

Plant Behaviour and Intelligence

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Preface

This book takes as its theme the statement by the Nobel prize winning botanist Barbara McClintock in 1984; 'a goal for the future would be to determine the extent of knowledge the cell has of itself and how it uses that knowledge in a thoughtful manner when challenged'. The response to 'challenge' is behaviour and 'thoughtful' responses are intelligent behaviour. Thus, the title of this book is Plant Behaviour and Intelligence. The knowledge cells have of themselves derives from the complex self-organizing system that constructs the cell from its constituent molecules and directly implies self-recognition. There is a further issue less well recognized—intelligent behaviour is inextricably linked to fitness. This issue is largely overlooked by all who either discuss intelligence or behaviour.

This book in 26 chapters fleshes out McClintock's superb insight in the cells and organisms to which she was referring, plant cells and plant organisms. It describes the elements and processes that bring cells to life, their origin four billion years back, and why they became multicellular to form recognizable higher plants. Behaviour some of it surprising is shown to require integration through the cambium. A further chapter highlights how leaves control their internal temperature homeostat. The analogous organizational and behavioural properties between social insect colonies (swarm intelligence) and large plants are described. Furthermore, how plant roots adjust their sensing systems to deal with

different predominant signals, and are able to self-recognize forms three critical chapters. Games that plants play are critically assessed. The phenomenon of intelligence is illustrated with a detailed discussion and reference to the numerous descriptions from those informed scientists that have spent time examining the question. Brains are not needed for intelligent behaviour and reflex behaviour is rejected. Intelligent genomes and intelligent foraging are outlined. Finally, in the context of McClintock's 'thoughtful', the vexed question of consciousness is discussed and in that context J. C. Bose's 'plant nervous system' receives its rightful recognition. Throughout the important issue of fitness is raised.

This book represents a suitable introduction for those who have an interest in the rapid developing areas of plant behaviour. Although some of the material is technical and molecular this has been kept to a minimum in favour of whole plant behaviour. Some overlap in idea and content between chapters is inevitable, but I have tried always to ensure that chapters can be read independently of others and that necessitates small amounts of occasional repetition for those that read right through. Much of the described material is fully referenced for those that seek to investigate further. For a more general readership, many of these chapters should be comprehensible and convey to them the excitement that encompasses our increasing understanding of Mc-Clintock's imaginative insight.

Foreword

The force that through the green fuse drives the flower.

(Dylan Thomas, 1952)

An author's justification for the organism

This book is concerned with behaviour and intelligence, but in plants, not animals and that makes it unusual. In this day and age, scientists are constantly required to justify what they research and, in this foreword, I have put some of the reasons that justify research on this group of organisms, rather than give personal reasons for the book, which come later in Chapter 1. It is my hope that, on reading this foreword, it will encourage the reader to delve further into other parts of the book.

Earth is a planet dominated by plants, a self-evident statement on any trip into the countryside. It is also the case that the words that describe some of our major ecosystems such as tundra, rainforest, prairie, etc., refer to the dominant plant life that characterizes such regions. Photosynthesis is responsible for the current composition and substantive presence of oxygen, a highly reactive gas, make this dominance very clear. It is one of those niceties of life that we require the oxygen that plants produce and they in turn require the carbon dioxide that we exhale.

One of the reasons that a Martian, if there were such, might conclude the possibility of life on earth is the potential greening of parts of the planet with the change in the seasons. He/she might also observe that with such a reactive gas, as oxygen, in the atmosphere that there must be an abundance of life on earth to produce it. By the same token, Professor James Lovelock FRS concluded that there was no life on Mars because its atmosphere was at chemical equilibrium. However, there are other more

common reasons that account for the popularity of plant life with the public.

Plants are some of the most beautiful objects

'From fairest creatures we desire increase, that thereby beauty's rose might never die'. Many green plants and flowers have particular effects on our emotions as William Shakespeare (sonnet 1), the author of this quotation, was well aware. If it is beauty in biology we are looking for, then flowers must rank as some of the most beautiful objects on this planet. Burns compared his love 'to a red, red rose that's newly sprung in June'. The similar thrill generated by a perfect flower is surely familiar to many. Perhaps it is no accident that Van Gogh's 'Sunflowers' is currently one of the world's most highly priced paintings. Members of the orchid family come, in my mind, closest to perfection in beauty. Many orchids excite collectors and public alike, and rare orchids rank as some of the most expensive and sought after plants in the world by collectors. Expect to pay up to £100,000 for a particularly rare specimen. Surely orchids can equal some of the most beautiful pictures that artists have painted. I have been fortunate enough to attend two exhibitions of flowering orchids, one in Germany (Minau) and the other in Scotland. The enormous variety of shapes and colours is almost overpowering.

However, others will have different reasons; 'Beauty is bought by judgement of the eye'. Shake-speare again, as accurate as ever in *Loves Labours Lost*. Beautiful objects do have an extraordinary

calming effect and with flowers being natural objects, the pleasure is greatly increased. Surely, this is the reason that we inundate those in hospital with flowers or decorate those that have died.

Biophilia is another reason

Many find enormous satisfaction to be gained from digging the soil—to nurturing plants from seed to flower, all the way to designing a garden. Certainly in the UK, this has become a tremendous industry and its popularity speaks of something quite basic in the human condition. Biophilia is a term coined by E. O. Wilson (1984) to describe the bond, the obvious kinship, between ourselves and other organisms. Orians (1980) has gone further and suggested that, in gardens and outdoor properties of all kinds, mankind attempts to construct a psychologically-satisfying environment that mimics the savannah with its open grassland, clumps of trees, and small areas of water. The evidence that early hominids evolved in such environments is quite strong and the implication is that this environment over millions of years became hard-wired into the brain. Carl Gustav Jung would have referred to this phenomenon as an aspect of the collective unconscious.

The evidence for this satisfying effect of plants has strong psychological support. Across different cultures there is a strong preference for natural over urban environments (Parsons 1991). Patients exposed to natural surroundings exhibit a much more rapid recovery with reduced dependence on drugs and better clinical assessment, than those who are not so exposed (Ulrich 1984, 1999; Franklin, 2012). The known effects of gardens on health, and direct measurements of brain alpha waves and EEGs indicate strong reductions of stress when looking at plants compared to other situations (Ulrich 2002).

The history of gardens seems lost in the mists of time. When did present mankind actually start to till the soil for purely decorative purposes, rather than food? The Hanging Gardens of Babylon and those in ancient Egypt, which can be seen carved on the walls of various temples and structures, speaks of a long history of biophilia.

Agriculture is the means whereby the hunter-gatherer changed his nomadic way of life to pastoral food collection, to living in villages and cities. Plants predominate in present-day agriculture, cereals and vegetables being the basis of most human diets. From slow beginnings, arable farming presently uses more than one billion hectares world-wide; about one-tenth of the earth's land surface. Crop production itself probably occupies at least half of mankind in one way or another. Could an early affinity with growing useful and highly decorative plants have been the first steps in crop domestication? The supposition has always been that food was the prime reason for domestication, but perhaps it was the other way round. We now know that early mankind decorated him/herself with simple ornaments and necklaces. Could flowers, although ephemeral, also have been used?

Trees excite a different kind of appreciation and are beautiful in an alternate way. Although many are enormous, compared with ourselves, they are completely benign. Again, trees are intimately involved in mankind's early history, providing wood as fuel, construction, and useful chemicals. The mature, deciduous trees of temperate climates or some of the splendid cedars, easily excite widespread admiration. My first visit to the Giant Redwoods and Sequoia dendrons of California induced in me an extraordinary feeling of rapture and awe similar to that of Darwin on his notable world-encompassing voyage when he first encountered the tropical forest; 'wonder, astonishment, and sublime devotion fill and elevate the mind'. Because of the high canopy, giant redwood forests are extraordinarily still and peaceful. Sound travels a considerable distance in these forests, no doubt reflected from the high canopy. These forests are one of the seven natural wonders of the world that everyone should visit. The sheer size of these trees dwarfs the observer; what is man, indeed, compared with trees and mountains?

Greater still is what goes on underground and unseen. The massive root system that anchors such enormous leviathans. The frenetic activity that drives water and minerals to the highest shoots a hundred metres up. 'The force that through the green fuse drives the flower . . . drives my red blood', Dylan Thomas (1952) echoing a common poetic sentiment of the oneness of nature, but with insight seeing a common thread to animals and

plants. Although not seen, the growing root system is in a remarkably dynamic state. Sensing mechanisms operate that enable accurate navigation of the soil mosaic. Soil organisms, pockets of water and minerals, soil characteristics and crumb structure, pockets of gases, soil chemicals, and stones are all recognized, and action taken to exploit or avoid.

In temperate climates, plants accurately mark the seasons. 'A thousand branches flowering in due rotation, each has his season coming early or late but to all alike the fertile soil is kind; the red flowers hang like a heavy mist, the white flowers gleam like a fall of snow' Pang chu-I (819, translation published 1961).

Even sleep movements are recorded 'Now sleeps the crimson petal, now the white . . . Now folds the lily all her sweetness up' (Tennyson 1949). Flora Poetica contains many examples.

Many plant biologists find fascination in uncovering the hidden beauty that underpins plant life. It is obvious reading Keller's book on Barbara McClintock, who gained the Nobel Prize for plant transposons that she shared many of these sentiments—a love of life and an embrace of the natural world, but more on her views later. Plants in general enable that easy embrace where, in many respects, many animals do not. Elephants, tarantulas, and lions excite our attention but usually only at a distance, or on film, or behind bars.

Practical reasons for investigating plant life

There are, of course, practical reasons for science to investigate the plant world that are equally crucial. Could we have evolved without the services that plants provide? The green forests and the great expanse of oceanic plankton of the world act as its lungs. The origin of the use of wood in all sorts of human activities (houses, furniture, etc.), again, is lost in the mists of time, but the use in house construction is still a dominant feature. Plants supply a multiplicity of basic foods and nutritional/medicinal chemicals and fibres for paper and clothes. Plants are the basis of all food chains. The *Dictionary*

of Useful Plants (Coon, 1974) lists 20,000 species out of about 300,000. Plants are inextricably linked with our survival.

So the justification for a book on plant behaviour finds its basis in an effective love of the organism. Plant behaviour is an enormous topic. Laboratory behaviour or physiology has, in the past, required 20 volumes to cover knowledge. Thus, this book contains merely subjects that interest me and I hope the reader, too. There are 26 chapters in this book, all of them relatively short and it is a book for dipping into, rather than reading through. The chapters describe the things that interest me—some are technical and may require some background knowledge, but the general reader will find plenty to get into. If nothing else it should increase respect for the organisms that are so much the unrecognized staff of life.

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A feeling for the organism

A goal for the future would be to determine the extent of knowledge the cell has of itself and how it uses that knowledge in a thoughtful manner when challenged.

(McClintock 1984)

Summary

This chapter starts with a brief introduction to Barbara McClintock's insights into cell behaviour, including her famous statement about cellular knowledge given above, which forms part of the basis for this book. It considers some of her insights into plant behaviour and describes my own reasons for writing this book. The basic problem with plant behaviour is its difficulty in general detection. The description of what is meant by the term 'plant', frequently used in this book, is described and justification given for using a dicot as an exemplar. The variety of types of plant in the plant kingdom are included, particularly those without roots, without a vegetative stem or leaves. The major tissues are indicated to provide a necessary background for the general reader. Finally, the problems of using domesticated plants for experimental purposes are raised since domestication usually involves elimination of numerous behaviours.

Introduction

This book is about plant behaviour and intelligence, terms rarely put together in a knowledgeable way. Behaviour is best described as what plants do and intelligence as a capacity for problem solving. I will justify those definitions of behaviour and intelligence in greater detail later, but accept them for the moment. To many, the notion that plants do anything at all is faintly ludicrous-are they not prime examples of still life or sculpture? However, the fact is that plants do many things and, for those plants in natural circumstances, there are plenty of problems to solve. To the extent that we come to understand the behaviour of all plants better, we will place a greater value on them and, in turn, on ourselves. A better and healthier perspective is gained of our position here on this earth and a more

realistic assessment of our position in this extraordinary universe. 'Respect yourself first and then all that surrounds you' is a Navaho precept that I believe in and underpins this text. We live on a planet dominated by plants and, hopefully, this book will indicate why respect should be shown to many members of the plant kingdom, but remembering all the time, 'respect yourself first'. I have to state that at the beginning, because some may misinterpret notions of plant intelligence to try and justify placing plants as necessitating a legal protection accorded to higher mammals.

My own commitment to plant biology

Occasionally, someone raises the question as to where you were when some dramatic or apocalyptic event happened. I can certainly recall where

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I was when I heard of President Kennedy's assassination, or when Armstrong put his foot on the moon. However, with less certainty of the precise date, I can identify what made me a plant biologist. My own entry into the plant world was determined by a superlative botanical teacher at school. Common enough reason, I can hear the reader say. Teachers often do not know the long-term effects of their teaching and in my case this teacher left as I was finishing my A levels. When young you are often too gauche to express your thanks and provide the appropriate plaudits that teachers need.

However it came about, my eyes were opened to the fascinating, but often still mysterious subjects of plant morphology, ecology, physiology, biochemistry, and everything plant-like. I can still recall the feeling of intense excitement in 1955 when joining the upper school that I was finally allowed to open the locked cupboard and to examine some of the books kept for advanced classes. They were full of mysterious terms and chapter headings and some remain as exciting mysteries. I acquired my own copies of some of these books in later years, but once bitten I never looked back. It has dominated my life as it has many others.

What had always interested me was the whole organism. However, when I finally entered post-doctoral research and later on as a lecturer at the University of Edinburgh, whole plant studies were no longer research priorities, so I spent a long research sojourn on things more molecular, but always to do with the signals (that is meaningful information) that plants sense and act upon. Plants continually react to the environment in which they live. My later investigations on how these signals do what they do in the responding plant, brought me back to my first compelling fascination—the behaviour of the whole plant itself.

The road to systems and plant intelligence

In 1972, I purchased a small book by Bertalanffy published in 1971 and entitled *General Systems Theory*. Although the material in the book was quite limited in amount, the way of thinking about cells, organism, and biology, and indeed economics and

politics was quite radical. Biology, it indicated, was constructed from networks or systems. Understanding required identifying the connections between the network constituents, since it was the connections that generated the novel properties of biological organisms and populations. I, like many of my time had been typically reductionist, probing the bits and pieces of the network. To make a living as a scientist required, and still requires, that mode of investigation. However, that small book changed my way of thinking. Systems thinking taught one to think sideways, as it were, to see the connections and, thus, the surrounding context into which any network constituent is embedded. The connections could be straightforward or more complicated with negative feedback or feedforward devices.

There were precedents to Bertalanffy and I read as much as I could find at that time. Jan Smuts, for example, who first used the word holism; the developmental biologist Paul Weiss, 'The science of life' (1973); Bernard Patten (1971), an ecologist who edited four volumes on systems thinking; Jay Forrester (1961), on economics systems theory; Stafford Beer (1972), management systems theory; Gregory Bateson (1972), systems approaches to mind. All of these were already on the shelves in 1972-73. In the University of Edinburgh, which I joined in 1970, Henrik Kacser and Jim Burns published the highly significant 'The control of flux' in 1973 and Conrad Waddington, Tools for Thought in 1977. I list these people in particular because, like many others at the time, they effectively educated me in systems approaches and understanding, and as others have said before, I stand on the shoulders of these superb intellects.

However, acquisition of the systems approach led me into serious controversy over plant growth regulation by hormones. I had written a long invited article (Trewavas 1981) emphasizing the context within which molecules worked as being crucial and no less important than the molecule itself. It countered the common research view of the time. I received over 600 reprint requests in 3 weeks (no websites at that time), so there was certainly interest, but there were subsequent meetings where what I had written was either damned or lauded as the new approach; my promotion was also temporarily blocked.

What directed me into the area of intelligence was not only a lifetime experience with plant behaviour (for so it turned out to be), but also Mc-Clintock's very challenging statement, published in 1984, which begins this chapter. What exactly did she mean by it? The words 'thoughtful' and 'knowledge' indicated someone with a profound understanding of plants and they resonated with conclusions that had slowly emerged from my own reading. Most of this book really is an exploration of McClintock's assessment of plant life. 'Thoughtful' directly implies intelligence and 'challenge' requires behaviour. As indicated in the preface to this book, its title, Plant Behaviour and Intelligence becomes an inevitable consequence of McClintock's insight. All self-organizing cells and organisms are very complex systems and the particular system structure at the time represents 'the knowledge it has of itself'. Chapter 3 amplifies the meaning of systems structure.

However, one consequence of controversy on plant hormones is that it led to numerous invitations to write articles for other scientific journals. In one of these subsequent invited articles, I illustrated a particular complex amino acid biosynthetic pathway in plants as a simple neural network (Trewavas 1986). It seemed to me that it was one way to use 'thoughtful' and 'knowledge' from Mc-Clintock's article. In turn, thinking about that led me to the realization that the complicated network inside every cell must have similar analogous organization and, thus, behaviour to the potentially more complicated ones found in brains. In fact, any self-organizing network of sufficient complexity, and capable of maintenance in the face of environmental perturbation and the active pursuit of food of any kind must be intelligent. Plants were certainly in that category. However, at the time, plants were the last organisms normally associated with intelligent behaviour. When I mentioned this possibility to some colleagues, the response was often ferociously negative. Thinking that way was obviously dangerous. The jottings on the issue went into the desk drawer and did not surface again until I was more confident, and could argue the case.

With time and data amassed in 1999 and 2002, I used the opportunities again of invited articles

to float the idea of plant intelligence gradually (Trewavas 1999, 2002) and then in 2003 published another long invited article entitled 'Aspects of plant intelligence' (Trewavas 2003). Inevitably, controversy surfaced again and, immediately, some of those who agreed with me 20 years earlier now seemed opposed, but with a new band of supporters, some of whom had already started down this road. This book 8 years in occasional writing is a consequence of thinking around that theme and, of course, new information has now emerged from elsewhere, which is to be found in its pages.

Just as outstanding scientists provided me in the past with systems education, two others are Barbara McClintock, already mentioned, and Charles Darwin who will surface now and again. Darwin wrote the first book on plant behaviour. A third much less well known, but of remarkable stature is J. C. Bose whose contributions will find reasonable reference later on in Chapters 2 and 25.

In some sense, the more I look into plant biology, the more I see and the more I appreciate how little is actually understood. In that sense, exploration has magnified my ignorance, the expansion of knowledge is now much greater than when I graduated; thus, my knowledge in relative terms has diminished. Like so many scientists, I need two or more lifetimes to explore further, but nature in its wisdom does not permit us that luxury. Perhaps that is the most fortunate aspect of our biology; there are too many who have lived too long already.

'A feeling for the organism'

In 1984, Barbara McClintock, a plant biologist, received the Nobel Prize, the highest honour and accolade any scientist can receive from other scientists. For many years, her pioneering research, decades ahead of others, contradicted one of the then-current dogmas that assumed that the genome, the sequence of nucleotides in DNA was stable throughout the lifetime of the individual. When scientific dogma takes hold, life becomes difficult for any scientist whose research does not fit; for Barbara the penalty was to be ignored and her observations, clear though they were, misunderstood or even trivialized (Keller 1983).

It did not help that she worked with a plant, Zea mays or corn, a crop that produces the familiar yellow sweetcorn. Although plants can be popular with the public, they are not a particularly popular organism for biological study or grant money, although that may be changing. The fact is plants do not seem to do anything, and if they do not seem to do anything, what is there for any young scientist to be challenged to investigate? An abundance of food in western countries has not helped either; plant research in terms of food provision and security no longer seems publicly so important.

However, recent surges in the price of food have reawakened us to the fact that we have a problem. The population of the world, currently now over seven billion and predicted to rise to nine billion by 2050 needs more and plentiful food. There is no more land available unless we cut down rainforest, so two ears of wheat must be provided where one was grown before. We need more knowledge about plants and their behaviour.

Evelyn Keller has written a biography of Barbara McClintock, a readable and enjoyable text that gives substantial insight into McClintock's thinking and attitudes. Keller talked with McClintock at length, so that we often have direct quotes from her and I have used several below.

'But just because they sit there, anybody walking down the road considers just as if they're not really alive' (Keller 1983, p. 200). One reason for writing this book is to modify that undoubtedly common perspective of the ordinary public 'walking down the road'.

What exactly is meant when I refer to a plant?

This question will be examined again and again in this text, because it is seminal to any study of plants. The real question is 'what is the essence of being a plant', because through that question the phenomenon of behaviour is more obviously displayed. I will use the word 'plant' frequently, as a shorthand for plants we are familiar with. While it is generally true that plants are photosynthetic, not all organisms that photosynthesize are plants.

The living kingdom used to be divided into animals and plants. So far as I can ascertain, the

division was based on the simple idea that all the interesting things moved and all the uninteresting ones did not. So, originally, both bacteria and fungi were classed as plants, together with the more obvious, algae, mosses, liverworts, ferns, gymnosperms, and finally, angiosperms. Once it was realized that bacteria caused disease and plants did not, attitudes changed. Microscopical studies established that bacteria lacked a nuclear membrane and thus a proper nucleus. Furthermore, obvious chromosomes during mitosis were absent and it is now known that, instead, bacteria possess a single circular chromosome containing their DNA. Bacteria are described as prokaryotes and placed in a kingdom all of their own. In contrast, virtually all other organisms, animals, the non-photosynthetic fungi, and plants are described as eukaryotes, meaning they have a true nucleus and obvious chromosomes.

More recent studies using genome and protein sequencing indicate that fungi left the main evolutionary tree at a different time to plants, so they, too, are now regarded as a kingdom of their own. If their present lifestyle of living off the decaying materials of other organisms was the same when the fungal branch occurred, then self-evidently they could only do so when there was sufficiently large number of dead organisms to provide the necessary substrate material. Yeast, truffles, and mushrooms are the public's main experience of fungi.

The reader should regard the word 'plant' in this book as synonymous with a higher plant, an angiosperm

In evolutionary terms, the first true plants are often regarded as members of the algae. The algae are eukaryotes, but these eukaryotes were preceded, probably by a billion years at least in photosynthetic terms, by photosynthetic bacteria and blue-green algae, both of which are part of the prokaryotic kingdom. Many algae live in marine conditions or in freshwater, and again, in evolutionary terms, are assumed to have preceded the mosses and liverworts; these, in turn, are assumed to have preceded the ferns. Tree ferns and horsetails, some 300 million years ago, formed the basis of the material that eventually became coal measures. The ancestors of

gymnosperms appeared about the same time and present day representatives are mainly large trees. Finally, about 150–200 million years ago, the angiosperms, probably the most familiar of plants to the reader, were first detected in the fossil record.

When I use the word 'plant' throughout this book, it is simply a shorthand for an angiosperm, a higher (i.e. more recently evolved) plant. In contrast to algae, mosses, and ferns, which use a motile, fast-moving, male sperm for fertilization, which swims to the ovule or egg cell, gymnosperms and angiosperms use pollen containing the male cell for fertilization. The reproductive cells in angiosperms are found in flowers and about 70% of species are hermaphrodites; the same flower contains both male and female cells, although both types may mature at different times. Others contain male and female cells either on other individuals or on other flowers.

A variety of ways are used to transfer pollen to the female stigma, but once arrived, pollen tubes germinate and form a tube that grows with astonishing accuracy and speed (e.g. 5 cm/day by effectively a single cell) through the female tissues. The male cells move inside the pollen tube and eventual targeting of the female cell by the pollen tube permits fertilization to occur initiating a process of embryogenetic development that eventually culminates in seed formation. Because the pollen tube grows internally in the female tissues, the film of water required for motile sperm movement is no longer needed. It is assumed that pollen evolved (so-called siphonogamy) as a response to the requirement for fertilization of plants in a drier climate. Alternatively, the evolutionary progenitors of both gymnosperms and angiosperms attempted to expand their habitat into the drier regions of the land surface in response to increased competition for light or root resources.

The commonest version of survival in dry conditions is perhaps exemplified by members of the grass family. Stigmas of most angiosperms contain a sticky fluid to which the transferred pollen grain adheres and these moist conditions enable pollen germination to start. The grasses, which survive in drier conditions quite happily, have a dry stigma. Germination of the pollen on dry stigmas can take place through a drop of liquid provided

by the pollen cell itself, once it senses contact with the stigma. The mechanism is extraordinary. The response to sensing may give rise to lipids synthesized by either stigma or pollen, and a number have been identified. Apply these chemicals to leaves and pollen tubes will penetrate and grow through the leaf, something it cannot ordinarily do (Wolters-Arts et al. 1998).

Gymnosperms (about a thousand species altogether) are largely distinguished from angiosperms by using cones instead of flowers as the reproductive organ. They, too, are wind pollinated. Photosynthesis takes place in needles instead of true leaves, although the Ginkgoales (e.g. Gingko biloba) have leaf-like structures, but are still recognizably gymnosperm. Reasonable numbers of the gymnosperms are important crop plants—larches, pines, and spruces, which are quick growing trees and efficient converters (relatively speaking) of light energy into wood. Among the gymnosperms are the giant redwoods and Sequoidendron found native in California. These gymnosperms contain individuals that are both the largest living things on earth (General Sherman, the largest Sequoia dendron weighing an estimated 6000-7000 tons) and the tallest still in existence is a coast redwood (Sequoia giganteum) at 362 feet.

The giant redwood forests are one of the greatest, jaw-dropping, and extraordinary wonders on planet Earth that all should make an effort to see. One's first view of any of these, simply instils wonder at what the natural world can produce. These giant trees are now protected, but a number were cut down in a typically unthinking act, perhaps similar in character to the virtual elimination of the bison in North America.

The bristlecone pines contain the longest living individual trees with estimated lives at 4500–5000 years. Sometimes these records of longevity are instead claimed for Pando, known as 'The Trembling Giant', that is actually a clonal colony of Aspen (*Populus tremuloides*). In total, Pando is estimated at over 6000 tons and believed germinated over 80,000 years ago. However, a clonal colony arises by vegetative suckers and the individual trees that arise could easily be isolated and live independently. As the older ones died new suckers took over. Thus, Pando consists of a set of joined individuals, but

there is no evidence yet, that these individuals are in any way dependent on each other.

Some fern communities have a similar clonal relationship and grow outwards in a circle with the original individuals dying off in the middle; rather like a large fairy ring. Some of these have been estimated at 40,000 years old. These abilities reflect a major difference with most animals; many plants can reproduce vegetatively, as well as sexually. For some higher plants like the small members of the Lemnaceae (duckweeds) that cover the surface of ponds, flowering is uncommon and most growth is by replication of individuals that separate from each other. In good conditions doubling in numbers of some duckweeds takes less than a day. Other members of the Lemnaceae, the Wolffiellas, are the smallest flowering plants known. The vegetative body of Wolffiella is about 1-2 mm across and the flower can only be seen with magnification.

The overall evolutionary trend in plants seems to be directed towards survival in drier climates. The algae largely live in water; mosses and liverworts also prefer moist habitats. Reproduction in ferns usually requires moist conditions with a film of water on the surface of a haploid organ, the prothallus, in which motile sperm swims towards the egg cell. Evolutionary convergence is described in Chapter 6.

Survival in a very dry climate is surely best exemplified by lichens, a symbiotic relationship between algal and fungal partners. These can survive in exceptional dry and harsh climates, but they pay for this capability by a low rate of growth.

The term 'plant' will also be generally used for a young dicotyledonous species

The angiosperms themselves contain about 240–270,000 species and originated 150 million to possibly 200 million years ago (Cornet 2007). The real surprise has been the rapidity of speciation, thought to be the result of direct interactions with insect pollinators and insect herbivores that were themselves undergoing rapid evolutionary change (Cornet 2007). It looks as though speciation in both organism groups was synergized by this interaction.

Very early on, an evolutionary split gave rise to progenitors that have produced, over time, two main classes. First, there are the monocotyledonous angiosperms (monocots for short) and, secondly, the dicotyledonous angiosperms (dicots). The cotyledon refers to an embryonic leaf in the seed and whether there is one or two, but there are other differences. Many monocots use bulbs or corms for vegetative propagation, and these act as a food store for the plant to grow in springtime. In some bulbs the decision to form a flower is taken either one or more years ahead of time. Many bulbs/corms produce contractile roots that are used to pull the bulb down in the soil to a pre-determined level of safety. Monocot leaves are usually parallel-veined, in contrast to dicot leaves that use a network of veins.

Veins are composed of two tissues—xylem and instead. Phloem—and these are the primary cell constituents of all vascular tissue in all angiosperms. As in animals, it is the function of vascular tissues to transport necessary materials around the plant. Leaves synthesize sugars (mainly sucrose), which is needed by non-photosynthetic tissues, while roots provide water and minerals from the soil. However, many other important chemicals are transported by the vascular tissues that act as carriers of information and initiate changes in behaviour. The critical concept of information is discussed later.

There is no need these days to provide simple diagrams of plants to illustrate the main parts, the web provides all. For those who do need a reminder, simply typing 'diagrammatic pictures of plants' into Google will summon up a large number; usually these are young dicot seedlings. Dicots contain about 170,000 species of which an estimated 100,000 are trees. The dicotyledonous tree life cycle is different in behaviour to annuals; many trees have juvenile periods that can range from 2 to 30 years before flowers are produced. Cycles of flowering can often appear, sometimes occurring every other year or even longer. As I write this section, all the local mature ash trees are covered in flowers; next year there will be hardly any.

Dicot trees contain a root and a shoot, and growth takes place at the tips of both in areas called meristems, which are basically undifferentiated embryonic areas, capable of generating new cell types by differentiation after division. Shoot and root meristems are the subjects of intense investigation at the present time. Branching occurs from buds (basically

a dormant meristem) in the stem, located at what are called nodes. One common method of dicot propagation requires only the grafting of a single bud onto a recipient plant, usually of the same species, but a different variety. This grafting method, for example, is used by gardeners for propagating virtually all roses. Below ground, branch roots originate from a main root and are formed *de novo* from an internal cellular tissue in the main root called the pericycle.

Increases in stem and root girth result from the activities of the cambium, another embryonic meristematic tissue that in form is like an internal skin under the stem bark or under the outer epidermis of mature roots and surrounding other internal tissues. The cambium produces new cells both to the inside and outside of itself by mitosis, that then differentiate further. The inner cells form the xylem, a word derived from the Greek for wood. Xylem cells eventually become lignified then die, providing essential support tissues as the plant increases in height. The tubular structure of xylem acts as a conduit for active water and mineral translocation up the stem and branches to the leaves and other growth points. The differentiation process and, thus, the life cycle of xylem cells is an excellent example of programmed cell death, a process called apoptosis.

The second important tissue produced on the outer ring from cambial differentiation is the phloem (from the Greek for bark), the tissue that is involved in the transport of sugars and other chemicals. The main phloem cells are anucleate.

The mitotic activity of the cambium in trees is based on an annual cycle and it is the xylem cells that differ in characteristics of size through the season that give rise to the characteristic rings seen in transverse sections of the cut trunk of dicot trees. Since the activity of the cambium is a sensitive indicator of the growth conditions each year, the thickness of individual tree rings acts as a potential proxy of the experienced climate for that year. Since cambial activities are part of the process of development, everything that modifies development, including mineral access, rainfall, general weather, light conditions, predation, and disease affect the size of the ring, as well as temperature. Temperature might be only a weak contributor as described in Chapter 12.

The science of tree rings is called dendrochronology and can be used not only to check carbon dating methods to at least 10,000 years past. It has, of course, been used to measure the length of life of old trees. By this means, we know that giant redwoods and Sequoidendrons in California are several thousand years old.

The oldest trees in Europe are generally considered to be slow growing yews (*Taxus* species) and some have been identified as at least 3000 years old. The Fortingall yew in Scotland was measured by Linnaeus as having a girth of 16 m, but is now sadly decayed and partly vandalized. There is a drawing of the signing of the Magna Carta in 1215 at Runnymede under a yew tree. Recent photographs indicate the tree is still there and looks very similar to its drawing eight centuries ago.

As needed, other anatomical and tissue characteristics will be introduced in the text. It is dicot species that I will generally refer to in discussing behaviour and intelligence.

The monocots have only some 60,000 species, monocot tree species are rare, the most well-known being the palms, although large bamboos, at about 20 m high, could be regarded as trees. However, many monocots grow initially from the base of the shoot, either they grow from a bulb or, like grasses, grow from a basal meristem. Vascular elements are distributed through the stem, whereas in dicots they form a ring. Shoot branches are often called tillers and the root characteristics are fibrous, with many numerous branch roots that stabilize surface soil. In other long-lived monocots, like bamboos, growth takes places at the nodes in a less distinct fashion than dicots. Monocots lack cambium, and it is expansion and growth of cells throughout the trunk that enables lateral expansion to occur. The grass family (Gramineae) are the most well-known group of monocots because members of them (e.g. wheat, maize, rice, oats, etc.) act as staple foodstuffs.

Is a dicot really representative of the plant kingdom?

Having chosen a dicot as representative of a plant, it is now necessary to provide adequate justification. Most readers, when asked to name a specific representative animal, will probably say a dog or