Some Distance from the Sun
Commentary for an Installation

A traveller should be a botanist, for on every hand plants form the chiefest vista.

Charles Darwin

Plants are not legless animals

Plants and animals present us with two methods for sustaining life on our planet. A typical animal is equipped with the means to move about and explore its environment. In this way it can search for food and mates, and avoid being caught by predators. The animal's food is chemically complex organic matter in the form of parts of plants or other animals. This is a more-or-less concentrated source of the energy and materials required to build and maintain the organism. By contrast a typical plant needs only simple inorganic material: carbon and nitrogen from the earth's atmosphere and a few salts dissolved in water that has been in contact with the minerals of the earth's crust. The plant also needs sunlight as a form of energy that can be trapped by the process of photosynthesis. This is the basic chemistry that drives most of our living systems. Light at the red and blue ends of the visible spectrum is absorbed by one of the green pigments we call chlorophyll; and the chemical energy thus made available is fixed, initially in the form of carbohydrate, by combining water with bicarbonate derived more-or-less directly from atmospheric carbon dioxide, CO_2. The process involves the splitting of the water molecule H_2O with the release of oxygen.

Photosynthesis is therefore also vital in maintaining the large reservoir of oxygen in the atmosphere which enables organisms to respire. Respiration is the process by which most organisms release the chemical energy that powers all their living processes.

Animals typically forage: they move about in search of items of food. In them evolution has tended to produce a compact body with a discernible front end where the mouth and many of the sensory organs are located. Sensory information is processed by a brain, often also near the front, to direct purposeful movement. The resources for plant life are not concentrated but dispersed in the environment. Plants tend to absorb them over a large part of their surface area so evolution has tended to produce a body form that is diffuse and without front-rear orientation. Such a body form is poorly adapted to purposeful movement so the typical plant spends most of its life anchored in one place and intercepts resources by means of outgrowths that occupy space. This contrast with animals is fundamental and profound. It confronts plants with challenging problems of reproduction and dispersal that have been solved in ways not seen in the animal kingdom. Because we are animals we find it harder to understand the nature of plants. They are so different from ourselves as almost to seem like alien invaders of our planet, yet without them life would be impossible.

Oceanic botany

The simplest plants are algae comprising single cells or groups of cells loosely attached as chains, nets or other geometrical arrays. These microscopic forms live in greatest variety in the sea, habitat of the earliest living organisms. Many bear flagella: minute hair-like organs that can move in corkscrew fashion to propel the cell through its watery medium. Thus the flagellates, as they are called, do not simply drift with the movements of the water round about, or sink to the unlit depths. Motility enables them to remain in the surface water where sunlight can penetrate and photosynthesis is possible. As it proceeds dissolved salts are absorbed by the cells but their swimming motion propels them towards fresh supplies. These plants are far too small to be shown here.

Seaweeds

The simplest plants visible to the naked eye are also mostly found in the sea. These are the seaweeds and are also called algae. They are generally found anchored to rock surfaces in shallow water at or near the shore. A seaweed comprises numerous cells that are strongly attached to each other and to the supporting surface. Strength allows them to withstand the forces of wave action that pull and toss the plants; but the

water currents also constantly renew the supply of mineral salts, which can thus be absorbed more efficiently than by free-floating single-celled flagellates. This makes possible a complex body in which only the outermost layer of cells need be in direct contact with the water. Cells can also become specialised: some for photosynthesis, others for moving its products to shaded parts of the plant, and some for strengthening the structure to withstand the enormous forces of breaking waves in stormy weather.

These anchored seaweeds have special mechanisms to reproduce and spread. Cells near the surface of the plant body transform their contents into minute units that look like some of the single-celled flagellates and can travel in water currents to new sites for colonisation. Some of these units are called zoospores: asexual cells able to attach themselves to rocks or adult seaweeds and grow into new plants. Others are male and female gametes that must fuse to form a zygote before becoming anchored. Many of the seaweeds have a life cycle of two alternating phases: one producing zoospores and called the sporophyte phase; the other called the gametophyte phase and producing gametes. In some species the two phases appear virtually identical; in others they differ greatly in size and form.

Seaweeds show a great variety of form and complexity. The simplest have their cells arranged in branching filaments or else in sheets formed into tubes or lettuce-like fronds. In the most complex, one can distinguish a stem-like structure that carries a frond at its apex and has a base which is specialised for attachment by branches resembling roots. However these holdfasts do not penetrate the supporting rock surface, for unlike land-living plants the seaweeds can absorb their nutrients directly from seawater all over their surface. We find a similar range of form among plants that are either green, or dark red, or else predominantly brown (but the yellow-green algae are microscopic and less varied). The colours of the red, brown and yellow-green algae are caused by pigments associated with their chlorophyll. They are linked with profound differences in the biochemistry of the four types of plant which show that they are distinct lines of evolutionary descent. It is among the brown seaweeds that we find most of the more complex plants with many layers of cells and clear division of the plant into root-like, stem-like and frond-like parts. Although this reminds us of the roots, stems and leaves of land-living plants, we cannot suppose that these brown wracks and kelps could have emerged successfully onto dry land, for it is with the green seaweeds only that land plants share fundamental features of their biochemistry.

Invading the dry land

Colonisation of the land by plants was a defining event in the history of the Earth. It occurred during the Silurian: a geological period that came to an end about 400 million years ago. Some of the fossil plants from this period bore stomata. These are the tiny pores through which the leaves of today's land plants exchange gases with the surrounding atmosphere during photosynthesis, taking in CO_2 and giving off oxygen.

Beneath the microscope a stoma is a distinctive object because the pore through which the tissue inside the leaf communicates with the open air is surrounded by a pair of guard cells whose movements open and close the aperture. Water is essential for photosynthesis but the physics of gas exchange at the cell surfaces inside the leaf means that it evaporates while CO_2 enters and oxygen leaves. In the sea, water is not in short supply, but its availability greatly limits the potential for plant life on land. The guard-cell mechanism controls the rate of water loss, so the presence of these structures in a fossil label it as the remains of a land plant.

Not all extant land plants have stomata but without them adaptation to the land environment is incomplete. The mosses and liverworts are familiar groups of plants that are widespread despite this constraint, but limited in their size and in the range of habitats they can occupy. They are most abundant in damp habitats such as peat bogs and woodlands where a lack of control over moisture loss is less significant.

All land plants have inherited from their marine ancestors life cycles with alternating gametophyte and sporophyte phases. In mosses and liverworts what we think of as "the plant" is the gametophyte phase and this is the dominant episode in the life of these organisms. It takes the form of a forking seaweed-like strap of photosynthetic tissue or a branching system of shoots covered with phylloids. These are minute structures arranged rather like leaves but for the most part comprising a sheet of tissue one cell thick and thus without

the highly organised internal cellular structure we find in true leaves. There are no roots. Instead the gametophytes are fixed in place by short hair-like rhizoids which absorb moisture, but only from the soil surface.

As in seaweeds the male gametes of these plants have flagella and swim in water, which is another cause of their dependence on dampness. Fusion of male and female gametes from the gametophytes gives rise to a zygote that develops into an embryonic sporophyte. In mosses and liverworts this phase remains attached to the gametophyte on which it depends for anchorage, water and (in sporophytes lacking chlorophyll) for the products of photosynthesis. In most cases the adult sporophyte comprises an un-branched stalk with a bulbous base embedded in the gametophyte, and an expanded capsule, the sporangium, at its apex. Sometimes the sporangium is photosynthetic, with green internal tissues linked to the atmosphere through stomata. Fertile tissue in the capsule gives rise to spores. These are minute cells surrounded by a highly resistant coat of sporopollenin: a characteristic feature of all land plants that is readily fossilised. Structures and mechanisms in the capsule cause the ripened spores to be released into dry air where they may be carried long distances by wind, achieving dispersal if they land where there is enough moisture for them to germinate and develop into a new gametophyte.

Plant-like but not plants

The fungi are generally thought of as saprophytes (organisms that live by absorbing dead organic matter) or as parasites. Although plant-like in features of their growth and dispersal they do not photosynthesise and are regarded as a separate kingdom equivalent to plants and animals. For green plants on land they are important in two ways.

First numerous kinds of fungi are symbiotic with algae, the association being what we call a lichen. These composite organisms are stable, tough, long-lived, and with distinct body forms and chemical characteristics. Of the two components the alga provides energy and organic materials from its photosynthesis while the fungus provides the alga with mineral salts, anchorage, some protection from desiccation and an extended structure within which to operate. Lichen habitats include the bark and branches of trees, various man-made objects and bare rock surfaces. Some lichens even live just below the rock surface (rocks being translucent in thin layers), and in this way they survive some of the harshest conditions found anywhere on the Earth's surface.

Secondly, for their exploitation of the resources of the soil many land plants depend on symbiotic associations between their roots and fungi. Many toadstools are involved in this way with forest trees, for instance, and the arrangement is so important for the life of land plants as to be given the special name of mycorrhiza. As in the lichens the green plant nourishes the fungus enabling it to permeate the soil with a dense weft of minute threads called hyphae. These absorb water and mineral nutrients, including some nutrients that are not readily mobilised in other ways. Since a large volume of soil can be exploited by a small volume of living tissue the mycorrhizas provide an efficient mechanism for gathering resources.

Doing it properly: ferns and their allies

Fossils show that the green land plants became increasingly elaborate during the Devonian period and by the Upper Carboniferous, which came to an end about 300 million years ago, forests of tall trees covered the humid tropical regions of the Earth. Those trees, many preserved in coal deposits, have since become extinct but allied forms are still found living. Many belong to the pteridophytes: a diverse set of plant groups that seem not to be closely related but have similar life cycles. By contrast to the mosses and liverworts, in these plants it is the sporophyte phase that dominates and is called "the plant". In the ferns, for instance, this is the phase that bears the elaborate compound leaves known as fronds. Most of the pteridophytes are anchored by roots that are also involved in absorbing water and minerals from deep in the soil. Roots and foliage are connected through the intervening stem by a tract of vascular tissue, the xylem, whose elongated cells provide a ready pathway for replenishing the water evaporated from the leaves during photosynthesis. This water-conducting xylem is visible microscopically in fossils; together with stomata and spores it is part of the signature of a land plant.

As well as ferns with complex feather-like fronds that expand by uncurling, the pteridophytes include clubmosses, horsetails quillworts and *Psilotum*, with sporophytes in which the leaves are reduced to scales. In many pteridophytes the sporangia are closely associated with the leaves. The fronds of ferns typically bear groups of sporangia that appear as brown patches on the lower surface. On ripening they release clouds of spores that can germinate on damp surfaces to form an inconspicuous gametophyte. This is the

sexual phase of the life cycle, producing male gametes that swim in water films to fertilise the egg cell (female gamete); and from the resulting embryo there develops a new sporophyte. In other pteridophytes, especially some aquatic or marsh-dwelling forms, spores of two kinds are produced. Some are small and numerous and give rise to male gametophytes; others are large, few in number and form female gametophytes only. Thus sex becomes a property of the sporophyte phase and the function of the spores is fertilisation rather than dispersal, reducing reliance on male gametes swimming in films of water.

Trees short and thick; trees tall and thin: the gymnosperms

Many living pteridophytes are herbs although the tree ferns remind us of their loftier fossil ancestors. By contrast the gymnosperms are almost all tree-like in their growth habit. Some of them attain great size and age, their elaborately branching trunks made possible by the mechanical properties of wood, evolution's response to life in a medium offering little buoyancy but much turbulence. Wood is the water-transporting xylem accumulated year-by-year as the thickening trunk or branch lays down a further layer that appears as one of a series of concentric annual rings. These are revealed when the structure is sliced across and are most clearly developed when the tree's growth is regulated by a seasonal climate. The surface of the trunk is covered by a layer of cork. This is the bark that protects the tree from water loss and attack by fungi and other parasites. Beneath it is a very delicate tissue in which cell division generates new xylem inwards and new cork outwards. This is a vigorous metabolic process driven by respiration, with oxygen and CO_2 being exchanged with the atmosphere through perforations in the bark called lenticels. As the xylem grows the cork splits to accommodate the trunk's increasing thickness. The outermost and oldest layers of cork fall off and the remaining pattern of lenticals and crevices gives the bark an appearance that is typical of the species of tree .

Most plants have an elongated branching structure that exposes the largest possible surface to the environment supplying them with light. In land plants this habit is developed by a mechanism that depends on the properties of the growing cells. In these there is a central vacuole that absorbs water by osmosis, generating a powerful hydrostatic pressure that would burst the cell were it not enclosed by a strong wall of cellulose. During growth the cell walls stretch in response to the internal pressure, but not uniformly. In shoots, for example, it is only the longitudinal walls that are sufficiently plastic to respond, so the structure enlarges by elongation rather than by swelling in all directions. Amongst animals there is no counterpart to the cell wall or the vacuole-cell-wall mechanism of growth. This appears to be a property fundamental to plants, as organisms that exploit the resources of their environment by growing a diffuse structure into it from a fixed anchorage, rather than by moving purposefully about hunting for food: a foraging process that demands a compact structure.

Shoots, branches and the leaves they bear originate in buds. Cell division in these produces an embryonic shoot in which all the organs appear telescoped, often within a protective envelope of scales. Water absorbed by osmosis then causes the shoot to elongate and the leaves to expand. When the process is complete we find the leaves attached to nodes that became separated as the intervening internodes elongated. In this way the lower leaves escape becoming shaded by those above. Each node generally bears another bud at the base of every leaf: a bud with the potential to form a new branch. The development of these lateral buds is controlled by hormones generated in the bud at the shoot apex. These prevent development until the apex has been carried aloft by a sufficient distance to prevent leaves on the new branch becoming too shaded by those on the main shoot. Large apical buds produce enough hormone to suppress side branches completely. Such buds are found in the cycads where they give rise to a crown of fronds resembling those of ferns, except that they are hard, leathery and long-lived. Cycad trunks are relatively thick and short, with few or no side branches thanks to the large apical bud. This is a growth habit seen also in palms and pawpaws: large-leaved trees that seem strange to those of us unfamiliar with tropical vegetation.

In the more familiar small-leaved gymnosperms the buds are much smaller and regular branching is the rule. With few exceptions their leaves are narrow and more-or-less needle-shaped or else reduced to scale-like appendages. The conifers are the largest group of living gymnosperms. Their female gametophytes are retained in the cones of the sporophyte phase, and only the small spores that give rise to male gametophytes are liberated and spread by wind. These spores are the yellow dust we call pollen; and in

pine and fir for instance, they are released in vast quantity in late spring by specialised male cones that are nconspicuous and soon fall off the tree. The more familiar female cones emerge soft and herbaceous but then become woody structures lasting several years, during which reproduction proceeds at a leisurely pace. An egg cell is first fertilised by a male gamete from a pollen grain. The sporophytic tissues of the female cone then provide the zygote and embryo with an energy-rich food supply called the endosperm, and with a protective integument. To this is attached an aerofoil. This complex structure is termed a seed and is a better protection for the tree's reproductive investment than the much simpler fern spore. When the seed is finally released the aerofoil helps dispersal by breaking the seed's fall, so that wind currents are more likely to carry it away from the parent tree to a site where germination can occur and the new plant can become established using the food reserves of the endosperm.

Flowers, fruits and modules

The angiosperms (flowering plants) are the final stage of land-plant evolution. They appear rather suddenly in the fossil record during the Cretaceous period that began about 150 million years ago. They include trees, which are especially diverse in the humid tropics, as well as herbaceous plants that are more typical of higher latitudes. These share their bark and trunk structure with the gymnosperms, though with more efficient water-conducting cells in the xylem. They show a great range of adaptation to different habitats, including the succulents and short-lived annuals of dry deserts, the bulbous perennials of alpine meadows, the helophytes of bogs and marshes, the insectivorous plants of habitats where minerals are in short supply, hydrophytes in lakes and streams, and the sea grasses that have become re-adapted to shallow marine habitats. They also show interesting adaptations enabling them to retain water, discourage grazing, fix atmospheric nitrogen, survive without soil on tree branches, trap and digest insects as a source of mineral salts, and parasitise other plants or climb up them. They are the main source of food for terrestrial animals including humans and their livestock. They synthesise a far greater range of complex chemical compounds than any other group of organisms and were the main source of medicines until the late 19th Century. Their leaves show a great variety of colour, form and mode of development. Some grow from the base and have parallel veins like those of grasses. Some are delicate and are shed in the hostile season while others are thick and leathery, and persist for several years; and yet others have shapes adapted to disperse rainwater quickly or promote rapid gas exchange in still air.

Some of these adaptations are foreshadowed in the pteridophytes and to some extent also in the gymnosperms. But it is to two properties that the angiosperms owe much of their evolutionary success.

First the hormonal control of bud development has become the basis of a highly flexible system of responses to external stimuli. Most gymnosperms die back when too much top growth is cut off, as we frequently see in badly maintained suburban cypress hedges; and a felled conifer does not re-sprout from the stump. In angiosperms the response is often quite different. Gardeners use pruning as a means of rejuvenating flowering plants of many kinds, including trees such as hawthorn and beech when used for hedging. Coppicing is a traditional way of managing broad-leaved woodlands by cutting them over at intervals and allowing new shoots to regenerate from the stumps. Grasses react to grazing or mowing by new growth at the base that creates a sward tough enough to withstand ball games or trampling by livestock. These are all responses to interrupting the supply of bud-suppressing hormones when the shoot apex and its dominant bud are removed. Unlike most animals, plants show a modular structure in which growth is accomplished by the addition of indefinite numbers of new organs (roots, stems, leaves and reproductive structures) that resemble those already formed. This feature, first seen among the larger seaweeds, confers great ecological advantage on the flowering plants which recover readily when damaged and can reproduce even when a stressful environment stunts their growth.

Secondly the flower, an incompletely expanded bud-like organ, is a far more efficient means of reproduction than the cone. There are several reasons for this. While some angiosperms are wind-pollinated the flower seems to have evolved primarily to enable insects (and other flying animals) to transfer pollen between plants in less wasteful ways than by wind. The sweet nectars, attractive scents and conspicuous petals of flowers provide guiding mechanisms for this. Seed production can follow pollination very rapidly: in days or weeks rather than the years taken by many gymnosperms. Seeds are formed inside an ovary that becomes a fruit; and fruits display a bewildering variety of adaptations to dispersal. They may be carried about inside or outside animals, blown about by the wind often over long distances, or else they may squirt or catapult

away the seeds they contain. Moreover the chances of successful germination and establishment are increased by mechanisms involving dormancy and responses to varying light and temperature that are located in the complex structure of the integument (the seed coat).
Conquest of the land by plants has made possible most of the life that surrounds us. Yet in their nutrition, their manner of growth and in the remarkable story of their reproduction they seem for ever strange to us despite the ubiquitous vista they create.

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