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# RESOURCE COMPETITION

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James P. Grover  
*University of Texas at Arlington*



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# 1 Introduction

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Resources are entities which contribute positively to population growth, and are consumed in the process. They may be classified as biotic or abiotic: the former are capable of reproduction, but the latter are not. Supply processes for biotic resources are potentially complex, but in many cases, the dynamics of abiotic resources are adequately described by simple expressions of mass conservation. Such mass-balance properties characterize systems for which all resource transformations are budgeted.

At equilibrium, a population's loss rate determines its resource demand, and in many simple models of abiotic resources, the equilibrium is stable. Biotic consumer-resource interactions may have unstable equilibria or multiple equilibria. When an equilibrium is stable and unique, resource availability goes to a long-term value  $R^*$ , which can be calculated from the population's resource-dependent growth function and its loss rate. This number is a synthetic parameter summarizing much biology in an informative way.

Competition refers to mutually negative interactions among two or more individuals or populations. At the population level, such mutually negative interactions cause reductions in growth rates. This phenomenon can arise from consumption of the same resources, whence the term resource competition. The well-known Lotka–Volterra equations of competition describe the population phenomenon of competition, but attempts to relate their parameters to mechanisms of resource utilization have not been wholly successful. An alternative approach, taken in this book, is to build towards an understanding of the phenomenon of competition from an elementary knowledge of resource consumption and resource-dependent population growth.

## 1.1 RESOURCES

Living beings inherit a meagre stock of materials and energy from their parents, and begin their existence armed mostly with a plan. According to their genome's instructions, they grow in size through the accumulation of more materials and energy. They reproduce if they survive long enough, acquire enough materials

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and energy and a mate, if necessary. This acquisition of materials and energy over a lifetime follows conservation laws: what one individual obtains is not immediately available to another. These fundamental processes of life and the universal conservation laws give rise to subject of this book – resource competition – which concerns some of the ecological implications of the consumption of materials and energy, arising at the population and community levels.

Loosely speaking, competition may be defined as mutually negative effects between individuals or populations. At the individual level, fitness is reduced on the part of every individual engaged in the competition; at the population level, the net rate of change is reduced on the part of every population so engaged. Resource competition, then, refers to situations where these negative effects arise through consumption of resources – materials and energy – required for growth, survival and reproduction. Neither this loose definition of competition as mutually negative effects, nor that of resources as the materials and energy required for life, is wholly satisfactory.

The definition of competition is discussed below. First, we address defining resources, in the context of population dynamics. Ecologists have defined resources in various ways (Tilman, 1982; Price, 1984; Wiens, 1984; Abrams, 1988a). All reasonable definitions include the notion that the per capita rate of population growth is an increasing function,  $\mu$ , of resource availability,  $R$ , at least through some range of variation in  $R$  (Figs 1.1–1.4). Thus, formal modeling of consumer-resource dynamics with differential equations begins with the step:

$$\frac{dN}{Ndt} = \mu(R) + \text{other terms}, \quad (1.1)$$

where  $N$  is the density of the population in question (see Table 1.1 for mathematical notation). The ‘other terms’ include all losses affecting the population, and other processes, including immigration and emigration. For much of this book, immigration into and emigration from the local habitat in which equation (1.1) applies will be assumed negligible (this assumption will be relaxed in Chapter 7). Thus our population increases only by growth within a given habitat, in relation to local resource availability. Interference among the members of a population is neglected, so that competition between members of a population occurs only through depletion of the resource, mediated by the growth function,  $\mu(R)$ .

A commonly used growth function is that of Monod (1950), originally proposed for growth of bacteria on organic substrates:

$$\mu(R) = \frac{\mu_{\max} R}{K_\mu + R}, \quad (1.2)$$

where  $\mu_{\max}$  is the maximal per capita rate ( $\text{time}^{-1}$ ) at which the population can grow, and  $K_\mu$  is the substrate concentration ( $\text{mass volume}^{-1}$ ) at which half this maximal growth rate is reached (Fig. 1.5). Two features of equation (1.2) are biologically reasonable for many populations. First, even if resource availability became infinite, population growth rate would plateau at a finite rate, and second, a principle of diminishing returns (saturation) applies at every resource

Table 1.1 Mathematical notation for Chapter 1

Symbol	Meaning
$N$	Population density (numbers or biomass per unit area or volume)
$R$	Resource availability, e.g. concentration of a nutrient (mass volume $^{-1}$ )
$\mu(R)$	Resource-dependent population growth rate, per capita (time $^{-1}$ )
$\mu_{\max}$	Maximal per capita growth rate in Monod function (time $^{-1}$ )
$K_\mu$	Resource availability at which population growth is 1/2 of $\mu_{\max}$ (mass volume $^{-1}$ , for example)
$Q$	Resource quota, units of resource contained in one unit of population
$Y$	Yield, units of population produced from consumption of one unit of resource (reciprocal of quota)
$S$	Resource supply, the maximum possible resource availability in a habitat (mass volume $^{-1}$ , for example)
$m$	Per capita mortality rate (time $^{-1}$ )
$r_i$	Intrinsic rate of natural increase of species $i$ , its maximum per capita growth rate in the Lotka–Volterra equations (1.9) (time $^{-1}$ )
$K_i$	Carrying capacity of species $i$ , in the Lotka–Volterra equations (1.9) (units of population density)
$\alpha_{ij}$	Effect of species $j$ on the population growth rate of species $i$ due to competition, in the Lotka–Volterra equations (1.9) (dimensionless)

availability. Successive increases in resource availability cause less than proportional increases in the rate of population growth. Mathematically, these properties of the growth function are specified by assuming that for all  $R$ ,  $\mu(R)$  is bounded,  $d\mu/dR > 0$ , and  $d^2\mu/dR^2 < 0$ . Many other possible mathematical definitions of  $\mu(R)$  share these properties, but few are as algebraically convenient as equation (1.2), so it is widely used, although other functions may better describe the population growth of some organisms.

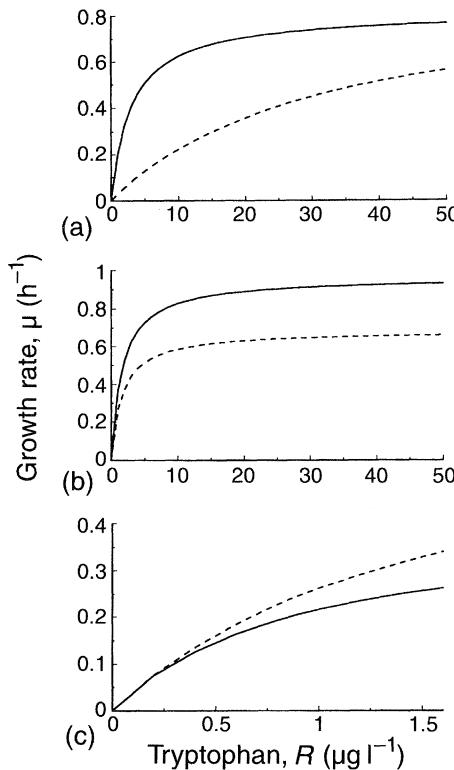
So far we have defined resources in terms of what they do to populations. We must also recognize that populations consume resources, i.e. availability decreases as a population grows. Using differential equations, consumption is expressed formally as

$$\frac{dR}{dt} = -\mu(R)QN + \text{other terms}, \quad (1.3)$$

where  $Q$  is the **quota**, which tells how many units of resource are contained in a unit of population, and which need not be a constant. The consumption term in this expression,  $\mu(R)QN$ , can alternatively be written  $\mu(R)N/Y$ , where  $Y$  is the **yield coefficient**, which again, need not be a constant. Quota and yield are reciprocals,  $Q = 1/Y$ , so that yield tells how many units of a population are produced from the consumption of one unit of resource. Writing a model in terms of quota or yield is a matter of taste and tradition.

For the purposes of this book, resources are entities which stimulate population growth, at least over some range of availability, and which are consumed.

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*Figure 1.1* Growth rates ( $\mu$ ) of several bacterial strains as a function of tryptophan concentration ( $R$ ), drawn from data of Hansen and Hubbell (1980): (a) *Escherichia coli*, strain C-8 (dashed line); *Pseudomonas aeruginosa*, strain PAO 283 (solid line). (b) Strain C-8 nal<sup>1</sup> spec<sup>8</sup> (dashed line); strain C-8 nal<sup>1</sup> spec<sup>1</sup> (solid line); grown in the absence of nalidixic acid. (c) The latter two strains grown in the presence of  $0.5 \mu\text{g l}^{-1}$  nalidixic acid.

That is, if we can model the interaction of a population  $N$  with an entity  $R$ , using eqs (1.1) and (1.3), or their finite difference analogs, then  $R$  is a resource. This is a very broad definition, allowing many kinds of interactions and dynamics. Resources clearly include various forms of materials and energy, and could also include space, shelter, and other things. To make progress, the general definition of ‘resource’ must be subdivided into categories that share important features. There are many ways to do this (e.g. Tilman, 1982; Price, 1984), but rather than present a catalogue, we shall introduce important distinctions as they are needed.

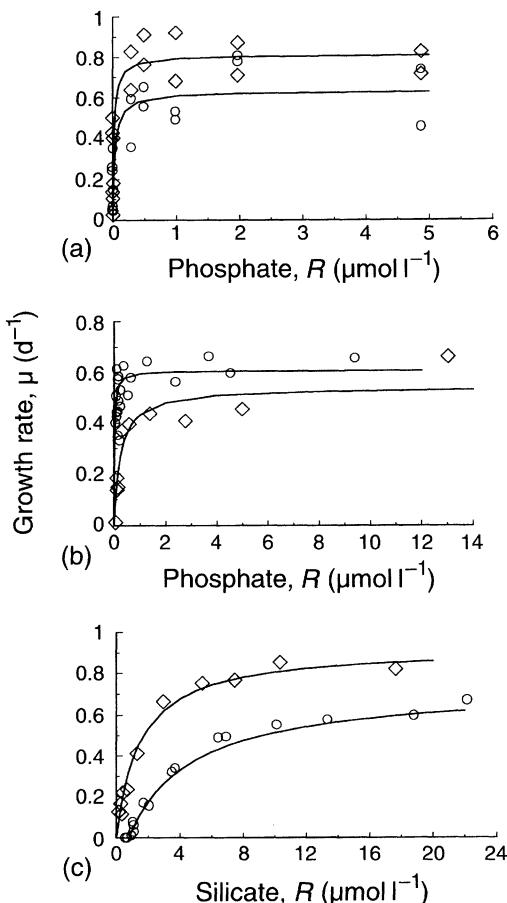


Figure 1.2 Growth rates ( $\mu$ ) of several freshwater algae as a function of inorganic nutrient concentration ( $R$ ): (a) *Chlorella* sp. (diamonds); *Scenedesmus quadricauda* (circles). Reproduced with permission from Grover (1989c). (b), (c) *Cyclotella meneghiniana* (diamonds); *Asterionella formosa* (circles). Reproduced from Tilman and Kilham (1976), with permission.

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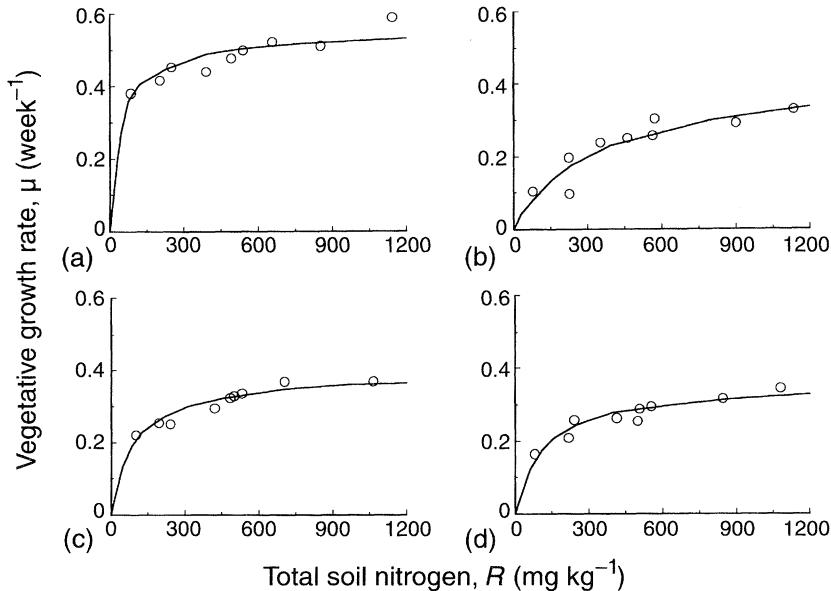


Figure 1.3 Growth rates ( $\mu$ ) of plant biomass for several grasses as a function of soil nitrogen ( $R$ ): (a) *Agrostis scabra* (b) *Agropyron repens* (c) *Schizachyrium scoparium* (d) *Andropogon gerardi*. Reproduced with permission from Tilman and Wedin (1991a).

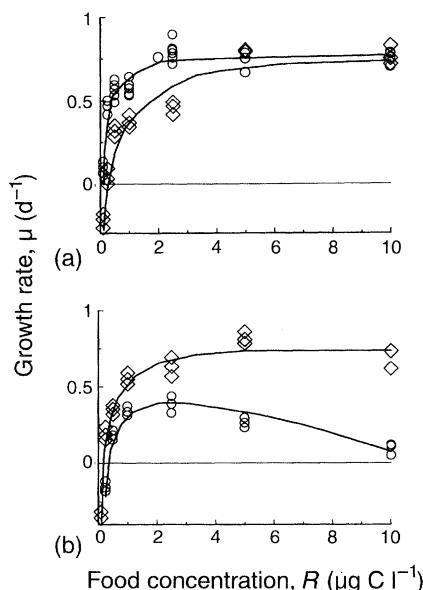


Figure 1.4 Growth rates ( $\mu$ ) of two freshwater rotifer species as a function of food (algal) concentration ( $R$ ): *Brachionus rubens* (diamonds); *Brachionus calyciflorus* (circles). (a) *Chlamydomonas sphaeroides* supplied as food. (b) *Monoraphidium minutum* supplied as food. Reprinted from Rothhaupt (1988), with permission.

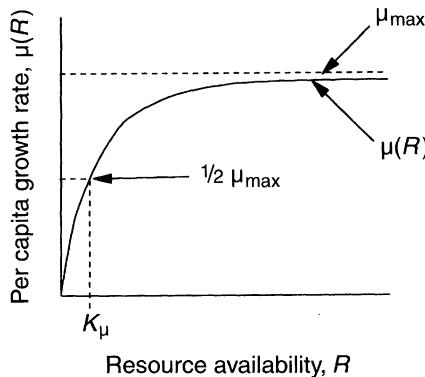


Figure 1.5 The Monod growth function (equation 1.2).

## 1.2 A PARADIGM OF POPULATION GROWTH

### 1.2.1 Abiotic resources

One important distinction is between abiotic and biotic resources. Intuitively, **abiotic resources** are those which are not living things: entities such as mineral nutrients and organic substrates are examples. **Biotic resources** are living things – organisms or parts of organisms. Whether or not something is alive means, basically, whether it can reproduce. Abiotic resources cannot, and so must be supplied by processes other than their own reproduction. This greatly simplifies mathematical models, and facilitates experimental manipulation. Armstrong and McGehee (1980) offered a definition of abiotic and biotic resources formalizing this intuitive distinction between non-living and living. Here is their verbal definition:

At any given time a parcel of abiotic resource exists either in a ‘free’ state or in a ‘bound’ state. In the free state it is available for use by any individual, while in the bound state it is in use by some individual. ... A parcel of abiotic resource is regenerated from the bound state to the free state through the death of the individual by which it was bound.

This verbal definition has a technical, mathematical version. The dynamics of an abiotic resource need not be written in the form of a differential equation like equation (1.3). For an abiotic resource, the amount of available resource at any time is given by an algebraic equation of the form:

$$R = S - F(N). \quad (1.4)$$

Here,  $S$  is the **resource supply**, and constitutes an upper bound on the amount of available resource that can ever exist in a habitat, and  $F$  is an increasing function of  $N$ . Whenever  $N$  increases by population growth, available resource

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decreases, i.e. it is consumed; and whenever  $N$  decreases by mortality, available resource increases, in keeping with the verbal definition cited above. In many applications where the resource in question is a mineral nutrient, equation (1.4) is simply a mass conservation law.

Those resources whose dynamics do require a differential (or difference) equation to represent reproductive dynamics, are defined as biotic by Armstrong and McGehee (1980). Abiotic and biotic resources in mathematical models can usually be clearly distinguished by these criteria. In the real world, the distinction between resources which reproduce and those which do not is sometimes less clear. In many cases, however, the distinction comes easily enough to justify it as a first approximation.

Much of the theory used to study resource competition, and many of the key experimental results, concern abiotic resources. Working with biotic resources is usually more difficult. In theoretical studies, reproduction by the resource population(s) produces a range of possible dynamics that do not complicate the study of abiotic resources. For example, coupled consumer-resource models based on eqs. (1.1) and (1.3), and representing an abiotic resource, cannot give rise to limit cycles in the absence of time lags or environmental heterogeneity, but similar models with a biotic resource often do. Such models can also have multiple equilibria. Experimentally, the supply and dynamics of an abiotic substance is relatively easy to control and manipulate, compared to the difficulties of manipulating a resource population, in addition to the consumer population.

### 1.2.2 Resource-dependent growth in a closed system

Having made the distinction between abiotic and biotic resources, we can now specify the ‘other terms’ in eqs (1.1) and (1.3), for an idealized ‘closed’ system. Of course, all systems in biology are open in a thermodynamic sense – life cannot be maintained without an input of free energy. In the study of resource dynamics, a closed system is one with no material exchange across the boundary defining the habitat in question. Few real biological systems are closed in this sense. Closed systems are of interest mainly as a tractable limiting case, whose properties fortunately generalize to at least some kinds of open systems (Chapter 2 and Appendix B). Closed systems are emphasized here to avoid unnecessary clutter at an early stage. When we come to grips with more sophisticated analyses, the details of open systems can be crucially important (especially when spatial heterogeneity is considered, see Chapter 7).

The following equation system is derived in Appendix A, based on the assumption that the per capita mortality rate,  $m$ , is constant and independent of population density:

$$\frac{dN}{dt} = \mu(R)N - mN \quad (1.5a)$$

$$R = S - NQ. \quad (1.5b)$$

Here, equation (1.1) is refined to equation (1.5a), and equation (1.3) to equation (1.5b).

### 1.2.3 A paradigm of resource-dependent population growth

This system (equation 1.5) is a basic paradigm for growth of a single population, through which equations of resource competition theory are reached by extension to accommodate additional populations. Therefore, it is important to understand the patterns of population dynamics predicted by equation system (1.5). By setting the right-hand-side of equation (1.5a) to zero, a ‘trivial’ equilibrium is found at  $(R, N) = (S, 0)$ , with no organisms present. A second equilibrium, with a positive population density, is also possible if there is a value  $R^*$  for which  $\mu(R^*) = m$  (in this book, an equilibrium quantity will always be denoted with a \* superscript). In most biologically realistic cases,  $\mu(R)$  has a finite upper bound, so that this second equilibrium exists only if

$$m < \max_R [\mu(R)]. \quad (1.6)$$

This says that a population has an equilibrium density, where growth balances losses, only if its loss rate is less than the maximal rate at which it can grow. Graphically, we find the equilibrium resource availability,  $R^*$ , by superimposing a horizontal line representing the loss rate ( $m$ ) on a plot of the growth curve  $\mu(R)$  (Fig. 1.6). The intersection of the line and the curve occurs at a value  $R = R^*$ . The solution of equation system (1.5) for its nontrivial equilibrium is

$$R^* = \mu^{-1}(m) \quad (1.7a)$$

$$N^* = (S - R^*)/Q, \quad (1.7b)$$

where the ‘ $-1$ ’ superscript on  $\mu$  means ‘inverse function’.

To determine whether these equilibria are stable to small perturbations, the

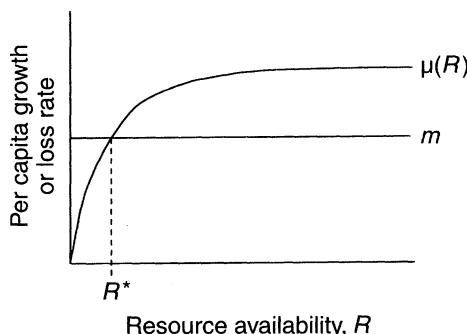


Figure 1.6 Graphical representation of the equilibrium of a simple consumer-resource system. The equilibrium resource availability ( $R^*$ ) occurs where the growth function ( $\mu(R)$ ) intersects the line ( $m$ ) representing the loss rate.

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mathematical machinery of linearized stability analysis could be used (see May, 1974; Nisbet and Gurney, 1982). In this simple case, however, the machinery is overkill. Starting with the trivial equilibrium, suppose it is perturbed by the addition of a small population of organisms, so that  $N$  is now positive, but close to zero. The per capita rate of change of this small population is now  $\mu(S) - m$ , which is positive. If  $S > R^*$ , the small population grows away from the equilibrium value of zero, and the trivial equilibrium is unstable. The condition  $S > R^*$  simply means that for a population to increase when rare, resource supply must exceed the resource availability that the population requires to balance its losses. Alternatively, if  $S < R^*$ , then  $\mu(S) < m$ , the small population cannot grow, and the trivial equilibrium is stable.

If  $S < R^*$ , then equation (1.7b) has no positive solution for a nontrivial equilibrium population,  $N^*$ ; the logically possible negative solution is biologically meaningless, and the nontrivial equilibrium is ‘infeasible’. Thus, the condition for instability of the trivial equilibrium is also a condition for feasibility of the nontrivial equilibrium. Biologically, if a population successfully invades an empty habitat in which all resource is available, then there is a feasible equilibrium with a positive density for that population. That this nontrivial equilibrium is stable is easy to see: suppose  $N$  is perturbed below  $N^*$ , without changing the total resource supply. Then, equation (1.5b) implies that  $R > R^*$ , and in turn, equation (1.5a) implies that  $\mu(R) > m$ , so that the population grows back towards  $N^*$ . If  $N$  is perturbed above  $N^*$ , then equation (1.5b) implies that  $R < R^*$ , and equation (1.5a) implies that  $\mu(R) < m$ , so that the population declines back towards  $N^*$ . A more technical analysis by Armstrong and McGehee (1980) proves that the equilibrium  $(N^*, R^*)$  is globally stable, when it is feasible.

These results apply to any increasing function  $\mu(R)$ , regardless of its detailed shape. Several features of the properties just sketched for equation system (1.5) are characteristic of models describing population growth that depends on abiotic resources, and recur in more elaborate models. First, there are threshold conditions on the parameters representing the consumer population’s mortality rate and the habitat’s total resource supply, which must be met for the population to be able to invade when rare, or to persist at an equilibrium. The mortality rate must be lower than the maximal growth rate of a consumer population, and the resource supply must exceed the level of resource availability required for the population to persist in the face of its losses. Similar thresholds apply when equation system (1.5) is extended to include additional, competing populations, and additional resources.

Second, the quantity  $R^*$ , which plays a critical role in the dynamics of this consumer-resource system, is a synthetic parameter summarizing everything that affects both growth and loss of the consumer population. As this modeling framework is extended, similar synthetic quantities emerge as critical. The derivation of threshold conditions and critical synthetic parameters is important, because it provides predictions that can be experimentally tested, and guides experimentalists towards measuring highly informative quantities.

Finally, the intraspecific competition that leads to stability of the equilibrium

is mediated entirely through the consumption of the resource. The population biologist's **density dependent regulation** is indirect, involving encounters of individuals with parcels of resource, not encounters of individuals with other individuals. The density dependence arises because a larger population depletes more of the resource, reducing the capacity for further growth. In the models used to study resource competition, density dependence and interspecific competition also arise indirectly, through consumer-resource interactions, and not through direct interactions of individuals of the same or different populations. Some cases where this representation is clearly inadequate are discussed in Chapters 3 and 10.

### 1.3 COMPETITION AND RESOURCES

In Chapter 2, we will add more populations (usually interpreted as different species) to eqs. (1.1) and (1.3), in addition to other elaborations to make them more realistic. With several competing populations present, we must discuss the fate of each, and hence the range of possible outcomes is enlarged. One or more populations may go extinct, in which case it is customary to speak of **competitive exclusion**, or two or more populations may persist, in which case we speak of **coexistence**. In either case, it may prove that one population maintains high abundance in the long term, while others are rare or extinct. A population with high abundance in the long term is often called a **superior competitor** or **dominant competitor**.

The appropriate definition of competition, superior competitor, and related terminology has been a matter of some discussion (Grime, 1979; Thompson, 1987; Tilman, 1987a; Thompson and Grime, 1988; Keddy, 1989). One definition of **competition** refines that offered above: it is the interaction occurring between species when increased abundance of a first species causes the population growth rate of a second to decrease, and there is a reciprocal effect of the second on the first. This definition focuses on an effect, mutually negative interactions between species, regardless of the processes involved. Historically, a variety of processes leading to such mutually negative interactions have been studied under the name 'competition'.

There are clear disadvantages to such a definition; the same term will often be attached to very different processes, potentially obscuring important biological differences (Grime, 1979; Thompson and Grime, 1988). For this reason, the term competition is often qualified. Most commonly, a distinction between **interference competition** and **resource or exploitative competition** is drawn. Further distinctions have also been suggested (e.g. Schoener, 1983). Resource competition is a mutually negative interaction between species that arises because individuals of both species consume the same resources. What one individual gets, another does not, whence the mutual negativity. No further direct actions of interference between individuals are postulated. This definition of resource competition preserves the attention to the effects at the population level of consuming shared resources, but also draws attention to the process, or mechanism,

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whence the effects arise. Perhaps it would be best to divorce mechanism and effect entirely. Thus Grime (1979) suggests defining competition only as the consumption of shared resources, reserving other terms for attendant effects at the population level.

Because of historical usage, and correspondence to common practice in field studies aimed at documenting mutually negative interspecific interactions, I prefer to retain the population-level components of the definitions of competition and resource competition. In this book, competition means a mutually negative interaction between populations, and resource competition such an interaction arising from consumption of resources. One possible consequence of competition, so defined, is that the negative effect of a first species on a second is consistently stronger than the reciprocal effect. If this is so, the first species will over time replace the second. In such a case, the first species is said to be a **superior competitor**, or **dominant**. If such dominance is clearly due to consumption of shared resources, then I call the first species a **superior resource competitor**. The ultimate end may be competitive exclusion, wherein the dominant species alone persists.

If mutual negativity at the population level is removed from the definition of competition, as suggested by Grime (1979), then a superior competitor is one that maintains a higher rate of resource consumption than an inferior competitor. Plausibly, the superior competitor may also be dominant, but this is not logically necessary when the definition of competition does not reach to the population level.

### 1.4 CLASSICAL COMPETITION THEORY

#### 1.4.1 Logistic and Lotka–Volterra equations

Theoretical ecology has only recently, incompletely, and perhaps reluctantly, accepted the resource-based paradigm of population growth sketched above. Traditionally, theory has focused on the effects of competition at population level, hoping to identify general features independent of the mechanism producing them. The starting point is the logistic equation:

$$\frac{dN}{dt} = rN(1 - N/K). \quad (1.8)$$

Population density is the only state variable. Any role of resources is subsumed in the idealized parameters  $r$  and  $K$ , conventionally called the **intrinsic rate of increase** and **carrying capacity**, respectively.

The extension of this equation to competition between two populations, indexed by subscripts  $i = 1, 2$ , assigns each an intrinsic rate of increase ( $r_i$ ) and a carrying capacity ( $K_i$ ). The negative influence of a population's own density on its growth rate is retained, and the other competing population is assigned a similar effect, to arrive at the coupled equations:

$$\frac{dN_1}{dt} = r_1 N_1 \left( 1 - \frac{N_1}{K_1} - \frac{\alpha_{12} N_2}{K_1} \right) \quad (1.9a)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left( 1 - \frac{N_2}{K_2} - \frac{\alpha_{21} N_1}{K_2} \right), \quad (1.9b)$$

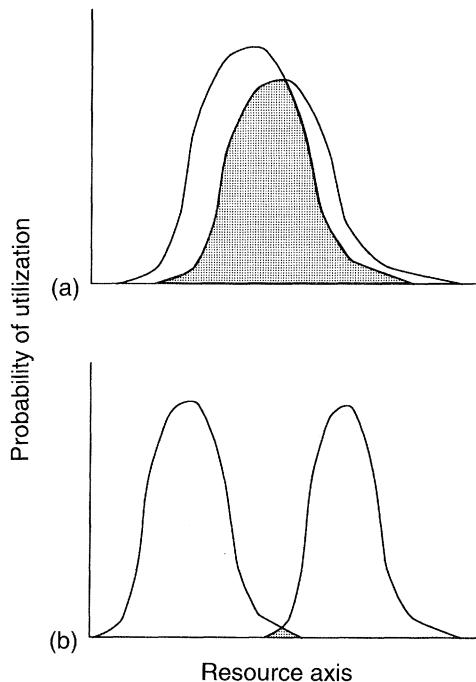
where the parameters  $\alpha_{ij}$  are the **competition coefficients**, describing the effect of species  $j$  on the growth rate of species  $i$ , arising from competition. Once again, any role of resources is hidden in the parameters of these equations.

Ecologists have traditionally regarded equation system (1.9) as a theory of competition, even as a theory of competition for resources. Its status as a theory is questionable, however, because as it stands it cannot be used to predict anything – it leads to no conjectures about nature that might be refuted by observation or experiment. Equation system (1.9) make no reference to any entities other than the densities of the two competing populations, and thus its critical parameters, the competition coefficients, cannot be estimated prospectively, before an instance of competition is observed. Hence no prediction of the outcome of competition can be made. The competition coefficients can only be estimated retrospectively, after competition has occurred (Tilman, 1987b).

This deficiency has been recognized for a long time, and a remedy was suggested by Gause (1934). The parameters  $r_i$  and  $K_i$  are unproblematic – they can be estimated from observations of single populations in isolation, prior to any competition. What is needed are auxiliary hypotheses, postulating relations between the competition coefficients and some entities beyond the competitors' population densities. An expanded theory, consisting of equation system (1.9) plus rules for determining the competition coefficients independently, could then predict population trends under competition, whether competitors coexist or not, and whether one or the other is dominant. Gause (1934) tested such predictions experimentally, using yeast that interacted by consuming sugar and producing alcohol (in modern terms, both resource competition and allelopathy were present in his experiments). He could not always achieve quantitative predictions, and concluded that his understanding of the competition coefficients was deficient.

Gause's programme of appending a theory for competition coefficients to the Lotka–Volterra equations lay dormant for about 25 years, until MacArthur and Levins (1967) revived it. In their approach, populations consume a single resource, but one which cannot be described by a simple scalar quantity, such as used in eqs. (1.1) and (1.3). Instead, the resource is continuously or discretely distributed, according to some attribute – for concreteness, imagine birds eating a variety of insects which differ in size. Size of insects is then an axis along which the resource is distributed, and the utilization of various size classes by a population is represented as a probability distribution along the size axis (Fig. 1.7). The competition coefficient is then assumed to be related to the extent of

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*Figure 1.7* Representation of resources in the competition theory of MacArthur and Levins (1967). The resource is a distributed variable, characterized by a single attribute, e.g. size, on the abscissa. Curves show the probabilities of consumption for two competitors, as functions of the resource attribute: (a) High overlap in utilization, which leads to high values of competition coefficients. (b) Low overlap in utilization, which leads to low values of competition coefficients.

overlap between the utilization curves of two competitors: high overlap produces a large competition coefficient (Fig. 1.7a), and low overlap a low competition coefficient (Fig. 1.7b).

MacArthur and Levins (1967) proposed a formula relating resource overlap to competition coefficients to be inserted in the Lotka–Volterra competition equations. This approach was greatly elaborated by them and others, leading to a set of propositions summarized by Schoener (1982):

1. Species that are too similar in resource use cannot coexist indefinitely – competitive exclusion of all but one eventually takes place.
2. Species that coexist in nature do so by virtue of differences in resource use.
3. Interspecific competition selects for adaptations that result in divergence of resource use between species.
4. Species whose resource utilization curves do not differ sufficiently to coexist will have disjunct geographical ranges.

For convenience, I will refer to these statements and their underpinnings as **classical competition theory**.

Classical competition theory is attractive. The resource utilization curves at its heart are widely documented, especially for vertebrates, by direct observation of foraging, examination of stomach contents, and less directly by the morphology of structures involved in resource capture and use. From such data, the theory makes predictions about evolutionary and biogeographical patterns that are of broad interest. A number of studies appear to corroborate these predictions (reviewed by Schoener, 1982). Nevertheless, classical competition theory is not currently fashionable.

Its problems are both empirical and theoretical. First, the evolutionary and biogeographical patterns cited in evidence of the theory have been questioned. Under some analyses, putative patterns evaporate as indistinguishable from randomness (Strong, Szyska and Simberloff, 1979; Simberloff and Boecklen, 1981), and reasonable alternatives to the competition hypothesis are often difficult to exclude (Grant, 1972). Analysis of the patterns predicted by classical competition theory has been contentious, and although its predictions have not been conclusively falsified, they have proven very difficult to test. Were the predictions of classical competition theory easier to test, it might today be held in greater favor.

Second, classical competition theory has been found to be unduly sensitive to changes in how competition coefficients are computed from resource use. Most theoretical work deducing the predictions listed above simply used the original formulation of MacArthur and Levins (1967), but these predictions are not robust to alternative formulations (Abrams, 1975). Unfortunately, the original formula was based more on mathematical convenience than biology, undermining confidence in the theory's predictions. Moreover, building theory from first principles of resource consumption and population growth need not lead to dynamics that can be represented by Lotka–Volterra equations (Abrams, 1975), and the extension of these equations to multispecies, rather than pairwise competition, is problematic (Tilman, 1987b).

#### 1.4.2 The emergence of resource competition theory

As dissatisfaction with classical competition theory grew, a new approach to competition for resources emerged. It is based on the definition of resources advanced above, and on the use of a scalar variable to represent the availability of each distinct resource. Thus, the ability to describe complexity in the nature of a single resource and its utilization (as in Fig. 1.7) is given up, in exchange for eqs (1.1) and (1.3) with their explicit linkage of resource dynamics, consumption, and population growth. MacArthur and Levins (1964) and MacArthur (1972) sketched some of the implications of assuming competition for two such resources, and a more thorough analysis was provided by León and Tumpson (1975) (see Chapter 2). The historical association of resource competition theory and classical competition theory should not obscure their significant differences

## 16 Introduction

in how resources are represented, and how relations between populations and their environment are portrayed (see Leibold, 1995 for a detailed discussion).

The change in the theoretical representation of resources occasioned a change in the organisms for which the theory was designed. Classical competition theory was constructed with reference to vertebrates, which often consume an array of similar prey types, differing principally in size. The use of a distributed variable to represent such a resource is reasonable. In contrast, the scalar variables suggested by MacArthur and Levins (1964) to denote resource availability are easier to accept when the resources are nutrients. Not surprisingly, application of the scalar theory was first developed for microorganisms, where a considerable body of research on nutrient competition already existed (Chapter 3), by Phillips (1973), O'Brien (1974), Taylor and Williams (1975), and Tilman (1977). The latter showed that resource competition theory held up under laboratory tests with phytoplankton. Later work extended this theory to plants (Tilman, 1982, 1988) and zooplankton (Rothhaupt, 1988).

### 1.5 CONCLUDING REMARKS

The subject of resource competition, as presented in this book, follows this last line of research. Rather than the logistic and Lotka–Volterra equations, it takes resource dynamics and resource-dependent population growth as its mathematical starting point. The programme proceeds by extending the model of one resource and one population to include additional resources and competitor populations (Chapter 2). These theoretical efforts have prompted a number of experiments (Chapter 3), but the related empirical research says very little about the birds, lizards and fishes that have attracted other competition researchers. Instead, microorganisms and plants, and to a lesser extent invertebrates, are prominent. Keddy (1989) noted that such humble organisms not only constitute most of the earth's biomass, but are also often more experimentally tractable than vertebrates, and he wondered what ecological theory would look like if it were constructed predominantly around microorganisms and plants. For the subject of resource competition, this book attempts to answer that question. It has other goals: to review the central body of work that has developed (Chapters 2 and 3), consider its weaknesses (Chapter 4), and sketch developments that might strengthen it (Chapters 5–10).

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## 2 Theoretical and experimental foundations

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Growth of a single population on a single resource is the basic building block of resource competition theory, which is constructed by expansion of simple growth models to represent many species. Assuming first that there is competition for a single abiotic resource, the quantity  $R_{(i)}^*$  can be computed, which is the resource availability at equilibrium when a single species  $i$  grows in the absence of competing species. When several species compete this quantity is critical, and a simple rule governs competitive outcomes. At equilibrium, the species with the lowest  $R_{(i)}^*$  competitively excludes all others.

With more than one resource, coexistence and priority effects are also possible. A necessary condition for these latter outcomes is that for each species, there are combinations of availabilities of both resources for which only that species grows (Phillips, 1973). For two resources, stability conditions enunciated by León and Tumpson (1975) are sufficient for equilibrium coexistence: each competitor must consume relatively more of the resource that most limits its competitor. These conditions are summarized by graphical models of resource-dependent population growth isolines and resource consumption and supply vectors. In theory, a common pattern often emerges for competing species: if coexistence is possible for any resource supply condition, then the ratio between supplies of different resources is critical, and coexistence of competitors occurs only at particular supply ratios.

Competitive outcomes according to these theories are predictable from knowledge of the resource-dependent consumption and growth rates of each competitor population studied in isolation. Laboratory studies with various organisms demonstrate this predictive capability.

### 2.1 INTRODUCTION

In the first chapter, we introduced a framework for modeling resource-dependent population growth, which we now extend to situations of competition. First, we keep the simple assumption of a single resource, and explore competition between many species. Then, we explore competition for two resources. The first

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goal of this presentation is to introduce two hypotheses, which predict the outcome of such competition based on the biological properties of the competitors, and characteristics of the environment they inhabit. The first hypothesis, the **R\*-rule**, applies to competition for one resource and claims that only a single superior competitor persists, that which most depletes the available resource. The second hypothesis, the **resource-ratio hypothesis**, applies to competition for two resources, and claims that two competitors at most coexist, setting out conditions under which coexistence or competitive exclusion occur.

The second goal of this chapter is to briefly review some experiments that support these hypotheses, and which have played a crucial role in the study of resource competition. Some familiarity with the experimental systems employed is necessary, because their properties have both stimulated and constrained the development of theory. In particular, the mathematical models represent processes occurring in continuous cultures of microorganisms (chemostats). Their unaltered extension to other organisms and habitats thus rests upon an analogy to such systems, and it would not be surprising if modifications of the basic theory proved necessary. A more extensive review of experimental literature follows (Chapter 3).

### 2.2 CHEMOSTAT MODELS

The equations of resource-dependent population growth constructed in Chapter 1 are extended to many species in a natural way:

$$\frac{dN_i}{dt} = (\mu_i(R) - m_i)N_i \quad \text{for } i = 1, \dots, n \quad (2.1a)$$

$$R = S - \sum_{i=1}^n N_i Q_i, \quad (2.1b)$$

where the subscript  $i$  indexes the population densities ( $N_i$ ), growth functions ( $\mu_i(R)$ ), loss rates ( $m_i$ ) and resource quotas ( $Q_i$ ) of the different species (see Table 2.1 for mathematical notation). As in Chapter 1, the resource is abiotic (as defined by Armstrong and McGehee, 1980). Taken literally, equation system (2.1) represents a closed system with a constant concentration ( $S$ ) of total resource, of which the concentration  $R$  is available.

Despite the apparent artificiality of a closed system, equation system (2.1) approximates the long-term dynamics of certain open systems. In Appendix B it is shown how to approximate the system

$$\frac{dN_i}{dt} = \mu_i(R)N_i - DN_i - d_i N_i \quad \text{for } i = 1, \dots, n \quad (2.2a)$$

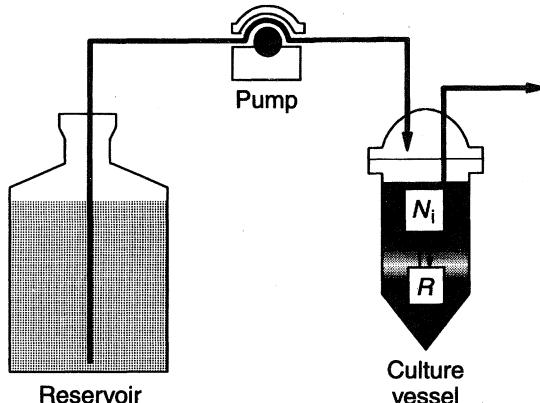
$$\frac{dR}{dt} = D(S - R) - \sum_{i=1}^n (\mu_i N_i Q_i - d_i N_i Q_i), \quad (2.2b)$$

Table 2.1 Mathematical notation for Chapter 2

Symbol	Meaning
$N_i$	Population density of species $i$ (numbers or biomass per unit area or volume)
$R$	Resource availability, e.g. concentration of a nutrient (mass volume $^{-1}$ )
$Q_i$	Resource quota of species $i$ , units of resource contained in one unit of population
$\mu_i(\cdot)$	Resource-dependent population growth rate of species $i$ , per capita (time $^{-1}$ ), a function of resource availability or quota, depending on growth model
$m_i$	Per capita mortality rate of species $i$ (time $^{-1}$ )
$S$	Resource supply, the maximum possible resource availability in a habitat (mass volume $^{-1}$ , for example)
$D$	'Dilution rate', a per capita loss rate applying to all organisms and to available nutrient in a chemostat (time $^{-1}$ )
$d_i$	Per capita loss rate of species $i$ resulting from processes other than dilution, e.g. death within the habitat (time $^{-1}$ )
$Q_{\min,i}$	Subsistence quota of species $i$ , the value of resource quota at which population growth ceases (units of resource per unit of population)
$Q_{\max,i}$	Maximal quota of species $i$ (units of resource per unit of population)
$\mu'_{\max,i}$	Apparent maximal per capita growth rate of species $i$ in the internal storage model (eqs. 2.5–2.7), population growth rate that would occur if quota were infinite (time $^{-1}$ )
$\mu_{\max,i}$	True maximal growth rate of species $i$ , occurring at the finite maximal quota, $Q_{\max,i}$ (time $^{-1}$ )
$\rho_i(R)$	Resource uptake rate of species $i$ (units of resource consumed per unit time per unit population)
$\rho_{\max,i}$	Maximal resource uptake rate of species $i$ (units of resource consumed per unit time per unit population)
$K_{\rho,i}$	Resource availability at which uptake is half-maximal (e.g. concentration for a nutrient)
$\Psi(\dots)$	Resource supply function (units of resource per unit time), which potentially depends on many quantities (see Appendices A and B)
$l_i$	Proportion of a plant devoted to leaves (dimensionless)
$b_i$	Proportion of a plant devoted to roots (dimensionless)
$s_i$	Per capita loss rate of plant matter due to shedding of litter (time $^{-1}$ )
$c_i$	Per capita loss rate of plant matter due to processes other than shedding of litter (time $^{-1}$ )
$h_i$	Nutrient (resource) content of plant tissues shed as litter (nutrient mass per unit plant mass)
$k_i$	First order decay rate for plant litter (time $^{-1}$ )
$\mathbf{u}$	Supply vector (in two-resource models, see eq. 2.22)
$\mathbf{c}$	Consumption vector (in two-resource models, see eq. 2.22)
$\mathbf{S}$	Supply point (in two-resource models)

which has a distinguished pedigree. Models of this form have long been used to describe the growth of microorganisms in a culture system called a **chemostat** (Novick and Szilard, 1950; Monod, 1950). In a chemostat, a sterile nutrient medium is continuously pumped through a culture vessel (Fig. 2.1). The ratio of

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*Figure 2.1* The chemostat, an experimental model corresponding to many of the mathematical models of resource competition. Organisms grow in a culture vessel, consuming a resource supplied by pumping in sterile medium at a dilution rate  $D$ , with resource concentration  $S$ . Inflow is balanced by an outflow removing both available nutrient (at a concentration  $R$ ) and organisms (at densities  $N_i$ ).

the flow through the vessel to its volume imposes a hydraulic turnover at a rate  $D$ , called the **dilution rate**. This turnover removes both available resource and organisms from the habitat (the culture vessel). This efflux of materials is balanced by an influx of the resource at the rate  $DS$ , where  $S$  is now the concentration of the resource in the inflowing medium. The constant  $d_i$  represents losses of organisms by death within the habitat, and the terms  $d_i N_i Q_i$  in equation (2.2b) express an assumption that the nutrient contained in dead organisms is instantaneously recycled to available form, in keeping with the definition of an abiotic resource. (Often, this death-and-recycling term is assumed to be small, and is neglected in many presentations of the chemostat model.) The loss rate  $m_i$  in equation (2.1a) is thus partitioned into an outflow component shared by all species ( $D$ ), and a specific component ( $d_i$ ) pertaining to other losses.

The long-term properties of an open chemostat system with a single species are very much like those of a corresponding closed system (Appendix B). Namely, there is a trivial equilibrium  $(R, N_i) = (S, 0)$ , which can be invaded by a small population of species  $i$  if

$$m_i = D + d_i < \max_R [\mu_i(R)], \quad (2.3)$$

and

$$S > R_{(i)}^* = \mu_i^{-1}(m_i) = \mu^{-1}(D + d_i). \quad (2.4)$$

Under these conditions, the single-species equilibrium  $(R_{(i)}^*, N_{(i)}^*)$  is feasible and stable, and has a formal solution exactly like that of the closed system (equation 1.5). The long-term dynamics of the open system resemble closely those of the

closed system, though transient dynamics differ when the initial total resource concentration,  $T(0)$ , differs from the equilibrium value,  $S$ . Concerning notation: it is convenient to distinguish  $R^*$  for different species  $i$  by subscripts, and to emphasize that this  $R^*$  refers to a particular system, namely that containing only population  $i$ , we let  $R_{(i)}^*$  be the value of  $R^*$  characterizing population  $i$ .

### 2.2.1 Biotic resources

The salient feature that distinguishes biotic from abiotic resources is that the former are alive – they reproduce – and the dynamics of the reproduction must be explicitly accounted in any reasonable model. Of course, a system with a biotic resource and a consumer is a predator-prey system, in the broadest sense, covering herbivores, parasites and pathogens. Competition for biotic resources is harder to study than competition for abiotic resources, both theoretically and experimentally. One of the difficulties in studying predator-prey interactions as a basis of resource competition is the well-known tendency for predator-prey systems to oscillate. This tendency was emphasized by Volterra (1926), and is a recurring theme in predation theory (e.g. Gilpin, 1972; May, 1972).

The simple models for abiotic consumer-resource interactions introduced above do not generate oscillations, either as a sustained long-term behavior or during their approach to equilibrium. Many predator-prey models, however, have long-term dynamics that converge to a limit cycle with sustained oscillations (May, 1974; Nisbet and Gurney, 1982), and oscillations have been observed experimentally in predator-prey systems (Huffaker, 1958; Salt, 1967; Tsuchiya *et al.*, 1972; Jost *et al.*, 1973a; Luckinbill, 1973, 1974). It is also not uncommon for biologically reasonable models of predator and prey to have multiple stable equilibria (May, 1977).

For consumer-resource systems characterized by a unique stable equilibrium for a single species growing alone, the associated resource availability  $R_{(i)}^*$  is a natural measure of resource depletion, and it is also the basis for a predictive rule for competitive outcomes which may apply to both biotic and abiotic resources. For biotic consumer-resource systems characterized by sustained oscillations or multiple stable equilibria, a simple measure of resource depletion is not so readily ascertained, and prediction of competitive outcomes is more difficult. Because the study of competition for biotic resources is so strongly linked to nonequilibrium phenomena, we defer its detailed consideration to Chapter 5.

## 2.3 COMPETITION FOR A SINGLE ABIOTIC RESOURCE

### 2.3.1 The $R^*$ -rule

So far, we have examined growth of one population on one abiotic resource. Members of the population compete for the resource only with members of the same population, depleting it to the level  $R_{(i)}^*$ , and stabilizing population density at an equilibrium. The extent of resource depletion, of which  $R_{(i)}^*$  is an inverse

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measure, gauges the intensity of this intra-population competition. This quantity also measures a given population's competitive impact on other populations.

A very simple principle governs competition in model systems following eqs. (2.1) and (2.2) (Powell, 1958; Stewart and Levin, 1973; O'Brien, 1974; Tilman, 1976, 1977; Hsu, Hubbell and Waltman, 1977; Armstrong and McGehee, 1980). Competitive outcomes follow the  **$R^*$ -rule**, based on the quantity  $R_{(i)}^*$ . If we determine  $R_{(i)}^*$  for each species when it is growing alone, then the rule says that the species with the lowest  $R_{(i)}^*$  competitively excludes all other species in the long term, in a constant habitat. Starting with all species present, eventually the densities of all but one go asymptotically to zero, while the one species with the lowest  $R_{(i)}^*$  goes asymptotically to the equilibrium density that it would obtain if growing on its own, without competing species. Moreover, this outcome is independent of competitors' initial densities. If we start with an inferior competitor (high  $R_{(i)}^*$ ) on its own at equilibrium, and introduce a very small population of a superior competitor (low  $R_{(i)}^*$ ), the latter will increase in density, eventually supplanting the former. If we start with a superior competitor (low  $R_{(i)}^*$ ) on its own at equilibrium, and introduce a very small population of an inferior competitor (low  $R_{(i)}^*$ ), the latter will decrease in density, going asymptotically to zero.

The verbal explanation of this result is that in the long term, resource availability goes to the level defined by the lowest  $R_{(i)}^*$  among the competing populations. If  $R$  is below this level, then no population can increase, all decrease, and consequently  $R$  increases towards this  $R_{(i)}^*$ . When  $R$  is above this level, at least one population can increase (the one with the lowest  $R_{(i)}^*$ ). Consequently,  $R$  decreases, and will do so until it reaches this lowest  $R_{(i)}^*$ . For  $R$  very near  $R_{(i)}^*$ , the net growth of the superior competitor is near zero – it is approximately at equilibrium – while all other populations have negative net growth and decline. As time goes on,  $R$  converges to  $R_{(i)}^*$  for the superior competitor, which goes to its own equilibrium population density.

An elegant mathematical proof of the  $R^*$ -rule formalizes this scenario in terms of Lyapunov functions (Armstrong and McGehee, 1980), and is global, applying to any set of initial conditions (for which the ultimate winner does not have zero initial density). Although this proof relies on a mass balance constraint (equation 2.1b), it extends to systems in which total resource concentration is not constant, but merely bounded (Wolkowicz and Lu, 1992).

The action and implications of the  $R^*$ -rule are easily explored graphically. Note that  $R_{(i)}^*$  depends on both growth and loss processes, so that a superior competitor could achieve a low value of  $R_{(i)}^*$  either by possession of superior growth characteristics, or by suffering minimal losses.

For simplicity, suppose that  $m_i = m$ , a common constant for all species, and that the growth functions of different species do not intersect. Then the superior competitor among a set of species is the one whose growth curve has the highest elevation (e.g. Fig. 2.2a). In such a simple case, one species wins regardless of the magnitude of the common loss rate suffered by all populations. The competitive superiority conferred by a growth curve of higher elevation is not robust to differing loss rates (Fig. 2.2b). When species do not share the same loss rate, and again assuming that growth functions do not intersect, a species with a high

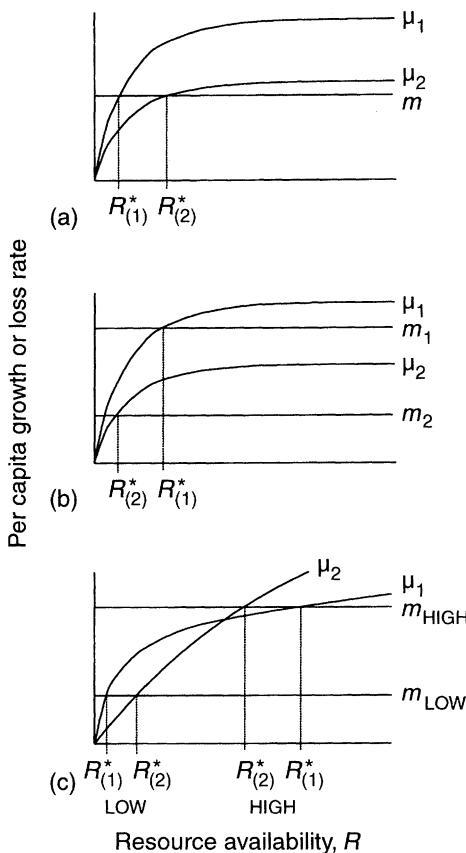


Figure 2.2 Graphical analysis of competition between two species for one abiotic resource: (a) The growth curve of species 1 ( $\mu_1$ ) lies above that of species 2 ( $\mu_2$ ) for all resource availabilities, and both species suffer the same loss rate ( $m$ ). Therefore, species 1 equilibrates at a lower resource availability ( $R_{(1)}^*$ ) than species 2 ( $R_{(2)}^*$ ). According to the  $R^*$ -rule, species 1 competitively excludes species 2. (b) The growth curve of species 1 lies above that of species 2 for all resource availabilities, but species 1 suffers a higher loss rate ( $m_1$ ) than species 2 ( $m_2$ ). Therefore, species 1 equilibrates at a higher resource availability ( $R_{(1)}^*$ ) than species 2 ( $R_{(2)}^*$ ). According to the  $R^*$ -rule, species 2 competitively excludes species 1. (c) The growth curves of the two species intersect, and the two species suffer the same loss rate. Competitive outcomes depend on whether their loss rate is high ( $m_{\text{HIGH}}$ ) or low ( $m_{\text{LOW}}$ ), because the rank order of the quantities  $R_{(i)}^*$  changes.

growth curve could be competitively inferior, if its loss rate is also high. For the two species illustrated in Fig. 2.2b, the outcome of competition depends critically on loss rates, and a sufficient reduction in population 1's loss rate, or a sufficient increase in population 2's, could reverse the outcome by giving an ordering  $R_{(1)}^* < R_{(2)}^*$ .

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If the growth functions of different species intersect even once, then competitive outcomes depend on loss rates, even if the same loss rate applies to all species (Fig. 2.2c). For two species, when loss rates fall below the point at which growth curves intersect ( $m_{\text{LOW}}$  in Fig. 2.2c) the dominant species has the highest growth curve at low resource availabilities. For loss rates above the intersection point ( $m_{\text{HIGH}}$  in Fig. 2.2c), the dominant species has the highest growth curve at high resource availabilities.

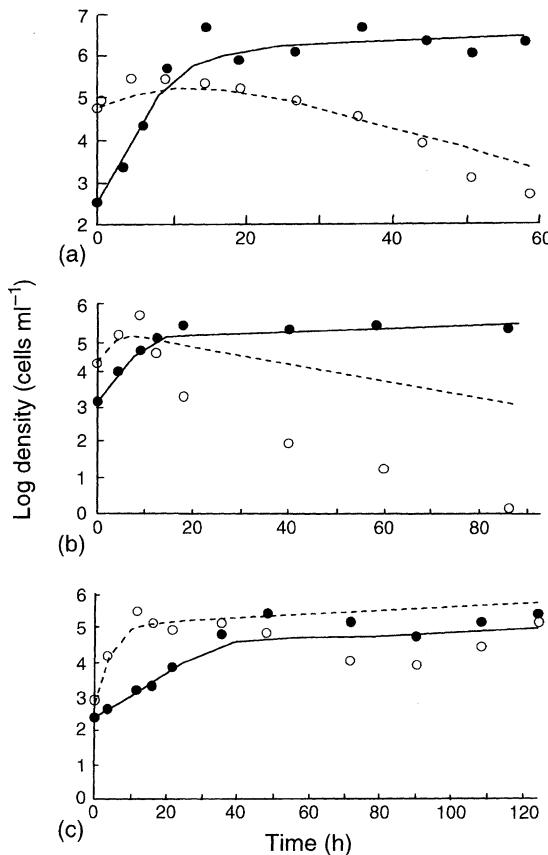
There are only a few special cases of competition for a single abiotic resource, to which the  $R^*$  rule does not apply in theory. These arise when competing species have the same value of  $R_{(i)}^*$ . In these cases, there is no competitive displacement at all: the relative abundances of the species remain at their initial values forever. The species may be said to coexist, but such coexistence depends on an initial configuration which is forever carried forward in time.

Equality of  $R_{(i)}^*$ 's might arise only for particular parameter values. For example, if loss rates are equal, and two populations' growth curves intersect, then a loss rate exactly at the point of intersection gives equal values of  $R_{(i)}^*$ . In such cases, the delicate balancing of parameters permitting coexistence is fragile to any change affecting either species' growth functions or loss rates. Changes in external conditions, or evolutionary change in either of the competing species will destroy this balance. Equality of  $R_{(i)}^*$  for two or more species could also arise from identity of their growth functions and loss rates. From the standpoint of theory, there is no need to distinguish such populations. Whether they represent distinct named species, genetic variants within species, or other entities, if they have identical growth functions and loss rates, there is no need to describe them mathematically as distinct populations.

### 2.3.2 Experimental verification of the $R^*$ -rule

Hansen and Hubbell (1980) tested the predictions of the  $R^*$ -rule using several strains of bacteria growing under limitation by tryptophan. They first fitted the Monod equation (1.2) to their strains' growth rates (Fig. 1.1), permitting calculation of  $R_{(i)}^*$ . Then, in their first experiment, they competed *Escherichia coli* strain C-8 against *Pseudomonas aeruginosa* strain PAO283. From the growth curves of these strains (Fig. 1.1a), the  $R^*$ -rule predicts that the former should win in a chemostat experiment, regardless of the loss rate imposed. This outcome was observed (Fig. 2.3a), and the dynamics of competitive exclusion were quantitatively predicted by simulations based on a parameterized version of equation system (2.2).

Hansen and Hubbell (1980) also examined two strains of *E. coli* C-8: one sensitive to the growth inhibitor nalidixic acid (strain C-8 nal<sup>s</sup> spec<sup>c</sup>), the other resistant (strain C-8 nal<sup>r</sup> spec<sup>s</sup>). Without inhibitor, the sensitive strain is predicted to be a superior competitor, based on the  $R^*$ -rule (see Fig. 1.1b). In a chemostat experiment, the sensitive strain won, although the dynamics of competitive exclusion were more rapid than predicted (Fig. 2.3b). By adding the inhibitor at 0.5 µg/l, Hansen and Hubbell (1980) altered the growth curves of these competitors, producing a region of approximate equality of their values of  $R^*$ , at loss



**Figure 2.3** Competition in chemostats for tryptophan between pairs of bacterial strains. Lines show predicted strain dynamics based on resource competition theory, as indicated. (a) *E. coli* strain C-8 vs. *P. aeruginosa* strain PAO283. (b) *E. coli* strain C-8  $\text{nal}^8 \text{ spec}^r$  vs. strain C-8  $\text{nal}^1 \text{ spec}^8$ ; no nalidixic acid present. (c) *E. coli* strain C-8  $\text{nal}^8 \text{ spec}^r$  vs. strain C-8  $\text{nal}^1 \text{ spec}^8$ ; nalidixic acid present at  $0.5 \mu\text{g l}^{-1}$ . Reprinted from Hansen and Hubbell (1980), with permission.

rates less than about  $0.1 \text{ h}^{-1}$ . In a chemostat with such a low loss rate, theory thus predicts coexistence. This was indeed observed (Fig. 2.3c).

### 2.3.3 Critiques of the $R^*$ -rule

There are now many other studies (Chapter 3), showing that where the assumptions of the models written above are well approximated, the dynamics of competition between real organisms conform to the  $R^*$ -rule remarkably well. Most of these supportive studies were done in laboratory systems, where the simplifying

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assumptions of the theory are satisfied by contrivance. Nature is not generally so congenial to the assumptions employed by mathematical biologists, and real systems are probably rare in which space is homogeneous, population structure is simple, a single abiotic resource limits all species' growth, sufficient time is allowed to reach a equilibrium before abiotic factors change, and no intra- or interspecific interactions other than resource competition occur. Not only are the assumptions of the simplest resource competition theory unrealistic, so are the predictions. The strong tendency to competitive exclusion predicted by this theory suggests that the world should be dominated by only a few species. It is not.

One might suspect that the theoretical tendency to low diversity found in simple models of resource competition can be reconciled with the great diversity of the natural world by changing the unrealistic assumptions to more realistic ones. In fact, changing nearly any of the assumptions listed above often increases possibilities for coexistence and diversity, as detailed in later chapters. The greatest challenge lies in determining which assumptions must be relaxed to describe and predict a given system adequately, and which ones may be retained as convenient and harmless fictions.

### Optional section

#### 2.3.4 Robustness of the $R^*$ -rule

Some elaborations of simple theory do not upset the  $R^*$ -rule, and the associated tendency to dominance by a single superior competitor. Equations (1.2) and (2.1a) are very simplified descriptions of the processes underlying resource-dependent population growth. One might worry that more realistic descriptions of growth would frustrate such a simple principle as the  $R^*$ -rule, but this is not so for many useful elaborations of these basic models (e.g. Tilman, 1990a).

One common elaboration is to allow the quota of resource per individual ( $Q_i$ ) to vary, representing storage of the resource, and severing the direct connection between population growth and resource availability. In this approach, commonly applied in algal ecology, the per capita rate of population increase is assumed to depend on the amount of resource an individual has captured. That is, population growth depends on the 'internal' state variable  $Q_i$ , not on the 'external' state variable  $R$ , the availability of the resource in the organism's environment. Thus, the growth function is written  $\mu_i(Q_i)$ , where  $\mu_i$  is now an increasing function of quota. An empirically justified and algebraically convenient function was suggested by Droop (1968):

$$\mu_i(Q_i) = \mu'_{\max,i} (1 - Q_{\min,i}/Q_i), \quad (2.5)$$

where  $Q_{\min,i}$  represents a subsistence quota, the value at which population growth ceases. According to equation (2.5)  $\mu_i(Q_i)$  is a rectangular hyperbola (Fig. 2.4a), intercepting the quota axis at the subsistence quota, and rising to an asymptotic value  $\mu'_{\max,i}$ . This asymptote is an 'apparent' maximal growth rate, since it could only be achieved if  $Q_i$  were infinite. In reality, there is a finite maximum for quota,  $Q_{\max,i}$ , at which  $\mu_i(Q_i)$  is truncated, giving a true maximal

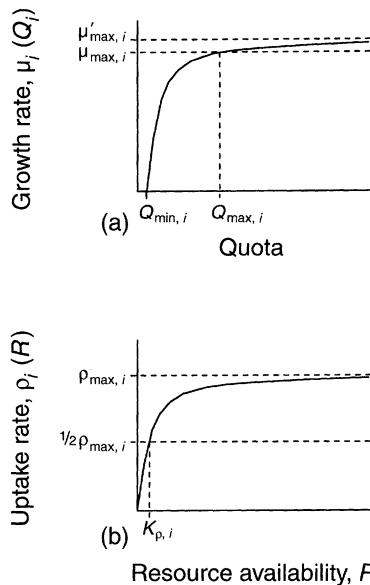


Figure 2.4 Extending the basic consumer-resource model to accommodate resource storage in the form of a variable resource quota: (a) Growth rate as a function of quota, according to Droop's equation (2.5). (b) Resource uptake rate as a function of availability, according to the Michaelis–Menten equation (2.6).

growth rate  $\mu_{\max,i}$ , which is less than  $\mu'_{\max,i}$ . These latter two quantities should not be confused.

If a population grew without resource consumption, then quota would decrease as more members of the population were added, and a fixed amount of resource divided among them. This 'dilution by growth' implies that quota decreases at a rate  $-\mu_i(Q_i) \cdot Q_i$ . Quota increases through consumption at a rate  $\rho_i(R)$ , where  $\rho_i$  is an increasing function of resource availability. For example, algae and other microorganisms acquire dissolved nutrients via transport proteins situated in the cell membrane, for which Michaelis–Menten kinetics are a reasonable assumption. This leads to the expression

$$\rho_i(R) = \rho_{\max,i} R / (K_{\rho,i} + R), \quad (2.6)$$

where  $\rho_{\max,i}$  is the maximal rate of nutrient uptake, and  $K_{\rho,i}$  a half-saturation constant, giving the nutrient concentration at which uptake is half the maximal rate (Fig. 2.4b).

When eqs. (2.5) and (2.6) are used to describe population growth and resource consumption, the resulting model is called the **variable-internal-stores**, or **cell quota** or **Droop** model (Droop, 1974; Morel, 1987; Turpin, 1988). Here, a

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general formulation with  $\mu_i(Q_i)$  and  $\rho_i(R)$  unspecified, is explored as a basis for a competition model. For several species, the model is

$$\frac{dN_i}{dt} = \mu_i(Q_i)N_i - m_i N_i \quad \text{for } i = 1, \dots, n \quad (2.7a)$$

$$\frac{dQ_i}{dt} = \rho_i(R) - \mu_i(Q_i)Q_i \quad \text{for } i = 1, \dots, n \quad (2.7b)$$

$$\frac{dR}{dt} = \Psi(\dots) - \sum_{i=1}^n \rho_i N_i. \quad (2.7c)$$

Each species suffers density-independent losses at a rate  $m_i$ , and the function  $\Psi(\dots)$  represents resource supply processes characteristic of a habitat (see Appendices A and B).

Although it is physiologically more realistic than equation systems (2.1) and (2.2), competition according to the variable storage model (equation system 2.7) follows the same  $R^*$ -rule. To see this, consider the dynamics of the amount of resource sequestered by population  $i$ . At any instant, this is the product  $N_i Q_i$ ; applying the chain rule to calculate its derivative, we find

$$\frac{d(N_i Q_i)}{dt} = \left[ \left( \frac{\rho_i(R)}{Q_i} \right) - m_i \right] (N_i Q_i). \quad (2.8)$$

This derived equation is in the form of equation (2.1a), with the quantity  $\rho_i(R)/Q_i$  playing the role of  $\mu_i$  in that equation. The quantity  $\rho_i(R)/Q_i$  is the ‘per capita’ rate of increase, with dimensions of time<sup>-1</sup>, for population  $i$  measured in units of resource. For a microorganism, this might mean measuring population density as moles of a nutrient sequestered by that population per unit volume, rather than as cells per unit volume. Because  $\rho_i(R)$  is an increasing function of  $R$ , so is the entire term in brackets on the right-hand side of equation (2.8), for any fixed  $Q_i$ . Additionally, for appropriate choices of the supply function  $\Psi(\dots)$ , a mass-balance constraint of the form of equation (2.1b) governs population densities, quotas and available resource.

We have now collapsed the description of population growth in equation system (2.7) down to equation (2.8) coupled to equation (2.1b), which constitute a system following the  $R^*$ -rule (Smith and Waltman, 1994). For a given population, the first step in finding  $R_{(i)}^*$  is to calculate

$$Q_i^* = \mu_i^{-1}(m_i), \quad (2.9)$$

from setting equation (2.7a) to zero, and to substitute this into the inversion of  $\rho_i$ , which results from setting equation (2.7b) to zero:

$$R_{(i)}^* = \rho_i^{-1}(m_i \mu_i^{-1}(m_i)). \quad (2.10)$$

When the Droop equation (2.5) and Michaelis-Menten equation (2.6) are used, these quantities become

$$Q_i^* = \frac{\mu'_{\max,i}}{\mu'_{\max,i} - m_i} Q_{\min,i} \quad (2.11a)$$

$$R_{(i)}^* = \frac{m_i K_{p,i} Q_i^*}{\rho_{\max,i} - m_i Q_i^*}, \quad (2.11b)$$

solutions which are valid for loss rates ( $m_i$ ) less than the true maximal growth rate, and nutrient supplies ( $S$ ) exceeding  $R_{(i)}^*$ . In the context of this model, the quantity  $R_{(i)}^*$  synthesizes a population's uptake, storage, growth and loss processes into a single critical number measuring its competitive success.

Equation system (2.7) is an appropriate model for a unicellular organism whose entire surface takes up nutrient, and whose entire cell participates in processes leading to population growth. For multicellular plants, only the roots acquire nutrients from soil, and the above-ground parts carry out much of the biosynthesis leading to growth. Tilman (1990a) provided an appropriate modification of equation system (2.7) to represent this physiological partitioning:

$$\frac{dN_i}{dt} = \mu_i(Q_i) l_i N_i - m_i N_i \quad \text{for } i = 1, \dots, n \quad (2.12a)$$

$$\frac{dQ_i}{dt} = \rho_i(R) b_i - \mu_i(Q_i) Q_i \quad \text{for } i = 1, \dots, n \quad (2.12b)$$

$$\frac{dR}{dt} = \Psi(\dots) - \sum_{i=1}^n \rho_i b_i N_i. \quad (2.12c)$$

where  $l_i$  is the proportion of a plant devoted to leaves, and  $b_i$  the proportion devoted to roots, both assumed to be constant.

Proceeding as above, to consider the dynamics of the amount of nutrient sequestered by a given population,  $N_i Q_i$ , eqs. (2.12a) and (2.12b) can be collapsed to

$$\frac{d(N_i Q_i)}{dt} = \left[ \left( \frac{\rho_i(R) b_i}{Q_i} \right) - m_i \right] (N_i Q_i). \quad (2.13)$$

Again, the bracketed term is an increasing function of  $R$ , and for an appropriate choice of supply function, applying mass balance on total nutrient will lead to equation (2.1b). Thus, competition according to this model also follows the  $R^*$ -rule, with

$$R_{(i)}^* = \rho_i^{-1} \left( \frac{m_i}{l_i b_i} \mu_i^{-1} \left( \frac{m_i}{l_i} \right) \right). \quad (2.14)$$

Another complication is that of litter production by plants (Tilman, 1990a). Assume that a plant's total loss rate  $m_i$  is partitioned into losses shed as litter at a rate  $s_i$ , and other losses at a rate  $c_i$ . Before shedding tissues as litter, the plant

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adjusts the nutrient concentration of those tissues to a level  $h_i$ , where  $h_i \leq Q_i$ , so that a plant reabsorbs nutrient from tissue before shedding it. Litter from each population ( $L_i$ ) then accumulates at a rate  $s_i N_i$ , and assume that litter decay is a first-order process with a rate constant  $k_i$ . Our competition model thus becomes

$$\frac{dN_i}{dt} = \mu_i(Q_i)N_i - s_i N_i - c_i N_i \quad \text{for } i = 1, \dots, n \quad (2.15a)$$

$$\frac{dQ_i}{dt} = \rho_i(R) + s_i(Q_i - h_i) - \mu_i(Q_i)Q_i \quad \text{for } i = 1, \dots, n \quad (2.15b)$$

$$\frac{dL_i}{dt} = s_i N_i - k_i L_i \quad \text{for } i = 1, \dots, n \quad (2.15c)$$

$$\frac{dR}{dt} = \sum_{i=1}^n k_i h_i L_i + \sum_{i=1}^n c_i N_i Q_i - \sum_{i=1}^n \rho_i N_i. \quad (2.15d)$$

The supply function chosen in equation (2.15d) describes a closed system, in which plant losses that do not go into the litter pool are immediately recycled. This choice is made for convenience.

Considering the dynamics of nutrient sequestered by plant population  $i$  leads to the equation

$$\frac{d(N_i Q_i)}{dt} = \left[ \left( \frac{\rho_i(R) - s_i h_i}{Q_i} \right) - c_i \right] (N_i Q_i), \quad (2.16)$$

where again, the bracketed term increases in  $R$ . For this system, mass-balance relationships are complicated by the presence of litter, but as a consequence of equation (2.16), competitive outcomes follow the  $R^*$ -rule.

More elaborate models describing population growth on a single abiotic resource in greater detail could be given. Many such models would conform to the  $R^*$ -rule governing competitive outcomes at equilibrium. The necessary conditions are not biologically restrictive:

- an increase in resource availability must cause the total amount of resource sequestered by the population to increase
- an increase in the total amount of resource sequestered by the population must cause a decrease of available resource.

Certain kinds of structured population models, which have been used to represent growth of zooplankton and other animals, also lead to the  $R^*$ -rule for competitive outcomes. Cushing (1989) analyzed a model describing the size-distribution of individuals of each competing species. Individual growth, reproduction and consumption rates were functions of individual size, and availability of a single resource. Population and resource dynamics followed a system of partial integrodifferential equations based on the McKendrick–Von Foerster equations, which have often been used to represent size- and age-structured populations

(e.g. Sinko and Streifer, 1967, 1969; DeRoos *et al.*, 1990; DeRoos, Diekmann and Metz, 1992). These equations have potentially rich dynamics, and their application to competition theory remains under-explored. However, in some circumstances, Cushing (1989) showed that competition between size-structured populations for an abiotic resource follows the simple  $R^*$ -rule.

The critical assumptions are that

- the allocation of resource to maintenance is negligible compared to allocation to growth and reproduction
- there is no juvenile period prior to reproductive maturity.

Under these assumptions, Cushing (1989) integrated over the size distribution of each species, and applied a clever matrix transformation to demonstrate that the long-term dynamics of the structured population model are equivalent to those of a system of ordinary differential equations. The result is simply equation system (2.2), except that  $N_i$  is now not population density, but a synthetic quantity related to the cumulative size of all individuals. Thus competition follows the  $R^*$ -rule. The necessary assumptions are rather restrictive – there are probably few organisms that are born reproductively mature. Nevertheless, Cushing's (1989) derivation shows that a complex biology does not necessarily negate a simple conclusion.

From the preceding analyses, the  $R^*$ -rule emerges as a fairly robust principle, in the face of at least some level of realism. This result allows the models listed above to be used to explore the biological bases of competitive ability. For example, equation system (2.12) leads to equation (2.14), which relates competitive ability to a plant species' allocation of biomass to roots (Tilman, 1990a).

## 2.4 COMPETITION FOR TWO ABIOTIC RESOURCES

Although it is satisfying to have found a robust, simple rule governing resource competition, the theory of competition for a single resource falls far short of describing many natural systems. One step towards real applicability is to allow for several potentially limiting resources. An important principle was stated by Levin (1970), who proved that at equilibrium in a single homogeneous habitat, the maximum number of coexisting populations cannot exceed the number of 'limiting factors' (see also Armstrong and McGehee, 1980). A limiting factor is an entity that affects the rate of change of a population, negatively or positively, and is not necessarily consumed or otherwise affected by any population. Because resources are clearly a special case of limiting factors, the conclusion becomes:

the maximum number of populations coexisting at equilibrium cannot exceed the number of resources, unless other limiting factors are invoked.

As noted by many (Hutchinson, 1961; Armstrong and McGehee, 1980, Tilman, 1982; Huston and DeAngelis, 1994), this conclusion is still too restrictive. Nevertheless, it is worth exploring its basis. If there are no other limiting factors, the number of resources imposes only an upper limit to the number of

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coexisting populations. Without further conditions, there is no guarantee that even two populations will coexist. For the upper limit on diversity at equilibrium to be obtained, there are some biological properties that populations coexisting by virtue of diverse resources must display. One important principle was enunciated by Phillips (1973): for each population, there must exist at least one set of resource availabilities at which only this population can grow, while all others go extinct. This condition guarantees the existence of at least one equilibrium in which all populations coexist.

This condition is not sufficient to guarantee long-term coexistence, however, because the equilibrium in question must also be stable to small perturbations. Taylor and Williams (1975) and León and Tumpson (1975) examined stability conditions for some particular examples involving two resources. Tilman (1982) synthesized much of the earlier work on these problems, emphasizing the general principles applying to a wide range of possible resource types.

As a starting point, consider the following generalization of equation system (2.2), in which  $n$  populations compete for  $m$  resources:

$$\frac{dN_i}{dt} = (\mu_i(R_1, R_2, \dots, R_n) - m_i)N_i \quad \text{for } i = 1, \dots, n \quad (2.17a)$$

$$\frac{dR_j}{dt} = \Psi_j(\dots) - \sum_{i=1}^n \mu_i N_i Q_{ij}. \quad \text{for } j = 1, \dots, m. \quad (2.17b)$$

Here, the growth function  $\mu_i$  of a given population now depends, potentially, on all  $m$  resources. The supply function for each resource,  $\Psi_j(\dots)$ , will be chosen so that long-term resource dynamics follow a mass-balance equation

$$R_j = S_j - \sum_{i=1}^n N_i Q_{ij}, \quad (2.18)$$

where  $S_j$  is the maximum concentration of resource  $j$  possible in the habitat, and  $Q_{ij}$  is the amount of resource  $j$  contained in a unit of population  $i$ , assumed for now to be constant (see eqs. B.20 and B.21 in the Appendix).

For now, we need only consider the case of two resources, which allows a transparent graphical presentation of the major results (Tilman, 1980, 1982). Rigorous mathematical treatments of some of these results are presented by Hsu, Cheng and Hubbell (1981) and Butler and Wolkowicz (1987). It is useful to classify resources based on their joint effects on the per capita growth rate of a population. For two resources, this amounts to examining the surfaces or contours defined by

$$\mu_i(R_1, R_2) = \text{const.} \quad (2.19)$$

Tilman (1982) considered many classes of resources in detail: two of these cover most published theoretical and experimental studies.

### 2.4.1 Essential resources

The first of these cases is that of **essential resources**, as defined by Tilman (1982); the adjective **complementary** has also been used (e.g. León and Tumpson, 1975; Hsu, Cheng and Hubbell, 1981). Here, the population growth requires consumption of each of the two resources  $R_1$  and  $R_2$ . The best examples are the mineral nutrients required by autotrophs – carbon, nitrogen, phosphorus, sulfur, and so on – which cannot be substituted one for another. In the simplest cases, it could be that population growth is limited in a Liebig fashion, at a rate dictated by the availability of the one resource that most constrains growth. Formally,

$$\mu_i(R_1, R_2) = \min\{\mu_{i1}(R_1), \mu_{i2}(R_2)\}, \quad (2.20)$$

where  $\mu_{ij}$  gives the relation between the per capita increase of population  $i$  and resource  $j$  when that resource alone limits growth (with other resources available in excess). For example, Monod's rectangular hyperbola (equation 1.2) might be used for each function  $\mu_{ij}$ .

The contours of such a growth function, obtained by applying equation (2.20) are rectilinear, L-shaped curves in the  $R_1R_2$  plane (Fig. 2.5a), with growth rate increasing with distance from the origin. The corners of the contours lie along a curve defined by  $\mu_{i1}(R_1) = \mu_{i2}(R_2)$ ; below this curve, population growth is limited by  $R_2$ , above it, by  $R_1$ .

Consider first the equilibria arising from growth of a single population on two such essential resources. Setting equation (2.17a) to zero specifies one of the contours illustrated in Fig. 2.5a to be the zero-net-growth isocline (hereafter, simply the **isocline**) for the population (Fig. 2.5b). This is the set of points  $(R_1, R_2)$  such that

$$\mu_i(R_1, R_2) = m_i. \quad (2.21)$$

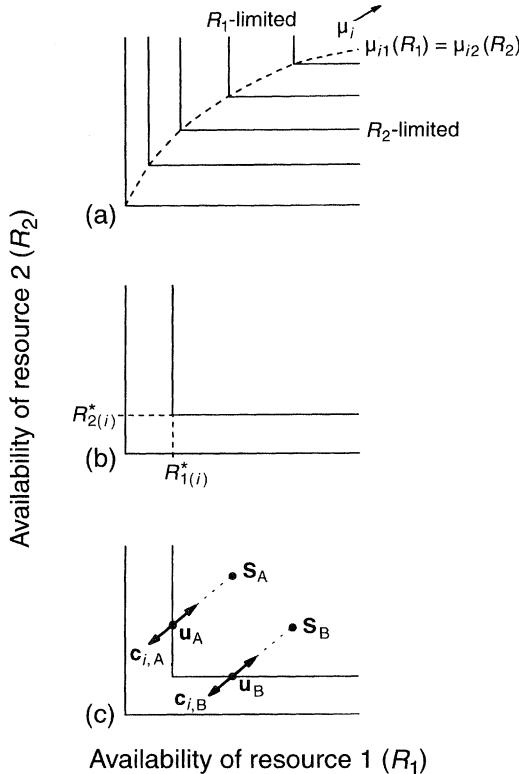
In the region of the  $R_1R_2$ -plane lying between the isocline and the coordinate axes, growth of the population is negative because resource availabilities are too low to support a growth rate balancing the loss rate  $m_i$ ; on the other side of the isocline, resource availabilities support growth at a rate exceeding  $m_i$ . The corner of this isocline sits at the point  $(R_1, R_2) = (R_{1(i)}^*, R_{2(i)}^*)$ , where the quantity  $R_{j(i)}^*$  is the resource availability at which population  $i$  growing alone, reaches equilibrium under limitation only by resource  $j$ . Thus  $R_{j(i)}^*$  is equivalent to the quantity denoted  $R_{(i)}^*$  above, when only a single resource was considered.

The isocline graphically represents the conditions for equilibrium of equation (2.17a) for population growth, but equation (2.17b) for resource dynamics must also be at equilibrium. For appropriate choices of  $\Psi_j(\dots)$ , the conditions for resource equilibrium reduce to a vector equation

$$\mathbf{u} = \begin{bmatrix} S_1 - R_1^* \\ S_2 - R_2^* \end{bmatrix} = \begin{bmatrix} N_i^* Q_{i1} \\ N_i^* Q_{i2} \end{bmatrix} = \mathbf{c}_i, \quad (2.22)$$

where the vector  $\mathbf{c}_i$ , on the right-hand side, is the **consumption vector**, and the vector  $\mathbf{u}$ , on the left-hand side, is the **supply vector**, indicating the trajectory that

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*Figure 2.5* Graphical model of one population growing in dependence on two essential resources: (a) Contours of growth rate are rectilinear, with corners lying on a curve (dashed) separating the  $R_1, R_2$ -plane into regions where availability of resource 1 only limits growth, and where availability of resource 2 only limits growth. (b) One of these contours provides a growth rate that just balances the population's loss rate, and it thus defines a zero net growth isocline. The corner of this isocline lies at the point  $(R_{1(i)}^*, R_{2(i)}^*)$  explained in the text. (c) Representation of the equilibria for two supply points ( $S_A$  and  $S_B$ ). These occur at points where the vector equation (2.22) is satisfied, balancing the resource consumption vectors ( $c_{i,A}$  and  $c_{i,B}$ ) against resource supply vectors ( $u_A$  and  $u_B$ ). For supply point A, growth of population  $i$  is limited by resource 1 at equilibrium; for supply point B, growth of population  $i$  is limited by resource 2 at equilibrium.

$(R_1, R_2)$  would take if consumption ceased (MacArthur, 1972; Tilman, 1982). Simultaneous solution of eqs. (2.21) and (2.22) for the unknowns  $R_{1(i)}^*$ ,  $R_{2(i)}^*$  and  $N_{(i)}^*$  defines the equilibrium for a single population.

The isocline and the consumption and supply vectors provide graphical tools to represent this equilibrium (Fig. 2.5c). First, any point in the  $R_1 R_2$ -plane representing an equilibrium must lie on the isocline. The slope of the consumption vectors is fixed by the parameters  $Q_{i1}$  and  $Q_{i2}$  – it is simply the ratio  $-Q_{i2}/Q_{i1}$  (the minus sign indicates that consumption vector points toward the origin of the

$R_1R_2$ -plane, since consumption reduces resource availability). Solution of equation (2.22) requires that the supply vector have the same slope, but point in the opposite direction. In fact, the supply vector is directed towards a point  $\mathbf{S} = (S_1, S_2)$  in the  $R_1R_2$ -plane, called the **supply point**. Therefore, the graphical representation of the equilibrium of equation system (2.17) consists of finding the point lying on the isocline such that a supply vector of slope  $Q_{i2}/Q_{i1}$  also points toward the supply point (as shown for two supply points  $\mathbf{S}_A$  and  $\mathbf{S}_B$  in Fig. 2.5c).

The remaining equilibrium requirement is that the magnitudes of the supply and consumption vectors be equal; solving this condition determines the equilibrium density  $N_{(i)}^*$ , for population  $i$  alone. No such solution is possible with positive  $N_{(i)}^*$ , unless the supply point lies on the side of the isocline away from the origin; if the supply point lies between the coordinate axes and the isocline, then the habitat is too poor in resources to support a population at equilibrium. For equilibria lying above the curve defined by  $\mu_{i1}(R_1) = \mu_{i2}(R_2)$ , growth of population  $i$  will be limited by resource 1 (e.g. point  $\mathbf{S}_A$  in Fig. 2.5c); for equilibria lying below this curve, growth will be limited by resource 2 (e.g. point  $\mathbf{S}_B$  in Fig. 2.5c).

Competition between two species for two essential resources is represented by superimposing the graphical elements derived above. Coexistence requires that the isoclines of the competing populations intersect (as drawn in Fig. 2.6a), implying that there is a set of resource availabilities for which each population alone can increase (regions I and II, Fig. 2.6a), thus satisfying Phillips' (1973) coexistence condition. For essential resources following the Liebig principle of limitation (equation 2.20), satisfaction of Phillips' condition requires that

$$R_{l(1)}^* < R_{l(2)}^* \quad \text{and} \quad R_{2(2)}^* < R_{2(1)}^* \quad (2.23a)$$

or

$$R_{l(2)}^* < R_{l(1)}^* \quad \text{and} \quad R_{2(1)}^* < R_{2(2)}^* \quad (2.23b)$$

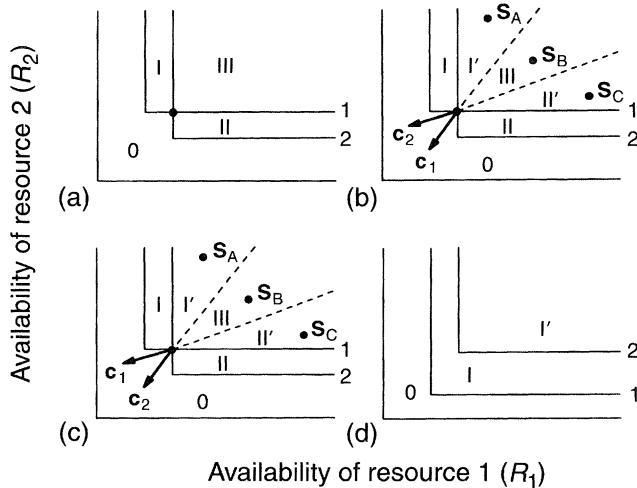
These conditions say that one population must be a superior competitor for one resource and an inferior competitor for the other, and the other population must be a superior competitor for the other resource, and an inferior competitor for the other.

Intersection of the isoclines guarantees that there is an equilibrium point for both species. To see whether this point represents feasible and stable coexistence, consumption and supply vectors must be examined. The overall consumption vector is the resultant ( $\mathbf{c}$ ) of the single-species vectors  $\mathbf{c}_1$  and  $\mathbf{c}_2$ ; formally,

$$\mathbf{c} = \mathbf{c}_1 + \mathbf{c}_2 = \begin{bmatrix} N_1^* Q_{11} \\ N_1^* Q_{12} \end{bmatrix} + \begin{bmatrix} N_2^* Q_{21} \\ N_2^* Q_{22} \end{bmatrix}. \quad (2.24)$$

For meaningful equilibrium solutions (with positive densities for both populations) the resultant lies between  $\mathbf{c}_1$  and  $\mathbf{c}_2$ . This is possible only for supply points that lie between the two lines sharing the slopes of the consumption vectors, and projected along them away from the origin (e.g. point  $\mathbf{S}_B$  in Fig. 2.6b).

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*Figure 2.6* Graphical model of two species competing for two essential resources: (a) Isoclines for species 1 and 2 intersect, partitioning the  $R_1R_2$ -plane into four regions. The following outcomes occur for supply points falling in these regions: 0, neither species can persist, regardless of whether the other is present; I, species 1 only can persist, regardless of whether species 2 is present; II, species 2 only can persist, regardless of whether species 1 is present; III, both species can persist if the other is absent, and when both are present, resource competition determines which species persist. There is an equilibrium with both species present at the point indicated by the solid circle. (b) Coexistence is possible for some supply points, because the equilibrium (solid circle) is stable. Realization of this possibility requires that the supply point fall in region III, between the dashed lines projected from the species' consumption vectors ( $c_1$  and  $c_2$ ). The relative positions of the consumption vectors imply that the coexistence equilibrium is stable for such supply points. For supply points in region I', species 1 competitively excludes species 2; for supply points in region II', species 2 competitively excludes species 1. (b) A priority effect is possible for some supply points, because the equilibrium (solid circle) is unstable. Realization of this possibility requires that the supply point fall in region III, between the dashed lines projected from the species' consumption vectors ( $c_1$  and  $c_2$ ). The relative positions of the consumption vectors imply that the coexistence equilibrium is unstable for such supply points, so that the eventual outcome depends on initial conditions. For supply points in region I', species 1 competitively excludes species 2; for supply points in region II', species 2 competitively excludes species 1. (d) Neither coexistence nor priority effects are possible. Isoclines do not intersect, and species 1 competitively excludes species 2 for supply points in region I'. For supply points in region I, species 1 only can persist, whether or not species 2 is present. For supply points in region 0, neither species can persist. Reproduced from Tilman (1982), with permission.

Thus coexistence is feasible only for a restricted set of supply points (region III in Fig. 2.6b). For supply points falling outside of this region, one or the other competitor goes extinct (or both do). For supply points lying in regions I and I' of Fig. 2.6b (such as point  $S_A$ ), species 2 goes extinct. In region I it would do so

whether or not species 1 was present. However, for supply points in region I' species 2 persists in the absence of species 1, but not in its presence, because it is competitively excluded. Similarly, for supply points lying in regions II and II' (such as point  $S_C$ ), population 1 goes extinct. In region II it would do so whether or not species 2 was present, and in region II' species 1 persists in the absence of species 2, but is competitively excluded in its presence. Finally, for supply points lying in region 0 of Fig. 2.6b, neither species persists – the habitat is too resource-poor for either of them.

León and Tumpson (1975) applied a standard, linearized stability analysis to the equilibrium just derived. Each competitor is limited by a different resource at this equilibrium, and sufficient conditions for stability are that a given population must consume proportionally more of the resource limiting its own growth, than of the resource limiting its competitor's growth. Figure 2.6b illustrates a case where coexistence at equilibrium is stable. The equilibrium point falls on the portion of species 1's isocline that is parallel to the  $R_1$  axis, indicating that under conditions of equilibrium coexistence, growth of species 1 is limited by the availability of resource 2. Conversely, the equilibrium point falls on the portion of species 2's isocline where resource 1 limits population growth. Graphically, the stability conditions for this equilibrium are satisfied if the consumption vector for population 1 has a steeper slope than that for population 2, so that it consumes more of resource 2 (which limits population 1) than of resource 1 (which limits population 2).

When the stability conditions are not met, consumption vectors are arranged as in Fig. 2.6c, indicating that each species consumes relatively more of the resource that limits its competitor's growth, and relatively less of the resource that limits its own growth. In such a case, when the supply points fall in regions 0, I, I', II and II', outcomes are as described above: at least one species goes extinct, sometimes as a consequence of competition. For supply points in region III of Fig. 2.6c (such as point  $S_B$ ), there is a feasible, but unstable equilibrium for both competitors. Instead of going to this **interior equilibrium**, system dynamics will tend towards one of the two **stable boundary equilibria** of the system's phase space – where species 1 persists alone, and where species 2 persists alone. Initial conditions determine which outcome is obtained in a particular case, thus generating a **priority effect**, such that the competitor having the initial advantage in relative abundance (usually) wins. Without knowledge of initial conditions, long-term outcomes in the unstable case cannot be predicted for all resource supply conditions. In contrast, when coexistence at equilibrium is stable, long-term outcomes for all resource supply conditions are predictable without knowledge of initial conditions.

For completeness, cases where isoclines do not intersect (Fig. 2.6d) also have long-term outcomes that do not depend on initial conditions. Here, one species' isocline lies closer to the origin than the other population's, throughout the entire  $R_1R_2$ -plane. The species with the isocline closer to the origin is a superior competitor for both resources (species 1 in Fig. 2.6d). For supply points in regions I or I' of Fig. 2.6d, species 2 goes extinct; for supply points in region I', population 2

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would be able to persist if growing alone, but is competitively excluded by population 1.

### *Storage of essential resources*

The simple model just sketched can be extended to include internal storage of resources, by extending equation system (2.7) to an additional resource. Quotas of both resources vary, becoming larger as growth rate increases. At equilibrium, equation (2.22) still determines consumption vectors, but the slopes of these vectors vary with a species' growth rate at equilibrium, hence with its loss rate. It is then possible that coexistence of competitors will be stable or unstable, depending on loss rates.

This possibility has been examined for phytoplankton and inorganic nutrients. The greatest impact of resource storage and quota variation on competition occurs when one resource has a relatively fixed quota, and the other a relatively flexible quota (Turpin, 1988). This situation arises when one nutrient plays a predominantly structural role in algal cells (e.g. carbon or silicon), and shows little variation in quota, because of the relatively constant amount needed to constitute a viable cell, while the other nutrient plays more varied biochemical roles (e.g. nitrogen or phosphorus), some of which can be reduced while remaining viable, leading to greater variation in quota (Table 2.2). For those resources with which it can be parsimonious and reduce its quota, a population increases its competitive ability considerably (Turpin, 1988).

*Table 2.2* Ranges of the ratio of maximal to minimal quota (per cell) for nutrient elements for phytoplankton. In some cases,  $Q_{\max,i}$  was calculated from related quantities according to formulae derived by Morel (1987). Silicon is used only by some phytoplankton species, while carbon, nitrogen and phosphorus are used by all

<i>Nutrient element</i>	<i>Range of <math>Q_{\max,i}/Q_{\min,i}</math></i>	<i>References</i>
C	1	Goldman, Oswald and Jenkins, 1974
Si	1.9–3.1	Tilman and Kilham, 1976; Paasche, 1973; Harrison <i>et al.</i> , 1977
N	1.3–9.1	Morel, 1987; Goldman and McCarthy, 1978; Laws and Bannister, 1980; Elrifi and Turpin, 1985; Caperon and Meyer, 1972a, b; Caperon and Ziemann, 1976; Thomas and Dodson, 1972; Harrison <i>et al.</i> , 1977; Mickelson, Maske and Dugdale, 1979
P	2–427	Morel, 1987; Healey and Hendzel, 1988; Tilman and Kilham, 1976; Holm and Armstrong, 1981; Kilham, Kott and Tilman, 1977; Gotham and Rhee, 1981a; Kennedy, 1984; Grover, 1991a; Sandgren, 1988; Elrifi and Turpin, 1985; Droop, 1974, 1975; Fuhs <i>et al.</i> , 1972

Using laboratory cultures, Tilman (1977) studied competition between two freshwater diatoms, *Asterionella formosa* and *Cyclotella meneghiniana*, for two resources, silicon and phosphorus. The former nutrient is primarily structural (a cell wall constituent), with restricted variation in quota, while the latter varies widely. Based on underlying physiological data (Tilman and Kilham, 1976), Tilman parameterized a model of the form of equation system (2.17); the growth functions are shown in Fig. 1.2b, c. He also parameterized a model allowing for variable quotas, appending another nutrient to equation system (2.7). His predictions and results are summarized in Fig. 2.7. The dilution rate of each experimental culture sets the loss rate for both species, and at each loss rate, the

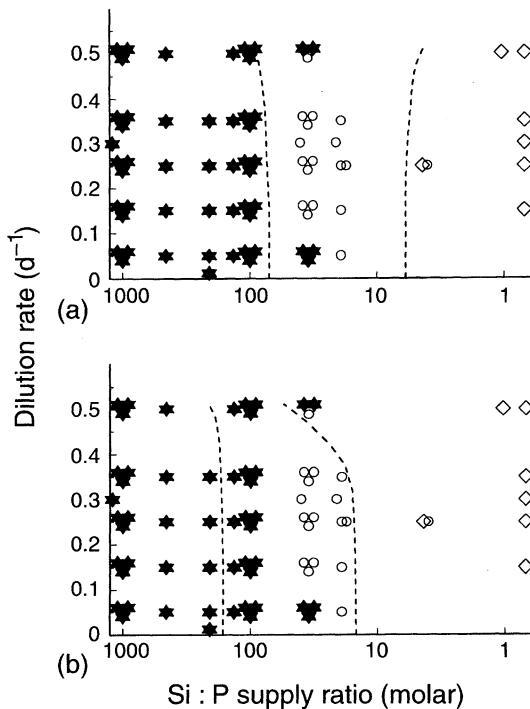


Figure 2.7 Competition between the algae *Asterionella formosa* and *Cyclotella meneghiniana* for silicon and phosphorus. Predictions of competitive outcomes for different dilution rates and supply ratios of silicon to phosphorus are summarized as the dashed lines: for high supply ratios, *A. formosa* is predicted to dominate; for intermediate supply ratios, coexistence is predicted; and for low supply ratios *C. meneghiniana* is predicted to dominate (note that the abscissa decreases from left to right). Experimental outcomes are shown by symbols: stars, *A. formosa* dominated; circles, coexistence; diamonds, *C. meneghiniana* dominated: (a) Predictions based on a simple model ignoring resource storage. (b) Predictions based on a model allowing resource storage. Reproduced from Tilman (1977), with permission.

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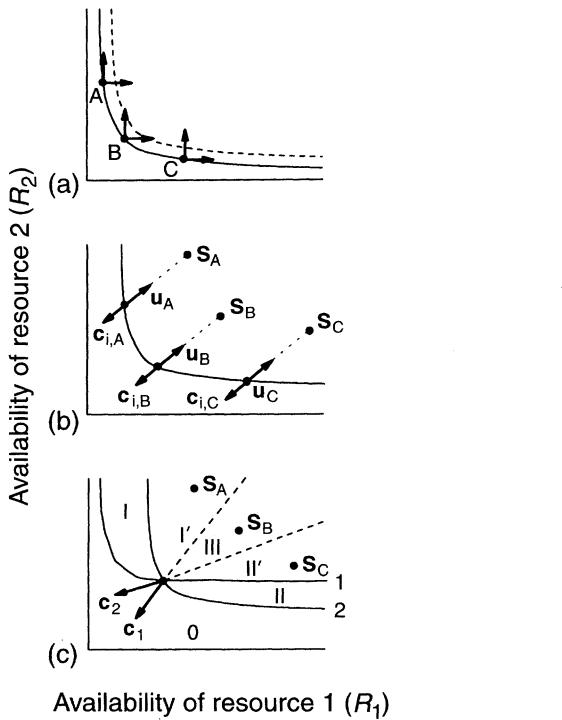
experimental gradient in the supply ratio of silicon to phosphorus corresponds to a shift in supply like that drawn for points  $S_A$ ,  $S_B$ , and  $S_C$  in Fig. 2.6b, passing through a region of coexistence.

The predictions of Fig. 2.7 differ between the fixed and variable quota models, with the degree of disagreement increasing with loss rate. The simpler, fixed quota model gave better predictions of the experimental results, suggesting that it may be an adequate approximation. However, because the underlying physiology demonstrably involved quota variation, Tilman (1977) noted that a judicious choice of the fixed value of  $Q_{ij}$  was essential to quantitative prediction. For both species and both resources, he used quotas allowing growth at half the maximum rate. His experiments were performed at relatively low equilibrium growth rates (less than half-maximal), and use of quotas characterizing more rapid growth would have been less accurate. The greater realism of the variable-internal-stores model did not provide better predictions – possibly due to the compounded errors of estimating its many parameters. This result suggests that for understanding competitive outcomes at equilibrium, well-chosen simple models may be preferable to more realistic, but also more error-prone, models.

### *Interactive-essential resources*

In the theory developed above, population growth switches distinctly between states of limitation by one resource or another. Such simple switching closely describes the growth of microalgae in relation to mineral nutrients (Droop, 1974; Rhee, 1978), but may be an oversimplification for other organisms. Even if two resources are each required for positive net growth, it may be possible for a consumer to vary its phenotype in an adaptive manner, to acquire more of a resource more limiting to its growth rate, at the cost of reduced consumption of another resource less limiting to growth. Tilman (1988) suggested that isoclines for population growth should then resemble those of Figs. 2.5 and 2.6, but have rounded corners (Fig. 2.8), based on arguments of optimal foraging for two resources. Chen and Christensen (1985) suggested that non-adaptive variability in consumer phenotypes (e.g. due to age-structure) might also generate the same shape of isocline, and Loreau and Ebenhöh (1994) derived similar isoclines for consumers with complex life cycles.

Resources giving such isoclines are called **interactive-essential** (Tilman, 1982), because population growth is determined by the availability of both resources, rather than by the availability of just one of the two growth-limiting resources at a time. For interactive-essential resources, there is a point on the isocline that represents equal limitation by the two resources, in that a unit increase in either resource gives the same increment to population growth (point B in Fig. 2.8a). At points further out on the limbs of the isocline, population growth responds greatly to an increase in one of the resources, and hardly at all to an increase in the other (points A and C on Fig. 2.8a). Thus it is possible to characterize such a population as being more or less limited by a particular resource, or



*Figure 2.8* Graphical model of two species competing for two interactive-essential resources: (a) Isocline for growth of a single population. Vectors illustrate the response to enrichment of one or the other resource at various points on the isocline, by reference to a contour (dashed line) showing a higher growth rate. (b) Representation of equilibria for one population growing in equilibrium with three supply points ( $S_A$ ,  $S_B$  and  $S_C$ ). Supply ( $u$ ) and consumption ( $c_i$ ) vectors are constructed as for essential resources; where these vectors balance, the system is in equilibrium (solid circles). (c) Two species that can coexist. Their isoclines intersect, creating a potential coexistence equilibrium (solid circle), and the relative positions of their consumption vectors ( $c_i$ ) imply stability (as explained in the text). Projecting along the slopes of these vectors defines region III of the  $R_1R_2$  plane, where supply points lead to coexistence (e.g. point  $S_B$ ). For supply points in region I' (e.g.  $S_A$ ), species 1 competitively excludes species 2. For supply points in region II' (e.g.  $S_B$ ), species 2 competitively excludes species 1. For supply points in region I, species 1 only can persist, whether or not species 2 is present. For supply points in region II, species 2 only can persist, whether or not species 1 is present. For supply points in region 0, neither species can persist. Reproduced from Tilman (1988), with permission.

equally limited by both. However, there is continuous variation in the degree to which a particular resource is limiting.

Competition for interactive-essential resources proceeds much like that for essential resources. Vectors describing consumption and supply again represent conditions for equilibrium growth of a single species (Fig. 2.8b). With two

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competing species, the cases presented in Fig. 2.8 all have their parallels for interactive-essential resources. Figure 2.8c presents a case of stable coexistence. Unless the coexistence equilibrium lies exactly on the point at which one or the other competitor is equally limited by both resources, each competitor can be classified as relatively more or less limited by a given resource. Stability of the coexistence equilibrium depends on the relative slopes of the consumption vectors, and requires that each population consume proportionally more of the resource that more limits its own growth, than of the resource that more limits its competitor's growth (León and Tumpson, 1975). As drawn, species 1 in Fig. 2.8c is more limited by resource 2 than resource 1, and the steeper the slope of its consumption vector relative to that of species 2 indicates that species 1 consumes proportionally more of resource 2, satisfying the stability conditions.

For interactive-essential resources, as opposed to essential resources, there is one qualitatively new possibility. If two species' isoclines differ greatly in curvature, they could intersect twice, producing a complicated set of competitive outcomes, including priority effects (Taylor and Williams, 1975).

### 2.4.2 Substitutable resources

Thus far, we have considered only resources that cannot be substituted by another, because each fills a unique biological role. Most heterotrophs, however, probably consume resources that are substitutable. Herbivores and predators consume preformed packets of organic matter: potentially each such resource includes a full complement of the substances required for growth. Saprotrophs consume preformed organic molecules, which may be substitutable within broad categories. Thus, many of the resources consumed by animals may be substitutable. Indeed, this may be a fundamental difference between competition among plants and among animals (León and Tumpson, 1975).

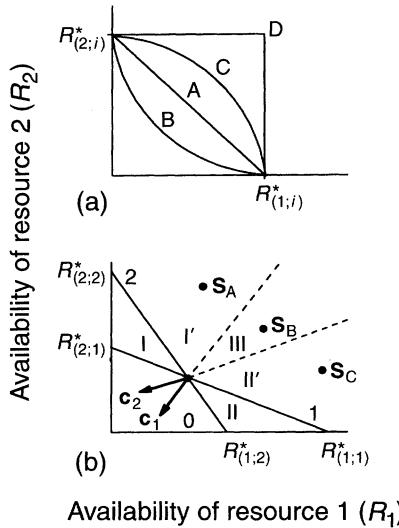
Of course, another difference is that the resources consumed by many animals are biotic resources, with their own population growth dynamics. For the moment, however, we treat substitutable resources as abiotic. In some cases, this is not unrealistic. For decomposers, consuming dead organic matter, resource dynamics may be adequately described while ignoring resource reproduction.

In the simplest cases, consumer population growth is a function of a linear combination of two substitutable resources (MacArthur and Levins, 1964),

$$\mu_i(R_1, R_2) = \mu_{i1}(R_1) + \mu_{i2}(R_2), \quad (2.25)$$

so that the isocline for population growth is linear in the  $R_1, R_2$ -plane (Fig. 2.9a). The two resources are then called **perfectly** or **linearly substitutable**, and the isocline is the line connecting the points  $R_{(1;i)}^*$  and  $R_{(2;i)}^*$ , which are the equilibrium resource availabilities in respective subsystems containing population  $i$  and resource 1 only, and containing population  $i$  and resource 2 only (Fig. 2.9a). The notation is that an equilibrium subscripted ' $(j;i)$ ' pertains to a system of only consumer population  $i$  and resource  $j$ .

Curved isoclines may also occur. If the isocline lies below the line connecting



**Figure 2.9** Graphical model of two species competing for two substitutable resources: (a) Possible shapes for the isocline of a single population: A, linearly substitutable resources; B, complementary resources (reproduced from Tilman, 1982, with permission); C, antagonistic resources; D, switching resources. (b) Two species that can coexist while competing for the two resources. Their isoclines intersect, creating a potential coexistence equilibrium (solid circle), and the relative positions of their consumption vectors ( $c_i$ ) imply stability. Projecting along the slopes of these vectors defines region III of the  $R_1R_2$  plane, where supply points lead to coexistence (e.g. point  $S_B$ ). For supply points in region I' (e.g.  $S_A$ ), species 1 competitively excludes species 2. For supply points in region II' (e.g.  $S_B$ ), species 2 competitively excludes species 1. For supply points in region I, species 1 only can persist, whether or not species 2 is present. For supply points in region II, species 2 only can persist, whether or not species 1 is present. For supply points in region 0, neither species can persist.

$R_{(1;i)}^*$  and  $R_{(2;i)}^*$ , then both resources together provide higher growth rates than a linear combination would predict (Fig. 2.9a); Tilman (1982) called such resources **complementary**, citing as an example protein sources with complementary spectra of essential amino acids. If the isocline lies above the line connecting  $R_{(i;1)}^*$  and  $R_{(i;2)}^*$ , then both resources together provide lower growth rates than a linear combination would predict (Fig. 2.9a); Tilman (1982) called such resources **antagonistic**, and suggested that such an isocline could arise if the two resources have synergistic toxins, or must be obtained in spatially separated habitats. The limiting case of antagonistic resources is a rectilinear isocline (Fig. 2.9a), characterizing what Tilman (1982) called **switching** resources, because at equilibrium a consumer population relies on one resource or the other, but not both.

Provided that the isocline decreases monotonically from  $R_{(2;i)}^*$  to  $R_{(1;i)}^*$ , the

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graphical machinery presented above applies to substitutable resources. An increasing portion of the isocline would indicate that one resource is inhibitory to population growth. Ignoring such a possibility graphical analysis proceeds similarly for all cases shown in Fig. 2.9a, so only the simple linear case is presented.

In the case of substitutable resources, determination of consumption vectors may be more tricky than for essential resources. One possibility is a single slope  $-Q_{i2}/Q_{i1}$  for all consumption vectors belonging to species  $i$ . However, optimal foraging theory suggests that this is unlikely (Tilman, 1982): depending on the underlying foraging constraints, either consumption of resources in proportion to their availability, or specialization on only one of the resources, are the likely cases. In the latter case, the population growth isocline is the rectilinear form for switching resources, even though the resources themselves might be substitutable from a nutritional standpoint. In some cases, the consumption vector's slope may result from complex behaviors of predator and prey not adequately anticipated by optimal foraging theory.

Figure 2.9b shows a graphical example in which stable coexistence is possible, for at least some supply conditions of two substitutable resources. Species 1 is the superior competitor for resource 2, which is indicated by  $R_{(2;2)}^* > R_{(1;2)}^*$ , so that when resource 2 alone is available, species 1 is the superior competitor. Growth of species 1 is also more limited by resource 2 than by resource 1: assuming the isoclines are all parallel, then a unit increase of resource 2 causes a larger increase in species 1's growth rate than a unit increase of resource 1. Conversely, species 2 is the superior competitor for resource 1, because  $R_{(1;1)}^* < R_{(2;1)}^*$ . Growth of species 2 is also more limited by resource 1 than by resource 2. To satisfy the conditions for stability (León and Tumpson, 1975), the consumption vector for population 1 is drawn with a steeper slope than that for species 2. Thus each species consumes proportionally more of the resource that most limits its growth.

The predictions of the theory of competition for substitutable resources were tested by Rothhaupt (1988) for two herbivorous rotifers, *Brachionus calyciflorus* and *B. rubens*, growing on two green algae, *Chlamydomonas sphaeroides* and *Monoraphidium minutum*. Using studies of ingestion and population growth rates (Fig. 1.4), Rothhaupt (1988) successfully predicted competitive outcomes at equilibrium, for 11 of 12 experimental treatments (Fig. 2.10).

In these experiments, the two algal foods were supplied in a fashion approximating chemostat supply, by daily removing a fixed volume from each culture, and replacing it with a mixture of algae at fixed ratios, and algal growth was suppressed by keeping the cultures in the dark. Thus, the influence of algal population growth on resource dynamics was minimized, allowing the algae to be treated as abiotic resources. For rotifers feeding on algae in nature, and for many other animals, prey population growth probably dominates resource dynamics. Thus, we now ask: how must this approach be altered for biotic resources?

Part of the answer was provided by MacArthur (1972), who analyzed competition for substitutable, biotic resources. The same isoclines as sketched above

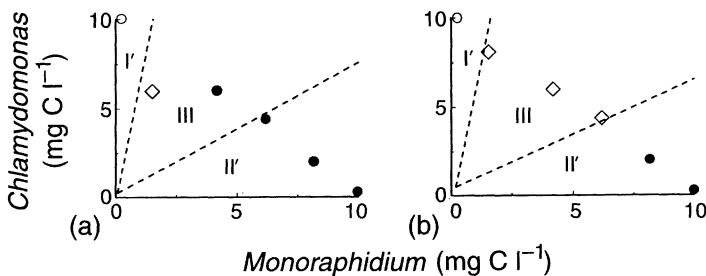


Figure 2.10 Competition between the rotifers *Brachionus rubens* and *Brachionus calyciflorus* for two algal species as food: *Chlamydomonas sphaeroides* and *Monoraphidium minutum*. Dashed lines separate the plane of resource availabilities into regions of dominance and coexistence, according to the theory illustrated in Fig. 2.9b: region I', *B. calyciflorus* is predicted to dominate; region II', *B. rubens* is predicted to dominate; region III, coexistence is predicted. Experimental outcomes are shown by symbols: open circles, *B. calyciflorus* dominated; diamonds, coexistence; solid circles, *B. rubens* dominated. (a) Loss rate ( $D$ )  $0.2 \text{ d}^{-1}$ . (b) Loss rate  $0.45 \text{ d}^{-1}$ . Reprinted from Rothhaupt (1988), with permission.

apply to population growth, and coexistence at equilibrium again requires their intersection. A balance of consumption and supply vectors is also required, but for biotic resources, the supply vector is not simply determined by a supply point. Instead, it points in a direction determined by the growth dynamics of the resource populations. It would be possible for coexistence at equilibrium to be infeasible, due solely to a direction of the supply vector which cannot be balanced by any resultant of the competitor's consumption vectors, even if all other coexistence conditions are satisfied.

León and Tumpson (1975) considered biotic resources in their stability analyses, under the assumption that the supply function considered as a function of  $R_j$  was a 'generalized logistic' function. That is,  $\Psi_j(R_j)$  was assumed to have the following properties: for a unique value of  $R_j = K$  (the **carrying capacity**), population growth is zero ( $\Psi_j$  vanishes); population growth is positive when  $R_j < K$ , and negative when  $R_j > K$ ; and  $\Psi$  is a decreasing function of  $R_j$ . Then, the same stability condition given above applies: coexistence is stable when each competitor consumes proportionally more of the resource that most limits its own growth, which is again a statement about the slopes of consumption vectors at equilibrium. However, this result depends critically on noninteraction among resource populations. Stability conditions are more complex and perhaps more stringent, when the resource populations themselves compete, or otherwise interact. In Chapter 5, it is argued that when competition for biotic resources is likely, so too is instability, so that these equilibrium analyses may be inadequate to study competition for biotic resources.

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### 2.4.3 Resource-ratio gradients

There is a common pattern to all of the cases presented above, in which two species compete for two resources. In any configuration in which coexistence is possible for at least some conditions of resource supply, the  $R_1R_2$ -plane is divided into six disjoint regions, such that long-term outcomes are determined by which of these regions contained the resource supply point. On Figs. 2.6b, c, 2.8c, and 2.9b, there is a region, labelled 0, corresponding to extinction of both species, because supply points in this region represent habitats too impoverished for either. There are also regions, labelled I and II, where only species 1 or 2, respectively, persist for supply points contained in those regions. Such regions must exist for any system in which coexistence is possible (Phillips, 1973). In the regions labelled I' and II', species 1 and 2, respectively, competitively exclude the other species. These regions are separated by the sixth region, labelled III, for which coexistence occurs, when stability conditions are met.

When these latter conditions are met, patterns of population abundance and competitive outcomes follow a general pattern with respect to the ratio at which the two resources are supplied. Coexistence of two competitors occurs only when the supply ratio,  $S_2/S_1$ , is moderate. For extreme supply ratios, when one resource is in short supply while the other is abundant, competitive exclusion occurs. For all the cases of coexistence shown above, a plot of population abundance at equilibrium versus supply ratio has the same general pattern (Fig. 2.11a), with species 1 alone persisting for low supply ratios, coexistence for intermediate ratios, and species 2 alone persisting for high ratios. Moreover, when several species compete (Fig. 2.11b), at most two persist for any resource supply ratio, and their peaks of population abundance are arrayed along the resource-ratio axis. In such a case, each species that persists is a superior competitor to all other species, at some resource supply ratios, but not others. The **resource-ratio hypothesis** proposes that such patterns are common.

## 2.5 CONCLUDING REMARKS

In many examples presented here, competitive outcomes are predictable from knowledge of the resource-dependent consumption and growth rates of each competitor population studied in isolation, independent of any observations of competitive dynamics. This predictive capability and its theoretical basis have survived testing in laboratory studies with various organisms. This predictive ability is also a major advantage of mechanistic theories of resource competition, which distinguishes them from the Lotka–Volterra and related theories. Working from knowledge of species’ characteristics, an understanding of evolved adaptations to competition may be developed, and some measure of predictability might be achievable in real-world applications. The central results of simple resource competition theory – the  $R^*$ -rule and the resource-ratio hypothesis – exemplify these predictions for competition for one and two resources. In the next chapter, we review experiments that test these predictions.

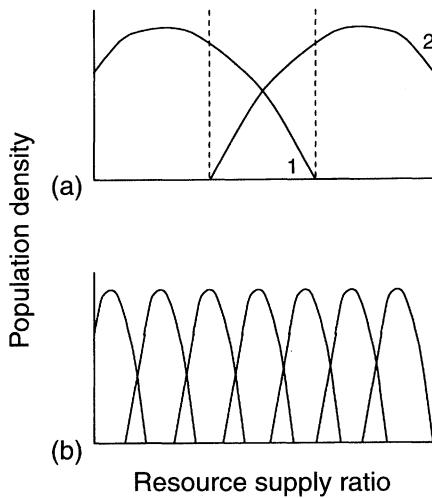


Figure 2.11 The resource-ratio hypothesis: (a) Population densities of two competitors in relation to the supply ratio of the resources. At extreme supply ratios (to the left or right of the two dashed lines), competitive exclusion of one or the other competitor occurs, while for intermediate supply ratios (between the two dashed lines), there is coexistence. (b) More than two competing species.