the study of the distribution of organisms on Earth

Introduction to Biomes

Biomes are the major regional groupings of plants and animals discernible at a global scale. Their distribution patterns are strongly correlated with regional climate patterns and identified according to the climax vegetation type. However, **a biome is composed not only of the climax vegetation, but also of associated successional communities, persistent subclimax communities, fauna, and soils.**

The biome concept embraces the idea of community, of interaction among vegetation, animal populations, and soil. A biome (also called a biotic area) may be defined as a major region of distinctive plant and animal groups well adapted to the physical environment of its distribution area.

To understand the nature of the earth's major biomes, one needs to learn for each:

- The **global distribution pattern**: Where each biome is found and how each varies geographically. A given biome may be composed of different taxa on different continents. Continent-specific associations of species within a given biome are known as formations and often are known by different local names. For example, the temperate grassland biome is variously called prairie, steppe, pampa, or veld, depending on where it occurs (North America, Eurasia, South America, and southern Africa, respectively).
- The general characteristics of the **regional climate** and the limitations or requirements imposed upon life by specific temperature and/or precipitation patterns.
- Aspects of the physical environment that may exert a stronger influence than climate in determining common plant growth forms and/or subclimax vegetation. Usually these factors are conditions of the **substrate** (e.g.,

1

waterlogged; excessively droughty, nutrient-poor) or of disturbance (e.g., periodic flooding or burning).

- The **soil order(s)** that characterize the biome and those **processes** involved in soil development.
- The dominant, characteristic, and unique **growth forms; vertical stratification; leaf shape, size, and habit; and special adaptations** of the vegetation. Examples of the last are peculiar life histories or reproductive strategies, dispersal mechanisms, root structure, and so forth.
- The types of **animals** (especially vertebrates) characteristic of the biome and their **typical morphological, physiological, and/or behavioral adaptations to the environment**

Tropical Rainforest

The tropical rainforest is earth's most complex biome in terms of both structure and species diversity. It occurs under optimal growing conditions: abundant precipitation and year round warmth. There is no annual rhythm to the forest; rather each species has evolved its own flowering and fruiting seasons. Sunlight is a major limiting factor. A variety of strategies have been successful in the struggle to reach light or to adapt to the low intensity of light beneath the canopy.

Climate:

Mean monthly temperatures are above 64° F; precipitation is often in excess of 100 inches a year. There is usually a brief season of reduced precipitation. In monsoonal areas, there is a real dry season, but that is more than compensated for with abundant precipitation the rest of the year.

Vegetation:

A vertical stratification of three layer of trees is apparent.. These layers have been identified as A, B, and C layers:

A layer: the emergents. Widely spaced trees 100 to 120 feet tall and with umbrella-shaped canopies extend above the general canopy of the forest. Since they must contend with drying winds, they tend to have small leaves and some species are deciduous during the brief dry season.

B layer: a closed canopy of 80 foot trees. Light is readily available at the top of this layer, but greatly reduced below it.

C layer: a closed canopy of 60 foot trees. There is little air movement in this zone and consequently humidity is constantly high.

Shrub/sapling layer: Less than 3 percent of the light intercepted at the top of the forest canopy passes to this layer. Arrested growth is characteristic of young trees capable of a rapid surge of growth when a gap in canopy above them opens.

Ground layer: sparse plant growth. Less than 1 percent of the light that strikes the top of the forest penetrates to the forest floor. In such darkness few green plants grow. Moisture is also reduced by the canopy above: one third of the precipitation is intercepted before it reaches the ground.

Growth forms:

Various growth forms represent strategies to reach sunlight:

Epiphytes: the so-called air plants grow on branches high in the trees, using the limbs merely for support and extracting moisture from the air and trapping the constant leaf-fall and wind-blown dust. Bromeliads (pineapple family) are especially abundant in the neotropics; the orchid family is widely distributed in all three formations of the tropical rainforest. As demonstration of the relative aridity of exposed branches in the high canopy, epiphytic cacti also occur in the Americas.

- **Lianas:** woody vines grow rapidly up the tree trunks when there is a temporary gap in the canopy and flower and fruit in the tree tops of the A and B layers. Many are deciduous.
- **Climbers:** green-stemmed plants such as philodendron that remain in the understory. Many climbers, including the ancestors of the domesticated yams (Africa) and sweet potatoes (South America), store nutrients in roots and tubers.
- **Examplers:** these plants begin life as epiphytes in the canopy and send their roots downward to the forest floor. The fig family is well represented among stranglers.
- **Heterotrophs:** non-photosynthetic plants can live on the forest floor.
	- 1. Parasites derive their nutrients by tapping into the roots or stems of photosynthetic species. *Rafflesia arnoldi*, a root parasite of a liana, has the world's largest flower, more than three feet in diameter. It produces an odor similar to rotting flesh to attract pollinating insects.
	- 2. Saprophytes derive their nutrients from decaying organic matter. Some orchids employ this strategy common to fungi and bacteria.

Common characteristics of tropical trees:

Tropical species frequently possess one or more of the following attributes not seen in trees of higher latitudes.

4

- **Buttresses**: many species have broad, woody flanges at the base of the trunk. Originally believed to help support the tree, now it is believed that the buttresses channel stem flow and its dissolved nutrients to the roots.
- **Large leaves** are common among trees of the C layer. Young individuals of trees destined for the B and A layers may also have large trees. When the reach the canopy new leaves will be smaller. The large leaf surface helps intercept light in the sun-dappled lower strata of the forest.
- **Drip tips** facilitate drainage of precipitation off the leaf to promote transpiration. They occur in the lower layers and among the saplings of species of the emergent layer (A layer).

Other characteristics that distinguish tropical species of trees from those of temperate forests include:

- **Exceptionally thin bark**, often only 1-2 mm thick. Usually very smooth, although sometimes armed with spines or thorns.
- **Cauliflory**, the development of flowers (and hence fruits) directly from the trunk, rather than at the tips of branches.
- **Large fleshy fruits** attract birds, mammals, and even fish as dispersal agents.

Soils:

Oxisols, infertile, deeply weathered and severely leached, have developed on the ancient Gondwanan shields. Rapid bacterial decay prevents the accumulation of humus. The concentration of iron and aluminum oxides by the laterization process gives the oxisols a bright red color and sometimes produces minable

deposits (e.g., bauxite). On younger substrates, especially of volcanic origin, tropical soils may be quite fertile.

Subclimaxes:

Distinct communities (varzea) develop on floodplains. Jungles may line rivers where sunlight penetrates all layers of the forest. Where forests have long been cleared and laterites have developed to cause season waterlogging of the sub strate, tropical grasslands and palm savannas occur.

Fauna:

Animal life is highly diverse. Common characteristics found among mammals and birds (and reptiles and amphibians, too) include adaptations to an arboreal life (for example, the prehensile tails of New World monkeys), bright colors and sharp patterns, loud vocalizations, and diets heavy on fruits.

Distribution of biome:

The tropical rainforest is found between $10 \degree$ N and $10 \degree$ S latitude at elevations below 3,000 feet. There are three major, disjunct formations:

- **Neotropical** (Amazonia into Central America)
- **African** (Zaire Basin with an outlier in West Africa; also eastern Madagascar)
- **Indo- Malaysian** (west coast of India, Assam, south east Asia, New Guinea and Queensland, Australia.

The species composition and even genera and families are distinct in each. They also differ from species of temperate forests. Species diversity is highest in

6

the extensive neotropical forest; second in the highly fragmented Indo-Malaysian formation; and lowest in Africa, Where 5 to a maximum of 30 species of tree share dominance in the Temperate Broadleaf Deciduous Forest, there may be 40 to 100 different species in one hectare of tropical rainforest. Tropical species of both plants and animals often have very restricted distribution areas.

Altitudinal Zonation on High Mountains in the Tropics

Vegetation zonation on mountains in the tropics does not replicate the latitudinal belts of vegetation of the middle and higher latitudes even though mountain peaks may extend well above snowline. In part this is due to the fact that the seasonal cool and cold temperatures of the middle and high latitudes are not experienced in the tropics. Instead, it is diurnal temperature patterns that are important. At high elevations nocturnal frosts may occur nearly every day throughout the year; while daytime temperatures are quite warm. Seasons in the tropics are distinguished on the basis of precipitation patterns.

Plant species of the alpine zones of the tropics, particularly in the southern hemisphere, are taxonomically related to the southern hemisphere temperate zone and antarctic floras. There are interesting convergences in lifeforms between the alpine flora of the Old World and New World tropics and, indeed, between some animal taxa, too. For example, the hummingbirds (Trochilidae) of the high Andes have their counterpart in East Africa in the sunbirds (Nectarinidae).

For all the similarities, there are also distinct differences between the mountain zones of South America and of East Africa reflecting the very different geologic history of the two continents. The Andean Cordillera of South America is a continuous range of mountains stretching along the entire west coast of the continent, the result of mountain building associated with continental drift. In east African a disjunct chain of mountains ranges from Ethiopia to South Africa.

Individual peaks and ranges have different ages, origins, and geologies. Instead of forming a long corridor as the Andes do, Africa's mountains are more or less islands onto themselves. Thus we will examine each continent's tropical mountain vegetation separately.

Vegetation Zonation on East Africa's Highest Mountains

Spectacular mountains rise above snow line in the equatorial region of East Africa. Included among these are Africa's highest peak, Mt Kilimanjaro (5,895 m or 19,340 ft) in Tanzania; Mt. Kenya (5199 m or 17,058 ft) just 200 miles to the north in Kenya; and the Ruwenzori range (with peaks above 5000m or 16,000 ft) the fabled Mountains of the Moon--along the Uganda-Zaire border.

8

From 4000 m to snowline at about 5000 m, is the **Afro-alpine Zone** (similar in many respects to the paramos of the northern Andes of South America),dominated by tussock sedges (*Carex* spp.) and rushes, proteas, red-hot pokers (*Kniphofia*), and-most distinctively-giant lobelias (*Lobelia* spp.) and tree groundsels (*Senecio* spp.). The lobelias-familiar North American forms of the genus are small herbaceous plants-may be 7 to 8 feet tall, while the arborescent groundsels may stand 30 feet high.

A **Montane Zone** exists from 1300-1500 m to 4000 m. It has two or three distinct subzones. At the lowest elevations is the montane forest. On wetter slopes this will be broadleaf and evergreen, but composed of species not found in the lowland forest. On drier slopes a coniferous forest of junipers and podocarps occurs. At the upper margins of the montane forest, bamboos may occur in patches or as a nearly continuous belt. The uppermost belt of the Montane Zone is composed of giant heaths (Ericaceae) up to 60 ft tall and

draped with lichens.

The regional vegetation of the lowlands (broadleaf evergreen forest west of the Ruwenzori and tropical savanna to the east, as shown here) extends up to elevations of about 1300 m.

All photographs were taken on Mt. Kenya

Endemism

There is a high degree of endemism among the plant species of the Afroalpine zone, which have been isolated on individual peaks since the late Pleistocene. See the table below for examples.

Seasonal Forests of the Tropics

As one proceeds pole ward from the equatorial rainforests, one finds a progressively longer dry season until one finally encounters truly arid climates. This latitudinal and moisture gradient is reflected in the natural vegetation. The forests poleward of the rainforest become shorter in stature and simpler in structure. The proportion of trees that are deciduous increases as the dry season becomes more pronounced. Leaves become smaller and thorns or spines more frequent. At the drier extremes of this gradient, succulents become common.

The general sequence of vegetation from about 10° to 25° of latitude is semi-evergreen forest; deciduous seasonal or dry forest; and thorn forest or thornscrub.

Tropical Semi-evergreen Forests

These are broadleaf forests, some species of which are evergreen and some of which are deciduous. Two tree layers are evident: an upper canopy of deciduous trees with large leaves and an understory of small-leafed evergreen species. Frequently stands are composed of a single-species, such as teak in Africa and Southeast Asia and miombo (*Brachystegia* spp. and *Isoberlinia* spp.) in Africa. There are many fewer tree species than in the rainforests, but still many lianas. Epiphytes are infrequent. The seasonal leaf fall produces abundant nutrients and more fertile soils than found under tropical broadleaf evergreen forests but also creates fuel for fires. The fire factor in the environment may explain the thicker bark of tree species in this formation compared to those of the rainforest. Some researchers consider teak woodlands to be a fire subclimax.

Tropical Deciduous Broadleaf Forests or Dry Forests

This forest type occurs where two of the dry season months receive less than 1 inch of rain. It is not found in Africa. Two layers are again evident. In this case both the upper story of trees 60 to 80 feet tall and the understory trees some 10 to 30 tall are small-leafed and deciduous. Bamboo (a member of the grass family) thickets are common. The forest is poor in lianas, epiphytes, and herbs. The shrub layer is dominated by members of the pea family (Leguminosae) such as *Mimosa* spp. and *Acacia* spp. Palms are also common.

Thorn Forest or Thornscrub

This vegetation type, comprised of low-growing trees, shrubs, and frequently stem-succulents, occurs where annual precipitation averages 20 to 25 inches and the dry season extends for 6 or 7 months.

The woody species are deciduous and small-leafed; many have thorns or spines. Stem succulents in the neotropics include members of the cactus family (Cactaceae) and a member of the Bombacacae, the barriguda or Brazilian bottletree, *Chorisia glaziovii*. Xerophytic palms and epiphytes (esp. genus *Tillandsia*, family Bromeliaceae) are common. Terrestrial bromeliads also occur.

In the neotropics, this vegetation type is represented by the **caatinga** in northeast Brazil and by the thornscrub communities of the Mexican state of Oaxaca.

11

Desert scrub

Desert areas are rarely devoid of life. Instead, they abound with wonderfully adapted plants and animals that have evolved various mechanisms for tolerating or avoiding the extremes of aridity and temperature that might be encountered in their environment. Deserts develop under four distinct geographic conditions:

- Under zones of high atmospheric pressure associated with the subtropics and centered near 30° latitude. Air descending from the upper atmosphere at these latitudes causes evaporation to exceed precipitation. Much of the Sahara and the Australian desert can be associated with this phenomenon.
- **•** West coasts of continents between 20° and 30° latitude. In these latitudes, prevailing winds are easterly and prevent moist air from coming onto the west coast. Cold ocean currents also occur in these locations and moisture in the sea air condenses as fog along the shore. Some of the world's driest deserts are located right on the coast; they received most of their limited precipitation from fog. Such fog deserts include Baja California in North America, the western Sahara in northern Africa; the Atacama in South America, and the Namib in southern Africa.
- Rainshadows of high mountain ranges. When air masses are forced over mountains and downslope, they warm and their capacity for holding water vapor increases. Evaporation exceeds precipitation and an arid environment or rainshadow is created on the leeward side. Such conditions account for some of the North American deserts (exemplified in Death Valley, CA), the Patagonian desert in Argentina; and the Peruvian desert.
- Interiors of continents. Usually in combination with the rainshadow effect, distance from a major source of moist air results in dry climates in the interior

of a land mass. The Great Basin desert of the US, the Australian desert, and the Gobi desert of Mongolia can all be explained in large part to their interior positions.

Climate:

Arid climates (BWh and BWk) are those which average less than 10 inches of precipitation a year. Potential evaporation exceeds precipitation in the annual water budget. Furthermore, rainfall is highly localized and relatively unpredictable in terms of when it will occur, although usually there are seasons of highest probability for precipitation. Annual variation in total precipitation may also be great. Temperatures are also variable. They may exceed 100° F on summer afternoons, but dip by 20-30 degrees or more at night. Winters are cool to cold: "hot deserts" rarely experience frost; "cold deserts" may have prolonged periods of below freezing temperatures and snowfall.

Vegetation:

Shrubs are the dominant growth form of deserts. They may be evergreen or deciduous; typically have small leaves; and frequently have spines or thorns and/or aromatic oils. Shallow but extensive root systems procure rainwater from well beyond the canopy of the shrub whenever it does rain. These are the true xerophytes adapted to tolerate extreme drought. They form an open canopy and, except after rains when annuals may cover the desert floor, the ground between shrubs is bare of vegetative growth.

Water is not entirely lacking in the desert environment and several other growth forms represent strategies to reach water or to store water:

- **Phreatophytes** are plants with long taproots that may extend downward 20 to 30 feet to tap ground water supplies. Especially along intermittent streams or under dunes, underground water may be readily available. Mesquite is a good example here in North America. One of the world's most unusual phreatophyes is *Welwitschia mirabilis* of the Namib.
- **Succulents** store water accumulated during rains for use during the intervening dry spells. Different species store water in different parts of the plant; hence we can recognize stem succulents, leaf succulents, root succulents, and fruit succulents. Many plant families have members that evolved succulence. Most prominent among stem succulents in the Americas are the Cactaceae; in Africa succulent euphorbias have evolved shapes and sizes resembling the cacti. The agaves (Liliaceae) are examples of leaf succulents in the Americas; their role is filled by aloes (Liliaceae) in Africa. Most succulents do not tolerate freezing temperatures so they are essentially limited to the hot deserts.
- **Ephemerals** are another growthform adapted to desert conditions. This is an especially short-lived annual forb that completes its life cycle in two-three weeks. The seeds are encased in a waterproof coating that prevents desiccation for years if necessary. These plants essentially avoid drought by occurring as seeds most of the time.
- **Perennial forbs** with underground bulbs store nutrients and water in undergound tissues and also remain dormant most of the year. They can sprout rapidly after sufficient rains and replenish their undergound stores.

Soils:

Calcification is the dominant soil-forming process, if indeed soil forming even occurs. There is poor development of horizons, with accumulation of calcium

carbonate at or near the surface. Sparse vegetative cover and tiny leaves results in little humus and soils typically have a light gray color. Aridosols are the dominant soil order.

Fauna:

Like the plants, the animals of the desert have evolved an array of strategies for dealing with aridity.

- Behavioral adaptations such as being nocturnal or crepuscular, being fossorial, and staying the shade during the heat of day are common.
- Morphological adaptations include those noticed by Bergmann, Allen, and Golger. The better to radiate body heat to the environment from warm-blooded animals, body sizes are small and appendages long. Pelage and plumage is light colored to reflect sunlight and help prevent the absorption of heat form the environment.
- Rarer, but important, are physiological adaptations such as aestivation (dormancy during summer), the absence of sweat glands, the concentration of urine, localized deposits of fat in tails or humps; and salt glands to secrete salt without losing fluids.

Reptiles with their waterproof skin, production of uric acid instead of urine, hard-shelled eggs, and ability to gain body heat directly from the sun and to retreat to shade or underground to avoid heat are exceptionally well adapted to drylands and, not surprisingly, diverse there.

Many birds in the North American deserts, so fragmented by mountains offering humid habitats and permanent streams, simply fly to free water and so are not limited by the lack of open water. They maintain breeding seasons like other temperate zone birds synchronized by changing photoperiods. In Australia, where

the desert geography is quite different and aridity more pervasive, bird populations synchronize their breeding readiness according to cues of rainfall.

Tropical Savannas

Tropical savannas or grasslands are associated with the tropical wet and dry climate type (Koeppen's Aw), but they are not generally considered to be a climatic climax. Instead, savannas develop in regions where the climax community should be some form of seasonal forest or woodland, but edaphic conditions or disturbances prevent the establishment of those species of trees associated with the climax community. Seasonal forests of the tropics are also widespread and vary along a latitudinal/moisture gradient between the tropical broadleaf evergreen forest of the equatorial zone and the deserts of the subtropics.

The word savanna stems from an Amerind term for plains which became Hispanicized after the Spanish Conquest.

Vegetation:

Savannas are characterized by a continuous cover of perennial grasses, often 3 to 6 feet tall at maturity. They may or may not also have an open canopy of drought-resistant, fire-resistant, or browse-resistant trees, or they may have an open shrub layer. Distinction is made between tree or woodland savanna, park savanna, shrub savanna and grass savanna. Furthermore, savannas may be distinguished according to the dominant taxon in the tree layer: for example, palm savannas, pine savannas, and acacia savannas.

Climate:

A tropical wet and dry climate predominates in areas covered by savanna growth. Mean monthly temperatures are at or above 64° F and annual precipitation averages between 30 and 50 inches. For at least five months of the year, during the dry season, less than 4 inches a month are received. The dry season is associated with the low sun period.

Soils:

Soils vary according to bedrock and edaphic conditions. In general, however, laterization is the dominant soil-forming process and low fertility oxisols can be expected.

Regional expressions:

- East African savannas are typically, perhaps stereotypically, acacia savannas. Many survive in the famous game parks of Kenya and Tanzania, and also those of Zimbabwe, Botswana, South Africa, and Namibia. The savannas are actually a mosaic of communities controlled (and today managed) by fire and grazing pressures. The famous Serengeti Plains in Tanzania are a grass savanna developed on droughty but nutrient-rich volcanic sands.
- The llanos of the Orinoco basin of Venezuela and Colombia are grass savannas maintained by the annual flooding of the Orinoco and Arauca rivers and their tributaries. The long periods of standing water inhibit the growth of most trees.
- Brazil's cerrado is open woodland of short-stature, twisted trees. It is species-rich, second only to the tropical rainforest in plant diversity. There are many endemic species, and several plants have adaptations to tolerate the high aluminum content of soils resulting from laterization on the ancient Gondwanan Shield of South America.
- The pine savannas of Belize and Honduras, in Central America, occur on sandy soils.
- Savannas as subclimaxes.

Edaphic Subclimaxes:

Waterlogged conditions occur when the A-horizon of lateritic soils is exposed to the atmosphere. Alternating wet and dry seasons and baking by the sun create a brick-hard layer impermeable to water. This usually red hardpan is called a laterite (from the Latin for brick). During the rainy season, there is standing water above the hardpan for several months, preventing the establishment of most tree species. During the dry season, the laterite prevents penetration of roots, also inhibiting the growth of most trees. Several species of palms do tolerate these conditions and, along with grasses, occur above laterites.

Droughty substrates, such as quartz or volcanic sands, also inhibit the growth of most trees. The pine savannas of Central America are examples of savanna vegetation developed on droughty, low-nutrient conditions of quartz sands; the grass savanna of the Serengeti–with its herds of large mammals–is virtually treeless.

Low-nutrient soils. The cerrado of Brazil occupies a broad expanse of the Brazilian Highlands that characterized by the low-nutrient level of the heavilyleached soils, would be occupied by a seasonal forest.

Fire subclimaxes. Two groups of plants that are pre-adapted to survive fire become dominant in areas where burning is frequent and periodic. Such fires have both natural and human origins. The savannas of South east Asia are generally considered to be man-made.

Palms have the advantage of being monocots: their vascular bundles are scattered throughout the stem so that scorching of the outermost layer of the trunk will not kill the plant. (Dicot trees, on the other hand, have their vascular bundles arrnaged around the outer, living part of their stems where they may be easily destroyed by fire.)

Perennial grasses have underground stems or rhizomes and so their growth nodes are protected by the soil during a ground fire. Trees and shrubs–with renewal buds above the surface–are selected against by fire and the balance tips toward the grasses.

Grazing subclimax. Large mammals such as the elephant open woodlands by debarking the trees and by knocking them over. This opens the woodland to grass invasion and attracts a variety of grazing animals, including zebras, wildebeest, and the diverse antelopes of the Ethiopian province. Grazers will both eat and trample tree seedlings, inhibiting the regrowth of the woodland. Only well-armed species of shrubs and trees can establish themselves in the clearings, leading to thickets of thorny acacias. Protected in the thicket, some acacias and other thorny trees will grow to mature specimens.

Overgrazing: if a grass savanna is overgrazed, patches of bare ground will be created. The grassland will no longer carry a ground fire and invasion by trees becomes possible. The bare ground will suffer from increased evaporation and a dry microhabitat quickly develops. Well-armed, drought-resistant species like the acacias tolerate both grazing and drought, so again an acacia savanna can become established.

Fauna:

The world's greatest diversity (over 40 different species) of ungulates (hoofed mammals) is found on the savannas of Africa. The antelopes are especially diverse and including eland, impalas, gazelles oryx, gerenuk, and kudu. Buffalo, wildebeest, plains zebra, rhinos, giraffes, elephants, and warthogs are among other herbivores of the African savanna. Up to sixteen grazing and browsing species may coexist in the same area. They divide the resources spatially and temporally; each having its own food preferences, grazing/browsing height, time of day or year to use a given area, and different dry season refugia.

The species-rich herbivore trophic level supports a diverse set of carnivores, including cats (lions, leopards, cheetahs, servals), dogs (jackals, wild dogs), and hyenas. Most herbivorous mammals of the open savannas are herd animals, often organized into groups of females and their young with a single dominant male and groups of bachelor males.

In South America a distinct savanna fauna is not well-developed. The capybara, the large semi-aquatic rodent, is associated with the llanos, but is found elsewhere and in other vegetation types as well. Indeed, few if any neotropical mammals are restricted to the savannas. The highest diversity of mammals is found in the dry or seasonal forests. Similarly, most bird species are not restricted to savanna-type habitats.

Termites are especially abundant in the tropical savannas of the world, and their tall termitarias are conspicuous elements of the savanna landscape. These detrivores are important in soil-formation; their termitaria provide shelter for other animals; and they are the beginning of the food chain for anteaters (Neotropical endemics) and aardvarks and pangolins (Ethiopian endemics).

Mediterranean Scrub

Regions of Mediterranean-type climate occur roughly between 30° and 40° latitude on the west coasts of continents, where offshore there are cold ocean currents. Each region in which the Mediterranean shrublands and woodlands occur is island-like in character and thus there is frequently a high degree of endemism. Comparative studies of the several regional expressions of this biome reveal interesting examples of convergent evolution in plant families and birds (but not among reptiles or small mammals) on the different continents.

Climate:

The Mediterranean Climate (Cs) is unique in that the wet season coincides with the low sun or winter period. Summers are dry. Total annual precipitation ranges between 15 and 40 inches per year. Temperatures are those of the subtropics moderated by maritime influence and fogs associated with the cold ocean currents. The result is a very limited, but predictable, growing season when

there is both sufficient soil moisture and adequately warm temperatures. Many plants are adapted to

Vegetation:

Throughout the world, the Mediterranean biome is characterized by shrubs. In most regions these shrubs are evergreen and have small, leathery (sclerophyllous) leaves with thick cuticles. Sometimes the leaves are so reduced as to appear needle-like. Many typical members of the shrub flora are aromatic (for example, sage, rosemary, thyme, and oregano) and contain highly flammable oils.

Mediterranean regions have long been impacted by humans especially through the use of fire and the grazing of livestock. The Mediterranean proper, we know from classical Greek literature, was formerly forested with live oaks, pines, cedars, wild carob and wild olive. The shrublands of California, likewise, are believed much more extensive today than before aboriginal burning and Spanish livestock grazing.

Major regional expressions

The Mediterranean proper–Europe, North Africa, and Asia Minor: around the Mediterranean Sea, which penetrates deeply into the Old World land masses, the biome reaches its maximum extent. Much of the formation is considered a subclimax developed on degraded and eroded soils and maintained in part by fire and goats. It is from this region that many culinary herbs associated with Italian cuisine originate. The shrublands are known locally as *maquis*.

California: The *chaparral* (from the Spanish *chapa* or scrub oak) of southern California consists of two plant associations, the coastal sage and the foothills

chaparral. The former is indicated by the presence of "soft" shrubs such as true sage (Salvia spp.). Inland, the latter is represented by a rich variety of "hard" woody shrubs that occurs in a mosaic reflecting fire history. A twenty-year cycle of fire maintains a subclimax of chamise (*Adenostoma fasciculatum*). In communities with less frequent or regular burns, chamise gives way to ceonothus, mountain mahogany, sumac, toyon, and manzanita. Dwarfed oaks and droughtresistant, closed-cone pines also occur. Adaptation or preadaptation to fire is important among various plant taxa: for example,

- the flammable oils of chamise and other shrub species promote fire;
- chamise sprouts from the roots after a burn;
- the resin coating the cones of closed-cone pines melts in a hot fire and allows the cones to open and disperse their seeds;
- perennial forbs survive as underground bulbs and sprout quickly in response to the addition of nutrients to the soil after a burn;
- the rosette shape of yuccas protects the inner growth bud from destruction in all but the hottest fires.

Where fires have been prevented (and grazing also) for 50 years or more on Catalina and Santa Cruz islands (Channel Island group), an "elfin forest" of live oaks has developed. Some believe with even more prolonged suppression of fire, an oak savanna–perhaps the real climatic climax–would occur.

California's Mediterranean region is restricted mor or less to coastal areas by the surrounding mountain ranges.

Chile: In Chile the formation is known as *matorral* (from the Spanish *mata* for shrub), and as in California, is confined to the coast by high mountains. The flora consists of many more deciduous species than are found in California's chaparral and many species also have thorns. Overgrazing during the Spanish colonial period has been implicated in prevalence of these thorny, deciduous shrubs.

South Africa: The *fynbos* of the Cape region of the Republic of South Africa displays a high degree of endemism and high diversity in each family represented in the flora. (An endemic fauna is also present.) Among the more biogeographically interesting components of the flora are the proteas, with 69 endemic species. Their closest relatives are in South America and Australia. While the protea family (Proteaceae) is very old and very primitive, the species are considered quite young. Cycads, ancient gymnosperms that look superficially like palms, are also part of this formation. Their nearest relatives are in Mexico and Australia. Perennial forbs such as amaryllis and gladiolus are found in the fynbos, as are the succulent aloes.

Australia: The mallee scrub vegetation of subtropical Australia is dominated by pungent, evergreen shrubs of the genus Eucalyptus, close relatives of Australian forest species. The prevailing grey-green color of the eucalypt leaves makes this vegetation appear uniform in composition, but actually dozens of families are represented. The mallee scrub occurs in two regions of southern Australia separated by the arid Nullarbor Plain.

Fauna:

The fauna of the various expressions of this biome are characterized by endemism that seems more a product of isolation than of peculiar adaptations to the Mediterranean environment. There is close convergence in the bird species found in California and those in Chile in terms of morphology, ecological niche, and even color and vocalization! Approximately the same number of species is found in both regions, another interesting convergence.

Temperate Grasslands

Temperate grasslands are composed of a rich mix of grasses and forbs and underlain by some of the world's most fertile soils. Since the development of the steel plow most have been converted to agricultural lands.

Climate:

Semiarid, continental climates of the middle latitudes (Koeppen's BSk climate type) typically have between 10 and 20 inches of precipitation a year. Much of this falls as snow, serving as reservoir of moisture for the beginning of the growing season. Warm to hot summers are experienced, depending on latitude.

Vegetation:

Perennial grasses and perennial forbs [especially Compositae (or Asteraceae, depending on the taxonomic system used) and Leguminosae--the sunflower and pea families, respectively] are dominant growthforms. Two or more strata of grasses (erect grasses and recumbent species) are recognized in the more humid expressions of the biome.

Grasses. Perennial grasses, with their growth buds at or just below the surface, are well-adapted to drought, fire, and cold. The tiller or narrow, upright stem reduces heat-gain in the hot summers; the intricate root systems trap moisture and nutrients. Two basic types are:

- Turf- or sod-forming grasses, with rhizomes or underground stems from which new plants spring forth; associated with the more humid grasslands
- Bunch grasses, without rhizomes, that reproduce by seed; associated with the drier parts of the biome.

Major regional expressions:

- North America: the **prairies** of the Central Lowlands and High Plains of the US and Canada. The Palouse Prairie of eastern Washington state, the California grasslands, and the desert grasslands of the Southwest are also temperate grasslands.
- Eurasia: the **steppes** from Ukraine eastward through Russia and Mongolia.
- South America: the **pampas** of Argentina, Uruguay, and southeastern Brazil
- Africa: the **veld** in the Republic of South Africa.

Soils:

Calcification is the dominant soil-forming process in semiarid regions. Mild leaching, high organic content, and concentration of calcium carbonate in the B horizon typifies the dark brown mollisols developed under the temperate grasslands. When this process works on a loess that itself is rich in calcium, the world's most fertile soils are created, the *chernozems* (A Russian term meaning black soil). Loess and hence chernozem underlie the eastern prairies of the US, the pampas of South America, and the steppes of Ukraine and Russia.

Fauna:

The temperate grassland fauna is very low in diversity, especially in comparison with the tropical grasslands or savannas of Africa. In North America the dominant herbivores are bison Bison bison) and pronghorn (the sole member of

the Nearctic endemic family, Antilocapridae). Rodent herbivores include the pocket gopher (another Nearctic endemic), ground squirrels, and the prairie dog. Carnivores include coyote (actually an omnivore), badger, and the federally endangered black-footed ferret, the last two members of the weasel family.

On the Russian steppes the fauna formerly included wisent (*Bison bonasus*), tarpan or wild horse, and saiga antelope, among others. Mole rats, fossorial members of one of the two mammal families endemic to the Palearctic, are conspicuous by virtue their many mounds. Polecats and other members of the weasel family are among the larger, extant carnivores.

Temperate Broadleaf Deciduous Forest

The Temperate Broadleaf Deciduous Forest (TBDF) - especially in eastern North America, where is remains most intact - is known for the turning of the colors of its leaves to brilliant reds, oranges, and golds in autumn. The shortening days of fall stimulate the plants to withdraw chlorophyll from their leaves, allowing a brief but beautiful display of other pigments before the leaves are shed completely and plants enter an extended period of dormancy.

Climate:

Associated with warmer continental and humid subtropical climates (Dfa, Cfa, and–in Europe, Cfb). There is an approximately 6 month growing season. The 20 to 60 inches of precipitation is distributed evenly throughout the year. The nongrowing season is due to temperature-induced drought during the cold winters.

Vegetation:

Many of the same genera, previously part of an Arcto-Tertiary Geoflora, are common to all three of the disjunct northern hemisphere expressions of this biome. Included among these genera are *Quercus* (oak), *Acer* (maple), *Fagus* (beech), *Castanea* (chestnut), *Carya* (hickory), *Ulmus* (elm), *Tilia* (basswood or linden), *Juglans* (walnut), and *Liquidamber* (sweet gum). Different species of these genera occur on each continent.

Structure and Growthforms: Five layers are recognized:

- a tree stratum, 60 -100 feet high, dominated regionally by various combinations of the genera listed above;
- a small tree or sapling layer, with not only younger specimens of the tall trees with species limited to this layer such as (in Virginia) Allegheny serviceberry or shadbush, sourwood, dogwood, and redbud;
- a shrub layer often with members of the heath family such as rhododendron, azaleas, mountain laurel, and huckleberries;
- an herb layer of perennial forbs that bloom primarily in early spring; and
- a ground layer of lichens, clubmosses, and true mosses. Lichens and mosses also grow on the trunks of trees.
- Lianas such as wild grape, poison ivy, and Virginia creeper climb the trees to flower and fruit high in the forest canopy.

Soils:

Brown forest soils (alfisols, in the American soil taxonomy) develop under the TBDF. Broadleaf trees tend to be nutrient-demanding and their leaves bind the

major nutrient bases. Thus the litter under this forest is not as acidic as under needleleaf trees and aluminum and iron are not mobilized from the A horizon. The autumn leaf fall provides for an abundant and rich humus which begins to decay rapidly in spring just as the growing season begins. The humus content gives both A and B horizons a brown color. [Until John Deere's invention of the steel plow in the 1800s and the subsequent ability to break the prairie sod, the alfisols were considered the most fertile, most easily worked, and most easily cleared of northern hemisphere temperate zone soils. Many have been under continuous cultivation since the Neolithic.]

Ultisols replace alfisols in the southeastern US, where the older soils of unglaciated regions have been weathered to a much greater degree and are more completely leached than the younger soils to the north. Distinctive red or yellow subsoils have developed under the warmer climate. Ultisols are generally less fertile than alfisols and in the southeast were frequently further degraded under plantation and subsistence agriculture in both the colonial and post-colonial periods.

Subclimaxes: On sandy substrates, pines replace broadleaf species. Hence the New Jersey pine barrens, the pineywoods of the Deep South, and the tall (longneedled) pines of Georgia and other areas of the Atlantic Coastal Plain. On waterlogged sites in more northerly latitudes, bogs develop. In the south one finds instead pine savannas and bald cypress swamps.

Fauna:

Characteristic members of the fauna are either mast-eaters (nut and acorn feeders) or omnivores. Mammals show adaptations to an arboreal life; a few hibernate during the winter months.

- North American herbivores include white-tail deer, gray squirrel, and chipmunk.
- Omnivores include raccoon, opossum, skunk, and black bear.
- Carnivores have been largely eliminated through the deliberate effort of humans but should include timber wolves, mountain lions, and bobcats. The coyote, native to the western grasslands and deserts, has recently dispersed east and taken over the niche of its departed cousin, the timber wolf.
- Resident bird species also tend to be seed-eaters or omnivores. Many, like the several species of woodpeckers and the chickadees, are cavity-nesters. The loud, conspicuous blue jay is a major agent in the dispersal of oaks onto abandoned farmland and pastures. Migratory species tend to be insectivorous and include many so-called neotropical migrants, including warblers, wrens, thrushes, tanagers, and hummingbirds.

Distribution:

The TBDF occurs in three major, disjunct expressions in western and central Europe; eastern Asia, including Korea and Japan; and eastern North America.

- In Europe, a species-poor forest reflects widespread extinctions during the Pleistocene. Oaks, beeches, and elms dominate. Most of the forest was cleared for agriculture, with remnants surviving only in some royal hunting preserves.
- The TBDF of China is known primarily from the fossil record; intensive agriculture has caused this region to be cleared of natural vegetation for at least 4,000 years. Japan has a largely artificial forest, but in the mountains of Korea the forest is more or less intact and fall foliage is reminiscent of New England's.

▪ Almost all the forests of eastern North America are second growth, but they preserve the world's greatest diversity of TBDF flora and fauna. This is especially true of the unglaciated Appalachian Plateau of eastern Kentucky and Tennessee and western North Carolina and Virginia. The Great Smoky Mountains have been designated a world biosphere reserve.

Southern hemisphere expressions of the biome: Regions of humid subtropical climate occur in the southern hemisphere, but their vegetation and flora differ. Such regions have a mixed (broadleaf and needleleaf) evergreen forest whose biogeographic interest stems from the occurrence of Gondwanan relicts: *Araucaria* pines (South America and Australia), *Podocarpus* pines (South America, Africa, and Australia), and the evergreen southern beech *Nothofagus* (South America, Australia, and New Zealand).

Boreal Forest (Taiga)

The boreal forest or taiga exists as a nearly continuous belt of coniferous trees across North America and Eurasia. Overlying formerly glaciated areas and areas of patchy permafrost on both continents, the forest is mosaic of successional and subclimax plant communities sensitive to varying environmental conditions. *Taiga* is the Russian name for this forest which covers so much of that country. However, the term is used in North America as well.

Climate:

The taiga corresponds with regions of subarctic and cold continental climate (Koeppen's Dfb, Dfc, and Dwd climate types). Long, severe winters (up to six months with mean temperatures below freezing) and short summers (50 to 100 frost-free days) are characteristic, as is a wide range of temperatures between the lows of winter and highs of summer. For example, Verkhoyansk, Russia, has recorded extremes of minus 90 ° Fand plus 90 ° F. Mean annual precipitation is 15 to 20 inches, but low evaporation rates make this a humid climate.

Vegetation:

Needle leaf, coniferous (gymnosperm) trees are the dominant plants of the taiga biome. A very few species in four main genera are found: the evergreen spruce (*Picea*), fir (*Abies*), and pine (*Pinus*), and the deciduous larch or tamarack (*Larix*). In North America, one or two species of fir and one or two species of spruce are dominant. Across Scandanavia and western Russia the Scots pine is a common component of the taiga.

Broadleaf deciduous trees and shrubs are members of early successional stages of both primary and secondary succession. Most common are alder (*Alnus*), birch (*Betula*), and aspen (*Populus*).

Growthforms:

The conical or spire-shaped needleleaf trees common to the taiga are adapted to the cold and the physiological drought of winter and to the short-growing season:

• Conical shape – promotes shedding of snow and prevents loss of branches.

- Needleleaf narrowness reduces surface area through which water may be lost (transpired), especially during winter when the frozen ground prevents plants from replenishing their water supply. The needles of boreal conifers also have thick waxy coatings–a waterproof cuticle–in which stomata are sunken and protected from drying winds.
- Evergreen habit retention of foliage allows plants to photosynthesize as soon as temperatures permit in spring, rather than having to waste time in the short growing season merely growing leaves. [Note: Deciduous larch are dominant in areas underlain by nearly continuous permafrost and having a climate even too dry and cold for the waxy needles of spruce and fir.]
- Dark color the dark green of spruce and fir needles helps the foliage absorb maximum heat from the sun and begin photosynthesis as early as possible.

Soil:

Podzolization occurs as a result of the acid soil solution produced under needleleaf trees. The main soil order associated with the taiga is spodosol.

Subclimaxes: Edaphic conditions result in sometimes extensive, persistent patches of vegetation other than spruce and fir:

- Bogs (muskeg) occur in poorly drained, glacial depressions. Sphagnum moss forms a spongy mat over ponded water. Growing on this mat are species of the tundra such as cottongrass and shrubs of the heath family. Black spruce and larch ring the edge.
- Pine forests, in North America dominated by the jack pine (*Pinus banksiana*), occur on sandy outwash plains and former dune areas. These are low nutrient, droughty substrates not tolerated by spruce and fir.

▪ Larch forests claim the thin, waterlogged substrate in level areas underlain with permafrost. These forests are open with understories of shrubs, mosses and lichens. In Alaska stands of *Larix larichina* are localized phenomena, but in Siberia east of the Yenesei River the extreme continentality and nearly continuous permafrost give rise to vast areas dominated by *Larix dihurica*.

Fauna:

Fur-bearing predators like the lynx (*Felis lynx*) and various members of the weasel family (e.g., wolverine, fisher, pine martin, mink, ermine, and sable) are perhaps most characteristic of the boreal forest proper. The mammalian herbivores on which they feed include the snowshoe or varying hare, red squirrel, lemmings, and voles.

Large herbivores are more closely associated with successional stages where there is more nutritious browse available and include elk or wapiti (*Cervus elaphus*, known as red deer in Europe) and moose (*Alces alces*, known as elk in Europe). The beaver (*Castor canadensis*), on which the early North American fur trade was based, is also a creature of early successional communities, indeed its dams along streams create such habitats.

Among birds, insect-eaters like the wood warblers are migratory and leave after the breeding season. Seed-eaters (e.g., finches and sparrows) and omnivores (e.g., ravens) tend to be year-round residents. During poor cone years, normal residents like the evening grosbeak, pine siskin, and red crossbill leave the taiga in winter and may be seen at bird feeders here in Virginia.

Distribution patterns within the boreal forest biome:

The boreal forest is restricted to the northern hemisphere. It is circumpolar in distribution, as are many of the species which comprise it and even more of the genera. In general, plants have different species represented on North America and Eurasia; the mammals of both continents tend to be conspecific.

There are latitudinal zones within the forest. Running north to south, one finds

- A tundra/taiga ecotone
- An open coniferous forest (the section most properly called taiga) the characteristic closed-canopy needleleaf evergreen boreal forest; and
- A mixed needleleaf evergreen-broadleaf deciduous forest, the ecotone with the Temperate Broadleaf Deciduous Forest. In the US, this southern ecotone is dominated by white pine (*Pinus strobus*), sugar maple (*Acer saccharum*), and American beech (*Fagus americanus*).

Alpine expressions of the biome: In Merriam's Life Zones, the Hudsonian and the Canadian zones correspond with the Boreal Forest

In North America, several variants of the boreal forest occur in the mountains of the West:

- In the Pacific Northwest, what amounts to a temperate rainforest is dominated by needleleaf species such as Douglas fir, western hemlock, and other giants. This forest type is the center of a major controversy regarding timber operations in old growth forests.
- On the windward (western) slopes of the Sierra Nevada at elevations between 4,000 and 8,000 feet, the tall western conifers are joined by the magnificent
giant sequoia (*Sequoia gigantea*). The specimen named General Sherman is some 3,800 years old, 272 feet tall, and has a diameter of 37 feet. The congener of this sequoia, the redwood (*S. sempervirens*) grows along the northern California coast. Their closest relative is the Dawn Redwood, a deciduous conifer of the genus *Metasequoia* from China.

- In the Rocky Mountains, where fire is an important part of the environment, lodgepole pines (*Pinus contorta*) form nearly pure, single-aged stands. The great fire of Yellowstone National Park demonstrated once again the association of this species and its ecosystem with repeated burns.
- Along the Appalachian Mountains in eastern North America the boreal forest of eastern Canada, dominated by red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*), extends southward with little change in species composition until Virginia. The southern limit of balsam fir occurs in Shenandoah National Park; southward to the Great Smokies, on isolated mountain tops, is found Fraser fir (*A. fraseri*)

Tundra

The word tundra derives from the Finnish word for barren or treeless land. The tundra is the simplest biome in terms of species composition and food chains.

Vegetation:

Lichens, mosses, sedges, perennial forbs, and dwarfed shrubs, (often heaths, but also birches and willows)

Growthforms:

Typical are ground-hugging and other warmth-preserving forms including:

- tussock-forming graminoids
- mats or cushion plants, often evergreen members of the heath family
- rosettes
- dwarf shrubs, some of which are deciduous in habit

Climate:

The high latitude conditions of Koeppen's ET climate type that impact life in this biome include

- extremely short growing season (6 to 10 weeks)
- Long, cold, dark winters (6 to 10 months with mean monthly temperatures below 32° F or 0° C.)
- Low precipitation (less than five inches/year) coupled with strong, drying winds. Snowfall is actually advantageous to plant and animal life as it provides an insulating layer on the ground surface.

Edaphic controls:

Permafrost, not cold temperatures per se, is generally believed to be what prevents tree growth. Furthermore, freeze-thaw activity, a thin active layer, and solifluction during the warmer months contribute to strong controls on vegetation patterns and create a mosaic of microhabitats and plant communities.

Soil:

No true soil is developed in this biome due to the edaphic factors mentioned above.

Fauna:

Strategies evolved to withstand the harsh conditions of the tundra can be divided among those species that are resident and those that are migratory.

Among the small number of bird (e.g., ptarmigan) and mammal (e.g., muskox, arctic hare, arctic fox, musk ox) species that reside year-round on the tundra one commonly finds:

Morphological adaptations such as:

- large, compact bodies following Bergmann's and Allen's rules
- a thick insulating cover of feathers or fur
- Pelage and plumage that turns white in winter, brown in summer.

Physiological adaptations: such as ability to accumulate thick deposits of fat during the short growing season. Fat acts as insulation and as a store of energy for use during the winter, when animal species remain active.

Population adaptations such as cyclical fluctuations in population size, best seen perhaps in the lemming, a small rodent which is the major herbivore in the tundra's simple food chain. Predator populations and plant populations respond in kind to the peaks and crashes of the herbivore populations.

Migratory species such as waterfowl, shorebirds and caribou adapt to the tundra by avoiding the most severe conditions of winter. Each year at the end of the short growing season they move southward into the boreal forest or beyond, but return to the tundra to breed.

Aperiodic emigration from the tundra is exhibited by the snowy owl during those years that the lemming populations have crashed. Those winters see snowy owl irruptions as far south as Virginia. Most owls are found with empty stomachs and do not survive to return to the Arctic.

Distribution:

The tundra biome is restricted to the high latitudes of the northern hemisphere in a belt around the Arctic Ocean. Many of its species, both plant and animal, have circumpolar distribution areas.

Within the tundra biome a **latitudinal zonation of communities** is realized:

High Arctic Tundra: essentially confined to the islands of the Arctic Ocean and characterized by scattered lichens and mosses on care rock surfaces and perennial forbs growing in protected crannies among sharp, ice-fractured rock debris.

Middle Arctic Tundra: restricted to the Arctic Coastal plain where level terrain, a thin active layer, and freeze and thaw result in patterned ground, or rock polygons. The sorting of particles by freeze-thaw activity results in a waterlogged center to the polygons, a microhabitat conducive to sphagnum moss and sedges; and an outer ring that is drier and provides a microhabitat favorable to forbs and some dwarf heaths.

Low Arctic Tundra: the majority of the tundra lies on better drained slopes with greater depth to permafrost than is encountered on the Arctic coastal plain. Here there is a greater frequency of woody shrubs: willow, birch, and various berrybearing members of the heath family. Along streams willows and alders may be 10 feet high. On south-facing slopes needleleaf evergreen trees (spruce and fir) are established and represent the northernmost extensions of the great boreal forest to the south. (Such areas where two biomes interdigitate are known as ecotones.)

Alpine Tundra: Many tundra species can be found at high elevations in the mountains of the northern hemisphere. The arctic-alpine lifezone of high elevations

experiences a different climate–in terms of daylength and seasons–than does the true tundra of the Arctic. However, thin soils and cold temperatures create an environment that many middle latitude trees cannot tolerate and thus allow tundra species to invade and thrive.

In the tropics, the climate of very high elevations is extremely different than that of the Arctic. Freeze-thaw, instead of following a seasonal cycle, follows a diurnal cycle. Also, the peaks are isolated from the Arctic tundra. Often endemic species derived from a tropical flora or from Antarctic flora create the unique communities of tropical high mountain tops.

Marine Biomes

Life Zones in the Ocean

I. Horizontal zones (those extending from land out to sea).

- *Coastal Zone:* that region in which tides expose the sea bottom for some part of each day. The habitats are alternately submerged under salt water and waterlogged for hours and then exposed to the air and dried out for hours. Also known as **littoral**, **nearshore**, and **intertidal zone**.
- *Pelagic Zone:* located seaward of the coastal zone's low-tide mark, this contains the vast open waters of the ocean. Two subdivision are recognized:
	- 1. *Neretic Zone:* the water overlying the continental shelf. With the exception of Antarctica, these waters usually extend to a depth of 600 ft. Sunlight penetrates the entire water column.
	- 2. *Oceanic Zone:* The region of the sea extending from the edge of the continental shelf, over the continental slope, and over ocean floor. It is characterized by darkness and tremendous pressure. Vertical life zones are significant here.

II. Vertical life zones of the oceanic zone.

- *Neustic zone:* the thin film or "skin" formed by surface tension at the surface of the water
- *Euphotic zone*: The top of the water column as far down as light is available for photosynthesis. Depending upon water clarity, the bottom of the euphotic zone is about 500 ft below sea level. Also known as **epipelagic** zone.
- *Aphotic zone:* the remainder of the water column below the euphotic zone. Food chains usually begin with detritus or living algae and bacteria sinking from above. This zone is further subdivided by depth as follows:
	- **Mesopelagic zone:** 500 to 3,280 ft below the sea surface.
	- **Bathypelagic zone:** 3,280 to 13,000 ft below the sea surface
	- **Abyssopelagic zone:** 13,000 to 20,000 ft below the sea surface
	- **Hadal zone:** 20,000 to 35,000 ft below the sea surface.

III. Benthic Zone

This zone contains all the habitats of the sea bottom, whether in coastal, continental shelf, or deep sea environments. Organisms may live within the bottom material or on its surface.

Major Environmental Factors in Marine Biomes

a) Water is much more than a passive medium in which life exists. Its unique chemistry with hydrogen bonds and high specific heat allow it to store latent heat and moderate global temperatures. Its movements transport heat energy from the equatorial region poleward into both hemispheres. Water is able to dissolve many compounds, including important nutrients.

b) Light. Most marine food chains begin with photosynthetic single-celled organisms (the phytoplankters) which are affected by daily and seasonal

changes in light intensity and duration. Sunlight penetrates transparent water, but different wavelengths are absorbed at different depths. The longest wave lengths (reds and oranges) are absorbed in the first 50 ft of the water column. Most other wavelengths are absorbed in the next 130 ft. The shortest wavelengths (blues and violet) penetrate the deepest, making the sea appear blue on a sunny day. (Actual depths vary with the clarity or murkiness of the water. The clearer the water the deeper light can reach. When only one percent of the sunlight received at the sea surface remains, photosynthesis is only sufficient to maintain life. No growth or reproduction can occur. The depth at which this occurs is called the **compensation zone**. It represents the bottom of the euphotic zone. Below 3,000 ft there is no light.

- **c) Pressure.** On average, at sea level, the weight of the atmosphere exerts 14.7 lbs/in² of pressure or 1 atmosphere. In the ocean, due to the added weight of water, pressure increases 1 atmosphere for every 33 ft of depth. On the deep sea floor pressure may reach more than 500 atmospheres.
- **d) Dissolved gases:**
	- **Oxygen,** a product of photosynthesis, is greatest at the surface where the sea water is in contact with the atmosphere. The colder the water, the more oxygen it can contain.
	- **Carbon dioxide** is absorbed from the atmosphere, a process which may slow global warming. Its levels, however, may be lower in the euphotic zone due its use by algae and bacteria during photosynthesis.
	- **Nitrogen** must be fixed into nitrates before used by most marine algae. This accomplished by other microorganisms, such as cyanobacteria. Nitrogen is a major limiting factor in the sea.
- **e) Nutrients.** Macronutrients in marine ecosystems include carbon, nitrogen, phosphorus, silicon, sulfur, potassium, and sodium. Micronutrients include

iron, zinc, copper, manganese and some vitamins. Nitrogen is the most common limiting factor for algal growth; phosphorus the second most common.

- **f) Temperature** varies with depth and with latitude. Infrared wavelengths (heat energy) of sunlight are absorbed in the top 3 ft of the water column. Waves mix the warmed water into the top 30 ft, the surface layer. Below this layer is a transition zone wherein temperature decreases rapidly with depth. This is the *thermocline*. Below the thermocline is the deep zone, where temperature decreases only slightly with increasing depth. Most seawater in the deep zone stays at about 37 \degree F all year. Colder water (33 \degree to 35.5 \degree F) may be found at or near the seafloor. Due to its salt content, which acts as an antifreeze, sea water does not freeze until 28.5° F. As the freezing point is approached, the density of water decreases. Very cold water rises to the surface, where ice forms.
- **g) Salinity** refers to the amount of dissolved matter (salts) in seawater. The Average is 35 ppt. Salinity varies geographically according to precipitation, discharge from rivers, and evaporation (a function of temperature). The formation of ice increases salinity in the unfrozen water. Generally salinity is highest in the surface layer, below which is a transition zone known as the *halocline*. Below the halocline, salinity remains fairly constant.
- **h) Density** is a function of temperature and salinity. Warmer water is less dense than cooler water and floats upon it. Freshwater is less dense than seawater and so floats atop it. The lowest density usually occurs in the surface layer since particles tend to sink and the wataer is warmer than that below. The transition zone in which there is a rapid increase in salinity with depth is called the pycnocline. The pycnocline is a barrier to the exchange of nutrients between layers, but also helps keep phytoplankton in the sunlit waters near the surface. Wave action helps return sinking nutrients and phytoplankters to the surface.
- **i) Waves.** A wave is actually just energy moving toward shore. The water molecules do not move laterally, but rotate up and down in circular orbits. Each orbit sets water below into motion to form a vertical chain of ever smaller orbits with less energy than the one directly above. The chain extends downward to a depth 1.2 times the wave height. Below that level, water is unaffected. Waves are generated by wind action. As a wave approaches the shore, the friction created when orbits contact the sea bottom slows the base of the wave. The crest then gets ahead of the base and crashes. This creates a breaker, landward of which lies the surf zone. The energy remaining in the wave after the formation of a breaker raises the water level and thrusts the water upon the shore. Sand, gravels, shells, and other abrasive particles are picked up as the water moves onto land.
- **j) Tides** are the product of the gravitational pull of the sun and, especially, the moon on the oceans. The shape and orientation of coastlines and their seafloors determine the frequency and the tidal range at a particular place. Most coasts experience two high tides and two low tides each day, but a few $-$ such as along the Gulf of California $-$ have only one high tide and one low tide per day.

Life in the Ocean: Introduction

Marine life can be grouped according to size, mobility, and location within the water column or benthic zone:

- 1. **Pleuston:** Organisms, such as the colonial cnidarians known as the Portuguese man-of-war, that live at and above the surface, half in and half out of the water. These buoyant creatures are wind-blown.
- 2. **Neuston:** Mostly carnivorous animals that cling to the surface film and drift or "walk" on the very top of the water column (e.g., sea skater) or hang just below the surface (e.g., the gastropod *lathina*)
- 3. **Plankton:** Small organisms that float in the water, unable to propel themselves against tides or currents. Flagella, however, do allow them to move up and down the water column. *Phytoplankton* is photosythetic and consists mostly of algae and cyanobacteria; they are confined to the

euphotic zone. The *zooplankton* consists of animals such as copepods, salps, and krill.

- 4. **Nekton:** Active swimmers. Those that live in the upper part of the water column, such as sharks, tuna, and whales, are known as *pelagic* forms; those that live close to the bottom, such as cod, flounder, and rays, are *demersal* forms.
- 5. **Benthos:** Organisms restricted to the benthic zone. Sessile forms, such as kelps, seagrasses, and corals attach themselves to the sea bottom; motile forms, such as worms, seastars, mussels and crabs, move through or on top of the sea bottom.

Coast Biome

The coast is where the land meets the sea. This highly variable region begins where salt spray reaches and affects land-based plant communities and extends seaward through the surf zone as far as wave action still disturbs the sea bottom, usually to depths of about 200 ft. Indeed, the coast environment has the greatest diversity of habitats and microhabitats on Earth.

Coastal life must be adapted to environmental factors that grade from one extreme to another, especially from wet to dry; wave action; and particle sizes of bottom materials.

Zonation of habitats is the rule. Running parallel to the shoreline, each zone reflects conditions at specific elevations above or below sea level. Characteristic groups of organisms occupy each zone, although actual species composition varies geographically. Zonation is obvious on exposed rocky shores, but much more subtle on soft-sediment coasts, where most invertebrates retreat below the surface during low tide.

Visible zonation on a rocky coast

Three broad belts of coastal habitat are recognized:

- **Supralittoral** or sea spray zone: upper part of coast which is never submerged
- **Eulittoral** or intertidal zone: area between extreme high tide and extreme low tide which experiences alternating conditions of inundation by seawater and exposure to the air
- **Sublittoral**, subtidal, or nearshore zone: lower levels of coast that remain submerged at all times but are affected by wave action.

Vertical zonation of seaweeds (algae) also occurs because different photosynthetic pigments absorb different wavelengths of sunlight. Green seaweeds are restricted to shallow waters in the upper eulittoral zone because the chlorophyll that gives them color only absorbs the longest, red wavelengths. In red algae chlorophyll is masked by other pigments that absorb in the orange to green parts of

the spectrum. They can absorb most wavelengths and can occur at just about all depths in the coastal zone. Finally, brown algae such as kelps have both chlorophyll and fucxanthin, a pigment which absorbs short blue-green wavelengths. Brown algae are usually found in themed- to lower eulittoral zone and to depths of 30 to 50 feet in the sublittoral zone.

Rocky Coasts

Rocky coasts are areas of active erosion, where pounding waves and abrasive particles held in the water work away at the bedrock foundations of continents and islands. Life on these shores has evolved ways to tolerate the force of the waves and to cling to the rocks to avoid being swept away. Small size is one adaptation, larger forms being more easily dislodged by moving water. A thin film of slow-moving water—the **boundary layer**—coats wetted rock, so small, flat organisms such as isopods, sea stars, and chitons can avoid the full force of the wave action and thrive on rocky shores. Crabs simply squeeze into cracks and crevices to find shelter from crashing waves.

Colonies of **sessile**, or attached, forms trap fine sediments and create habitat for motile invertebrates such as polychaetes, gastropods, and crustaceans.

Hard surfaces, living and nonliving are coated with a **microbial film** of bacteria, cyanobacteria, diatoms, and protozoans—important food sources for grazing invertebrates.

Waves carry oxygen and dissolved nutrients, plankton, and organic debris to sustain attached organisms and carry away their wastes. **Filter-feeders** hence dominate on more exposed coasts. Barnacles are widespread on the upper shore of such habitats; mussels are common. Motile limpets graze on encrusted red algae and the biofilm of cyanobacteria.

a. barnacles (dark) and limpets (light); b. mussels; c. isopod

Soft-Sediment Coasts

Under conditions suitable for deposition, particles of various sizes accumulate to form a loose substrate of pebbles, sands, silts, or clays, as opposed to the solid rock of rocky coasts. Actual particle size is a function of the velocity of longshore currents, strength of wave action, and the types of particles available for transport to the site.

Four main kinds of soft-sediment habitats are recognized:

- **Shingle or pebble beaches** with steep slopes and strong wave action
- **Open sandy beaches** semi-exposed to the open sea and experiencing significant wave action. The sands and profile of the beach are often reworked during storms. Wind-blown dunes form along the landward margin.
- **Protected sandy beaches** sheltered from strong wave action. Their gentle slopes are formed in finer sands.
- **Protected mudflats** at the heads of inlets and on the landward sides of barrier islands. Wave action is minimal, allowing silts and the finest particles of organic detritus to settle out. Salt marshes characterize such habitats in temperate climes; mangroves in tropical regions.

Soft-sediment environments differ from rocky coasts in two key ways:

- 1. They are *three dimensional*: not only are horizontal zones formed according to elevation and tidal range, but vertical layers are formed within the substrate. Organisms live on the beach as well as in the beach.
- 2. *Instability* is a given since small particles move in the swash and backwash of waves on the beach. Bioturbation—disturbance of the sediments by the action of the beach's inhabitant also commonly occurs. Inhabitants of the beach, themselves, are highly mobile and their distribution patterns change frequently in response to the physical changes in the habitat that occur daily and seasonally. Indeed, the entire beach may disappear and reappear after storms and from summer to winter.

A major control of the distribution of life on a beach is the rate at which water infiltrates the sediments. In coarser deposits, upper levels are dry at low tide and the ebb and flow of seawater removes wastes and re places nutrients. Fine particle beaches and tidal flats, on the other hand, remain saturated even at low tide and become stagnant.

Vertical stratification develops in sandy beaches at low tide. The **surface zone** becomes dry due to evaporation and the downward draining of water due to gravity. A **zone of retention** lies below the surface where water is lost by gravity but replaced by water drawn upward by capillary action. This zone has the best

combination of water, oxygen, food, and substrate stability to support life. Below it is a **zone of resurgence** which receives the water pulled down from above by gravity. Deepest is the **zone of saturation**; it becomes stagnant and depleted of oxygen

Inhabitants of Sandy Shores

Photosynthesis is conducted by a **microflora** of bacteria, cyanobacteria, diatoms, and autotrophic flagellates living in the interstices between sand grains or attached to the surface of the grains. Macroalgae are rare but will occur if hard surfaces such as shells or buried stones are available. The microorganisms and small macroalgae may also grow as epiphytes on the stems of salt marsh grasses, the leaves of seagrasses, or the aerial roots of mangroves.

Many of the animals of the beach are tiny and serves as links in **detritus food chains**, feeding on decomposers such as bacteria and fungi or themselves consuming organic detritus. Among the many permanent residents in the infauna are rotifers, some copepods, ostracods, flatworms (turbellarians), and nematodes.

The **macrofauna** of exposed beaches consists of polychaetes (bristleworms), crustaceans (isopods, amphipods, crabs, and ghost shrimp), and mollusks. They include both **filter-feeders and deposit-feeders**. Burrowing is a common strategy to avoid dessication and predators during low tide.

Scavengers and predators are abundant, searching for prey just below the surface at low tide or for sealife that has been stranded on the shore. Fish visit the beach during high water. Shorebirds, however, are the most visible predators, probing the sand at low tide or chasing scurrying prey as waves roll onto the beach. Sandpipers, plovers, and oystercatchers are common. Most shorebirds breed in the Arctic and migrate along well-defined flyways to wintering grounds in both the Northern and Southern hemispheres. Estuaries, beaches, and salt marshes are important stopover places along the way.

Invertebrates of the sandy shore:

a. beachflea (amphipod); b. copepod; c. ostracod

Inhabitants of Mudflats

Most photosynthesis occurs in a **biofilm** of diatoms, cyanobacteria, and flagellates (e.g., euglena) that is visible at low tide. Coloring the tidal flats green or brown, these microorganisms migrate 1 or 2 millimeters down into the mud just before the tide returns. Green filamentous algae (*Enteromorpha* spp.) will grow if attachment sites are available.

Crabs and snails are common members of the **epifauna**, permanent residents of the surface. Fiddler crabs are active at low tide; Europe's shore crabs are active when the mudflat is under water. These animals consume detritus and scavenge beached carcasses.

An **infauna** of copepods, nematodes, and flatworms (turbellarians) is abundant and lives with a macrofauna of bivalves, crustaceans, various types of worm, anemones, and brittlestars—the last two burrowing into the mud. In order to survive low oxygen levels, many have evolved ways to draw oxygenated water into their burrows during high water and store it for use during low water.

Shorebirds such as herons and egrets are common predators at low tide; fish such as flounders hunt when the flats are inundated.

Salt Marsh

Salt marshes are found in sheltered intertidal areas, especially in the temperate regions of the world. (In the tropics similar environments usually support mangroves.) Perennial grasses, the cordgrasses (*Spartina* spp.) in particular, dominate, but forbs and succulent subshrubs also occur. All are halophytes, plants adapted to highly saline conditions. Various strategies have evolved to deal with salt. Plants may:

- Prevent the uptake of salts by their roots;
- Secrete excess salts via specialized glands on the leaves;
- Accumulate salts in leaves, which are then shed, thereby removing the salts, as some cordgrasses do; or

▪ Dilute the salt solution in their tissues by accumulating water in the tissues (succulence), as do pickleweeds or glassworts (*Salicornia* spp.).

Many close relatives of salt marsh plants are found in deserts, where high salt concentrations can also occur.

Salt marsh grasses actually build up their habitat as they trap fine sediments washed from the uplands in their masses of stems, roots, and rhizomes. As the level of the marsh rises, tidal creeks erode deep channels through it. The surface becomes uneven and a variety of habitats are created: lagoons, salt pannes and pools, and natural levees among them.

Zonation of plant communities occurs from the upper shore to the lowest part of the marsh. In the **high marsh**, which is only submerged during the highest spring tides and severe storms, rainfall and runoff dilute salt concentrations and flush them from the sediments. Cordgrasses, reeds, and glassworts grow in this region. The **midshore** tends to be the most saline habitat and is occupied primarily by succulents such as sea blites (Suaeda spp.) and glassworts. In the **low marsh**, evaporation rates are depressed (since exposure time to the air is less) and accumulated salts are flushed out by the tide. However, sediments remain saturated at low tide and oxygen depletion becomes a problem. Many plant species in the low marsh have fine roots at the surface through which take in oxygen from the air and send it via specialized tissues called *aerenchyma* to deeper roots. Some oxygen leaks from these roots and oxygenates the bottom sediments. Smooth cordgrass *(Spartina alterniflora*) dominates.

Salt marshes are among the world's most productive plant communities, yet relatively few herbivores consume salt marsh plants. Sucking insects such as aphids and grasshoppers are important grazers, as are vertebrates such as geese and muskrats. Huge amounts of dead plant material amass each year. Its decay further depletes oxygen, often to the extent that **anaerobic bacteria** take over the decay process. The distinctive odor of exposed mudflats comes from hydrogen sulfide gas, a by-product of anaerobic decay.

Detritus food chains are predominant in the low marsh. Marsh periwinkles and amphipods shred dead grasses as they consume them. Unconsumed particles fall to the floor of the marsh, where they feed fiddler crabs and snails as well as filter-feeders such as ribbed mussels and oysters. Carnivores in the detritus food web include fish such as killifish, rails, herons, and raccoons.

b

SOME INVERTEBRATES of THE SALT MARSH:

a. Marsh periwinkles (Wikipedia Commons; b. Ribbed mussel (USGS); c. Fiddler crab (NOAA)

Animals in the marsh must deal with exposure to rapidly changing salinities and periodic flooding and exposure to the air. Furthermore, tidal movements could sweep them out of the marsh. Many burrow into the bottom sediments to escape predators and dessication during low tide. Fiddler crabs, which feed on the surface during low tide, plug their burrows with mud as the tide comes in; preserving a

pocket of air for the time the marsh is inundated. Marsh perwinkles, in contrast, must escape predators such as blue crabs during high water, so they climb up the cordgrass stems ahead of the rising tide.

THE MARSH and a KEY PREDATOR:

Left: Clapper Rail (Wikipedia Commons); Right: Winter marsh at Plum Island, MA.

Mangroves

Mangrove refers to both a habitat type in the intertidal zone and to the specialized, salt-tolerant trees and shrubs that grow there. Approximately 75 percent of coasts located between 25° N and 25° S support this vegetation type. Mangroves grow in both wet and dry climates within this latitudinal belt.

Global distribution of mangrove (Wikipedia Commons)

Mangrove habitat is found on river deltas that form in brackish estuaries (riverine mangrove), on intertidal flats along more exposed coasts (fringing mangrove), and on the landward side of fringing mangrove where wave action and tidal influences are greatly reduced (basin mangrove).

Mangrove (plants) occurs in at least 19 plant families. Two stand out: the black mangroves (Avicenniaceae) and the red mangroves (Rhizophoraceae). Two genera (*Avicennia* and *Rhizophora*) occur throughout the tropics. Most others are geographically restricted to the coasts of either the Indo-Pacific region or the Atlantic Ocean.

In desert areas the mangroves are low shrubs, but in tropical rainforest areas they can be trees 120 ft or more tall. All have evolved ways to tolerate waterlogged soils and high salinity. To overcome the constraints of a saturated substrate, many produce some kind of aerial root (**pneumatophore**). Black mangroves produce thin, vertical projections from their roots that are completely underwater when the tide is in, but exposed to the air at low tide. Red mangroves have prop roots arching from their trunks to the ground. In both structures, pores in the surface allow air to penetrate to the underground ground roots during low water levels.

Strategies to deal with high salinity are similar to those found among salt marsh plants. Some, such as *Rhizophora*, prevent salt uptake by their roots. Others, such as *Avicennia*, allow salt to enter the roots but have salt glands on their leaves to rid the plants of excess salt. A few species allow salt to accumulate in bark and leaves and then shed these tissues to eliminate excess salt.

The embryos of many mangroves develop while the fruit is still on the tree (**vivipary**). The resulting seedling or capsule looks like a long bean pod hanging from the branches. Seedlings drop from the tree into the water and float for weeks until they reach sites favorable for their further growth.

In the Americas, mangroves are usually arranged in three zones. Red mangroves prefer the seaward edge of the stand, black mangroves grow inland of them, and white (*Laguncularia racemosa*) and button mangrove (*Concarpus erectus*) concentrate at the landward edge.

Sessile barnacles and oysters attach to mangrove trunks and aerial roots, on which periwinkles, snails, and tree-living crabs feed. On the floor of the mangrove, fiddler crabs, mangrove crabs, snails, and air-breathing mudskippers find a home. The invertebrates aerate the soil as they build burrows and mounds and thereby improve growing conditions for the plants.

Mangrove leaves are rarely consumed by animals, Borneo's proboscis monkey being the main exception to the rule. However, flowers and fruits attract an array of insects and other terrestrial animals. Wading birds such as Scarlet Ibis and Roseate Spoonbill, probe the floor at low water; fish are predators hunting during high water.

PNEUMATOPHORES

Left: Arching prop roots of red mangroves, the Everglades Wikipedia Commons); Right: Upright, pencil-like pneumatophores of black mangroves. Madagascar

MANGROVE ANIMALS

Left to right: Fiddler crab, mangrove crab (Wikipedia Commons), mudskipper (Wikipedia Commons)

Left: Roseate Spoonbill (Wikipedia Commons); Upper right: Proboscis Monkey (David Dennis, Wikipedia Commons); Lower right: The endangered Red Ibis (Wikipedia Commons)

- a. Black Oystercatcher (South Africa); b. The rare and endangered Piping Plover (New Jersey);
- c. Dunlin-a sandpiper (Ontario, Canada) (Wikipedia Commons)

Continental Shelf

Introduction

Continental shelves are the submerged margins of continent that stretch seaward from the extreme low-tide mark to depths of approximately 600 ft below sea level, at which point the sea bed drops precipitously (continental slope) to the sea floor.

The continental shelf is depicted in light tourquoise.

The width of the shelf depends upon the area's geologic history: narrow shelves occur at active plate boundaries, the broadest on the trailing edges of moving plates. Continental glaciation also plays a role by depressing the continental mass, such as currently seen on Antarctica, and by lowering sea level, as happened during the Pleistocene glaciations. Interglacials and contemporary

climate change equate with higher sea levels, extending the shelves farther onto the continent.

The seabed (benthos) together with the shallow, sunlit waters of the neritic zone comprises some of the most productive and economically significant parts of the ocean. As much as 90 percent of the global catch of shellfish and finfish comes from the continental shelf biome. Many seabirds and marine mammals also find sustenance in this biome.

The nutrients supporting the rich and diverse marine life comes from both the land and the sea. Stream runoff is an extremely important source. Wind, tide, and tidal and shelf-edge fronts serve to keep the nutrients in the euphotic layer of the water column. Upwelling returns nutrients than had settled to depth to the surface at specific west coast locations associated with the major cool eastern boundary currents (the California, Humboldt, Canary, and Benguela currents).

Highly productive communities in the continental shelf biome include:

Seagrass meadows

Seagrasses are flowering plants. Forty-nine species in 12 genera are known. Most are dioecious-i.e., there are separate make and female plants. The flowers are simple and open underwater; pollen is transported by waves and currents. However, they also reproduce vegetatively via rhizomes and form dense mats or meadows often composed of a single species.

Totally immersed in seawater, the long, linear leaves have no stomata. The plants never exchange gases with the atmosphere. They absorb carbon dioxide that is dissolved in the water and utilize the oxygen they themselves produce during photosynthesis.

Eelgrass (NOAA)

Eelgrasses (*Zostera* spp.) and wigeongrasses (*Ruppia* spp.) dominate temperate seagrass meadows. Turtlegrasses (*Thalassia* spp.) and tapeweeds are important in the tropics.

Sea grasses grow on fine sediments in the subtidal zone at depths where sunlight is adequate for photosynthesis. Actual depth depends on water clarity. Along the east coast of the US, the favorable zone may only extend 3 ft deep, but elsewhere—in clearer waters—it can be more than 100 ft deep.

The meadows are highly productive, but few animals feed directly on the grasses. Those that do tend to be vertebrates such as sea turtles, dabbling ducks, geese, and manatees and dugongs.

Left: Green seaturtle; Right: West Indian manatee

Tiny epiphytes cover seagrasses (NOAA)

The leaves of sea grasses are often covered with epiphytic algae, bacteria and small invertebrates such as protozoa, nematodes, and hydrozoans. Amphipods and isopods graze the algae; snails and fish eat both the algae and the invertebrates.

Much of the primary production of the seagrass meadow enters detritus food webs. Detritovores include members of the infauna such as polychaetes and

members of the epifauna such as crabs, shrimps, and fish. Other crabs and fish hunt and scavenge through the canopy of grasses. Sea horses hide among the leaves, waiting in ambush; stingrays lurk in the sediments. Fish predators are mainly after detritus-feeding crustaceans.

The meadows provide food and shelter and therefore are important nursery areas for shellfish and finfish, as well as refuges for adults. They serve as essential wintering grounds for such Northern Hemisphere migratory waterfowl as Brant and American Wigeon. The abundance of fish attracts Ospreys and fish-eating eagles.

Osprey, a top predator in the seagrass ecosystem (Terry Spivey, USDA Forest Service, bugwood.org)

Kelp forests and beds

Kelps are large, rubbery brown algae that from in sense stands off sheltered to moderately exposed rocky coasts in cool $(\leq 68^{\circ} \text{ F})$ temperate waters of both hemispheres.

They flourish where the continental shelf has a gentle slope and where hard surfaces are available for the attachment of their holdfasts. Kelps can be found at depths up to 130 ft and as far as 6 miles off the coast. Anchored on the seafloor, individuals reach to the surface, where their blades rock on the waves. Smaller kelps and red algae form an understory. Together they create a three dimensional habitat that hosts diverse animals.

Kelp forests are highly productive and they quickly recycle nutrients so that most stay in the system. Waves break off tips of blades and uproot kelps during storms, releasing DOM, which bacteria absorb and direct through the everimportant microbial loop. Bacteria are consumed by zooplankters; or adhering to marine snow, they sink to the bottom, where filter-feeding benthic organisms such as tunicates, mussels, and sponges fed upon them.

Uprooted kelps drift out to sea or onto beaches, where they are stranded and become wrack. Terrestrial amphipods and isopods feed on the dead kelp. At sea, sea urchins graze living kelp. Occasionally, for reasons not well understood, populations explode and overgrazing leaves an empty patch covered only with diatoms, encrusting red algae, and filamentous green algae. It may take 4-6 years for the forest to recover.

Off the west coast of North America, sea otters are predators of sea urchins and abalones, which also graze living kelp. Off the east coast, before overfishing decimated their numbers, Atlantic cod were important urchin predators.

In the kelp beds in the Gulf of Maine, the dominant kelps are horsetail help, sugar kelp, and sea colander. The Red alga known as Irish moss is a major component of the understory. Limpets and periwinkles, as well as sea urchins, feed on the kelps. In the understory, amphipods, isopods, shrimps, and young crabs comprise the motile invertebrate community. Sessile invertebrates include hydroids and tunicates that grow on the kelps and red algae. Predators include lobsters, crabs, sea stars, and fish—including winter flounder, haddock, and wrasse. Sea ducks feed on invertebrates and small fish. Among those visiting the kelp beds are Red-breasted mergansers, Common Goldeneye, and Long-tailed Duck.

Kelp wrack at the Cape of Good Hope, South Africa:

Wrack along beach at Cape of Good Hope; close-up showing rubbery nature of kelp.

68

Life in a west coast (US) kelp forest:

Left: Anemone and starfish in kelp Forest (Wikipedia Commons); Right: Sea otter with young (Caleb Slemons, bugwood.org)

Deep Sea

The deep sea biome occurs in that part of the ocean and seafloor beyond the continental shelves. It covers 65 percent of the planet's surface and reaches depths of -650 ft to -36,198 ft at the bottom of the Challenger Deep in the Mariana Trench. Much of the seafloor region consists of the flat **abyssal plain**, located on average 3.5 mi below sea level and covered with muds and **oozes**. Bottom water temperatures are a steady 28° F. The fine sediments on the seafloor come from stream runoff and from a constant rain of debris and organisms from the upper layers of the sea. They are mostly made up of the shells of plankton: silica-based shells from diatoms, radiolarians and silicoflagellates and calcium carbonate shells form foraminiferans, coccolithophores, and pteropods. Calcareous oozes dominate at mid-oceanic ridges; silicaceous oozes are found on the abyssal plain. The abyssal plain is punctuated by mid-oceanic ridges and seamounts.

Hard substrates are scarce but important for life in the deep sea. Among the main sites are exposed volcanic rocks on the mid-oceanic ridges, the steep slopes of seamounts where sediments are unable to collect, concretions of iron and manganese on the seafloor, tubes and shells of invertebrates, and the skeletons of whales and large fish resting on the seafloor. These all become attachment sites for sessile animals, which in turn attract motile animals seeking prey or sheltering habitat.

Important **communities** with the deep sea biome include:

Deep Sea Pelagic Communities

In the open sea beyond the continental shelf, five life zones can be recognized. In the euphotic or **epipelagic zone** (the first 500 feet below the sea surface) cyanobacteria and phytoplankters receive enough light for photosynthesis. These tiny organisms are the primary producers of the entire pelagic regions. Beneath this zone, consumers either feed on sinking algae and bacteria, are scavengers of the rain of organic debris coming from above, or are predators of the other consumers. All life in the pelagic region either drifts or must swim in the water column all of the time.

At depths greater than 3,500 ft below sea level, the pelagic habitat is fairly uniform and dark. Pressure increases with increasing depth, which poses problems for body structure and buoyancy, but an even bigger challenge is limited food availability. Species have evolved to meet these challenges, but biodiversity is relatively low.

Atlantic blue marlin demonstrates countershading in fish of the epipelagic zone. (NOAA)

In the epipelagic zone, tiny zooplankters consume the one-celled phytoplankters larger, and zooplankters rely upon globs of particulate organic matter (POM) known as "marine snow." At night the zooplankters rise toward the surface to feed on algae and bacteria. Most predators, both invertebrate (e.g., copepods) and vertebrate (e.g. fishes) also feed at night. Many of the carnivores hunt by sight, so natural selection has favored "invisible" zooplankters transparent gelatinous creatures such as salps (planktonic tunicates), siphonophores, medusae (jellyfish), ctenophores (com jellies), squids, and chaetognaths (arrow worms). Fish typically are counter-shaded (dark on top; light on the undersides) and have disruptive patterns that make them less visible to predators from below; still they are safer feeding in night-time darkness when their prey is more concentrated.

In the **mesopelagic zone**, the same groups dominate as in the epipelagic zone, but different species occur: copepods and siphonophores are especially abundant. Shrimp in this region of the sea are often transparent and red or orange, pigments that absorb the shorter wavelengths of sunlight that penetrate into this zone, rendering them more or less invisible to predators.

Left: Copepod (Russ Hopcroft, NOAA) ; Right: Deep sea shrimp (NOAA)

Fish in the upper parts of this zone are strongly muscled, usually have welldeveloped eyes, dark backs, reflective flanks, and light-producing organs (photophores) on their bellies. Gas-filled swim bladders help them control buoyancy. Predators tend to have upward-oriented eyes and mouths. Fishes in the lower parts of the zone are dark all over and do not have reflective flanks.

The highest diversity of pelagic organisms is found in the **baythypelagic zone** at depths between -3,000 and -8,000 ft. Fishes here are black and have tiny, simple eyes. They have fat-filled swim bladders or lake them altogether. Featherlike bristles and antennae may aid buoyancy. Bioluminescence is important in species and gender recognition, in luring prey, in spotlighting prey, and/or in confusing predators. Musculature is greatly reduced to save energy. Many fish look like a large mouth with fins.

Mysid shrimp (NOAA)

The **abyssopelagic zone**, an area of immense pressure and constant cold (35°-37° F) is inhabited primarily by decapods and, in the deepest waters, by mysid shrimp.

The **hadopelagic zone** (or hadal zone) occurs in oceanic trenches. Many species found in the zone are colorless, but may have some form of bioluminence. Jellyfish and viperfish are among inhabitants of the water; other organisms such as sea cucumbers and tubeworms may live on the seafloor.

Head of Pacific viperfish (NOAA)

Within 300 feet of the seafloor at various depths a transition between the benthic and pelagic zones occurs. Food is more available than in many of the overlying waters. Benthic organisms float up into the zone and the larvae of both pelagic and benthic organisms may congregate here. Gastropods, amphipods,and sea cucumbers are other members of a diverse community that attracts deep sea predators.

Deep Sea Soft-Sediment Communities

Soft-sediments (muds and oozes) dominate across the abyssal plain and in oceanic trenches. Organisms from most of the phyla and classes found in softsediments in shallow water situations occur in the deep but are represented by

different genera and species. Foraminiferans, nematodes, tiny copepods, isopods, amphipods, polychaetes and bivalves are common members of the community. Larger animals include sea anemones, brittlestars, sea stars, sea cucumbers, and bottom-dwelling fishes.

Xenophyophore (Wikipedia)

The xenophyophore is a unique, one-celled foraminiferan found only in soft sediment on the deep seafloor. A huge, one-celled organism, it is covers itself in slime that traps sediments and debris. The slime hardens to form a hard protective coating called a test. *Syringammina fragilissima,* at a maximum 20 cm in diameter, is one of the largest protozoans known. Xenophyophores enrich the benthic habitat and areas dominated by them have been shown to have several times the number of benthic crustaceans, echinoderms, and areas dominated by xenophyophores have several times the number of benthic crustaceans, echinoderms, and mollusks than areas where they are absent.

Most animals are deposit feeders. Exceptions are suspension-feeders such as sea anemones, glass sponges, horny corals, sea pens, and stalked barnacles that have some type of apparatus for catching drifting food items. Other suspension feeders (brachiopods, tunicates, bryozoans, and some bivalves) secrete mucus to trap floating particles.

Predators are poorly known. A number of species, called croppers, are omnivores and ingest sediments, dead organic material, and live prey items. Among them are octopuses, decapods, and fishes.

Seamount Communities

Seamounts are steep volcanic mountains rising at least 3,500 ft above the seafloor, but not high enough to break the surface and be islands. Most occur in chains at hot spots or along plate boundaries. Some, such as those northwest of the Hawaiian Islands were formerly mountains: but when they moved off the hot spot and became extinct volcanoes, they sank beneath the sea. Flat-topped seamounts are known as guyots.

Orange roughy. Drawing by Robbie Cada

Seamounts divert ocean currents and force upwelling, creating isolated areas of highly productive waters in the otherwise nutrient-poor open sea. Shallow seamounts support kelps and crusts of coralline algae on exposed rocks and phytoplankters in the water. Dense populations of mysid shrimp, squid, and lanternfish will form, with large congregations of fish such as orange roughy consuming them. Open sea predators—sharks, rays, tunas, and swordfish—are attracted to the abundance of prey species.

A lanternfish (NOAA)

On deeper seamounts, an attached or sedentary fauna dominates: various kinds of corals, sponges, tunicates, and crinoids. Also present are motile forms such as polycheates, sea stars, sea urchin, sea cucumbers, mollusks, crabs, and lobsters.

Rocky outcrops exposed to fast currents that bring in food and take away wastes support deep sea coral forests and gardens. They are built by **cold-water corals** such as tuft coral, black corals, hydrocorals, octocorals, and host many other cnidarians, as well as sponges. Some (too many) of the corals, especially gold, red (or precious), and pink deep sea corals, are exploited by the jewelry industry as semiprecious gems. Among the fish visiting the coral structures are blackbelly rosefish, morid cod, and red bream, and roughy, conger eel. Groupers, snappers, and sharks comprise the top carnivore biota.

Cold-water corals: a. gold coral and pink coral; b. an octocoral; c. bubblegum coral with grenadier (all photos courtesy of NOAA)

Locations of major seamounts (Wikipedia)

Hydrothermal Vent Communities

Hydrothermal vents occur at both diverging and converging plate boundaries. Heat is released as magma rises and cracks the ocean floor and overlying sediments. Seawater drains into the fractures and becomes superheated, dissolving minerals and concentrating sulfur and other compounds. When the water is blocked in its downward path it spews forth as a jet of water with temperatures approaching 750° F.

Coming into contact with the cold bottom waters of the deep sea, the dissolved minerals quickly precipitated out of solution and form tall towers or chimneys. Plumes of water stream from these waters, often rising 1,000 ft above the vent. The water of so-called "black smokers" is rich in sulfides; that of "white smokers" contain compounds of barium, calcium, and silicon. The temperature of the plume of white smokers is usually lower than that of black smokers.

Left: Black smoker; Right: white smoker (both courtesy of NOAA)

Water also seeps through the walls of the chimneys and cools enough (35^o-210° F) to allow a highly specialized fauna (see below) to live in the vent.

Vents usually occur in clusters or wide fields above a given body of magma. More tectonically active plate boundaries (e.g., the East Pacific Rise) tend to have more numerous and denser clusters of vents than less active (e.g., the Atlantic Mid-Oceanic Ridge) locations. Vents are temporary features on the seafloor. They become inactive when seafloor-spreading moves them away from the rising

magma or when they become clogged. Some vent fields may remain active for 10,000 years, but individual vents are much shorter-lived.

Chemosynthetic bacteria obtain energy from the chemical bonds of hydrogen sulfide. In hydrothermal vent communities, these bacteria are the first step in the food chain. Many of these bacteria exist in symbiotic relationships with species in the vent fauna. They are hosted by vestimentiferan tubeworms, vesicomyd clams, and bathymodiolid mussels. The tubeworms have no gut at all and depended completely on the bacteria living in their tissues. Vent tubeworms range in size from less than an inch to almost 3 ft long. The largest, *Riftia pachyptila*, lives on the East Pacific Rise.

The bivalves are filter-feeders as well as recipients of energy from symbiotic bacteria. Clams have reduced digestive systems, indicating a greater dependence on the chemosynthetic microbes than mussels, which have fully functional digestive systems. The giant vent clam (*Calyptogena magnica*) can reach a length of nearly 8 inch.

There are shrimps that also host sulfur-dependent bacteria. At least some "farm" the bacteria on specialized mouthparts.

Left: Tubeworms (C. Van Dover.NOAA); Right: Galathied crabs, shrimp, graze bacteria on vent mussels (NOAA)

In addition to bacteria living in hosts, there are also free-living chemosynthetic bacteria living at vents. Some live as small blobs resembling marine snow within the rising plume. Others grow as mats or biofilms on hard rock or animal surfaces and are grazed by copepods, amphipods, and shrimps.

Top carnivores at vents include the eel-like zoarchid fish, which apparently feeds on snails, limpets, and amphipods. Vent crabs and squat lobsters prefer clams and tubeworms. These animals are all restricted to vent habitats. More widely distributed octopuses visit the vent to feed on clams and mussels.

Scavengers (gastropods, decapods, and copepods) arrive when the vent community is in decline because the vent itself is clogged or its activity is declining as the vent moves away from the magma source.

Cold Seep Communities

First discovered in 1983 off the Gulf Coast of Florida with the aid of the research submersible, ALVIN, cold seeps are now known from all oceans. They occur at tectonically active places in the seafloor where hydrogen sulfide, oil, highly saline water, and methane leak out to form brine pools. The reaction between seawater and methane, coupled with bacterial activity, leads to the production of carbonate rocks and reefs.

Methane is initially the main energy source for the cold seep community as bacterial mats metabolize both methane and hydrogen sulfide. Early on, symbiotic methane-oxidizing bacteria allow dense mussel beds (*Bathymodiolus* spp.) to develop. Bivalves from 4 other families also occur. As carbonate rock forms, it permits the establishment of tubeworms that have bacteria in their tissues requiring hydrogen sulfide. The tubeworms are able to "mine" hydrogen sulfide from the substrate to supply their symbionts. There are also free-living sulfur-oxidizing bacteria (*Beggiatoa* spp.) occurring as mats.

Brine pools in Green Canyon, Gulf of Mexico (NOAA)

Left: Orange mat of Beggiatoa bacteria (NOAA); Right: Tube worms at a cold seep (NOAA)

A cold seep community at a depth of 9,800 ft below sea level in the Gulf of Mexico includes tubeworms, soft corals and chemosynthetic mussels; eelpouts, a galatheid crab and a deep-water shrimp. (NOAA)

Lophelia pertusa, a cold-water coral lacking symbiotic algae and hence color. (NOAA)

When methane seepage decreases, the mussels die off and tubeworms become dominant. In turn, as the seep becomes inactive, the tubeworms, too, disappear. Cold-water corals, settling on the carbonate deposits, take over once the seep community is gone. In the North Atlantic, *Lophelia pertusa*, unusual in that it lacks xoozanthellae, is a common deep-water coral.

Chapter 1 Absorption of Water

Water

Life originated in an aqueous environment and in the course of evolution became fully dependent upon water in a number of ways. In general, water is essential for life and its importance to plants may be summarised as follows:

(1) Water is the main constituent of the protoplasm comprising up to about 90 to 95 %of its total weight. In the absence of water, protoplasm becomes inactive and is even killed.

(2) Different organic constituents of plants such as carbohydrates, and proteins, nucleic acid and enzyme etc. , lose their physical and chemical properties in absence of water.

(3) Water participates directly in many metabolic processes. Interconversion of carbohydrates and organic acids depends upon hydrolysis and condensation reactions.

(4) Water increases the rate of respiration. Seeds respire fast in presence of water.

(5) Water is a source of hydrogen atom for the reduction of carbon in the reactions of photosynthesis.

(6) Water acts as a solvent of and carrier of many substances. It forms the medium in which several reactions take place.

(7) Water present in the vacuoles helps in maintaining the turgidity of cells, which is a must for proper activities of life. The turgidity of cells help s in the elongation of cells resulting in growth. The difference in the amount of available water during summer and winter season for the formation of annual rings in the higher plants. In summer, the turgidity is less and as a result smaller cells are formed.

(8) A network of thin layer of water surrounding each cell plays an important role in the entry and movement of dissolved substances.

(9) Water helps (I) in the transactions of solutes , (II) in the mobility of gametes , (III) in the dissemination of spores , fruits and seeds , and (iv) provides support to aquatic plants .

(10) In tropical plants, water plays a very important role of thermal regulation against high temperatures. Some people think the plants lose about 95 per cent of the absorbed water just to maintain the optimum temperature.

(11) Thousands of characters develop for balancing the water content of planes. Even atmospheric moisture affects plants growth. Different plants absorb water from their general surface while in higher plants roots are the organs concerned with absorption of water.

Soil water

Plants absorb water from the soil by their roots. The water is found in different forms in the soil. The chief source of water to the soil is rain or irrigation. After a rainfall or irrigation some of the water penetrates downwards, under the influence of gravity until it reaches the water table. This is called "the gravitational water" and it is of little benefit for the plants. Moreover, it may be injury to plants. Because it replaces the air between the soil. A major portion of the water is retained by the soil particles against the force of gravity which keep the soil moist. Some of this water is adsorbed by the soil colloids and is held tightly by them in very thin films. This called the "hygroscopic water" and it is non- available for the plants. Another portion of water fills the spaces between the soil particles and called the "capillary water" which is the greatest important for the plants, because it easily absorbed by root hairs. A portion of the gravitational water rises by capillarity and becomes ready available to plants. This portion depends on the structure of the soil, which is generally depend on the size of the soil particle. As soils with relatively small particles held more capillary water than that of relatively large ones.

Movement of water in the plants

- 1. Absorption of water (root system)
- 2. Ascent of sap (shoot system)
- 3. Loosing of water (transpiration) (leaves)

Water absorbing parts of plants

Major portion of water required by plants is absorbed by the roots, but the absorption of water by leaves and stem has also been found in a few plants hydrophytes absorb water by general surface.

The uptake of water by leaves is influenced by:

(i) Structure and permeability of cuticle and epidermis,

(ii) The hairiness of leaf surface,

(iii) The case of wetting surface, and

(iv)The internal environment of deficiency of water in parenchymatous cells closes to the epidermis

Roots play the principle role in absorption of water. Even orchids absorbing water from atmosphere develop modified roots for the purpose.

ROOTS

Roots absorb water mainly from the apical region. Apical organization of root shows three clear demarcations, the zone of elongation and the zone of absorption or differentiation.

The zone of differentiation consist of three different types of tissue system, i.e. dermal, cortical and stellar. Dermal tissue include surface layers of cells. Epidermis in the region has enormous number of unicellular root hairs. Cortical tissue system is complex and consists of pericycle, phloem and xylem etc. Important ones are described here.

Root hair

 \bullet

Root hair is the special modified cell of epidermis meant for the absorption of water. It is specialised not only in appearance but also in its internal structure. The wall of root hair consists of cellulose and pectic substances have great capacity of water absorption.

The cell wall act as permeable layer. Next to cell wall is plasma membrane enclosing cytoplasm, nucleus and vacuole. Vacuole is quite large in size so as to give peripheral arrangement of cytoplasm. The role of vacuole during absorption of water is just like a controller.

MECHANISM OF WATER ABSORPTION

Entry of water in root hair

Root hair maintains contact with soil water and in nature it acts as a soil water – absorbing organ. The water diffuses in to the root hair as a result of diffusion pressure deficit (DPD) gradient. The cell sab contains a more concentrated solute than the water present outside.

Water enters as long as DPD of cell sap is greater distending the cell until the elasticity, of stretched wall is sufficient to balance the osmotic pressure of solutes.

How exactly water enters in the root hair and what is the precise mechanism of water absorption have been explained by two different approaches.

(i) Active absorption.

 (ii) Passive absorption.

Active absorption

When we speak about water being absorbed actively, we mean that water is being absorbed through expenditure of metabolic energy. Active absorption occurs as a result of activities in root and does not concern the shoot. Generally it is thought that the active absorption of water may occur in one of two ways, as a result of the active absorption and accumulation of salts or through nonosmotic mechanisms.

a) Osmotic active absorption: actually water absorbed by osmosis and this means that it is does not directly require an expenditure of energy. Water is thought to move from the soil to the interior of root along an increasing osmotic pressure gradient. That is water moves through the root epidermis, cortex, and into the xylem ducts because of increasing solute concentrations as it passes from the exterior to the interior cells of the root. The water absorbed by this manner does not directly require an expenditure of energy. The energy is expended in the absorption and accumulation of salts.

(b) Non-osmotic active absorption: Thimann (1951) and Kramer (1959) suggested that the absorption of water is an active process but occurs due to non-osmotic reason even against diffusion pressure gradient. The process requires an expenditure of energy obtained from respiration. How is the energy utilised is not well explained. It may be used directly.

Following are supporting points of this theory that water is absorbed nonosmotically and there is participation of energy (respiration):

(1) Wilting of roots occurs in non-aerated soils such as flooded areas. It indicates that water is absorbed by living cells under aerobic atmosphere.

(2) Use of respiratory inhibitors such as KCN, reduces the rate of water absorption and exudation from the cut end of stems. Thus, there is some correlation between the processes.

(3) The occurrence of distinctive diurnal variation in water uptake and root pressure. It is faster during day time and slower during night. This fact is also true for respiration.

(4) The water absorption is also influenced by hormones such as auxin. Low auxin concentration increases water uptake and exudation.

(5) The process of absorption occurs in living cells.

Passive absorption

This theory explains that the forces responsible of absorption of water into the roots are governed by other cells. The governing force originates in the cells of transpiring shoots rather than in root itself. This forces develop due to transpiration. With the occurrence of transpiration, the DPD of leaf cells increases, which results in the movement of water from the xylem cells to adjacent mesophyll cells. Due to presence of continuous column of water from leaves to roots through xylem channels, the deficit is transmitted to the xylem of roots and finally to root hairs along which radial movement of water takes place and puts these cells under tension.

Path of Water

We should by now be familiar with the tissues encountered by water moving from the soil to the leaves of plant. In figure 7.8 the path of water through a plant is diagrammatically shown. Water is first absorbed from the soil by root hairs and other epidermal cells in or near the root hair zone. Water then move through the cortex tissue and across the endodermis and pericycle and finally into the xylem ducts. The xylem tissue of the roots connects directly with the xylem tissue of the stem. The xylem of the stem, thus allowing water to move out of the root and into the stem, the xylem of the stem is divided and subdivided many times to form a complex network of water–conducting tissues, finally ending in the fine veins of the leaf. Water moves from the leaf veins into the mesophyll cells, is evaporated from their surfaces, and finally moves as water vapour through the stomates into the surrounding atmosphere.

Figure 7.8

Movement of water through plants

Ones the water entered in root hair, it moves first to root stele and then to leaves passing through the different parts of the plant. The movement of water inside the plant shows two different directions. In the first stage, it moves from the root hairs to the stellar region of root via cortex and endodermis, i.e. radial movement of water,

And in the second stage, it moves from the root stele to the top of leaves i.e. upward movement of water. The upward movement is popularly known as "A SCENT OF SAP"

Radial movement of water: (movement of water from root hair to stele):

There are two ways of radial movement of water:

(1) Cell to cell movement of water across the root (osmotic flow).

(2) Movement of water across the cortex along the water filled spaces into the cell walls forming a continuous system from soil water film to endodermis.

Both this mechanisms operate together and help the water to reach up to endodermis.

As a result of the absorption of water from the soil, the root hair cell becomes fully turgid, it is osmotic pressure falls due to dilution and its turgor pressure increased. As a consequence, its suction pressure will fall below that of the adjacent cortical cell **B** as a result water will pass from **A** to **B**.(**Fig. 2).**

The diffusion of water in to **B** likewise reduces its suction pressure which falls below that of the next cortical cell **C**, with the result that water passes from **B** to **C**. in the same manner water pass from the cell **C** to **D**, and from **D** to **E**, from **E** to **F** and from there in to the endodermal cell **N**. from here it is passed on to the pericycle cell **O** which will eventually become turgid. It will then exert no suction pressure and hence, will readily give up water to the xylem vessel with which it is in contact. The walls of the xylem vessel are in elastic so, that there is not turgor pressure and the whole of the osmotic pressure of the xylem sap constitutes its suction pressure. This being higher than the reduced suction pressure of the parenchyme (pericycle) cell **O**, water will draw in to the xylem vessels.

Fig. 2 diagram indicated the movement of water (radial movement) after absorbing from the soil.

FACTOR AFFECTING WATER ABSORPTION RATE

The plant gets two types of environment includes factors such as (a) available soil water , (b) concentration of soil solution , (c) soil temperature and (d) aeration while internal environment includes factors such as (a) transpiration , (b) absorbing root system and (c) metabolism .

External Environmental Factors

(a) Available soil water:

The water in the soil is present in a different forms such as capillary, hygroscopic, gravitational etc, of which capillary water is readily available for absorption. This is in between field capacity and permanent welting percentage where the rate of absorption of water is generally uniform and is not affected. With an increase in water beyond field capacity, aeration of soil is badly affected which reduce s the rate of absorption and under severe conditions wilting results in. The similar wilting is observed in extremely dry soils and a decrease in soil water reduces the rate of absorption.

(b) Concentration of soil solution:

Large number of elements are dissolved in soil water called soil solution. On account of these elements, the concentration of soil solution changes. If the soil solution is highly concentrated, it increases greatly osmotic pressure and when it reaches higher to that of cell sap, water is not absorbed. It is one reason that the plants fail to grow in highly saline fields. This is popularly known as physiological dryness.

(c) Soil temperature

The variation of temperature affect the rate of absorption .20 to 30 ℃is the most suitable temperature for absorption. The low temperature reduces and moderately high temperature increases the rate of absorption. A very high temperature kills the cell. How the low temperature exercises its negative influence in absorption has been explained as follows that it results in:

(I) slower rate of elongation of root thus preventing its contact with areas.

(II) Slower rate of metabolic activities.

(III) Reduce of soil water diffusion into the roots.

(IV) Increased viscosity of water, protoplasts and colloidal gels in the cell wall.

(V) Decreased permeability of cell membrane.

(d) Soil aeration:

Water is absorbed more efficiently in a wall aerated soil than in a poorly aerated soils. Probably the reason may be the respiration as normally roots fail to respire anaerobically and plants shortly die in floated areas. The deficiency of oxygen inhibits the growth and the metabolism and accumulation of $CO₂$ increases the viscosity of protoplasts and decreases the permeability of cell membrane. Both this factors affect severely and reduce the rate of water absorption. These may be the reasons for plant death in flooded areas. Only few plants such as rice and Typha can grow normally in poorly aerated soils as these are specially adapted to such environments.

Internal Environment Factors

(a) Transpiration.

The rate of absorption of water is nearly directly proportional to that of transpiration. A higher rate of transpiration increases the rate of absorption because of cohesion theory of ascent of sap, i.e. transpiration produces a tension or pull, transmitted to roots through hydrostatic system of plants creating a favourable condition for entrance of water.

(b) Absorbing root system.

The efficiency of water absorption depends upon the absorbing system. The presence of number of root hairs accounts for the rate of absorption. However, the development of root hairs depends upon environment. The maize plants does not produce root hairs in culture solution but produces large number of root hairs when grown in soil. In moist conditions root hairs are well developed and large in quantity. The coniferous plants (gymnosperms) bear few or no root hairs but absorb large amount of water with the help of mycorhizal hyphae. Thus root systems play a major role in absorption of water

(c) Metabolism.

The metabolism and absorption are closely related. Although doubt exist in use of energy during absorption, but factors inhibiting rate of respiration-such as poor aeration application of anaesthetics and KCN reduce the absorption rate . Thus metabolic activities are expected to participate indirectly by forming a constantly elongated root system and always providing newer contacts with soil water.

Chapter 2

Various elements found in plants

Major elements

Serious attempts to determine experimentally the mineral content of plants were made by **Sachs and knop** as far back as 1860. Using liquid cultures, they were able to show that ten elements are essential to the plant. these they listed as carbon (C) hydrogen (H), oxygen (O), nitrogen (N), Phosphorus (P), potassium (K) , Calcium (Ca) , Sulfur (S) , Magnesium (Mg) , and Iron (Ca) Fe) . These ten elements were generally accepted as all that a plant needed for normal growth and development. However, we know today that there are growth of most plants and several additional elements specifically required by certain plants.

Method of detections

Several of the methods used in the early study of plant nutrition are still in use today. The analysis of plant ash and the use of liquid and sand cultures are techniques used for the study of plant nutrition in laboratories throughout the world. However, these methods have been refined and improved upon.

Ash analysis

A reasonably reliable means of detecting the mineral element content of a plant is to subject the plant to high temperatures (about $600 \degree C$) and then analyse its ash content. Only ten mineral elements are present all of the organic compounds having been decomposed and passed off in the front of gases. These primary elements (carbon, hydrogen, and oxygen) are therefor given off as $CO₂$, water vapour and oxygen. In addition to carbon, hydrogen, and oxygen, the element nitrogen cannot be detected accurately with this method, since some of it is given off in the form of ammonium or nitrogen gas. All of the other mineral elements that were absorbed from the soil are present in plant ash.

Although the analysis of plant ash may be thought of as a method of determining the relative quantities of mineral elements in a plant, it is, at best, a crude technique. Too many variables are present to give accurate, reliable results. For example, vaporization or sublimation of some of the elements may

be caused by the high temperatures. Generally, elements are not present in pure state in the ash, but are in the form of oxides. finally , the qualitative and quantitative analysis of the ash for the different elements present is depended on different chemical treatments the accumulative error resulting from this facts quantitative data obtained from the ash analysis of plant tissue.

Solution cultures

It did not take scientists long to realize the impracticality of using soil as a medium for growth in any serious study of plant mineral requirements. To render a soil free of the mineral elements used by plants and then control the amounts of nutrients made available to the roots imbedded in the soil is impossible. On the other hand, solution cultures provide an excellent means for controlling the quantity and relative proportions of minerals salts given to a plant in any of one experiment. Two other good reasons for using solution cultures in mineral nutrition studies are the excellent solvent characteristics of water and the relative ease with which water can be freed of most contaminating influences.

Good quantitative studies may be made of the nutritional need of plants using water as a medium. However careful attention to small details is necessary to achieve good results. Due to the fact that satisfactory growth may be achieved with extremely small amounts of trace elements, contamination problems are always present. Some of the sources of the contamination are the rooting medium, reagents used containers, the water, cutting implements, seeds and the dust in the surrounding atmosphere. Obviously, total elimination of these contaminating influences is impossible, but they can be kept to a minimum.

Several studies have shown that the best container for solution cultures are made of borosilicate grass or natural polyethylene **(Hewitt, 1963)**. However, even with the use of these materials, some contamination may be expected, such as the presence of boron in borosilicate glass and, perhaps, molybdenum and cobalt in polyethylene. Water distilled in metal stills usually is contaminated with trace amounts of copper, zinc, and molybdenum. Redistillation of water in stills made entirely of borosilicate glass is necessary to remove this elements **(Piper, 1942; Ston and Arnon, 1939)**. Another satisfactory method of ridding water of contaminating trace elements is to pass it over cation and anion exchange resins **(Hewitt et al., 1954).**

In early studies of plant nutrients reagents used presented a major source of contamination. These reagents had to be purified by various means before trace elements deficiencies could be demonstrated. Reagents may be purchased today that are pure enough for most studies. But even this contain trace amounts of contaminants.

From the discussion above, one can see that most of difficulties encountered in mineral nutrition studies are associated with trace element contamination. A study of deficiencies caused by major nutrients can be easly accomplished because of the relatively large amounts needed for normal growth. Here, a small amount of contamination is not a serious problem.

With proper attention given to the problems discussed above, the next step is to prepare stock solutions from inorganic salts containing the necessary elements for normal plant growth. Once stock solutions are prepared and the proper containers obtained and filled with deionized water, nutrient solutions may be prepared by simply adding, in the correct proportion, the necessary inorganic salts from the stock solutions. Several satisfactory formulas for nutrient solutions have been prepared.

Sand cultures

Solid media, such as sand or crushed quartz, are generally easier to work with than a liquid medium. On the other hand, purification problems are more difficult to cope with. However, today it is possible to purchase highly purified silica sand or crushed quartz that is very low in available trace elements. The added attraction a solid culture is that the roots are growing in a nature medium and no means of support needs to be provided. Nutrient solutions are added to the solid culture by three different ways: pouring over the surface (slop culture), dripping on the surface (drip culture), and forcing solution up from the bottom of the container (subirrigation). In the all three systems, the nutrient solutions added drain out through an opening in the bottom of the container. In subirrigation, the system may be attached to a timing mechanism, which may be set to give periodic irrigation to the sand.

Of the three methods, the slop culture is the easiest to manipulate, but offers the least control. The drip culture may be set up so that the amount of solution being added equal to the amount of solution draining off. This method allows for continuous nutrients supply and partial control of the amount of nutrients reaching the root system. The last system, subirrigation, may be set up to work

 $\hat{}$

automatically and also gives partial control of the amount of nutrients reaching the plant roots. The subirrigation system is the most desirable of the three systems, but the hardest and most expensive to set up initially.

Chapter 3

Occurrence of the various elements

Because of their relative importance and abundance in the plant carbon, hydrogen, oxygen, and nitrogen will not be covered in this chapter but will receive more extensive attention in separate chapters**.**

Phosphorus

Phosphorus is present in the soil in two general forms, inorganic and organic. In the organic form, phosphorus may be found in nucleic acid, phospholipids, and inositol phosphates, compounds common to the organic fraction of the soil. To the author's knowledge, there have been no reports of plants absorbing organic phosphorus, either from the solid or solution phase of the soil. Therefore, organic phosphorus represents an unusable form of the element with respect to the plant. However, organic compounds are eventually decomposed and phosphorus is released in an inorganic form, which is readily taken up by the plant.

Much of the phosphorus of the soil solution is present in the inorganic form, mainly as the phosphate ions H_2PO_4 ⁻ and HPO_4^{2-} (wiklander, 1958). The quantity of either ion present is dependent upon the PH of the soil solution, the lower pH favouring the H_2PO^{4-} ion and the higher pH, HPO_4^2 .

Calcium

Generally, calcium is the major exchange cation of fertile soils (**marshall, 1951**) .However, the major portion of calcium in the soil is found in a nonexchangeable form, chemically bound in primary minerals such as anorthite $(CaA₁S₁O₈)$. Through a weathering, this calcium can be made available. We have already mentioned the presence of calcite $(CaCO₃)$ of soils in semiarid and arid regions and the general occurrence of insoluble calcium is available to the plant, depending upon the solubility of the salt and the degree of alkalinity.

Liming

The most effective and economical method of controlling soil pH is the application of the lime. lime to the chemist is calcium oxide (CaO) , but to the farmer , it is any compound containing calcium or magnesium capable of counteracting the harmful effects of an acid soil **(Millar et al ., 1951) .**

In an acid soil, we have clay micelles with a predominance of exchangeable hydrogen ions absorbed to their surfaces. With the addition of lime compounds, such as calcium carbonate $(CaCO₃)$ or calcium oxide (CaO) many of hydrogen ions are replaced by calcium ions. In addition, the released hydrogen ions are tied up in the form of water. The final result is a rise in pH and an increase in the supply of exchangeable calcium ions (figure 13-4).

Figure 13-4

One should be cognizant of the harmful effects of liming, as well as the beneficial effects. Over liming a soil may cause the pH of the soil to rise above 7.

Magnesium

Magnesium is present in the soil in water-soluble exchangeable and fixed form and is present in primary minerals (**Bould, 1963**).

Magnesium in minerals such as magnesite ($MgCO₃$), olivine ($MgCO₃2SiO₄$) , and dolomite ($MgCO3$.CaCO₃) is available to plants in satisfactory amounts for growth .

Potassium

Potassium is present in the soil in a nonexchangeable or fixed form, an exchangeable form, and a soluble form. Although there is a relatively high content of this element in the soil, most of it is nonexchangeable and, therefore unavailable to the plant.

When we speak of an element being unavailable, especially with respect to potassium, we mean that utilization of the element in its present form by the plant is not possible. However, availability of potassium in potassium-bearing minerals, such as biotite, muscovite, and illite , is made possible through normal weathering processes .

An equilibrium exists between the soluble, exchangeable, and fixed forms of potassium

Soluble $K =$ exchangeable $K =$ fixed K

Sulfur

Soil sulfur is found primarily in the organic fraction (**Quastel, 1963**), but may also be found in minerals such as pyrite, cobaltite, gypsum, and epsomite and in the soil solution as the sulfate ions $(SO₄)²$. Sulfur is the phosphate ion, the sulfat ions is weakly adsorbed, the adsorption increasing with a decrease in soil pH. Adsorption is favoured by the presence of hydrated oxides of iron fate ion is generally thought of as replacing hydroxyl ions in clay minerals , a process known as anion exchange.

Organic sulphur is made available to the plant through biological oxidation. Through the activity of certain microorganisms, sulfur is transformed from the organic form to the sulfataion, the form of sulphur that higher plants absorb. Not only do soil microorganisms oxidize organic sulphur, but also sulphide minerals, such as ferrous sulphide (FeS). Where there is good aeration, moisture and suitable temperature, FeS canbe chemically oxidized to elemental sulfur.

The elemental sulfur is then oxidized sulfate by sulfur bacteria. The two-step oxidation of ferrous sulphide in soil was first demonstrated by **Wiklander et al. (1950).**

And may be written as follows:

 $FeS + H₂O + \frac{1}{2}O_2 \rightarrow Fe(OH)₂ + S$

 $2S + 2H_2O + 3O_2 \rightarrow 2H_2SO_4$

Biological oxidation in the soil of pyrite $(F \in S_2)$ has also been demonstrated, sulphuric acid being the final product **(Wiklander, 1958)**

Another source of soil sulfur is the atmosphere, the sulfur being brought to the soil by rain and snow.

Iron

Soils generally are not deficient in iron, but may be deficient in exchangeable and soluble forms of iron. Appreciable quantities of iron are present in minerals in hydrated oxides such as limonite $(Fe₂O₃·3H₂O)$, and in the sulfide form (**Bould, 1963**). Iron is most available to the plant in the ferrous form, but significant quantities of the ferric ion may also be absorbed.

The availability of iron to the plant is controlled rather sharply by the soil pH. In acid soils, appreciable amounts of iron are dissolved in the soil solution and available to the plant. However, in neutral or alkaline soils, iron is much more insoluble. In fact, one of the dangers of overliming is that the resulting increase in pH will cause symptoms of iron deficiency to appear on plants. However, even in soils poor in soluble iron, this element may be available by the direct contact of plant roots with iron-containing soil particles **(Chapman, 1939).**

Manganese

According to **Leeper (1947)**, the manganese of the soil may exist in the bivalent, trivalent, and / or tetravalent forms. The bivalent ion may be found dissolved in the soil solution or as an exchangeable ion adsorbed to the soil colloids, both of which are available to the plant. The exchangeable bivalent ion is significant in manganese nutrition, since very little of the soil manganese is likely to be found dissolved in the soil water **(Stiles, 1961).**

Copper

The major portion of the copper of primary rock is present as chalcopyrite $(CuFeS₂)$, which is the probable source of natural deposits of copper sulfide in the soil **(Bould, 1963).**

The divalent copper cation is adsorbed very strongly to the soil colloids and organic materials of the soil **(Hasler, 1943)** a form of which it is relatively exchangeable. adsorption of copper as a complex monovalent ion (CuOH⁺, CuCl⁺) has been demonstrated in organic soils **(Llucas , 1948**) and on clay minerals **(Menzel and Jakson , 1950) .**

Zinc

According to **Bould (1963)**, zinc occurs in the ferromagnesium minerals, magnetite, biotite, and hornblende. Weathering of these minerals releases zinc in the divalent form, which is readily adsorbed onto soil and organic matter in exchangeable form.

As with many other essential elements, one of the factors controlling the availability of zinc is the soil pH. The availability of zinc decrease with increase in pH, making it very likely that symptoms of zinc deficiency may occur in plants growing in alkaline soils.

Boron

Boron appears in exchangeable , soluble , and nonexchangeable forms in the soil, that is, as boric acid (H_3BO_3), calcium or manganese borates, and as a constituent of silicates **(Bould , 1963 ;Wiklander , 1958) .** Like zinc, the dissolved boron content in the soil solution is very low.

Molybdenum

According to (**Wiklander, 1958**), molybdenum is present in soils in three forms:

- dissolved in the soil solution as molybdate ions $(MoO₄²$ or $HMoO⁴$),

- adsorbed to soil particles in an exchangeable form,

- In a nonexchangeable form as a constituent of soil minerals and organic matter.

Chapter 4

Phosphorus

Function

- Phosphorous is found in plants as a constituent of nucleic acids and nucleoprotein so, it is found in the meristematic regions with higher concentration.
- It is found as a constituent of phospholipids which form the cell membrane.
- Also, it is found as a constituent of the coenzymes NAD and NADP that are important in oxidation reduction reactions in which hydrogen transfer takes place.
- In addition, Phosphorous is found in the most important constituent ATP which acts as an energy transfer compound.

Deficiency symptoms of phosphorus

1-Falling of the premature leaves.

2- Formation of purple or red anthocyanin pigmentation.

3-Developing of dead or necrotic areas on the leaves, petioles or fruits.

4-With more severe deficiency, leaves turn pale brown and die, and roots may turn dark and discolored in sorghum

5- Stunted growth.

6-Sickle leaf disease is caused in P deficiency, which is characterised by chlorosis adjacent to main veins followed by leaf asymmetry.

Nitrogen

Function

- Nitrogen has an important role as it found in the structure of protein molecule
- It is found in such important molecules as purines, pyrimidines and prophyrines.
- Purines and pyrimidines are found in the nucleic acids, DNA and RNA which are essential for protein synthesis.
- The prophyrines are important for the metabolism of some compounds such as chlorophylls and the cytochrome enzymes.

Deficiency symptoms of nitrogen

1-the chlorophyll content of the plant leaves is reduced which results in pale yellow color.

2-young leaves are pale as the older leaves are yellow and drop early

3- Purple color formed on leaf, petioles and vines of tomato as a result of production of anthocyanin pigment.

4-Reduction in cell size and cell division

5-low of nitrogen availability must cause a decrease in protein synthesis.

6-Reduction in protein results in stunted growth and dormant lateral buds

7- Flowering, fruiting, protein and starch contents are reduced.

8- Shoots are thinner and shorter.

Magnesium

Function

- Magnesium is a constituent of chlorophyll molecule without it photosynthesis would not occur.
- Many of enzymes involved in carbohydrate metabolism require magnesium as an activator
- Magnesium acts as activator for those enzymes involved in the synthesis of nucleic acids (DNA, RNA).
- It has a role in protein synthesis.

Deficiency symptoms of magnesium

1-The first sign of magnesium deficiency is the chlorosis of old leaves which progresses to the young leaves as the deficiency progresses.

2- The low amounts of Mg lead to a decrease in photosynthetic and enzymatic activity within the plants.

3- After prolonged magnesium deficiency, necrosis and dropping of older leaves occurs.

4- Production of smaller fruits.

5- Stem becomes yellowish-green, often hard and woody.

Calcium

Function

- Act as a constituent of cell walls in the form of calcium pectate
- Calcium is important in the formation of cell membranes and lipid structure.
- Calcium has a role in normal mitosis
- It acts as activator of some enzymes.

Deficiency symptoms of calcium

- 1- Necrosis leading to stunted plant growth
- 2- Curling of the leaves
- 3- Reduction of plant height, fewer nodes, and less leaf area.
- 4- Death of terminal buds and root tips.
- 5-cell walls become rigid or brittle.

6- The common disease is blossom-end rot of tomato (burning of the end part of tomato fruits.

Potassium

Function

- It has a major role in varies process as respiration, photosynthesis, chlorophyll development and water content of leaves.
- Potassium acts as activator for enzymes involved in protein synthesis.
- Also, it acts as activator for enzymes involved in carbohydrate metabolism.
- It has an essential role in apical dominance in the plants.

Deficiency symptoms of potassium

1-Brown scorching and curling of leaf tips as well as chlorosis (yellowing) between leaf veins.

2- Purple spots may also appear on the leaf.

3- Reduction in plant growth, root development, and seed and fruit development.

4- Potassium deficiency symptoms first appear on older (lower) leaves.

5- Stunted in growth and shortening of internodes.

6- Two common diseases are known **"Rosette** "in beet and carrot, bushy growth or rosette condition develops due to potassium deficiency."**Die back".** In acute deficiency cases, there is a loss of apical dominance and regeneration of lateral buds and bushy of growth. In prolonged cases, die back of lateral buds are also resulted.

Zinc

Function

- It participates in the metabolism of plants as an activator of several enzymes.
- It involved in the biosynthesis of the plant auxin (IAA).
- It plays an important role in protein synthesis.

Deficiency symptoms of zinc

1-An interveinal chlorsis of the older leaves starting in the tips and margins.

- 2- White necrotic spots.
- 3- Seed production and fruits size is greatly reduced.
- 4- Leaves are often narrower or have wavy margins.
- 5- Smaller leaves and shortened internodes resulting in stunted growth.

6- The common disease is **little leaf** disease. Yellow mottling of leaves, reduction of leaf size with rosette appearance (due to reduced internodal distance) and die back of the affected branches are symptoms of the disease.

Sulfur

Function

- Sulfur is the constituent of amino acids cysteine, cysteine and methionine
- It also participates in the constituent of vitamin B, co-enzyme A and volatile oils.
- It may be found in sulfhydryl groups, which are present in many enzymes. \sim \sim \sim

Deficiency symptoms of sulfur

- **1-** Sulfur deficiency causes yellowing (Chlorosis) of leaves. Young leaves are affected first.
- **2-** Tips and margins of leaves roll inward.
- **3-** Accumulation of starch, sucrose and soluble nitrogen.
- **4-** Young leaves develop orange, red or purple pigments.

Manganese

Function

- It acts as an activator for enzymes in respiration and nitrogen metabolism.
- It plays an important role in nitrate reduction.
- Manganese thought to be involved in the destruction and oxidation of indol-3-acetic acid (IAA).

Deficiency symptoms of manganese.

1-The leaves start to turn yellow and undergo interveinal chlorosis.

2- The younger leaves near the top of the plant show symptoms first.

3- The chloroplasts of tomato leaves lose chlorophyll and starch grains becoming yellow green in colour.

Copper

Function

- Copper acts as a component of some enzymes.
- It has a role in photosynthesis process as a constituent of chloroplast.

Deficiency symptoms of Copper.

1-It causes a necrosis of the tip of young leaves that proceeds along the margin of the leaf, giving it a withered appearance.

2- Under sever condition the leaves may be lost, and the whole plant may appear wilted.

3- *Reclamation disease*: It is also called as White Tip disease and is found in legumes, cereals, oats and beet. The tips of the leaves become chlorotic followed by a failure of the plants to set seed.

Iron

Function

- Iron has a number of important functions in the overall metabolism of the plant.
- It appears to be essential for the synthesis of chlorophyll
- It has a major role in the biosynthesis of cytochromes.
- It acts as an activator of some enzymes.

Deficiency symptoms of iron

1- Extensive chlorosis of leaves specially the younger one.

2-The lack of iron may inhibit formation of chloroplasts through inhibition in protein synthesis.

Boron

Function

- Boron has an important role in the transport of carbohydrate within the plant.
- It participates in cellular differentiation, in nitrogen metabolism, fertilization, active salt absorption, hormone metabolism, phosphorous metabolism and photosynthesis.

Deficiency symptoms of boron

- **1**-death of stem and root tips.
- 2- Abscission of flowers.
- 3-the leaves may have a coppery texture.

4-leaves sometimes curling and becoming quit brittle.

5- Root growth is stunted.

Molybdenum

Function

- It has an important role in nitrogen fixation and nitrate and phosphorous assimilation.
- It maintain the concentration of ascorbic acid in the plant.

Deficiency symptoms of Molybdenum

1-Chlorotic interveinal mottling of the lower leaves followed by marginal necrosis and infolding of the leaves.

2- Under sever conditions; mottled areas may become necrotic, causing the leaf to wilt.

3-Flower formation is inhibited and if flowers do form, they abscise before setting fruit.

4- A common disease of molybdenum deficiency in cauliflower plants is whiptail in which the leaves show an interveinal mottling and leaf margins may become grey and finally brown. The leaf tissues wither, leaving only the midrib and a few small pieces of leaf blade, giving the appearance of a whip or tail.

Chapter 5

Mineral Salt absorption And Translocation

It was thought that osmotically active substances diffused along concentration gradients from soil solution into the plant. The osmotic concentration inside the cell was continuously kept a low point through utilization of the absorbed substances in metabolism. The osmotic theory sufficiently explained the absorption, but did not account for the rapid translocation of the salts once they were absorbed. Again the transpiration stream was implicated, this time as only aiding in the dispersal of the salts, not their absorption. Thus, early attempts to explain salt absorption and mineral nutrition

Translocation only emphasized physical mechanisms, neglecting almost entirely the participation of metabolic energy.

However, during this time, a statement was made by the brilliant physiologist, **Pfeffer**, which contrasted sharply with prevalent theories on salt absorption and remarkably foreshadowed a popular theory today (**Pfeffer, 1900**). **Pfeffer** claimed:

The nature of the plasma is such as to render it possible that a substance may combine chemically with the plasmatic elements, thus being transmitted internally, and then set free again.

This statement agrees very nicely with the carrier theory in salt absorption generally accepted today.

As is usually the case when one tries to buck the tide of popular thought, this provocative theory in absorption was not taken too seriously, and physical mechanisms and models were continuously produced to explain salt absorption. It was finally recognised, from work done in the 1930, that salt absorption is largely dependent upon metabolic energy, that the uptake of salt is predominately active, not passive as was earlier thought.

Passive absorption

Outer and apparent free space

Salt absorption takes place through the intimate contact of the root system with the soil colloids or soil solution. What are the mechanisms involved in the passage of dissolved inorganic salts from the soil solution into the plant? passive or non-metabolic absorption of ions has been demonstrated by numerous investigators (see review by **Briggs and Robertson , 1957**) it has been found frequently that when a plant cell or tissue is transferred from a medium of low salt concentration to a medium of relatively high salt concentration there is an initial rapid uptake of ions this is followed by a slow steady uptake that is under metabolic control . The rapid initial uptake is not affected by temperature or metabolic inhibitors; that is, metabolic energy is not involved. If the above tissue is returned to the low salt medium, some of the ions taken up will diffuse out into the external medium. In other words, a part of cell or tissue immersed in the salt solution is opened to free diffusion of ions. since free diffusion implies that ions can move freely in or out of the tissue , the part of the tissue opened to free diffusion will reach an equilibrium with the external medium and the ion concentration of this part will be the same that found in the external medium .

That part of a plant cell or tissue which will allow for free diffusion to take place is referred to as outer space.

With the establishment with the concept of 'outer space ', workers turned to the task of calculating the volume of plant cell or tissue involved. This may be accomplished by immersing a tissue in a solution of known concentration, allowing it to come to equilibrium, and then determining the amount of salt taken up. Assuming that the ion concentration is the same both in outer space and in the external medium and knowing the amount of salt taken up, we can calculate the volume of outer space.

Under the above circumstances, active absorption must be inhibited (e.g., by metabolic inhibitors or by low temperature) or the calculated volume will be greater than the actual volume.

Ion exchange

Ions adsorbed to the surfaces of the cell walls or membranes of a tissue may exchange with ions from the external solution in which the tissue is immersed.

We have already encountered analogous ion exchange mechanisms between the soil solution and the soil colloids in a previous chapter. Suppose, for example, the cation, K^+ , of external solution exchanged with a hydrogen ion, H^+ , adsorbed to the surface of the cell membrane. The action would then become adsorbed to the surface of the membrane and rendered osmotically inactive. Anions could exchange with free hydroxyl ion in the same manner. Thus, ion exchange mechanism would allow for a greater absorption of ions from the external medium than could normally be accounted for by free diffusion.

Diagrammatic representation of (a) The contact-exchange theory and (b) The carbonic acid exchange theory

Donnan equilibrium

The Donnan equilibrium theory takes into account the effect of fixed or in diffusible ions. Take, for example, a membrane that is permeable to some ions and not to others and which separates the cell from the external medium. Suppose in the inner side of this membrane there is a concentration of anions to which the membrane is impermeable (fixed anion). Now, if the above membrane is freely permeable to the cations and anions in the external solution equal numbers of cations and anions from the external solution will diffuse across from the membrane until an equilibrium is established. Normally, this equilibrium would also be electrically balanced. However, additional cations are needed to balance the negative charges of (fixed) anions. Therefore, the cation concentration would be greater in the internal solution than in external solution. also , it must be remembered , because , of the excess of negative charges due to fixed anions , the concentration of anions in the internal solution will be less than that of the external solution . As shown in figure 5.3.

Donnan equilibrium ion diffiusion across membranes. (a) Membrane is impermeable to the cation, X^+ , causing additional anions, B^- , to diffuse across from the outside (accumulation of anions) . (b) membrane is the impermeable to the anion, Y , causing additional cations, A^+ , to diffuse across from the outside (accumulation of cations) .

Mass flow

Some of investigators believe that ions can move through roots along with the mass flow of water (**Hylmo, 1953; 1955; Kylin and Hylmo 1957**). According to this theory, an increase in transpiration should cause an increase in absorption of ions. That this is so has been generally accepted (**Russell, and barber, 1960**) but weather the effect of transpiration is direct or indirect is not clear. some authors claim that transpiration in directly effects ion absorption by removing ions after they have been released into the xylem ducts , causing by this dilution an increase in ion absorption activity (**Brauwer , 1956 ; Broyer et al . , 1943 ; Honert , 1955**) .

From this discussion, we have learned that at least part of the total salt taken up by a plant may result from passive absorption. This may be accomplished

through free diffusion of ions into the apparent free space of a tissue. Accumulation of ions against a concentration gradient is possible under the above circumstances due to Donnan equilibrium. Accumulation may also take place against an apparent concentration gradient due to ion exchange mechanisms. Finally, the mass flow of ions through root tissue may be possible with the aid of transpirational 'pull'. All of this mechanisms occur in the absence of metabolic energy. Let us now turn to an analysis of active transport.

Active transport

Direct analyses of the vacuolar sap of plants immersed in solution of known salt concentration have demonstrated an equivocally that both anions and cations are accumulated by plants against concentration gradients. Furthermore, the extent of accumulation is such as known physical mechanisms, such as ion exchange and donnan equilibrium, cannot account for the extent of accumulation that occurs, analyses of the ion accumulation in the sap of *Nitella clavata* and *Valonia macrophysa* by **Hoagland (1944**) give an excellent picture both of the accumulation and selective properties of salt absorption mechanisms in plants.

Since ion accumulation is inhibited when the metabolic activity of the plant is inhibited by low temperature, low oxygen tension, metabolic inhibitors, etc., we can only assume that ion accumulation as it occurs in plants requires metabolic energy. The transport of ions with the aid of metabolic energy has been termed active transport. Various mechanisms have been devised to explain active transport, none of which have been universally accepted. All of this suggested mechanisms, however, generally accept the concept that the active transport of an ion across an impermeable membrane is accomplished through the mediation of a carrier compound present in the membrane.

The carrier concept

The space in a tissue or cell to which ions penetrate, through the mediation of metabolic energy, is termed inner space. Where outer space ends and inner space begins has not been clearly established. however , it is thought that this dividing line begins somewhere in the middle of the cytoplasm , since apparent free space volume measures have implied that part of cytoplasm allows for free diffusion of ions . The area between outer and inner space is impermeable to free ions. Passage across this area is thought to require the intercession of specific carriers, which combine with ions in outer space and release them in inner space. This impermeable barrier is usually spoken of as a membrane and the carriers as existing within it.

The most important feature of the carrier theory is the assumption of an intermediate carrier-ion complex, which is capable of moving across the above mentioned impermeable membrane. The direction of movement of the complex is from outer to inner space only. Ions released into inner space cannot move out and thus are accumulated. A model giving a simplified description of the carrier concept is shown in figure 22.4.

The carrier concept has received impressive support by numerous investigators since its formulation by **Van den honert in 1937**. We will discuss three characteristics of salt absorption and active transport that appear to suggest strongly the validity of the carrier concept.

Fig. 22.4

Saturation effects

The fact that a level maximum rate of absorption may be maintained over a relatively long period of time suggests the participation of a finite number of carriers working, so to speak at maximum efficiency. That is, the active sites on the carriers in the above situation are occupied all of the time. As soon as a carrier released an ion to inner space, it is immediately occupied by an ion from the outer space areas in the tissue. Thus, at the saturation point of cycle is kept in continuous motion and cannot be made to proceed faster by increasing the salt concentration.

Specificity.

The carrier concept offers a reasonable explanation of the fact that roots selectively absorb ions. That is, ions are absorbed at different rates and have different levels in accumulation in the root tissue, suggesting the presence of specific carriers. This specificity is rather rigid with ions of dissimilar chemical behaviour, but weak or non-existent with ions of similar behaviour.

Cytochrome pump

Early workers observed that although salt accumulation is depended upon metabolic energy, there appeared to be no quantitative relationship between salty absorption and respiration. However, **lundeggardh and burstrom (1933)** claimed that such a relation exists between anion absorption and what they called 'anion' or 'salt' respiration. They observed that the rate of respiration increases when a plant is transferred from water to salt solution. The amount by which respiration is increased over normal or ground respiration by the transfer of a plant or tissue from water to a salt solution is known as salt respiration. The original observations of **lundegardh and Burstro** have since been expanded and developed to a workable theory in active salt absorption by **lundegardh (1950, 1954)**.

Lundegardh theory assumes the following:

1. Anion absorption is independent of cation absorption and occurs by a different mechanism.

2. An oxygen concentration gradient exists from the outer surface to the inner surface of a membrane, thus favouring oxidation at the outer surface and reduction at the inner surface

3. The actual transport of the anion occurs through a cytochrome system.

Since there is a quantitative correlation between anion absorption and salt respiration and since this correlation does not exist with cation absorption it was assumed that only anions are actively transported. The inhibition of salt respiration and consequent inhibition of anion absorption by cyanide or carbon monoxide led lundegardh to propose that transport of anions is mediated through cytochrome oxidase and that cytochromes may be anion carriers. A diagrammatic representation of lundegardh cytochrome theory is shown in figure 7.3. According to lundegardh theory, dehydrogenase reactions on the inner surface produce protons $(H⁺)$ and electrons (e \cdot). The electrons produced move outward via a cytochrome chain, while anions move inward. At the outer surface of the membrane the reduced iron of the cytochrome in oxidized, losing an electron and picking up an anion. The released electron unites with a proton and oxygen to form water.

At the inner surface the oxidized iron of the cytochrome becomes reduced by the addition of an electron released in a dehydrogenase reaction. The anion is released on the inside in this last reaction. Cations are absorbed passively to balance the potential difference caused by the accumulation of anions on the inner surface.

Fig. 7.3 Diagrammatic representation of the Lundegardh's cytochrome pump theory.

Although the cytochrome transport theory des give a clear picture of how metabolic energy might participate in ion absorption, it has not been universally accepted and has been criticized by a number of investigators. For example, **Robertson et al. (1951)** found that 2, 4- dinitrophenol (DNP), an inhibitor of oxidative

Phosphorylation, increases respiration but decreases salt absorption. This implies that phosphorylation should be included in any theory of ion accumulation. The original proposal that only anions are capable of stimulating respiration has come under considerable attack. For example, **Handley and overstreet (1955)** found that both potassium and sodium ions simulated respiration. Finally, if there is only one carrier for all anions, then competition for binding sites among anions should be apparent.

On the contrary, as pointed out in an earlier discussion, the anion sulfate, nitrate, and phosphate do not compete with one another.

Carrier mechanism involving ATP

A mechanism for active salt absorption that utilizes ATP has been proposed by **Bennet – clarck (1956).** This investigator has suggested that phospholipids may be important in the transport of ions across membranes otherwise impermeable. In this transport **lecithin**, a phospholipid, is synthesized and hydrolysed in a cyclic manner, picking up ions on the outer surface and releasing them on hydrolysis into inner space. The synthesis of at least one of the components of this phosphatide cycle requires ATP. A diagram showing the 'phosphatide cycle' and how it might proceed in ion transport is given in figure 7.4.

Fig. 7.4. Diagrammatic representation of the Bennet-Clark's Protein-Lecithin theory.

Factors affecting salt absorption

The physical and biochemical activities of living organisms are subject to the influences of their external and internal environments. Salt absorption is not an exception, being speeded up, slowed down, or kept in dynamic equilibrium by a complex of ever changing factors. The scientist has learned to study the influence of individual factors by controlling the environment and studying the effect of the one factor in question. This has been done with the process of salt absorption, and we now have an extensive, if incomplete, picture of how this process might proceed in nature's ever changing environment. We will discuss the effects of temperature, pH, light, oxygen tension, interaction, and growth on salt absorption.

Temperature

In general, an increase in temperature results in an acceleration of salt absorption.

However, the influence of temperature in salt absorption is confined to a relatively narrow range. In addition to accelerating salt absorption, increase in temperature past a maximum point will inhibit and eventually terminate the process. Most likely, the inhibitory effects of high temperature are because of the denaturation of enzymes involved either directly in salt absorption or in the synthesis of some necessary component of salt absorption.

Boss passive and active absorption process are affected by temperature changes. The rate of free diffusion, for example, depends upon the kinetic energy of the diffusing molecules or ion which is, in turn, dependent on temperature. Therefore, lowering of temperature will slow down any process dependent upon free diffusion. Low temperature will, of course, slow down the biochemical reactions found in active transport.

Hydrogen ion concentration

The availability of ions in the soil solution, discussed in a previous chapter, is profoundly affected by the hydrogen ion concentration. Ionization of electrolytes or the

Valence numbers of different ion species are influenced by changes in pH. For example, the monovalent phosphate ion, H_2PO^{4-} , is the form of phosphorus most readily taken up by plants. However, as a medium approaches a more

alkaline pH, production of first the bivalent phosphate $(HPO₄²)$ and then the trivalent phosphate $(PO₄³)$ is favoured. The bivalent ion is only sparingly available to the plant, while the trivalent ion is not available at all. Since the monovalent ion is absorbed more readily than the bivalent ion, absorption of phosphate is accelerated at an acid pH. **Robertson (1958)** has pointed out that since boron is taken up as the undissociated acid, H_3BO_3 , or as the $H2BO³$ ion, it too must be absorbed more readily at a lower pH. In contrast to the above observations, with anions increase in pH will favour the absorption of cations.

There have been numerous experiments showing little pH effect, as judged by growth (**Robertson, 1958**). Marked pH effects most likely occur when ion availability is inhibited. However, if the concentration of ion is high enough, it will be difficult to show a deficiency for that ion in the plant over a physiological range of pH values. Of course, at pH values outside the physiological range, damage to plant tissues and carriers will inhibit salt absorption.

Light

The effects of the light in the opening and closing of stomates and on photosynthesis indirectly affect salt uptake. Opened stomates increase the mass flow of water in the transpiration stream and thus may indirectly influence salt absorption. The energy derived from the photosynthetic process provides energy for salt uptake and the oxygen given off improves conditions for the active absorption of ions

Oxygen tension

The active phase of salt absorption is inhibited by the absence of oxygen. Indeed, it was this observation that most strongly supported early theories active transport.

Chapter 6

PLANT GROWTH REGULATORS

Plant growth regulators or phytohormones are organic substances produced naturally in higher plants, controlling growth or other physiological functions at a site remote from its place of production and active in minute amounts. **Thimmann (1948)** proposed the term *Phyto hormone* as these hormones are synthesized in plants*. Plant growth regulators* include auxins, gibberellins, cytokinins, abscisic acid and ethylene.

Plant growth regulators

An endogenous compound, which is synthesized at one site and transported to another site where it exerts a physiological effect in very low concentration. But ethylene (gaseous nature), exert a physiological effect only at a near a site where it is synthesized.

• Defined as organic compounds other than nutrients, that affects the physiological processes of growth and development in plants when applied in low concentrations.

• Defined as either natural or synthetic compounds that are applied directly to a target plant to alter its life processes or its structure to improve quality, increase yields, or facilitate harvesting.

Five major classes of plant hormones are known in plants. With progressing research, more active molecules are being found and new families of regulators are emerging.

- (1) Auxin
- (2) Gibberellin
- (3) Cytokinin

(4) Abscisic acid

(5) Ethylene

Auxins

The term auxin is derived from the Greek word 'auxein' which means to grow. They are a class of plant hormones which has a cardinal role in coordination of many growth and behavioral processes in the plant's life cycle essential for development of plant. Auxin is the first plant hormone to be identified. They have the ability to induce cell elongation in stems and resemble indole acetic acid (the first auxin to be isolated) in physiological activity.

Discovery of auxin: **Darwin (1881)** was the first person who discovered the existence of auxin in plants, the first phytohormone known. He noted that the first leaf (coleoptile) of canary grass (Phalaris canariensis) was very sensitive and responsive to light and he demonstrated the bending of the grass coleoptiles towards unilateral source of light. This bending occurred only when the coleoptile was also illuminated. When the tip of the coleoptiles was covered with a black cap, it resulted in loss of sensitivity of the plant towards the light as shown in Figure 2. Darwin concluded that some influence that causes curvature is transmitted from the coleoptile tip to the rest of the shoot. Boysen – Jensen (1913) also made similar observations on oat (Avena) coleoptiles as shown in Figure 2. Paal (1918) demonstrated that when the decapitated coleoptiles tip was replaced on the cut end eccentrically, more growth resulted on the side which causes bending even when this is done in complete darkness.

Sites of biosynthesis of auxin: IAA is synthesized primarily in actively growing tissue in leaf primordia and young leaves, fruits, shoot apex and in developing seeds. It is made in the cytosol of cells.

Classification of auxins: Auxins are classified into two types based on its occurrence, if they occur naturally or are synthesized artificially.

- 1. Natural auxins
- 2. Synthetic auxins

Natural auxins: The four naturally occurring (endogenous) auxins are Indole-3 acetic acid, 4-chloroindole-3-acetic acid, phenylacetic acid and indole-3-butyric acid; only these four are synthesized by plants.

Synthetic auxins: Synthetic auxin analogs include 1-naphthaleneacetic acid, 2,4dichlorophenoxyacetic acid (2,4-D) and many others. Some synthetic auxins, such as 2,4D and 2,4,5-trichlorophenoxyacetic acid (2,4,5-T), are used also as herbicides. Broad-leaf plants (dicots), such as dandelions, are much more susceptible to auxins than narrow-leaf plants (monocots) such as grasses and cereal crops, so these synthetic auxins are useful as synthetic herbicides.

Distribution of auxin in plants

In plants, auxin (IAA) is synthesized in growing tips or meristematic regions from where; it is transported to other plant parts. Hence, the highest concentration of IAA is found in growing shoot tips, young leaves and developing auxiliary shoots.

Within the plants, auxin may present in two forms. i.e., *free auxins* and *bound auxins*. Free auxins are those which are easily extracted by various organic solvents such as diethyl ether. Bound auxins on the other hand, need more drastic methods such as hydrolysis, autolysis, enzymolysis etc. for extraction of auxin. Bound auxins occur in plants as complexes with carbohydrates such as glucose, arabionse or sugar alcohols or proteins or amino acids such as aspartate, glutamate or with inositol.

Some physiological effects of auxin

- **1-Cell division and elongation**
- **2- Apical dominance**
- **3- Root initiation**

1. Cell division and elongation

The primary physiological effects of auxin are cell division and cell elongation in the shoots. It is important in the secondary growth of stem and differentiation of xylem and phloem tissues.

2. Apical dominance

In many plants, if the terminal bud is intact and growing, the growth of lateral buds just below it remains suppressed. Removal of the apical bud results in the rapid growth of lateral buds. This phenomenon in which the apical bud dominates over the lateral buds and does not allow the lateral buds to grow is known as *apical dominance*.

Skoog and Thimmann (1948) pointed out that the apical dominance might be under the control of auxin produced at the terminal bud and which is transported downward through the stem to the lateral buds and hinders the growth. They removed the apical bud and replaced it with *agar* block. This resulted in rapid growth of lateral buds. But when they replaced the apical bud with agar block containing auxin, the lateral buds remained suppressed and did not grow.

3. Root initiation

In contrast to stem, the higher concentration of auxin inhibits the elongation of roots but the number of lateral roots is considerably increased i.e., higher concentration of auxin induces more lateral branch roots. Application of IAA in lanolin paste to the cut end of a young stem results in an early and extensive rooting. This fact is of great practical importance and has been widely utilized to promote root formation in economically useful plants which are propagated by cuttings.

4. Phototropism

Photo means "**Light**" and tropism means "**Turning**". Therefore phototropism merely refers as the bending of plants towards the light for its growth by absorbing solar energy.

When a growing plant is illuminated by unilateral light, it responds by bending toward the light. The bending of the plant is caused by cells elongating on the shaded side at a much greater rate than cells on the illuminated side. This differential of growth response of the plant to light, called phototropism, is caused by an unequal distribution of auxin, the higher concentration of the growth hormone being on the shaded side. Many attempts have been made to explain why there is a higher concentration of auxin on the shaded side of unilaterally illuminated coleoptile. There is a large evidence supporting the theory that unilateral illumination is capable of inducing lateral transport of auxin.

5. Geotropism

If an intact seedling is placed in a horizontal position it will respond to the earth's gravitational field with a particular pattern of growth. Growth of the stem under these circumstances will cause it to curve upward until it is vertical again and the root system will curve downward until it too is vertical again. Like phototropism, the geotropic response is controlled by an unequal distribution of auxin but, unlike phototropism, gravitational pull instead of light is the influencing factor in geotropic auxin distribution. The **colony-went** theory provides an explanation for geotropism as well as phototropism. They proposed that the differential growth exhibited by a horizontally placed organ is due to the accumulation of auxin on the lower side. They suggested that auxin is laterally transported from the upper to the lower side under the influence of gravity. The accumulation of auxin on the lower side of a horizontally placed stem causes an accelerated growth to occur on the lower side causing the stem to curve upward. The horizontally placed root, however, will exhibit a positive geotropic response even though auxin concentrates on the lower side. Roots are much more sensitive to IAA than stems and the concentrations of IAA which stimulate cell elongation in stems are actually inhibitory to cell elongation in roots. The accumulation of auxin on the lower side of a horizontally placed root would, therefore, retard cell elongation on that side.

Gibberellin

Gibberellin was first discovered in Japan by **Kurusowa**. He observed from his field that some of the rice seedlings had grown much taller than the others. On further observation, he found that such taller rice plants had shown unusual internodal elongation. This internodal elongation is known as the 'bakanae' or 'foolish seedling' disease of rice. Later, it was discovered that the elongation was due to the action of a substance produced by a fungus, Gibberella fujikuroi. This substance was successfully isolated from the fungus and it was named as gibberellic acid.

There are over 90 different gibberellins isolated from fungi and from higher plants. Gibberellins occur in various plant organs.

They are named as GA1, GA2, GA3, etc. These phytohormones occur in all groups of plants.

Physiological effects of gibberellin

- 1. Gibberellins produce extraordinary elongation of stem. The elongation of stem is caused by the cell division and cell elongation induced by gibberellic acid.
- 2. One of the most striking effects of the gibberellins is the reversal of dwarfism in many genetically dwarf plants. For e.g. 'Rosette' plant of sugar beet, when treated with GA undergoes marked longitudinal growth of axis attaining the normal size.
- 3. Rosette plants usually show reduced internodal growth. These plants exhibit excessive internodal growth when they are treated with gibberellin. This sudden elongation of stem followed by flowering is called bolting.
- 4. Many biennials usually flower during the second year of their growth. For flowering to take place, these plants should be exposed to cold season. Such plants could be made to flower without exposure to cold season in the first year itself, when they are treated with gibberellins.
- 5. Formation of seedless fruits without fertilization can also be induced by gibberellin treatment in many plants. e.g. Tomatoes, apples, cucumbers, etc.,

6. Some of the light sensitive seeds can germinate by the treatment of gibberellic acid even in complete darkness. e.g. barley, gibberellin breaks dormancy in potato tubers.

Cytokinins

The effect of cytokinins was first reported when it was found that adding the liquid endosperm of coconuts to developing plant embryos in culture stimulated their growth. The stimulating growth factor was found to be cytokinin, a hormone that promotes cytokinesis (cell division). Almost 200 naturallyoccurring or synthetic cytokinins are known, to date. Cytokinins are most abundant in growing tissues, such as roots, embryos, and fruits, where cell division is occurring. Cytokinins are known to delay senescence in leaf tissues, promote mitosis, and stimulate differentiation of the meristem in shoots and roots. Many effects on plant development are under the influence of cytokinins, either in conjunction with auxin or another hormone. For example, apical dominance seems to result from a balance between auxins that inhibit lateral buds and cytokinins that promote bushier growth.

Abscisic acid

Abscisic acid (also called ABA) is one of the most important plant growth inhibitor. It was discovered and researched under two different names before its chemical properties were fully known, it was called *dormin* and *abscicin II*. Once it was determined that the two compounds are the same, it was named abscisic acid. The name "abscisic acid" was given because it was found in high concentrations in newly abscissed or freshly fallen leaves.

This class of PGR is composed of one chemical compound normally produced in the leaves of plants, originating from chlorplasts, especially when plants are under stress. In general, it acts as an inhibitory chemical compound that affects

bud growth, and seed and bud dormancy. It mediates changes within the apical meristem, causing bud dormancy and the alteration of the last set of leaves into protective bud covers. Since it was found in freshly abscissed leaves, it was thought to play a role in the processes of natural leaf drop, but further research has disproven this. In plant species from temperate parts of the world, it plays a role in leaf and seed dormancy by inhibiting growth, but, as it is dissipated from seeds or buds, growth begins. In other plants, as ABA levels decrease, growth then commences as gibberellin levels increase. Without ABA, buds and seeds would start to grow during warm periods in winter and be killed when it froze again. Since ABA dissipates slowly from the tissues and its effects take time to be offset by other plant hormones, there is a delay in physiological pathways that provide some protection from premature growth. It accumulates within seeds during fruit maturation, preventing seed germination within the fruit, or seed germination before winter. Abscisic acid's effects are degraded within plant tissues during cold temperatures or by its removal by water washing in out of the tissues, releasing the seeds and buds from dormancy.

In plants under water stress, ABA plays a role in closing the stomata. Soon after plants are water-stressed and the roots are deficient in water, a signal moves up to the leaves, causing the formation of ABA precursors there, which then move to the roots. The roots then release ABA, which is translocated to the foliage through the vascular system and modulates the potassium and sodium uptake within the guard cell, which then lose turgidity, closing the stomata. ABA exists in all parts of the plant and its concentration within any tissue seems to mediate its effects and function as a hormone; its degradation, or more properly catabolism, within the plant affects metabolic reactions and cellular growth and production of other hormones. Plants start life as a seed with high ABA levels. Just before the seed germinates, ABA levels decrease; during germination and early growth of the seedling, ABA levels decrease even more. As plants begin to produce shoots with fully functional leaves, ABA levels begin to increase, slowing down cellular growth in more "mature" areas of the plant. Stress from water or predation affects ABA production and catabolism rates, mediating another cascade of effects that trigger specific responses from targeted cells. Scientists are still piecing together the complex interactions and effects of this and other phytohormones.

Ethylene

Ethylene is a gas that forms through the breakdown of methionine, which is in all cells. Ethylene has very limited solubility in water and does not accumulate within the cell but diffuses out of the cell and escapes out of the plant. Its effectiveness as a plant hormone is dependent on its rate of production versus its rate of escaping into the atmosphere. Ethylene is produced at a faster rate in rapidly growing and dividing cells, especially in darkness. New growth and newly germinated seedlings produce more ethylene than can escape the plant, which leads to elevated amounts of ethylene, inhibiting leaf expansion. As the new shoot is exposed to light, reactions by phytochrome in the plant's cells produce a signal for ethylene production to decrease, allowing leaf expansion. Ethylene affects cell growth and cell shape; when a growing shoot hits an obstacle while underground, ethylene production greatly increases, preventing cell elongation and causing the stem to swell. The resulting thicker stem can exert more pressure against the object impeding its path to the surface. If the shoot does not reach the surface and the ethylene stimulus becomes prolonged, it affects the stem's natural geotropic response, which is to grow upright, allowing it to grow around an object. Studies seem to indicate that ethylene affects stem diameter and height: When stems of trees are subjected to wind, causing lateral stress, greater ethylene production occurs, resulting in thicker, more sturdy tree trunks and branches. Ethylene affects fruit-ripening: Normally, when the seeds are mature, ethylene production increases and builds-up within the fruit, resulting in a climacteric event just before seed dispersal. The nuclear protein Ethylene Insensitive2 (EIN2) is regulated by ethylene production, and, in turn, regulates other hormones including ABA and stress hormones.

Seed dormancy

Plant hormones affect seed germination and dormancy by acting on different parts of the seed.

Embryo dormancy is characterized by a high ABA: GA ratio, whereas the seed has a high ABA sensitivity and low GA sensitivity. In order to release the seed from this type of dormancy and initiate seed germination, an alteration in hormone biosynthesis and degradation toward a low ABA/GA ratio, along with a decrease in ABA sensitivity and an increase in GA sensitivity, must occur.

ABA controls embryo dormancy, and GA embryo germination. Seed coat dormancy involves the mechanical restriction of the seed coat. This, along with a low embryo growth potential, effectively produces seed dormancy. GA releases this dormancy by increasing the embryo growth potential, and/or weakening the seed coat so the radical of the seedling can break through the seed coat. Different types of seed coats can be made up of living or dead cells, and both types can be influenced by hormones; those composed of living cells are acted upon after seed formation, whereas the seed coats composed of dead cells can be influenced by hormones during the formation of the seed coat. ABA affects seed coat growth characteristics, including thickness, and effects the GA-mediated embryo growth potential. These conditions and effects occur during the formation of the seed, often in response to environmental conditions. Hormones also mediate endosperm dormancy: Endosperm in most seeds is composed of living tissue that can actively respond to hormones generated by the embryo. The endosperm often acts as a barrier to seed germination, playing a part in seed coat dormancy or in the germination process. Living cells respond to and also affect the ABA:GA ratio, and mediate cellular sensitivity; GA thus increases the embryo growth potential and can promote endosperm weakening. GA also affects both ABA-independent and ABA-inhibiting processes within the endosperm.

 \bigcirc

References

Else MA, Coupland D, Dutton L, Jackson MB (January 2001). "Decreased root hydraulic conductivity reduces leaf water potential, initiates stomatal closure, and slows leaf expansion in flooded plants of castor oil (Ricinus communis) despite diminished delivery of ABA from the roots to shoots in xylem sap". Physiologia Plantarum. 111 (1): 46–54. [doi](https://en.wikipedia.org/wiki/Digital_object_identifier)[:10.1034/j.1399-](https://doi.org/10.1034%2Fj.1399-3054.2001.1110107.x) [3054.2001.1110107.x.](https://doi.org/10.1034%2Fj.1399-3054.2001.1110107.x)

Feurtado JA, Ambrose SJ, Cutler AJ, Ross AR, Abrams SR, Kermode AR (February 2004). "Dormancy termination of western white pine (Pinus monticola Dougl. Ex D. Don) seeds is associated with changes in abscisic acid metabolism". Planta. 218 (4): 630–9. [doi:](https://en.wikipedia.org/wiki/Digital_object_identifier)[10.1007/s00425-003-1139-8.](https://doi.org/10.1007%2Fs00425-003-1139-8) [PMID](https://en.wikipedia.org/wiki/PubMed_Identifier) [14663585.](https://www.ncbi.nlm.nih.gov/pubmed/14663585)

Gerhard W (2000). ["Seed Dormancy".](http://www.seedbiology.de/dormancy.asp) *The Seed Biology Place*. Royal Holloway University of London.

Kermode AR (December 2005). "Role of Abscisic Acid in Seed Dormancy". J Plant Growth Regul. 24 (4): 319–344. [doi](https://en.wikipedia.org/wiki/Digital_object_identifier)[:10.1007/s00344-005-0110-2.](https://doi.org/10.1007%2Fs00344-005-0110-2)

Ren H, Gao Z, Chen L, Wei K, Liu J, Fan Y, Davies WJ, Jia W, Zhang J (2007). ["Dynamic](https://archive.is/20120710210532/http:/jexbot.oxfordjournals.org/cgi/pmidlookup?view=long&pmid=16982652) [analysis of ABA accumulation in relation to the rate of ABA catabolism in maize tissues under](https://archive.is/20120710210532/http:/jexbot.oxfordjournals.org/cgi/pmidlookup?view=long&pmid=16982652) [water deficit".](https://archive.is/20120710210532/http:/jexbot.oxfordjournals.org/cgi/pmidlookup?view=long&pmid=16982652) Journal of Experimental Botany. 58 (2): 211–9. [doi](https://en.wikipedia.org/wiki/Digital_object_identifier)[:10.1093/jxb/erl117.](https://doi.org/10.1093%2Fjxb%2Ferl117) [PMID](https://en.wikipedia.org/wiki/PubMed_Identifier) [16982652.](https://www.ncbi.nlm.nih.gov/pubmed/16982652) Archived from [the original](http://jexbot.oxfordjournals.org/cgi/pmidlookup?view=long&pmid=16982652) on 2012-07-10.

*Robert M. Devlin (1969)***:** plant physiology, university of Massachusetts. Second edition. Mineral nutrition part.

Wang Y, Liu C, Li K, Sun F, Hu H, Li X, et al. (August 2007). "Arabidopsis EIN2 modulates stress response through abscisic acid response pathway". *Plant Molecular Biology*. **64** (6): 633–44. [doi:](https://en.wikipedia.org/wiki/Digital_object_identifier)[10.1007/s11103-007-9182-7.](https://doi.org/10.1007%2Fs11103-007-9182-7) [PMID](https://en.wikipedia.org/wiki/PubMed_Identifier) [17533512.](https://www.ncbi.nlm.nih.gov/pubmed/17533512)

Yan J, Tsuichihara N, Etoh T, Iwai S (October 2007). "Reactive oxygen species and nitric oxide are involved in ABA inhibition of stomatal opening". Plant, Cell & Environment. 30 (10): 1320– 5. [doi:](https://en.wikipedia.org/wiki/Digital_object_identifier)[10.1111/j.1365-3040.2007.01711.xPMID](https://doi.org/10.1111%2Fj.1365-3040.2007.01711.x) [17727421.](https://www.ncbi.nlm.nih.gov/pubmed/17727421)