Plants: Evolution and Diversity

Plants are so much part of our environment that we often take them for granted, yet beautiful, fascinating and useful plants are everywhere, from isolated moss colonies on stone walls to vast complex communities within tropical rainforests. How did this array of form and habitat come about, and how do we humans interact with the plant kingdom? This book provides a refreshing and stimulating consideration of these questions and throws light in a new way on the complexity, ecology, evolution and development of plants and our relationship with them. Illustrated throughout with numerous line diagrams and beautiful colour photographs, the book provides a unique source of information about the fascinating lives that plants lead and the way in which our lives are inextricably linked to theirs. It will be particularly useful to those seeking a more ecological and process-oriented approach than is available in other textbooks.

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Preface

Dancing is surely the most basic and relevant of all forms of expression. Nothing else can so effectively give outward form to an inner experience. Poetry and music exist in time. Painting and architecture are a part of space. But only the dance lives at once in both space and time. In it the creator and the thing created, the artist and the expression, are one. Each participant is completely in the other. There could be no better metaphor for an understanding of the . . . cosmos.

Lyall Watson (*Gifts of Unknown Things*)

The metaphor of dance is a very apt way to portray the unfolding and increasing complexity of plant-life on Earth. The dance of plants is the dance of plant form in space and time. From a reductionist point of view, the conversion of solar energy is what plants are really all about, either at the level of the individual, or the community, or even in the characteristics of the plant-life of a given region. Form, is the physical expression of the energy captured and transformed by plants, and it provides the basis for all ecological relationships. It is not surprising then that, broadly speaking, the plants of tropical regions that have access to the greatest input of radiant energy also have the greatest exuberance, while those of energy- and nutrient-limited environments, such as alpine moorlands and bogs, have a more restricted range of body plans.

In the continuum of time the dance of plants is both developmental and evolutionary. From this perspective the unity of all life can be seen in its infinite diversity. No longer can organisms be viewed in isolation but must be seen in the context of environment – they **are** environment. The dancers are the plants and the music is their physical and biotic relations with their environment. They are simultaneously the creators and the created for they themselves contribute to the music.

As the orchestra of life tuned up, the first steps of sub-cellular and cellular structure and physiology were rehearsed. Initially it was a slow dance and the first notes of the evolution of life were the solar and thermal energy driving the chemistry of simple living organisms. The overture only hinted at what was to come and, for a long time, there was a simple melody where the principal players were not heard and the dancers were few, but even at an early stage the dance was one of innovation and improvisation. It was a dance of increasing sophistication accompanied by harmonies in a major key as plants

arose. They were the first truly terrestrial organisms and they transformed the landscape making it habitable for other organisms.

The dance of plants is complex beyond our wildest dreams. Plants perform epic dances of cooperation and competition. They dance with their environment, adapting in step with it and modifying it, by cooling the air, changing atmospheric carbon dioxide concentration, providing oxygen, making soil and by altering the relative abundance of the biotic components. They dance with each other in complex communities, exploiting water, mineral nutrients and sunlight, each finding a place to grow. They dance with other organisms, avoiding or repelling herbivores, attracting and feeding pollinators and dispersers of seeds and fruits, and cooperating with fungi to exploit the soil's nutrients. There is an endless variation in the music and the dance, and the degree of complexity of their interrelationship.

The growth of plants from seed is the source of some powerful metaphors for human life but mostly plants do not have immediate impact on us in terms of their adaptive evolution and developmental processes. We appreciate them more for their beauty of form and colour, and grow them in our gardens and homes to lend harmony to our lives and as a reminder of wild nature. There may be more to 'phyto-psychology' than we realise. Humans have highly developed senses of colour and spatial order and there may be a connection here with our love of highly symmetrical plants such as cacti and succulents, or rosette plants such as African violets and primulas. Many bird-pollinated species such as fuchsias and columneas with their bright scarlet flowers, or herbs of the rainforest floor such as marantas with their strange metallic pigments, are perennial favourites in our homes.

Plants lack the spontaneity of animals, whose movements, grace, complex behaviour, and often intricate and bizarre colours and patterns attract us in profound yet familiar ways. Animals arouse our curiosity. They are like us in so many ways, yet are different, and this novelty requires investigation. Plants live in a different time dimension and television documentaries often resort to the use of time-lapse photography in order to 'animate' plants. This is perhaps unfortunate because it fails to convey the true nature of the relationship between the spatial and temporal organisation of the plant world.

While plants could also be said to lack the 'aloofness' that is so tantalising about wild animals, we can easily touch plants and we can imagine that they pose for our photographs, but they still remain somewhat alien. Their texture is not that of the animal, although we can be intrigued when some leaf textures seem fur-like. Plants appear to lack movement or, if they do move, we are bemused. We know they are formed by the conversion of radiant energy, but the nature of their nutrition remains mysterious, and when they occasionally devour insects we are amazed. They are living organisms but we cannot quite comprehend the nature of their experiences of the world, what it means to actually be a plant. Perhaps it is no great surprise that some of the earliest space invaders of science fiction were plant-like creatures, the triffids.

Ironically, plants are so much part of our environment that we also tend to take them for granted, and that is part of the problem for conservation. How do we become aware, how do we redirect our attention? To comprehend the grandeur of these organisms, a visit to the silent groves of coastal redwoods of California, the towering dipterocarps of a Bornean rainforest, or the remnant primeval kauri forests of New Zealand may be necessary. For others it requires the crazy kaleidoscopic colours of an alpine meadow, or a desert after rain, to take the breath away. But plants also impress us on a tiny scale. Some of the loveliest flowering plants are tiny ephemeral beauties that can be found only on the highest mountains. But, at this scale there is still much to be seen in our immediate, even urban, environment, especially the enchanting, if largely unsung, world of bryophytes. On an even smaller scale is the world of plants through the microscope. We can remember the first time we viewed the jewel-like appearance of moss leaf cells through a microscope, a truly wondrous sight.

Aesthetic appeal will probably have a more profound influence on the conservation of plants than economic arguments, and to encourage the conservation of the world's flora is one of the main aims of writing this book. For more than 30 years we have studied plants in laboratory and field and they have led us to some very exciting places as well as the more mundane. Even industrial slag-heaps have provided raw data for theories of plant adaptation. Beautiful and fascinating plants are everywhere, from the bryophyte communities of old walls, to the scattered plants holding a tenacious grip on the scree slopes of glaciated mountains, or the weedy fringe at the high-tide marks of sandy seashores. Even old derelict buildings can be a source of pleasure. When travelling in the middle of a city such as London one can see buddleias, growing in such incongruous sites. The wonder of being a botanist is that literally almost anywhere you can find something beautiful and fascinating. In the words of Alan Paton from his moving novel, *Cry, the Beloved Country*:

> *. . . the train passes through a world of fancy, and you can look through the misty panes at the green shadowy banks of grass and bracken. Here in their season grow the blue agapanthus, the wild watsonia, and the red-hot poker, and now and then it happens that one may glimpse an arum in a dell.*

The writing of this book has taken much longer than we intended, and many of our ideas have evolved in keeping with the progress of the book. Inevitably this meant more changes. Originally, our plan was to write a celebration of plant diversity as a successor to *Diversity and Evolution of Land Plants* (Ingrouille, 1992). However, it soon became obvious that there was a definite need for a new kind of approach, one that would go beyond the bounds of conventional textbooks, of which there are several excellent examples already available for students. The research for such a book meant that the material we acquired would fill several volumes, so painful decisions were made to cut the ever-expanding prodigy down to an acceptable size. Meanwhile, other events, including a lengthy research post overseas, intervened to delay publication even further.

Some of our personal views of plant-life and the ideas expounded in this book might be considered unorthodox by the standards of mainstream science. For example, we have aimed to bring into the foreground the work of botanists whose work no longer fits current orthodoxy, but whose views we believe still have value today. There are past masters, such as Goethe, Hoffmeister, Church, Arber, and Corner, and undoubtedly many others, to whom we are happy to pay our dues, as well as those whose works we have consulted for this book. In the words of John Bartlett,

> *I have gathered a posie of other men's flowers, and nothing but the thread that binds them is mine own.*

Generally speaking, we believe that science and art are but two ways of comprehending the world, two forms of creativity, and that the scientific method, particularly in the realm of botany, could be applied in a more phenomenological way, and even augmented by intuitive approaches. Like art, science provides a way of knowing, of making sense of the world, but the best scientists must go beyond the scientific method. Current scientific procedures and methodologies are inadequate to explain much of the complexities of plantlife, which often require subtle, broader-based holistic approaches. For example, we have always been struck by the similarity of forms throughout many unrelated plant families, be it at the level of gross morphology or confined to the flower. Such phenomena are usually explained away as instances of parallelism or convergence (or homoplasy, to use a currently popular term), and the explanation is always framed in Darwinian terms of adaptation and natural selection. However, we feel that there is a deeper, underlying law of form or morphogenesis that constrains expression of form to within certain boundaries, and which cannot be understood simply in terms of linear cause and effect. From a holistic perspective, the genome may also be portrayed as a self-organising network capable of producing new forms of order. In addition, the aesthetic dimension has undoubtedly great potential in promoting empathy for plants at the personal level as well as a more widespread conservation ethic.

It is unfortunate that, in this age of instant information, general botany and its long history are no longer taught, at least to the extent that we would prefer. How we react to plants and how we ultimately treat them is intimately bound up with our ways of regarding them. Western science, at least since the time of Descartes and Bacon, has promoted the idea that plants and other living organisms are objects (*res extensa*) existing in isolation from the subject observer (*res cogitans*). The disinterested objective method became the scientific method and a cornerstone of the philosophy of science. We strongly believe that this philosophy is flawed and has contributed to many of the difficulties facing science today.

Thus, initially it may be difficult for some students to get situated in this book, to see it in its entirety, for, at first sight, the combination of different approaches is apparent. We make no apologies for this

because we do not reject the advances made in botany over the last four hundred years. There is no doubt that reductionist science has been singularly successful in elucidating much of our current knowledge of plantlife, particularly relating to anatomy and physiology, and in the fields of genetics, development and systematics. However, in the age of the expert, plant science courses in universities are often so narrowly specialised that we are in danger of losing sight of the plants altogether, and therefore we feel that certain new approaches or new perspectives are needed.

The traditional role of the amateur is the foundation upon which botany was built. Without disparaging the importance of modern computerised methods, and molecular and theoretical developments, we encourage a return to a broad approach to botany that would reinstate the importance of the amateur. Botany is an immense and deeply satisfying subject and one that we can attest to providing a lifetime of riches and rewards. It is therefore difficult for an undergraduate to get the flavour of botany in three or four short years, especially to develop a feeling for plants, and to understand the role of plants in diverse ecosystems.

Where possible, we have tried to keep abreast of the multifarious changes that have revolutionised so much of current biology in recent years. Chapter 1 has been strongly influenced by developments in complexity theory, including phenomena such as hypercycles and autopoiesis (see Kauffman, 1993). It was felt necessary to touch on such topics in order to give as complete a picture of the events leading to the early evolution of plant life, and for this reason we have also included many aspects of the evolution and diversity of the algae, although technically we would normally exclude them from the category 'plant'. There are several excellent and complementary texts on the biology, evolution and diversity of the algae that we recommend.

In Chapter 2, although we have basically adopted a conventional reductionist approach, we have tried to integrate this with some of the most recent ideas in plant morphology and developmental genetics, including the 'theory of morphospace'. Much of this chapter was influenced by the 'process morphology' of Rolf Sattler and his colleagues, although the philosophy behind this approach goes back to A. N. Whitehead (see Whitehead, 1929), in addition to more recent theories on developing and transforming dynamic systems and biological form (Webster and Goodwin, 1996). There is no doubt that morphology and developmental genetics has benefited from this trend away from a static typology to a more dynamic process-orientated approach but it has to be admitted that, by including the dimension of time, practical difficulties in the analysis, interpretation, and description of form are also introduced. This is particularly the case with respect to descriptive morphology and the use of homology in classification.

There have been changes in the world of evolutionary botany over the past 20 years. The familiar Neo-Darwinian paradigm is being augmented by views that see evolutionary change as a result of life's inherent tendency to create novelty, and which may or may not be

accompanied by adaptations to changing environmental conditions. Some believe that we are in the process of a paradigm shift (in the sense of Kuhn) while others believe that the Neo-Darwinian paradigm is sufficient to explain evolution, or that it only needs some amendments. There is no doubt, however, that, in biology, we are witnessing a general move from a mechanistic world view to a systems view of life involving the triple helix of phenotype, genotype and environment.

In Chapters 3 and 4, we have tried to explore the processes of evolution and plant reproduction within an evolving Darwinian framework that gives more weight to phenotypic plasticity and the ability of plants to harmonise their form and life cycles with changing physical parameters, rather than to simply view plants in more orthodox terms of mutation and selection within populations. We have also tried to emphasise the recognition of both constraint and relaxation in form-making and the resultant phenomena of convergence and novelty, respectively. In addition, we have highlighted processes that might be pertinent to the evolution of plants, especially the founder effect on island populations, and those that may result in major genomic and morphological reorganisation. The reciprocal relation of space and time with form is central to Leon Croizat's panbiogeography and this approach to plant distribution has much to commend it rather than the viewpoint whereby organisms are treated a priori within the framework of a simple dispersalist model.

In Chapter 5, we have used the arrangements of plant families that have resulted from the most recent findings of molecular systematics. Of course, this may be a highly controversial and somewhat contradictory stance, especially in view of what we say about methodologies. However, we believe that this provides the student with the best means of gaining access to, and evaluating, current developments in plant systematics. Within the realm of plant systematics we take the view that cladistics and molecular methods are only several ways of handling data, and that a pluralistic approach involving time-honoured methods (e.g. morphology and biogeography) is essential.

In Chapter 6, which is an overview of the world's flora, we have deliberately taken an adaptationist approach knowing full-well the pitfalls of 'the adaptationist programme', which were so elegantly exposed by Gould and Lewontin in their seminal paper 'The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme' (1978). A naïve interpretation of functional morphology is certainly to be avoided but we feel that there is an overwhelming heuristic value in the adaptationist approach and, if soberly used, it can be an invaluable teaching aid and inspiration for students. Story-telling is fundamental to humans and can be the most effective way of inspiring an empathetic relationship with the plant world.

The earliest botanists were herbalists and plants were studied mainly for their culinary, curative and magical properties. In Chapter 7 we have emphasised some of the most important uses of

plants by humans, in addition to some of the more worrying aspects of globalised food production and distribution. For example, in many western countries, the larger supermarkets now stock a diversity of fruits and vegetables from around the world that would rival some of the traditional fruit markets in places such as Malaysia and Thailand. One wonders what the effect of such large-scale imports will have on local economies and traditional crops. Today, plants sustain a multi-billion dollar global pharmacy industry, and a growing research and development programme for genetically modified crops, but there has been a backlash to all these so-called technological improvements to our food supplies. There has been a tremendous resurgence of interest in recent years in herbal medicines, vegetarianism and organic farming.

All this has been happening at a time when we are witnessing widespread disaffection with modernity. We are now more acutely aware of the impacts of technological/industrial activities on the climate, and on plant and animal life of the planet, as well as the gross inequalities in human societies, owing to an unrestrained desire for material wealth and consumer goods. We suggest that political answers to these problems are, in reality, only short-term solutions, and that we will only realise a paradigm shift to a more eco-centric way of living in harmony with the Earth when, as individuals, we adopt a transpersonal way of relating to other living organisms. This is the essence of the movement known as Deep Ecology that was first formulated by the Norwegian philosopher Arne Naess. A *poesis* of life or 'living poetically' is what we try to live up to in our relationship with living organisms and the environment.

The evolutionary dance of plants has taken place during the past 400 million years. In the past 10 000 years a different tune in a minor key has been heard as plants have begun a new dance with humans. They have been manipulated and transformed by us for food and materials, and have enabled human civilisations to evolve. Simultaneously we have also damaged and destroyed much of the plant life on Earth and rendered numerous species extinct or nearly so. The book is about the relationships between plants and humans, how we perceive them, form concepts of them, study and analyse them, and enjoy them, although it does not provide clear answers as to why we do this. In the third millenium we need to adopt a new philosophy for the planet we inhabit and all its unique life-forms if we are to survive. We have tried to steer clear of metaphysics, but maybe we also need to retain a sense of the mysteries of life, especially if we are to develop a sane and non-exploitational relationship with the Earth.

Evolution is the polestar of the biological sciences, and this book says a lot about the evolution of plants, but it goes beyond scientific concerns to embrace our intuitive processes, our aesthetic senses and the human ability to wonder and to imagine. According to Wordsworth, imagination is 'reason in its most exalted mood'. Therefore, we have given much emphasis to the visual aspect of plants, their form and colour, and have promoted a return to a more

'in-depth seeing' as exemplified by phenomenology. The phenomenological method tries to take into account the subjective feelings of the observer within a more dynamic framework of observation and concept-formation ('reciprocal illumination'). To do this effectively we also have to have some grounding in epistemology, and therefore we have provided an outline in Chapter 8 of the philosophical traditions that impinge on botany, as well as the major developments in its history. Phenomenology was essentially the way of Goethe, and consequently his much maligned and overlooked contributions to botany are given due consideration.

We hope that this book will provide a much-needed stimulus to the student of botany with an inquiring mind, particularly advanced undergraduates, but it is not designed solely as a university textbook. It is also aimed at all who enjoy plants for their form and beauty but want to delve deeper into their complexity, their ecology, evolution and development, and who, hopefully, will find inspiration and seek out other sources of knowledge. We have tried to bear in mind Corner's words about botany texts.

> *. . . the books that deal with general botany have grown so tediously compendious, so canalised in circuitous fertility, so thoroughly dull and dully thorough*

The interaction with plants can invoke feelings of empathy, but the sheer pleasure of discovery, of finding things out, can invoke feelings of revelation. We have tried to present the material in a way that will stimulate the reader to find pleasure and wonder in the world of plants, much of which is unknown, and probably will remain unknowable. At the end of each chapter we have listed only a fraction of our sources but, hopefully, these works should provide a gateway to the larger literature.

. . . . . .

for the question is always

how

out of all the chances and changes

to select

the features of real signficance

so as to make

of the welter

a world that will last

and how to order

the signs and symbols

so they will continue

to form new patterns

developing into

new harmonic wholes

so to keep alive

in complexity

and complicity

with all of being -

there is only poetry.

(Kenneth White, 'Walking the Coast')