Simulation modelling of fynbos ecosystems: Systems analysis and conceptual models

F J Kruger, P M Miller, J Miller, and W C Oechel (eds)

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PREFACE

In the southern and south-western area of the Cape Province, South Africa, there is an exceptionally rich flora of sclerophyllous shrublands and heathlands known locally as fynbos. The flora and fauna of the various fynbos ecosystems are of considerable scientific and aesthetic interest and the mountain catchment areas of the fynbos biome are of particular economic importance both as sources of water and as recreational areas.

This unique area has been the focus of considerable research in the past and in order to synthesize available scientific information, coordinate current activities, and to stimulate new research within the region, the Fynbos Biome Project was initiated in 1977.

The Fynbos Biome Project is one of several national scientific programmes within the National Programme for Ecosystem Research administered by the CSIR. The National Programme is a cooperative undertaking of scientists and scientific institutions in South Africa concerned with research related to environmental problems. It includes research designed to meet local needs as well as projects being undertaken in South Africa as contributions to the international programme of SCOPE (Scientific Committee on Problems of the Environment), the body set up in 1969 by ICSU (International Council of Scientific Unions) to act as a focus for international non-governmental scientific effort in the environmental field.

This report is the first step in the development of a systematic approach to a synthesis of knowledge of the fynbos biome. The approach is based on simulation models which were developed over nearly 20 years and used in a diversity of biomes. Developing mathematical simulation models is a final, but not necessarily the most important, product of a systems analysis of an ecosystem. First the goals of the modelling and then the boundaries of the system to be modelled must be defined. This document deals with these two initial steps and presents preliminary word models that were modified or developed for application in the fynbos biome.

A second report describing the programming code and the parameter values used in the models will be written once the word models described here are fully formalized as mathematical models. The results of simulations directed toward testing specific hypotheses will also be presented in this second report.

Parallel development of compatible models in the chaparral of southern California and other mediterranean climate ecosystems will eventually provide a quantitative basis for comparing mediterranean-type ecosystems. These models should be thought of as dynamic, since they will be continually improved as the understanding and hypotheses about ecosystem dynamics develop. The insights gained during the process of modelling are far more valuable than the accuracy of the final product.

ACKNOWLEDGEMENTS

On behalf of myself and my family I would like to thank all those individuals and institutions who made possible our visit to South Africa to work on this project. I would especially like to thank Fred Kruger and the Directorate of Forestry of the Department of Environment Affairs, who extended the original invitation, and who have assumed the burden of financing the project, which, being of a theoretical nature, sometimes appears to be making little progress. I would also like to thank Margie Jarman and the Fynbos Biome Project, CSIR who provided the link with the "other half" of the fynbos research community and whose support and funding has also allowed one review of the project by international scientists interested in mediterranean-type ecosystems.

Finally, the computers which make this type of research possible need to be acknowledged, as do the owners of the fingers who get the computers and word processors to behave, namely Lisa Klaussner (Department of Environment Affairs) and Elma Mantle (CSIR). Pascale Chesslet and Pat Beeston (University of Cape Town) deserve thanks for undertaking the drawing of all the figures in the report; and Pat Beeston, in addition, for undertaking copy proof reading in the latter stages of production.

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1984

ABSTRACT

This report outlines progress with the development of computer based dynamic simulation models for ecosystems in the fynbos biome. The models are planned to run on a portable desktop computer with 500 kbytes of memory, extended BASIC language, and advanced graphic capabilities.

The FYNBOS model, which simulates seasonal ecosystems dynamics, is the central model of the Project. This model consists of 14 submodels of major ecosystem processes: climate; soil water balance; energy balance; decomposition; nitrogen cycling; phosphorus cycling; uptake of water and nutrients by roots; carbon balance; growth and demography of shrubs, growth and demography of graminoids; growth and demography of geophytes; seedling growth; propagule dynamics; and plant-animal interactions. An additional two models, which expand aspects of the FYNBOS model, are described: a model for simulating canopy processes; and a Fire Recovery Simulator. The canopy process model will simulate ecophysiological processes in more detail than FYNBOS over a one day time period. The Fire Recovery Simulator models successional dynamics after disturbance with less ecophysiological detail than FYNBOS, over periods of decades and longer.

The role of models in systems ecology, and the function of the three models described, as aids in the research and management of the fynbos biome, are also discussed.

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INTRODUCTION
(F J Kruger)

Resource managers have used mathematical models successfully to explore the possible results of management options and as aids in the choice of alternative courses of action. The tree stand simulators such as the COMPAS model used in South African forestry (Kassier 1980) are examples. In these models data and knowledge gained from experimental programmes are synthesized as formal mathematical expressions which describe the growth of forest stands of chosen species composition under various environmental conditions. These models simulate the growth of individual trees as well as the growth of the whole stand in response to thinning and other management. Results of these simulations can then be coupled with cost and income accounting procedures and so allow identification of management regimes that maximize productivity and income. The models can accommodate: different species and sites; different intermediate and end products; and different financial discounting rates. In these "decision models", complex biological information as well as economic and similar relationships are combined, so that a comprehensive analysis of the options open to the manager is possible.

The task of the natural resource manager can often be more complex than that of the forest manager because more diverse goals are pursued. For example, in the mountain catchment areas of the fynbos biome, the manager aims to simultaneously: maintain water yields and quality; maintain natural species and landscape diversity; sustain the yield of various products from the land; prevent wildfires; remove and then prevent the spread of invasive organisms; and regulate recreational and other uses. In lowland regions managers have similar needs, but also require an understanding of the minimum requirements for successful conservation of these areas in light of the increasing demands by agricultural development. In all areas management options must include the economic realities of the choices and provide the greatest benefit to society at the least cost. To make these decisions the manager is dependent upon the results of research programmes and the advice of expert staff. As the understanding of the natural systems increases there is a steady adjustment and refinement of managerial techniques and goals. At any given point in time the environmental conditions of an area can also greatly influence management options. Simulation models to be used like those in forestry, which would allow a manager to evaluate the possible outcome of his decision, could greatly enhance the efficiency of resource management.

Research in the fynbos has escalated rapidly over the past decade, involving many disciplines. Research has been organized around the theme of the structure and functioning of fynbos ecosystems. Most of this work has been directed toward questions underlying the management of fynbos ecosystems for their sustained use and a considerable body of information has become available. This information is not yet properly integrated for use in assisting management, or for the proper planning of future research programmes.

A dynamic system is required to integrate new research results and to realize their implications for management. Research needs a system to synthesize results from projects on various subcomponents of the ecosystem, or from various locations, which can also aid in deciding priorities for study and funding. Managers not only need tools to assist in deciding land use policies and practices on the broader scale, but also for making decisions on a finer scale. An example of this would be whether or not to burn a certain stand of vegetation in a given year or on a given day. At present there is no formal integrated system guiding research and there are only approximate guidelines for management decisions. These management guidelines are not properly based on new knowledge, nor are they structured so that they can be systematically and continually improved as new information becomes available. The first step toward satisfying these problems is the integration of research results into simulation models. From these, goal-oriented decision models can be developed to aid management. Mechanistic "explanatory" models, based on our understanding of ecological processes, are better for this purpose than statistical models, which summarize observed relationships without necessarily explaining any of the relationships. The complexity of the fynbos landscapes and the limited resources available for research makes the intensive sampling required for statistical models impracticable. Mechanistic models based on theoretical insights, rather than expensive data, are the more economical alternative. Knowledge of ecological gradients in fynbos can then be coupled with these models to treat the problem of spatial variation.

The problems facing scientists, managers and administrators can be separated into four time scales: diurnal, seasonal, successional and evolutionary; and two spatial scales: site specific and widespread. Limitations in modelling techniques and computer hardware prohibit development of a single model accommodating all spatial and temporal dimensions. A set of related models is therefore needed. No such set of related models exists although the various individual models are available. Early work on crop growth modelling has led to effective simulators of processes in crop and natural canopies that operate over the daily to annual time scales for specific sites. The ecosystem models developed in various International Biological Programmes (IBP) are effective over annual time scales, again for specific sites. Succession models, such as those developed to simulate forest succession in North America and, latterly, Australia, simulate processes that operate over decades or centuries. Spatial modelling of continuous ecosystems (rather than repeated point models with different environments) have been developed for the Glacier National Park in the

United States and elsewhere. In mediterranean-type ecosystems the programme of ecological modelling initiated at the Systems Ecology Research Group, San Diego State University in the mid-seventies has recently developed to the stage of simulating ecosystem processes at all three time scales, for specific sites.

In order to accelerate the modelling programme in the fynbos biome the Directorate of Forestry of the Department of Environment Affairs granted a research fellowship to Professor Philip C Miller to work in South Africa from October 1981 to June 1982. Local researchers collaborated in the modification and trial of the San Diego models which proved reasonably successful in simulating the dynamics of fynbos ecosystems. However, it was then necessary to rewrite the models so that they would reflect the theoretical understanding developed in the fynbos, rather than that in the United States. In rewriting the models, various new approaches and procedures were introduced, such as the plant shoot dynamics submodels and much of the succession model.

This report is an outline of progress to date and deals with the concepts which will be formalized as mathematical models. The report is the first of two which will describe the preliminary ecosystem models.

AN INTRODUCTION TO SYSTEMS ECOLOGY

(R Smart, J Miller)

BACKGROUND ON SYSTEMS ANALYSIS

A system is a set of connected or related components which form and/or act as an entire unit (Patten 1971). Systems analysis is a reductionist approach to understanding complex systems. The basic assumption is that the response of a complex system can be explained as the sum of the responses of the individual components of the system. A systems analysis involves a series of logical steps, the first of which is to divide the complex system into a number of manageable components. This can be done according to the internal logic of the system or according to some external requirements of the analyst. Each component can then be considered independently, although it is still linked to other components of the system. After each component is understood, the system can be reintegrated and understood in its entirety.

Any system with more than two components is more easily understood as a set of two component subsystems. If a problem concerning the dynamics of a multicomponent system can be divided into a set of problems concerning the dynamics of two component subsystems and their linkages, these smaller problems can be solved over a period of time, or by a group of people. One of the main uses of this approach has been in the organization and management of research projects. Projects with limited budgets may be confined to one subsystem at a time, whereas projects with large budgets may involve teams of specialists who each examine a specific subsystem.

Many problems are of a scale that will never allow a complete solution. In these cases, systems analysis has been used as the first step in the development of models of systems and in the simulation of their dynamics. Problems concerning the response of a system that continually changes through time are difficult to solve, since one has not only to understand the relationships between the components of the system, but to keep account of the state of the components to be used at the start of each modelling cycle.

Questions in ecology are often too complex for direct solution. By treating these as questions concerning the responses of ecological subsystems one can approach solutions. However, questions concerning the responses of ecosystems are usually too large to ever allow a complete solution, because of their physical and temporal scales. Through the use of systems analysis and the development of simulation models, systems ecology can investigate problems such as the dynamics of an ecosystem over a long time-period, or the response of an ecosystem to some external perturbation or management regime, without having to put the ecosystem itself at risk.

Ecological research projects are normally planned to span periods of at least a year in order to observe the effects of a seasonal range in environmental conditions. Some projects last several years in order to sample the year to year variability in the climate, but few continue for long enough to include the full range of environmental conditions that could be encountered in a given ecosystem. Thus the conclusions drawn from one period of study may not be applicable to the next, because the climate may be quite different. By being able to simulate the yearly cycles of ecosystem processes under a variety of climatic conditions, one can test the conclusions drawn from a short-term field study.

The purpose of a simulation model of an ecosystem is usually to follow the condition of various components of the ecosystem through time. Viewing an ecosystem solely in terms of trophic groups, ie as producers, possibly subdivided as a grass, a tree, and a bush; as consumers, possibly divided into grazers and browsers; and as black box decomposers (because of the usual lack of data), benefits neither the managers nor the scientists, since they work with species. It is a mistake to assume that developing a hypothetical "combined average organism" is expedient when there is a lack of data. This only allows for wild guesses at preliminary parameter values, provides no meaningful way of arriving at parameter values once data have been gathered and does not guide the manager. In a culling situation for example, the "combined average organism" does not exist and should not be thought of as the 30 per cent of species A, 10 per cent of species B and the rest species C, as it may be in the model. By using a computer, it is possible to follow a large number of components in an ecosystem. Processes, such as photosynthesis, can usually be described by one general equation for all of the plant species, which is made to fit the specific situation by changing its parameters. When the model is first described, it is probable that most of the parameters will have to be set equal to the only known values. However, this approach allows one to incorporate new data gathered for real species and to generate results which are interpretable in the real world.

TYPES OF MODELS

A model will be defined here as a set of interconnected, explicit hypotheses about the dynamics of a system. The results of a model will therefore be hypotheses about the behaviour of the original system.

Models can be physical objects, such as the models of molecules common in chemistry, but are usually constructed in words or sometimes in mathematical expressions. Language is a useful medium for models since it is generally understood, at least at a conceptual level. At a detailed level language can become less useful, because too much time is spent defining the exact meanings of the words and their allowable relationships. In developing an understanding of a complex system that will include the expertise of people in a variety of different fields, word models may be the most efficient choice within the field, where people may agree on terms; but a mathematical model in a "common language" is required for comparing the interactions between fields.

Two major categories of mathematical models should be distinguished: empirical models and analytical models. Empirical models are derived from data through statistical analysis; analytical models are derived from theoretical assumptions. Regression models are an example of empirical models. Empirical models make no attempt to examine the causality of the relationships involved in a data set and can only reconstruct its statistical properties. If an empirical model does not have the ability to simulate the original system within desired tolerances, then the only conclusion possible is that the model has been based on an insufficient data set which does not include the full range of the responses of the original system. No insight has been gained about the original system; only information on the sample size is required for meaningful statistics.

Analytical models consist of explicitly stated theoretical assumptions about the causal relationships of a system. Analytical models therefore depend on the depth of understanding one has of a system, rather than on the completeness of the data set on the system. If the results of an analytical model differ widely from the observations on the original system, then it is assumed that the theoretical assumptions in the model are at fault.

TECHNIQUES OF MODELLING

Computerized simulation modelling is an iterative process: the cycle involves stating the hypotheses concerning the dynamics of a system; expressing these relationships between the components as mathematical equations understood by a computer; testing their ability to simulate the system; and then revising the hypotheses. Once the model seems to simulate the dynamics of the original system within tolerances, the sensitivity of the model to changes in both its structure and data input can be tested. By comparing the sensitivity of the model to these changes with the sensitivity of the original system, it is possible to decide if the structure of the model adequately reflects the original system.

In developing a model to simulate the response of a system to an external influence, the first step is to accurately simulate the natural system. In building a model to simulate the response of an ecosystem to various management practices one first simulates the "steady state" of the ecosystem. Once the simulated ecosystem behaves within tolerances, the effects of the management practice can be included as modifications of the appropriate mechanistic relationships in the model.

In a model the components of the system are usually described by a set of quantities which are referred to as state variables, since they specify the condition or state of the system at any given point in time. The state variables can be related in two ways: firstly, through the transfer of material from one state variable to another; and secondly, through the transfer of information about one state variable to another. Usually there is only one material, or currency, that is exchanged between the state variables. The transfers or flows of material are simulated by rate variables, since they describe the movement of a quantity per unit time. The exchange of information, such as the response of the rate variable to the amount of material in the source or sink, is described by parameters. These three types of variables can be arranged in Forrester diagrams (box and arrow diagrams) to show their interrelationships (Forrester 1969).

Continuous functions can be described by differential equations, but because computerized integration techniques are complex, such functions are usually treated as difference equations and are solved over a given time interval. The condition of a state variable at the end of a time interval is determined by its condition at the beginning of the time step and any gains or losses to it during the time step.

Flows from one state variable to another are usually formulated as a potential maximum, multiplied by a series of functions which determine the per centage of the maximum that is possible as conditions vary from those that are optimal.

Models are usually constructed from a few common mathematical functions. These functions include: the exponential relation; the Mitscherlich function, which is an exponential relation; and the Michaelis-Menten function (Figure 1). Each is defined by two parameters: a rate constant, and a parameter which defines the sensitivity of the rate of the controlling variable. When these equations are used in the following models to describe one of the rate limiting functions, they are divided by a third parameter so that the response of the function varies between zero and one. This formulation allows the input and the output of the function to be in meaningful units, while the third parameter transforms the response into a decimal fraction.

A model designed to simulate a single season should be able to run for several seasons, since an obvious check of the model will be its year-end values. If the results of one year's simulation cannot be used as the initial conditions for a second year, because the simulated ecosystem is unacceptably out of balance, then the values within the first year are also probably not very realistic.

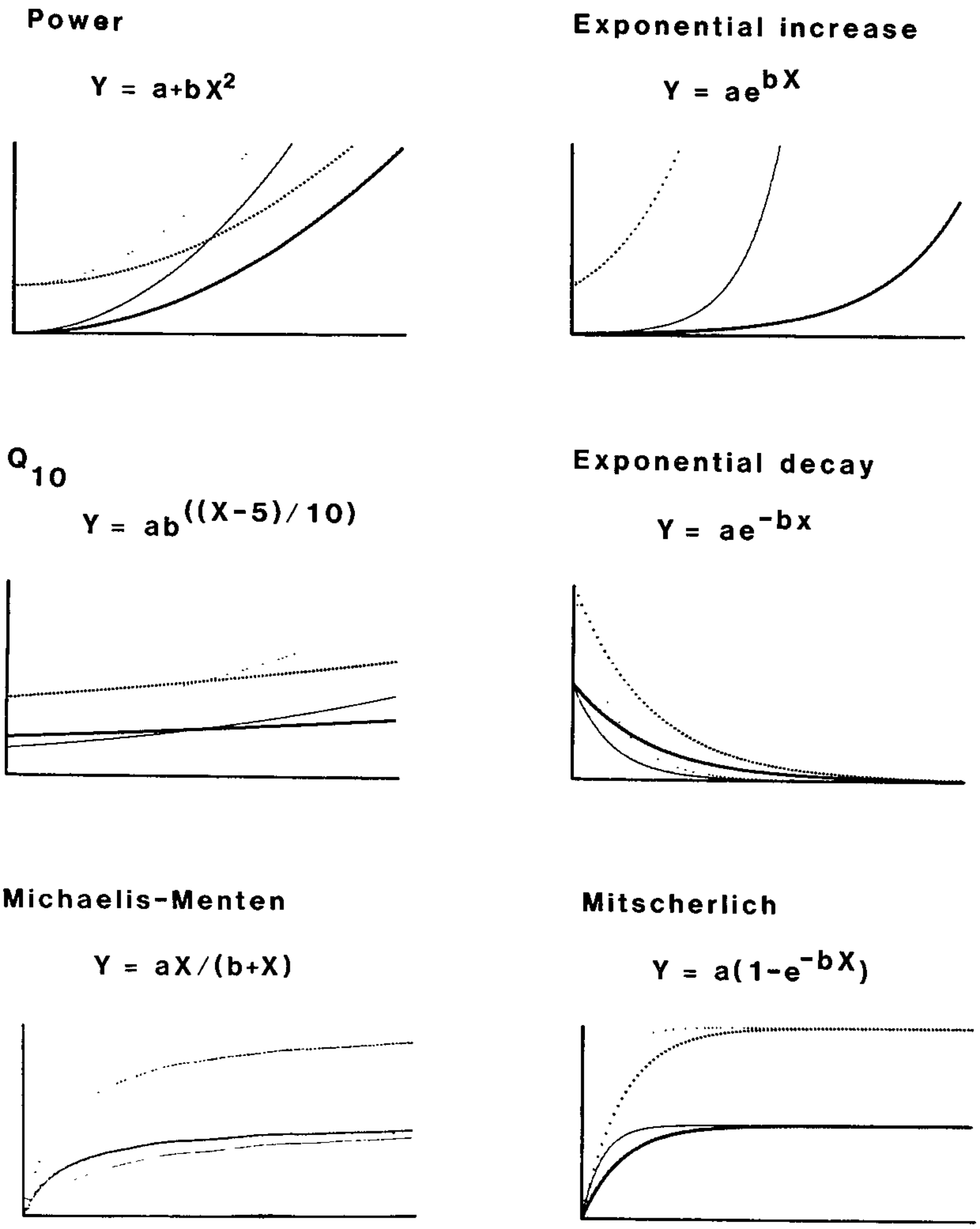

FIGURE 1. Some commonly used mathematical functions and the effect of doubling their parameters. From solid to dotted line there is a doubling of b, and from thick to thin line there is a doubling of a.

THE ROLE OF MODELS IN RELATION TO RESEARCH AND MANAGEMENT IN THE FYNBOS BIOME

(P M Miller, J Miller)

THE RELATIONSHIP OF MODELLING TO RESEARCH AND MANAGEMENT

The standard process of research deals with the real world, the conceptual model of the real world (ie our understanding of the real world) and the experiments designed to improve our conceptual model (Figure 2, Spain 1982). When a new phenomenon is observed, it is described in terms of other phenomena that are already known. From such comparisons, hypotheses about the potential behaviour of the new discovery can be developed and experiments designed. From the actual data gathered about the behaviour of the phenomena, the conceptual model is developed and improved. The disadvantage of this approach is that the conceptual model can only develop as fast as the data can be gathered and interpreted. In ecology this can involve long periods of time, especially in studies of succession.

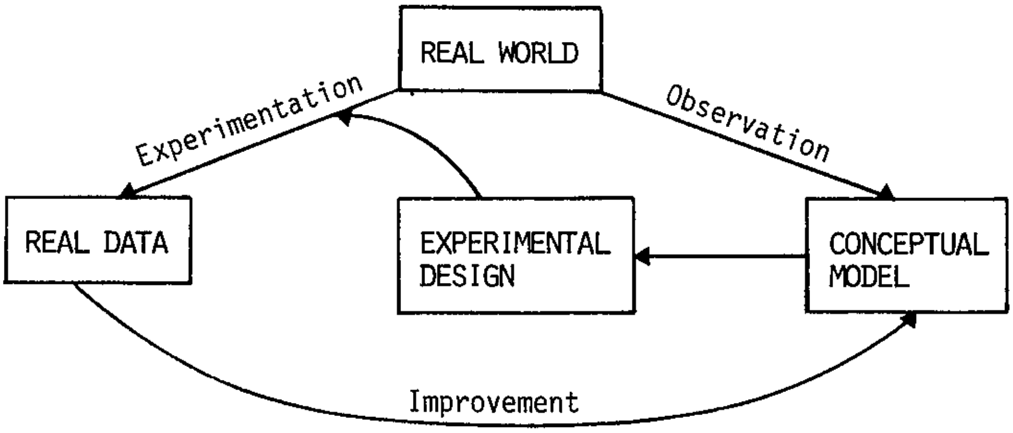

FIGURE 2. The standard research loop showing the relationship between the real world, the scientist's conceptual version of the real world, and his experiments to test his hypotheses.

Adding the development and testing of mathematical models to the standard process of research provides two further pathways for the development of the conceptual model (Figure 3). The process of formalizing the conceptual model as a mathematical model can in itself lead to improvements. Even without having precise parameters, the mathematical model should at least be as stable as the original system. If it is not, then some key process may have been omitted. By using the mathematical model to simulate experimental results and then comparing these with actual data, both the mathematical and the conceptual model can be improved.

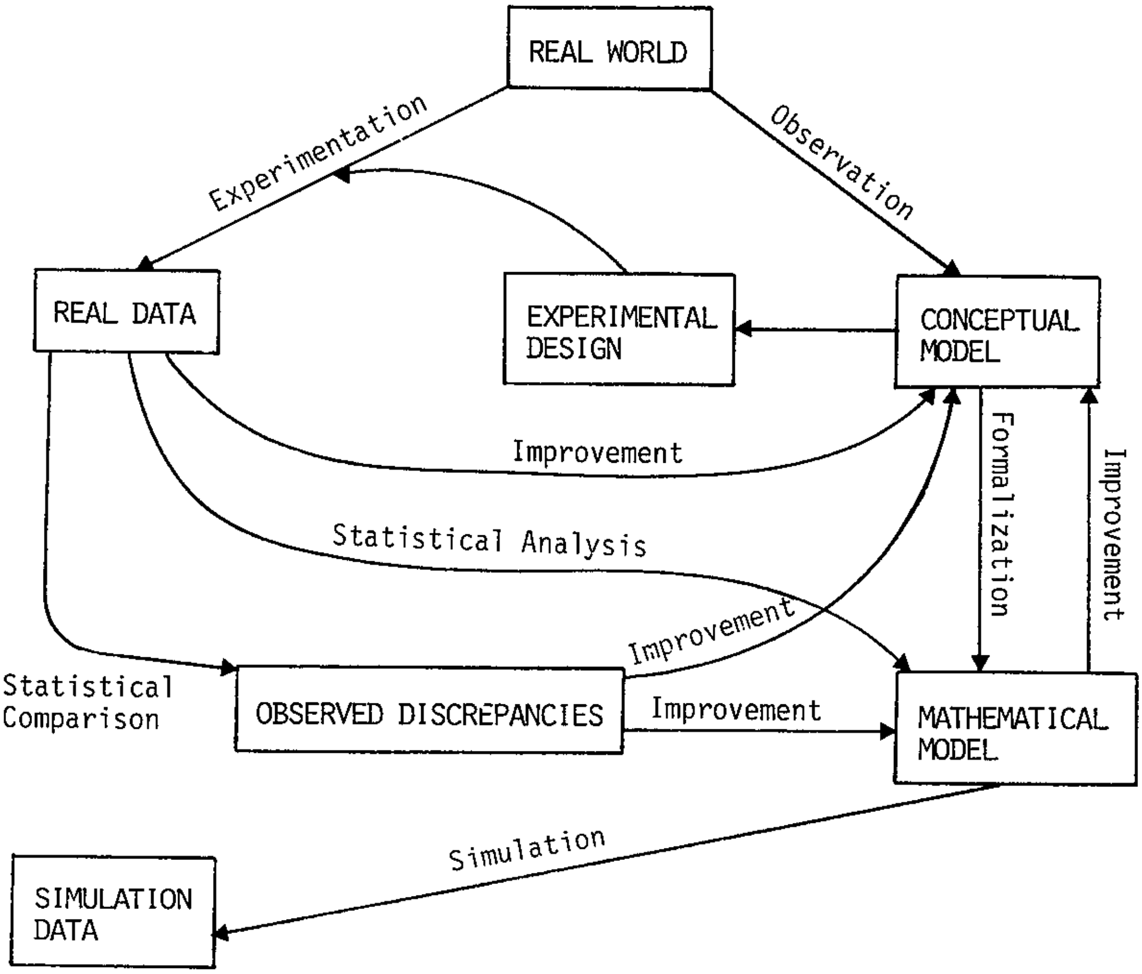

FIGURE 3. The pattern of research when it includes the construction of mathematical models. By formalizing the conceptual model into a mathematical model and comparing the simulation results with actual data a second pathway toward improving the conceptual model is available.

Decision makers can gain insight into the behaviour of the real world from the mathematical model and the simulated responses of the model (Figure 4). The management question "What would happen if ..." cannot only be answered from insights contained in the conceptual model, but also from simulation by means of the mathematical model (Spain 1982).

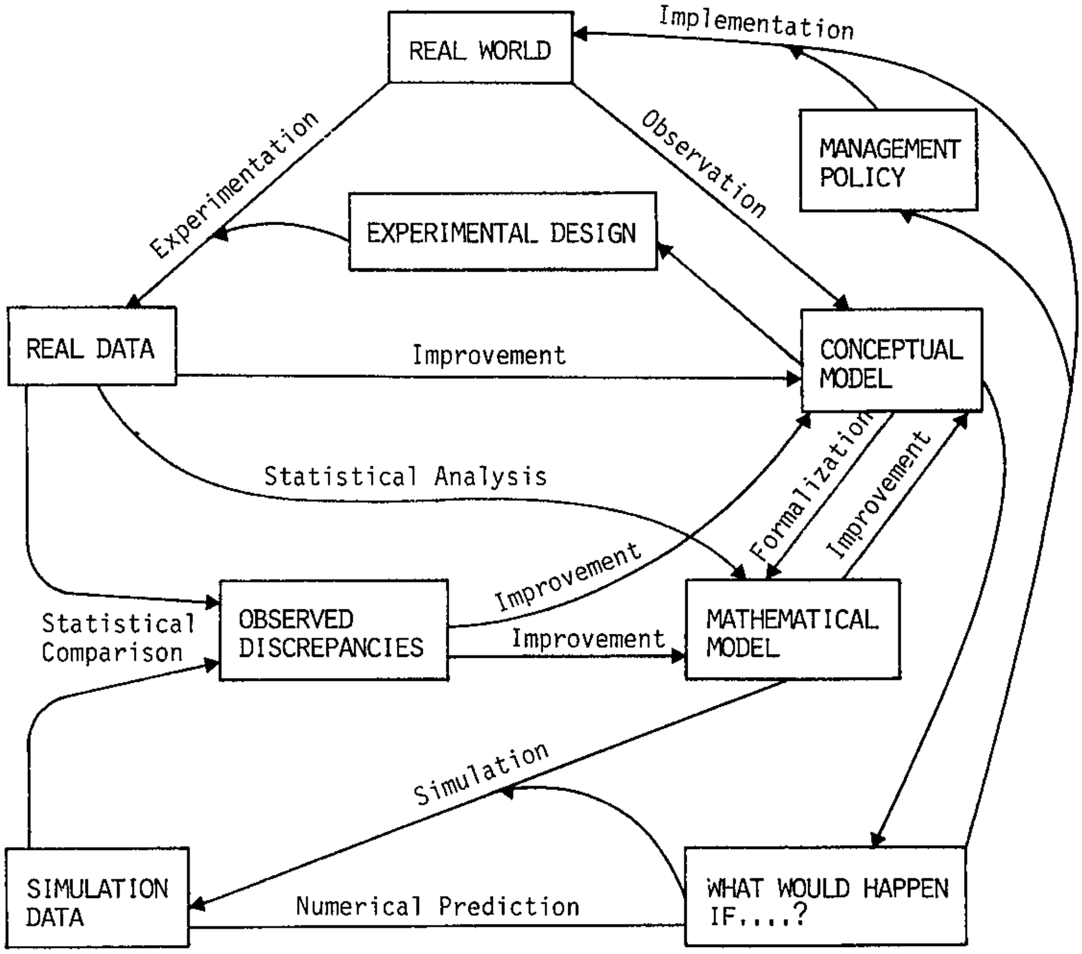

FIGURE 4. A diagram relating modelling and simulation to the development and improvement of management policy. Based in part on a diagram by Spain (1982).

Since modelling, like experimentation, is a tool available to the scientist, each scientist should be the one who actually does the modelling. The development of models need not become a project in itself in the organization of a large research effort, unless one of its main objectives is to help direct the management of the project. In this case, the project director should maintain a modelling framework, which can include the submodels of each individual scientist. The main concern of the project director would therefore be to make sure that the results generated by one project and submodel are compatible with and sufficient for the requirements of another project and submodel.

A manager who uses a simulation model to test his hypothetical management practices should either have a complete understanding of the model, or use a model that can be interrogated as to why it reached a certain result. This will allow the manager to decide if the model, which only includes a few of the major relationships in the original system, has provided a reasonable result.

Because it can be time-consuming to develop computer simulation models, individual scientists and managers often do not do the modelling themselves. A specialist in modelling is given the job and his main role is to communicate with those who should be doing the modelling. He has first to find out what the theoretical understanding of the scientists is and then to explain why the model based on this understanding predicts what it does. The step in the middle, ie programming the computer, becomes the easiest part. Many of the failures of large ecosystem simulation modelling projects can be traced to the fact that those who built the models and those who needed to use them were not the same people. When models are no longer understood by their users and are treated as black-boxes, they become not only worthless but dangerous.

OBJECTIVES OF THE MODELLING PROJECT

When the Fynbos Biome Project was initiated, three phases of research were envisaged. In Phase I, research was to focus on baseline studies, which included surveys of climate, soils, vegetation, fauna and land use patterns. In Phase II, detailed comparative studies of ecosystem structure and function were to begin. From these projects in Phase II, models were to be developed; and in Phase III of the project, validation studies to test the hypotheses and models were planned. Because of the availability of manpower and other considerations, the schedule was allowed to be flexible.

The broad goal of the Fynbos Biome Project is to provide a sound scientific understanding of the structure and function of the fynbos, which can be used as a basis for its conservation and management (Kruger 1978). For the modelling project, these goals have been more specifically defined and are:

(1) to simulate fynbos ecosystem processes and hence the impacts of fire and vegetation replacement on
  - volumes and quality of water yielded from mountain catchments
  - vegetation recovery after disturbance
  - species composition;

(2) to provide a framework and a means for comparing data and processes in the different mediterranean-type ecosystems, for testing the transferability of research results from one continent to another and to derive valid theory for mediterranean-type ecosystems in general;

(3) to improve our understanding of mechanisms controlling carbon, nutrient and water flux through the soil-plant-atmosphere continuum; and

(4) to contribute to research guidance and project organization at the ecosystem level.

THE MODELLING FRAMEWORK

Because the processes in an ecosystem are continuous, and the simulation models are constructions of difference equations rather than differential equations, the first requirement of the modelling process is to decide on a time step for the model. The condition of the system can be calculated once a minute, once a day, once a year, or for longer intervals. The shorter the time step the more detailed the model can be, though it will also be more prone to drift if used to simulate long periods of time. In studies of ecological processes, four main time scales exist: diurnal, seasonal, successional, and evolutionary. Two spatial scales exist: site specific, and widespread. In simulating diurnal dynamics, a time step such as five minutes is reasonable and the appropriate models would remain stable for a period of three to five days. In simulating seasonal dynamics, a one day time step is convenient, and the model should run for three to five years. For simulating successional dynamics, time steps of a month or a year can be used and the model should be able to simulate several successional sequences. Simulation of the mechanisms involved in biological evolution processes is beyond the scope of the project at present.

The modelling project for the fynbos has started with the site specific processes at the first three time scales. The central model is one of seasonal ecosystem dynamics. A more detailed model is used to simulate the diurnal courses of photosynthesis, transpiration and related processes in the plant canopy; and to derive parameters for the FYNBOS model. A less detailed model of successional dynamics based on the results of the ecosystem model is used to simulate processes on a longer time scale.

The Fynbos Ecosystem Simulator (FYNBOS) is a development of the Mediterranean Ecosystem Simulator (MEDECS) (Miller et al 1978; Miller 1981) and its latest revision as the Arctic Tundra Simulator (ARTUS) (Miller et al 1983). MEDECS was used as a tool to test theories of resource-use in the chaparral in southern California and the matorral in central Chile. ARTUS has been used to organize research in Alaska concerning the effects of oil exploration on ecosystem processes in the tundra and the effect of elevated carbon dioxide levels and temperatures on the carbon balance of the Arctic.

The diurnal processes simulator will be developed from the Canopy Process Simulator (CAPS), which simulates the energy, water and carbon dioxide balance of a continuous canopy and runs through the day in five minute time steps (Miller 1981). The CAPS model was developed from earlier models of canopy photosynthesis (Monteith 1965; Anderson 1966; Duncan et al 1967; Lemon 1967); of the penetration of irradiance through the canopy (Monsi and Saeki 1953; Idso and de Witt 1978); and of the transfer of heat, water vapour, and carbon dioxide within a canopy (Waggoner and Reifsnyder 1968; Murphy and Knoerr 1970; Steward and Lemon 1972).

The Fire Recovery Simulator (FIRES) is a model of succession following disturbance in mediterranean-type ecosystems. It is based on the JABOWA model of forest succession (Botkin et al 1972; Shugart et al 1977) and includes plant ecophysiology and nutrient cycling dynamics from Californian chaparral, Chilean matorral (Miller 1981) and South African fynbos. FIRES was first outlined in May 1981 and reviewed at a workshop held in San Diego in June 1981, which was attended by three to five persons from each mediterranean region. Between October 1981 and March 1982, South African scientists reviewed and revised the model in the context of their research and practical experience with fire in fynbos.

These models emphasize the soil-plant-atmosphere interactions in the ecosystem. Other models can be developed from these to put more emphasis on plant-animal interactions or the socio-economic aspects of management. Models designed to reconstruct the spatial variation in ecosystem dynamics, rather than the processes at a given site, may also prove to be of interest and may be feasible with the advent of larger, faster computers.

A PRELIMINARY ANALYSIS OF SEASONAL DYNAMICS: THE FYNBOS MODEL

(P C Miller)

INTRODUCTION

As currently structured, the Fynbos Ecosystems Simulator (FYNBOS) contains 14 submodels of groups of major components and processes (Figure 5). These include: climate; soil-water balance; energy balance; decomposition; nitrogen cycling; phosphorus cycling; uptake of nutrients and water by roots; carbon balance; the growth of three groups of plants (shrubs, graminoids, and geophytes); seedling growth; plant-animal interactions; and propagule dynamics.

This set of generic subdivisions reflects our understanding of the principal processes of fynbos ecosystems. At a more detailed level the grouping of ecological processes, in many cases, reflects the external needs of the analyst rather than what may be our intuitive description of the ecosystem. This is especially apparent in the sequence in which processes are calculated when the process is required by more than one submodel. Water, for example, moves into the soil in the soil water balance submodel, but because of the required energy terms in the calculations, it only completes the cycle by leaving the soil as evapotranspiration in the energy balance submodel.

The fynbos is rich in plant species and any single stand of vegetation may include 50-100 or more species (Kruger and Taylor 1981). However, a limited number of growth forms dominate the vegetation (Kruger 1979). A reasonable initial assumption is that the members of the same growth form category are functionally similar, irrespective of their identity. Fynbos is usually considered to consist of three major growth forms: tall proteoid shrubs occurring in an upper layer; proteoid and ericoid shrubs intermingled in an intermediate mid-high layer; and low shrubs and graminoid forms in a lower layer. In addition geophytes are often common. For Swartboschkloof, eight species have been selected as typifying the different growth forms: Protea repens (Proteaceae) represents the tall proteoid shrub form; female Leucadendron salignum (Proteaceae) represents the short proteoid resprouting shrub form;

female Cliffortia cuneata (Rosaceae) represents a tall but short-lived shrub form; Erica plukenetii (Ericaceae) and Psoralea obliqua (Fabaceae) represent the mid-height shrubs; female Restio filiformis (Restionaceae)

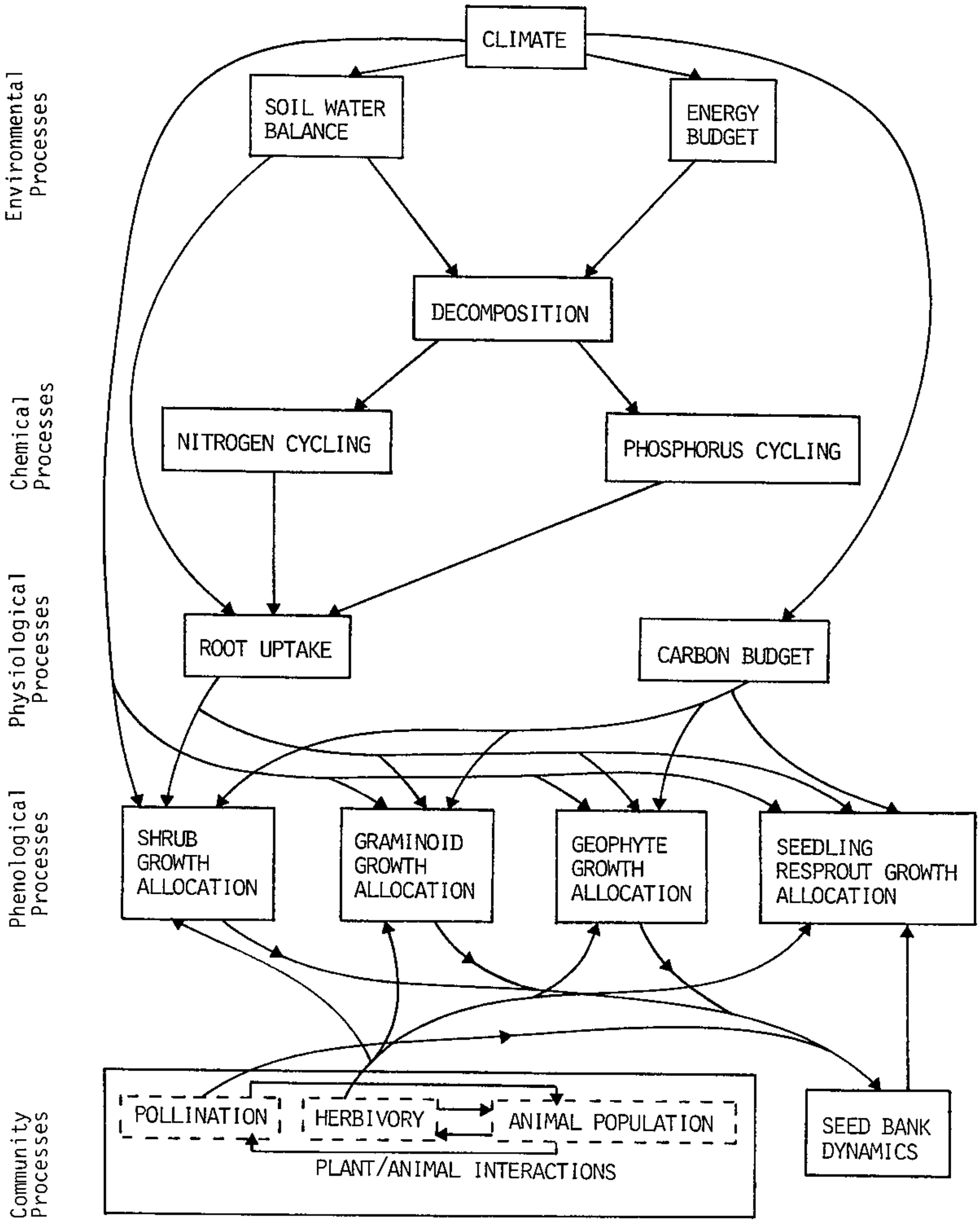

FIGURE 5. The 14 submodels in the FYNBOS ecosystem model. The arrows show the general interrelationships rather than the details of the flows between submodels.

and Tetraria ustulata (Cyperaceae) represent the graminoid forms; and Watsonia pyramidata, (Iridaceae) represent the geophytes. The notion is that any fynbos stand can be modelled by using submodels of the typical growth forms in the particular stand being represented.

Plant growth can be viewed as a set of physiological processes including: photosynthesis; transpiration; uptake and translocation of nutrients; and the uptake of water. Plant growth also involves seasonal patterns of the increase and allocation of biomass to aboveground and belowground plant parts and the development of the plant canopy. However, growth of a population of plants or a stand of vegetation also involves the birth and death of plants and plant parts, which are demographic processes. In the plant growth submodel of FYNBOS, we are concerned with the collective demography of established plants and make provision for the dynamics of shoot growth and development and reproduction. These processes of plant growth and development are described in three submodels: one that represents shrubs; another for graminoid plants; and a third that represents geophytes.

Conventions of the model

The basic unit of the plant is taken as the shoot system, which consists of a current shoot and that fraction of the old leaves, conducting tissue and absorbing root of the plant which supports the shoot. A shoot is defined as being composed of: a terminal meristem (or intercalary meristem in the case of monocots); new leaves; new stem leader; axillary buds; and inflorescences.

Processes are calculated variously on the basis of: an individual shoot system; a volume of soil; or a unit of soil area. Conversions between the shoot system, volume and area bases are made using: the number of shoots per plant; the thickness of the soil layers; soil bulk density; and plant and root densities of each species.

The model provides for six soil levels: 0,00 to 0,02 m; 0,02 to 0,10 m; 0,10 to 0,20 m; 0,20 to 0,30 m; 0,30 to 1,00 m; 1,00 to 2,00 m; and up to eight plant species. The species at Jonkershoek which are currently included in the model are: Protea repens; Leucadendron salignum; Cliffortia cuneata; Erica plukenetii; Psoralea obliqua; Restio filiformis; Tetraria ustulata; and Watsonia pyramidata. Possible species of interest at Pella include: Protea repens; Leucospermum parile; Phylica cephalantha; Staavia radiata; Staberoha distachya; and Thamnochortus punctatus.

About twenty plant state variables, consisting of 11 population and nine biomass parameters, are maintained for each species. The exact number of species parameters varies according to growth form. Population variables include: seed densities in the canopy, soil surface, and soil (#/m^2); plant density (#/m^2); vegetative shoot systems per plant (#/plant); flowering shoots and persistent cones per plant (#/plant); viable axillary buds (#/shoot system); and potential epicormic and crown sprouts after fire (#/plant). Biomass properties include: new and old leaf masses (g/shoot system); fine and coarse stem masses (g/shoot system); conducting and absorbing root masses (g/shoot system); carbohydrate, nitrogen and phosphorus reserves (g/shoot system); and average height (m). Active growing stems less than six millimetres in diameter are categorized as fine stems and those greater than six millimetres as coarse stems, following categories used in fire behaviour models (Countryman and Philpot 1970). Standing dead include attached dead plant parts and skeletons of dead shrubs. Litter includes unattached plant material lying on the soil surface.

The model currently involves 59 parameters defining the processes specific to each species. In addition the model includes the compartments: soil water (kg/m^3); soil heat (MJ/m^3); mass of dry matter, total non-structural carbon (TNC) (which includes sugars and storage carbohydrates), nitrogen and phosphorus in fine and coarse standing dead material (kg/m^2); mass of dry matter, TNC, nitrogen and phosphorus in litter (g/m^2); mass of dry matter, TNC, nitrogen and phosphorus in soil organic matter (kg/m^3); mineralizable soil nitrogen and phosphorus (g/m^3); soil ammonium and nitrate in solution and on the clay-organic matter or iron-aluminium exchange complexes (g/m^3); and nitrogen and phosphorus in dissolved organic compounds (g/m^3).

The water, carbon, nitrogen and phosphorus balances are simulated for the site as a whole. The site water balance is based on calculations of: interception; transpiration; soil evaporation; movement between soil layers; and deep drainage. The site carbon balance is calculated from: gross photosynthesis; plant respiration; plant growth; litter respiration; and decay of soil organic matter. The site nitrogen balance is based on: inputs from rain, dryfall, free-living fixation and symbiotic fixation; losses by drainage, mineralization, nitrification and exchange reactions and uptake by vegetation; and return in litterfall and decay. The site phosphorus balance is based on: inputs from rain and dryfall; losses by deep drainage, mineralization, exchange reactions and uptake by vegetation; and return in litterfall and decay.

Gross primary production, net primary production, total biomass and the nitrogen and phosphorus taken up and incorporated by the vegetation are based on the final calculated growth rates. Finally, the accumulation of carbon in the ecosystem is calculated as the balance between net primary production and the decay rates for litter and soil organic matter.

THE CLIMATE SUBMODEL

(J Miller, W Maliepaard, D B Versfeld)

Introduction

Climate influences most chemical and biological processes in the ecosystem since almost all are sensitive to temperature and moisture.

The climatic variables required by the various soil and plant submodels can be read as data or can be generated by a climate submodel. While data may be preferred for testing a submodel, it is usually of more interest to run the submodel under a variety of environmental situations in order to understand its full range of responses. Complete, long-term records of all the required climate variables are usually not available for all sites of interest. An analytically derived climate submodel which generates realistic stochastic climate data for various sites allows simulations in circumstances where recorded data are unavailable

Such a model also permits simulation of extreme conditions which have not been observed but are considered to be possible.

Requirements of the submodel

The climate submodel needs to satisfy three general requirements. Firstly, it has to provide all the necessary environmental input variables required by the other submodels. Secondly, the climate submodel should be easily parameterized or derived for any site of interest within the fynbos biome. Thirdly, it should be able to incorporate available sets of climatic data so that the response of the other submodels to recorded environmental conditions can be tested. If an incomplete climate record is used, the climate submodel should be able to generate the rest of the climate variables around the available data.

The required output variables of the climate submodel are: day length in hours; daily total photosynthetically active radiation photon flux density (400-700 nm) in Einsteins/m^2 soil surface/day; daily total solar irradiance (300-3 000 nm) in MJ/m^2 soil surface/day; daily total incoming infrared irradiance (3 000-11 000 nm) in MJ/m^2 soil surface/day; daily total wind run in km/day; daily average air temperature in degrees Celcius; daily total rainfall in mm/day; the occurrence of mist; daily average relative humidity as a dimensionless fraction; daily average saturated vapour pressure of the air in millibars; and daily average actual vapour pressure of the air in millibars.

Description of the submodel

The climate submodel assumes that most of the climate variables can be described by the location of the site, season and the effect of rain events. A rainfall generator drives the model and the remaining variables are modified by the presence or absence of rain and amount of rain. Two versions of the climate submodel are to be constructed: an empirical model, similar to the model developed by Richards (1981); and an analytical model. Because of the modular design of the climate submodel, parts of the empirical model and parts of the analytical model can be combined, or can be used with climate data sets depending upon what is required of the total submodel (Figure 6).

In the empirical model, the rainfall generator consists of a first-order Markov chain, which calculates the probability of rain on a given day from the conditions of the previous day. Whether or not it actually rains is then determined and if it does, the amount of rain is calculated from an appropriate frequency distribution. If data on other climatic variables are available, they are related to rainfall as dependent variables in a multivariate regression model (Richards 1981). Though the model requires reasonably long term climate records in order to generate its parameters, any site with a climate record anywhere in the fynbos biome can be quickly parameterized.

Where the empirically derived regression model cannot be developed because of the lack of data, explicit equations developed in other ecosystems, which relate climate variables to rainfall, can be used.

TABLE 1. Equations defining output variables of the CLIMATE submodel

Variable Name	Definition		Units
DAYL	Day length	= 12,151+2,2751*COS((DAY+99)/365*2*3,14)+0,8982	hours
MAXFLUX	Solar noon maximum PAR flux	= 1650+450*COS((DAY+99)/365*2*3,14)	uE/m^2/day
PARFLUX	Daily total PAR flux	= MAXFLUX*(2*DAYL*60*60/3,14)*1E-6	E/m^2/day
MAXRAD	Solar noon maximum solar radiation	= 700+300*COS((DAY+99)/365*2*3,14)	W/m^2
SOLAR	Daily total solar radiation	= MAXRAD*(2*DAYL*60*60/3,14)*1E-6	MJ/m^2/day
WIND	Total daily wind run	= 150+(2*RND-1)*150	km/day
TAIR	Daily average air temperature	= 16,1+5,5*COS((DAY+44)/365*2*3,14)	°C
PPT	Daily total precipitation	= RND*RND*48+0,5	mm/day
MIST	Daily total mist deposition on the soil surface	= if RND 0,1 then MIST=2	mm/day
ES	Daily average saturated vapour pressure of air	= 6,108*EXP(17,2674*TAIR/(TAIR+237,28))	mb
VAIR	Daily average actual vapour pressure of air	= ES*RH	mb
IR	Daily total incoming IR radiation	= 1440*3,4E-12*(TAIR+273)^4*(0,44+0,08*SQR(VAIR))*(1+0,9*FOV)	MJ/m^2/day

Note: RND is a computer generated uniform random number between 0 and 1.
EXP causes the following term to be used as the exponent of e.

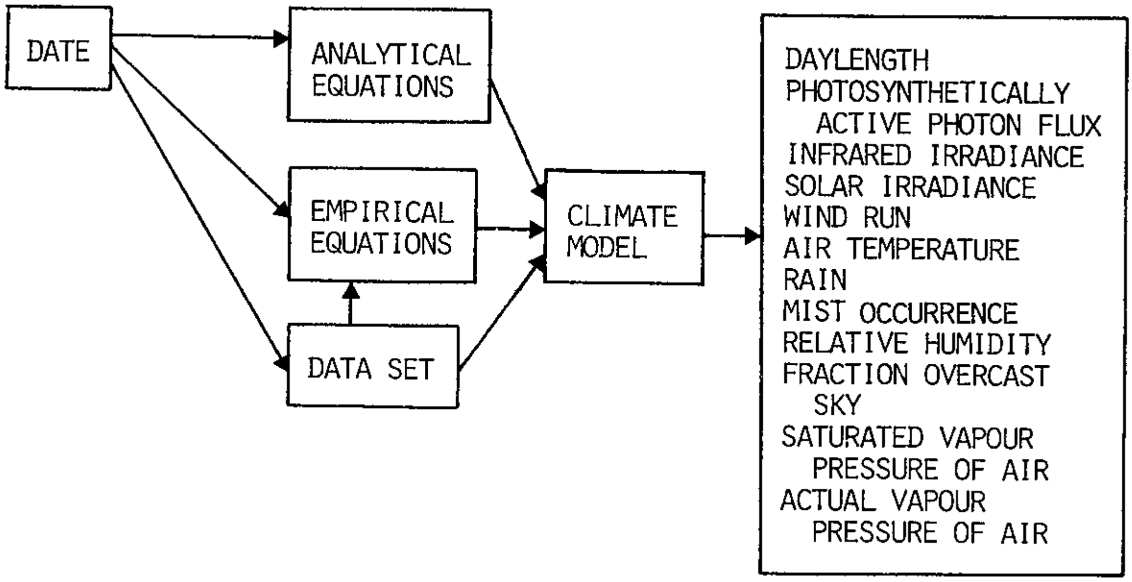

FIGURE 6. The environmental parameters generated by the CLIMATE submodel, and the approaches to configuring the submodels, using analytical equations, empirical equations, or data sets, or some combination thereof.

Day length, daily total photosynthetically active photon flux density, daily total solar irradiance and daily average air temperature are calculated from sine curves. Day length is calculated for 34° South from a yearly mean based on data from the Smithsonian Meteorological Tables (1963) and uses December 22 as the longest day of the year. Civilian twilight calculated for 34° South is then added to the length of each day (Savage and McGee 1980). The yearly mean for daily total photosynthetically active photon flux density and daily total solar irradiance are calculated following Monteith (1973). Photosynthetically active radiation photon flux density values are based on measurements by Miller et al (unpublished) and daily total solar irradiance values are based on measurements for the chaparral (Miller and Poole 1980). The sine curve for daily average air temperature uses February 15 as the warmest day of the year and a yearly mean of 16,1°C for Swartboschkloof. Daily total wind run averages 150 km/day and varies uniformly on a daily basis between 0 and 300 km/day.

Simulation of daily total precipitation depends on the estimated or observed probability of rain occurring and then on the variation in the amount of rain on that day. The probability of rain occurring on a day varies through the year. Based on data from Swartboschkloof, the calculated daily probabilities of rain are: 40 per cent in April and May; 55 per cent in June and July; 40 per cent in August and September; 20 per cent in October and November; 10 per cent in December and January; and 15 per cent in February and March. The daily probability of rain on a given day is compared to a computer-generated random number to determine if rain occurs on the simulated day. If it rains, the rain event lasts from one to three days. The amount of rain on a rain day is taken as a random number between 0,5 and 48,5 mm/day, with an average value of 12,5 mm/day for Swartboschkloof. Mist events are assumed to occur on 10 per cent of the non-rain days throughout the year.

On rain days, the daily average relative humidity is assumed to vary between 50 and 90 per cent (Table 2); the fraction of overcast sky varies between 10 and 100 per cent; and the daily average air temperature drops by up to 6°C. The daily average fraction of overcast sky decreases the daily total photosynthetically active radiation (PAR) and total solar irradiance by up to 90 per cent with fully overcast skies. The daily average saturated vapour pressure of the air is calculated from daily average air temperature (Table 1). Daily average actual air vapour pressure is the product of daily average relative humidity and the daily average saturated air pressure. Daily total incoming infrared irradiance is calculated from daily average air temperature, daily average actual air vapour pressure and daily average fraction of overcast sky, following the relationship found in chaparral (Miller 1981).

On non-rain days, the daily average relative humidity is simulated to vary uniformly between 40 and 70 per cent (Table 2); a 10 per cent chance of the presence of clouds is assumed; and the daily average fraction of overcast sky is assumed to vary uniformly between 0 and 80 per cent. The daily average air temperature is assumed to decrease linearly with the fraction of overcast sky up to a decrease of 2°C on fully overcast days. Because the simulated air temperature is a daily mean and rain events decrease mean daily air temperature, warm conditions occur on 50 per cent of the non-rain days and air temperature is increased by up to 10°C to maintain the yearly mean air temperature. On these warm days the daily average relative humidity varies uniformly between 10 and 30 per cent and the daily average fraction of overcast sky is zero. The presence of mist increases the daily average relative humidity by 10 per cent.

Results of the submodel

A preliminary version of the climate submodel using analytically derived equations has been developed (Table 3). The only climatic data presently available for Swartboschkloof are rainfall and air temperature. In this preliminary version of the model, the incoming energy parameters are based on data from Chile and the effect of cloudiness is based on data from California (Miller 1981). The relative humidity and vapour pressure of the air are estimates.

The annual total amount of rainfall seems to be reasonable, but the number of rain events and ammount of rainfall per event need to be improved. The simulated air temperatures are close to the actual values.

TABLE 2. Effect of a precipitation event on output variables of the CLIMATE submodel

Variable Name	Definition	Equation	Units
Non-rain days			
RH	Daily average relative humidity	= 0,4+RND*0,3	fraction
FOV	Daily average fraction of overcast sky	= if RND 0,1 then FOV=RND*0,8 else FOV = 0	fraction
TAIR	Daily average air temperature	= TAIR-2*FOV	°C
"Berg wind" days			
RH	Daily average relative humidity	= 0,1+RND*0,3	fraction
FOV	Daily average fraction of overcast sky	= 0	fraction
TAIR	Daily average air temperature	= TAIR+RND*10	°C
Mist days			
RH	Daily average relative humidity	= if MIST 0 then RH=RH+0,1	fraction
Rain days			
RH	Daily average relative humidity	if 0,4 PPT/32 then RH = 0,5 + 0,4 else RH = 0,5 + (PPT/32)	fraction
FOV	Daily average fraction of overcast sky	if 0,9 PPT/32 then FOV = 0,9 else FOV = 0,9 + (PPT/25)	fraction
TAIR	Daily average air temperature	TAIR - RND*6	°C
On all days			
PARFLUX	Daily total photosynthetically active radiation photon flux	= PARFLUX*(1-0,9*FOV)	E/m^2/day

Note: RND is a computer generated uniform random number between 0 and 1.

TABLE 3. Five year means of the parameters generated by the climate submodel using preliminary analytical equations based on data from other mediterranean-type ecosystems, and comparable data from Swartboschkloof where available

Parameter	Simulated	Actual	Units
Day length	13,0	n/a	hours
Daily total PAR flux	42,5	n/a	$E/m^2/day$
Daily total solar irradiance	18,5	n/a	$MJ/m^2/day$
Daily total incoming infrared radiation	27,6	n/a	$MJ/m^2/day$
Daily total wind run	150,5	n/a	km/day
Yearly average air temperature	16,6	15,9	°C
Yearly total rainfall	1575,2	1567,5	mm/year
Number of rain days	132,2	104,0	#/year
Rainfall per event	11,9	15,1	mm/day
Number of mist days	28,0	n/a	#/year
Yearly average relative humidity	0,52	n/a	fraction
Yearly average fraction of overcast sky	0,20	n/a	fraction
Yearly average saturated vapour pressure of the air	20,1	n/a	mb
Yearly average actual vapour pressure of the air	9,2	n/a	mb

n/a = not available.

THE SOIL WATER BALANCE SUBMODEL
(D B Versfeld, J Miller, W Maliepaard)

Introduction

Soil moisture conditions affect plant water status, may limit plant growth and affect species distribution. The movement of water through the soil-plant system is also a major factor in the movement of nutrients from the soil to plants and through the soil levels to streams and deep storage.

Water is often a limiting resource in mediterranean-type ecosystems. A knowledge of water availability, movement and yield; the effect of water balance on plant communities; and of vegetation on the water balance; is therefore essential for the management of these ecosystems.

Requirements of the submodel

The soil water balance submodel should simulate the movement of precipitation (rain and mist) through the plant canopy, into and through the soil levels, and out into stream flow. Gradients in soil and plant water potentials should be used as the driving force for water movement so that characteristics of different soils can be incorporated mechanistically.

The soil water balance submodel should calculate the interception loss in the plant canopy, the surface runoff and changes in the water content of the six soil levels. The submodel should provide for lateral flow into and out of each soil level. The soil water potential of each soil level should be calculated. Water flowing out of the deepest soil level should appear as stream flow. The potential evapotranspiration should be calculated as an aid in estimating a total water balance, though actual soil evaporation and transpiration are calculated in other submodels.

Description of the submodel

The soil water balance submodel uses as inputs the daily total rainfall and mist precipitation which are calculated in the climate submodel. The submodel calculates the interception of rainfall and mist in the canopy, the water contents and potential of the six soil levels, horizontal water movements, vertical water movement by rapid percolation and along water potential gradients and drainage. Water uptake by the plants is calculated in the root uptake submodel; soil evaporation and transpiration are calculated in the energy balance submodel. To simulate the complete water balance of a site, all four submodels are required (Figure 7).

Rainfall interception loss is the water captured by the canopy and evaporated. Interception is a function of canopy structure and storage, the rainfall rate and evaporative conditions during and between rain events. The daily interception of precipitation by the canopy is calculated by assuming that the storage capacity of the canopy is 0,2 mm per m^2 of leaf area and that the storage capacity is evaporated twice during each day of a rain or mist event. Net rainfall enters the top (0 to 0,02 m) soil compartment, since it is assumed that there is no surface runoff.

Water moves vertically between the six soil levels by two pathways. The first is rapid percolation, which accommodates inputs exceeding the maximum holding capacity of that level into a given soil level. The need for a rapid percolation pathway is a programming artifact and is a result of the one-day time step of the submodel. When the input of water to a soil level increases the water content beyond the maximum possible water content of that level, all the excess water is transferred to the level below within the same day. When soil levels are not supersaturated, the second pathway operates. Water moves according to the water potential gradient between the soil levels, modified by the hydraulic conductivity of the soil at that soil water content. The water holding capacities are reduced by the soil rock content. The submodel has the capacity to move water laterally into and out of each soil level, but under most situations it is assumed that lateral flow causes no net change.

Water draining out of the lowest soil level appears as stream flow. To adequately simulate hydrograph data of streamflows from actual rainfall

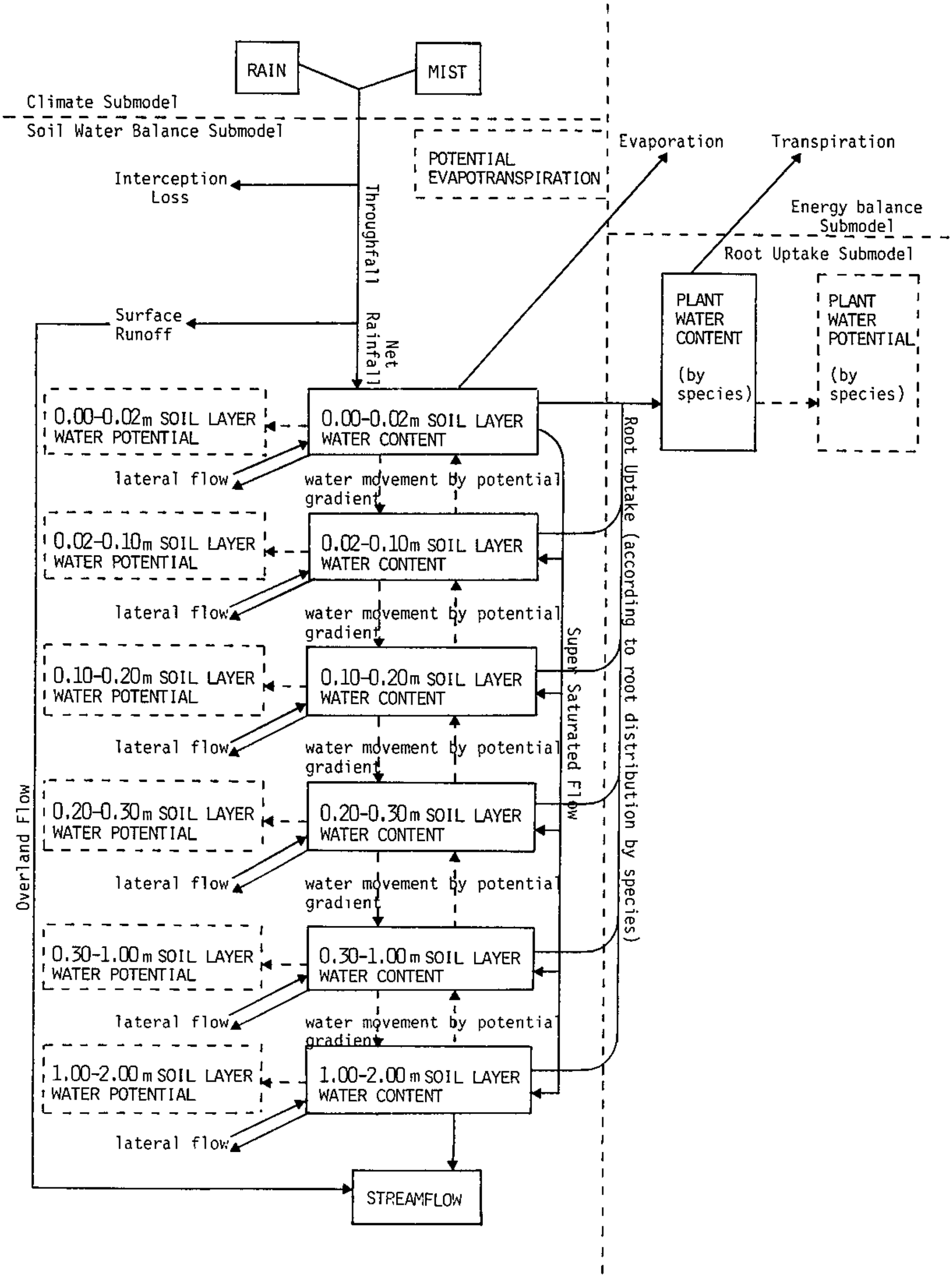

FIGURE 7. The processes in the soil water balance submodel, and those in the climate, energy balance, and root uptake submodels that are required to describe the complete site water balance.

records, some modifying site-specific lag equations may be needed in the submodel.

Potential evapotranspiration is calculated with the Monteith modification of the Penman equation (Penman 1948). The Penman-Monteith equation requires values for net irradiance, air temperature, vapour pressure and windspeed (Monteith 1973), which are calculated in the climate submodel. Data on canopy height, leaf area index and minimum canopy resistance are also required and are supplied by other submodels.

Results from an earlier submodel

An earlier water balance submodel which had a simpler method of calculating soil-water movement processes and evapotranspiration was run using two years of climate and stream flow data from the Bosboukloof catchment at Jonkershoek. Simulations with leaf area indices of 0,2 and six gave appropriate seasonal courses of deep drainage. Differences between the data and the simulations, ie that drainage was more rapid in the simulations, can be explained by the linear relationship used in the model to define the number of days required for the soil to drain from saturation to air dry. Precipitation in the Bosboukloof catchment was 1 443 mm in 1977 and 921 mm in 1978. The measured evapotranspiration was about 800-900 mm/yr (van Wyk, personal communication 1983). The simulated evapotranspiration in 1977 and 1978 was 317 and 357 mm/yr with a Leaf Area Index (LAI) of 0; 634 and 671 mm/yr with a LAI of 4,8; and 708 and 738 mm/yr with a LAI of 7,29 respectively. The higher simulated evapotranspiration with the lower measured precipitation was probably due to the greater simulated incoming solar irradiance during the year with lower precipitation.

THE ENERGY BALANCE SUBMODEL

(P C Miller)

Introduction

Processes of energy exchange determine plant temperatures, rates of water loss and uptake, photosynthesis, respiration, growth and phenological events. Plants intercept and absorb solar irradiance for photosynthesis, but they also must dissipate heat through the emittance of infrared radiation, evaporation, and convection. Energy exchange within the canopy affects the amount of energy reaching the soil surface. Soil temperatures affect the rate of many biological processes, including decomposition, mineralization, seed germination, root growth, and leaf growth in geophytes. The heat balance of the soil involves the partitioning of solar irradiance between the canopy and soil, the net infrared irradiance in the canopy and at the soil surface, and the soil temperature profiles.

Energy balance processes influence canopy structure and may affect species distributions. In the chaparral of southern California, narrow-leaved species are more common on equator-facing slopes (Miller 1979).

Requirements of the submodel

This submodel should calculate the energy balance of the plant canopy and the soil surface, including calculations of plant transpiration and soil evaporation. The submodel should also calculate the flow of energy between the six soil levels. The temperatures of leaves and soil levels can then be calculated as a function of their energy content.

Description of the submodel

The energy balance equation balances the incoming and outgoing energy flows and calculates the net change in the system. The incoming solar irradiance and infrared irradiance must equal the loss of energy by reflectance, emittance, evaporation, convection, conduction and the change in energy content (Figure 8).

The amount of solar irradiance absorbed by the canopy is calculated from the incoming solar irradiance, a climate variable, albedo and the interception of irradiance in the canopy. The interception of solar irradiance follows Miller and Poole (1980). The net infrared irradiance (long-wave) absorbed by the canopy is calculated from the infrared irradiance from the sky, minus the infrared irradiance from the canopy. The incoming infrared irradiance is calculated from air temperature, humidity and cloud cover, following Miller et al (1981). The equation fits California data well, but it has not been tested elsewhere. The infrared irradiance from the canopy is calculated from the air temperature in the canopy, using the Stefan-Boltzman law. The resultant values for net infrared irradiance are similar to those calculated with the Brunt equation (Brunt 1932).

The radiation balance at the soil surface is calculated from the solar irradiance which is not intercepted by the vegetation canopy, albedo of the soil surface, incoming infrared irradiance, infrared irradiance from the canopy, fraction of the soil surface covered by vegetation and infrared irradiance from the ground. The turbulent exchange term in the Penman equation involves wind velocity and air vapour pressure. Wind velocity is calculated for the average height in the canopy and for the soil surface. Vapour pressure is calculated for the canopy and for the soil surface.

The daily mean temperature at the soil surface is related to air temperature, solar irradiance and leaf area index such that with 30 MJ/m^2/day incoming solar irradiance and no leaf area index, the soil surface temperature is 5°C above the air temperature. With 11 MJ/m^2/day irradiance and no leaf area index, the soil surface temperature is 2°C above air temperature. With a leaf area index of one, the difference between soil and air temperature is reduced to 2,5°C and 1°C with irradiances of 30 and 11 MJ/m^2/day. A leaf area index of two reduces the difference to 1,3°C and 0,5°C respectively. This relation is based on measurements in chaparral and matorral (Miller 1981). The surface temperature is the same as air temperature on overcast and rainy days.

Soil heat contents and soil temperatures are calculated at the mid-point of the six soil levels. The calculation of change in temperature at different soil depths involves the thermal diffusivity of the soil.

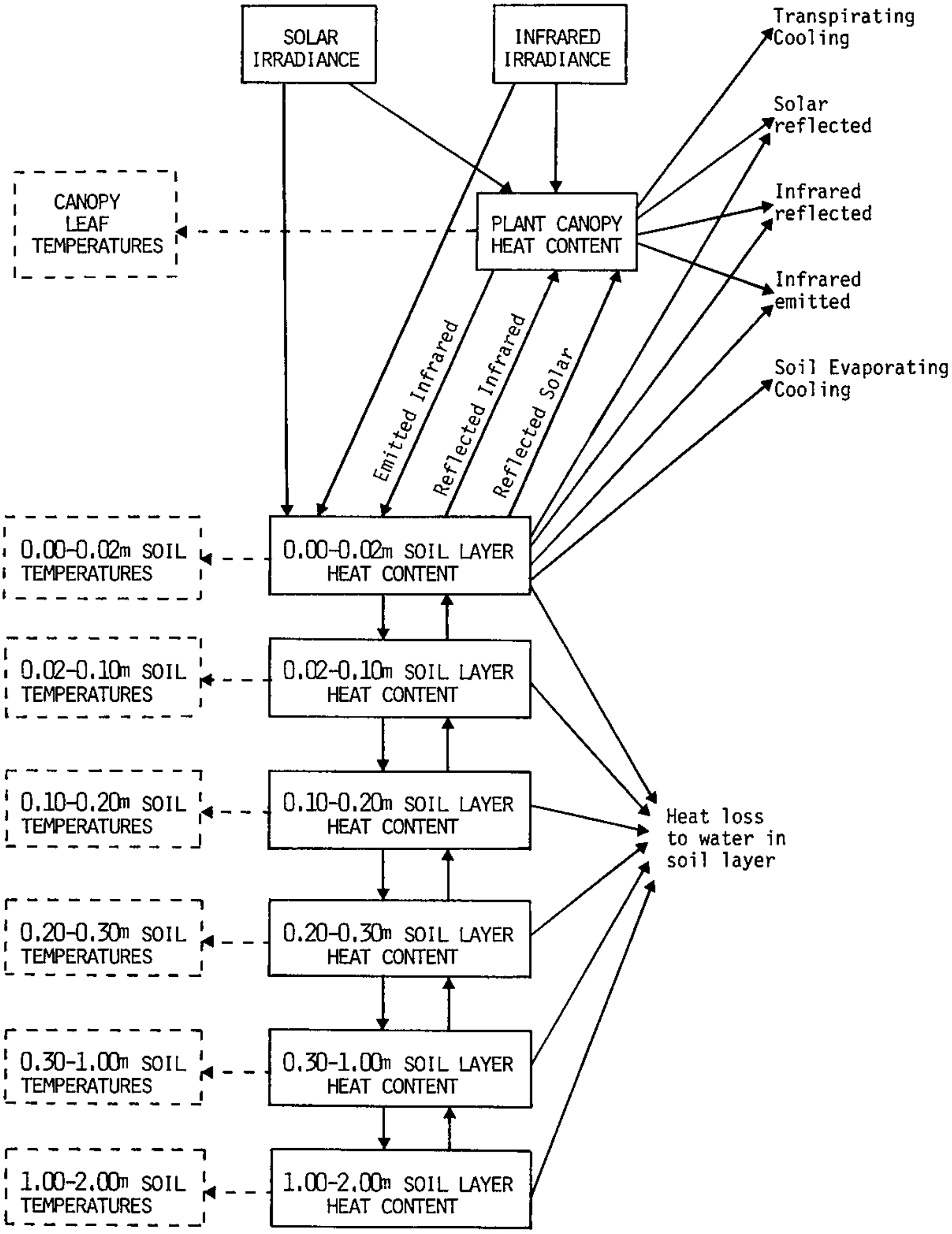

FIGURE 8. Energy transfer calculated in the energy balance submodel.

Thermal diffusivity involves the heat conductance and volumetric heat capacity of the soil, both of which vary with soil organic matter content and soil water content. The temperature at 6,6 m depth can be assumed constant through the year.

Soil evaporation is a function of the area of bare soil energy availability; hydraulic conductivity and the length of the diffusion pathway. Soil evaporation in kg per m^2 of soil surface is calculated by reducing the potential evaporation rate according to the water content of the surface level. If the water content is greater than 216 kg/m^3 no reduction occurs. The evaporation rate is reduced linearly to zero as soil water contents fall from 216 kg/m^3 to 24 kg/m^3. The latter is the soil water content when it is air-dry. On rain or mist days soil evaporation is reduced in proportion to the duration of the wetting event.

Transpiration is controlled by available energy and the stomatal resistance, which is a function of plant water potential, defined by plant root distribution and available soil moisture. A transpiration rate for the canopy is calculated from the vapour pressure deficit between the leaves and the air and the leaf resistance to water loss.

THE DECOMPOSITION SUBMODEL

(D T Mitchell)

Introduction

Decomposition is of particular interest in the fynbos biome, because the vegetation growing on oligotrophic soils of lowland and mountain regions is both evergreen and sclerophyllous; and when the vegetation dies it decomposes at an extremely slow rate. The decomposition submodel simulates several of the factors which control the release of nutrients for uptake by plant root systems. Both annual and seasonal variations in litter production are important, because the quantity of litter provides an indication of the potential availability of nutrients to the soil surface. The rate of decomposition depends on the ability of soil micro-organisms such as actinomycetes, bacteria and fungi to colonize the litter. This is governed by various climatic factors and the chemical nature of the decaying tissues. Soil moisture is important in the release of the soluble constituents such as potassium, soluble carbohydrates and soluble phenolics.

The release of leachates from the soils to streams may be of interest, as the concentration and combination of the chemical compounds in the leachates may distinguish black water from clear water streams in the fynbos biome. Analysing leachates may be a useful tool in determining the quality of drinking water in catchment areas.

Requirements of the submodel

The decomposition submodel should simulate the seasonal variations of decomposition and the release of carbon dioxide from the decomposition of litter, roots and soil organic matter. The submodel should also simulate the release of organic nitrogen and organic phosphorus compounds, which will then be used in the nitrogen and phosphorus submodels. In order to simulate the chemical controls on decomposition and the seasonal variation in litter quality, litter and soil organic matter should be broken down into groups of important classes of biochemical compounds such as: those that decompose quickly; those that are highly resistant and those that have an inhibitory effect. The submodel should be applicable over the full range of the sites in the biome, but data are not available for Strandveld and Renosterveld areas. Litter quality, seasonal waterlogging and frost at the high altitudes in Mountain Fynbos areas should also be included.

Observed patterns of decomposition

The measured annual litter production at Pella was 84 g/m^2 from randomly placed litter traps, 368 g/m^2 under the Leucospermum parile canopy and 247 g/m^2 under the Protea repens canopy. The period of peak litter production at Pella was from December until April for the proteoid shrubs, from September until May for the ericoid shrubs and from July until October for the restioids. Under the Leucospermum parile canopy, peak litter fall of leaves was from January until March and of flowerheads was from October to February. At Pella the annual per cent of Leucospermum parile leaf litter mass lost by decay was 11,42 per cent for the first and second years after the leaves fell. This represents a turnover rate of once in 8,03 years. Protea repens at Pella lost 25,5 per cent of the mass of leaf litter in the first year, but only 18 per cent of the Protea repens leaf litter mass was lost during the first year at Jonkershoek.

Description of the submodel

In the decomposition submodel, the aboveground litter, dead roots and rhizomes, and faeces are converted to organic matter. Leachates, organic nitrogen and organic phosphorus bearing compounds and carbon dioxide are the end products (Figure 9). The rate of microbial decomposition depends on the combination of different compounds present in the litter (Figure 10). Methanol-soluble phenolics may inhibit the growth rates of the decomposers; methanol-soluble carbohydrates have a rapid turnover rate and are consumed by the decomposers. Holocellulose, lignin, fats and waxes turn over slowly and are only broken down by specific microorganisms. As nitrogen and phosphorus are the two main elements in the nutrient cycling submodels, the turnover rates of these two elements from the litter are simulated in the decomposition submodel. The mineralization of both organic nitrogen and phosphorus in the soil is described in the nitrogen cycling and phosphorus cycling submodels.

Decomposition and release of components from the litter will be calculated according to either the overall fractional loss rate (k') or the instantaneous fractional loss rates (Olson 1963). The instantaneous fractional loss rate or k is useful for comparing decomposition rates for labile constituents (Olson 1963). The equations for k and k' are:

$\ln(X_0/X_t) = -kt$ (where X_t and X_0 are the mass remaining at times t and 0 respectively) and ; (1)

$k'=1-e^{kt}$ (2)

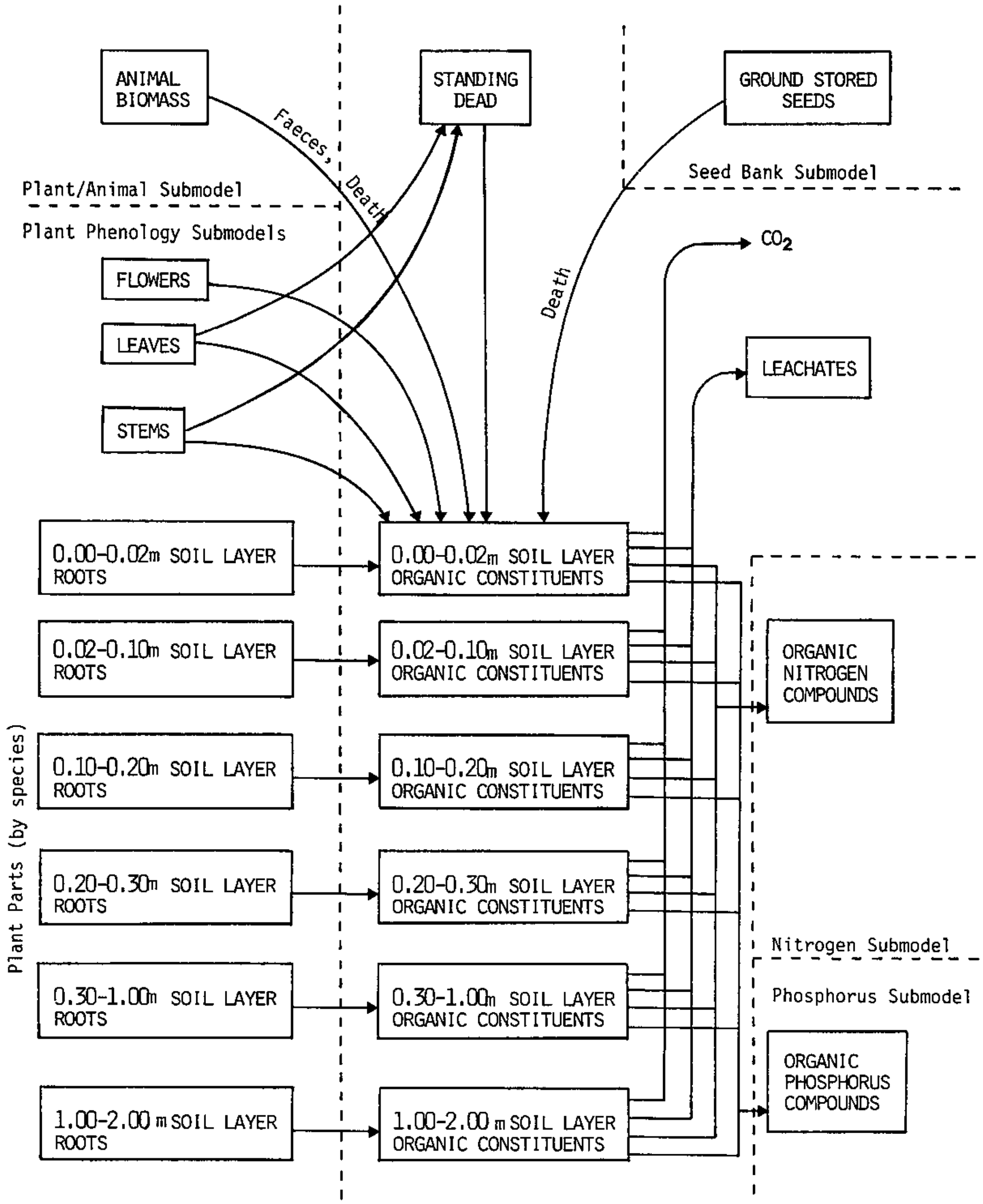

FIGURE 9. The general decomposition process including processes in the plant phenology submodel, plant/animal interactions submodel, the seed bank dynamics submodel, the nitrogen cycling submodel, the phosphorus cycling submodel, and the decomposition submodel.

Each component, eg dry mass, carbohydrates, phenolics, cellulose, lignin, fats and waxes, phosphorus and nitrogen, will have specific decomposition constants during the first, second and third years of the breakdown of the litter. Leaf litter will decompose at an annual loss rate related to the lignin content (per cent) and annual actual evapotranspiration (Figure 11). Soil organic matter decomposition will be related to soil moisture content and temperature using a multilinear regression equation similar to that used in the ARTUS model (Miller et al 1983) (Figure 12). Carbon-containing compounds, such as holocellulose and soluble carbohydrates, are converted to free sugars; lignin is broken down to phenolic compounds (Figure 9). All carbon containing compounds may be used as substrates for respiration by the soil micro-organisms. In the models, carbon dioxide production will be calculated as soil respiration excluding root respiration.

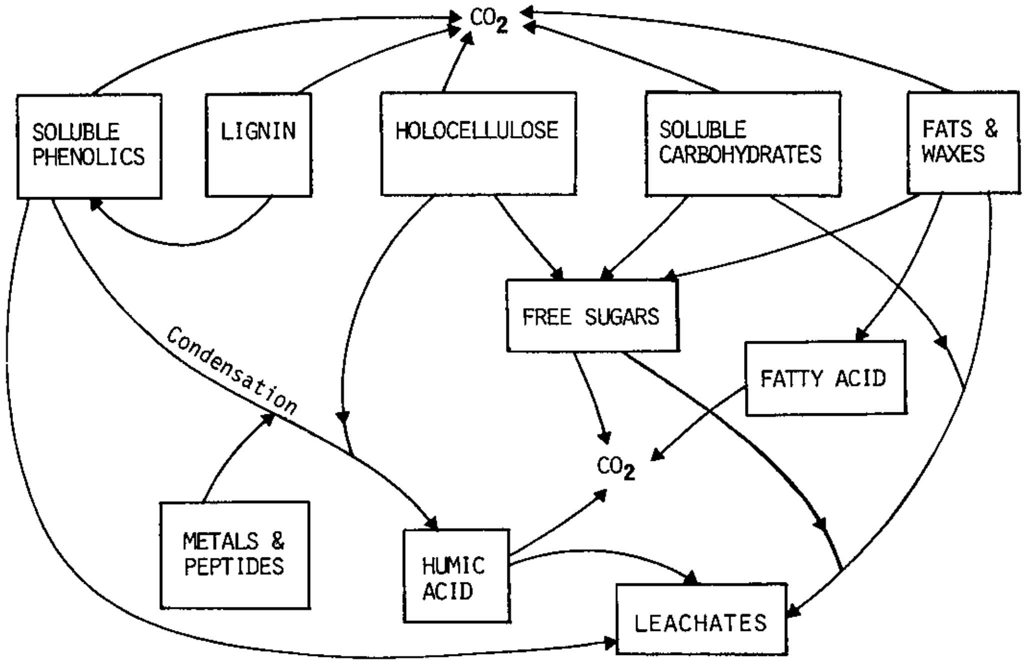

FIGURE 10. Flow diagram of the breakdown of carbon-containing compounds in the litter.

THE NITROGEN CYCLING SUBMODEL
(W Stock)

Introduction

Nutrient cycles in mediterranean-type ecosystems are dominated by the role of fire. Large stores of nutrients, especially of nitrogen, may be lost during a fire (Clark 1977). However, fire also releases nutrients which are tied up in woody canopy material and in types of litter that are highly resistant to decomposition. The fynbos is considered to be a nitrogen-limited system. Developing a submodel of nitrogen-cycling is a

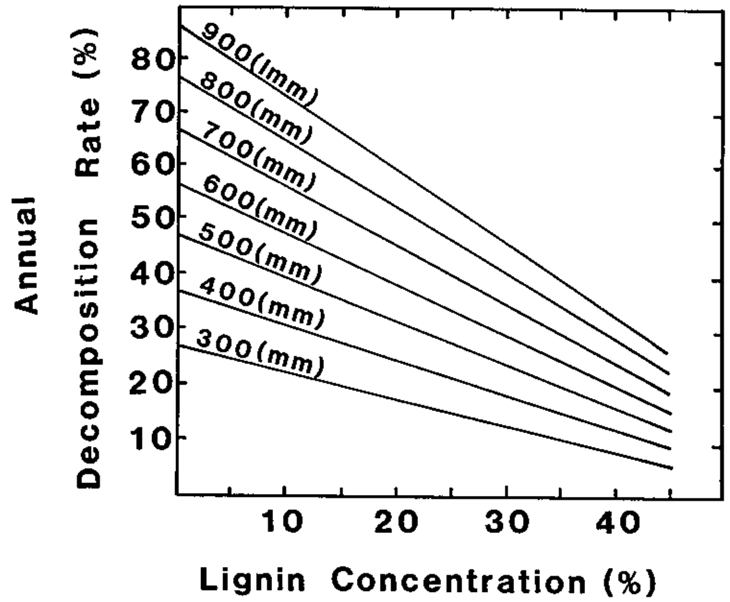

FIGURE 11. Model of the relationship between annual decomposition rate (per cent) and lignin concentration (per cent) at different values of annual actual evapotranspiration (AET). The slopes were obtained using the following linear equation:

$$Y = (-3{,}336 + 0{,}1\ X_1) - (0{,}013 + 0{,}002\ X_1)X_2 \qquad (3)$$

where Y_1 = annual decomposition rate (%),
X = annual AET (mm),
and X_2 = lignin concentration (per cent) (from Meentemeyer 1978).

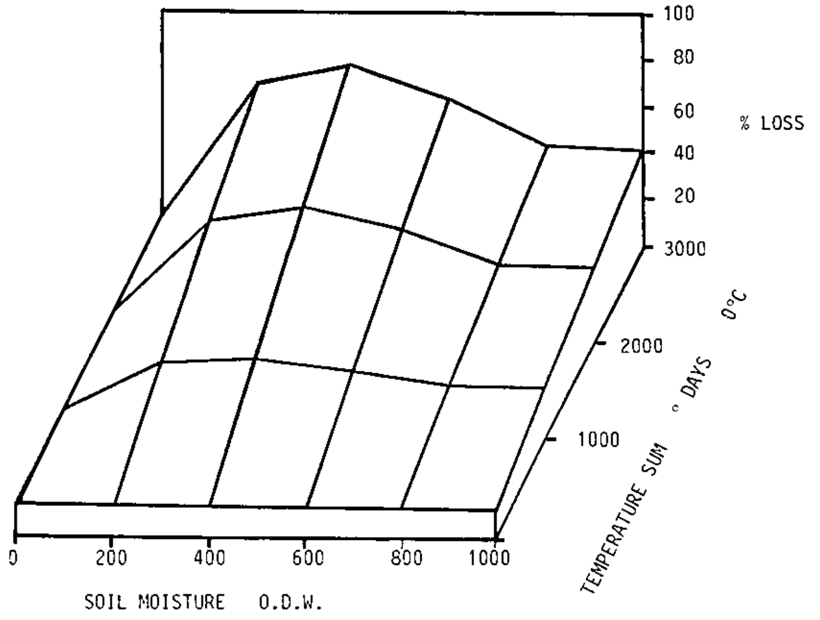

FIGURE 12. Regression surface for maximum first-year per cent losses in tundra sites, in relation to temperature sum and soil moisture. Per cent loss = $11{,}62 + 0{,}0147TW - 0{,}00289TW^2 + 0{,}000152TW^3$ ($R = 0{,}769$) where T = sum of degree-days for days with mean soil temperature (5 cm) above 0°C, W = $\frac{1}{2}$ (max + min) soil moisture (g/gdw) (from Heal and French 1974).

step towards understanding the processes that supply nitrogen to the ecosystem and the controls on the availability of nitrogen for plant uptake.

Requirements of the submodel

This submodel should simulate the major controls on the cycling of nitrogen in the fynbos. The submodel should start with the organic nitrogen compounds, which are released by the decomposition submodel; and include organic and inorganic nitrogen, which enter the system via precipitation. Nitrogen input by symbiotic fixation and mineralization should also be included. The submodel should then describe the various pathways by which nitrogen is made available for plants as ammonium and nitrate; and pathways by which it is lost from the system through leaching and denitrification. The submodel should be able to include the effects of seasonal waterlogging and periodic desiccation; and the competition for available nitrogen between plants and microbes. It should be possible to set parameters for the model for all major soil types in the fynbos biome.

Description of the submodel

The nitrogen cycling submodel maintains three organic nitrogen and four inorganic nitrogen pools (Figure 13). Organic nitrogen is divided into nitrogen in the microbial biomass, nitrogen in easily decomposable organic compounds and nitrogen in organic compounds resistant to decomposition. Inorganic nitrogen is in the form of available ammonium, ammonium bound on the exchange complex, nitrite and nitrate. The units for these pools are grams of nitrogen/m^2. Transfers between pools have the units grams of nitrogen/m^2/day.

As organic nitrogen in g/m^2/day is made available from the decomposition of litter, it is assigned to different compartments in the nitrogen cycling submodel. Based on data of Anderson and Domsch (1980), who found that the per centage of the total soil nitrogen in microbial biomass was approximately five per cent in agricultural soils and 0,22 per cent in forest soils, one per cent of the organic nitrogen in the litter is assigned to microbial biomass, 64 per cent to a decomposable organic nitrogen pool and 35 per cent is assigned to a resistant soil organic nitrogen pool. Exchanges within the three organic nitrogen pools maintain the pools at different nitrogen levels than those in the entering litter. One per cent of the total soil organic nitrogen is microbial nitrogen; 30 per cent is decomposable organic nitrogen; and 69 per cent is resistant organic nitrogen. Exchanges within the organic nitrogen pools favour the resistant pool, which is maintained near 69 per cent of the total organic nitrogen in the soil.

The rate of uptake of organic nitrogen by microbes is a function of the population growth of the microbes, which is affected by temperature and soil-water content (Figures 14 and 15). Fungi and bacteria have slightly different temperature and soil-moisture requirements for growth. As the amount of organic nitrogen in the microbial pool approaches two per

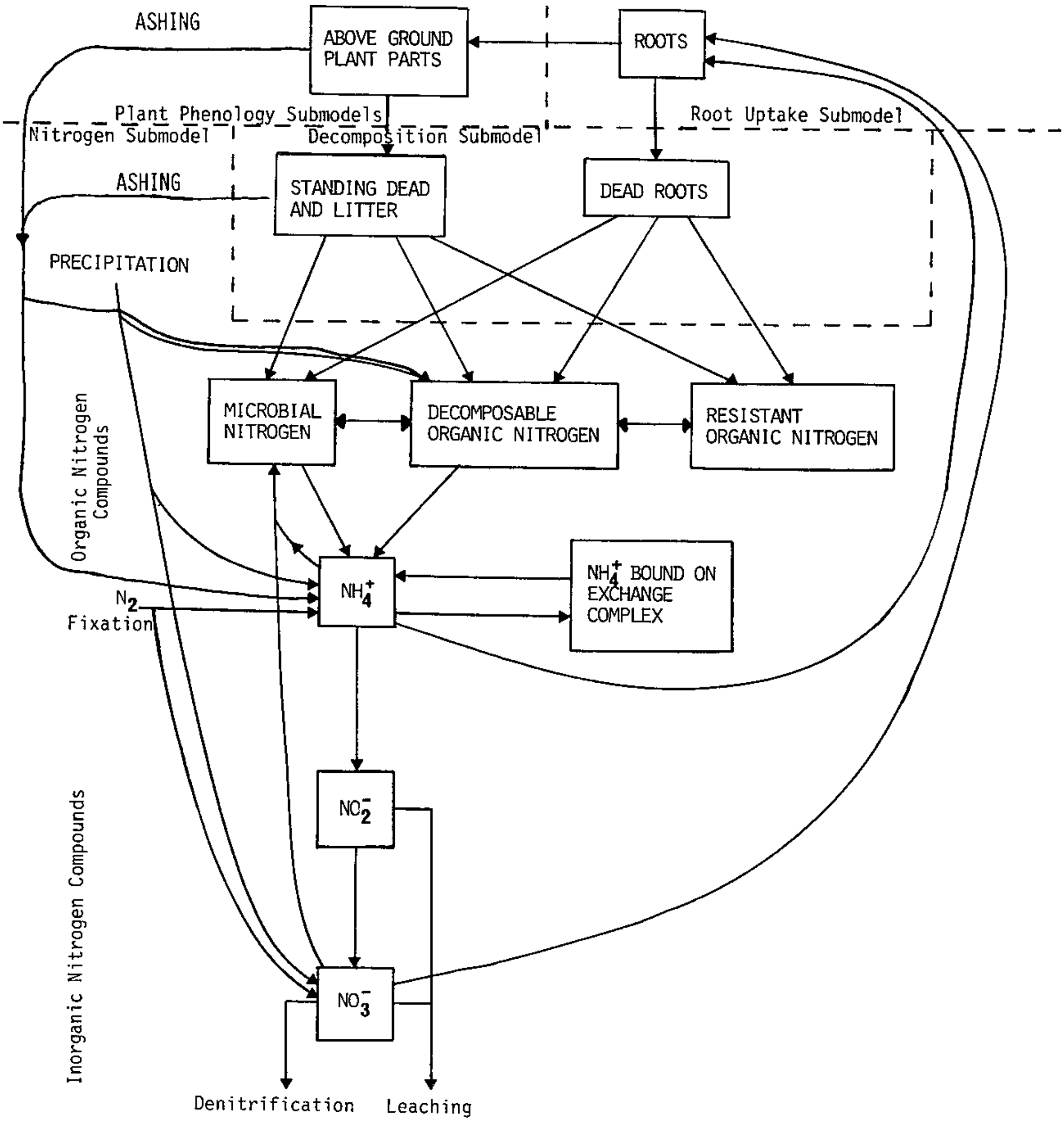

FIGURE 13. The complete nitrogen cycle which includes processes in the root uptake submodel, the plant phenology submodels, and the decomposition submodel, as well as the nitrogen cycling submodels.

cent, the exponential phase of microbial population growth stops (Figure 16). Microbes begin to die as soil temperature rises above 30°C and as soil-water content drops below -2 MPa (Figures 17 and 18). As microbes die, 90 per cent of their organic nitrogen is assigned to the decomposable pool and 10 per cent goes to the ammonium pool. This nitrogen is then available for plant uptake. The partitioning of nitrogen released from dead microbes into these two pools should mimic the nitrogen flush which is measured after soil desiccation.

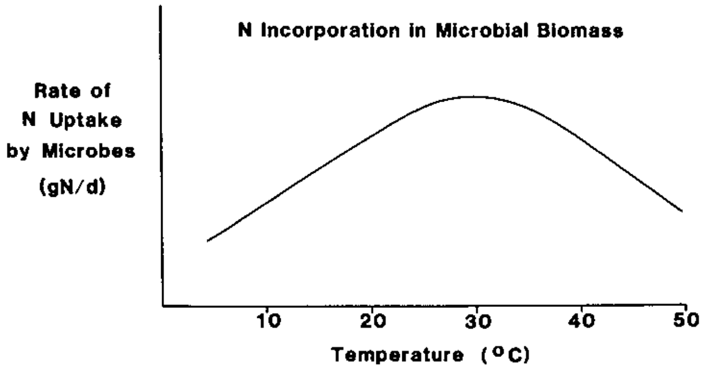

FIGURE 14. Nitrogen incorporation in microbial biomass as a function of temperature.

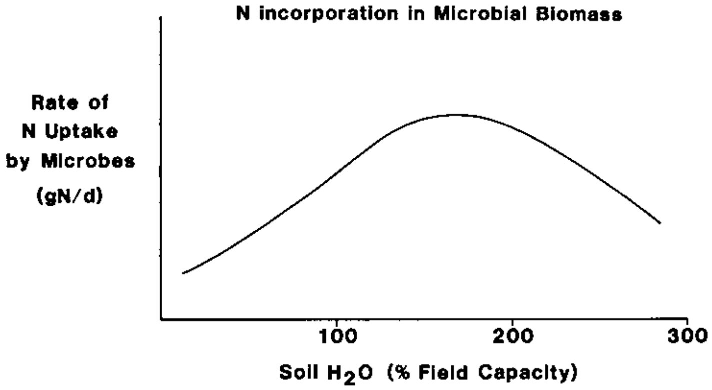

FIGURE 15. Nitrogen incorporation in microbial biomass as a function of soil-water content.

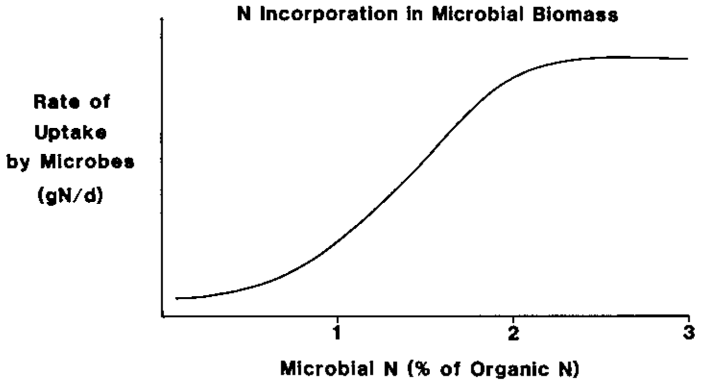

FIGURE 16. Microbial population growth rate as a function of microbial population size.

The mineralization of organic nitrogen in the soil is divided into ammonification and nitrification. Ammonification, which is the conversion of protein, peptides and amino acid compounds into free ammonium, is essentially the fungal and/or bacterial hydrolysis of protein by protease enzymes. This conversion is dependent on the soil temperature and water content (Figures 19 and 20). In incubation experiments Stock et al (in preparation) measured a mineralization rate of 0,916 mg N/g soil organic N/day for soils from Pella which were held at field capacity and a temperature of 30°C. The optimum temperature for ammonification in these soils is between 25 and 30°C, and the optimum soil-water content is between 75 and 100 per cent of field capacity. Ammonification is more sensitive to changes in temperature than to changes in moisture. It is known that soil fungi are relatively insensitive to changes in soil-water content and can operate at soil-water potentials as low as -5 MPa. Ammonification ceases when the pH is lower than 3,0.

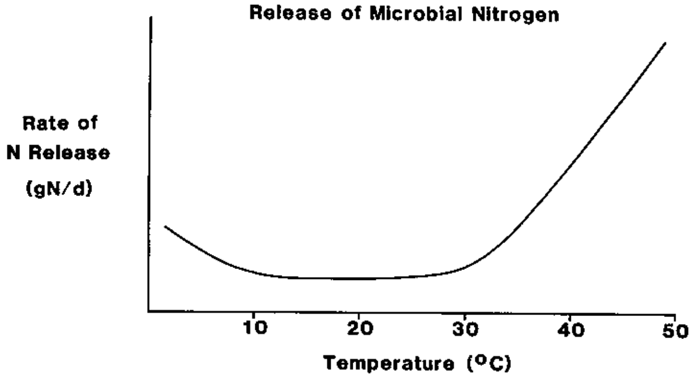

FIGURE 17. Microbial death rate as a function of soil temperature.

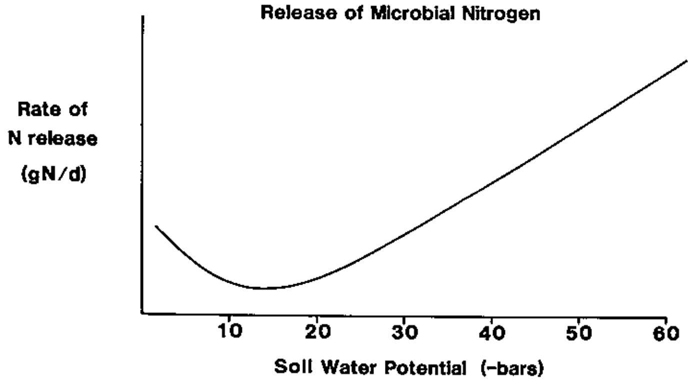

FIGURE 18. Microbial death rate as a function of soil-water potential.

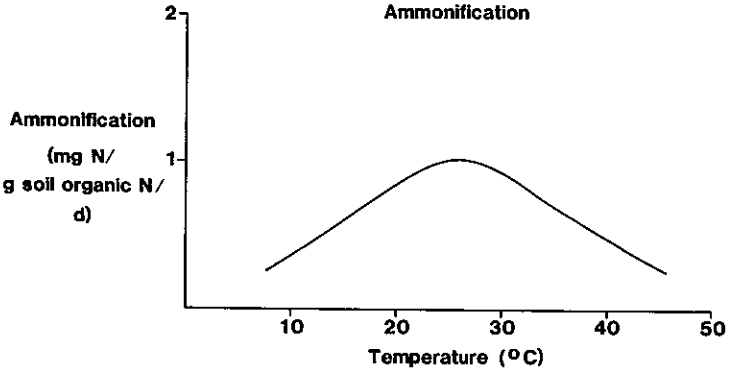

FIGURE 19. Rate of ammonification as a function of soil temperature.

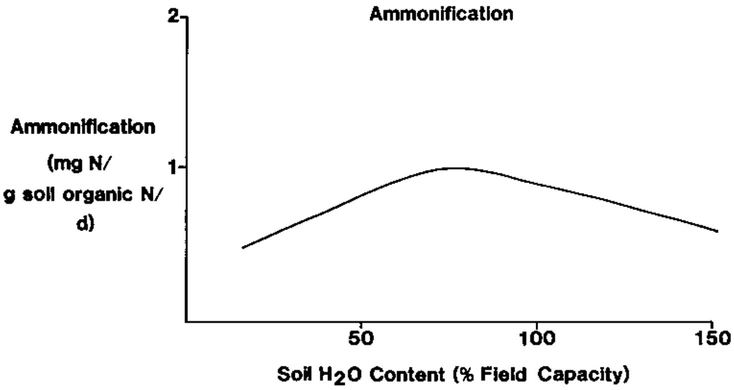

FIGURE 20. Rate of ammonification as a function of soil-water content.

Nitrification is assumed to be a two step process in which chemotrophic bacteria are dependent on the oxidation of ammonium and nitrite for their energy requirements. The two steps have slightly different temperature and moisture requirements (Figures 21-23). The step from ammonium to nitrite decreases slowly when soil moisture is above 100 per cent of field capacity. However, the step from nitrite to nitrate is sensitive to anaerobic conditions; the conversion decreases sharply when soil moisture is above 100 per cent of field capacity, which may cause nitrite to accumulate under anaerobic conditions. It is assumed soil oxygen tension is related to soil-water content and that waterlogging indicates anaerobic conditions. These relationships apply at a pH level of five. As the pH decreases from 5 to 3,5, the rate of nitrification decreases linearly to zero. Below a pH of 3,5, nitrification does not occur.

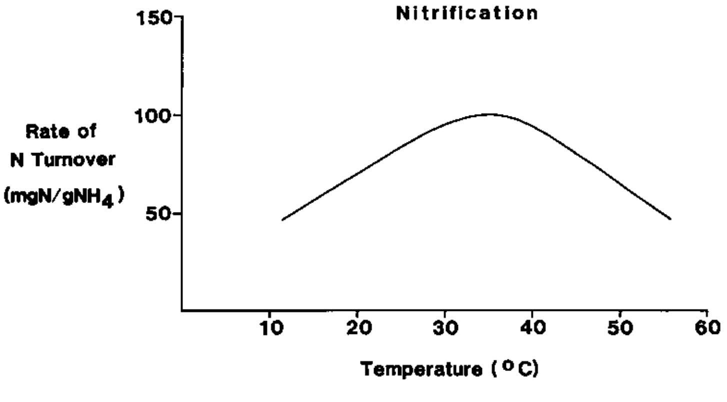

FIGURE 21. Conversion of ammonium to nitrite as a function of soil temperature.

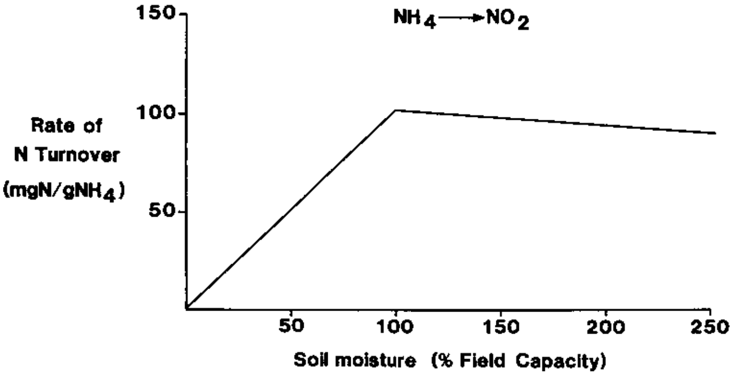

FIGURE 22. Conversion of ammonium to nitrite as a function of soil-water content.

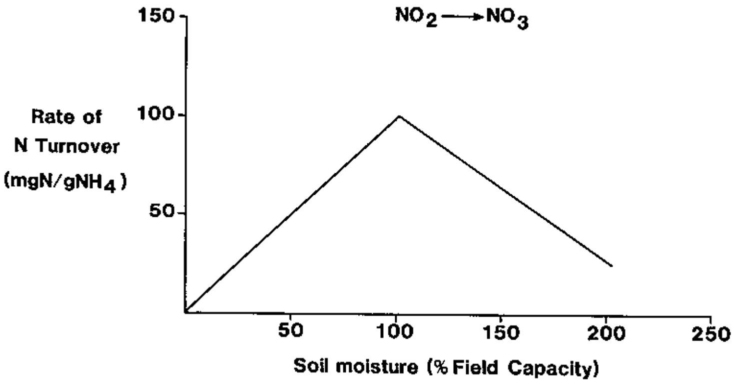

FIGURE 23. Conversion of nitrite to nitrate as a function of soil-water content.

The positive charge on the ammonium causes it to be held on clay and organic particles by electrostatic forces. It is assumed that, as ammonium is produced, there is a steady state between the soil solution and exchange complex. The ratio of exchangeable ammonium to soil solution ammonium does not change. It is only a change in the clay content of the soil or the amount of soil organic matter which would cause a change in the number of exchange sites. This will change the ratio of the bound to soluble ammonium (Figures 24 and 25). Ammonium and nitrate can be taken up by microbes. Ammonium and nitrate are taken up by plant roots in the various soil levels, depending on the amount of root length in each level, soil water and temperature. Nitrate and nitrite are lost from the system by leaching. Fox et al (1970) found that nitrate leaching in sandy soils could be predicted by the formula:

$$\text{depth of leaching} = \frac{\text{amount of leaching water}}{\text{field capacity of the soil}} * 100 \qquad (3)$$

It should be possible to describe the movement of nitrate in the soil profile as a distinct front. Thus all the nitrate could be leached from a soil level if the volume of precipitation is large. Nitrite probably has the same leaching pattern as nitrate.

Nitrate is also subject to loss by denitrification at a rate which is a function of soil water content. Denitrification occurs with soil-water contents above field capacity. Denitrification increases to 10 mg NO_3 reduced per gram NO_3 as soil-water capacity increases from field capacity to maximum soil-water content.

Nitrogen also enters the system as dry and wet fall. About two kilograms organic N/ha/yr, or about 0,04 g organic N/mm of precipitation, is added to the soil surface at Pella through dry and wet fall. This organic nitrogen enters the decomposable pool and is immediately available for uptake by microbes and plant roots. Bulk precipitation of inorganic nitrogen is between 1,2 and 2,0 kg inorganic N/ha/yr at Pella, but varies annually depending on the volume of precipitation. The input of inorganic nitrogen can be calculated as 0,03 g N/mm precipitation. With 500 mm/yr of precipitation, Pella receives about 1,5 kg inorganic N/ha/yr. Inorganic nitrogen in wet and dry fall is divided equally between the ammonium and nitrate pools. The input of organic and inorganic nitrogen through dry and wet fall is added to the surface soil level. Lower soil levels receive nitrate and nitrite by leaching. It is assumed that organic nitrogen and ammonium are not mobile down the soil profile.

The microbes and plant roots compete for different forms of nitrogen. Since nitrogen uptake by both microbes and roots are similarly controlled by temperature and soil water, the C:N ratio is the controlling factor which determines whether the microbes or the roots get the available nitrogen (Figures 26-28). The rate of microbial uptake of nitrogen is low with a C:N ratio of about 35.

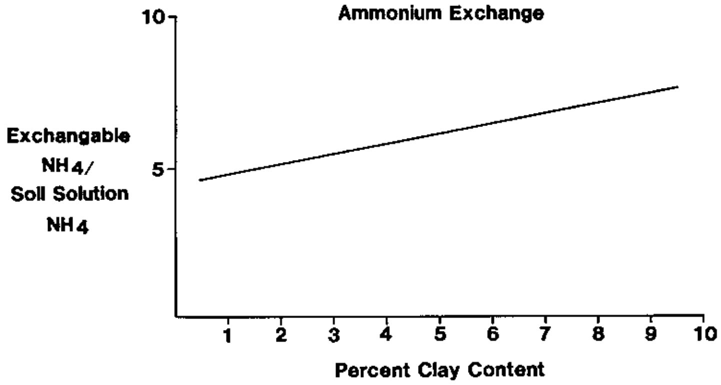

FIGURE 24. The ratio of ammonium bound on the exchange complex to soluble ammonium as a function of clay content of the soil type.

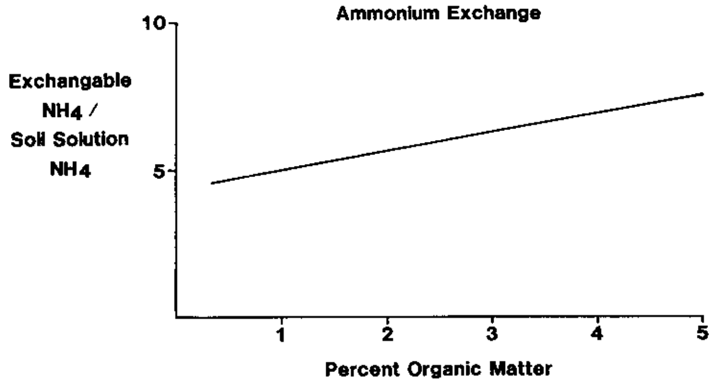

FIGURE 25. The ratio of ammonium bound on the exchange complex to soluble ammonium as a function of the organic matter in the soil.

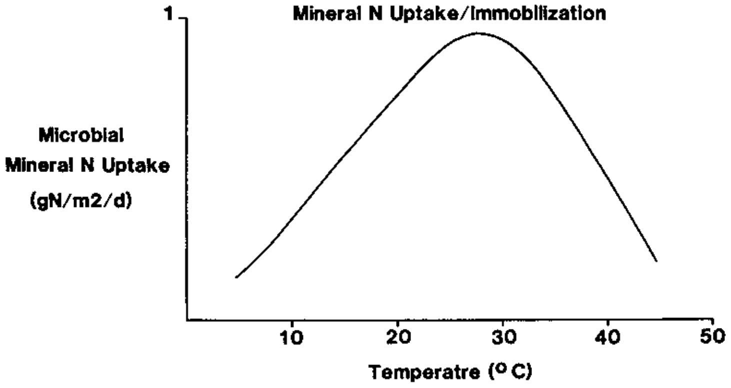

FIGURE 26. The ratio of nitrogen uptake by microbes to nitrogen uptake by plants as a function of soil temperature.

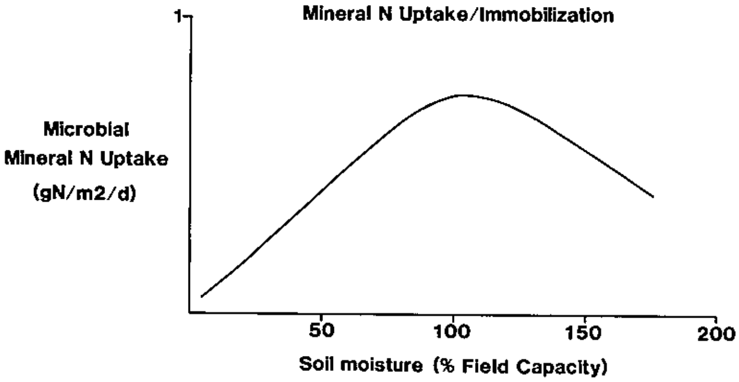

FIGURE 27. The ratio of nitrogen uptake by microbes to nitrogen uptake by plants as a function of soil water content.

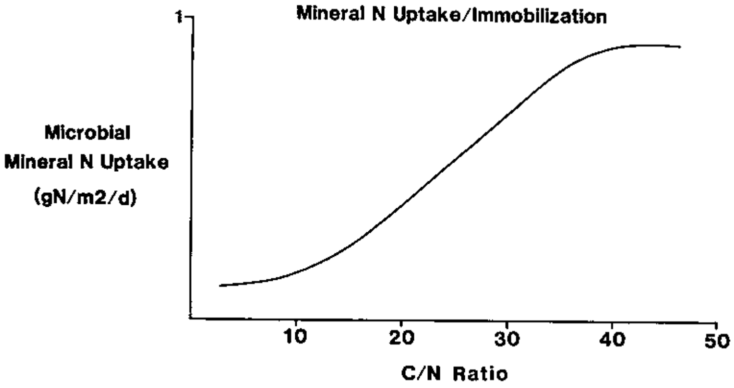

FIGURE 28. The ratio of nitrogen uptake by microbes to nitrogen uptake by plants as a function of the C/N ratio in the soil organic matter.

THE PHOSPHORUS CYCLING SUBMODEL
(G Brown, D T Mitchell)

Introduction

The phosphorus cycling submodel was originally structured using concepts and parameters developed in other ecosystems (Miller et al 1983). The results of detailed work on phosphorus availability in the soils at Pella are just now becoming available (Brown 1983). Some of the results of this work are presented here. The concepts developed by Brown will be encoded in the phosphorus cycling submodel so that it can approximate phosphorus availability in fynbos ecosystems.

Requirements of the submodel

The submodel should simulate the seasonal progression of phosphorus mineralization, phosphorus exchange reactions, input of phosphorus in dry and wet fall and loss of phosphorus in drainage (Figure 29).

Observed patterns of phosphorus availability

Brown (1983) found three factors that are involved in the adsorption and desorption reactions of extractable phosphorus in the soil: I_e, the equilibrium activity product of the phosphorus in the soil solution while in equilibrium with the soil; Q_0, the measured amount of surface

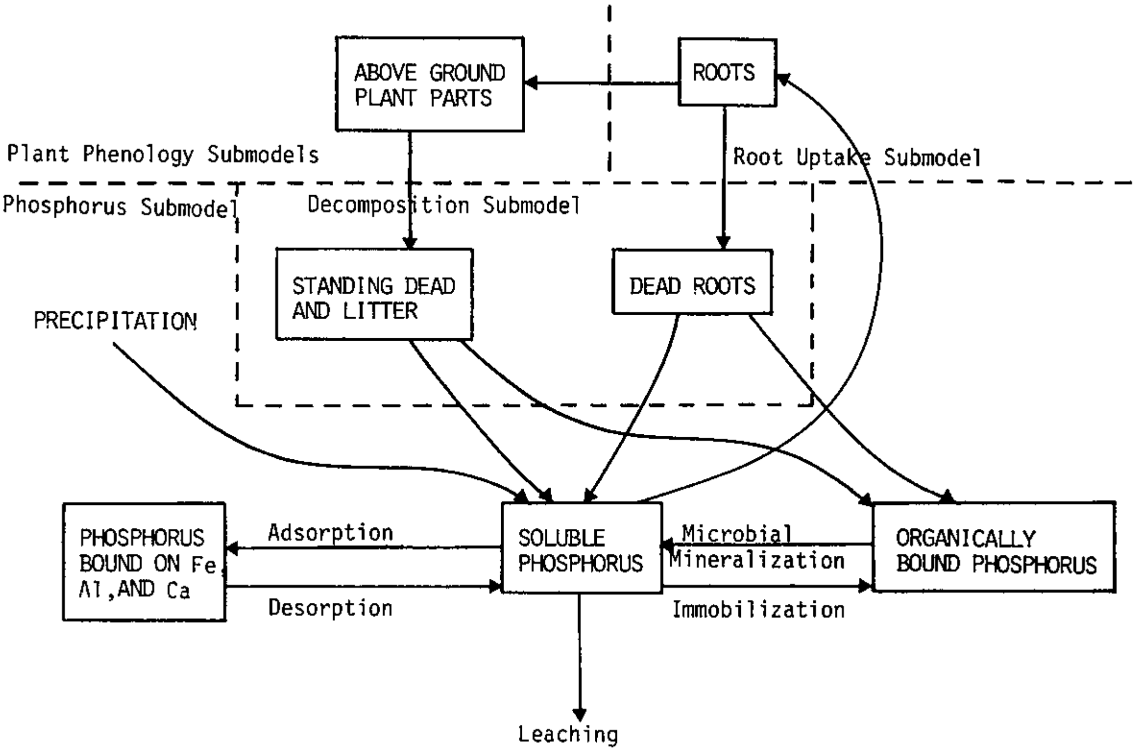

FIGURE 29. The complete phosphorus cycle including the processes the root uptake, plant phenology and decomposition submodels.

exchange sites present in the soil at equilibrium (I_e); and Q/I, the quantity of labile phosphorus that must be added to the soil to cause given changes in the soil solution. There is a negative relationship between the buffering capacity of the soil (Q/I) and the total amount of phosphorus desorbed by the soil in a given time:

$$Y = 191{,}65 - 52{,}51X \tag{4}$$

where Y is the total phosphorus desorbed and X = Q/I, r = - 0,82.
I_e values are positively correlated with the phosphorus levels measured using resin bags:

$$Y = 0{,}23 + 0{,}02X \tag{5}$$

where Y is the resin bag extractable phosphorus and X = I_e, r = 0,99.
Q/I is positively correlated with the amount of phosphorus extracted using the Bray #2 method:

$$Y = 0{,}17 + 0{,}17X \tag{6}$$

where Y = Q/I and X = Bray #2 phosphorus, r = 0,96.
Q_o is positively correlated with soil iron levels:

$$Y = 24{,}35 - 3{,}38X \tag{7}$$

where Y = Q_o and X is the soil iron level, r = - 0,83.

The amount of surface exchange sites in the soil is up to 10 times higher in waterlogged soils than dry soils. This increase in exchange sites persists for some time after the soils dry. The per cent of total phosphorus in resin extractable form is negatively correlated with soil iron levels:

$$Y = 10{,}19 - 1{,}80X \tag{8}$$

where Y is the per cent of total phosphorus in resin bag extractable form and X is the soil iron level, $r = -0{,}93$.

These relationships are for freely drained soils. If the soils become waterlogged, iron forms amorphous gels which have more binding sites per surface area. The decreased pH associated with waterlogging causes the iron fraction in the soil to become more important. Below a pH of 7, calcium bound phosphorus is not significant.

The major factors influencing the levels of organic phosphorus in the soil are soil moisture content and temperature; pH and the level of soil organic matter are also important. Increasing pH should increase rates of mineralization due to increased activities of bacteria in the soil. Higher levels of organic phosphorus in the soil will also increase the rate of mineralization of phosphorus.

Description of an earlier submodel

An early version of the phosphorus cycling submodel was based on North American experience. Organic phosphorus was taken to break down to TNC (total non-structural carbohydrate) and phosphate at a rate of 0,96 µg/g soil/day at 20°C and when soil water was at field capacity. The temperature relation used a Q_{10} of 2. The water relation was such that if the soil water was less than 0,67 times the field capacity, phosphorus mineralization decreased from 0,96 µg/g soil/day to 0,10 µg/g soil/day when the soil water content was at equilibrium with the air. With water contents above field capacity, the rate was reduced proportionally to water content, from 0,96 µg/g soil/day to 0,53 µg/g soil/day, at the maximum water content. The process involving immobilizaton of phosphorus by microbes was simulated just as for nitrogen, using the same relation with the C:N ratio. Mineralized phosphorus, as phosphate, was taken to be 0,14 of the organic phosphorus decomposed.

The available pool of phosphorus was divided between the solution and the exchange complex. Five to seven per cent of the inorganic phosphorus was taken to be in resin-bag-extractable form (Brown 1983), the rest being bound on iron, aluminium and calcium complexes. The ratio of phosphorus in the soil solution (mg P/kg soil) to that bound on the exchange complex was taken to be nine. This ratio was affected by the presence of iron and aluminium, pH and water.

The loss of phosphorus by drainage depended on the concentration of the soil solution, relative uptake and the drainage loss of water.

The concentration of phosphorus in rain was assumed to be 0,03 mg/l, which with 600 mm/yr of precipitation will give 18 g P/m^2/year, with no leaching of phosphorus from live plant material. This is reasonable since leaching of phosphorus from newly fallen litter is slow (Specht 1981), because most of the mobile compounds have been translocated from leaves by the time of abscission.

Results of an earlier submodel

Simulations using the earlier version of the phosphorus cycling submodel over several seasons indicated that phosphorus mineralization is extremely sensitive to soil-water content through several simulated years. Mineralization occurred throughout the year in the simulations but with peaks in autumn and spring.

THE ROOT UPTAKE SUBMODEL

(P C Miller, S Jongens-Roberts, D T Mitchell)

Introduction

In the FYNBOS model the uptake of water and nutrients is treated in a separate submodel to take advantage of the data available from current research. Available amounts of water, nitrogen and phosphorus are calculated in other submodels.

Requirements of the submodel

The root uptake submodel should simulate the uptake of water, nitrogen and phosphorus by the plant roots. Uptake should be based on the exploited radius around a root so that root interactions and species competition for water and nutrients can be simulated.

The uptake of water should be based on the water potential gradients between the soil and the plant. Nitrogen and phosphorus uptake mechanisms should include root growth into unexploited soil, diffusion and mass transport.

Description of the submodel

In the root uptake submodel, water moves from the six soil levels to the roots of the eight plant species according to the water potential gradient between each soil level and the density of absorbing roots of each species in each level. In a given level, water moves from the soil to the plant root if the water potential of the plant is lower than the water potential of the soil. For plants which are able to extract water from a soil level, the water is divided among the species according to the ratio of their respective root lengths in the level and the ratio of their water deficits. Water movement is slowed, because of the resistance of water movement into the rhizosphere and root resistance to water uptake.

Nitrogen and phosphorus uptake are assumed to occur through diffusion and mass transport and as roots grow into unexploited space. Uptake is directly proportional to the effective root length of a given species. The effective root length is the measured absorbing root length adjusted by an uptake adjustment factor, which is assumed to account for roots lost in excavations, mycorrhizae and variations in root mass in the soil relative to pockets of high nutrient availability. Uptake was first calculated for the vegetation as a whole and was then apportioned to the separate species according to their effective root length relative to that of the total community. Mass:length ratios for roots were calculated from Manders (unpublished), Kummerow (1981a), and Bowen (1981).

Roots are divided into primary roots, secondary roots and proteoid roots or mycorrhiza. Primary roots extend the root system into areas of the soil that were previously unexploited and take up nutrients while they are growing, but they do not continue to take up nutrients after they stop growing. Primary roots are considered to be perennial. In the submodel secondary and proteoid roots live for two to three months (Lamont 1981) and then die back, giving an average death rate of 0,013 g/g/day. Secondary and proteoid roots take up nutrients by diffusion and mass flow as they grow into unexploited soil; and continue to take up nutrients as long as they persist. Length to mass ratios were taken as 3 m/g for primary roots, 30 m/g for secondary roots and 90 m/g for proteoid roots. The analogous ratios for secondary roots in chaparral is about 10 m/g (Kummerow et al 1977); and for Banksia species is about 30 m/g (Bowen 1981).

Nitrogen and phosphorus uptake by root growth into unexploited soil is such that half of the nitrogen and phosphorus in the soil volume surrounding the new root is absorbed in one day. The exploited soil volume is a cylinder, with a length equal to the daily root growth increment and an exploited radius slightly greater than the length of root hairs of mycorrhizae. Bowen (1981) gives the length of root hairs on Banksia as one millimetre. Mycorrhizae may be two millimetres long. An exploited radius of one to two millimetres is used in the submodel. Zones of mineral depletion around roots have been well documented (cf review by Lamont 1981).

Phosphorus uptake over the assumed 75-day life of absorbing roots, as measured by Mitchell (unpublished), is 1 370 μgP/g absorbing root for Clovelly soil at Pella and 1 111 μgP/g absorbing root for Hutton soil at Jonkershoek.

Phosphorus uptake by diffusion depends on the diffusion coefficient of H_2PO_4 in solution ($77*10^{-6}$ m/day), the soil phosphate buffering capacity (0,11 $\mu gP/m^3$ water)/($\mu gP/m^3$ soil), the concentration of the soil solution away from the root (which is 857 μgP/kg soil solution for Clovelly soils at Pella and 588 μgP/kg soil solution for Hutton soils at Jonkershoek), the soil-water content (which is 84 kg/m^3 for Clovelly soils and 374 kg/m^3 for Hutton soils), and the length of the absorbing root. Nitrogen uptake by diffusion is taken to be higher for NH_3 than it is for NO_3.

Nitrogen and phosphorus uptake by mass flow of water depends on transpiration rates and soil solution concentrations. As water moves down through the soil levels past the roots, uptake can also take place depending on the cross-sectional area of the roots.

Uptake by transpiration will be equal to the transpiration stream multiplied by the concentration of soil solution. Transpiration is about 2 kg/m^2 leaf per day. Therefore, with 0,07 m^2 leaf per shoot and solution concentrations of 590 μgP/kg soil solution for Clovelly soil and 860 μgP/kg soil solution for Hutton soil, about 83 and 120 μgP/shoot/day are taken up by plants growing on Clovelly and Hutton soils respectively. The uptake is carried out by about 10 g root/shoot for the 75-day period of root activity. Thus about 622 and 900 μgP/g root/year are taken up in the transpiration stream by plants growing on Clovelly and Hutton soils. The uptake from water moving through the soil, past the root, depends on the cross-sectional area of the absorbing root; the solution concentration and the rate of water movement, which is 1,4 kg/m^2/day. If 20 per cent of the phosphorus is taken up as the solution passes, in 75 days a total of 1 121 and 1 634 μgP will be taken up from the passing water per gram of root, by plants growing on the Clovelly and Hutton soils. The total uptake for a gram of root with an extension of 30 m/g is 1 743 and 2 534 μg on the two soil types. The total phosphorus taken up is several times the 600 μ/g phosphorus used to make a root grow in either soil. Based on these calculations roots are not exporters of phosphorus to the plant.

In the simulation, as phosphorus decreases, mycorrhizal infection and proteoid roots increase, thus increasing the exploited volume of soil. As phosphorus decreases phosphatase secretion may increase thus increasing the available phosphorus in the vicinity of the roots. In the submodel the average diameter of absorbing root is 0,15 mm which is similar to values for Banksia (Bowen 1981; Lamont 1981). The average root diameter decreases as more proteoid roots are developed as root extension increases. As the average distance between roots decreases to less than twice the exploited radius, roots begin to compete for available nutrients. As root density increases, competition for nitrogen and water will appear before competition for phosphorus, because the exploited radii for nitrogen and water are larger than the exploited radius for phosphorus. This is because phosphorus is highly immobile and has a much lower diffusion rate.

More information is needed on the seasonal growth and death rates of absorbing roots, as the balance of the two rates gives the absorbing root mass. The mass of absorbing roots affects both the carbon and phosphorus balance of the simulated plant. A simulation which gives too much TNC and too little phosphorus can be corrected by increasing or decreasing the mass of absorbing roots.

THE CARBON BALANCE SUBMODEL

(P C Miller)

Introduction

The processes involved in photosynthesis are the keys to understanding the survival of plants. This is especially true in mediterranean-type ecosystems which are marked by repeated periods of drought and have low nutrient levels in the soils. In order to control the loss of water a plant may close its stomata, which restricts its ability to take up carbon. Low levels of light, possibly caused by the shading of the plant by its neighbour, will limit the energy avilable for carboxylation and therefore the rate of photosynthesis. Nutrient deficiencies may limit the production of important enzymes, which will also limit photosynthesis even though there may not be an increase in stomatal resistance.

While photosynthesis may be limited because of environmental or nutritional limitations, the plant must continue to maintain itself and satisfy its respiratory costs. At some point, the limitations imposed on carbon acquisition by the environment will exceed these costs to the plant and the negative carbon balance will lead to death.

In the mediterranean-type ecosystems of California and Chile, this pattern of environmentally limited carbon acquisition and the variation in photosynthetic rates and respiratory costs of different growth forms, has been hypothesized as the explanation for the distribution of plants in these areas (Miller 1979).

Requirements of the submodel

The carbon balance submodel should simulate the processes that control the rates of photosynthesis and respiration. The submodel should generate the daily photosynthate reserve, which can then be allocated to the growth of the various plant parts in the phenology submodels. Photosynthesis should be limited by such things as plant water status, atmospheric water vapour pressure gradients; photosynthetically active photon flux levels, and plant nutrient status. Respiration should be a function of parameters such as the plant tissue involved, temperature and protein content of the plant.

Description of the submodel

Plant physiological data for fynbos species are extremely limited. At present it is hard to do much more than make some broad general assumptions based on growth form (Table 4).

TABLE 4. Rates of photosynthesis assumed in carbon balance submodel (see text for explanation)

GROWTH FORM CATEGORY	Rate of photosynthesis, mg TNC assimilated per gram of leaf tissue (or stem tissue in <u>Restio filiformis</u>) per 13-hour day.	
	Mature	Juvenile
Shrub	40	-
Graminoid	54	90
Geophyte	64	-

In this submodel, photosynthesis is calculated as 10,8 g dry matter/m^2 of leaf per day, or 0,04 g/g leaf/day for a 13 hour day for the shrub species. Fynbos shrubs in Swartboschkloof have photosynthetic capacities similar to those in other mediterranean-type ecosystems (Mooney et al 1983), therefore assuming such an average rate is reasonable in the absence of detailed data. Photosynthesis is calculated to vary with day length throughout the year.

Respiration is divided into maintenance and growth components. Maintenance respiration occurs at rates of 0,64 mg dry matter/g shoot/day; 0,41 mg/g new secondary stem tissue/day; and 8 mg/g/day for the floral bud, flower, and seeds. The maintenance respiration of leaves is included in photosynthesis during the daylight period and is 4 mg/g leaf during the night. The maintenance respiration values are based on the nitrogen contents (van Wilgen and le Maitre 1980, 1981).

It is assumed that maintenance respiration is directly proportional to plant protein content and is 15 mg/g/day with a nitrogen content of 40 mg/g (Penning de Vries 1972, 1973; McCree 1970). Growth respiration is assumed to equal 0,3 of the growth (Penning de Vries 1972, 1973), except for roots. In roots, growth respiration is assumed to be an amount equal to 0,8 of the growth, because of the cost of producing root exudates and the costs of root cap formation, which is 0,4 of the new growth in roots. In mediterranean-type ecosystems, maintenance respiration should probably be expressed in terms of per cent nitrogen contents, rather than on a dry-mass basis, but due to the absence of data the above approximations are used.

In both of the graminoid species, photosynthesis is assumed to be 54 mg/g/day for shoots on a mature plant and 90 mg/g/day for shoots on the juvenile plant. Maintenance respiration is 0,64; 0,64; 4,0; 8,0; and 8,0 mg/g of shoot, rhizome, absorbing root, inflorescence and seed, respectively. Growth respiration values are 400; 400; 800; 300 and 700 mg/g new tissue for shoots, rhizomes, absorbing roots, inflorescences and seeds, respectively.

THE SHRUB GROWTH SUBMODEL

(P C Miller, F J Kruger, D C le Maitre, B W van Wilgen)

Introduction

The submodels of shoot growth, graminoid growth, geophyte growth and seedling growth all perform the same function. They describe the controls on the growth of the various plant parts and the subsequent plant phenology (Figure 30). Although all three growth forms have analogous anatomical structures, it is easier to think of stems in the case of shrubs, rhizomes in the case of graminoids and bulbs, in the case of geophytes, rather than connective tissue. It is hoped that within a growth form, the phenological patterns will be similar enough to necessitate only parameter changes in modifying a single set of equations. Equating plants, such as Protea repens with Psoralea obliqua, may be difficult, because the former shows two growth periods a year and has a multi-year reproductive cycle, whereas the latter seems to go through most of its phenological stages within a year. As our understanding of the controls on allocation and growth improve, it may be necessary to develop separate submodels for each species; or it may be possible to combine all three growth forms into a single universal submodel.

The shrub growth submodel describes physiological processes, including the controls of temperature and plant water status on growth, the allocation of total nonstructural carbohydrate to leaves, stems, and roots and the nitrogen and phosphorus limitations on growth of leaves, roots and inflorescences. The submodel simulates the seasonal course of shoot and inflorescence development and the death of plant parts.

Requirements of the submodel

The shrub growth submodel should partition photosynthate determined in the carbon balance submodel, as well as nitrogen and phosphorus reserves determined from calculations in the root uptake submodel, to the various plant parts based on the patterns of shoot system dynamics. The growth of each of the various plant parts can then be calculated from the reserves of total nonstructural carbohydrate (TNC), nitrogen and phosphorus in that plant part, taking account of phenological triggers and temperature, nutrient and water controls on growth.

The submodel should simulate the observed patterns of growth and phenological switching mechanisms which define the sequence of growth of the various plant parts. It should provide for: environmental cues, such as heat sums and day length for starting growth; and internal physiological cues, including TNC levels and plant-water potential for stopping growth and starting death.

The shrub submodel should receive inputs from the climate (light, temperature), energy balance (actual transpiration) and carbon balance (photosynthesis as TNC per unit tissue per day) and root uptake (nitrogen, phosphorus, and water) submodels, although it is presently configured with its own set of simplified environmental and nutrient cycling equations. The plant submodels output simulated data to the energy balance (leaf area index and in due course, canopy structure), root uptake (root length) and propagule bank dynamics (seed and/or resprout bud numbers) submodels. Simulated data are for individual species to allow for competitive interactions, but are aggregated for certain purposes, eg for calculation of light extinction in the canopy in the energy balance submodel.

Observed shrub phenology and growth patterns

Protea repens is the most common and most widely distributed of the Cape proteas, occurring throughout the south-western, southern and eastern Cape (Rourke 1980). Protea repens is usually found on the lower mountain slopes at elevations between sea level and 600 m, but it is also found at higher elevations on the high, drier inland mountains. It varies in its edaphic requirements, growing on Table Mountain Sandstone, Cape Granite, Witteberg Quartzite and on rare occasions on Bokkeveld Shale (Rourke 1980). It is a tall shrub, normally about 2,5 m tall, although it can reach 4,5 m; and often forms a dominant overstorey layer. Its common name, sugarbush, is derived from its copious nectar production during flowering (Cowling and Mitchell 1981).

FIGURE 30. Portion of the canopy of Protea repens, showing the structure of the shoot system. The branch was sampled in March, soon after rapid growth of the new inflorescence bud (A) had begun. The older inflorescence (C) would have been pollinated in the previous winter. The portion of shoot between A and B, including the inflorescence A, represents one shoot within a cohort of shoots. See text.

The growth pattern in Protea repens is sympodial and relatively simple. Axillary shoots develop when the terminal bud differentiates into an inflorescence; and growth flushes can be detected via budscale scars, which makes the aging of shoots relatively easy. During the first year the new shoot develops leaves and stem (Figure 31). The initiation of shoot growth generally begins between 10 September and 1 October; and growth continues until late December (Kruger 1981). In late January a second flush is initiated on some shoots, which continues until mid- or late March. The terminal bud becomes dormant about the end of March. Bond (1980a) found that the pattern of growth of Protea repens in the Swartberg was similar to that at Jonkershoek, although growth in the two areas may be out of phase by about two weeks. This pattern of growth may be an adaptation to the availability of soil moisture to deep-rooted species throughout the year.

The embryology of Protea repens was extensively studied and described by Jordaan (1944). The inflorescence bud develops over a period of 16 to 18 months until flowering, which occurs in May and June. Three to five days after the involucral bracts open, the outer florets open. Over a period of an additional three to five days, the remainder of the florets open. About three days after opening, the florets begin to senesce; 10 to 14 days later the bracts close; and a week later the inflorescence is tightly shut and the bracts are dry and brown. Following flowering and pollination, the fruits (achenes) mature for eight months, until February. One year after flowering some inflorescences may open.

The mature seeds usually remain in the dried cone and maintain their viability for at least two to three years (van Staden 1978; Kruger 1981). The process, from the development of the axillary bud to mature seed, takes 42 months. With favourable conditions during development of the floral bud, flowering may occur one to two months earlier (eg southern Cape). There are ecotypic differences, which result in varying patterns of flowering response to environmental factors (Rourke 1980).

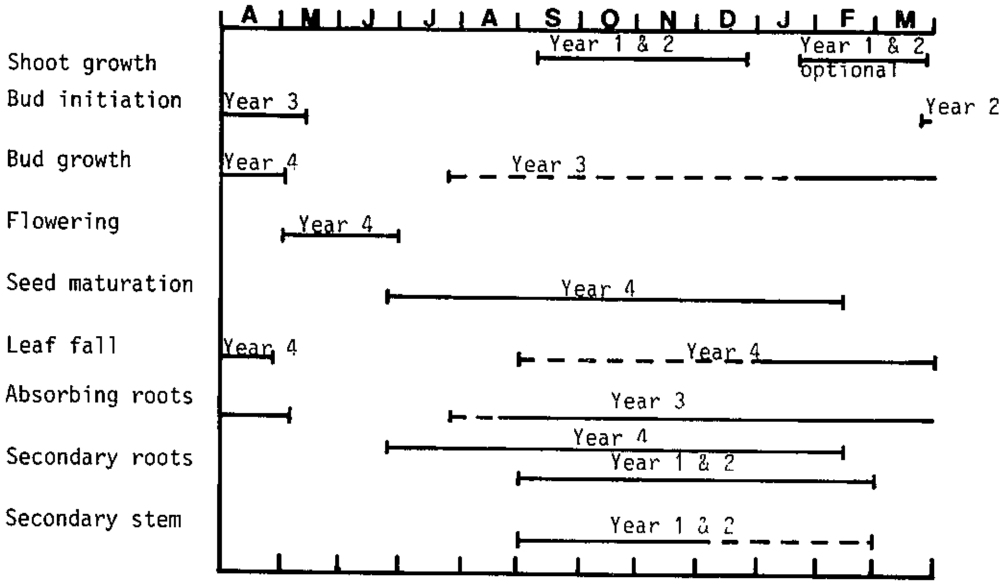

FIGURE 31. The timing of phenological stages in Protea repens.

The leaves die and fall from the plant mainly during the seed maturation period, but a minor leaf fall may occur just before flowering, at the height of the dry summer period (Lamb, unpublished data). The older leaves die first.

The growth pattern in Protea repens results in a shrub architecture or form that fits Leeuwenberg's model as described by Halle and Oldeman (1975).

Leucadendron salignum is a mid-height, broad-leaved, sclerophyllous shrub, which is common throughout the mountain and lowland regions of the south-western and southern Cape. It is the most widespread species of its genus and usually occurs as scattered individuals rather than in dense stands (Williams 1972). Leucadendron salignum is dioecious; some populations may have more male plants than female plants. After a fire Leucadendron salignum sprouts from a branched underground rootstock and forms a multiple-stemmed shrub that grows to 0,6 to 1,2 m, but may reach two metres in height, depending on the length of time since the last fire. Sprouts flower within two years after burning, but seedlings require about four years before they flower (Williams 1972). The numerous post-fire sprouts on an individual plant are rapidly thinned to two to ten major sprouts as leaders gain apical dominance.

Initial post-fire regrowth occurs irrespective of season and seems to be initiated solely by the fire event (Wicht 1948). After the initial period of post-fire regrowth, the phenological pattern of shoot development is regular. Most shoots form a flowering bud after two years. Axillary buds which are located below the male and female flowers, begin to grow in early January. Growth continues until about the end of April or the middle of May, but most shoot elongation occurs between 1 January and 15 April. Flower buds are set at the end of shoot growth and develop immediately; flowering occurs between early April and the middle of August. After pollination, which is probably by insects, especially beetles (Williams 1972), female cones close and develop until about the end of December. Seeds are retained for an additional two years or more in the cone. Seeds are presumably ripe within about six months after fertilization. The seed is winged and is probably wind dispersed (Williams 1972). Leaf-fall occurs from January to March, inclusively (Figure 32).

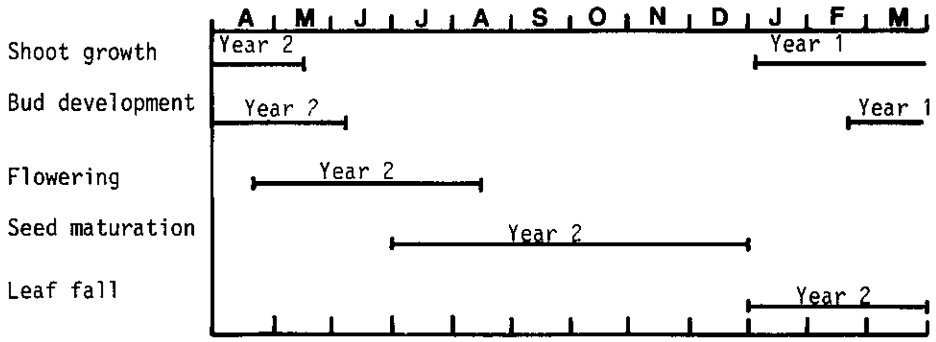

FIGURE 32. The timing of phenological stages of Leucadendron salignum.

Cliffortia cuneata is one of the more common mid-height shrubs at Jonkershoek. It usually grows on granitic substrates and is most frequent at elevations between sea-level and 600 m. Cliffortia cuneata can grow to more than two metres tall and has a relatively complex growth pattern, because the axillary buds develop into long shoots during the growth of the parent shoot. The terminal bud seems to have very little apical dominance. In adult plants, long shoots are initiated from axillary and terminal buds. During the first year the shoot develops leaves and stems (Figure 33). The initiation of shoot growth begins about 1 April and shoot growth continues until 1 August. Axillary buds on the one-year-old shoots become flower buds. Flowering occurs from July to September (van der Merwe 1966). Following flowering and pollination, seeds mature until January or February. Cliffortia cuneata is an obligate seeder and does not resprout after fire. The mature seeds fall to the soil surface and are probably collected by ants (Bond and Slingsby 1981). The leaves die and fall from the plant mainly during the seed maturation period after the leaves are one-and-a-half years old.

Ericoid shrubs and restioids form the primary components of the understorey in the South African fynbos. **Erica plukenetii** is one of the most widespread erica species in the fynbos and is distributed from Namaqualand to Mossel Bay (Baker and Oliver 1967). It is shallow rooted and has whorls of 12 to 16 mm long, filiform leaves which are loosely arranged around the terminal bud. Shoot growth begins in December and continues until January. Growth can continue from the terminal bud for several years without side shoots forming, or several shoots can form near the terminal bud giving the shrub a sparsely branched appearance.

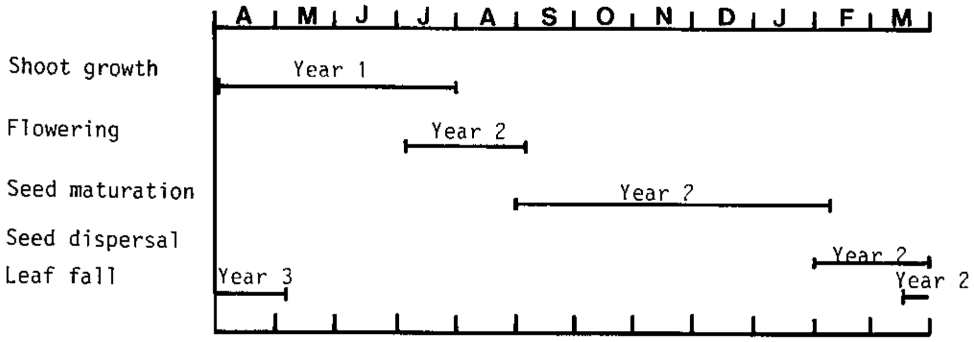

FIGURE 33. The timing of phenological stages of Cliffortia cuneata.

During the second year, axillary buds located on the previous year's shoot-growth develop into flower buds. Flowering occurs from October until January (Figure 34).

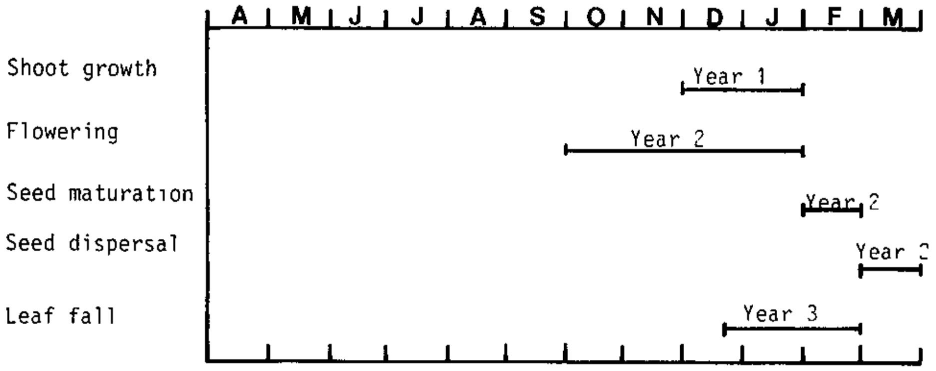

FIGURE 34. The timing of phenological stages of Erica plukenetii.

Following flowering, seeds mature for one month. The small seeds drop to the soil surface or are dispersed by wind when released. Leaves persist on the stem for about three years, then they die and fall from the plant mainly during the late summer. Erica plukenetti is associated with endotrophic mycorrhizae and is an obligate seed regenerator.

Psoralea obliqua is a mid-height sprouting shrub, 0,6 to 1,2 m tall, which is distributed from Paarl to Caledon. New shoots are initiated primarily from terminal buds early in July and growth continues until mid-October (Kruger 1981). During the second year, axillary buds develop into flower buds, but growth stops when the shoot is in flower.

Flowering occurs from August to October in Swartboschkloof (van der Merwe 1966), but the flowering season occurs between July and November in other regions (Figure 35). Nodules have been observed on the roots. The mature seeds fall to the soil surface and are probably dispersed by ants. Leaves die and fall from the plant during their second year, from mid-February to mid-May. The species is reported to regenerate only by sprouting (van der Merwe 1966).

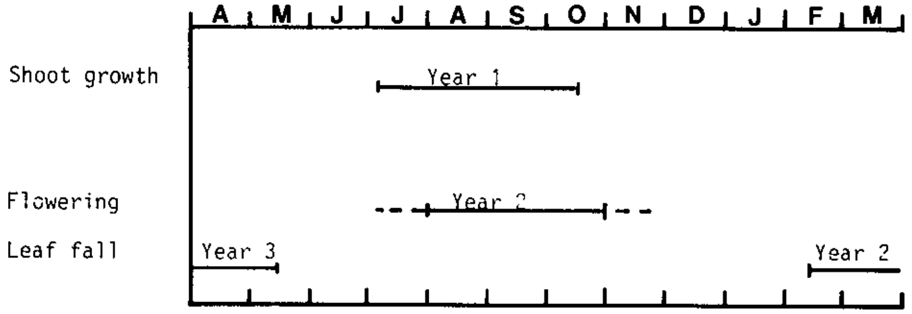

FIGURE 35. The timing of phenological stages of Psoralea obliqua.

Following a fire in the fynbos, short-lived non-sprouting legumes, such as certain Aspalathus species, can become locally abundant. These short-lived plants are presumably important in replacing nitrogen which has been lost during the fire. They are unable to survive in mature fynbos stands. Sprouting legumes are longer lived and are tolerant of the conditions in mature stands. These longer lived species presumably supplement the nitrogen pool in older stands. The model will accommodate these in later versions.

Description of the submodel

The shrub growth submodel can be run using parameters for any species with a similar pattern of growth. The submodels for the individual shrub species can then be linked to simulate a community. In addition to Protea repens, species parameters and phenological observations for Leucadendron salignum, Cliffortia cuneata, Erica plukenetii and Psoralea obliqua are available. Only Leucadendron salignum has a growth pattern analogous to Protea repens. The shrub growth submodel will have to be modified to reflect the observed shoot development and phenological patterns of the other shrubs.

The compartments of the shrub growth submodel are: leaves, shoots or primary stems, secondary stem and root tissue, primary absorbing roots, inflorescences, seeds and old stems. For the entire plant, the submodel calculates the total number of shoots, total plant height, canopy (crown) diameter and stem diameter. The processes included in the submodel are the growth of leaves in mass and area, shoot elongation and growth of secondary stems and absorbing roots.

The shrub growth submodel can be run independently from the rest of the FYNBOS submodel. If the submodel is run alone, it requires a simplified set of equations describing environmental and nutrient inputs.

In the simplified environmental driver, day length, which includes twilight, is calculated following Savage and McGee (1980). Temperature is calculated with a sine curve varying 5,1°C above and below a mean temperature of 16,1°C. Plant-water potentials are calculated with a sine curve varying 0,6 MPa above and below -0,1 MPa, but the curve is truncated so that the potentials do not rise above zero. The curve approximates data of Miller et al (1983).

The simplified version of nutrient uptake involves two basic processes. For immobile ions such as phosphates, uptake depends on root growth into unexploited soil. For mobile ions such as nitrate, the ion moves to the root by diffusion and mass flow. Mass flow involves the transpiration stream and percolation of water through the soil. If the uptake of an ion per unit mass root growth is less than the amount of the ion incorporated into the unit mass of root, the nutrient cost of root production is greater than the nutrient gain. In the submodel, a negative balance between the cost of root production versus nutrient gain by that unit of root, eliminates root growth as a process for providing nutrients to the plant. Without root growth, the plant must depend on diffusion and mass flow for uptake of nutrients.

Root growth on a mass basis is converted to length growth using a root length/mass ratio of 30 m/g which is based on data for *Banksia* (Bowen 1981).

In the submodel, the uptake of nutrients by diffusion and mass flow is similar and is currently set at between 0,25 and 0,30 μg/m root/day, based on data for *Leucospermum parile* (Mitchell unpublished) and for *Banksia* (Bowen 1981). Uptake should also be affected by water movement in the soil. A distinction should be made between the two processes, because shrubs may take up phosphorus during the spring and summer by diffusion into growing roots, while during the wetter winter season mass flow may be the more important process for nutrient uptake. When leaves and roots die, they are assumed to contain 50 μgP/g (Bowen 1981). At leaf senescence, *Leucospermum parile* leaves contain 1,8 to 2,8 per cent TNC and *Protea repens* leaves contain 8 to 13 per cent TNC (Mitchell unpublished).

In the carbon balance submodel, TNC contents are updated by adding photosynthesis and subtracting the respiration and growth needs. The resulting leaf TNC is adjusted when reserves permit, to a 120 mg/g content by translocation to the main stem. The translocation rate is half the rate which would equilibrate the TNC levels in one day. This lag in translocation gives the observed seasonal course of shoot TNC contents (Oechel and Lawrence 1981).

Once initiated, growth of all plant parts is affected by temperature, plant water potential, TNC and plant phosphorus.

The temperature relation of growth uses a Q_{10} of 2,0 and different mean temperatures for shoots and roots in the different species (Table 5), reflecting conditions prevailing during the respective growing seasons. Growth declines linearly with plant-water potential and is zero at a minimum pre-dawn water potential of -0,6 MPa (van Keulen 1975). The water potential used in this relationship should probably be a mid-day value, not the pre-dawn value, or should be some average of the two. Root-water potentials are assumed to be 0,2 MPa higher than shoot-water potentials.

The TNC controls on growth are calculated using equations of the Michaelis-Menten form, based on the TNC contents of the shoot. For leaves the half-saturation rate value (KM) is 10 mg TNC/g in the shoot; for the roots the half-saturation rate value is 120 mg TNC/g in the shoot. The leaf growth rates observed in the field are calculated to occur at 90 mg TNC/g and the observed root growth rates are calculated to occur at 120 mg TNC/g. The different half-saturation rate values give higher leaf than root growth rates at low TNC contents and are assumed to relate to plant priority systems and distance from the TNC source. With low light or low leaf area, which both lead to low TNC contents, leaf growth is favoured over root growth (Brouwer and de Wit 1969). With high light or leaf area, root growth is favoured over leaf growth. For leaves the Michaelis-Menten function is set to equal one at 90 mg TNC. The seasonal difference in the TNC values during periods of shoot and root growth are estimated from chaparral values (Oechel and Lawrence 1981).

TABLE 5. Growth relations in the shrub species included in the FYNBOS model for Swartboschkloof (see text for explanation)

Species	Base temperature °C		Daily growth rates at base temperature, zero plant water potential and TNC concentration of 120 mg/g							
	Shoots	Roots	mg leaf per g shoot	mg stem per g leaf	g leaf per m stem	mg abs root g shoot	g bud per bud	g flower per g flower	g flower head per g flower	g seed per secondary g seed
Protea repens	16,0	13,0	120	14	0,0067	120	0,005	0,08(a)(b) (max 21,7)		0,1
Leucadendron salignum	22,0	15,0	30	7,5	0,0067	30	0,005	0,08	1,0	0,1
Cliffortia cuneata	18,5	13,0	1,7	0,26	80	1,7	0,005	0,08 (max 2,7)		0,1
Erica plukenetii	16,0	13,0	1,0	0,1	0,006	1,0	0,1	0,001 (max 20 mg)		0,1
Psoralea obliqua	15,0	13,0	2,0	0,4	0,0067	2,0	0,005	0,08(c) (max 2,7)		0,1

(a) This refers to inflorescence growth.
(b) Requires 0,05 g per flower head per day.
(c) Requires 10 mg per flower per day.

The phosphorus controls on growth are also calculated with equations of the Michaelis-Menten form. The k_m and full rate parameter values are higher for leaves than for roots. For leaves the k_m is 3 000 µg/g and for roots the Km is 100 µg/g. The observed growth rate equals the average value at 4 000 µg/g for leaves and 600 µg/g for roots.

The submodel assumes that day length is a major trigger for the seasonal patterns of shrub growth and development and that day length is sensed by the aboveground parts. "Budbreak" allows absorbing root and secondary stem growth to begin prior to leaf growth. Budbreak does not occur in autumn when day length is decreasing. A cold sum requirement determines that budbreak is timed to occur when mean temperature rises above 12°C in *Protea repens*, *Leucadendron salignum* and *Psoralea obliqua*. A day length of 12,8 hours and increasing is required for *Cliffortia cuneata*. Budbreak occurs in autumn in *Erica plukenetii*, with no cold requirement. At the time of budbreak, it is assumed that the bud begins vigorous metabolic activity, although bud and leaf expansion do not occur until several weeks later, in early October in *Protea*. A second growth flush can be initiated 30 days after the initial flush.

Leaf and shoot growth occur under different conditions for the several species, as follows:

(a) *Protea repens*: when day lengths exceed 13,7 hours, although growth may be suppressed when day lengths are near 15,5 hours or when the accumulated leaf mass reaches a maximum;

(b) *Leucadendron salignum*: when day length begins to decrease after 21 December;

(c) *Cliffortia cuneata*: when day length decreases below 12,4 hours;

(d) *Erica plukenetii*: when day length exceeds 13,7 hours;

(e) *Psoralea obliqua*: as for *Protea repens*.

In all species, leaf and shoot growth do not occur when the plant is in the reproductive phase (during flower development, flowering and seed maturation), but growth of absorbing roots and secondary tissue can occur at this time, except that no secondary growth is possible in the Proteaceae during the reproductive phase.

Flowers or inflorescence buds are initiated and flowering occurs in the different species when different conditions are met:

(a) *Protea repens*. The inflorescence bud is initiated when three conditions are met: the day length exceeds 15,4 hours; day length is decreasing; and the leaf mass of the shoot exceeds 15 g. Flowering also requires three conditions: the day length is less than 11,4 hours; day length is decreasing; and the inflorescence mass exceeds 2,5 g. The shoot is assumed to flower for 60 days and seed development follows the 60-day flowering period without additional necessary conditions.

(b) *Leucadendron salignum*. The inflorescence bud is initiated on two-year-old shoots when the day length decreases below 11,8 hours. Flowering occurs when day length decreases below 11,7 hours. The plant is in flower for 120 days, but a shoot is assumed to be in flower for 60 days. Seed development follows flowering.

(c) *Cliffortia cuneata*. The flower bud is initiated when day length exceeds 12,0 hours and flowering occurs once day length exceeds 12,2 hours. The shoot flowers for 60 days and seed development follows on from the flowering period.

(d) *Erica plukenetii*. Flower bud initiation occurs once day length exceeds 12,4 hours and flowering when day length exceeds 12,5 hours and is decreasing. The shoot flowers for 60 days and seed development follows on the flowering period.

(e) *Psoralea obliqua*. Initiation once day length exceeds 14,8 hours and is increasing and flowering when the day length exceeds 13,8 hours and is increasing. The shoot flowers for 60 days and seed development follows on flowering.

The phenological sequence of belowground plant parts is not well known. In chaparral and Australian heathlands, fine root growth generally precedes shoot growth (Kummerow 1981b; Specht 1981a). In the Jarrah (*Eucalyptus marginata*) forests of the mediterranean-type climate area of western Australia, surface root growth was initiated in two peak periods: spring; and following autumn rain. However, short (primary) roots formed after even very light showers in late summer. Root growth did not occur in midwinter, but was otherwise governed by soil moisture (Dell and Wallace 1983). In the fynbos, root growth may be opportunistically dependent on soil moisture (S M Jongens-Roberts, personal communication 1983). In the submodel it is assumed that growth of absorbing roots can occur whenever plant-water potentials are above -0,9MPa; growth is directly related to water potential. Secondary stem growth must occur to support shoot and root growth. Secondary stem growth usually occurs throughout the year in chaparral and matorral shrubs. In chaparral shrubs, a seasonally high rate of secondary stem growth precedes shoot growth (Kummerow 1981a). However, Specht (1975) reports that radial stem growth follows shoot growth in Australian heathland shrubs. In the submodel, secondary growth follows the measured pattern of *Rhus ovata* in the chaparral, which has a peak of secondary growth in early spring. Some proteoid shrubs in the fynbos appear to have a pattern of water relations similar to that measured for *Rhus ovata*; it is a deep-rooted, broad-leaved shrub with conservative rates of water loss and moderate water potentials through the summer drought (Poole and Miller 1975, 1981; Miller et al 1983).

The submodel assumes features of chaparral and heathland when data are not available for fynbos (Miller 1981; Pate and McComb 1981). For Lowland Fynbos, Low (unpublished) gives values for aboveground biomass of 6 949 gdw/m^2 and for belowground of 1 867 gdw/m^2. This ratio is similar to that measured in chaparral (Kummerow et al 1977; Miller and Ng 1977). Chaparral has about 200 g of fine absorbing roots per m^2, below a leaf area of about 500 g of leaf per m^2 (Kummerow et al 1978, 1981b). The submodel assumes that the shrub should have a 2:1 ratio of leaf mass to absorbing root mass. Shoot (leader) stem growth is synchronous with leaf growth and equals 15 per cent of the leaf growth. Secondary growth can occur during or without leaf growth and occurs so that the annual increment of secondary material is 15 per cent of the leaf growth multiplied by the stem length. Secondary growth was estimated from measurements of mass per unit length of stem section for stem sections of different ages (Miller unpublished). The increase in mass of the stem section is divided by the mass of leaves on the stem. The daily rate of secondary stem growth is lower than that of shoot growth, but secondary growth occurs over a longer period of time.

Average seasonal growth rates of leaves, stems, secondary stem tissue and roots, with average temperature conditions, water potentials of zero, and TNC of 120 mg/g, are set differently for different species, based on estimates from measurements on plants sampled in the field. Once initiated, growth of all plant parts is affected by temperature, plant water potential, TNC and plant phosphorus.

Height growth is calculated by converting shoot stem growth into length, based on measured mass per unit length of primary shoot (0,17 m/g for the Proteaceae, 0,2 m/g for *Cliffortia*, 0,98 for *Erica*, and 35 for *Psoralea*) and multiplying by the cosine of the shoot angle from vertical. The shoot angle depends on the species and the age of the plant, or more strictly on the leaf area of the plant. Plant stems grow vertically until a leaf area index of 2,3 is reached, then the shoot angle changes. Since it is commonly observed that the leaf area index seldom exceeds 2,3, this is taken to be the upper limit of shrub leaf area. Limits on leaf area index presumably reflect the plant's light requirements. The number of shoots, multiplied by the leaf area per shoot and divided by $3{,}14 * r^2$, must then be less than 2,3, where r is the canopy radius. This means that when the canopy reaches a leaf area index of 2,3, which is almost reached by a single shoot, the radius increases according to:

$$\text{delta } r = \sqrt{\frac{\text{(the number of shoots *leaf growth/specific leaf density}}{3.14 * 2.3}} \qquad (8)$$

During the second year, the terminal bud initiates growth about 1 October and vegetative growth continues until late December. In late December, the terminal bud may differentiate into a flower bud unless shoot conditions are unfavourable. If the conditions are unfavourable for flower bud development, axillary shoots do not develop and the shoot system dies. The major unfavourable conditions apparently relate to shade, which affects levels of total nonstructural carbohydrates.

Results of the submodel

The shrub growth submodel has been run using parameters for *Protea repens*. The simulated pattern of leaf growth shows the sequence of development of four cohorts of vegetative and reproductive shoots in a mature Protea repens (Figure 36). A cohort of shoots begins growth in October and grows until about April. On 1 April, only three active cohorts of shoots exist, because the oldest cohort (D) from the previous year has dropped all of its leaves and is no longer active. On 1 April, cohort A has completed one growth phase, cohort B has completed its second growth phase and is supporting developing inflorescences and cohort C has dropped its leaves as its cone is maturing. During the second year, cohort A completes its second growth phase, which terminates in December with the initiation of flower buds. Shoots in cohort A do not grow during the third year, but support their developing flower buds. Some leaves drop from the shoots in cohort A in mid-summer of year three. The developing buds of cohort A produce a flower in about March. About 75 per cent of the leaves on cohort A shoots drop after flowering, during the seed maturation period. The other 25 per cent of the leaves drop after the seeds are mature, when the shoots of cohort A are about four years old.

In the model all four cohorts of shoots follow the same pattern, but are out of phase with each other by one year. On 1 October the cohorts are updated and a new cohort is initiated as the oldest cohort becomes inactive. Increasing summer temperatures and decreasing plant-water potentials caused a slight depression in growth during the late summer period.

The simulated pattern of growth of leaves, stem and roots of one Protea repens shoot through a four year period, shows the timing of growth within the shoot system (Figure 37). Stem growth is synchronous with leaf growth, but absorbing root growth has a seasonal pattern. During the third year, growth of absorbing roots is necessary to maintain the plant phosphorus content at adequate levels whilst the seeds are developing.

The simulations indicate patterns of translocation of TNC which must occur if the above observations and assumptions about growth in Protea repens are true. The seasonal pattern of the TNC concentration in a shoot system shows a depression of TNC during growth and recovery of TNC content during the autumn and winter. Following the initiation of the axillary shoots at budbreak, the growth of absorbing roots, secondary stem tissue, leaves and shoots draws on the carbohydrate produced by the mother shoot. The axillary shoot does not become autonomous until after the first leaf-growth flush is completed. The importation of TNC maintains the axillary shoot at more than 30 mg TNC/g, therefore shoot growth is only slightly suppressed by low TNC availability. Root, stem, leaf and shoot growth proceed without carbohydrate limitation, because of the use of carbohydrate from the mother shoot; but flower bud development may be suppressed if cone metabolic rates are high. About 23 g of TNC are required from the mother shoot before the axillary shoot is autonomous. Shoot autonomy occurs when photosynthesis of the axillary shoot is greater than its respiration rates and growth rates. Simulations indicate several features of the phosphorus balance of the Protea repens (Table 6). Phosphorus uptake occurs throughout the year. About 250 days of phosphorus uptake are required to replenish the phosphorus used by Protea repens in growth. By the time leaf growth is initiated, root growth has already reached 10 g/shoot or 300 m/shoot.

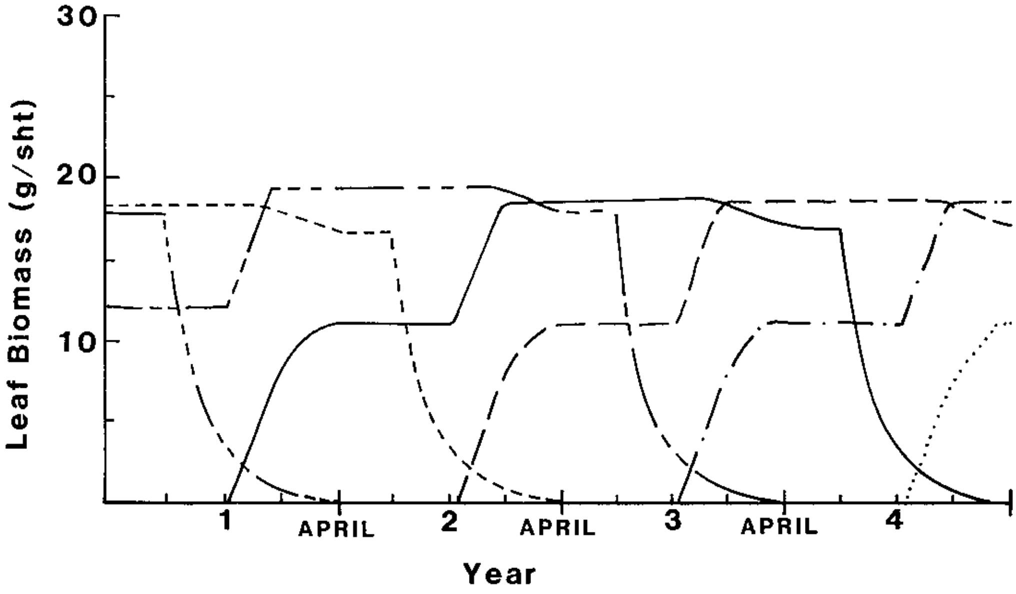

FIGURE 36. Seasonal pattern of leaf biomass showing the pattern of leaf cohort replacement.

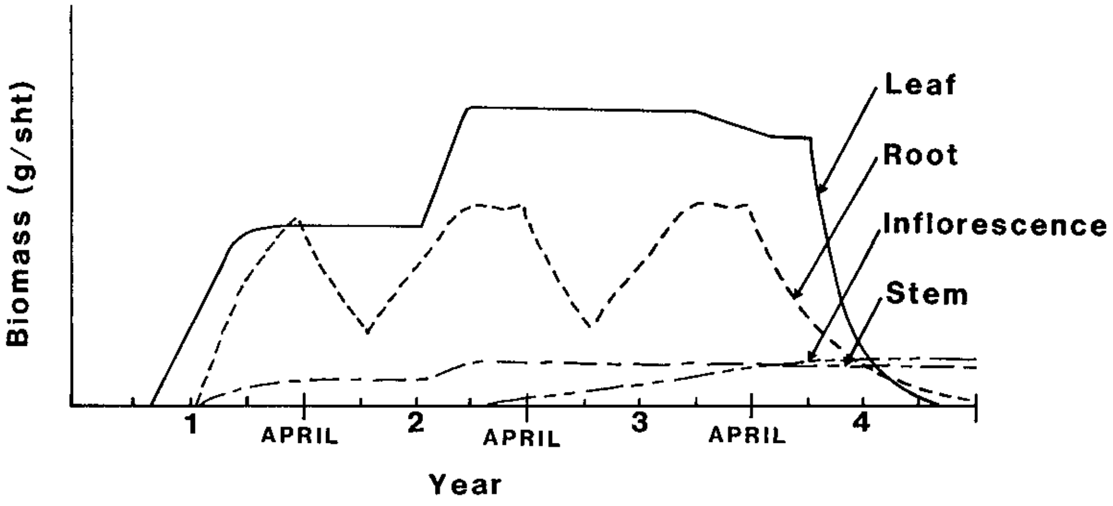

FIGURE 37. Pattern of growth of leaves, stems, roots and inflorescences of a single shoot system. Four years are required for the shoot to complete the cycle.

TABLE 6. Summary of the biomass and phosphorus balances of *Protea repens* for 4 cohorts of shoots during simulated year 4. The height of the plant is 5,35 m. The total number of shoots is 62. The total old stem mass is 71 g/plant. Plant TNC reserve is 14 362 g/plant. Plant phosphorus content is 241 392 g/plant

	Cohort			
	1	2	3	4
	Number of shoots (no/plant)			
Number	22	22	9	9
	Dry-mass Rates (g/sht/yr)			
Photosynthesis	89	228	259	37
Respiration, main	8	14	20	12
Growth	47	42	30	0
Respiration, growth	14	13	9	0
Export	16	156	198	27
	Masses (g/sht)			
Seed mass (mg/seed)	0,0	0,0	0,0	36,4
Flower bud mass	0,0	1,0	3,0	3,0
Leaf mass	11,1	18,3	16,9	0,0
Shoot (stem) mass	1,7	2,8	2,8	2,8
New stem mass	8,5	11,6	9,0	6,3
Absorb root mass	5,2	5,6	5,7	0,3
	Phosphorus Rates (µg/sht/yr)			
Uptake	5 494,7	6 315,2	6 359,8	400,0
Loss by leaf death	0,0	0,0	74,6	841,8
Loss by root death	1 051,9	1 388,3	1 411,5	268,8
Export	-1 046,3	1 799,9	4 768,4	4 044,1
	Masses (µg/sht)			
Seed mass	0	0	0	22
Flower bud mass	0	612	1 785	1 787
Leaf mass	2 212	3 668	3 372	7
Shoot (stem) mass	166	275	275	275
New stem mass	847	1 164	896	628
Absorb root mass	3 126	3 385	3 404	180

About 20 µgP is taken up by the roots to support new shoot growth. However, the growth of absorbing roots requires 600 µgP/g root or 18 000 µgP after 30 days of root growth. Secondary stem growth requires an additional 100 µgP tissue produced. The first year shoot and leaf growth requires 300 µgP/g leaf; first year stem growth requires 100 µgP/g stem. During the first year, leaf growth incorporates 6 000 µgP in leaves and 540 µgP in stems. In total, over 6 500 µgP are incorporated during the first year and about 6 000 µgP are taken up. In the second year almost 7 000 µgP are incorporated. Most of this phosphorus, 6 000 µg/yr, is made available through uptake and from back translocation from the one-year-old leaves, which supplies 800 µg. In the two years of vegetative growth, 13 000 µgP are incorporated in vegetative tissues and 12 000 µgP have been taken up or back translocated from senescent tissue.

In the model, about 6 036 µgP are incorporated in the sexual reproductive effort. About 6 800 µg of the phosphorus used to produce the inflorescence comes from uptake, if absorbing roots are allowed to grow during the third year, which is the sexual reproduction phase of the shoot system in Protea repens. About 1 000 µgP is retranslocated from the two-year-old leaves and is available to help support the growth of the inflorescence. The values as they stand do not quite balance. Actual phosphorus uptake by the roots appears to be higher than modelled values. Incorporation of values based on recent research should balance the phosphorus budget. Slower rates of phosphorus uptake than those currently used in the simulations should lead to slower growth and delayed floral bud initiation.

If the simulated growth and translocation scenario for Protea repens is true, then the removal of leaves from the shoot during the second year should suppress the growth of the axillary shoots which do not become autonomous until after they have completed their first growth flush. Removal of the one-year-old leaves from the shoot should delay floral bud initiation by one year, because one-year-old leaves contribute carbohydrate to the developing inflorescence. Removal of axillary shoots during their second year of growth should have no effect on the increase in cone weight because two-year-old shoots are autonomous and no longer received TNC from the rest of the shoot system. Two-year-old axillary shoots do not supply TNC to the cone, but use all the TNC they produce to support their secondary growth flush. Removal of the developing cone should have little effect on the development of the axillary shoots.

THE GRAMINOID GROWTH SUBMODEL

(P C Miller, F J Kruger, D C le Maitre, P M Miller)

Introduction

The graminoid growth form is present in nearly all fynbos vegetation, sometimes dominating the understorey (Taylor 1978; Kruger 1979). Members of the Restionaceae are normally prominent, but occur in association with various proportions of the Poaceae and Cyperaceae. Knowledge of the dynamics of the graminoid stratum is required for any general understanding of fynbos dynamics, as well as for proper management. Graminoids are an important component of the fuel for veld fires. Developing simulation models for representative species is a step toward understanding the ecological relations of these plant forms.

Requirements of the submodel

The requirements of the graminoid submodel are the same as those of the shrub growth submodel, except that a different set of plant parts is involved.

Observed graminoid phenology and growth patterns

Restio filiformis is widely distributed throughout Mountain and Lowland Fynbos (Pillans 1924), occupying sites with well-drained soils. It is a reed-like, tufted, perennial herb up to 0,5 m tall. The upright, photosynthetic stems are about 0,5 mm in diameter, sometimes sparsely branched at the nodes which are covered by the bract-like leaf sheaths and terminate in an inflorescence. Plants are dioecious.

New shoots arise from the distal ends of the lignified basal node and grow from about late September until about the end of June of the following year. Shoot growth is by intercalary meristems at the nodes of the shoot. The inflorescence develops as the shoot elongates, so that plants flower from about mid-August until late September in the first year. Seeds apparently develop and ripen over about four months, from the beginning of October until the end of January; they are then dispersed.

The shoots remain alive for about two years, so that two live cohorts are always present on the plant. In the second year some shoots may produce branches. Plants sprout after fire and produce sterile stems in the first and sometimes second years. The first flowering shoots appear after one full growing season (Figure 38).

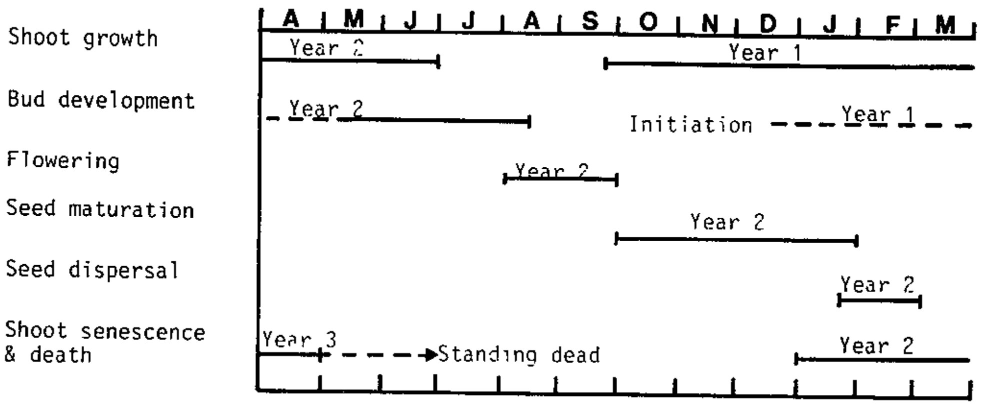

FIGURE 38. The timing of phenological stages of Restio filiformis.

Tetraria ustulata is widely distributed throughout Mountain and Lowland Fynbos (Harvey and Sonder 1859-1865), occupying sites with well-drained soils. It is a tufted perennial herb with flowering culms up to about 0,75 m tall. Flowering culms are about 4,0 mm in diameter and terminate in an inflorescence. New tillers arise intravaginally from the stem base and grow from about April until the end of August. Leaves originate from basal meristems at the tiller base and along the flowering culm.

The seasonal phenology presented here is based on experience with sedges elsewhere and on observations on Tetraria ustulata at Jonkershoek. During the first year, 13 leaves are produced from the new tiller. Leaves are initiated at about four-day intervals from within the dead leaf sheath surrounding the tiller base. During the second year 13 more leaves are produced and one to three of the leaves of the previous year may die back. In the third year, the flowering culm is produced and one to three daughter tillers are produced intravaginally. The dead leaves persist around the tiller base and provide a basis for estimating the age of the shoot since the age-classes of dead leaves can be distinguished (Figure 39).

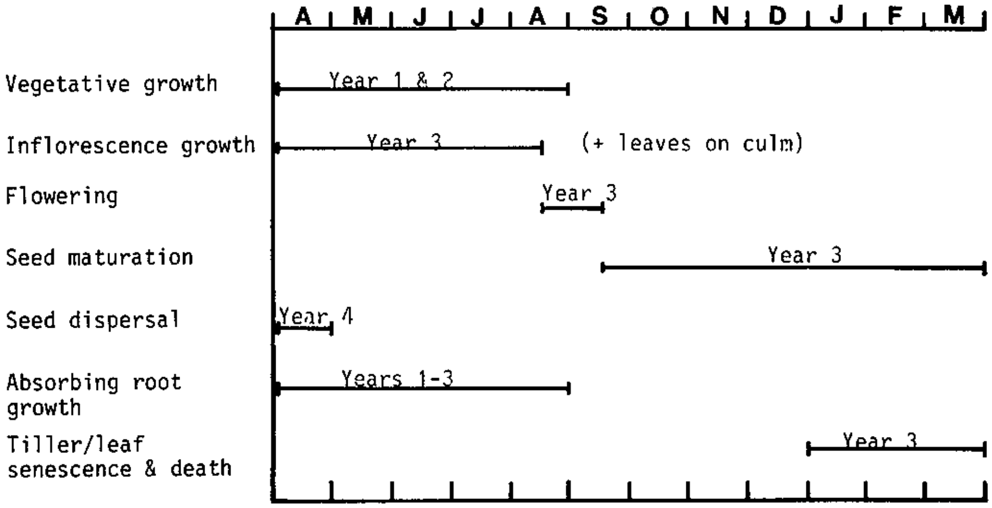

FIGURE 39. The timing of phenological events in Tetraria ustulata.

The tussock has two vegetative modes of expansion: vertical tillers, which arise intravaginally from the old tiller base; and the short (10 mm) horizontal rhizomes, which also arise from the tiller base and expand the tussock diameter. Growth of the flowering culm is by intercalary meristems near the nodes of the culm. Flowering culms develop until the plants flower from June to March (van der Merwe 1966). Herbarium specimens show that seeds apparently develop and ripen over about two months and are then dispersed. More work needs to be done to firmly establish the seasonal pattern of phenological events in Tetraria ustulata.

Description of the submodel

The submodel of graminoid growth dynamics was based on the observed phenological patterns of the female Restio filiformis and was then modified to fit the growth patterns of Tetraria ustulata.

The basic unit of the model is the shoot system (ramet), which is part of a tussock. The shoot system is divided into five compartments: lignified basal node (stem base in Tetraria), absorbing root, shoot, inflorescence, and seed. Roots should be further subdivided into primary and absorbing roots. The submodel calculates variables to describe individual tussocks in terms of old stem mass, TNC, phosphorus, tussock diameter and plant (tussock) height.

Growth of absorbing roots, daughter rhizomes, shoots and inflorescences depends on a rate constant for each plant part: 0,44 mg/day for absorbing roots, rhizomes and shoots; and 0,12 mg/day for inflorescences (Table 7). The rate of seed growth in the inflorescence is 0,15 mg/day. Growth also depends on temperature, plant-water content, TNC content and phosphorus content. Two seeds are produced per inflorescence. The temperature relation for growth uses a Q_{10} of 2 and a base temperature of 13°C for both root and shoot growth. The water potential at which growth is stopped is -0,7 MPa. Growth is decreased linearly as water potential decreases from 0 to -0,7 MPa. These water potentials are reached only periodically in the surface soil strata during winter, but are often reached during summer. Phosphorus and TNC contents at which growth is half the observed rate are, respectively: 0,14 µg/g and 25 µg/g for absorbing roots; and 0,01 µg/g and 15 µg/g for shoots. Given the controls on water, TNC, and phosphorus, roots are able to grow at any time. After 15 August the one-year-old shoot flowers. It remains in flower for fourteen days, though the population flowers over about forty days. Seed maturation proceeds until the seeds are dropped in February. Second year shoots grow absorbing roots, but basically they supply daughter shoots with TNC and phosphorus. After the first of January, second year shoots begin to senesce and release TNC and phosphorus through the basal node into daughter shoots. After the two-year-old shoot dies, it becomes standing dead. Shoot death is hastened by drought and by phosphorus deficiency. Shoot production is related to plant TNC levels, thus shading reduces shoot production. If

TABLE 7. Growth relations in the graminoid species included in the FYNBOS model for Swartboschkloof (see text for explanation)

Species	Base temperature		Daily growth rates at base temperature, zero plant water potential and TNC concentrations of 120 mg/g in shoot					
	Shoot	Root	Stem or leaf	Basal node	Abs root	Inflorescence	Seed	Daughter rhizome
Restio filiformis	13,0	13,0	0,44		0,44	0,12	0,15	0,44
Tetraria ustulata	13,0	13,0	0,87		0,87	0,12		

the plant is less than one year old and is a resprout, shoot height is lower. One-year-old shoots do not develop inflorescences and have higher photosynthetic rates than two-year-old shoots.

The submodel for Tetraria ustulata differs only in detail from the submodel used for Restio filiformis. Growth of absorbing roots and leaves on the one- and two-year-old tillers is set to begin on 15 April and continues until 28 August. The third-year tiller grows the flowering culm, leaves on the culm and absorbing roots. After 15 August,the three year old tiller flowers. It remains in flower for 30 days when seed maturation begins. Seeds drop in April. Daughter tillers are initiated when the flowering culm is initiated. It is assumed that the daughter tillers originate from buds in the axils of long leaves on thestem base, the rhizome develops from an axillary bud below the long leaf's bud and the flowering culm develops from the terminal meristem. The initiation of the flowering culm stops further vegetative development. After 1 January, the second year tiller begins to senesce, releasing TNC and phosphorus into the rhizome of the daughter tiller. On the death of the tiller, the tiller becomes standing dead and the rhizome goes to the old rhizome compartment. Shoot death is hastened by drought and by phosphorus deficiency. Shoot production is related to plant TNC levels, thus the effect of shading should be to reduce shoot numbers.

Phenological events are triggered by calendar day in the current model, although day length and whether day length is increasing or decreasing are probably more realistic controls. The model begins on 1 April (Day 1).

Results of the submodel

The model of the shoot dynamics of Restio filiformis runs but the unrealistic results emphasize the need for more accurate parameters, particularly for the physiological processes and their controls.

THE GEOPHYTE GROWTH SUBMODEL

(P C Miller, F J Kruger, D C le Maitre, M Viviers)

Introduction

Though often inconspicuous and generally dormant during the summer, geophytic plants are also important in the understorey of fynbos ecosystems. Bulb plants or analogous forms in the Liliaceae, Iridaceae, Amaryllidaceae, Orchidaceae, Asteraceae and several other families are often a significant component of the flora and respond readily to management. These geophytes are diverse in form and function, but share certain features that form the basis for generalizations.

Requirements of the submodel

The geophyte growth submodel has the same requirements as the shrub growth submodel, except that a different set of plant parts is involved.

Observed phenology and growth patterns of *Watsonia pyramidata*

Watsonia pyramidata is a common geophyte occurring in Mountain Fynbos communities and is abundant in parts of the mountains of the Cape Peninsula and the Stellenbosch and Caledon districts. The upright leaves of *Watsonia pyramidata* reach 1,0 m in length and flower spikes grow to 1,4 m tall. Vegetative reproduction results in clones of up to 28 or more individual ramets, which are strongly clumped and usually clearly delineated.

Watsonia pyramidata is dormant during summer. Before growth is apparent, the starch stored in the corm is mobilized, first by conversion to mucilaginous compounds and then to sugars (Waher 1974). Early in autumn at the beginning of the cool wet season, up to five or six leaves develop from concentric meristems that girdle the corm and new roots grow from the corm. Leaf elongation continues for about 60 days, until the middle or end of May, by which time the old corm is depleted of reserves and is reduced to a flattened disc about two millimetres thick. Old corm discs retain active primary roots for up to four years and are connected to one another and to the growing shoot by vascular tissue called the stele (Figure 40).

Populations consist of clumps of individual plants. Each plant consists of a corm (the shoot), old corm discs with roots, leaves and terminal bud or perhaps a flowering spike. The history of any given clone can be easily reconstructed after it is excavated, because the annually produced corm discs resist decay and remain in sequence; and because flowering is marked by the appearance of two daughter corms.

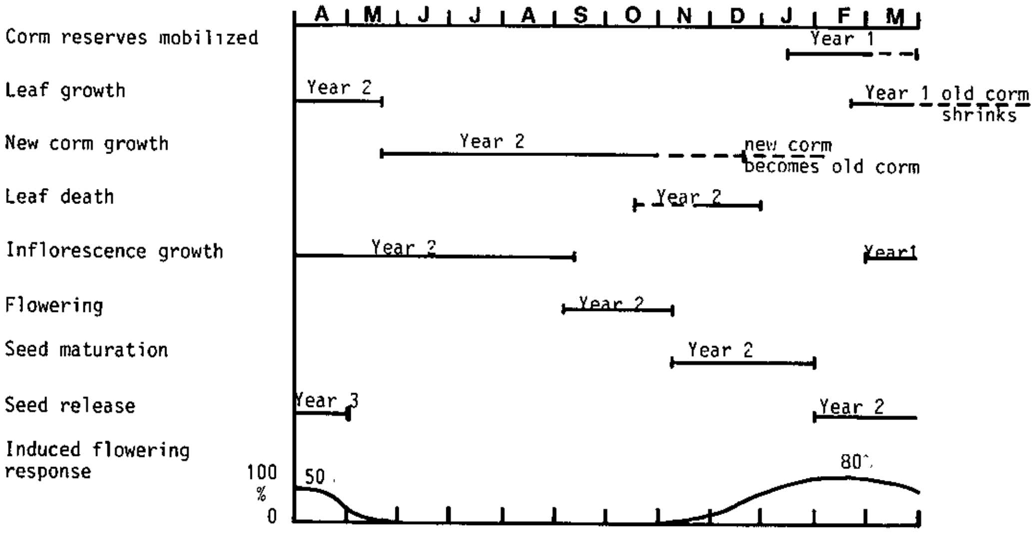

FIGURE 40. The timing of phenological events in *Watsonia pyramidata*.

The new corm is initiated from the terminal bud after leaf expansion, and accumulates starch until leaf death begins about the end of October. All leaves are dead by the end of January. Bases of old leaves form tough fibrous tunics around the new dormant corm.

In untreated populations, zero to five per cent of individual plants flower in a normal year. If Watsonia pyramidata is defoliated while dormant, ie between the beginning of January and around the end of April, 50 per cent or more of the population will flower. The triggering mechanism that induces flowering is not known and could involve decreased carbon dioxide levels in the soil, increased soil nutrient and/or moisture levels, heat, or defoliation (cessation of hormonal inhibition).

In flowering, the terminal bud does not form a new corm, but elongates to form a single inflorescence shoot. It does not form a new corm. Axillary buds in the upper leaf axils are activated and grow to form two independent daughter corms, thus the population multiplies vegetatively.

Abundant seeds are released from mature spikes during January and February. Seeds germinate during the following winter. Seedlings are quickly drawn into the soil by contractile roots. At Jonkershoek, twenty Watsonia pyramidata plants which were about one year old had a mean depth to the top of the corm of 26 ± 4,5 mm. Excavations show that a young plant continues as a single series of corms for 10 to 35 years without flowering, irrespective of the incidence of fire. After the corm grows to a diameter of about 60 to 70 mm, the plant is able to flower for the first time. Daughter corms from a flowering plant are smaller than the parent corm and weigh about 15 to 20 g. They require three or more years to grow to the size of the parent corm.

Description of the submodel

The compartments in the Watsonia pyramidata model are old corm, new corm, inflorescence (if it occurs), leaves, seeds and absorbing roots. TNC and phosphorus stored in the old corm are transferred to new leaves and roots as they grow; and from leaves and roots to the new corm as it develops. In general morphological terms, the old corm is equivalent to old stem and the new corm to new shoot stem. Leaf growth draws on reserves in the old corm through a period of 30 days. A new leaf supports its own photosynthesis and TNC requirements when green material appears. About a quarter of the length of the leaf is white and non-photosynthetic.

Absorbing root longevity is assumed to average 25 days through the winter and to fluctuate with surface water content in the upper two soil layers: 0,00 to 0,02 and 0,02 to 0,10 m.

In the model, leaf growth of Watsonia pyramidata occurs between 15 March and 15 May. The phenological triggering mechanisms which initiate leaf growth are not known because the exact timing of leaf growth has not been examined. The TNC and phosphorus contents for controlling leaf and root growth are calculated by pooling the TNC and phosphorus in old and new corms and the masses of old and new corms. Leaf growth occurs at a rate of 120 mg/g/day at 16°C, with an average water potential of zero. Leaf growth is zero when water potentials are -0,7 MPa in the absorbing root zone. The new corm grows 10 mg/g of structural tissue, which will become the tunic and disc. This tissue grows to two grams in 100 days.

The inflorescence spike elongates between 25 May and 15 September, at a rate of 30 mg/g plant/day to reach seven grams in 100 days. Flowering occurs between 15 September and 15 November. Seeds increase in weight during maturation at a rate of 54 mg/g plant/day for 100 days. One ramet can produce as many as 340 seeds, which each weigh about 16 mg.

THE SEEDLING GROWTH SUBMODEL

(P C Miller, W C Oechel)

Introduction

The growth and survival of seedlings and vegetative sprouts is critical in vegetation of fire-dominated ecosystems. In the fynbos, which is thought to be strongly nutrient limited, the patterns of nutrient uptake in seedlings are especially important. The growth pattern of seedlings described here is based on observations on *Protea repens*.

Requirements of the submodel

The seedling growth submodel should simulate seedling growth from germination until the plant flowers for the first time, which is usually after two to five years. It should also simulate the growth of sprouting species after a fire. The model should include requirements for germination and regrowth, so that the effects of a fire during any season of the year can be simulated. Seedling growth should be affected by availability of water, TNC, nutrients and irradiance. The submodel should interface with the mature plant growth submodel, so that the behaviour of seedlings under a mature canopy can be simulated.

Observed patterns of seedling growth

When a seed germinates, the root generally emerges first, followed by the cotyledons. From considerations of the carbon and phosphorus budgets, the early appearance of cotyledons or leaves is essential. The carbohydrate energy store in the seed is extremely limited relative to the needs of the seedling during the first year of growth. Once leaves have developed and the mechanisms to meet the requirement for carbohydrates are established, root growth to provide nutrients and water should become more important. In areas where the seasonal distribution of precipitation is uneven or annual precipitation is below about 500 mm, the seedling must develop roots that grow to a depth of at least 0,3 to 0,5 m by the end of spring, to ensure water uptake through the dry summer.

Description of the submodel

Initial seedling growth depends on stored nutrients in the seed. The stored energy and carbon can be in the form of protein, carbohydrates, or fats. In many small seeds, energy is stored as fat, which contains more energy per unit mass than does carbohydrate. However, Jordaan (1944) found that proteins are the dominant stored reserve in the embryo of *Protea repens*. The measured concentration of phosphorus in the seed is relatively large (van Staden 1966). It is therefore assumed in the model that in the very early stages of seedling growth, energy and nutrient stores are large relative to the needs of the emerging seedling. In the simulations, the initial root and leaf growth is not limited by total nonstructural carbohydrate (TNC) or nutrients. If the carbon stores in the seed are depleted before depletion of the phosphorus reserves, leaf growth is favoured over root growth. As carbohydrate reserves are replenished by photosynthates, phosphorus may become limiting and root growth is favoured over leaf growth.

The initial rate of growth of the seedling is slow. In the seedling submodel, the simulated relative growth rate of seedlings is five to 20 times lower than the rates used for shoots of mature plants. Using the same growth rate for seedlings and mature shoots led to mathematical instability in the seedling submodel. The seedling growth rate is calculated using a relative growth rate and an initial seedling leaf and root mass. The total nonstructural carbohydrate limitation on growth is calculated with a Michaelis-Menten relation. The relations for root and shoot growth were chosen to maintain a reasonable functional balance between leaves and roots. When carbohydrates are in short supply, leaf growth is favoured over root growth. Growth of leaves and roots are equal when total nonstructural carbohydrate content of the seedling is 150 mg/g. Above 150 mg/g, root growth is more rapid than leaf growth. Below 150 mg/g, leaf growth is favoured.

The phosphorus limitation on seedling growth is also calculated with a Michaelis-Menten relation. Compared to the relationship for carbohydrate, the k_m and full rate parameter values for phosphorus are reversed between leaf and root. For phosphorus in leaves, the k_m is 3 000 µg/g and for roots, the k_m is 100 µg/g. The growth rate equals the average value of 4 000 µg/g for leaves and 600 µg/g for roots.

Photosynthesis, respiration and plant carbon balance of the seedling are simulated to vary by approximately 30 per cent during the year, with seasonal changes in temperature and in solar irradiance related to changes in day length. Maintenance and growth respiration are separated and different respiration rates are assumed for different plant parts.

Stem growth is set at 0,15 of leaf growth. Secondary stem growth is calculated as 0,15 times the leaf growth, multiplied by the height of the plant in metres. The root to shoot mass ratio at 56 days and at one year should be about 1 to 18 (Manders unpublished).

Root growth in seedlings should be compared to the movement of the drying front in the upper soil layers. Then, if seedling roots do not grow downward more rapidly than the soil dries, the seedling would die; death would occur at a plant-water potential below -6 MPa. The soil-water model should be linked to the seedling model, so that the relationship between the rate of root growth and seedling mortality can be simulated.

Results of the submodel

Results based on the output of the seedling submodel for *Protea repens* indicate the importance of root growth and uptake, soil nutrient levels and root nutrient contents as factors affecting seedling survival and growth. The root must take up more phosphorus per unit root mass than is used in growing the same tissue. Concentrations of phosphorus in roots are not well known. Root length/mass ratios are also not well known. Data from the chaparral and northern heathlands indicate that the amount of phosphorus in roots is one-half of the amount of phosphorus in the leaves (Miller 1981; Specht 1981b). In Australian heaths, the phosphorus in Banksia roots is three times the amount of phosphorus in leaves (Bowen 1981). The absolute levels of phosphorus are similar in all mediterranean-type ecosystems but the amount of phosphorus in leaves varies widely between the ecosystems on different continents. This variation could provide a basis for a general picture of root phosphorus relations.

The simulation of seedling growth shows that certain combinations of root phosphorus concentrations, root length/mass ratios and available phosphorus are not viable for seedling survival. When the amount of available phosphorus in Hutton soil, 0,52 µg/g soil solution, is used in the model, the seedling cannot survive with a length/mass ratio of 30 mg/g or less and a minimum root phosphorus concentration of 100 µg/g. With the development of proteoid roots and an assumed length/mass ratio of 90 m/g, seedlings can survive even with a minimum root phosphorus concentration of 300 µg/g (Figure 41).

Phosphorus and water imbalance indicated by the seedling growth model, require consideration of the idea that seedlings must have primary roots which grow rapidly to depths of 300 mm, to maintain an adequate supply of water as the soil dries in the summer. The seedling must also have secondary and proteoid roots, which are more active in nutrient uptake. The increased exploited zone surrounding the root, caused by root hairs

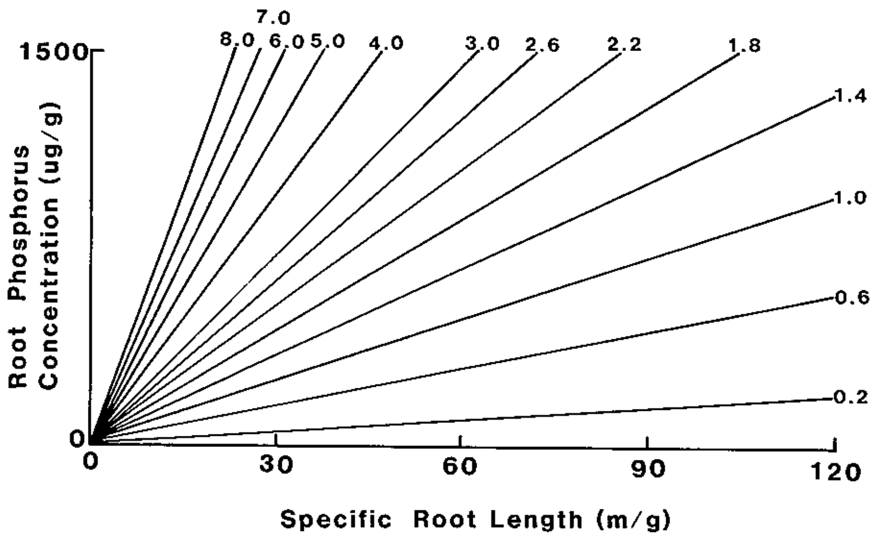

FIGURE 41. The relationship between root phosphorus concentration, specific root length, and the available phosphorus in the soil. In order for the plant to survive the root must be able to export more phosphorus than is used in growth. For a given soil phosphorus level (defined by the numbers on the lines) the root's phosphorus concentration and specific root length must be below the threshold line.

and the greater mineralization owing to the secretion of phosphatase, may also be important in the survival of the seedling.

THE PROPAGULE DYNAMICS SUBMODEL

(F J Kruger, G J Breytenbach)

Introduction

The processes which govern regeneration and recruitment of plants and the structure of the plant community, are all determined to a large extent by the incidence of fire in fynbos. The number of post-fire recruits to any suite of fynbos plant species are those which control the availability of viable seeds and/or resprouts. Any given species must survive the fire as either a seed or a sprout; or by seed dispersed to the site after the fire. Most fynbos plant species have short-range seed dispersal and survival is by means of in situ propagules.

Obligate-seeding species may be sensitive to the season of controlled burning. Even though it can be hypothesized that the most common period of natural fires is in summer and autumn, after the seed has been dropped and just before the rainy season starts; fynbos can burn any time of the year (Kruger 1979). Because of the dangers involved in managed burns during mid-summer, the management practice has favoured alternative seasons. This may increase the length of time that seed lies on the ground exposed to granivory, which is thought to be a major factor in deciding community composition in the southern and western Cape (Bond et al 1984; van Wilgen and Viviers in press).

In order to avoid the pressures of granivory, which could seasonally deplete a species' seed source and prevent recovery following an aseasonal fire, many seeding species in the fynbos are either serotinous, or have elaiosomes. Serotinous species protect their seeds by retaining them in the cone, only releasing them after a fire. Species with seeds which have elaiosomes utilize ants to transport the seeds below the surface of the ground, away from granivores. Unseasonal burning and the release of seeds from serotinous species when the environmental requirements for germination are not present, can still be disastrous. The life span of buried seeds is not well known, nor is their actual ability to germinate and contribute to the post fire community. Historical records show that seed longevity in myrmecochorous Proteaceae can be as long as 19 years (Boucher 1981).

The seasonal variation in a resprouting species' ability to recover after fire is not well understood. It can be hypothesized that immediately after a growth flush, plant reserves may be low and that this would be a poor time to burn and expect unhindered recovery.

In order to effectively manage the fynbos, it is necessary to have an understanding of the seasonality of seed reserves and resprouting potential. The effect of climatic conditions in the current season and those of last season's, which may have modified the plant's reproductive potential, can only be approached through simulation.

Requirements of the submodel

The seed bank dynamics should simulate the seasonal course in the size of the various seed pools and the seasonal course of the number of potential resprouts. The seed pools to be included should be seed stores in the canopy, seed stores at the soil surface and seed stores in the upper two soil levels. For each species, the number of viable and nonviable seeds stored in each pool should be maintained. Seed loss from these pools is through predation, loss of viability and germination. Seed production varies with the age and vigour of the plant. For resprouting species, the number of bud primordia should be maintained. The potential for vegetative regeneration also varies with the age of the plant. The regenerative processes, seed or vegetative, must be accomplished within the framework of the survivorship curve for the species population.

Description of the submodel

The detailed submodel has not yet been developed, but a similar submodel has been encoded in the FIRES model (see below).

THE PLANT-ANIMAL INTERACTIONS SUBMODEL

(G J Breytenbach)

Introduction

While the effects of interaction between animals and plants are often explicitly accommodated in models of grasslands, this has seldom been the case for other types of ecosystems. In fynbos, animals apparently do not have much effect on productivity, since consumption of foliage is low (less than two per cent of potential leaf area - Kruger unpublished). But effects on plant reproductive potential can be marked, through the influence of pollinators as well as a result of predation. For example, it is now obvious that small mammals play an important role in governing recruitment of seedlings in the post-fire environment. Consumption of seed and seedlings seems to be of critical importance in determining the structure of mature communities (Bond et al 1984). Therefore, any attempt to model the dynamics of fynbos communities must incorporate plant-animal interactions.

Requirements of the submodel

The plant-animal interactions submodel should simulate the seasonal course of seed and seedling predation and pollination by animals. The submodel should simulate the seasonal course of the various insect and vertebrate populations involved, as well as their activities; and should accommodate habitat influences determined by the structure of the vegetation.

The submodel should receive as inputs the leaf area index and in due course, the structure of the stand as calculated in the energy balance submodel; and should output rates of predation to the propagule dynamics submodel and of pollination to the shoot systems dynamics submodels.

Description of the submodel

The submodel as presently conceived deals only with granivory and seedling predation. Small-mammal communities of the fynbos normally consist of two to six species, of which one is always a grazer-browser (usually an Otomyinae). The rest of the community comprises Rodentia and Insectivora, which feed to a greater or lesser degree on seed (Bond et al 1980; Nel et al 1980; Rautenbach and Nel 1980; Breytenbach 1982). Several of the species in the southern Cape which feed extensively on seed, have been recorded feeding on insects in the western Cape (Rautenbach and Nel 1980).

Population density varies considerably, with four to 138 animals being recorded per hectare in the southern Cape (Breytenbach 1982). Density has been found to be a function of foliage profiles, where foliage profiles are measured by the inverses of the distances at which a board 100 mm wide x 200 mm high would be 50 per cent covered by vegetation. Small-mammal population density is related to the foliage profile as follows: $N = 20{,}6 + 0{,}286X + 0{,}982X^2$, where N is the small-mammal population (per hectare) and X is the density of foliage below 200 mm.

Small-mammal density fluctuates over seasons, but the patterns are not clear. Until more details about these fluctuations are known, the submodel should maintain small-mammal population densities at a constant level and relate them to annual changes in the foliage profile. However to achieve greater realism, small-mammal densities should fluctuate seasonally between -15 per cent and +60 per cent of the mean density for the year.

The number of seeds consumed by various rodent species in captivity varied between 150 and 450 per individual per day, depending on the size of the animal involved. However, a mean of some 200 seeds would be consumed by each individual present in the area when no other food is present. In mature veld, it is estimated that seeds constitute only 45 to 55 per cent of food consumed by the small-mammal community. It is fair to estimate that in a mature fynbos stand each individual rodent present would consume some 90 to 110 seeds per individual per day.

The largest rodents in the community are Otomys species, which are all grazer-browsers. They have a large indirect influence on the seed resources, since they feed extensively on the stems and flowers of plants. It was therefore deemed necessary not to eliminate them from the seed predator class. Calculations of density therefore incorporated the Otomyinae and it was assumed that they would probably also account for a similar loss from the seed bank.

This submodel has not yet been encoded in detail, but is incorporated in simple form in the FIRES model.

A PROPOSED MODEL OF THE DIURNAL PATTERNS OF PHOTOSYNTHESIS, TRANSPIRATION AND ENERGY BALANCE IN THE PLANT CANOPY

(W C Oechel)

INTRODUCTION

A model of the diurnal dynamics of plant and environmental processes has been conceptualized for the fynbos biome. When it is written, the model should simulate the diurnal patterns of evapotranspiration, plant carbon flux and energy exchange within the canopy for a 24 hour period, in five-minute time steps. The model can be used to interpret field measurements of diurnal patterns of leaf conductance to water loss, plant-water potentials, photosynthesis and soil evaporation. It will also aid in understanding the biotic factors affecting evapotranspiration in both riparian and non-riparian fynbos communities. This model can be used to develop and refine the parameters which define water and carbon dioxide flux in the plant growth and water balance submodels of FYNBOS. The proposed model will calculate leaf transpiration, leaf, stem, and soil surface temperatures, leaf and stem photosynthetic rates, leaf, stem, and root respiration rates, and abstraction of water from the different soil horizons.

REQUIREMENTS OF THE MODEL

The model of diurnal dynamics of plant and environmental processes needs as input, data values for the daily course of total solar irradiance, diffuse solar and infrared irradiance, relative humidity, air temperature and wind speed. Climate data can either be daily courses measured outside the canopy, or stochastically generated values for climate variables. Also required for the model are data on soil water-holding capacity; and the relationship of soil-water content to soil-water potential. The biotic inputs required include leaf and stem area indices, measured at appropriate levels in the canopy, and root area and length, measured at various soil depths. Other parameters and functions required are leaf angle and orientation at various levels in the canopy, the relationship of leaf-water potential to leaf conductance, the temperature and light controls on leaf conductance and on carboxylation resistance in the leaf, and net stem and leaf respiration as a function of temperature and light.

The diurnal model will produce daily courses of evaporation from leaf and soil surfaces, leaf transpiration as a function of climate, photosynthesis as a function of transpiration, respiration as a function of temperature and changes in soil-water content and soil-water potential as a function of climate. These daily output values can be used as input for models which run on a one-day time step, such as the FYNBOS model.

DESCRIPTION OF THE MODEL

This model is based on a similar one, the Canopy Process Simulator (CAPS), which was developed for the chaparral in California. CAPS simulates the diurnal patterns of irradiance, air, soil surface, and soil temperatures, humidity, respiration, transpiration and net photosynthesis of a continuous canopy. It runs in five-minute time steps for 24 hours.

Steady-state conditions are assumed for incident, direct and diffuse solar and infrared irradiance, temperature and humidity of the air and wind speed above the canopy. These parameters are entered as driving variables at the beginning of the simulation. The plant canopy is divided into layers 0,25 m thick. Calculations of plant parameters are based on one square centimetre of leaf; calculations of environmental parameters are based on one square metre of ground. CAPS has only one state variable and that is plant water content. The new model will include soil-water content as a state variable. Plant water-content at a given time step is a function of the previous plant-water deficit and the rates of water uptake and translocation.

Solar and infrared irradiance interact with the leaf and stem areas within each canopy layer, to produce profiles of direct and diffuse solar and infrared irradiance. Leaves and stems have varying inclinations, absorptivities, widths and water and photosynthetic functions. Air temperature, humidity and wind speed above the canopy then interact with leaves and the calculated irradiance profiles, to produce profiles of air temperature, humidity and wind within the canopy. Fluxes of energy are summarized using the energy balance equation for leaves and stems, which calculates leaf and stem temperatures. In a series of feedback relations, solar and infrared irradiance, air temperature, humidity and wind, affect leaf temperature and transpiration. Plant-water status is affected by transpiration, soil moisture and soil temperature. Because the movement of carbon dioxide, through the leaf, is affected by many of the same factors that control water movement, photosynthesis is calculated based on the movement of carbon dioxide as it is related to the movement of water vapour, through the leaf stomata. Photosynthetic rates are calculated for sunlit and shaded leaves; then photosynthesis is calculated for the entire layer and summed for the whole canopy.

RESULTS OF THE CAPS MODEL

The CAPS model has been used to simulate the effect of heated water for power plant effluents on a mangrove ecosystem (Miller et al 1976a); and to simulate photosynthesis in wet meadow tundra at Barrow, Alaska

(Miller et al 1976b). Irradiance parameters generated by the model were validated with data collected in a dwarf birch stand in Alaska (Stoner et al 1978). CAPS proved useful in predicting steady-state interactions between the environment and the plant canopy at the individual leaf level. Results with CAPS indicate that the new model should be able to simulate diurnal photosynthesis and transpiration.

A PRELIMINARY ANALYSIS OF SUCCESSIONAL DYNAMICS: THE FIRES MODEL

(P C Miller, F J Kruger, G J Breytenbach)

INTRODUCTION

Processes structuring plant communities can be categorized as predominantly demographic, dealing with numbers of individuals; or as predominantly physiological, involving flows of energy, carbon, water and nutrients. Much of the previous research in mediterranean-type ecosystems has dealt with physiological processes and models based on physiology. The views of Clements (1916, 1936) and Odum (1969), that succession is driven by competitive interactions for resources, lends itself to a physiological view of ecosystems. In ecosystems with a high frequency of disturbance, Noble and Slatyer (1977) emphasize that competitive ability may not be as important as other characteristics which allow the species to be present in a viable state after the disturbance.

Noble and Slatyer (1980, 1981) give a minimum set of vital attributes, which determine the persistence of a species in a fire-dominated ecosystem. In many cases, knowing the relative abundances of the species in an ecosystem after a fire may be just as important as knowing whether or not they will survive. Predicting this demographic information, such as the variation in seed production with plant age, or problems of mortality between and during fires, will probably be more informative than the vital attributes of age at which a species first produces seed, age to mortality and seed longevity.

Plant demography can be described on two levels of organization: genets (the genetic individuals); and ramets (the population of plant parts which constitutes the genet) (Harper 1980). It is possible to follow births and deaths of genets, but plants are enormously flexible in their ability to lose parts without death of the individual. Because of this, it is also often necessary to follow the births and deaths of ramets, which can be defined as functional individuals. Units of a shoot system can be treated as ramets.

Because the parameters defining the births and deaths of plant parts and whole plants are not constant, but vary with the state of the environment and of the plant, the interactions between environment and plant demography involve the physiology of the plant. Thus we arrive at an integration of basic demographic parameters and of physiology of the plant and we have a framework for considering the population biology of plants in the context of ecosystem processes. From this point we can begin to consider mechanisms of competition, physical stress, and species interactions and mechanisms of succession.

FIRES was first outlined in May 1981. It was then reviewed and model parameters were established for the chaparral of southern California, the matorral of central Chile, the fynbos of South Africa, the maquis and garrigue of the Mediterranean Basin and the mallee and heathlands of south and western Australia, at a workshop held in San Diego in June 1981.

REQUIREMENTS OF A SUCCESSION MODEL

A model such as FIRES should simulate the regeneration after fire of a stand of vegetation with a given history, as well as the post-fire succession. It should express changes in vegetation structure as the vegetation matures; and should simulate the capacity of the community to regenerate at any age after a fire. It must simulate successional changes in ecosystem properties that are important in management, such as the water balance of the site, species diversity and plant aboveground biomass as fuel. It is necessary to simulate the effects of different fire regimes, each differing in their frequency, seasonal timing and intensity of fire, therefore predicting longer-term changes in communities. The model must be useful in testing the effects of climate and other environmental changes on the rate and course of post-fire succession. Since fire has different effects in different seasons, it will be necessary in due course to determine the need for a model run on monthly time steps.

CONVENTIONS OF THE MODEL

FIRES proceeds in one-year time steps. It simulates the course of development of individual plants of different growth forms and densities; the dynamics of the soil and canopy seed banks, the processes of germination and seedling establishment, the development of the vegetation canopy and canopy light extinction, the growth and death of individual plants and the loss of plant parts, the site water balance, the site carbon balance, the site nitrogen and phosphorus balances, the probability and occurrence of fires of different intensities and the effects of these fires both on individual plants and on ecosystem processes. Plant-animal interactions have been added to FIRES, because it is becoming apparent that birds, rodents and ants are important agents in seed dispersal, seed mortality and protection from granivory (Bond and Slingsby 1983); and that they affect ecosystem production.

The model simulates the development of individual plants of each species and keeps account of eleven characteristics: age; number of vegetative shoots; number of flowering shoots and persistent inflorescences (flower heads); number of potential sprouts after fire; total biomass; leaf area; fine stem mass; coarse stem mass; root length; carbohydrate reserves; and height. Processes related to species characteristics are described by 55 parameters. Seed densities, plant densities and biomass are summed for each species. For the stand as a whole, the model tabulates fine and coarse standing dead material, litter, nitrogen in litter, phosphorus in litter, soil organic matter, total soil nitrogen and total soil phosphorus. The distinction between the fine and coarse standing dead categories is made at six millimetres diameter, following the similar distinction made in fire behaviour models (Countryman and Philpot 1970). Standing dead includes skeletons of dead shrubs and dead branches attached to living shrubs. Litter includes unattached material lying on the soil surface.

Each species simulated is assigned a characteristic area. This is necessary because the densities of common species can vary from less than 0,05 individuals/m^2 for the larger shrubs, to over 1 000 individuals/m^2 for annual grasses. The area assigned to each species was chosen so that a reasonable number of individuals of the species could be followed, to allow consideration of population age structures. Processes are calculated for an individual plant or summed for a square metre, whichever is most appropriate. Conversions between the individual and area bases are made using the characteristic area of each species.

Seasonal interactions between fire characteristics and effects, germination and establishment, will be included first as explicit mathematical relations; and later as simulated processes, as the model becomes more detailed in its time resolution.

DESCRIPTION OF THE MODEL

Climate, water balance, and heat balance

Presently, recorded climatic data are used to drive routines which simulate site processes. In the FIRES model rainfall interception is calculated so that with a leaf area index of 2,0, 10 per cent of the annual precipitation is intercepted and evaporated. Transpiration is currently calculated as an average annual rate multiplied by the leaf area index, but this formulation will be changed to allow more flexibility and consistency with physical principles. Soil evaporation is calculated to be 240 mm/yr from bare soils and decreases exponentially to 120 mm/yr as leaf area index increases to about 3,0. The balance between precipitation and evapotranspiration is given as drainage. The values for transpiration and soil evaporation are related to potential evapotranspiration through the relations encoded in FYNBOS, from which the annual values are derived.

Decomposition

The decay of litter and soil organic matter is calculated to be 23 per cent of the standing crop per year, following data from Swartboschkloof. The assimilation of carbon in the ecosystem is calculated from the net primary production and two decay rates.

Nitrogen and phosphorus cycling

The nitrogen and phosphorus balance include assumed values for inputs from precipitation and rhizobial fixation and outputs via drainage. Nitrogen and phosphorus are released from decaying litter and soil organic matter into the potentially mineralizable pool. Mineralization is taken as a fraction of the potential pool and is modified according to the annual precipitation. The main factor affecting the amount of mineralized nitrogen and phosphorus is the size of the mineralized pool.

Mineralization should be 20 per cent of the total pool, consistent with simulations with FYNBOS. In the FYNBOS model, the potential mineralization rate is adjusted according to the soil depth, temperature and changes in moisture through the year. In FIRES, 50 per cent of the nitrogen and phosphorus which falls from the plants in litter is assumed to enter the potential mineralizable pool directly. The other 50 per cent enters the soil organic pools and is released to the mineralizable pools at a rate of three per cent of the organic pools per year. These percentages should be modified, as simulation by means of the FYNBOS model and further experiments provide a more realistic picture.

Death of individuals

At each iteration for a one-year period the mortality of individual plants during the interval is calculated first. Growth of the surviving individuals is then calculated. The probability of death of the individual is related to the maximum age, which is a species parameter. Whether the individual actually dies depends on a random variable and the probability of death. On death, the plant mass, nitrogen and phosphorus are added to the standing dead, litter and soil organic compartments; according to the masses of leaves and fine stems, above- and belowground coarse stem material and absorbing roots.

Growth of individuals

The individual plant grows in response to an innate maximum rate and is limited by nitrogen and phosphorus uptake, water availability and light. The innate maximum rate is calculated from a maximum rate per vegetative shoot and the number of vegetative shoots per plant. The potential nitrogen and phosphorus uptake by the individual is calculated by multiplying that fraction of the total root length of the vegetation, which is the root length of the individual, multiplied by the mineralization rate of nitrogen and of phosphorus. The potential growth rates due to the potential uptake rates of nitrogen and phosphorus are then calculated by dividing the uptake rates by the nitrogen and phosphorus contents of the plant tissues. Potential transpiration is calculated from the annual water budget, ie from precipitation minus interception and soil evaporation. Photosynthesis is calculated from a photosynthesis-light curve and the light level at the midpoint of the plant canopy. Eventually, photosynthesis will be calculated for each stratum in the canopy. Transpiration is converted into potential photosynthesis by multiplying by the photosynthesis-transpiration ratio, ie the water-use efficiency. The two estimates of photosynthesis, one based on light and the other based on water, are then converted into potential tissue growth. In this conversion, maintenance respiration and flower and seed production are assumed to have priority over new vegetative growth. A growth respiration cost of 30 per cent is assumed. The final growth rate is the minimum of five separate potential growth rates. FIRES thus simulates inter- and intraspecific competition among plants for light, water and principal nutrients.

Leaf drop is calculated from the leaf longevity, allowing for longer leaf longevity in younger individuals. Leaf drop is calculated on the basis of dry mass per individual.

Shoot system dynamics and canopy architecture

The new growth is allocated to new leaf mass (area), fine and coarse stem mass and root mass (length). The height of the individual is recalculated according to the new fine stem mass, converting this to stem length and new height.

The number of shoots on the individual plant is calculated as the balance between shoot production and shoot loss. Shoot production decreases as the growth per shoot decreases from the maximum value to a minimum value. Different rates of shoot production in juvenile (non-flowering) and mature plants are allowed for. The production of flowering shoots depends on an average number of flowering shoots per shoot, plant age and whether a fire requirement for flowering is satisfied. Shoot death depends on the shoot turnover rate.

The leaf area index profile through the canopy is calculated in 0,2 m intervals between the soil surface and 4,0 m height. The height of each individual is taken to be the level of the highest leaves of that individual. The leaf area of the individual is assumed to be distributed vertically, according to a normal curve. Ninety-five per cent of the leaf area is included in the height interval, called the canopy thickness. The mean height of the canopy is calculated as two standard deviations below the height of the individual, whilst the canopy thickness is four standard deviations. The solar irradiance profile is then calculated from the leaf area index profile.

Seed germination and seedling establishment

In FIRES, germination can occur only if the fire and light requirements of the species in question are satisfied. The light requirement of a species may involve various inhibitory effects of the canopy. The number of seeds germinating depends on a species parameter, the seed density and the characteristic area of the species. The number of germinating seeds is simulated to vary between ±30 per cent of some expected value. A low first-year survival of germinated seeds is allowed for. Survival of two- to five-year-old seedlings is currently calculated following the adult mortality schedule, but survival should probably be calculated at a higher rate. The individuals which survive the first year are given a characteristic biomass, leaf area, fine stem mass and root length.

Vegetative resprouting

If the individual is a sprouter, the number of potential sprouts following removal of the aboveground portion of the plant is a function of the age of the plant and increases sigmoidally up to a maximum number of potential sprouts, as the plant ages. With old age the number of potential sprouts decreases.

Totals of plant processes

Gross primary production, net primary production, total biomass, nitrogen and phosphorus taken up and incorporated by the vegetation, are derived from the growth rates as finally calculated with the controls given to be operating for the current iteration.

Dynamics of seed banks

In fire-dominated ecosystems the availability of seeds and means of vegetative regeneration are important influences on the ultimate species composition of the stand (Specht et al 1958). The processes of seed storage, loss and germination are important. In the FIRES model, seed production depends on the number of flowering shoots and the number of viable seeds produced per inflorescence. Since the number of flowering shoots is calculated per individual plant, the seed production per m^2 is determined by the characteristic area of each species.

The model allows for seeds stored in the canopy (in bradysporous or "serotinous" species), at the soil surface and in the soil. The processes of gain and loss of the seeds in each storage location differs by species, although very little quantitative data are available on the number of seeds held in each location. Losses from these stores are due to consumption by insects, birds and rodents. The relative importance of seed predators differs depending on where the seed is stored. For canopy-stored seed consumption by insects and rodents is assumed to be relatively higher than that by birds.

Based on field observations, it is estimated that rodents can remove 30 per cent to 80 per cent of the flower heads of serotinous species during the first year after flowering. There is both regional and local variation (G J Breytenbach, personal communication, 1983). Older flower heads suffer little or no predation. Here, rodents are assumed to consume 40 per cent of the cohort of seeds in the first year. Insects are assumed to be responsible for continuous attrition of 30 per cent of the canopy-stored seed crop each year.

Seed loss is also assumed to be caused by decreased viability (van Staden 1978). All canopy-stored seeds are assumed to be viable for five years, with 20 per cent of a given cohort losing viability each year. Assuming that the processes of decreased viability and predation are independent, it follows that about 70 per cent of the canopy-stored seed crop is lost to predation during the first year. After this initial attrition, seed loss continues at a rate of 50 per cent per year due to loss of viability and insect predation. The total seed crop is lost by the third year after flowering.

The transfer of seeds from the canopy to the soil surface, involves the drying of the flower head following the death of the shrub in a fire or after a branch breaks. Consumption by insects and birds of the seeds at the soil surface can be high and may depend on the size of the seed crop, since these granivores can migrate freely between burned and unburned areas. Consumption by rodents depends on the size of the resident rodent population, which is simulated as a function of time since the last fire and leaf area index of the tall shrubs. The transfer of seeds from the soil surface to the soil store involves ants and is important in non-serotinous species which have elaiosomes. Seeds buried in the soil may be eaten by insects, but losses due to birds and rodents are probably low. Based on field observations, the loss of seeds from the buried seed bank is tentatively assumed to be five per cent per year because of consumption by insects; and 15 per cent due to the loss of viability.

In the simulations, one per cent of the balance of canopy-stored seed is transferred to the soil surface during each year without fire, as a result of branch or inflorescence mortality. Consumption of seeds stored on the soil surface is assumed to occur regardless of the occurrence of fire. Following a fire, all canopy-stored seeds are transferred to the soil surface. The total seed bank of canopy-stored seed which is available for germination after a fire is assumed to be 0,9 times the current year's seed crop, 0,3 times a one-year-old seed crop and 0,15 times the two year-old seed crop. In the model, birds are assumed to immigrate after a fire, and to remove five per cent of the seed crop on the soil surface within the first year. About 75 per cent of the pre-fire rodent population is assumed to survive the fire. These rodents consume large numbers of seeds and remove an additional 40 per cent of the seed crop. In the model, when the number of seeds on the soil surface drops to 10 per cent of seeds released at time of fire, it becomes energetically unfeasible for birds and rodents to survive on the remaining seeds. However, this assumption may be unrealistic. When animals are foraging for many smaller seeds, the occasional large seed will be found and eaten, resulting in a seed depletion of more than 90 per cent of the original pool.

Animal population dynamics

In the FIRES model, rodent populations and consequently their predation/consumption of seed, increase after a fire as leaf area index increases, until the total population reaches an average maximum, after which the population follows a sinusoidal fluctuation with a three- to four year period. Rodents are assumed to remove 90 per cent of the seed crop at the soil surface when the canopy is closed, ie where leaf area index (LAI) is 2,2. This rate is assumed to decrease linearly to one per cent when the canopy is open, ie LAI 0,2. The residence time of seeds on the soil surface beneath a closed canopy is short, ie less than a year. Loss of viability is assumed to reduce the soil surface seed bank by five per cent per year for soft seeds and one per cent per year for hard seeds. Transfer of seeds with elaiosomes to the buried seed store depends on the presence of ants. Seeds which are not buried are subject to large predation losses.

It has been observed that consumption of seed by rodents is directly related to rodent densities. The density of the foliage below 200 mm in the canopy can be used to estimate rodent density in fynbos plant communities (Breytenbach 1982). Foliage and rodent densities vary over time and seem to respond to rainfall, with a time lag of about one-and-a-half years. One-and-a-half years after a year with rainfall that is 30 to 50 per cent higher than the mean, the modelled populations of rodents will double; one year after drought, rodent populations drop to half the normal population size. Rainfall patterns could be used to indicate variations in rodent populations and therefore in granivory. A clearer estimate of seed losses could be obtained if granivory was expressed as grams of seeds consumed per gram of rodent body mass.

With more information on survival of rodents from fires and on post-fire succession, the amount of post-fire seed consumption can be more accurately estimated. In the FIRES model, the amount of seed consumed is a simple linear function of the density of seed predators. However it has been observed that rodent populations increase linearly with annual rainfall and hence plant productivity, only until density-dependent factors impose an upper limit on the size of the population. With further increases in plant production, seed production may increase, while rodent populations and therefore seed predation will remain constant. With particularly favourable rainfall regimes, the probability exists that excess seed may accumulate. These relationships need to be incorporated into the FIRES model.

As the FIRES model is developed and refined and as more information becomes available, aspects of modelling seed bank dynamics can be improved. The effect of the alien Argentine ant Iridomyrmex humilis on the dispersal and burial of seeds should be included. Iridomyrmex humilis may completely disrupt observed seed dispersal patterns (Bond and Slingsby 1983) which may result in much greater loss of seeds in myrmecochorous species.

Fire Probability and Effects

Sophisticated methods of modelling fire ignition and behaviour are under development (van Wilgen 1982, 1984), but a simple approach has been adopted in FIRES.

Fire requires an ignition source and fuel in a flammable condition. Ignition sources are lightning, falling rocks (unique in mediterranean-type ecosystems to South African fynbos), accidental ignition by man, and prescribed fire. The probabilities of ignition by the first three causes are presently set at 0,02, 0,01 and 0,03 respectively. For ignition to occur a random variable is selected and compared with these probabilities. The possible causes are additive. Fire is assumed not to occur if the fine standing dead and litter total less than 300 g/m^2. If this quantity is between 300 and 1 000 g/m^2, a moderate fire is assumed. If this plus the large standing dead are greater than 1 000 g/m^2, then a severe fire occurs.

The effects of fire on an individual plant depend on the severity of the fire and on whether the plant is a seeder or a sprouter. Seeders are killed and their above- and belowground biomass and nutrients are transferred to the dead organic compartments. Sprouters lose only their aboveground biomass and nutrients. The number of sprouts is calculated according to the potential number of sprouts. The leaf area of sprouters one year after the fire is set to 50 per cent of the leaf area before the fire. Fine stem mass is set to zero and coarse stem mass is reduced to 50 per cent of the mature coarse stem mass. The root length of sprouters is reduced to 90 per cent of that before the fire, to account for changes in the functional balance between leaves and roots and plant adjustments when leaves are removed.

Standing dead material thicker than six millimetres is reduced to 90, 75 and 50 per cent of that prior to the fire with fire intensities of light, moderate and severe, respectively. The losses of nitrogen and phosphorus to the atmosphere or through erosion are 60 per cent, 80 per cent and 100 per cent of the amount in aboveground plant parts consumed in light, moderate and severe fires, respectively. This will need changing when more is known of such losses, especially in the case of phosphorus.

Results of the model

Two sets of simulations were run with FIRES. After 33 years with repeated fires at two-year intervals, the community was dominated by Watsonia, a geophyte, which has the potential to double its population after each fire. With the same environmental conditions, but a different, random fire frequency and different random values assigned to the initial plant variables, Psoralea initially became abundant. It was then reduced by the next fire, but increased thereafter. In both simulations restios remain in the community throughout the simulated periods.

Some of the current problems with FIRES relate to the plant carbon balance, the maintenance of leaf area under nitrogen and phosphorus limitation and the seedling growth and survival rates. It is too early to suggest definitive patterns of fynbos community dynamics based on simulations using FIRES. However in most simulations, available nitrogen and phosphorus become limiting about 20 years after fire. With the probabilities currently used in FIRES, fire usually occurs before the twenty-fifth year. With a long period between fires, ie 40 years or more, litter is reduced because, as the community ages, production declines whilst the rate of decay remains constant. The emphasis in the model on the response of the total system, highlights the interactions between the size of the seed pool and the effects of the season of burn. A large seed pool reduces the influence of season of burn. However, if the seed pool is small, regeneration following a fire is highly dependent on the current year's seed crop and on the maturity of the seeds at the time of burn. Under these conditions the season of burn becomes important.

TOWARDS THE DEVELOPMENT OF A MODEL OF DISTURBANCE RECOVERY FOR THE MANAGEMENT OF THE FYNBOS BIOME

(B van Wilgen, F J Kruger)

The dynamic simulation models outlined in this report have present value as a means to improve understanding of fynbos ecosystems and the essential nature of their responses to disturbance and to manipulation. However, they are too complex and incorporate too many untested ideas and relationships for general use in management. Researchers will be able to use them to explore options and then advise managers as to appropriate courses of action. Simpler models are needed if the approach is to be useful for practical decisions and these would need to include knowledge gained from practical experience and judgement. The two lines of approach should converge progressively as knowledge and skills improve.

Fynbos catchment ecosystems should be managed to ensure the maintenance of optimum water yields and to maintain essential catchment processes. At present, management concerns are focused on a few major issues, including fire, weed control, grazing and flower-picking in natural fynbos areas. The destruction of fynbos and its replacement with crops is also a major issue. These major issues can be translated into day-to-day practical questions which a manager must deal with. Such questions relate to the timing of fires, stocking densities of domestic animals, or the number of flowers that must be left on a shrub to ensure survival of the species.

Designing a model to aid decision-making must take into account the information a manager has available to put into the model and the information he requires as output from the model. The manager should have data available on the fire history of the site, including the date of the last fire, basic climatic data since the last fire from some nearby climate station, degree of weed infestation and past and present domestic animal stocking rates. The manager should also be able to select the key species that occur in the area to be simulated in the model and to determine their basic vital attributes from information supplied as part of the model documentation. In due course, he should be able to obtain such information for a given location by reference to an appropriate managed data base, with the aid perhaps of gradient models.

Using these data as inputs into a management model, the manager should be able to select various fire regimes and have the model estimate their effect on water yield, species diversity and catchment quality.

Since it would be difficult to determine the vital attributes of all of the species in a fynbos catchment, it is necessary to develop criteria for selecting key species that are representative of the groups of species that occur in an area. Robust species that are able to withstand a wide range of treatments without noticeable change in numbers or importance are not suitable candidates. Sensitive species with long youth periods, limited life spans and vulnerable seed stores are more suitable. The species selected should represent a cross section of reproduction guilds such as serotinous (bradysporous) seed reproducing plants, annuals, resprouters, geophytes and so on. The assumption on which the model is based is that all species in a guild will follow the responses of the representative key species of their guild. Since the species of a guild co-exist in a community, their responses to a disturbance should be similar. If they responded differently, they probably would have been eliminated from the community by the past disturbance regime.

A model is merely an aid to decision-making in management and not something which makes actual decisions. The real value of a management model is that it guides the manager in gathering and using data which are to evaluate options.

The management model should be as well thought out and constructed as possible, but it will be continually updated as new knowledge comes to light. The value and accuracy of the model should improve as it is used and updated. Management decisions always have and will depend on the judgement of the manager - the model is merely an aid to that judgement.

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