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Excerpt
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Chapter 1

Plants and the origin of the biosphere

Energy flow and molecular complexity. Membranes. The serial endosymbiosis hypothesis for the origin of eukaryotes. Photosynthesis. The oxygen revolution. The ozone layer. Respiration. Multicellular life. Plant life moves onto land. Evolution and diversification of land plants. Plants, coal, and climate.

1.1 Introduction

Plants occur in almost every conceivable habitat on Earth – submerged on lake bottoms, exposed on wind-swept mountain tops, hidden within polar rocks, or perched perilously on branches in the rain forest canopy. They can be microscopic (oceanic plankton) or enormous like sequoias and eucalypts that may tower more than a hundred meters tall. Their flowers may span nearly a meter across (*Rafflesia arnoldii*) or extend the height of a human (*Amorphophallus titanum*), and be almost any color of the rainbow. Moreover, plants comprise *more than 99 percent* of all the Earth's living matter! We can also say with confidence that the history of the biosphere is largely the history of the origin and diversification of plants. Without plants, conditions on Earth – including temperature, types of rocks, the composition of the atmosphere, and even the chemical composition of the oceans – would be vastly different.

While plant ecology is generally defined as "the study of relationships between plants and the environment," plants do not, as this definition implies, merely inhabit environments. Plants also modify the environments, and they may even control them. Where, then, should one begin a book on plant ecology? The answer is clearly genesis – the origin of plants and the processes that created the current biosphere.

As we all learned in our first biology course, plants live by capturing sunlight. The first chemical process we were expected to memorize may well have been photosynthesis. This was a world-changing process. Yet by even this early phase in education, too many students are already convinced that plants are boring and can be ignored. Without them, however, none of us would exist. One of my objectives in writing this text was to try to recapture an appreciation of plants and basic botany, while also illustrating the importance of studying plants and their environments.

The world will always need botanists and plant ecologists. Many of the students in my courses seem to want to use their skills to protect wild species and improve the human condition, but I often find it necessary to explain that it is rarely possible to be effective at these tasks without some understanding of botany and ecology. If you want to contribute to ecology, or to conservation, or to many kinds of human welfare, you have to know something about plants first.

Since plants have a broad impact, those of you planning to work in fields including forestry, zoology, fisheries management, geography, planning, or environmental studies (not to mention molecular biology and medicine), may find it helpful, if not absolutely necessary, to know something about plant ecology. Indeed, one could suggest further that there is little point in going on a tropical holiday if you are unable to appreciate the remarkable plants and vegetation. If this book inspires you to continue with the study of plant ecology, and provides some resources to guide you in doing so, it will have succeeded. Equally, however, if it enriches another scholarly discipline that you intend to follow, or at least helps you better appreciate parts of the world that you one day visit, then it will have succeeded.

Before we examine the details of individual plants and types of vegetation, it seems essential that we begin by considering them as a unified whole – as a part of the biosphere. Hence this first chapter. Most newer students that I teach appear to know relatively little about global processes and geological time scales. I will therefore start with the story of plants and the origin of the biosphere in a quite general way, emphasizing long-term consequences for the atmosphere, the oceans and the land. The list of readings will allow you to pursue a deeper understanding of the impacts of plants on biogeochemical cycles, energy flow and the greenhouse effect. In Chapter 2 we will examine global patterns in plant distribution, and some of the explorers who made these important discoveries, which might inspire you to visit new areas of Earth and explore them yourself. Then and only then will we encounter the material with which most text books begin: resources and plant growth. In Chapters 4 to 8 we will work our way through the processes by which plants interact with other plants, fungi, and animals (including competition, herbivory, and mutualism), and the ecological consequences of these interactions. In Chapter 9, we will return to time, including the impacts of meteor collisions and ice ages upon plants and vegetation. Chapters 10 and 11 have more advanced work on patterns in vegetation and how they are studied. We will conclude, in Chapter 12, with the large scale again: the growth of human populations, and its consequences for the biosphere and the Earth's 300 000 plant species.

The word **biosphere**, which refers to that relatively thin layer on the surface of the Earth within which life exists, is now rather familiar to students. Yet the concept, according to Hutchinson (1970), was introduced into science rather casually by the Australian geologist, Eduard Suess in 1875. The idea was largely overlooked until the Russian mineralogist, Vladimir Vernadsky, published *La Biosphère* in 1929 (Box 1.1). The word has now attained a general usage and significance that Vernadsky probably could not have imagined.

Box 1.1 | The biosphere

La Biosphère by Vladimir Vernadsky (1863–1945, Figure B1.1) was published in 1929, based upon a Russian edition in 1926. In this slim book, Vernadsky publicised the term biosphere, which he attributes to E. Suess, a professor at the University of Vienna, an eminent nineteenth century geologist, who introduced the term in 1875. Vernadsky then lays out some basic principles that would become important themes in ecology as the century progressed. These included:

1. That the rates of reproduction of organisms such as termites will lead to geometric rates of increase in population size. A queen termite, for example, produces 60 eggs per minute, or 86 400 in 24 h, in which case in a few years they could cover the entire surface of the Earth, which he estimates at 5.10065×10^8 square kilometres (pp. 39–41). (Darwin, of course, used this observation in formulating the principles of natural selection and evolution.)
2. That, as all organisms could multiply to this extent, an external force (obstacle extérieur) sets an upper limit to their population size. There must be, he adds, some maximum numbers for different life forms, and these abundances, N_{max}, are characteristics of different species (pp. 46–48). (Today this upper limit is termed the carrying capacity, and finds its way into the Lotka-Volterra equations as K.)
3. That the gases of the atmosphere are identical to those created by the gaseous exchange of living organisms. These are oxygen, nitrogen, carbon dioxide, water,

Figure B1.1 Nataliia and Vladimir Vernadsky, 1910 (from Bailes 1990).

hydrogen, methane, and ammonia. This, he adds, is not accident (ne peut être accidentel). The amount of oxygen produced by plants, some 1.5×10^{21} g, corresponds to the amount of living matter that has been produced by plants (p. 57). (The origin of life on Earth is now traced back to gases such as these, leading Morowitz to observe that life is not an accident but an inevitable outcome of energy flow through the atmosphere. In spite of this, too many people, scholars and creationists, insist that life arose by accident.)

Of course, Vernadsky was not always correct. For example, he asserts on p. 63 that:

> The green micro-organisms in the ocean are the principal transformers of solar energy to chemical energy on the planet.

(While promises of oceans feeding the world persisted into the late twentieth century, better measures of production revealed that most of the oceans are unproductive, with pockets of high production along coasts, in estuaries, and where upwellings are produced by ocean currents.) None-the-less, one can see in this book an attempt to chart the major processes on Earth in terms of chemical and biological process calculated for the entire planet. The extensive literature on biogeochemical cycles can be traced back to early work such as this.

The biosphere has conditions that are rare in the universe as a whole – liquid water in substantial quantities, an external energy source (the Sun), and temperatures at which there are interfaces between solid, liquid, and gaseous forms of water. Liquid water exists under a rather narrow range of conditions of temperature and pressure. It was once abundant present on Mars and may still occur beneath the ice on Jupiter's moon Europa. New information is continually emerging from interplanetary space probes. At one end of the galactic temperature gradient there are temperatures of trillions of degrees inside stars, and, at the other end, there are conditions near absolute zero in the vastness of space. Neither extreme provides the conditions where biological chemistry, at least as humans understand it, can occur. The Earth offers an intermediate set of environmental conditions, and if it did not, we would not be here to write or to read this book.

1.2 Energy flow and photosynthesis

For life to exist, energy flow is required. Such a requirement is met when a planet is situated near enough to a star for sufficient energy released by solar fusion to pass the planet before dissipating into outer space. This is the case for our particular planet, situated near a star we know as the Sun. While it is not known how often life occurs, it may not be infrequent, given the enormous size of the universe – our own galaxy has some 100 billion suns, and there now appears to be convincing evidence that some of these suns have their own solar

Table 1.1. *The early atmosphere of Earth probably resembled the composition of gases produced by volcanoes such as these two on Hawaii (from Strahler 1971).*

Volcanic gases from basaltic lava of Mauna Loa and Kilauea	Percent composition
Water, H_2O	57.8
Total carbon, as CO_2	23.5
Sulfur, S_2	12.6
Nitrogen, N_2	5.7
Argon, A	0.3
Chlorine, Cl_2	0.1
Fluorine, F_2	–
Hydrogen, H_2	0.04

systems. This provides many opportunities for other possible planets to be affected by flowing energy. Proximity to a source of solar energy is essential for life because that energy flow, by itself, organizes matter. Life, at least as it is presently understood, is matter that has been organized by energy flow. Morowitz (1968) has examined the relationships among energy flow, thermodynamics, and life asserting that in order to properly understand life, one must look at the relationship between physical laws and biological systems. He demonstrates that flowing energy can create complexity out of simplicity.

Once the requirement for energy is met, life then requires resources. This begs the question of what those early resources might have been. One way to answer such a question is to ask what conditions would have existed in the early Earth's atmosphere before there was life, since the early atmosphere would likely have been one source of resources for the precursors of living cells. Determining what the early atmosphere was like, however, requires considerable detective work (e.g., Oparin 1938, Strahler 1971, Levin 1994). It seems that this atmosphere would have come, in part, from volcanic out-gassings. For clues about its composition one can measure the current composition of volcanic gases. Table 1.1 shows that the early atmosphere would likely have been composed of water, carbon dioxide, and sulfur. It was an atmosphere rather different from that of today. Yet, some billions of years later, these basic molecules remain as the principal constituents of cellulose, the dominant structural molecule of plants, and the most abundant (by mass) molecule in the biosphere (Duchesne and Larson 1989).

Morowitz (1968) presents thermodynamic calculations illustrating how energy flow stimulates chemical interactions and creates molecules with higher potential energy. From chemical interactions taking place within the volcanic gas mixture given in Table 1.1, molecules such as methane and ammonia will result. These molecules are thought to have been major constituents of the early atmosphere. Morowitz demonstrates mathematically that, with energy flow

Table 1.2. *The equilibrium concentration of chemical compounds formed in the mixed gas with the composition $C_2H_{10}NO_8$ at 1 atm and 500 °C (from Morowitz 1968).*

Compound	Equilibrium concentration	Compound	Equilibrium concentration
Water	2.24	Glycine	0.48×10^{-21}
Carbon dioxide	0.88	Acetylene	0.11×10^{-22}
Nitrogen	0.50	Lactic acid	0.20×10^{-23}
Methane	0.12	Acetamide	0.11×10^{-23}
Hydrogen	0.18×10^{-1}	Ethylene glycol	0.62×10^{-24}
Ammonia	0.15×10^{-3}	Benzene	0.52×10^{-25}
Carbon monoxide	0.54×10^{-4}	Alanine	0.97×10^{-27}
Ethane	0.34×10^{-7}	Furan	0.14×10^{-28}
Formic acid	0.93×10^{-9}	Pyrrole	0.31×10^{-30}
Acetic acid	0.25×10^{-9}	Pyridine	0.16×10^{-30}
Methanol	0.73×10^{-11}	Cyanogen	0.77×10^{-31}
Formaldehyde	0.13×10^{-11}	Benzoic acid	0.65×10^{-31}
Ethylene	0.88×10^{-13}	Pyruvic acid	0.31×10^{-31}
Hydrogen cyanide	0.73×10^{-13}	Pyrimidine	0.13×10^{-31}
Methylamine	0.64×10^{-13}	Phenol	0.10×10^{-31}
Acetaldehyde	0.81×10^{-14}	Xylene	0.17×10^{-33}
Ethanol	0.49×10^{-15}	Benzaldehyde	0.12×10^{-35}
Acetone	0.92×10^{-17}	Naphthalene	$<10^{-38}$
Ketone	0.19×10^{-17}	Anthracene	$<10^{-38}$
Methyl ether	0.30×10^{-19}	Asphalt	$<10^{-38}$
Formamide	0.24×10^{-20}	Oxygen	$<10^{-38}$

and simple mixtures of gases, increasingly complex molecules are formed. For example, a gaseous mixture of carbon, hydrogen, nitrogen, and oxygen at 500 °C yields mostly water and CO_2 with smaller amounts of other molecules, such as methane and ethane, which have higher potential energy (Table 1.2). The latter molecules are less likely to form because they are larger and therefore more energy is required to create them. As energy flows through the molecular system, however, the energy distribution shifts upward toward more and more complicated molecules.

Morowitz postulates that energy flow through the early atmosphere yielded similar results: starting off with simple low energy molecules such as water, CO_2, and nitrogen, more complex molecules were produced. The production of molecules was driven by the external energy source, which on Earth is the Sun. While some authors suggest that the origin of life by such means contradicts the second law of thermodynamics, what they fail to appreciate is that the second law applies to closed systems. The biosphere is an open system where, so long as energy flow occurs, organization will increase.

Another important physical condition of the early environment on Earth was the abundance of water. It is not surprising that water is still a major constituent of the bodies of living organisms. Given the probable temperatures on Earth at that time, water would be evaporating from some areas, condensing in the atmosphere, and then falling as rain. As it flowed back into the sea, water would dissolve elements from the rocks – elements that would rise in concentration as water evaporated from the ocean again. These elements could interact in solution, and concentrate in locations where seawater was evaporating most rapidly.

Of course, while energy flow tends to produce larger and more complex molecules, there is a natural countervailing tendency – complex molecules will also tend to fall apart into simpler molecules. But here is the crucial point – some molecules will be more stable than others. These stable ones will tend to persist and accumulate. They will steadily become more common than those other molecules that are unstable. It does not require any great scientific insight to appreciate this, nor does it require us to imagine any sort of magical complexity or life force – this process is simply a logical consequence of what we mean by the terms "stable" and "unstable." Nothing lasts forever. Some things fall apart quickly, some things fall apart slowly. So long as both kinds of things are being steadily built by energy flow, the long-lived ones will tend to become more common than the short-lived ones. It is so very simple – yet note that even at the chemical level, long before there is anything that one might be tempted to call life, there is a crude process of natural selection. Some things are surviving longer than others, and hence are becoming more common. Ammonia and methane are two such molecules that likely accumulated in the Earth's early atmosphere.

Once a reservoir of larger and more stable molecules forms, these molecules can in turn interact with each other, yielding molecules with greater complexity and higher levels of potential energy. Like the simpler molecules, these more complex molecules will have varying degrees of stability. Again, molecules that are unstable will fall apart and those that are stable will accumulate. Imagine this process continuing, with increasingly complex molecules forming as a consequence of external energy flow. In this simple scenario, there is ongoing natural selection for stability and persistence, even at the molecular level (Figure 1.1).

Such ideas are based upon thermodynamic calculations, simple chemistry, and logic. Experimental work nicely complements them. In an early experiment, Miller and Urey (Miller 1953) set up a simple atmospheric system with a hydrological cycle (Figure 1.2). Water was evaporated and then cooled and condensed while sealed within glass tubes. Miller and Urey then let the hydrological cycle run, created electrical sparks to simulate lightning (the electrical sparks were used as an alternative to sunlight as a possible external energy source), and found that primitive amino acids formed. This classic

Figure 1.1 Solar energy creates high-energy molecules out of simpler low-energy molecules. Complex molecules and multicellular organisms are inevitable thermodynamic consequences of energy flow in the biosphere. For any arbitrary level of potential energy there is a restricted pool of substrate molecules at the next-lower level, so that even in simple molecular systems a form of resource competition can be observed (from Keddy 2001).

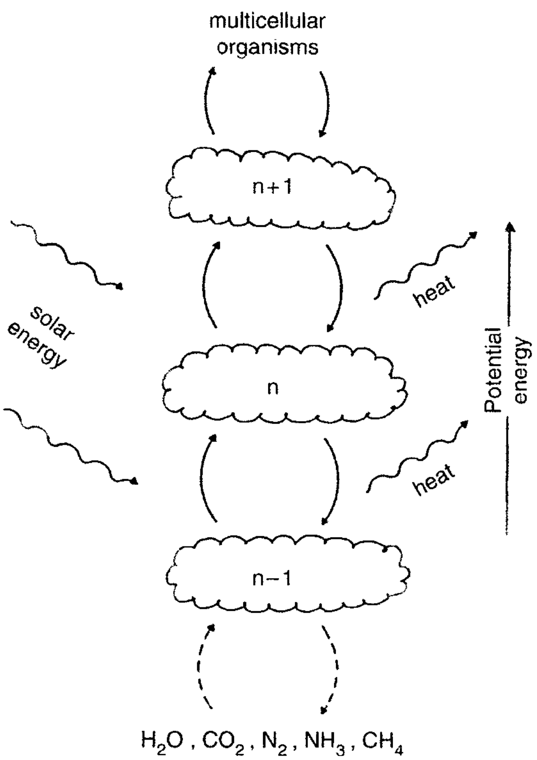
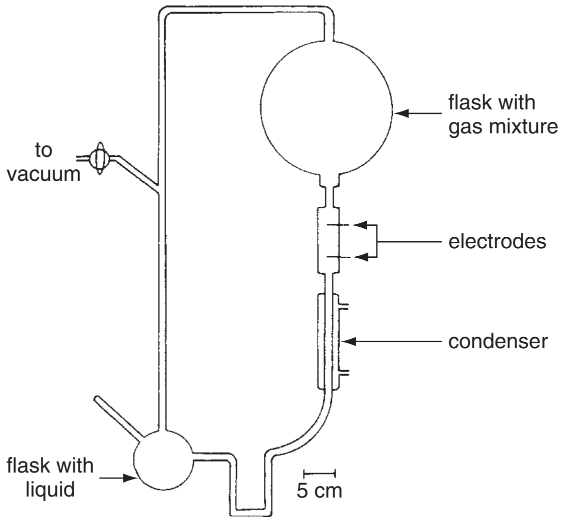


Figure 1.2 The original illustration of the apparatus used in the classic Miller and Urey experiment (from Miller 1953).



piece of work was done in the early 1950s, and it is worth emphasizing that it was done by a graduate student. Miller was fishing around for a research project to do for graduate work and had already tried one project that did not work. Then he and his advisor heard a seminar about early conditions on Earth that stimulated them to try their experiment. This single study led to a large series of experiments wherein researchers created all manner of artificial atmospheres and utilized different types of energy flow to explore what kinds of molecules could be produced.

One could ask what factors might allow complex molecules to further increase in stability and further accumulate. Such factors would likely include: (1) protective walls, (2) the direct use of sources of energy such as sunlight, and (3) the ability to form larger aggregations to buffer against short-term periods of unsuitable conditions. Consciousness would be another step, but this is not a step that plants have taken. In *The Selfish Gene*, Dawkins (1976) argues that consciousness can be thought of as the ability to develop predictive models for future events. For example, if an organism knows that certain conditions are likely to bring winter, then it can store up food. Such ideas will not be explored further here, but Dawkins does raise other issues, one of them being the way in which molecules that copy themselves will proliferate.

Returning to Figure 1.1, let us try to mentally reconstruct the circumstances on Earth some 4 billion years ago. Pools of increasingly complex molecules are accumulating as water evaporates and energy flow stimulates chemical interactions. Molecules that are stable are accumulating, those that are unstable are falling apart. Now consider the possibility of replication. Any molecule that tends to create copies of itself will accumulate more rapidly than other molecules. Dawkins suggests that the occurrence of such replicators was a critical event in the origin of life. Although he uses the word "replication," "reproduction" is the analogous biological term. From this perspective, then, molecular stability is survival, and molecular replication is reproduction. Thus, in a very basic and non-living molecular system, it is possible to find the sorts of ecological and evolutionary processes that occur in whole organisms. Further, one can also find larger ecological processes such as competition and predation (Keddy 1989).

Margulis and Sagan (1986) describe the circumstances on Earth at this time:

> The ponds, lakes and warm shallow seas of the early Earth, exposed as they were to cycles of heat and cold, ultraviolet light and darkness, evaporation and rain, harbored their chemical ingredients through the gamut of energy states. Combinations of molecules formed, broke up, and reformed, their molecular links forged by the constant energy input of sunlight. As the Earth's various microenvironments settled into more stable states, more complex molecule chains formed, and remained intact for longer periods. By connecting to itself five times, for example, hydrogen cyanide (HCN), a molecule created in interstellar space and a deadly poison to modern oxygen-breathing life, becomes adenine ($H_5C_5N_5$), the main part of one of the universal nucleotides which make up DNA, RNA and ATP.
>
> (p. 52)

Now we will turn from this very general discussion of the origin of life and look at more specific issues such as the origin of cellular envelopes, mitochondria, and chloroplasts.

1.3 Membranes

Membranes are essential to all life as we know it, and it seems probable that they originated rather early in the history of life. In the most basic way, there is no life without a membrane to divide the world into inside (living organism) and outside (environment). The importance of membranes is emphasized by Day (1984) in his book *Genesis on Planet Earth*. One line of inquiry into the origin of membranes has examined various colloids, mixtures of finely dispersed organic matter suspended in water. Depending upon the composition and concentration, small droplets called coacervates appear.

Coacervates appear prominently in *The Origin of Life*, published in 1938 by another Russian scientist, Aleksandr Oparin. He too emphasized how energy flow drove the assembly of molecules from elements in the early biosphere, and, like Morowitz, emphasized that life did not arise by chance, but as a consequence of the principles of physics and chemistry. He stresses that "...the formation of complex coacervates ... was unavoidable because their formation requires very simple conditions, merely the mixture of two or more high-molecular organic substances ...." (p. 159)

A good deal of later research examines what kinds of circumstances create coacervate droplets. In some cases, coacervate droplets actually have the ability to grow by absorbing from solutions around them. Under other conditions, coacervate droplets start dividing thereby simulating a simple form of cellular replication. They also have the ability to protect their contents from ultraviolet light irradiation (Okihana and Ponnamperuma 1982). Day argues that coacervates are only pseudo cells, that they look cell-like under the microscope, but that the walls around these coacervate droplets do not behave like or have the structure of the membranes cells have today. He concludes that one must look to other examples for origins of the cellular envelope.

On natural freshwater bodies such as lakes, one finds a surface film that tends to accumulate organic matter; this occurs because of the presence of proteins. Proteins have hydrophobic and hydrophilic components and will orient with the hydrophilic end in the water and the hydrophobic end pointing out. A thin type of membrane results. Day offers a model wherein four steps produce the modern membrane (Figure 1.3): (1) first a surface film forms with the lipid facing the atmosphere and with the protein in the water, (2) turbulence from wind causes the film to buckle, (3) eventually the film buckles so much that the edges of the film touch each other, and (4) finally the air dissolves into the water, leaving a vesicle with lipids inside and proteins outside. This lipid bilayer membrane is one of the most basic structures of life. These lipid bilayers have now been experimentally produced in laboratories and have demonstrated the ability to selectively accumulate certain substances in the