Learning unit 3: How plants colonised land

3.1 Introduction

To complete the learning unit, you will need to refer to pages 674–691 chapter 29 in Campbell et al. (2015)

Looking at a lush landscape, it is difficult to imagine the land without any plants or other organisms. For more than the first 3 billion years of Earth's history, the terrestrial surface was lifeless. Since colonising land, plants have diversified into approximately 290,000 living species. Plants have shown to have ability to inhibit all but the harshest environments, such as some mountaintop and desert areas and the polar ice sheets.

Take into consideration that we will refer to all plants as land plants, even those that are now aquatic, in order to distinguish them from algae, which are photosynthetic protists.

Land plants make it possible for other life-forms to survive on land. Plants supply oxygen during photosynthesis process and ultimately most of the food eaten by terrestrial animals. Moreover, plant roots create habitats for other organisms by stabilising the soil. The history of the plant kingdom is a story of adaptation and changing terrestrial conditions. In this learning unit, we are going to trace the first 100 million years of plant evolution, including the emergence of seedless plants such as mosses and ferns. This learning unit concentrates on the development of different groups of plants to live exclusively on land.

3.2 Learning outcomes

By the end of this learning unit you should be able to

• name and discuss the evolutionary adaptations to living on land characteristic of the four main groups of land plants

• distinguish between the main groups of land plants

• discuss derived characters unique to land plants

• name the characteristics common to land plants and charophycean algae

• describe the life cycle of mosses as well as the structure of their gametophyte and sporophyte generations

• describe the life cycle of ferns as well as the structure of their gametophyte and sporophyte generations

3.3 Evolutionary adaptations to terrestrial living and the phyla of extant plants

Recommended reading: pages 674–680 of chapter 29 in Campbell et al. (2015)

Land plants evolved from green algae

Charophyceans are the green algae most closely related to land plants. Land plants probably are probably derived from a group of green algae called charophytes. Land plants share with the charophyceans the following traits:

- Rosette cellulose-synthesizing complexes: land plants and charophyceans possess a rosette-shape array of proteins that synthesise cellulose microfibrils in their cell wall. Other cellulose wall-containing algae (e.g. brown algae, dinoflagellates), have linear arrays of cellulose-producing proteins. This suggests a common ancestor between the charophytes and land plants. This rosette synthesizing system evolved independently of the cellulose making system of other green algae.
- Peroxisomes enzymes: the charophyceans and land plants have enzymes in their peroxisomes that minimise the loss of carbohydrate due to photorespiration. Other alga groups do not have these enzymes in their peroxisomes.
- Structure of the flagellate sperm: details of the sperm of charophyceans resemble those of land plants that have flagellated sperms.
- Cell plate formation during cytokinesis: cell division features a complex network of microtubules and Golgi vesicles, the phragmoplast, again as found in all land plants.
- DNA and RNA sequences support their close relation to the charophytes, especially *Chara* and *Coleochaete*.

3.3.1 Terrestrial adaptation of land plants

A layer of sporopollenin protects charophytes from desiccation; sporopollenin is found in the spore wall of land plants. Danger of desiccation required new adaptations: transport tissue, cuticle, etc.

Support against gravity. Plants are eukaryotic, multicellular, mostly autotrophic organisms, with haploid-diploid life cycles, which retain embryo within female sex organ on parent plant; the cell wall contains cellulose. Scientists are studying the ultrastructure of cells, analysing macromolecules and comparing morphology with life cycles.

There are several proposals to rearrange the boundaries of the kingdom Plantae:

i) Only the **Embryophytes**; the present and traditional system.

ii) Expand it to include the charophyceans: Kingdom **Streptophyta**.

ii) Expand it further to include all the green algae, Chlorophyta: Kingdom **Viridiplantae**.

3.3.2 Derived traits of plants

The following characteristics are common to all four groups of land plants but are absent in the charophyceans.

ii. *Apical meristem*: cluster of embryonic cells found at the tip of shoots and roots.
iv. *Alternation of generations*: a characteristic life cycle. Alternation of generation does not occur in the charophyceans. This suggests that alternation of generation arose independently in land plants. A life cycle characterized by a multicellular haploid gametophyte stage followed by a multicellular diploid sporophyte stage.
vi. *Multicellular, dependent embryos*: The zygote is retained surrounded by tissues of the gametophyte. The parental tissue provides the embryo with nutrients. Placental transfer cells present in the embryo and sometimes in the gametophyte as well, enhance the transfer of nutrients.
viii. *Spores produced in sporangia*: haploid reproductive cells that become a multicellular haploid gametophyte by mitosis. The multicellular sporangium contains sporocytes, the cells that undergo meiosis to form spores. Sporopollenin, the most durable organic material known, makes the walls of the spores.
x. *Multicellular gametangia*: the gametes of land plants are produced in multicellular organs called gametangia. Algae produce their gametes in unicellular gametangia, inside a single cell.

Adaptations for water transport and conservation.

ii. Waxy cuticle to protect against desiccation.
iv. Stomata (sing. stoma) for gas exchange and control of transpiration.
vi. Transport system or vascular tissue

Secondary metabolic compounds

Land plants make many metabolic compounds that are produced by side branches off the primary metabolic pathways that make lipids, carbohydrates, proteins and other compounds common to all organisms. Cell wall contains lignin, a polymer, to strengthen and support upright structures. Other secondary compounds are alkaloids, tannins, and phenolics (flavonoids). These compounds functions as a protection against herbivores, absorb harmful UV radiation, and are involved in the symbiotic relationship with soil microbes.

3.3.3 Origin of land plants

About 475 million years ago, in the mid-Ordovician, plants were widespread all over the world as shown by the many spores found in sediments of this period.

In a relatively short time of about 50 million years, plant diversified abundantly and colonised many land areas. ***There are four main groups of land plants:***

(i) Bryophytes, including mosses. (ii) Pteridophytes, including ferns and seedless vascular plants. (ii) Gymnosperms, including conifers. (iv) Angiosperms including flowering plants.

Land plants are distinguished from algae by the *production of multicellular embryos* that remain attached to the mother plant, which protects and nourishes the embryos.

Bryophytes are distinguished from the other three groups of land plants by *the lack of a vascular tissue* made of special cells called xylem and phloem. Some bryophytes have water and nutrient transport system made of a different kind of cells.

Pteridophytes do not produce seeds. Gymnosperms and angiosperms produce seeds. A seed consists of a plant embryo with a food storing tissue and a surrounding coat for protection. The first vascular plants to produce seeds evolved about 360 million years ago. Their seeds were not enclosed in any specialized chamber.

Angiosperms produce flowers and conifers produce "cones", a specialized reproductive structure. Angiosperms produce their seeds in specialized chambers called ovaries. Gymnosperms do not produce seed in ovaries. The word grade is used to designate a collection of organisms that share a common level of biological organization or adaptation.

3.4 The gametophyte and sporophyte generations of the Bryophytes

Recommended reading: pages 680–684 of chapter 29 in Campbell et al. (2015)

There are about 17 000 species worldwide divided into three divisions or phyla: **Bryophyta**, the mosses; **Hepatophyta**, the liverworts; and **Anthocerophyta**, the hornworts. Their life cycle is similar but the three groups may not be closely related. The bryophytes may form a polyphyletic group. Bryophyta refers to the phylum of mosses only; bryophytes refer to the three phyla mentioned above.

Characteristics of the bryophytes:

ii. Small plants found in moist environments, lack woody tissue and usually form mats spread over the ground.
iv. Gametophyte generation is dominant; sporophyte is parasitic on the gametophyte.
vi. Bryophytes have cuticle, stomata and multicellular gametangia that allow them to survive on land.
viii. Bryophytes need water to reproduce and most species lack vascular tissue (xylem and phloem).
x. Water transport is mostly through capillary action, diffusion and cytoplasmic streaming. They lack true roots, stems and leaves.

The gametophyte of mosses is a one-cell-thick filament known as the protonema that eventually produces buds having meristematic tissue. These meristems produce an upright structure called the gametophore. These gametophytes are one to a few cells thick and obtain nutrients and water by direct absorption from the environment.

Most mosses do not have conducting tissue. Some species have specialized cells that conduct water and nutrients but lack lignin in their cell walls. The gametophores are anchored by fragile rhizoids. Rhizoids are either single elongated cells as those found in liverworts and hornworts, or filaments of cells as those of mosses. Rhizoids are not made of tissues and do not absorb any significant amount of water. In that way they differ from roots.

Bryophytes have smallest and simplest sporophyte of any group. The sporophyte remains attached to the gametophyte throughout its lifetime, dependent of the gametophyte for food, water and minerals. The mature sporophyte of mosses consists of a foot embedded in the archegonium, a seta or stalk is present in the phylum Bryophyta, and a capsule or sporangium. The cap or calyptra closes the peristome or opening or the capsule.

3.5 Origin of vascular plants - the gametophyte and sporophyte generation of the Pteridophytes

Recommended reading: pages 684–690 of chapter 29 in Campbell et al. (2015)

During the first 100 million years of plant evolution, bryophytes were prominent types of vegetation. But it is vascular plants that dominate most landscapes today. As in bryophytes, however, the sperm of ferns and all other seedless vascular plants are flagellated and swim through a film of water to reach eggs. In part because of these swimming sperm, seedless vascular plants today are most common in damp environments.

3.5.1 The origin of vascular plants

Ferns and other seedless vascular plants formed the first forests.

The next step in land plant evolution included the development of an independent sporophyte. At first this sporophyte was of equal size as the gametophyte. *Cooksonia caledonica*, from the Silurian (~420 million years ago) rocks of Europe and North America, is the oldest known land plant. Small, leafless, rootless, dichotomous axes with terminal sporangia.

Transport in xylem and phloem. Phloem for the transport of dissolved carbohydrates. Xylem for water and mineral transport. Lignin strengthens the vascular tissue cells.

Evolution of roots. Roots anchor plants and allow the absorption of water and nutrients from the soil. Root tissues of living plants closely resemble stem tissues of early vascular plants preserved in fossils. Roots may have evolved from the lowest subterranean parts of the stem. The oldest lycophyte fossil had simple roots 400 million years ago.

From an evolutionary perspective, there are two kinds of leaves: Microphylls are single veined leaves associated and evolved as superficial outgrowth of the stem. Microphylls first appear in the fossil record about 410 million years ago. Megaphylls have a complex venation pattern, and evolved from a branch system. Megaphylls appeared about 370 million years ago, at the end of the Devonian.

The sporophyte became the dominant generation. Sporophylls are modified leaves that bear spores. Sporophylls may be grouped into cone-like structures called strobili (sing. strobilus). Homospory: production of one kind of spores. Spores produce a bisexual gametophyte that produces eggs and sperms. Heterospory: production of two kinds of spores. Haploid megaspores develop into a female gametophyte. Haploid microspores develop into a male gametophyte.

3.5.2 Classification of seedless vascular plants

There are two phyla of pteridophytes found in the modern flora: Licophyta and Pterophyta.

(i) Phylum Lycophyta. There are about 15 genera of lycophytes and approximately 1000 living species. This phylum includes the *Lycopods* (club mosses), *Selaginella* (spike moss) and *Isoetes* (quillwort). This evolutionary line extends back into the Devonian (409-363 mya) but were most prevalent in the wet swamps of the Carboniferous period (363-290 mya). They eventually split up into two evolutionary lines.

The first were very large woody trees that did not survive in the drier climate at the end of and after the Carboniferous age. In the Carboniferous some lycophytes were forest-forming trees more than 35 meters tall. The second and the surviving group of *Lycopods* are the small and herbaceous trees. Lycophyta remains became the largest coal deposits of all geologic time. The sporophytes of lycophytes consist of true roots, stems and leaves (microphylls). Some *Selaginella* are heterosporous; *Lycopodium* is homosporous. Sporophylls are specialized leaves that bear sporangia and are organized into a structure called the strobilus (pl. strobili).

(ii) Phylum Pterophyta

Psilophytes (whisk ferns). It includes two living genera, *Psilotum* and *Tmesipteris*, from tropical and subtropical regions of the world. Sporophyte with a dichotomously branching aerial and subterranean stem system. True roots lacking. Underground stems with rhizoids and with a fungal association. Aerial stems lacking leaves but with scale-like or larger leaf-like structures (enations). Until recently they were placed in a phylum of their own, but DNA sequences analysis and sperm ultrastructure study has shown that they are related to present day fern. The lack of roots and leaves may be due to simplification, a derived or secondary characteristic, rather than a maintained characteristic from ancient ancestors, a primitive characteristic.

Sphenophytes (Horsetails). Sphenopsids extend back to the Devonian (409-363 mya) and reached their maximum development in the Carboniferous (363-290 mya). A family of one extant genus, *Equisetum* (ca. 15 species), of nearly worldwide distribution in damp habitats such as riverbanks, lakeshores, and marshes. Michigan is a centre of diversity for the genus with nine native species.

The sporophyte of *Equisetum* is differentiated into an underground rhizome that bears adventitious roots and an upright, photosynthetic stem with whorls of microphylls. Tough perennial herbs with jointed, ridged aerial stems with distinct nodes. Stems rough, accumulating silica and metals, and complex anatomically. The aerial stems contain a large central pith region, which in mature plants is hollow. Surrounding the pith cavity are discrete bundles of vascular tissue; this arrangement of conducting tissue is known as a eustele. Recent molecular data suggest that they are closely related to ferns and should be classified with them.

“True” ferns. The fossil record of ferns extends back into the Carboniferous (363-290 mya) but their origins is in the Devonian (409-363 mya). There are about 12,000 species of ferns in the world. Most species are tropical. Sporophyte is differentiated into true roots, stem (rhizome) and leaves (megaphylls). Leaves usually differentiated into Stipe (petiole) and blade with a central rachis or vein. Most ferns are homosporous; a few aquatic genera are heterosporous. The sporangia are produced in clusters called sori (sing. sorus.) the sori can be arranged in various patterns, e. g. rows or lines.

3.5.3 The significance of seedless vascular plants

The Lycophyta and Pterophyta represent the modern lineages of seedless vascular plants that formed forests during the Carboniferous period about 290-363 million years ago. The coal beds, oil fields and natural gas deposits that are mined in modern times are derived from these ancient forests. From there comes the name fossil fuels. During the Carboniferous Europe and North America were closer to the equator and covered with extensive swamps. As plants died, their body did not completely decay in the stagnant water and great depths of organic material accumulated forming peat.

3.6 Activity 3.1

Do this activity and add it to your portfolio.

Refer to your textbook and answer the following questions:

b. Which group of algae is believed to be the ancestors of land plants?
d. How are spores dispersed?
f. How do mosses absorb water? How is it distributed?
h. Like the Bryophyta, ferns are most common in damp environments. What feature of their reproduction requires them to live in a moist habitat?
j. Ferns are vascular plants. Why can vascular plants grow to be very tall, but nonvascular plants?

3.7 Feedback on activity 3.1

Feedback on activity 3.1

a) Charophytes which are a lineage of green algae.

Try to answer the remaining questions (from b to e) on your own.

3.8 Summary

Evolutionary adaptations to terrestrial living characterize the four main groups of land plants. Charophyceans are the green algae most closely related to land plants. Several terrestrial adaptations distinguish land plants from charophycean algae. Land plants evolved from charophycean algae over 500 million years ago.

The three phyla of bryophytes are mosses, liverworts and hornworts. The gametophyte is the dominant generation in the life cycles of bryophytes. Bryophyte sporophytes disperse enormous numbers of spores. Bryophytes provide many ecological and economic benefits.

Additional terrestrial adaptations evolved as vascular plants descended from moss-like ancestors. A diversity of vascular plants evolved over 400 million years ago. Pteridophytes provide clues to the evolution of roots and leaves. A sporophyte-dominant life cycle evolved in seedless vascular plants. Lycophyta and Pterophyta are the two phyla of modern seedless vascular plants. Seedless vascular plants formed vast "coal forests" during the Carboniferous period.