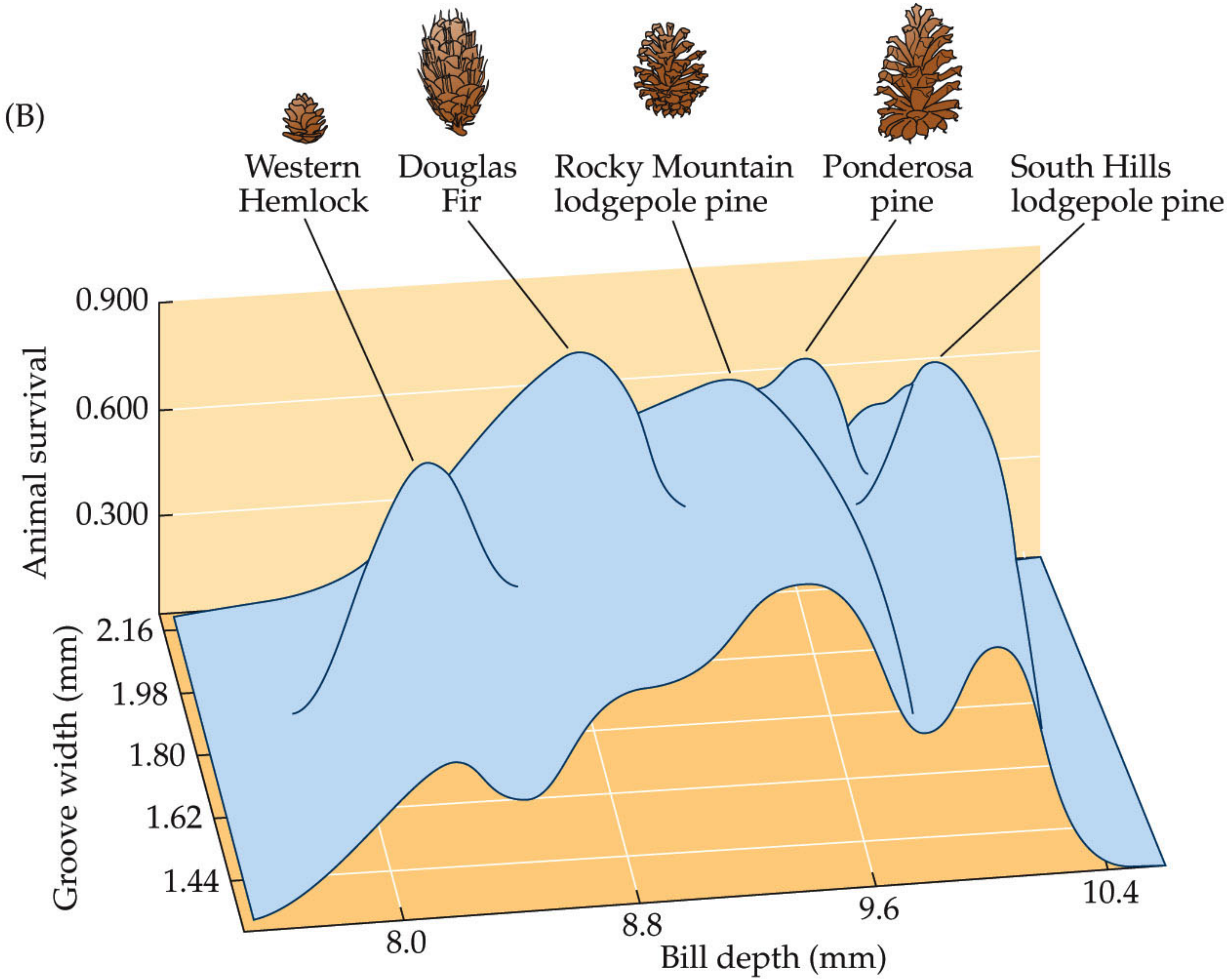
In studies of crossbills, Benkman (1993, 2003) tested the hypothesis that bill morphology was related to the morphology of the conifer cones they ate seeds from.

He showed that speed of seed extraction from a given cone was associated with bill depth, and speed of seed husking was associated with width of the groove where the seed is held.

(A)

ECOLOGY, Figure 5.18 (Part 1)

Figure 5.18 Crossbill Morphology, Food Preference, and Survival (Part 2)



ECOLOGY, Figure 5.18 (Part 2)

Each crossbill species was most efficient on one conifer species' cones.

There was a positive correlation between a species' bill depth and seed depth in the cone of its preferred conifer species.

Annual survival rate for each species was related to its feeding efficiency, which varied with conifer species.

Heterotrophy

Benkman (2003) concluded that red crossbills are currently undergoing evolutionary divergence (speciation) as a result of selection associated with available food sources.

Heterotrophy

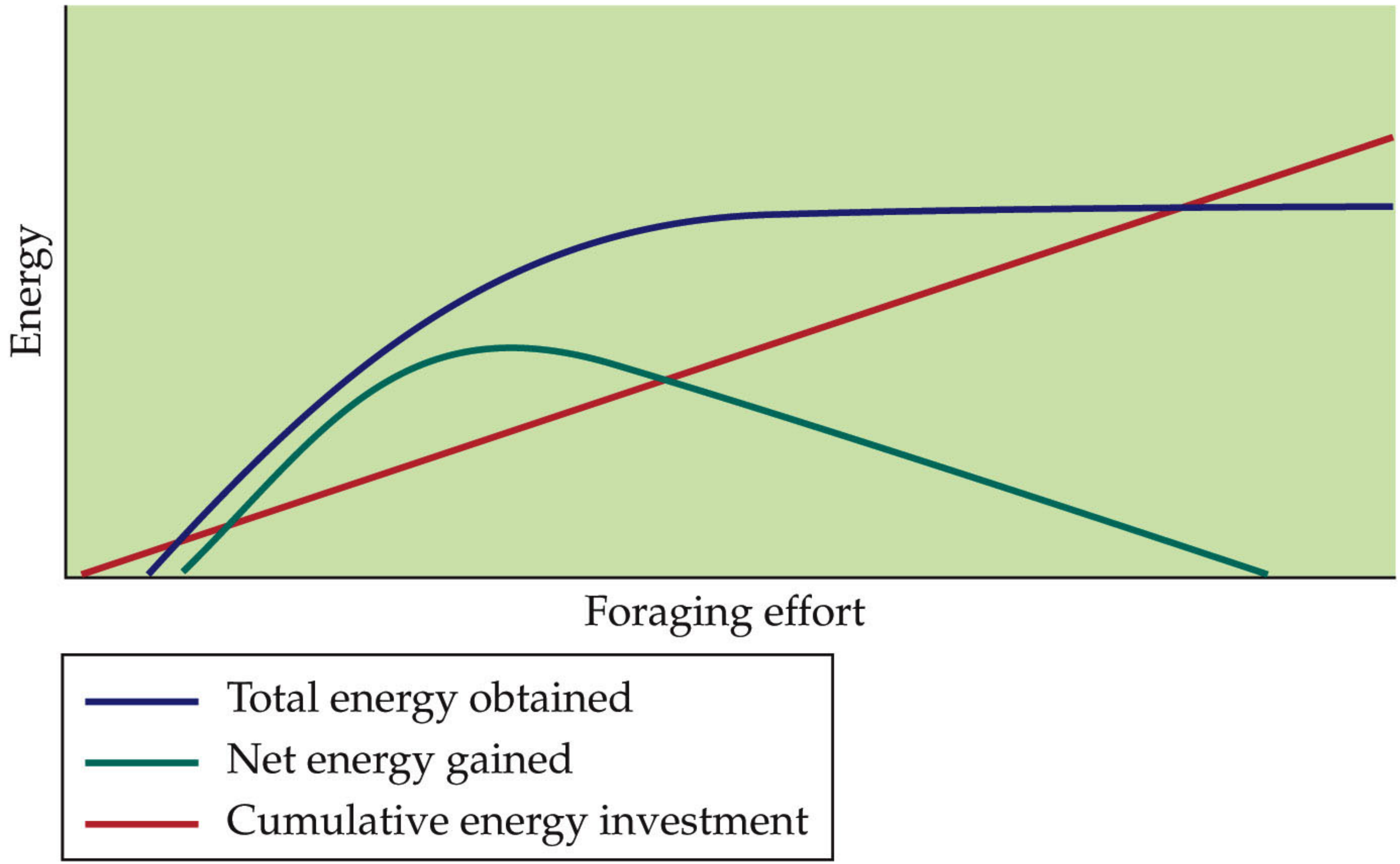
Food availability can vary significantly over time and space.

If energy is in short supply, animals in a heterogeneous landscape should invest their time obtaining the highest-quality food possible, which is the shortest distance away.

Optimal foraging theory proposes that animals will maximize the amount of energy gained per unit time, energy, and risk involved in finding food.

It assumes that evolution acts on the behavior of animals to maximize their energy gain.

Figure 5.19 Conceptual Model of Optimal Foraging



ECOLOGY, Figure 5.19

Heterotrophy

An animal's success in acquiring food increases with the effort it invests; but at some point, more effort results in no incremental benefit, and the net energy obtained begins to decrease.

Tests of the model can be made in the field or lab.

The independent variable (*x*-axis) could be size of food items; the dependent variable (*y*-axis) could be growth.

Is there an optimum food size that provides the greatest benefit per unit energy invested?

Heterotrophy

If optimal foraging is an adaptation to limited food supplies, then we must be able to relate the dependent variable to the survival and reproduction of the animal.

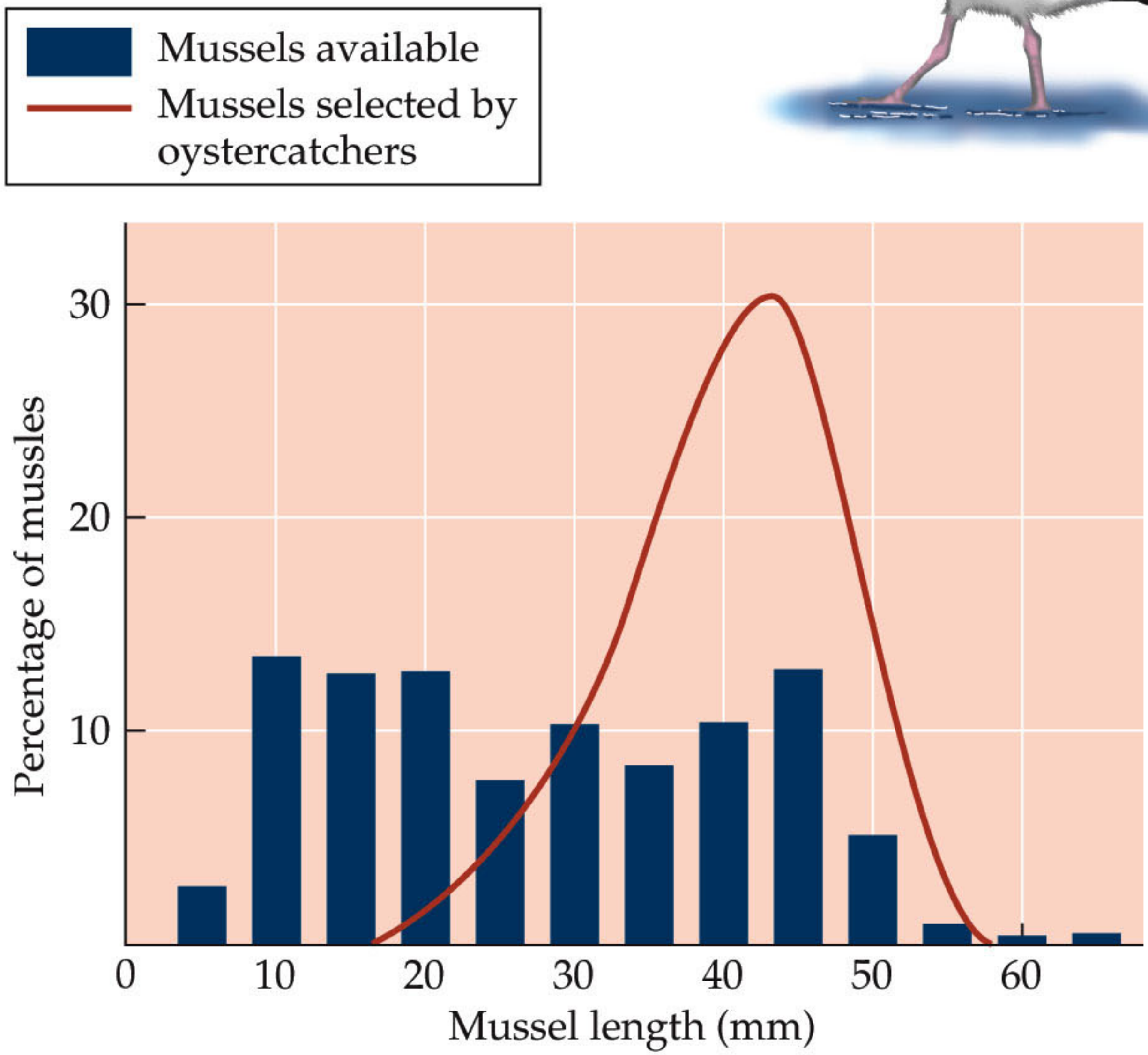
Research on the Eurasian oystercatcher, a shorebird that eats clams and mussels (Meire and Ervynck 1986):

The bird selects prey items of a size that provides the most energy per unit effort, even though this prey is relatively scarce.

Heterotrophy

Small mussels provide marginal net energy benefit; large mussels have thick shells and are difficult to open which increases energy expenditure.

Figure 5.20 Food Size Selection in Oystercatchers



ECOLOGY, Figure 5.20

Heterotrophy

Northwestern crows (*Corvus caurinus*) forage for shellfish and use gravity to open their shells.

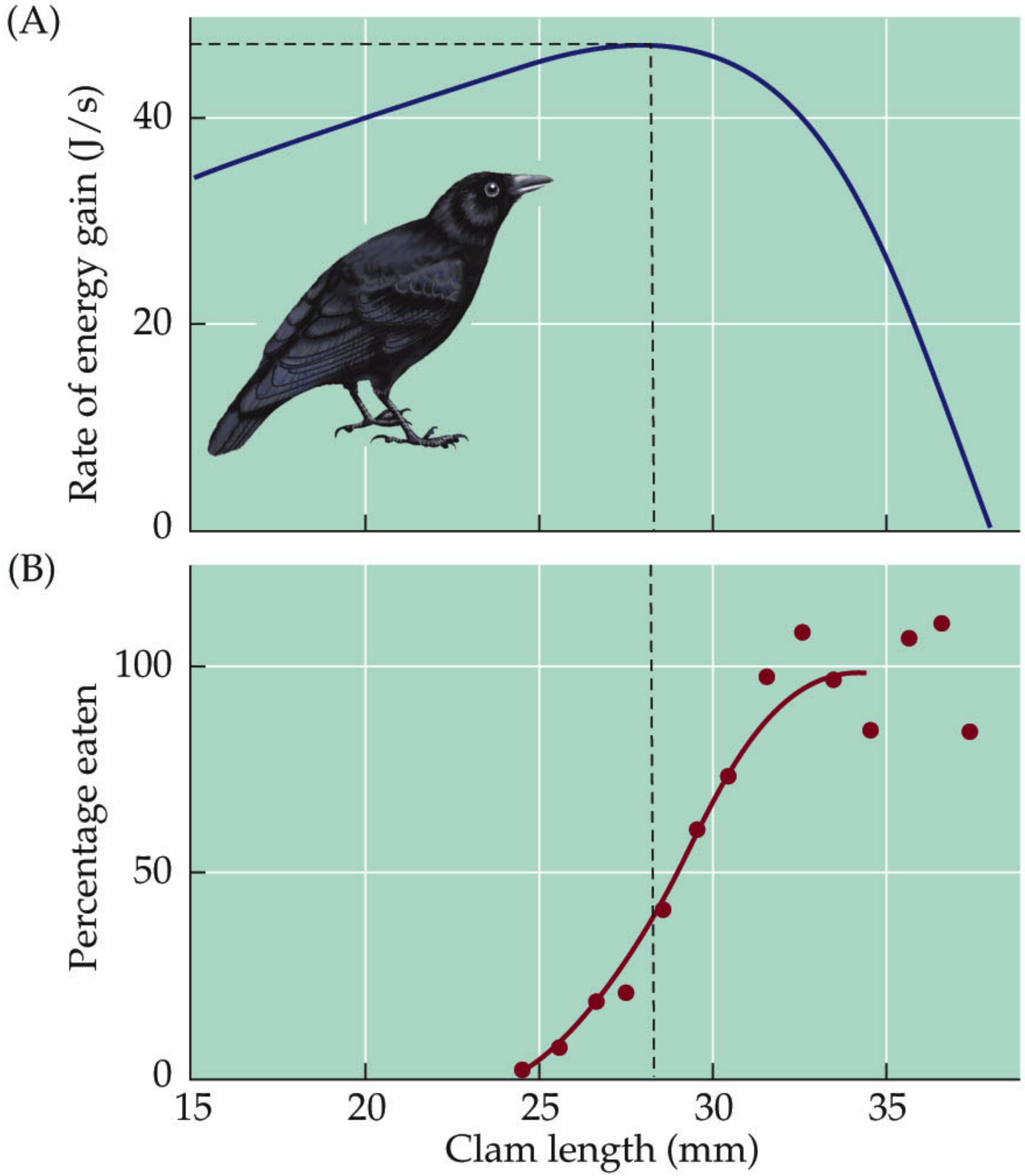
Crows pick up shellfish, fly into the air, and drop them on the rocks to crack them open.

Heterotrophy

The net energy from large prey items is greater, but so is the time spent in handling.

Richardson and Verbeek (1986) estimated the size of clam that provided most energy benefit, based on energy content of clams, abundance of size classes, and time required for handling.

Figure 5.21 Optimal Food Selection by Clam-Dropping Crows



Their estimate of optimal clam size closely matched the size the crows most often ate.

When crows were provided with both clams and whelks (less energy content), the crows chose larger items, even though they might get more energy from small clams versus large whelks.

Optimal foraging theory considers the habitat to be heterogeneous, having patches with different amounts of food.

To optimize energy gain, an animal should remain in a patch with highest food density, until food density becomes equal to nearby patches.

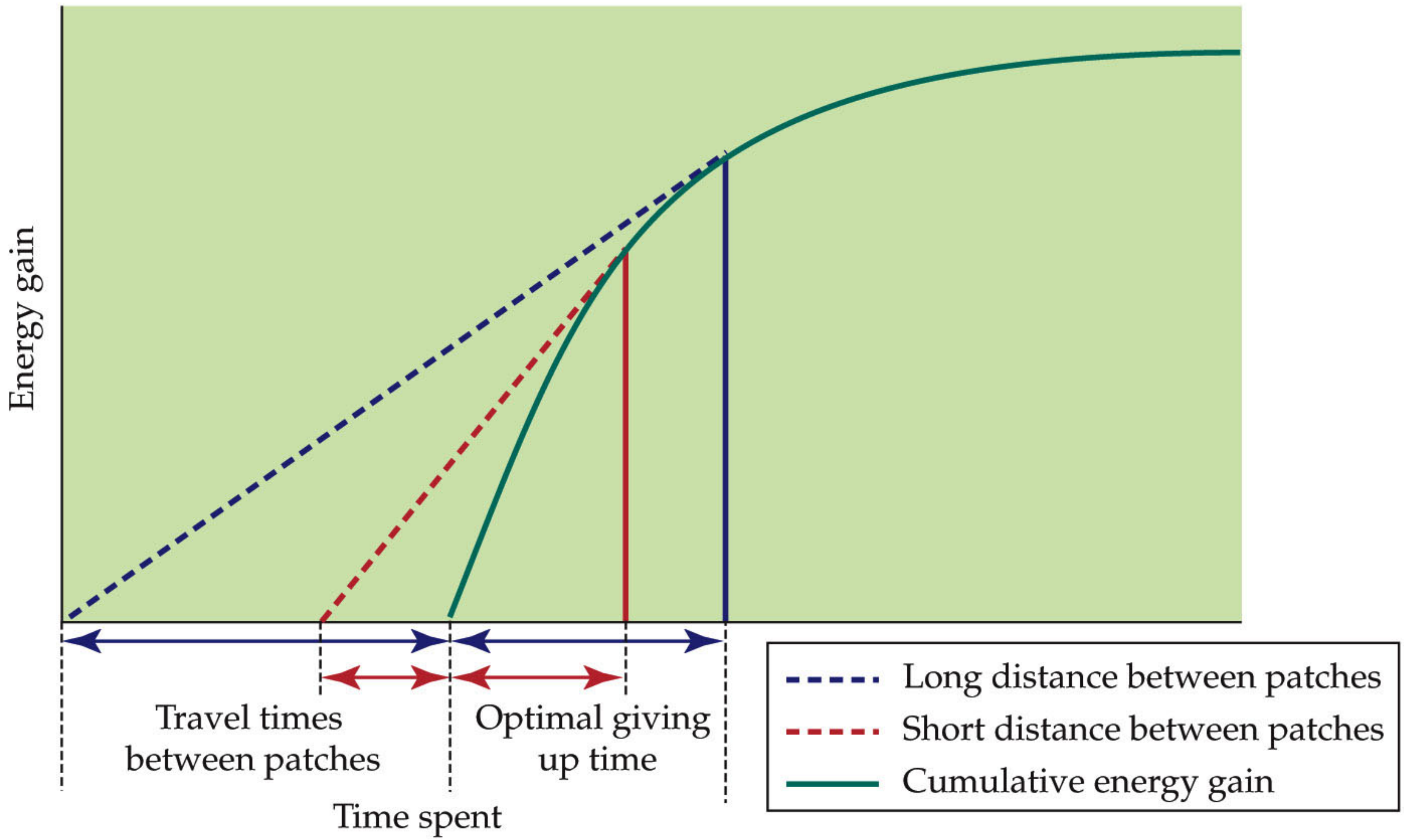
Marginal value theorem (Charnov 1976):

As a forager depletes the food supply, its energy gain decreases.

When energy gain is equal to the average rate for the habitat, the forager should move to another patch—*giving up time*.

The marginal value theorem can be used to evaluate the influences of distance between patches, quality of the food in a patch, and the energy extraction efficiency of the animal on the giving up time.

Figure 5.22 The Marginal Value Theorem



The longer the travel time between food patches, the longer an animal should spend in a patch.

This was tested by Cowie (1977) in laboratory experiments with great tits (*Parus major*).

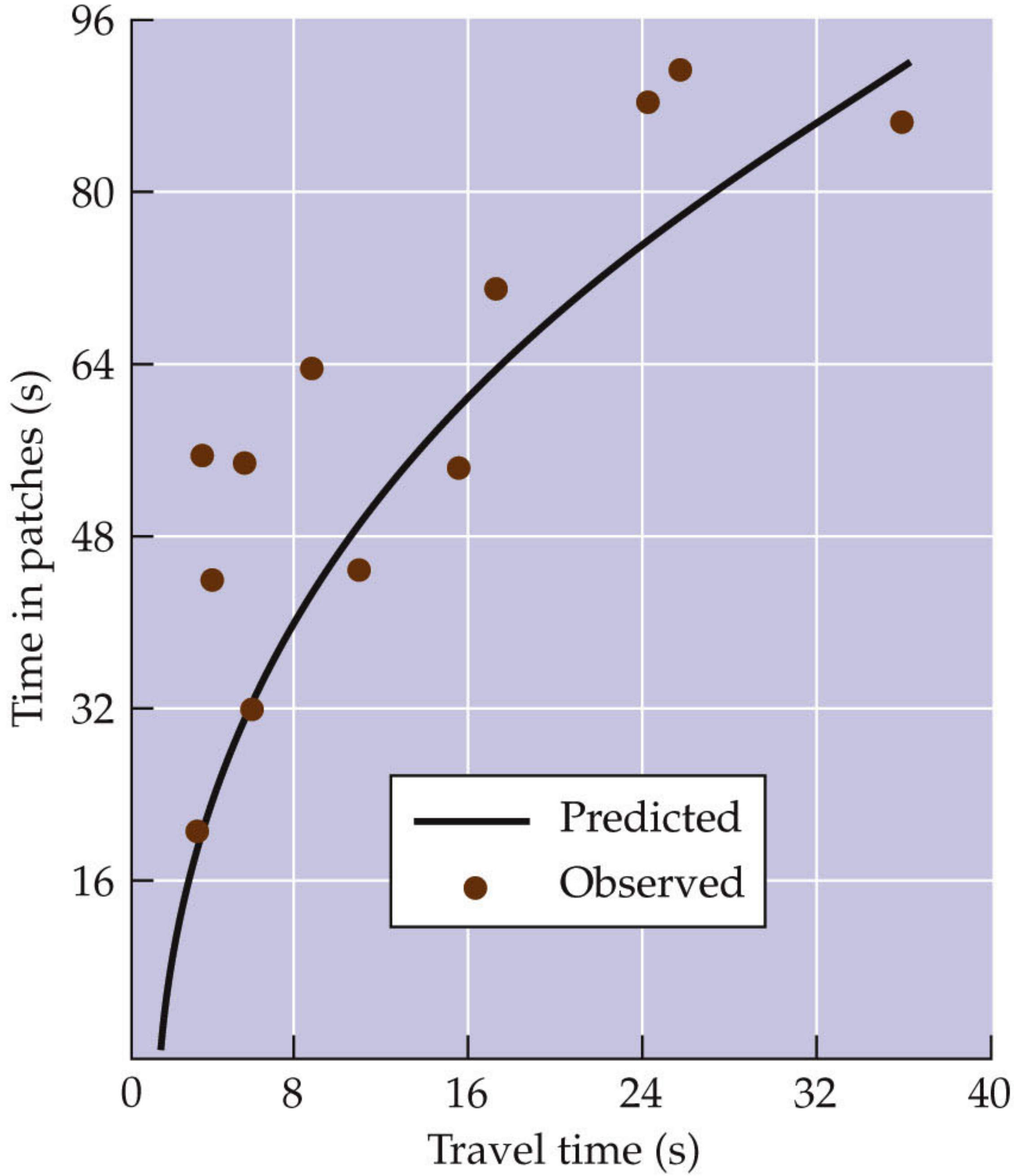
A “forest” of wooden dowels contained food “patches” of sawdust-filled plastic cups containing mealworms.

Heterotrophy

"Travel time" was manipulated by covering food cups, and adjusting ease of mealworm removal.

Results matched predictions made by the theorem fairly well.

Figure 5.23 Effect of Travel Time between Patches on Giving Up Time



ECOLOGY, Figure 5.23

Heterotrophy

Munger (1984) made a test of the theorem in a natural setting, using horned lizards.

The lizards eat ants that occur in patches of varying densities.

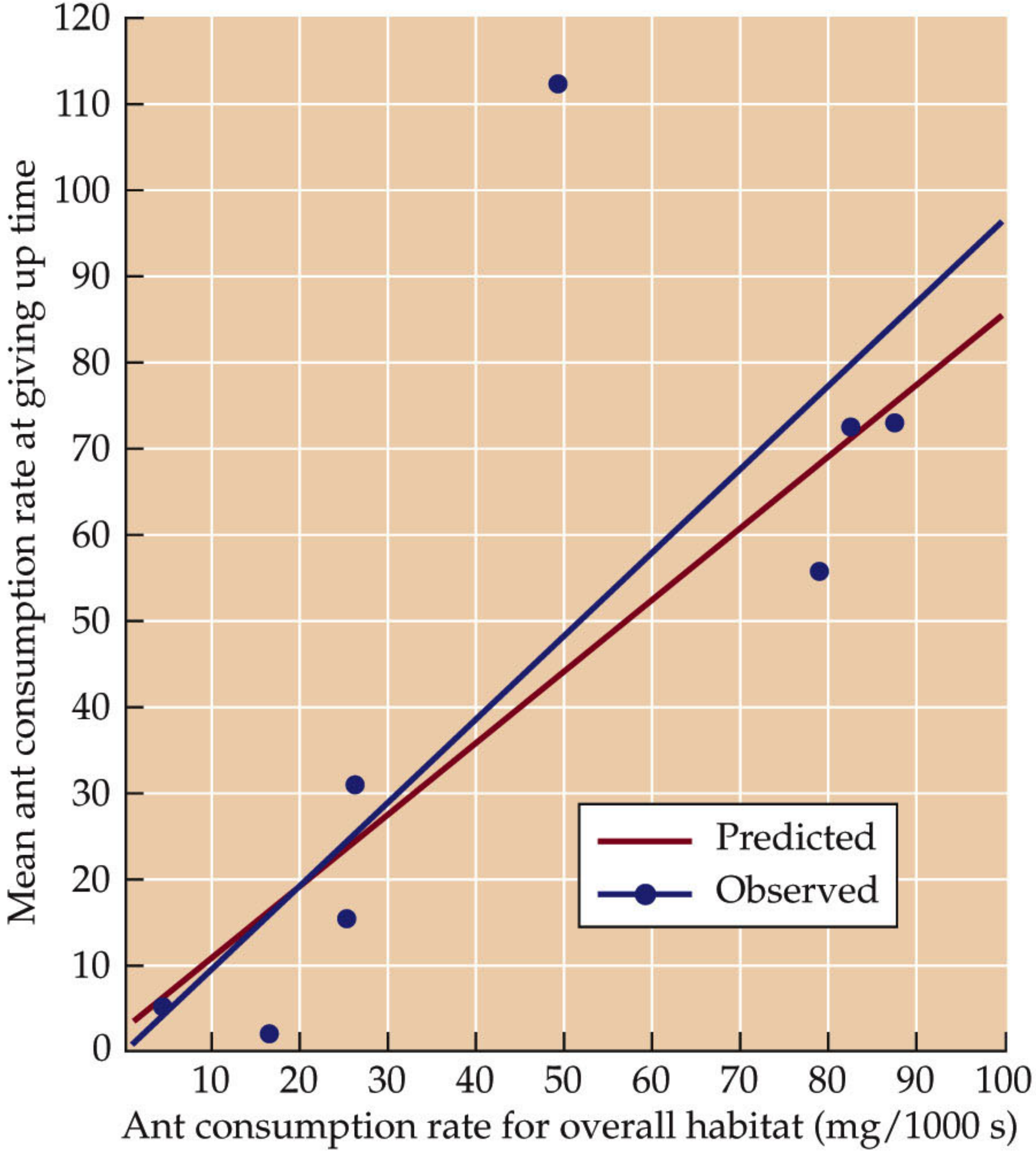
The rate of ant consumption at the giving up time was compared with overall consumption rate.

Heterotrophy

According to the theorem, the consumption rate at giving up time should be equal to the overall consumption rate for the habitat, and consumption rate should be higher when ant density was higher.

Again, results matched the predictions.

Figure 5.24 Giving Up Time in a Natural Setting



ECOLOGY, Figure 5.24

Optimal foraging theory does not apply as well to animals that feed on mobile prey.

The assumption that energy is in short supply and that dictates foraging behavior may not always hold.

Resources other than energy can be important, such as nitrogen or sodium content of the food.

Additional considerations for foragers include risks of exposure to their own predators.

The defensive behavior of prey also influences the costs and benefits to foragers.

Case Study Revisited: Toolmaking Crows

Do the New Caledonian crows inherit their knowledge of toolmaking?

Are they predisposed to learn how to make tools?

Or does the ability to learn toolmaking occur widely among birds?

Case Study Revisited: Toolmaking Crows

Kenward et al. (2005) reared crows without exposure to adult crows. Some received toolmaking tutoring from human foster parents, others did not.

The crows developed toolmaking skills, whether they had been tutored or not.

They concluded that this skill was partially inherited.

Figure 5.25 Untutored Tool Use in Captive Crows

ECOLOGY, Figure 5.25

Case Study Revisited: Toolmaking Crows

Different groups of New Caledonian crows make different styles of tools—there is a potential for technological evolution.

A survey of stepped-cut tools made from *Pandanus* tree leaves revealed three styles, and ranges of the three did not overlap (Hunt and Gray 2003).

Case Study Revisited: Toolmaking Crows

They suggested that the three tool designs were derived from one tool type, subjected to additional modifications.

This suggests ongoing innovation in toolmaking by the crows.

This crow engineering challenges our traditional view of technological advancement in nonhuman animals.

Connections in Nature: Tool Use and Innovative Foraging

There is much anecdotal evidence of toolmaking in nonhuman species.

A green heron in Florida was observed to collect bread fed to it and put it back in the water to attract fish.

When a flock of coots arrived, the heron chased them away, grabbed the bread and waited until the coots were gone to continue its fishing.

Connections in Nature: Tool Use and Innovative Foraging

The energy and nutrient content of the fish is much higher than bread.

Similar reports of using bait to attract fish have been documented for other heron species and great egrets.

Connections in Nature: Tool Use and Innovative Foraging

In some species, toolmaking is learned.

Some bottlenose dolphins pluck sponges from the seafloor to cover their noses (rostra). The sponges protect the rostra from stinging animals when the dolphin probes the seafloor for fish to eat.

Figure 5.26 Dolphin Nose Gear at Shark Bay, Australia

Connections in Nature: Tool Use and Innovative Foraging

Krützen et al. (2005) determined the "sponging" dolphins were mostly females, and belonged to a single family line.

They concluded that sponging was a learned behavior passed from mother to daughter.

This challenges the notion that cultural learning is unique to humans.