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Editors

Physical and Physiological Forest Ecology

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Preface

Photosynthesis is the source of energy for nearly all life on Earth and the source of the carbon in all the organic compounds within the bodies of organisms. Photosynthesis is the biochemical reaction through which all green plants, including trees, live and grow. We started field measurements of photosynthesis in Hyytiälä, the Forestry Field Station at the University of Helsinki, in the year 1972, and this was the beginning of a still continuing work in the forests around the station. We had the vision that physical and physiological knowledge in addition to the quantitative methods, especially field measurements and dynamic modelling, should have an important role in forest ecology. We introduced into our vision the important role of mass and energy fluxes when we studied the Chernobyl fallout in the summer of 1986. The construction of the SMEAR II measuring station clarified our vision, and we included the fluxes in the soil and between the soil and trees into our approach.

Some members in our team have had good knowledge in tree physiology, and they introduced the physiological aspect into the research. We have been lucky to work with physicists who are deeply interested in the role of physical phenomena in forests. Dr. Taisto Raunemaa (1939–2006) started common projects with us, and the physicists become a natural component in our research team. The co-operation between the Academy of Finland and Soviet Academy of Sciences enabled common research in Finland, Soviet Karelia and Estonia. Physicists, Academician Juhan Ross (1925–2002), Dr. Leo Kaipiainen (1932–2004) and Dr. Tiit Nilson have been the key persons in the team.

The co-operation with physicists was intensified when Dr. Markku Kulmala began to lead the team of young aerosol physics at the Department of Physics, Helsinki University. He was the other principal planner of the measuring systems SMEAR I and II. In addition, he is interested in the role of boreal forest in the formation and growth of aerosols. Dr. Timo Vesala introduced the important role of measurements of ecosystem fluxes with the Eddy Covariance method. He is also interested in the role of nitrogen in forest ecosystems.

The feedback from our measurements has been clear and positive. The developed model structures have been able to explain well the behaviour of trees and ground vegetation in field conditions. We have published our results in international literature, although some of the most relevant papers have remained unpublished in scientific journals. During the last 20 years, we have actively participated into European research co-operation.

The Academy of Finland and Helsinki University have been the main financial supporters during the whole long period.

Our first reader, Dr. John Grace from Edinburgh, has made valuable comments on our manuscript and we express our gratitude to him. We acknowledge Dr. Kourosh Kabiri Koupaei, for his contribution to the editing of the book.

Our book is the summary of our work during 40 years at the present Department of Forest Sciences, previously Department of Forest Ecology and Department of Silviculture at Helsinki University. Our vision stressing the importance of physics and physiological knowledge, quantitative methods, material and energy fluxes and field working in the forests has had the central role in the planning of the research.

Helsinki
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Chapter 1
Introduction to Physical, Physiological and Causal Forest Ecology

Pertti Hari, Liisa Kulmala, and Mikko Havimo

Contents

Abstract H. T. Odum proposed that energy flows are the key factors in understanding the interactions between ecosystems and their environment. He used electric analogue models and analogue computers in his approach. The development of quantitative methods, measurements, dynamic modelling and digital computing, has opened novel possibilities to analyse the energy and material flows between living organisms and their environment. In addition, the applications of ecological knowledge to the responses of forests to present climate change and forestry should be based on causal effects in trees, atmosphere and soil. The conservation principle of mass and energy, a cornerstone of Newtonian physics, results in dynamic models that can utilise physiological and physical background knowledge to provide causal explanations for the theory and models. The aim of our book is to develop and test a quantitative and causal theory of forest ecology that utilises physics and physiology as background knowledge.

Keywords Mass and energy fluxes • Physical knowledge • Physiological knowledge • Conservation principle

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1.1 Climate Change: A Challenge for Forest Ecology

The atmospheric CO_2 concentration has increased from 280 ppm (parts per million) to nearly 400 ppm during the last 200 years due to use of fossil fuels and deforestation. The increase continues at a rate of nearly 2 ppm annually. The extra CO_2 in the atmosphere reduces the thermal radiation escaping from the planet, and this inevitably causes an increase in temperature: the observed increase in the global mean temperature is nearly 1°C over the last century, very similar to the increase expected from climate modelling. As concentrations of CO_2 in the atmosphere continue to increase, the rise in temperature is expected to continue (IPCC 2007).

The forests of the world respond to the changes in the atmospheric CO_2 concentration and temperature: photosynthesis, for example, is enhanced and decomposition of organic matter in the soil is accelerated. Thus, trees have more raw materials for growth and the carbon pool in the soil is reduced. These changes generate a complicated web of responses to climate change in forests.

The forests have several important effects on the atmosphere by, for example, storing carbon, transpiring water and absorbing solar radiation. All these responses affect the climate change generating feedbacks from forests to climate change. The role of the feedbacks is under debate.

Ecology may be defined in several different ways, with different emphasis on the biological versus the physical and chemical aspects. The idea is, however, rather consistent in the different versions. Ecology studies the interactions between living organisms and their environment and the distribution and abundance of living organisms.

Knowledge on the interactions between forests and their environment is needed for the proper analysis of climate change, for example, because the responses of forests and other carbon-rich ecosystems play an important role in the global climate models (GCM). However, the forests are treated very roughly in the GCMs, and they introduce additional uncertainty in the simulations of the expected climate change.

1.2 Quantitative Knowledge in Ecology

For ages, human activities such as agriculture, fishing and hunting have been built on practical experience of the natural world. Ecological knowledge as a science grew slowly within biology during the early twentieth century gaining momentum in the later part, to some extent due to environmental movement. The present climate change and its effects on life on the Earth have further increased the need of causal understanding of the interactions between living organisms and their environment.

A qualitative approach dominated ecology in the early phase of the discipline. Typical studies of this era were the exploration and classification of plant communities, which resulted in definitions of vegetation zones and forest site types.

The still ongoing classification studies have successfully systematised the versatile life formations, but on the other hand, they have rarely given causal explanations on the interaction between organisms and their environment.

The quantitative ecological tradition developed parallel with the qualitative one. Alfred J. Lotka (1880–1949) pioneered in the field of quantitative ecology already in the early twentieth century. His famous predator–prey model is still in common use. System analysis and dynamic modelling were emerging methods in studying complex systems in 1950s. At the time, H. T. Odum (1924–2002) greatly influenced the development of ecology by applying physical principles and studying energy flows in ecosystems. He stressed the importance of emergent properties in large and complex systems. He also realised that it is not possible to derive the behaviour of ecosystems only from detailed knowledge concerning small objects in the system. The classical physics, especially electronics, played an important role in his thinking.

H. T. Odum based his models on the flows of energy using electric analogue, especially Ohm's law that describes electric current with resistors and voltages. These models were rather easy to construct, but the analogue of ecosystems with electric systems was not explicit and required rather strange concepts. The causal interpretation of the models was, in most cases, impossible, and the applications of the models were problematic. In addition, the analogue computers of his day were inadequate for further development of this technique. Moreover, the present numerical methods were not available 50 years ago. Therefore, the proper analysis of the energy flows in ecosystems was impossible with the methods available in 1950s and 1960s.

H. T. Odum widely utilised physical knowledge and methodology and applied them in an ecological context, but he knew rather little about the metabolism of living objects. It was not until the 1970s that the new research disciplines of ecophysiology and physiological ecology were introduced. Sporadic field measurements and experiments were used to study the relationships between metabolic activity and environment. Photosynthesis, for example, received much attention following the development of the infrared gas analyser. The results were used in an attempt to understand ecosystems, and they were applied even at the global scale, but the problems with transitions between scales and emergent properties were omitted rather commonly.

The lack of causal and emergent features is the major problem when extrapolating sporadic experiments and measurements on ecosystem and global scale. Applications such as studying the responses of forests to climate change and silvicultural actions require causal interpretation of the available knowledge. In addition, the emergent properties should be properly understood so that they can be introduced, too. Theoretical knowledge is needed to bridge fieldwork with the applications on very aggregated levels. However, theoretical work has received rather limited attention in forest ecology during the last decades.

1.3 Energy and Material Fluxes Through Ecosystems

Ecology includes research of a very versatile set of phenomena from predator–prey interactions to photosynthesis. Earlier, the focus was often on the interactions between animals whilst the vegetation played a minor role. However, the role of mammals and birds in forest ecosystems, for example, is generally small as their masses per hectare are negligible when compared with that of vegetation. The material and energy flows through mammals and birds are very small as well, although of course these organisms may exert a disproportionate effect on ecosystems as, for example, through dispersal of seeds and their role as ecological engineers.

Metabolism of living organisms synthesises numerous and often complicated molecules from simple substances such as carbon dioxide (CO_2) and water, utilising the energy captured from the solar radiation. The synthesised molecules are used by organisms to construct new leaves, roots, etc. or store energy for metabolic needs.

Metabolism and physical phenomena generate concentration, temperature and pressure differences that call for mass and energy fluxes between vegetation and environment at several spatial scales. These fluxes convey the interactions between living organisms and their environment. Water uptake by roots and loss in transpiration are the biggest mass fluxes, whilst carbon dioxide intake by leaves is the second biggest one. The nutrient flux from soil to vegetation is rather small in terms of mass, but very crucial in the functioning of plants. All the fluxes originate from the energy input by solar radiation. The heat exchange between vegetation and the atmosphere is also large (Fig. 1.1).

Long distances between the locations of material and energy inflows and their usage call for a need of transport within living organisms. The water uptake takes place in roots whilst transpiration occurs in leaves. The distance between these places is often over 10 m in trees and up to 100 m in the tallest trees; thus, an efficient water transport system is needed. Sugars, formed in photosynthesis, are the main building block in the synthesis of large molecules, and sugars are also used to store and release energy for metabolism. Thus, the distance between the formation and usage of sugars is large, and so an efficient transport system for sugars is necessary as well.

The forest stand components – trees, ground vegetation and soil – are interacting with each other and the atmosphere. A stand interacts very little with the neighbouring forests since the connecting material and energy fluxes are usually small. The material and energy fluxes between large forested areas and the atmosphere can be obtained as the sum of the fluxes from the separate ecosystems in the area. Thus, a forest ecosystem should be in the focus of forest ecological theory.

In several milliard years of evolution, organisms have developed the means to control the flows of material and energy between the organisms and their surroundings as well as within their own structures. For example, there are small pores in leaves that serve to reduce the evaporative loss of water in transpiration

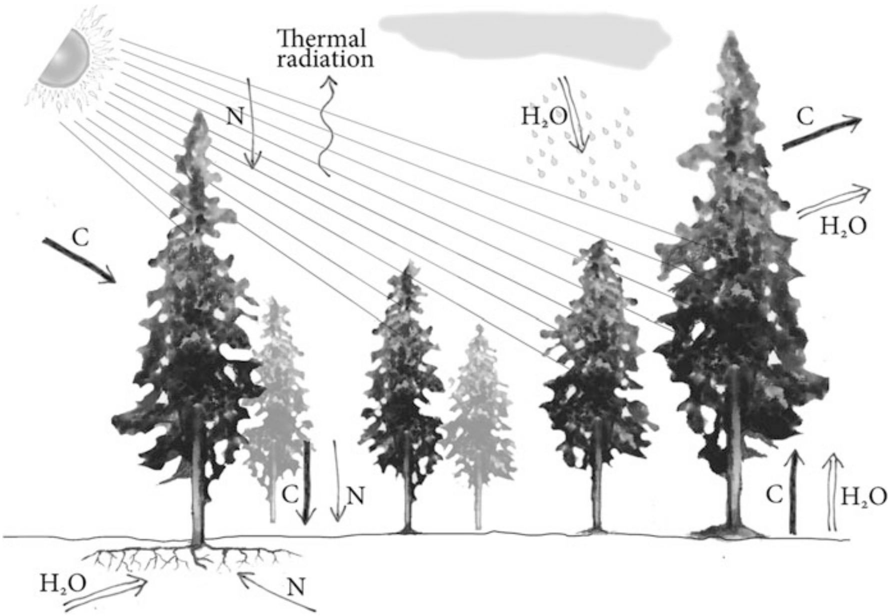

Fig. 1.1 Interactions in a forest ecosystem. Solar energy, carbon (C), nitrogen (N), water (H_2O) and thermal fluxes connect the forest with the atmosphere

and simultaneously allow the intake of carbon dioxide. The exchanges of water and carbon between leaves and atmosphere are thus intimately linked. The surfaces of roots have special structures for capturing water and nutrient, whilst in the leaves pigments are present to capture the radiation energy. Complex biophysical and biochemical systems convert the captured energy into a chemical form that can be used by the plant to build its structure.

Novelty in metabolism and transport arises during evolution. These novelties are tested against the prevailing ones. If the novelty is more efficient than the present one, it has a tendency to become more common and later it may replace the older one. This development of novelties and their continual testing against the prevailing ones lead to slow improvement, and therefore, efficient mechanisms for metabolism and transport have developed in evolution.

Conservations of mass and energy are cornerstones of Newtonian physics. The theory of relativity replaces these conservation principles with more general ideas, but Newtonian physics and the theory of relativity do not differ from each other under normal macroscopic conditions on the Earth. Evolution has a similar fundamental role in ecology. Biological entities are results of evolution during the past milliard years, and their properties should be considered in the evolutionary framework. If any consideration in ecology is in conflict with the conservations of mass or energy or with evolution, it should be rejected as fundamentally erroneous.

1.4 Towards Physical and Physiological Theory of Forest Ecology

The methodological and technological progress during the last few decades has created novel possibilities for ecological research. System analysis and dynamic modelling enables better processing of theoretical ideas. The efficiency of digital computers is usually sufficient for calculations. Numeric methods allow solution of equations, and automatic monitoring systems can be used to measure material and energy fluxes in ecosystems and between ecosystems and the atmosphere. These novel possibilities should be fully utilised in ecological research.

We are facing unprecedented climate change: the forests will respond to the changes in the composition of the atmosphere, in temperature and in rainfall. The responses of forests generate feedbacks to the climate system. To quantify these feedbacks, we need understanding of the metabolic and physical responses to environmental change as well as interpretation of the changes on the ecosystem and global levels. Providing the urgently needed knowledge, with a sound physiological and physical basis, is the challenge for ecological research in the near future.

We wanted to explore the possibilities that the development of research methodology and technology together with physical and physiological knowledge has opened for forest ecology. *The aim of our book is to develop and test a quantitative and causal theory of forest ecology that utilises physics and physiology as background knowledge*. The flows of material and energy combined with the conservation principle play a key role in the analysis of different phenomena such as photosynthesis, respiration and transport of water or sugars. Efficient metabolism and transport structures have arisen in the evolution.

Reference

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Chapter 2
The Approach to Construct and Test the Theory of Forest Ecology

Pertti Hari

Contents

Abstract This chapter gives the main lines of biological and methodological thinking applied in the whole book. The vision that mass and energy fluxes convey the interactions between forest ecosystem and its surroundings at different levels is the starting point of the theory formation. We formulate a common framework, called cover theory, to deal with different phenomena in the ecosystem. We analyse the fluxes generated by metabolism, and we use conservation of mass and energy for derivation of differential equations to describe each phenomenon under study. We test the dynamic models with field data to obtain feedback from nature. Finally, we combine the theories to form the physical and physiological theory of forest ecology.

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Keywords Vision • Cover theory • Background knowledge • Basic concepts and ideas • Dynamic models • Field test • Corroboration

2.1 Outline

Forests are complex ecosystems including very different groups of organisms ranging from trees to soil microbes. Thus simultaneous, comprehensive and coherent treatment of the versatile phenomena in ecosystems is needed, and it can be obtained with a hierarchy of theories: *The cover theory* outlines the great lines of research, and *specific theories* deal with different phenomena within the cover theory. From the coherent framework of theories, it follows that the methods, i.e. modelling and measurements, share a common basis, and the tests of specific theories with field measurements are based on the same approach. The construction of specific theories under the guidance of the cover theory and common methodology allows proper flow of knowledge in all research concerning these versatile and complex forest ecosystems and the formation of the general theory of forest ecology.

The construction of the cover theory begins with the formulation of the vision that outlines roughly the most essential features in the interactions between forest ecosystems and their environment. It introduces in general terms the framework for the theory. Theories of physics, physiology, chemistry, anatomy and evolution provide essential background knowledge. The definition of *basic concepts* introduces tools for clarifying the vision. Basic concepts allow the formulation of the *basic ideas* to express the most essential relationships in a more exact form.

The cover theory is too general for research into all the different phenomena in trees, in ground vegetation and in soil. Therefore, specific theories are needed to be formulated and specified under the guidance of the general ideas presented in the cover theory. The specific basic concepts and ideas outline the thinking in the studies of each phenomenon, and they are intended to capture the most essential features of the study object. The construction of theoretical models is based on the analysis of material and energy fluxes and conservation of mass and energy resulting in differential or difference equations that can be tested with field measurements. The relationship between specific theories and the cover theory is visualised in Fig. 2.1.

The formation of specific theories proceeds via basic concepts and ideas to the formation of theoretical models. We need feedback from forests to evaluate and develop the theory formation. The severe testing of theoretical models puts strict requirements for the data to be used. The arrangement of measurements is a highly technical but necessary sidetrack in the theory formation. Tests of theoretical model with high-quality data are the last phase in clarifying the theory. The feedback from test to the previous phases in the theory formation is essential. The different steps in the theory formation are visualised in Fig. 2.2. The feedback from the test will result in improvements of the theory. Our methodological approach follows the ideas presented by Tuomivaara et al. (1994), Bunge (1996) and Hari (2008).

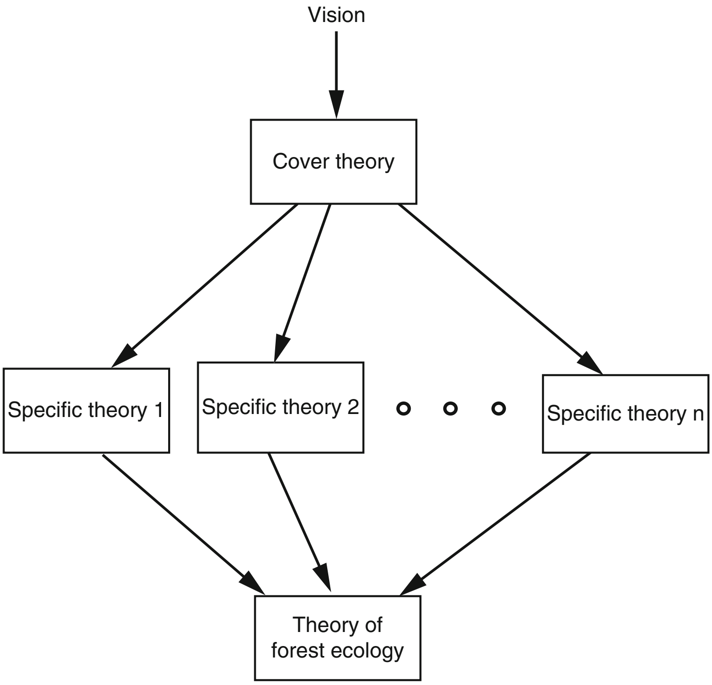

Fig. 2.1 The relationship between the cover theory and specific theories. We construct specific theories in the common framework provided by the cover theory. In this way, we can combine a coherent set of specific theories that enable knowledge flow between specific theories and construction of the theory of forest ecology. *Boxes* describe theories and *arrows* the flow of knowledge

2.2 Cover Theory of Forest Ecosystems

2.2.1 Vision

Solar radiation is the source of energy in forests. Vegetation has specialised structures that are able to convert energy in light quanta into a chemical form that is stored as carbohydrates such as sugars and starch. The chemical energy in sugars is further utilised in the synthesis of large carbon-, hydrogen- and oxygen-rich molecules. In addition, small amounts of nitrogen, phosphorus, potassium and other elements are needed for biosynthesis and the formation of special structures in vegetation. The metabolism of vegetation and microbes consumes O_2 and produces CO_2, H_2O, NH_4 and other simple compounds or ions generating material fluxes between forests and their environment. Already over 50 years ago, H. T. Odum stressed the important role of material and energy fluxes between ecosystem and their environment.

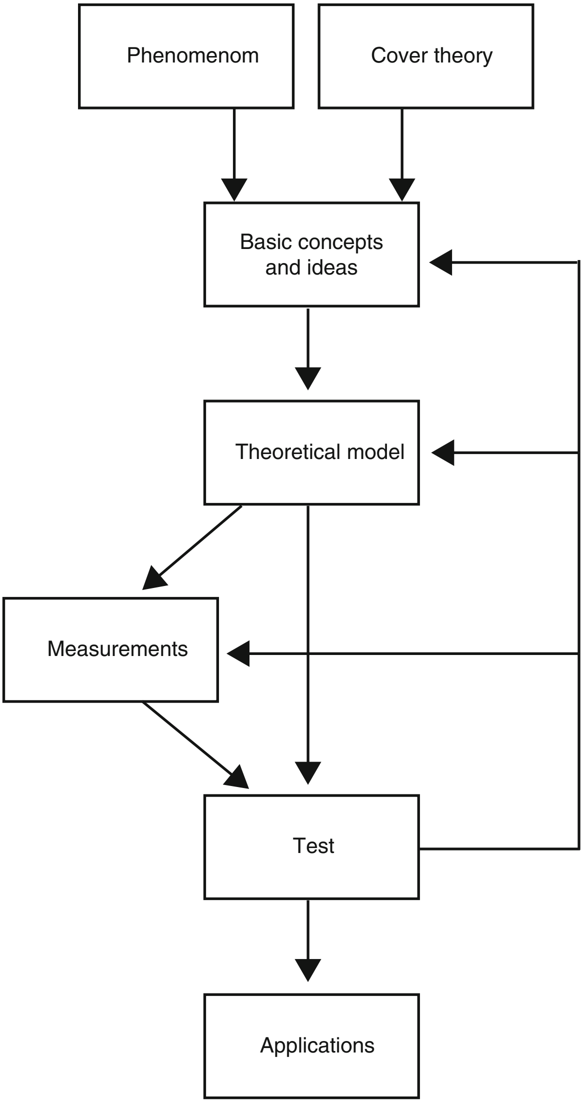

Fig. 2.2 The phases of formation of the specific theories utilising the cover theory as backbone. The feedback from the test to theory development and measurements is essential for the progress of the research. *Boxes* describe phases in the research and *arrows* the flow of knowledge

The physical distance for transport between sites of material intake and usage is in tall trees often over 20 m. Trees have effective transport structures connecting the roots and leaves with each other.

The strong annual cycle caused by the orbiting of the globe in a tilted position around the Sun is a stable characteristic for the Earth's environment. Forests have to tolerate the regular alternation of favourable and critical conditions during each year, and living organisms have means to cope with the cyclic behaviour in the environment.

Vegetation and microbes in soil have developed by evolution since the beginning of life on the Earth. The slow development during milliards of years has generated strong regularities in the structure and metabolism of living organisms. Evolution provides important insights into the present metabolism and structure of forests.

Conservation of energy and material, the cornerstone of Newtonian physics, is also a valid principle in the metabolism of vegetation and microbes in forests. Metabolism and physical phenomena convert material and energy in other forms, but the atoms and energy do not disappear. Both the environment and the state of the vegetation have effect on the conversion of material and energy, and by that they provide the causal explanations for the phenomena in forests.

The variation in the involved temporal and spatial scales is huge: from picoseconds in photosynthetic light reactions to century in the growth of a forest stand and from micrometres in the cell to hundreds of kilometres in a vegetation zone. Individuals are the basic units of the forests; they have complicated fine structure for metabolic tasks.

The vision outlines the basic features in forest ecosystems in very general form. These general ideas guide the formation of the theory of physical and physiological forest ecology. We proceed stepwise in the theory formation from background information, via definition of concepts, basic ideas and formulation of dynamic models, to their testing to give more concrete form to the vision.

2.2.2 Background

The physical and physiological theory of forest ecology utilises knowledge from very different disciplines as background. However, physics and physiology play dominating role in the argumentation.

Living organisms in forests have special structures to convert energy from light to chemical form and to utilise that chemical form in their metabolism. The intake and release of material and transport within trees take place as well via specialised structures. The discipline of anatomy provides an important insight into these rather complicated features of living organisms.

Several steps are involved in the conversion of solar energy into chemical energy as sugar. Vegetation synthesises a large number of macromolecules from sugars and ions. Each step in photosynthesis and in the synthesis of macromolecules is based on specialised enzymes, membrane pumps or pigments. The chains of steps are well balanced in such way that the sequence runs smoothly from the first step to the final product.

The enzymes, membrane pumps and pigments needed for the synthesis of new compounds are unstable proteins. They are unstable in the sense that they are fugitive over time. Their amounts and activation states fluctuate; thus new ones must be synthesised to replace the damaged ones and maintain the proper amount or activation state. This is a very demanding task for the metabolism of cells.

The annual cycle in light, temperature and other properties in the environment is an additional challenge for the metabolism of vegetation and microbes. Living processes and life in general must utilise effectively the favourable periods and tolerate the hard conditions during winter or drought. This is an additional complication in the control of the concentrations and activities of enzymes, membrane pumps and pigments. Physiology is the discipline that provides insight into the metabolism of vegetation and microbes.

Metabolism and physical phenomena generate concentration, temperature and pressure differences that cause diffusion or convection flows of mass and energy within individuals and between forest ecosystems and the environment.

The fundamental principle, conservation of mass and energy, allows the combination of metabolic and physical phenomena in a chain of conversion of energy or material. In this way, the causal relationships are introduced into the theory of forest ecology.

Effective structures, metabolism and control of enzymes, membrane pumps and pigments have developed in evolution.

Instrumentation has developed very rapidly during the last decades, and several phenomena can rather easily be measured in forests. Thus we can obtain important feedbacks from material and energy fluxes to theoretical thinking. This novel instrumentation is based on the discipline of electronics. Physical knowledge is essential for the proper understanding of fluxes, causality and electronics.

2.2.3 Basic Concepts

The construction of the cover theory begins with the definition of basic concepts. They are needed to cover the most important aspects in the interactions between forests and their environment. We should be able to introduce such concepts that characterise the most important ecological phenomena and that enable effective utilisation of the background knowledge.

The definition of basic concepts begins with the introduction of process. Large carbon molecules are characteristic for trees and other living organisms in forests. They are formed in the metabolism in long chains of biochemical reactions. The concept process is defined to characterise the conversion of material and energy in the metabolism and physical phenomena. Thus a *process*, by definition, converts material and/or energy into a new form or moves material through a membrane. For example, sugars are formed in photosynthesis from carbon dioxide and water using solar energy. Thus photosynthesis is a process according to the definition in the cover theory. Similarly, formation of new tissues and nitrogen uptake by roots are processes. They are characterised by the amounts of material converted to new forms or penetrated through a biological membrane. Processes are quantified by the fluxes of material or energy generated by the process under consideration.

The processes respond to the environment and also to the state of the living organisms. Thus concepts are needed to characterise the environment and the state of the living individual. *Environmental factors*, by definition, are those features in the environment that have effect on the processes. For example, light intensity, temperature and carbon dioxide concentration have substantial effects on photosynthesis. Thus at least these three are environmental factors.

Stable carbon compounds form the *structure* of living organisms. Cells are basic structural units of living organisms. Similar cells form tissues: They build up organs and finally organisms to form ecosystems. The structure involves several levels that have their characteristic phenomena. Geometrical features, chemical composition and mass characterise the structure.

Metabolic processes are non-spontaneous and special biological structures make them possible. *Functional substances* enable the metabolic processes in living organisms. Most of the structure of plant cells is formed by cell walls and lipid bilayers, which are passive skeletons for the metabolism. All biochemical processes have specific catalysing enzymes, membrane pumps actively transport material through membranes, and pigments capture light quanta. Thus enzymes, membrane pumps and pigments form the functional substances, and they play a key role in the utilisation of physiological knowledge in the formation of our forest ecological theory.

Functional substances are often non-stable large molecules; thus their lifetime is shorter than that of cell walls. In addition, the functional substances have often active and passive forms. Thus synthesis, decomposition, activation and deactivation of functional substances must take place in all living cells. Several processes and subprocesses are interrelated, and the functional substances of different processes and subprocesses have to match with each other to produce balanced metabolism, and the functional substances form large chains and webs to fulfil the metabolic needs. Living organisms have proteins, under the control of genetic system, that synthesise, decompose, activate and deactivate the functional substances. We call, by definition, these proteins and their genetic background as a *biochemical regulation system* and their action as *regulation*.

The metabolism of living organisms and physical phenomena convert material and energy to other forms. Thus metabolism and physical phenomena require new material or energy often from distant places. *Transport* moves material or energy in space. The long distances to be traversed by materials within trees have intrigued scientists for a long time, and transport phenomena are still being actively researched. *Fluxes* are material or energy flows per a unit of area during a unit time. Transport plays an important role when physical knowledge is utilised as background knowledge in ecology.

Forest ecosystems are very versatile and size differences between acting individuals are huge, ranging from microbes to large trees. In addition, the timescale runs from picoseconds to 100 years. Thus we need means to handle all these different space and timescales. An ordered structure is called a *hierarchy*. Proper knowledge flow between the different hierarchical levels of our analysis allows utilisation of knowledge gained on detailed level in the analysis at more aggregated one.

Forest ecosystems are complex hierarchical systems, and several simultaneous phenomena occur in the hierarchy. The interactions at lower levels generate new phenomena and properties at higher levels. These novelties are *emergent properties* in the system. There are several definitions of the emergence, and our definition is often called as weak emergence. The characteristic emergent properties at each level in the hierarchy should be identified and introduced into the treatment of phenomena.

The globe has orbited the Sun during the whole period of development of life on the Earth. This is why biochemical regulation systems have developed in evolution to cope with the very regular and strong annual cycle of light and temperature that is a characteristic feature of the environmental factors. The *annual cycle of metabolism* covers the changes in the biochemical regulation systems, in functional substances and in structures matching vegetation with the annual cycle of environment. The processes in living organisms have their own annual cycle since biochemical regulations system changes the concentrations and activities of the functional substances.

Besides the annual cycle, there are slow (i.e. during the lifetime of individuals) and irregular changes in the environment such as extreme weather events. *Acclimations of processes* are changes in functional substances and in the biochemical regulation system matching processes in vegetation with the slow and irregular changes in environment. *Acclimations of structure* are slow changes in structure matching it with irregular changes in the environment such as changes in light environment after collapse of a neighbour tree. In contrast to adaptations, which occur over evolutionary timescales, acclimations occur over days, months and years, and they do not involve alterations in the genetic composition.

Vegetation synthesises annually large amounts of energy-rich macromolecules, especially into cell walls. The senescent tissues are the source of energy and raw material for life in the soil. In *decomposition* microbes transform the large organic molecules into smaller molecules that are utilised in the microbial metabolism. The nutrients in the senescent tissues are released into the soil, and they are available for reuse by the vegetation.

Individuals are the fundamental functional units in a forest ecosystem, they are first born, and they metabolise and finally die. The ecosystem is not only the sum of the individuals but novel features emerge. The effects between individuals in an ecosystem are called *interactions*. The behaviour of the individuals determines the interactions, but they are characteristic for the ecosystem. The reduction of photosynthesis in the canopy caused by shading is the dominating interaction in forest ecosystems.

The regularities in phenomena in forests can now be analysed with the basic concepts: process, transport, environmental factors, hierarchy, regulation, annual cycle, interaction, emergence, acclimation and decomposition. The basic concepts are used to characterise the essential features of the study object. Visual symbols for most of the basic concepts are introduced (Fig. 2.3) to clarify the ideas dealing with the behaviour of the object. Material/energy flows, process, biochemical regulation system, transport, structure and functional substances have their own symbols in the visual language; thus flows can be visualised utilising physiological, physical and anatomical knowledge as background in each phenomenon under study.

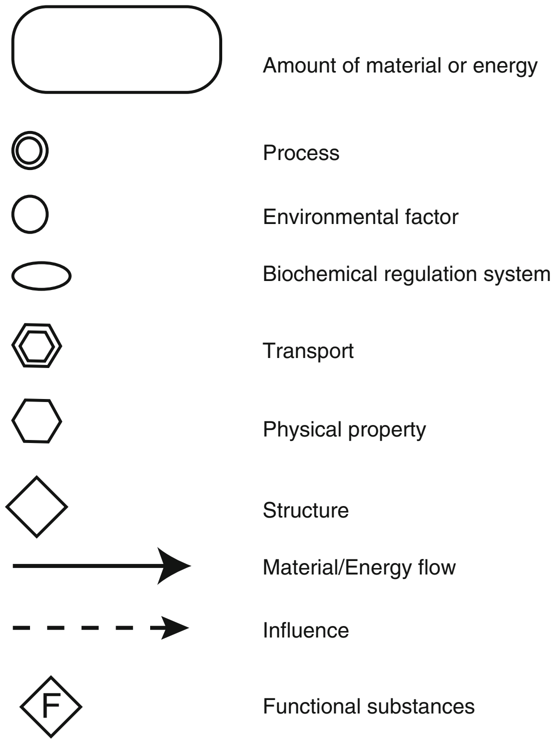

Fig. 2.3 Symbols describing the basic concepts to be used in the visualisation of theoretical ideas

2.2.4 Basic Ideas

The basic ideas link the basic concepts with each other and they enable the clarification of the vision. The basic ideas in the cover theory are:

1. The environmental factors vary greatly both in time and space. The orbiting of the globe around the Sun generates strong annual cycle, whereas the spinning of the globe creates strong daily cycle in environmental factors such as light and temperature. Spatial processes give rise to spatial and temporal variation in environmental factors. For example, photosynthesis decreases and respiration increases the surrounding CO_2 concentration near leaf surface.
2. The determination of environmental factors is problematic due to their great variability in time and space. Environmental factors can be well defined only in sufficiently small space and time elements. The scales of the environmental factors determine the most detailed level in the hierarchy. The great variability is characteristic for light, but also, e.g. concentrations and temperatures vary strongly in space and time.
3. The properties of the environment and of living organisms are reflected in the metabolism of living organisms. Environmental factors and the functional substances determine the conversion of material and energy in processes.

The relationships between processes and environmental factors can be determined properly only at the level of space and time elements due to the great variability of environment. The space and time element has to be so small that the variation in environmental factors is negligible within the element.

4. Cells (space element), individuals and ecosystems are natural spatial units. The metabolism responds very rapidly to environmental factors, i.e. during a short time element. The other evident timescales are year and rotation period. Thus the spatial levels of hierarchy are space elements of tissue, individual and ecosystem. The temporal levels of hierarchy are time element, year and rotation period. The flow of knowledge between the hierarchical levels, especially from detailed to more aggregated ones, is important in the analysis of the interactions between ecosystems and their environment.
5. The short lifetime of functional substances calls for a need to maintain the concentrations of the enzymes, membrane pumps and pigments in a long chain of steps generating the metabolic process. The biochemical regulation system synthesises, decomposes, activates and deactivates the functional substances. The actions of biochemical regulation systems keep the concentrations of the functional substances stable or change them, and the resulting regularities in the involved functional substances are emergent properties. The changes in the concentration or activity of functional substances are reflected in the effects of environmental factors on processes.
6. Material and energy fluxes mediate the interactions between ecosystems and their environment. In addition, the material fluxes within individuals are important due to the long distances between the locations of production and consumption. This is why transport plays a key role in forest ecology. Physical properties such as pressure, temperature or concentration difference generate material and energy fluxes, and in this way, physical knowledge is necessary in forest ecology.
7. Living organisms are the consequence of evolution over milliards of years. The emergence of novel features and their test against the existing ones result in effective metabolic, structural and regulation solutions. Thus efficient processes, transport structures and biochemical regulation systems have developed during evolution. Efficient solutions can, at least in some cases, be found as mathematical solutions of optimisation problems.
8. The strong and regular annual cycle in environmental factors has been a characteristic feature in the environment during the entire period of evolution, and a clear annual cycle in metabolism has developed to utilise the regular sequence of favourable and critical periods. In addition, the annual cycle of metabolism has been well tested during evolution, and it enables individuals to utilise the very regular alternation of warm and freezing or rain and dry periods in the climate of forests.
9. Acclimations are common in forests and they benefit the individuals since most of them have been tested in evolution. The acclimations of processes, structures and biochemical regulations have been tested during evolution only if the environmental factors generating the acclimation have varied during

the lifetime of individuals. Responses to increasing shading and drought are examples of well-tested acclimations. The atmospheric CO_2 concentration has varied considerably during the last million years, but during the lifetime of individuals, the concentration has been stable due to slow concentration changes. The present increase, about 100 ppm/100 years, is outside the range tested during evolution. Thus acclimation to CO_2 can benefit or harm the individual, and the predictions of the acclimations of forests to increasing CO_2 are problematic.

10. Important metabolic processes and transport phenomena have their own specialised structures. Actions of the biochemical regulation systems, together with the genetic code, determine the properties of the structure. The resulting regularities in the tree structure are emergent properties. The genetic code determines the great features, and regulation tunes it to the prevailing situation resulting in acclimations of the structure.
11. The interactions between individuals in a forest ecosystem are numerous and versatile. However, some interactions are more important and dominate the development of the forest ecosystem. Environmental factors convey the interactions in a plant community. Extinction of light and reduced photosynthesis in lower parts of a canopy is the most important interaction. The spatial variation in other environmental factors, especially between individuals, is small, and the different plants experience about the same environment. Thus spatially homogeneous environment is unable to convey interactions between individuals.
12. Conservation principles are cornerstones of Newtonian physics, and huge evidence has piled to support this theoretical idea. The living objects cannot violate the fundamental physical laws. The form of chemical compounds and energy may change, but the overall number of atoms and the total amount of energy do not change during processes or in transport.
13. The flow of information from the space and time element to the ecosystem level plays an important role in the analysis of the fluxes between forest ecosystems and their environment. However, it is very problematic to utilise detailed knowledge at the aggregated level, because the analyses become heavy and the small details easily hinder the researcher's view of important aspects. There are emergent properties at the various levels in ecosystems, and these new features allow the utilisation of the detailed knowledge at lower level in the hierarchy in condensed forms. The emergent features should be carefully analysed at each level, and the possibilities to utilise knowledge on more detailed level as emergent properties should be carefully analysed.
14. The carbon flow through ecosystem and circulation of nitrogen within the ecosystem, via photosynthesis, synthesis of macromolecules and finally decomposition of macromolecules in soil by soil invertebrates and microbes, are characteristic features for forests. In the soil, microbes decompose the macromolecules through the action of extracellular enzymes and utilise the resulting small energy-rich molecules in their metabolism. Without microbial activity, the organic matter would accumulate in the soil and nutrient cycling would be impossible.