3 Nutrients and autotrophs

3.1 INTRODUCTION

The inclusion of living components in models of nutrient kinetics changes the nature of these models from the simple systems reviewed in Chapter 2, in which compartments were passive recipients of nutrient molecules and had no control over their rate of input. Living organisms grow and actively incorporate energy and nutrients into their own biomass and biomass of their progeny. They acquire these nutrients by either uptake from the abiotic environment or consumption from the biomass of other organisms in the food web. The movement of nutrients in food webs thus becomes largely determined by biological and ecological processes, which can be far more complex than the geochemical processes that otherwise control the movements of material elements.

Autotrophs, or primary producers, are at the base of the food web and acquire most of their energy and nutrients from abiotic sources (though there exist some autotrophs, such as carnivorous plants, that supplement their abiotic nutrient supply by capturing and consuming small animals). However, the methods of nutrient acquisition differ somewhat across autotroph types. Phytoplankton cells, for example, are immersed directly in the water medium that supplies their nutrient needs. Nutrient ions, such as nitrate (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^{4-}, HPO_4^{3-} or $H_2PO_4^{2-}$, depending on pH), and sulphate (SO_4^{4-}), are transported from the external medium to the interior of the cell by specialized enzymes called permeases. In the higher terrestrial plants the root systems, which are in contact with soil water, are the primary means of acquiring needed mineral nutrients, while carbon is largely taken up through stomata on the leaves. Then the nutrients, through diffusion or, in higher plants, translocation, move to sites (usually in the roots and leaves of higher plants) where they are assimilated into organic compounds needed for growth and regulatory functions. Plants store the nutrients for various periods of time in their biomass, eventually releasing these nutrients through processes of excretion and organism death and decomposition.

The biological processes of growth and regulation are dependent on a sufficient supply of nutrients. The primary atomic components of biomass are carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorus (P), sulphur (S), calcium (Ca), potassium (K) and magnesium (Mg). The first three of these elements make up carbohydrates, which constitute most of the

dry weight of plant tissues. The latter six are needed in smaller, but still relatively large concentrations, and so are referred to as macronutrients. Among other things, N is a major component of proteins, nucleic acids and chlorophyll, P is found in adenosine triphosphate (ATP), nucleic acids and cell membranes, S occurs in proteins, K actuates some enzymes and plays a role in plant water balance, and Mg is a component of chlorophyll. Also essential to living tissues are sodium (Na), chlorine (Cl), and a number of micronutrients in percentages less than 0.05%: iron (Fe), manganese (Mn), zinc (Zn), iodine (I), boron (B), silicon (Si), copper (Cu), molybdenum (Mo) and cobalt (Co).

As introduced in Chapter 1, stoichiometry refers to the ratios of chemical constituents of matter. In living biomass some generalizations concerning stoichiometry are possible. A frequently observed set of uptake ratios for carbon, nitrogen and phosphorus by ocean plankton is (by atom) 106 C:16 N:1 P or (by weight) 42 C:7 N:1P, which is known as the Redfield ratio. This figure is certainly not fixed, however, and Boyd and Lawrence (1966) found freshwater phytoplankton with ratios (by weight) of 116 C:9.9 N:1P. The ratios of the six major elements (by atom) in plankton have been estimated by Stumm and Morgan (1981) and Trudinger *et al.* (1979) to be 106 C:263 H:110 O:16 N:1 P:0.7 S.

An equivalent of the Redfield ratio is seldom given for terrestrial plants, as the ratios tend to vary considerably among species due to differences in the support structures. However, Attiwill (1980) calculated concentrations of several macronutrients in green foliage and litter in various forest types. For example, the concentrations of these macronutrients (in g kg^{-1} dry weight) in green foliage are shown in Table 3.1. Such concentrations are highly variable and change continually (e.g. Fife and Nambiar, 1982).

The existence of rather well-defined, if often variable, ratios of bioelements in green plant (referred to equivalently as primary producer or autotroph) biomass means that the nutrient needs of autotrophs will best be satisfied when the amounts of nutrients available in the surrounding medium occur in approximately the same proportions as the proportions of these elements in the biomass. When the proportion of one particular nutrient to the other nutrients available in the environment is below that needed for plants or

Table 3.1 Concentrations (g kg^{-1} dry weight) of five macronutrients in three forest types (from Attiwill, 1980)

Forest type	*N*	*P*	*K*	*Ca*	*Mg*
1. Australian eucalypts (wet sclerophyll)	14.73	1.05	4.60	6.77	3.87
2. Mixed *Quercus*, *Betula* and *Fraxinus*	24.41	1.32	11.08	11.94	2.71
3. Equatorial forests	25.92	1.62	12.72	18.99	1.73

animals to grow and perform biological functions, it may act as a limiting factor in biomass growth, as discussed in the next section.

3.2 BIOMASS GROWTH AND LIMITING NUTRIENTS

To grow successfully, green plants need physical space, solar radiation, water, carbon dioxide and sufficient amounts of all of the macronutrients and micronutrients. Any of these factors can become limiting to plants, but of most interest here are situations where nutrients are factors that are or can be limiting.

In general, plants are adapted to their environments through physiological mechanisms that balance their growth demand for various nutrients to the supply from the surroundings. Since environmental conditions are highly variable, however, it is unlikely this balancing will be perfect.

Justus Liebig, a pioneer in the study of various factors affecting the growth of plants, had the insight that the growth rate would be regulated by the 'foodstuff' obtainable in smallest amount relative to its needs. This idea is now called Liebig's law of the minimum (e.g. Odum, 1971, p. 106). One qualification on this principle is that it is strictly applicable only under steady-state conditions. Even under those conditions, it is unusual for the limitation on growth to be governed by only one limiting nutrient. It is more likely that when two or more nutrients are in short supply, each contributes to some degree in limiting growth, not only the nutrient that is 'most limiting'. This has been observed, for example, in studies in arid grasslands, where increases in either water or nitrogen improve growth rates of some species (Lauenroth, 1979). Pot and chemostat experiments have documented numerous cases where at least two nutrients were simultaneously limiting (e.g. Droop, 1974; Gates and Wilson, 1974; Shaver and Melillo, 1984).

The implications of multiple limiting nutrients will be discussed in Chapter 9. Throughout most of this book, however, the analysis of the effects of limitation on food web dynamics will be restricted to cases of only one potentially limiting nutrient. If this nutrient is abundantly available, then the growth rate of the autotroph will be assumed to approach a maximum value that is, for present purposes, a constant depending on a combination of the physiological characteristics of the organism that limits its processing rates and factors such as physical space, water and solar radiation.

In principle, every one of the essential elements can be limiting and, no doubt, examples of limitation by a given nutrient can be found somewhere on earth, especially in terrestrial systems, which are more heterogeneous by nature than are aquatic and marine systems. However, in a very large number of cases either N or P appear to be limiting. Table 3.2 lists a variety of studies of different ecosystem types and the nutrient(s) determined to be limiting in each study. The analyses of this book are, for the most part,

Table 3.2 Some studies in which nutrient limitations in natural systems were discussed. The * means that no particular nutrient, but nutrient limitation in general is discussed and ** means that nutrient limitation in a wide variety of ecosystems is discussed

Paper	*Nutrient(s)*	*Type of ecosystem*
Beadle (1954)	P	Dry sclerophyllous forests of southeastern Australia
Penning de Vries *et al.* (1974)	N	Loblolly pines in southeastern US
Weinstein *et al.* (1982)	N,Ca	Temperate forests
Jordan and Herrera (1981)		Tropical forests
Kliejunas and Ko (1974)	N,P	'Ohi' a forest in Hawaii
Tanner (1985)	N,K,P,Ca	Tropical mor ridge forest
Golkin and Ewel (1984)	P	Forests and lakes in Florida
Reuss and Innis (1977)	N	Temperate grassland
Black and Wight (1979)	N,P	Northern great plains
Shaver and Chapin (1980	N,P	Cotton grass-tussock tundra
Kachi and Hirose (1983)	N	Coastal sand dune soils
Hopkinson and Shubauer (1984)	N	Salt Marsh
Howard-Williams and Allanson (1981)	P	Littoral zone of South African lake
Boynton *et al.* (1982)	N,P	Estuarine phytoplankton
Kalff (1983)	P	Algal biomass in tropical lakes
Schindler *et al.* (1971), Schindler (1977)	P	Canadian shield lakes
Robarts and Southall (1977)	N	Algal growth in reservoirs
Morris and Lewis (1988)	N,P	Phytoplankton in mountain lakes
Caraco *et al.* (1987)	N,P	Phytoplankton in coastal brackish ponds
Peterson *et al.* (1985)	P	Algae in a tundra river
Smith (1979)	P	Phytoplankton in lakes
Sakshaug and Olsen (1986)	N,P	Phytoplankton in coastal waters (fresh to marine)
Hecky and Kilham (1988)	N,P	Phytoplankton in fresh to marine water
Smith (1984)	N,P	Phytoplankton in marine ecosystems
Howarth (1988)	N,P	Marine ecosystems
Steele (1962)	*	Marine ecosystems
Harvey (1963)	*	Marine ecosystems
Riley (1963)	*	Marine ecosystems
Dugdale (1967)	*	Marine ecosystems
Gutschick (1981)	N	**
Lovstad (1984)	P,N	**
Agren (1985)	N	**

general in the sense that no particular nutrient is assigned the role of limiting nutrient. The results should apply equally to a variety of potentially limiting nutrients. Whenever the term 'nutrient' is used, it will generally refer to a nutrient that is potentially limiting.

The concept of a limiting nutrient is relatively simple in the case where the nutrient availability is completely controlled externally by geochemical processes. In actuality, however, the autotrophs and other organisms in an ecosystem also exert their own degree of control over nutrient availability by forming internal nutrient cycles in which nutrients are continually released from biomass back into the available pool to be used again. Available nutrient is thus composed of both 'new' and 'regenerated' or 'recycled' nutrients, the latter being determined by the ecological system as a whole.

Switzer and Nelson (1972) identified three levels of the circulation of nutrients in forest ecosystem: geochemical, biogeochemical and biochemical (Figure 3.1). Geochemical cycles encompass inputs from and losses to the larger abiotic environment. Biogeochemical cycles encompass the recycling of nutrients between the soil and plants and heterotrophs. Biochemical cycles encompass internal transfers or translocations of nutrients within plants. There are major differences in the degree to which these cycles govern the movement of different nutrients. The need for phosphorus in tree metabolism, for example, is met largely through internal translocation, with only about 5% coming as new input from the geochemical cycle (the left-hand side of Figure 3.1). Interesting differences in the timing of translocation of nutrients between different tree types have been noted. For example, the seasonal pattern of translocation of phosphorus and nitrogen between leaves, stems and roots differs between tundra deciduous and

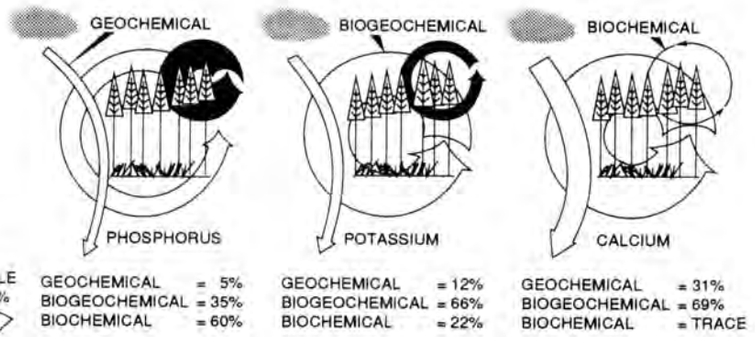

Figure 3.1 A comparison of the contributions of geochemical, biochemical and biogeochemical cycles to the phosphorus, potassium and calcium requirements of a 20-year-old loblolly pine plantation in southeastern US. (From Switzer and Nelson, 1972.)

evergreen shrubs (Chapin *et al.*, 1980). In deciduous shrubs, up to 14% of the total plant N and P was translocated from stems and large roots to leaves during the three weeks following snow-melt. In contrast, evergreen shrubs translocate N and P to leaves gradually through the growing season. Stems and large roots do not appear to act as large nutrient stores.

The plant's K needs are met predominantly through uptake from the soil, where it is the product of decomposition of plant detritus. The proportion of Ca used by the plant that is new input from the geochemical cycle is much greater than that of either P or K. This results from the great accumulation of Ca in the permanent tissue of plants, whereas K and P are primarily used in the more transient biomass and regulation processes of foliage where turnover rates are much higher.

Biogeochemical recycling may also be important in aquatic and marine ecosystems, especially oligotrophic systems. Dugdale and Goering (1967), Dugdale (1967) and others have distinguished between new nutrients supplied externally to the photic zone of marine ecosystems from outside through eddy diffusion, and recirculated nutrients within the photic zone. The latter may account for up to 94% of production in oligotrophic systems. As a final example, in dense aquatic macrophyte beds (*Potamogeton pectinatus L.*) the movement of phosphorus has been shown to be almost a closed cycle, in which the phosphorus released from decaying macrophytes was rapidly taken up again by epiphytic algae (Howard-Williams and Allanson, 1981).

It is not surprising that plants have special adaptations to help recover and thus conserve nutrients that are limited in their rate of supply by the geochemical cycle. Particularly important for terrestrial plants on nutrient-poor soils are extensive root systems concentrated near the soil surface (Jordan and Herrera, 1981). This reduces the likelihood of loss of nutrients through leaching and helps the plants compete with decomposers for nutrients. In tropical forests, aerial roots are another adaptation. These roots can penetrate and obtain nutrients from mats of dead epiphytes, such as bromeliads.

Headley *et al.* (1985) discussed a number of strategies that tundra evergreen plants, such as the moss *Lycopodium annotinum*, use to recycle nutrients internally and to improve the efficiency of nutrient uptake from the soil, and thus to conserve nutrients. These include increased root:shoot ratios and surface areas of roots, internal recycling from old to new tissues, efficient use of nutrient at low internal concentrations and a temporal extension of the period of photosynthetic activity through the evergreen habit.

A highly effective adaptation of virtually all forests is the symbiosis between trees and mycorrhizal fungi. The hyphae of these fungi are efficient at taking up nutrient from decomposing litter (they may actually participate in decomposition; Janos, 1983). They pass much of these absorbed nutrients on to the plant roots with which they are associated, receiving some

carbohydrates from the plant in return. This symbiosis enhances nutrient uptake by the plants.

Using information from a variety of forest ecosystems organized into the form of linear flow models, Finn (1976, 1978, 1980) calculated the cycling indices for various nutrients. The cycling index represents the recycled atoms as a proportion of the total nutrient throughput. This ratio for forest ecosystems ranged between 0.6 and 0.8. The cycling index will be discussed in more detail later in this chapter.

Kelly and Levin (1986) reviewed data from more than 200 natural areas on the relative importance of internal cycling and external sources. They noted patterns of decreasing nutrient use efficiency as a function of the amount of external loading. Whether or not there is nutrient limitation under these circumstances is hard to determine. The significance of the nutrient limitation can only be understood in the context of the complete system. The next few sections study the effects of nutrient limitation through formulation and analysis of simple mathematical models for systems in which the autotroph is the highest trophic level.

3.3 FORMULATING A MODEL OF NUTRIENT CYCLING

As Dugdale (1967) pointed out, the importance of nutrient limitation lies in its effects on the dynamic behaviour of systems. It can equally be said that the nutrient limitation is to some extent a function of the dynamics of the system. Both aspects will emerge from a model analysis of a system with nutrient cycling.

In this and the following chapter the only living organisms considered are primary producers. To simplify matters for the present, all autotrophic organisms are lumped into one compartment, so that autotophic biomass can be represented by a single variable. This is a reasonable representation when all the autotrophs in the system are members of the same species. When a mixture of different species is considered, the validity of aggregation is questionable, but the advantage of simplification to model analysis is so great that the approach seems justified, at least as a first step. In many cases a simple model will capture the essence of a phenomenon. Disaggregation into competing autotrophic species will be considered in Chapter 9.

There are two general ways of modelling the dynamics of nutrient-limited autotrophs, depending on whether nutrient uptake by the autotroph is assumed to be controlled solely by the external levels of available nutrient, or whether the intracellular nutrient level of the autotroph also exerts some control. Modellers assuming the former type of control usually assume that growth is described by a Monod-type function (e.g. Riley *et al.*, 1949; DiToro *et al.*, 1971, 1977; Thomann *et al.*, 1974). The second model type is often referred to as the cell quota model (e.g. Droop, 1968; Caperon, 1968). By including a mechanism for the effect of internal nutrient levels, such models

may be more appropriate for looking at details that require separation of the nutrient uptake and primary production processes. However, there is evidence that in many situations the simpler assumption of only external nutrient control of autotroph growth rate is an adequate approximation of growth dependence on nutrients (e.g. Caperon, 1965; Eppley and Thomas, 1969; Golterman *et al.*, 1969; O'Brien, 1974; Button, 1978; DiToro, 1980; Auer *et al.*, 1986). Because of the analytical simplification afforded by this assumption, it will be made throughout this chapter. The implications of the cell quota type of model will be explored in Chapter 4.

Both of the model types discussed above were derived for phytoplankton or bacteria and so neither can be expected to be appropriate for higher plants, where tissue differentiation and complex internal storage and translocation processes can occur. However, because models that lack internal differentiation may still adequately describe plant growth over long time scales, these models are frequently used to describe growth in higher plants, and will be used here also. The use of models with greater internal differentiation for higher plants will be discussed in Chapter 4.

In the present chapter the nutrient uptake per unit biomass of autotroph and the growth rate of the autotroph are assumed to be controlled solely by the external nutrient level or 'pool'. In addition, the amount of the nutrient in a given quantity of autotroph biomass, X, is assumed to be a fixed mean fraction γ of the biomass, so that the amount in the biomass is γX. Thus, an increase in autotroph biomass X must be accompanied by an uptake of an amount of nutrient γX from the nutrient pool.

Biomass is a convenient variable to use for modelling the flows of energy and matter in an ecosystem. Let $X(t)$ represent the instantaneous autotroph either as a density such as biomass (in $g\,m^{-2}$ or $g\,m^{-3}$, or an amount or standing stock such as g or kg, in a given system) in the primary producer trophic level. The most general possible model for the changes in $X(t)$ through time is

$$dX/dt = (\text{Production of } X) - (\text{Loss of } X) \tag{3.1}$$

where X is used as shorthand for $X(t)$. Here 'Production of X' includes both the growth in biomass of individual autotrophic organisms and the reproduction of new individuals, and 'Loss of X' encompasses both the decreases in biomass of individuals through processes such as respiration, litterfall and biomass sloughing as well as losses of whole individuals through mortality and emigration (by drift of phytoplankton in a lake or washout of periphyton and macrophytes in a stream, for example). For the purposes of this chapter, a special form of Equation (3.1) is used; that is,

$$dX/dt = r(N)X - (d_1 + e_1)X \tag{3.2}$$

where

$r(N)$ = the intrinsic rate of growth of X, which depends on the amount of available nutrient, N.

d_1 = the rate coefficient for the loss of autotroph biomass, where the biomass goes to a detrital compartment but stays in the system (i.e. the nutrient molecules can be recirculated back to living biomass);

e_1 = the rate coefficient for the loss of autotroph biomass, where the biomass is completely removed from the system, by harvesting or washout, for example, so that the nutrient molecules are lost forever from the system.

Input of biomass through autotroph immigration (transport of phytoplankton in water flow into the system, for example) has also been omitted for simplicity, though the term e_1 can be thought of as including, among other types of flux, the net difference between emigration and immigration.

The biomass of the detritus component will be represented by D(t). It will be assumed that the same mean ratio of nutrient weight to biomass weight, γ, exists in detritus as in autotroph biomass. The consequences of this assumption will be examined in Chapter 7. The dynamics of the detrital biomass can then be described by

$$dD/dt = d_1 X - (d_D + e_D)D \tag{3.3}$$

where

d_D = rate coefficient for decomposition of detritus, releasing nutrients into the available pool;

e_D = loss of detritus from the system, due to burial or transport from the system.

The possible complications that may arise from explicit inclusion of a community of decomposers (e.g. bacteria and fungi), such as immobilization of available nutrients, are put off until Chapter 7. In Chapter 2, the equations of solute dynamics [e.g. Equation (2.2)] described the solute in terms of concentration C (say, g solute l^{-1} water). This is an inconvenient variable for present purposes, as we would like to have a more flexible measure of nutrients that is more compatible with biomass X, which may have a variety of units (either a density such as g m^{-2}, g m^{-3}, kg ha^{-1}, or amount or standing stock such as g or kg, in a given system depending on the situation). Therefore, the variable N(t), or N for short, will be used from now on and will have units compatible with whatever units X has. The variable N is related to C through

$$C = L_C N \tag{3.4}$$

where L_C is a factor that can convert N from whatever its units are to g solute l^{-1} water. N represents the 'pool' of limiting nutrient in whatever unit of volume or area is chosen for the model system. If we assume homogeneity within these effective volumes, N should be able to play the same role as concentration, aside from a constant factor.

A conservation equation for N can easily be derived. In the absence of biotic uptake and release, N is described by

$$dN/dt = I_n - r_n N \tag{3.5}$$

where

I_n = rate of input of nutrient; for example, in g s^{-1}.

r_n = rate coefficient of output of nutrient in s^{-1}.

Note that I_n refers to input via the geochemical cycle; that is the input of new nutrient. Equation (3.5) is precisely analogous to Equation (2.2), except that in Equation 2.2, C describes grams of the nutrient per unit volume of water, while in the present case N means grams in the system of interest.

When biotic uptake by the autotroph and release by the detritus are included, the equation for N takes the form,

$$dN/dt = I_n - r_n N - \gamma r(N)X + \gamma d_D D \tag{3.6}$$

Figure 3.2 illustrates the arrangement of compartments. Recall that γ is the ratio of nutrient to biomass (e.g. g g^{-1}).

The remaining question in specifying a complete model is how to describe the effect of available nutrient on the growth rate, $r(N)$. One possibility is simply to let $r(N) = r_1 N$, where r_1 is a constant. This assumes there is no limit on the rate of biomass production, as long as nutrient is available in sufficient supply. This is an unrealistic assumption since the genetic and environmental limits on growth will ultimately prevent further increases in $r(N)$. A description frequently used is an analogue of the Monod function, which was used initially to describe bacterial growth, and which is itself based on the Michaelis–Menten function for enzyme kinetics. In the present

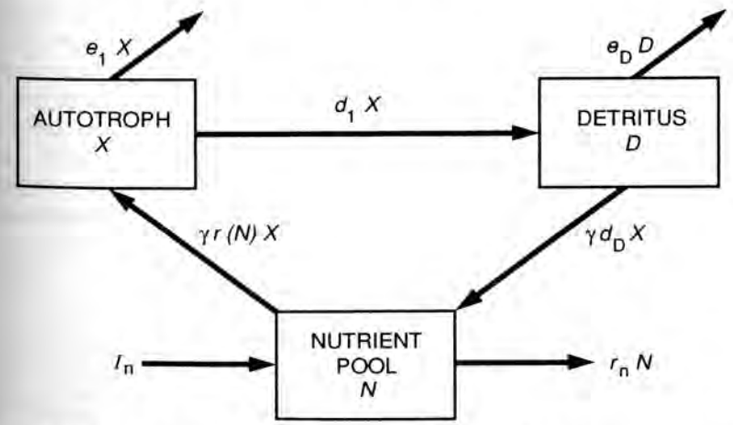

Figure 3.2 Schematic diagram of nutrient and biomass fluxes in a system with a nutrient pool, autotroph and detritus, as described by Equations (3.8a,b,c).

application, this function can be written as

$$r(N) = r_1 N/(k_1 + N) \tag{3.7}$$

The use of this function to describe the growth of phytoplankton was pioneered in the 1960s by, among others, Dugdale (1967), Caperon (1965), Eppley and Thomas (1969) and Golterman *et al.* (1969). This function should not be thought of as a 'law' in any sense, but as an empirical relation that often provides a good fit to data. The parameters can be described as follows:

r_1 = maximum rate of biomass growth (units of $g\,s^{-1}$)
k_1 = half-saturation concentration; that is, the concentration of nutrient at which the rate of biomass production is one-half the maximum rate of production (units of g).

The complete set of equations describing the system is thus

$$dN/dt = I_n - r_n N - [\gamma r_1 NX/(k_1 + N)] + \gamma d_D \tag{3.8a}$$

$$dX/dt = r_1 NX/(k_1 + N) - (d_1 + e_1)X \tag{3.8b}$$

$$dD/dt = d_1 X - (d_D + e_D)D \tag{3.8c}$$

These equations will form the basis for a study of the behaviour of the steady-state values, the local stability, the resilience, the ratio of new production to production based on regenerated nutrients and other properties of the system.

3.4 STEADY-STATE CONDITIONS

The steady-state solutions of Equations (3.8a,b,c) are of particular interest, because they will allow us to predict values of autotroph biomass from nutrient input values, a prediction of importance in the management of real systems, whether one wants to estimate the beneficial effects of fertilization on forest production, the harmful effects of nutrient loading in causing eutrophication of bodies of water or any number of related problems. The determination of the steady-state values is found easily by setting $dN/dt = dX/dt = dD/dt = 0$ and solving the right-hand sides for the steady-state values N^*, X^* and D^*. The results are

$$N^* = k_1(e_1 + d_1)/(r_1 - d_1 - e_1) \tag{3.9a}$$

$$X^* = (I_n - r_n N^*)(d_D + e_D)/[\gamma(d_1 e_D + d_D e_1 + e_1 e_D)]$$
$$= (I_n - r_n N^*)/(\gamma e_1) \qquad (\text{if } e_D = 0) \tag{3.9b}$$

$$D^* = d_1 X^*/(d_D + e_D) \tag{3.9c}$$

Two important features of the steady-state values are that N^* is a constant with respect to changes in I_n, whereas X^* increases linearly with

increasing I_n. This is exhibited in Figure 3.3 for values shown in Table 3.3. A better understanding of the steady state can be achieved by the detailed study of an abbreviated set of equations, leaving out the detritus (which is merely a passive, linear component in this model, anyway) and shunting

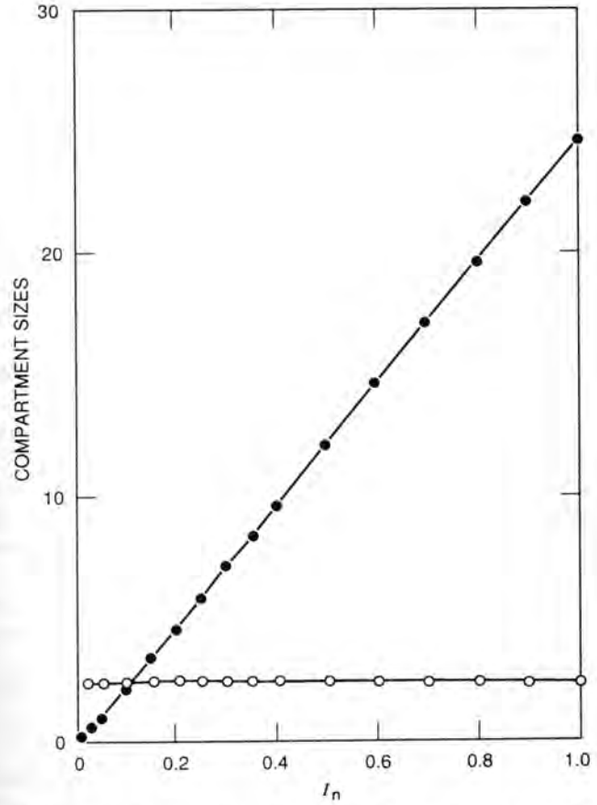

Figure 3.3 Plots of the steady-state pool of nutrients, N^*, multiplied here by 10^3 (open circles) and autotroph biomass (closed circles) as functions of nutrient input, I_n (multiplied here by 10^3). Based on parameter values in Table 3.3.

Table 3.3 Parameter values used in Equation 3.9 for producing the simulation results shown in Figure 3.3. These are hypothetical values and do not relate to any particular system

$I_n = 0.00005$ to 0.001	$d_1 = 0.1$	$e_1 = 0.001$
$r_1 = 0.3$	$d_D = 0.1$	$e_D = 0.001$
$r_n = 0.005$	$\gamma = 0.02$	$k_1 = 0.005$

autotroph losses directly to nutrient regeneration. This is completely equivalent to assuming that the detritus decomposes instantaneously. The condensed model is

$$dN/dt = I_n - r_n N - r_1 NX/(k_1 + N) + d_1 X \tag{3.10a}$$

$$dX/dt = r_1 NX/(k_1 + N) - (d_1 + e_1)X \tag{3.10b}$$

The characteristics of this system can be explored by plotting the zero isoclines, obtained by setting $dN/dt = 0$ and $dX/dt = 0$. These are, respectively

$$X = (I_n - r_n N)(k_1 + N)/[(r_1 N - d_1 N) - k_1 d_1] \tag{3.11a}$$

$$N = k_1(e_1 + d_1)/(r_1 - e_1 - d_1) \tag{3.11b}$$

These isoclines are plotted in Figure 3.4.

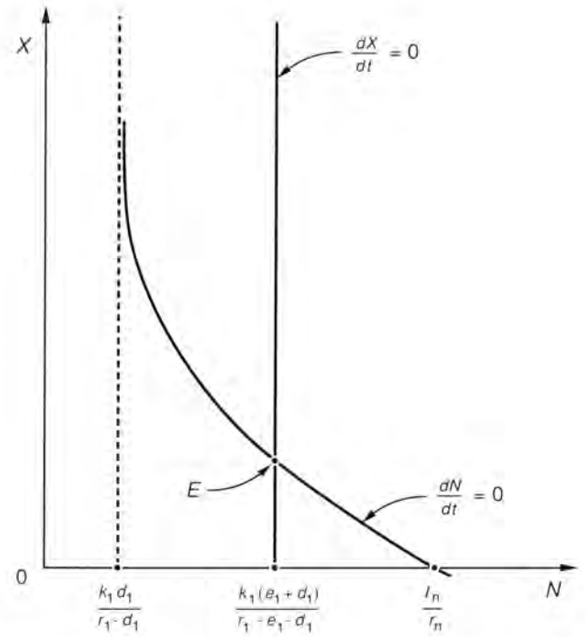

Figure 3.4 Plots of the zero isoclines, $dN/dt = 0$ and $dX/dt = 0$ of the pair of Equations (3.10a,b). The point of intersection of the two isoclines, E, is the equilibrium point of this system (N^*, X^*). The point $N = I_n/r_n$ is the nutrient level in the system described by Equations (3.8a–c) when autotrophs are absent and the point $N = k_1 d_1/(r_1 - d_1)$ is the nutrient level when autotrophs are present and the limit of complete nutrient recycling is approached.

Two properties of the set of equations (3.10a,b) are made clear by Figure 3.4:

1. The possible range of steady-state values of available nutrient, N^*, assuming that there is a non-zero autotroph biomass in the system, lies between $k_1 d_1/(r_1 - d_1)$ and I_n/r_n, as indicated along the N axis in Figure 3.4. When there is no autotroph present ($X^* = 0$), then $N^* = I_n/r_n$. When the autotroph is present, then $N^* = k_1(e_1 + d_1)/(r_1 - d_1 - e_1)$ and the smaller the loss rate e_1, the smaller N^* is.
2. The autotroph will go to extinction if either

$$r_1 < e_1 + d_1 \tag{3.12a}$$

or

$$k_1(e_1 + d_1)/(r_1 - e_1 - d_1) > I_n/r_n \tag{3.12b}$$

An explanation at an intuitive level is possible for both of these properties. The expression (3.12a) implies that no matter how large the available nutrient pool N is, the loss rate of the autotroph biomass may exceed its production, leading to extinction. This can be seen from the right-hand side of Equation (3.10b). Inequality (3.12b) is a more stringent condition on survival. This is equivalent to the fact that if production, $r_1 N/(k_1 + N)$, is less than losses, $(d_1 + e_1)$, even when N takes on its largest achievable steady-state value in the present system, which is I_n/r_n, the autotroph must necessarily go to extinction; that is, autotrophic production must exceed losses when the available nutrient is at its highest reachable steady-state value.

Property 1 can also be interpreted. First, it is impossible for N^* to exceed I_n/r_n because, from Equation (3.10b), $d_1 X^*$ must be less than or equal to $r_1 N^* X^*/(k_1 + N^*)$, so that, from Equation (3.10a), N^* must always be less than or equal to I_n/r_n. The behaviour near the lower limit of possible values of N^*, $k_1 d_1/(r_1 - d_1)$, is more curious. At first it seems strange that decreases in the loss rate of autotroph biomass from the system, e_1, should cause decreases in N^* and, simultaneously, cause X^* to increase towards infinity. To understand this, we should first recall that N^* is entirely controlled by the coefficients of the autotroph: k_1, e_1, d_1 and r_1. The input I_n has no effect on N^*. However, I_n controls the rate of increase of nutrients in the whole system, as can be seen by adding Equations (3.10a) and (3.10b) together after multiplying the latter by γ:

$$d(N + \gamma X)/dt = I_n - r_n N - \gamma e_1 X \tag{3.13a}$$

or, since N is held fixed at $N^* = k_1(d_1 + e_1)/(r_1 - e_1 - d_1)$

$$dX/dt = I_n - r_n N^* - \gamma e_1 X \tag{3.13b}$$

When $e_1 > 0$, X will approach an upper limit because the term $\gamma e_1 X$

increases until $dX/dt = 0$:

$$X^* = (I_n - r_n N^*)/(\gamma e_1) \qquad \text{(3.14, same as 3.9b)}$$

When $e_1 = 0$, however, the right-hand side cannot be made to equal zero for any values of $I_n > r_n N^*$, since N^* is fixed and the loss rate of nutrient, $r_n N^*$, cannot balance the input. The total amount of nutrient in the system, $N + \gamma X$, must continually increase when both $e_1 = 0$ and $I_n > r_n N^*$. All of this increasing nutrient goes into autotroph biomass, so that $X^* \to \infty$ as $t \to \infty$.

Are the types of behaviour exhibited by the model (Equations 3.8) typical of any systems in nature? The strong positive relationship between nutrient input, I_n, and autotroph biomass, X^*, appears to be qualitatively supported by data on algal biomass in lakes. Welch *et al.* (1975) plotted algal biomass against input of the limiting nutrient on a log–log scale, phosphorus (g loading per unit volume) for a set of lakes in the United States and Sweden (Figure 3.5). Actually, the biomasses plotted in this graph were normalized by being divided by phosphorus residence time in the lake. The rationale for this normalization is that it helps correct for the fact that in lakes with small residence times, notably smaller lakes with a large throughput of water, the limiting nutrient has less chance to be taken up through the autotroph and through the food chain.

It is interesting to compare this empirical behaviour with the expression for standing stock autotroph biomass, X^*, from the model. This expression,

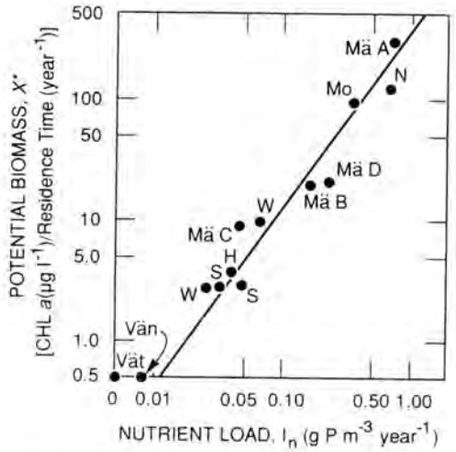

Figure 3.5 Relationship between loading of a limiting nutrient (phosphorus) per unit volume of lake water and biomass (expressed as CHL *a* or chlorophyll *a*, the most common type of chlorophyll, (normalized by nutrient residence time in the lake). (From Welch *et al.*, 1975.)

shown in Equation (3.9b), predicts that X^* will increase linearly with nutrient loading, I_n. Recall that the approximate nutrient residence time for nutrient in the lake is $T_{res} = 1/r_n$. It is 'approximate' because it is the residence time that would exist in the absence of autotrophic biomass in the lake. According to the expression (3.9b) for X^*, the smaller the residence time is, or the larger r_n is, the smaller X^* will be. This agrees entirely with the argument of Welch *et al.* (1975) that a smaller residence time of phosphorus, and thus a smaller potential probability of uptake by autotrophs, will lead to smaller standing stocks of biomass. By multiplying the expression (3.9b) for X^* by r_n, which is equivalent to dividing it by the phosphorus residence time, one could possibly neutralize some of the effects of the $-r_n N^*$ term and make X^* relatively independent of different lake residence times. It is clear from the expression that this normalization will not do this precisely, but the effect would certainly be in the same direction as the results plotted by Welch *et al.* Therefore, we can say tentatively that the model prediction of a linear increase of autotrophic biomass as a function of per unit volume input of limiting nutrient, corrected for variations in residence time of the nutrient atoms in the system, reflects data on lake ecosystems.

One final point regarding Figure 3.5 is worth noting. This is that the increase in autotroph biomass with increasing nutrient input depends on a shift in the phytoplankton community from species that are predominantly edible to species that are predominantly non-edible to zooplankton with increasing nutrient. Otherwise, much of the increase in autotroph productivity occurring with increases in nutrient input would go straight into increases in herbivore production and not be seen in increases in autotroph biomass.

3.5 PRODUCTION RESULTING FROM NEW AND RECYCLED NUTRIENTS

An important distinction can be made between the amount of autotrophic production that utilizes nutrient molecules that have just entered the system from outside and the amount of production that uses nutrient molecules that have already circulated internally through the autotroph and detrital biomass at least once. The ratio of these quantities would give a measure of the dependence of production in the system on the recycling of nutrients. This ratio is also interesting to know because it can have some relationship to other properties of the system, such as stability and resilience.

The rates of inflow to the available nutrient pool of new and recycled nutrient molecules, respectively, are I_n and $\gamma d_D D^*$ (Figure 3.2) where, from Equation (3.9b,c)

$$\gamma d_D D^* = d_1(d_D + e_D)(I_n - r_n N^*)/[(d_1 e_D + d_D e_1 + e_1 e_D)] \qquad (3.15)$$

As the rates of loss of biomass from the system, e_1 and e_D, decrease, $\gamma d_D D^*$ increases, and recycling plays a greater role in production.

Finn (1976, 1978, 1980) has developed formal expressions, which he called the cycling efficiency and the cycling index, to describe differences in the cycling of different nutrient atoms in different ecosystems. These indices can be discussed in terms of our analysis. To do this it is useful to generalize the fluxes in Figure 3.1 by representing them as F_{ij}'s (in $g\,s^{-1}$), where i is the donor and j is a receptor compartment (Figure 3.6). Steady state will be assumed here, although Finn's approach is general enough to apply to non-steady-state systems also.

Finn (1976) defined cycling efficiency, RE_k, of a compartment k as the fraction of throughflow through the compartment that is recycled. To apply this to the model in Figure 3.6, note first that the throughflows for the nutrient pool, autotroph and detrital compartments in steady state are, respectively, $F_{0N} + F_{DN}$ (or equivalently, $F_{N0} + F_{NX}$), F_{NX}, and F_{XD}. Then the cycling efficiency of the nutrient pool compartment, or the ratio of recycled throughput (that which has passed through compartment N in the past and is reentering it) to total throughput (all nutrient entering the N compartment), is

$$RE_N = F_{DN}/(F_{0N} + F_{DN})$$

and, likewise, the cycling efficiencies for the other compartments are,

$$RE_X = (F_{XD}/F_{NX})(F_{DN}/F_{XD})[F_{NX}/(F_{0N} + F_{DN})]$$
$$= F_{DN}/(F_{0N} + F_{DN})$$

$$RE_D = (F_{DN}/F_{XD})(F_{XD}/F_{NX})[F_{NX}/(F_{0N} + F_{DN})]$$
$$= F_{DN}/(F_{0N} + F_{DN})$$

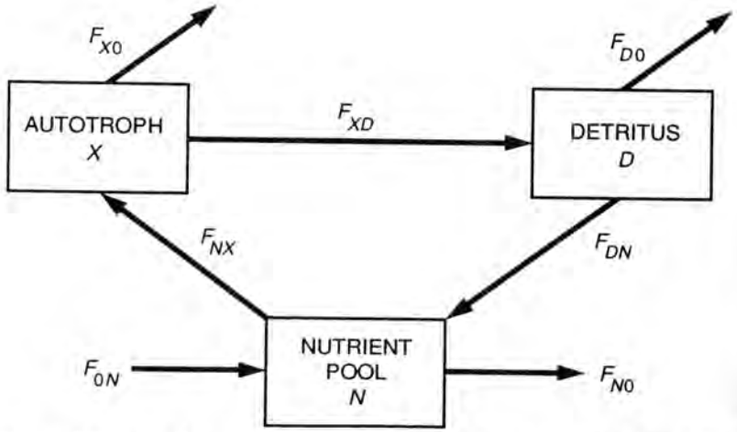

Figure 3.6 Schematic diagram of system with nutrient pool, autotroph and detritus compartments and general fluxes of nutrients between them.

To understand how RE_X and RE_D are derived, consider RE_X. The ratio F_{XD}/F_{NX} is the ratio of nutrient throughput of the autotroph that passes on to the detrital compartment, while F_{DN}/F_{XD} is the ratio of the nutrient throughput of the detrital compartment that passes to the nutrient pool, and $F_{NX}/(F_{0N} + F_{DN})$ is the ratio of the nutrient throughput of the nutrient pool that passes to the autotroph. The product of all three ratios, each of which is less than or equal to unity, is the fraction of nutrient molecules passing through the autotroph that returns to the autotroph. Similar logic holds for RE_D.

In this simple system, because all three compartments are in a single loop, the cycling efficiencies of all the compartments are identical. This has a further simplification regarding Finn's other index, the cycling index of the whole system, *CI*. Finn defines *CI* as

$$CI = TST_c/TST \tag{3.16}$$

where TST is the sum of all the throughputs of all the compartments in the system and TST_c is the sum of the cycling efficiencies of each compartment weighted by the throughput for that compartment. Thus, for the system in Figure 3.6

$$TST = F_{0N} + F_{DN} + F_{NX} + F_{DN}$$

Because the cycling efficiency for each compartment in Figure 3.6 is the same, TST_c is simply the sum of the same cycling efficiency, $F_{DN}/(F_{0N} + F_{DN})$, multiplied by each throughput;

$$TST_c = [F_{DN}/(F_{0N} + F_{DN})](F_{0N} + F_{DN} + F_{NX} + F_{DN}) \tag{3.17}$$

and, thus,

$$CI = F_{DN}/(F_{0N} + F_{DN}) \tag{3.18}$$

which, in this case, is the same as the cycling efficiency of each compartment.

The cycling index of nutrients in a system may be of less interest, for some purposes, than the mean length of time a nutrient molecule stays in the system; that is, the time between its first entry into the available nutrient pool N and its exit from the system through N, X or D. As described in Chapter 2, the mean residence time a nutrient molecule spends in a particular compartment per pass through that compartment is the standing stock of that compartment divided by the steady-state flux through the compartment. Analogously, for a multicompartment system, the mean residence time or turnover time of a nutrient molecule in the system in steady state is

$$T_{res} = N_T^*/I_n \tag{3.19}$$

where N_T^* is the total nutrient stored at any time in the steady-state system:

$$N_T^* = N^* + \gamma X^* + \gamma D^* \tag{3.20}$$

where N^*, X^* and D^* are given by Equations (3.9a,b,c).

It is interesting to look in the high recycling case to study how recycling affects the dynamics of the system. In the limit that I_n is very large and e_1 and e_D are very small, so that recycling is high (there is little loss of nutrient from the system due to biomass losses), the nutrient stored in biomass, $\gamma X^* + \gamma D^*$, far outweighs the available nutrient pool, N^*, so that N_T^* approaches

$$N_T^* = I_n[(d_D + e_D) + d_1]/(d_1 e_1 + d_D e_1 + e_1 e_D) \tag{3.21}$$

and

$$T_{res} = (d_1 + d_D + e_D)/(d_1 e_1 + d_D e_1 + e_1 e_D) \tag{3.22}$$

What this means is that T_{res} varies inversely with the loss rates e_1 and e_D and is independent of the nutrient input I_n and of the loss rate r_n from the nutrient pool. The reason for the independence from I_n is that an increase in I_n causes a proportional increase in N_T^*; thus turnover time will not change. The independence of T_{res} from r_n reflects the fact that the nutrient pool N^* is very small so that the nutrient loss rate $-r_n N^*$ is small and does not contribute to the residence time.

Later in this chapter, we show that T_{res} is closely related to the time it takes the system to return to equilibrium, T_R, following a perturbation. What is interesting is that T_{res} is independent of I_n, depending only on loss rates. For small values of I_n, it is easy to show that T_{res} can depend on I_n, although the precise form of this dependence is too complex to be predicted intuitively.

3.6 LOCAL STABILITY

The steady-state equilibrium point (N^*, X^*, D^*) was found above and some of its properties were explored. An additional feature of crucial importance is the local stability of this equilibrium point. As explained in Chapter 2, local stability refers to the tendency of system variables to return to the steady-state point following a very small perturbation.

It is possible to show that the set of Equations (3.8a,b,c) are locally stable. Unlike the model equations analysed in Chapters 1 and 2, Equations (3.8a,b,c) are non-linear and cannot be solved by the linear techniques used in Chapter 2. However, the equations can first be linearized about the steady-state equilibrium and the resultant linear equations can be solved and examined for stability.

To linearize Equations (3.8a,b,c), we introduce new variables, N', X' and D', which correspond to small deviations from equilibrium;

$$N' = N - N^* \quad \text{or} \quad N = N^* + N' \qquad (N' \ll N^*) \tag{3.22a}$$

$$X' = X - X^* \quad \text{or} \quad X = X^* + N' \qquad (X' \ll X^*) \tag{3.22b}$$

$$D' = D - D^* \quad \text{or} \quad D = D^* + D' \qquad (D' \ll D^*). \tag{3.22c}$$

When N, X and D are substituted for in terms of N', X' and D' in Equations (3.8a,b,c), the resultant equations are (see Appendix C)

$$dN'/dt = -r_n N' - \gamma r_1 k_1 X^* N'/(k_1 + N^*)^2 - \gamma r_1 N^* X'/(k_1 + N^*) + \gamma d_D D' \tag{3.23a}$$

$$dX'/dt = r_1 k_1 X^* N'/(k_1 + N^*)^2 \tag{3.23b}$$

$$dD'/dt = d_1 X' - (d_D + e_D)D' \tag{3.23c}$$

The equation for the eigenvalues of this set of equations is given by the determinant

$$\det \begin{vmatrix} -r_n - \dfrac{\gamma r_1 k_1 X^*}{(k_1 + N^*)^2} - \lambda & -\dfrac{\gamma r_1 N^*}{k_1 + N^*} & \gamma d_D \\ \dfrac{r_1 k_1 X^*}{(k_1 + N^*)^2} & -\lambda & 0 \\ 0 & d_1 & -(d_2 + e_2) - \lambda \end{vmatrix} = 0 \tag{3.24}$$

It can be shown (Appendix D) that this eigenvalue equation only has roots λ that have negative real parts, so that the system is always stable.

The local stability of pairs of autonomous equations such as Equations (3.10a,b) (autonomous meaning that none of the coefficients are time-dependent) can often be determined graphically by noting the slopes of the intersecting zero isoclines. This will be described in Chapter 5.

The fact that Equations (3.8a,b,c) are stable does not mean that the dynamic behaviour of this system is uninteresting. In fact, Equations (3.8a,b,c) can produce striking behaviour under typical natural conditions. O'Brien (1974) applied a model similar to this one to a single phytoplankton population starting at low numbers in a nutrient-rich medium, such as might occur in a pond or lake in spring.

O'Brien's (1974) model differs from Equations (3.8a,b,c) in several ways: (1) the detrital component is ignored; (2) nutrient feedback from organic matter to the nutrient pool is ignored; (3) the loss of nutrient from the lake by outflow, $r_n N$, is ignored; and (4) instead of autotroph biomass, cell number is chosen as the variable, so that r_1 (g_m in O'Brien's model) represents the rate of increase in cell numbers (assumed proportional to total biomass) rather than biomass growth directly. Thus, the parameters r_n, d_1, d_D and e_D are set to zero in Equations (3.8a,b,c). The remaining parameter values are, in current notation,

$r_1 = 0.5$ cell divisions d^{-1}

$d_1 = 0.15\,d^{-1}$

$k_1 = 10$

$I_n = 2\,\mu g\,l^{-1}\,d^{-1}$

$\gamma = 2.36 \times 10^{-7}\,\mu g$ cell^{-1}

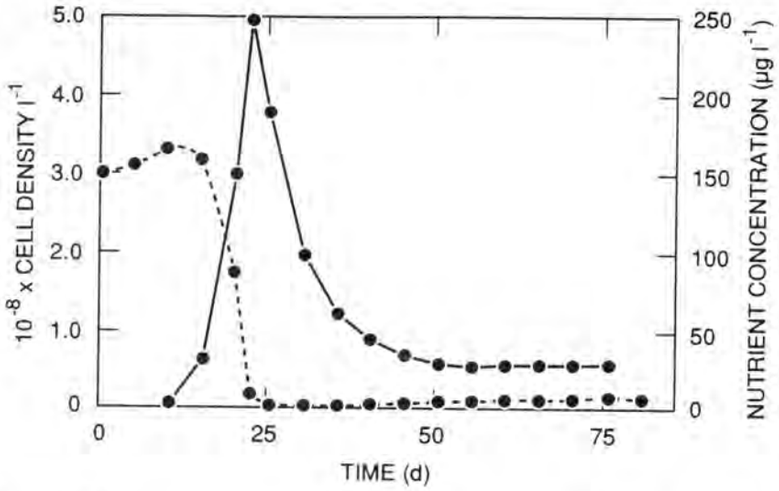

Figure 3.7 Cell number density as numbers l^{-1} (solid line) and nutrient concentration as $\mu g\ l^{-1}$ (dashed line) through time from simulations of Equations (3.8a,b) with parameters similar to those used in Figure 1 of O'Brien (1974).

Initial values of nutrient concentration $N = 150\,\mu g\ l^{-1}$ and $X = 500\,000$ cells were chosen. The results of the simulation over 100 days are shown in Figure 3.7. The phytoplankton population, starting from very low numbers, exploded in size within several weeks to over 5×10^8 cells per litre, causing a drastic decline in the available nutrients. This led to a crash of the phytoplankton population towards a steady-state equilibrium level, accompanied by a gradual rise in nutrient concentration towards steady state. As O'Brien (1974) pointed out, the model results indicate that phytoplankton crashes can easily be caused through nutrient limitation. The presence of zooplankton consumers is not a necessary factor.

The rate at which the system eventually settled to steady state is its resilience. Some generalizations concerning system resilience are discussed in the next section.

3.7 RESILIENCE

If a model system is shown to be locally stable, as is the case for Equations (3.8a,b,c), the question of next greatest significance is how resilient the system is, that is, how fast it returns to the steady state following a perturbation (or the inverse of the return time, T_R; see Chapter 2). Resilience has received attention from theoretical ecologists because of its possible role in the structure of ecological food webs.

Imagine a region of land receiving abundant rainfall and solar radiation

but only a very low rate of input of essential nutrients from the outside (in solution in precipitation or from rock weathering). Suppose that when the system reaches steady state, trees growing on this land have extremely efficient mechanism of recovery and retention of nutrients that are released in the soil through litter decomposition, so that only a tiny percentage of released nutrient is lost through leaching and runoff. This efficient recycling of nutrient enables a majestic forest of massive trees to grow, although it may take thousands of years to reach steady state because of the small input of nutrients. If this steady-state forest is perturbed by removal of, say, one-half of the biomass from the site, as long as the parameters of uptake and loss remain unaltered (which may not be the case in real situations), it will take thousands of years to replace the lost nutrients. In particular, the turnover time, $T_{res} = N_T^*/I_n$, where N_T^* is the total amount of nutrient stored in the biomass, litter and soil, while I_n is the input of the limiting nutrient, is a good estimate of the return time to steady state, as will be shown below.

If, under the same rate of nutrient input by precipitation and rock weathering, instead of a high steady-state rate of nutrient recovery and recycling, the forest system tends to lose nutrients rather rapidly and not to recycle them more than a few times on average, the steady-state forest biomass will be relatively small. Now the turnover time, $T_{res} = N_T^*/I_n$, will be proportionally lower than in the first case. If one-half of the biomass of the trees is removed, it should take a much shorter time for this amount of biomass to recover.

These two examples illustrate the concept of resilience, or the rate of recovery, as a function of the turnover time of a limiting nutrient. Resilience is often roughly the inverse of turnover time, or $1/T_{res}$.

Some results concerning the effect of nutrient limitation and recycling on food web resilience have already been derived from models (Jordan *et al.*, 1972; Dudzik *et al.*, 1975; DeAngelis, 1980; Harwell *et al.*, 1981). It was shown that the return time of the system tends to be negatively related to the rate of nutrient input, I_n, to the system per unit standing stock of system biomass (to which the standing stock of nutrients, N_T^*, is proportional). This is an intuitively reasonable conclusion since a faster rate of nutrient input per unit biomass should decrease the nutrient turnover time and thus increase the rate at which a system can recover from a loss of biomass.

To examine the resilience of the system in Figure 3.2, Equations (3.8a,b,c) were solved numerically on a computer. The set of parameters shown in Table 3.3 was used for all of the simulations and analyses performed on the model equations. These parameters are hypothetical and no units are assumed. However, the values, viewed as a whole, form a plausible set for describing typical dynamic behaviour of a nutrient-limited system. We describe here the observed resilience characteristics of the perturbed system as a function of I_n.

The return time T_R of the system after a removal of 10% of each compartment from the steady state was computed for a series of values of

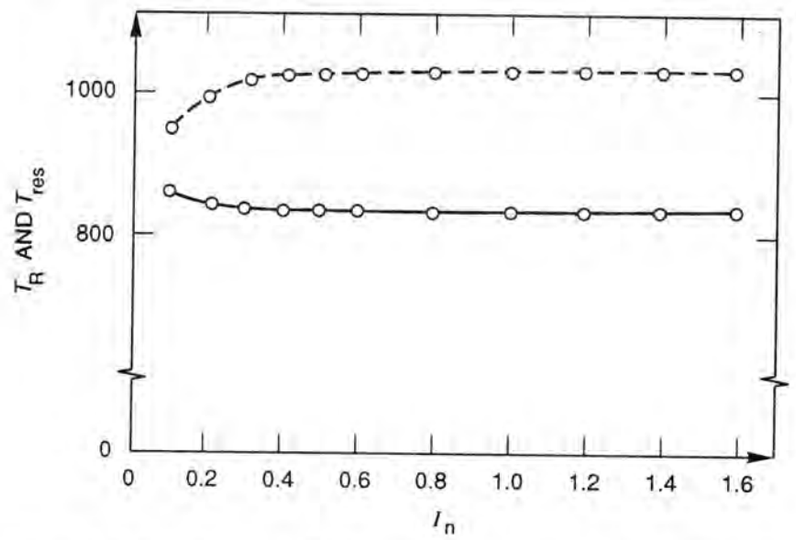

Figure 3.8 Return time, T_R (solid line) and nutrient turnover or residence time, $T_{res} = N_T^*/I_n$ (dashed line) for system described by Equations (3.8a,b,c), as a function of nutrient input, I_n ($\times 10^3$). Parameter values are specified in Table 3.3.

I_n by solving Equations (3.8) numerically and then using expression (2.8). The return time as a function of I_n is shown in Figure 3.8 (solid line). The value of T_R is observed to remain at a relatively constant level for all values of I_n that are large enough for the autotroph to persist.

To attempt to interpret the behaviour of T_R as a function of I_n, let us see if the generalization $T_R \cong T_{res} = N_T^*/I_n$, discussed earlier (Equation 3.19) has any explanatory power here. In this case, $N_T^* = N^* + \gamma X^* + \gamma D^*$, where N^*, X^* and D^* are the steady-state values. We have already solved for these values [see Equations (3.9)]. Note that the available nutrient is held at a fixed level by the autotroph, so that it does not increase as I_n increases (Figure 3.3). On the other hand, X^* and D^* are increasing functions of I_n.

When N_T^*/I_n is plotted as a function of I_n, this ratio is roughly constant as a function of I_n for all values of I_n (dashed line in Figure 3.8). For large values of I_n, the closeness of the return time predicted by N_T^*/I_n (dashed line) to T_R calculated from Equation (2.8) is remarkable, since, in a non-linear system, N_T^*/I_n is expected to provide only a rough estimate of T_R.

The resilience of forest ecosystem with respect to nutrient loss must be considered in commercial harvesting of trees. For example, whole-tree harvesting of southern New England hardwoods may remove 530 kg ha^{-1} of calcium directly, plus additional runoff losses of about 28 kg ha^{-1} (Tritton *et al.*, 1987). Only 2 kg ha^{-1} year^{-1} of calcium are added by

precipitation. A much larger amount is probably added by weathering of soils and bedrock, but since this is not known accurately, it cannot be excluded that the recovery time of the forest following whole-tree harvesting will be slow.

3.8 FURTHER CONSIDERATIONS

The Monod-type function used for $r(N)$ in the above model [Equation (3.7)] has the virtue of simplicity, but that does not mean that it provides the only possible description of uptake. Alternative models of uptake have been examined and found useful.

One obvious alternative follows from noting that growth of the autotroph may be impossible to sustain unless the level of limiting nutrient exceeds some critical level N_c. In this case, $r(N)$ has a negative value until N exceeds N_c. The function

$$r(N) = r_1(N - N_c)/[k_1 + (N - N_c)] \tag{3.25}$$

can be used to represent this situation. When this function is used in Equations (3.10), which are a truncated form of Equations (3.8) in which the detritus compartment is ignored, the zero isoclines that are equivalent to Equations (3.11a,b) are

$$N = N_c + k_1(e_1 + d_1)/(r_1 - e_1 - d_1) \tag{3.26a}$$

$$X = (I_n - r_n N)[k_1 + (N - N_c)]/[r_1(N - N_c) - d_1] \tag{3.26b}$$

While these zero isoclines differ quantitatively from Equations (3.11a,b), the basic shape of the curves is the same (Figure 3.4) and the properties of stability and resilience are similar to those discussed for Equations (3.10a,b).

3.9 SUMMARY AND CONCLUSIONS

The introduction of an autotrophic component complicates the dynamics of material elements that are nutrients for the autotroph. Because autotroph biomass actively accumulates the nutrients from the available pool and grows in size, the equations describing the system are non-linear. Nutrient limitation of autotrophic growth is common in natural systems, with nitrogen or phosphorus commonly being the limiting bioelement. Many types of adaptations have evolved in autotrophs to alleviate this limitation on growth due to the scarcity of one or more nutrients, including symbiotic associations with mycorrhizal fungi. The effect of most of these adaptations is to increase the proportion of biomass production in the autotroph that utilizes recycled nutrients, either through cycling within the autotroph itself or in biogeochemical cycles between the soil and aboveground and below-ground living matter.

A model of the dynamics of a nutrient–autotroph–detritus system was

constructed in which nutrient-limited autotroph growth was described by a Monod growth function and which included recycling of nutrients from detritus back to the nutrient pool. The model was analysed for steady-state solutions, local stability and resilience. One of the important properties of the steady-state solution was that the available nutrient level stays constant as a function of nutrient loading, but the autotroph biomass increases linearly. This prediction with regard to autotroph biomass seems to be corroborated qualitatively by data from a number of lakes.