

# 1

## CHAPTER

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# Elementary Population Dynamics



In many contexts it is important to understand the characteristics of single populations of organisms. A wildlife manager, for example, needs to predict what the density of a population of deer or cod would be under different management plans. Or an agronomist may wish to know the yield of a population of maize plants when planted at a particular density. In more theoretical applications, we are interested in knowing, for example, the rate at which a population changes its density in response to selection pressure. These topics are typical of the field called population ecology.

The unit of analysis is, not surprisingly, the population, a concept that is at once simple and complicated. The simple idea is that a population is a collection of individuals. But, as most ecologists intuitively know, the idea of a population is considerably more complex when one deals with the sort of real-life examples mentioned above. To know what size limits one should place on catch for a fish species, one must know not only how many fish are in the population but also the size distribution of that population and how that distribution is related to the population's overall reproduction. To decide when to take action on the emergence of pest species in forests or farms, one must know the distribution of individuals within life stages. In the determination of whether a species is threatened with extinction, its distribution in space and the amount of movement among subpopulations (i.e., metapopulation dynamics) are far more important than simply its numerical abundance. And, to cite the most cited example, the absolute abundance of the human population has little to do with anything of interest com-

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Jellyfish sometimes form large populations that grow exponentially, at least for a while.

pared with the activities undertaken by the members of that population.

Thus, the subject of population ecology can be very complicated. But, as we do in any science, we begin by assuming that it is simple. We eliminate the complications, make simplifying assumptions, and try to develop general principles that might form a skeleton upon which the flesh of real-world complications might meaningfully be attached. This chapter covers the first two essential ideas of that skeleton: density independence and density dependence.

### **Density Independence: The Exponential Equation**

It is surprising how quickly a self-reproducing phenomenon becomes big. The classic story goes like this: Suppose you have a lake with some lily pads in it and suppose each lily pad replicates itself once a week. If it takes a year for half the lake to become covered with lily pads, how long will it take for the entire lake to become covered? If one does not think too long or too deeply about the question, the quick answer seems to be about another year. But a moment's reflection retrieves the correct answer, only one more week.

This simple example has many parallels in real-world ecosystems. A pest building up in a field may not seem to be a problem until it is too late. A disease may seem much less problematical than it really is. The simple problem of computing the action threshold (the density a pest population must reach before you have to spray pesticide) requires the ability to predict a population's size on the basis of its previous behavior. If half the plants have been attacked within 3 months, how long will it be before they are all attacked?

To understand even the extremely simple example of the lily pads, one constructs a mathematical model, usually quite informally in one's head. If all the lily pads on the pond replicate themselves once a week, then, in a pond half-filled with lily pads, each one of those lily pads will replicate in the next week and thus the pond will be completely filled up. To make the solution to the problem general we say the same thing, but instead of labeling the entities lily pads, we call them something general, say organisms. If organisms replicate once a week and the environment is half full, it will take only one week for it to become completely full. Implicitly,

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the person who makes such a statement is saying out loud the following equation:

$$N_{t+1} = 2N_t \quad (1)$$

$N$  is the number of organisms, in this case lily pads. Instead of  $t$ (time), say this week, and instead of  $t + 1$ , say next week, and equation 1 is simply “the number of lily pads next week is equal to twice the number this week.”

Of course, writing down equation 1 is no different than making any of the statements that were made previously about it. But by making it explicitly a mathematical expression, we bring to our potential use all the machinery of formal mathematics. And that is actually good, even though beginning students sometimes do not think so.

Using equation 1, we can develop a series of numbers that reflect the changes of population numbers over time. For example, consider a population of herbivorous insects: if each individual produces a single offspring once a week, and those offspring mature and also produce an offspring within a week, we can apply equation 1 to see exactly how many individuals will be in the population at any point in time. Beginning with a single individual we have, in subsequent weeks, 2, 4, 8, 16, 32, 64, 128, and so on. If we change the conditions such that the species replicates itself twice a week, equation 1 becomes

$$N_{t+1} = 3N_t \quad (2)$$

(with a 3 instead of a 2, because before we had the individual and the single offspring it produced, now we have the individual and the two offspring it produced). Now, beginning with a single individual, we have, in subsequent weeks, 3, 9, 27, 81, 243, and so on.

We can use this model in a more general sense to describe the growth of a population for any number of offspring at all (not just 2 and 3 as above). That is, write,

$$N_{t+1} = RN_t \quad (3)$$

where  $R$  can take on any value at all.  $R$  is frequently called the finite rate of population growth (or the discrete rate).

It may have escaped notice in the above examples, but either of the

series of numbers could have been written with a much simpler mathematical notation. For example, the series 2, 4, 8, 16, 32, is actually  $2^1, 2^2, 2^3, 2^4, 2^5$ , and the series 3, 9, 27, 81, 243, is actually  $3^1, 3^2, 3^3, 3^4, 3^5$ . So we could write,

$$N_t = R^t \quad (4)$$

which is just another way of representing the facts as described by equation 3. (Remember, we began with a single individual, so  $N_0 = 1.0$ .)

We now wish to represent the constant  $R$  (of equation 4) in a different fashion, to make further exposition easier. It is a general rule that any number can be written in many ways. For example, the number 4 could be written as  $8/2$ , or  $9 - 5$ , or  $2^2$ , or many other ways. In a similar vein, an abstract number, say  $R$ , could be written in any number of ways:  $R = 2b$ , where  $b$  is equal to  $R/2$ , or  $R = 2^b$ , in which case  $b = \ln(R/2)$  (where  $\ln$  stands for natural logarithm). If we represent  $R$  as  $2.7183^r$ , a powerful set of mathematical tools becomes immediately available. The number 2.7183 is Euler's constant, usually symbolized as  $e$  (actually 2.7183 is rounded off and thus only approximate). It has the important mathematical property that its natural logarithm is equal to 1.0.

So, rewrite equation 4 as,

$$N_t = e^{rt} \quad (5)$$

which is the classical form of the exponential equation (where  $R$  has been replaced with  $e^r$ ). One more piece of mathematical manipulation is necessary to complete the toolbox necessary to model simple population growth. Another seemingly complicated but really rather simple relationship that is always learned (but frequently forgotten) in elementary calculus is that the rate of change of the log of any variable is equal to the derivative of that variable divided by the value of the variable. This rule is more compactly stated as,

$$\frac{d(\ln N)}{dt} = \frac{1}{N} \frac{dN}{dt} \quad (6)$$

So, if we rewrite equation 5 as,

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$$\ln(N_t) = rt$$

we can differentiate with respect to  $t$  to obtain,

$$\frac{d(\ln N)}{dt} = r \quad (7)$$

and we can use equation 6 to substitute for the left-hand side of 7 to obtain,

$$\frac{dN}{Ndt} = r$$

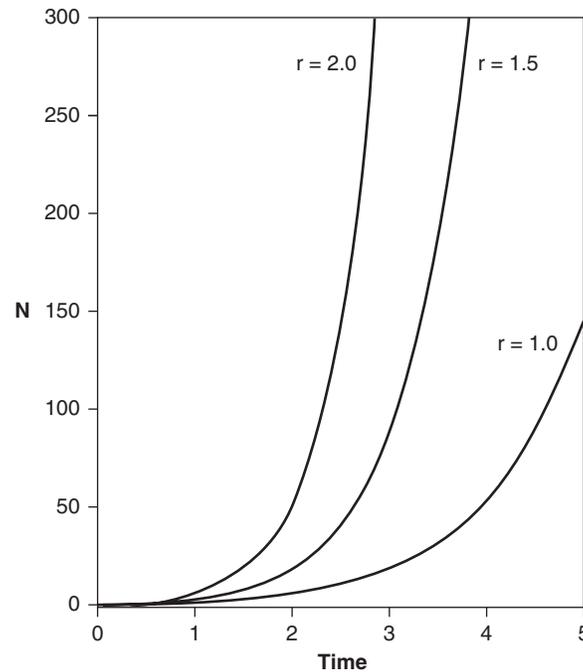
and after multiplying both sides by  $N$ , we obtain,

$$\frac{dN}{dt} = rN \quad (8)$$

Equations 5 and 8 are the basic equations that formally describe an exponential process. Equation 8 is the differentiated form of equation 5, and equation 5 is the integrated form of equation 8. They are thus basically the same equation (and indeed are quite equivalent to the discrete form—equation 3). Depending on the use to which they are to be put, any of the above forms may be used, and in the ecological literature one finds all of them. Their basic graphical form is illustrated in figure 1.1.

In the examples of exponential growth introduced above, the parameter ( $r$ , or  $R$ ) was introduced as a birth process only. The tacit assumption was made that there were no deaths in the population. In fact, all natural populations face mortality, and the parameter of the exponential equation is really a combination of birth and death rates. More precisely, if  $b$  is the birth rate (number of births per individual per time unit), and  $d$  is the death rate (number of deaths per individual per time unit), the parameter of the exponential equation is

$$r = b - d \quad (9)$$



**Figure 1.1.** Graphs of equation 5.

where the parameter  $r$  is usually referred to as the intrinsic rate of natural increase.

One other simplification was incorporated into all of the above examples. We presumed always that the population in question was initiated with a single individual, which almost never happens in the real world. But the basic integrated form of the exponential equation is easily modified to relax this simplifying assumption. That is,

$$N_t = N_0 e^{rt} \quad (10)$$

which is the most common form of writing the exponential equation. Thus, there are effectively two parameters in the exponential equation: the initial number of individuals,  $N_0$ , and the intrinsic rate of natural increase,  $r$ .

Putting the exponential equation to use requires estimation of the two parameters. Consider, for example, the data presented in table 1.1.

**TABLE 1.1**

Number of Aphids Observed per Plant in a Corn Field

<i>Date</i>	<i>Number of Aphids</i>	<i>ln(Number of Aphids)</i>
March 25	0.02	-3.91
April 1	0.5	-0.69
April 8	1.5	0.40
April 15	5	1.61
April 22	14.5	2.67

Here we have a series of observations over a 5-week period of the average number of aphids on a corn plant in an imaginary corn field.

As a first approximate assumption, let us assume that this population originates from an initial cohort that arrived in the milpa on March 18 (one week before the initial sampling). We can apply equation 10 to these data most easily by taking logarithms of both sides, thus obtaining,

$$\ln(N_t) = \ln(N_0) + rt \quad (11)$$

which gives us a linear equation of the natural logarithm of the number of aphids versus time (where we code March 18 as time=0, March 25 as time=1, April 1 as time=2, etc. . . .). Figure 1.2 is a graph of this line along with the original data to which it was fit, and figure 1.3 is a graph of the original data along with the fitted curve on arithmetic axes.

From these data we estimate 1.547 aphids per aphid per week added to the population (i.e., the intrinsic rate of natural increase,  $r$ , is 1.547, which is the slope of the line in figure 1.2). The intercept of the regression is -4.626, which indicates that the initial population was 0.0098 (that is, the anti ln of -4.626 is 0.0098), which is an average of about one aphid per 10 plants. Now, if we presume that once the plants become infected with more than 40 aphids per plant the farmer must take some action to try and control them, we can use this model to predict when, approximately, this time will arrive. The regression equation is,

$$\ln(N \text{ of aphids}) = -4.626 + 1.547t$$

which can be rearranged as,

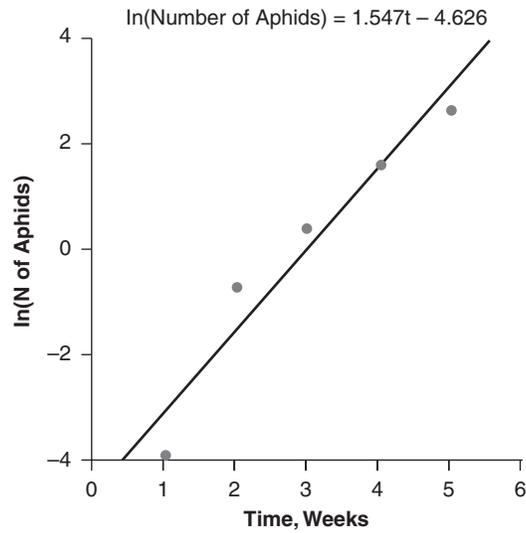


Figure 1.2. Plot of aphid data (from table 1.1).

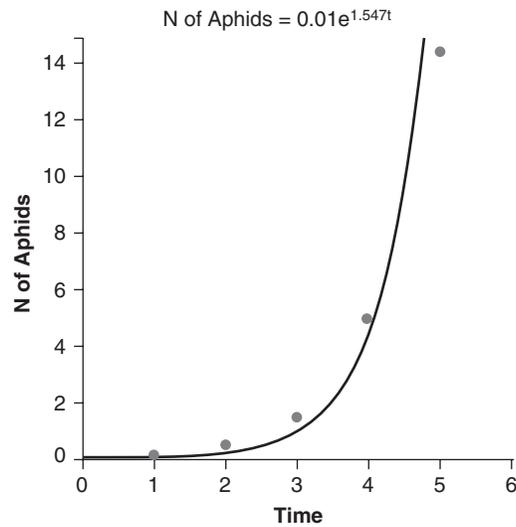


Figure 1.3. Aphid data from figure 1.2 plotted arithmetically.

$$t = [\ln(N \text{ of aphids}) + 4.626]/1.547$$

The natural log of 40 is 3.69, so we have,

$$t = (3.69 + 4.626)/1.547 = 5.375$$

Translating this number into the actual date (April 22 was time = 5), we see that the critical number will arrive about April 24 (actually at 3:00 P.M. on April 24, theoretically).

Naturally, the natural world contains many complicating factors, and the exact quantitative predictions made by the model could be quite inaccurate. As we discuss in later chapters, including some of the complicating factors will increase the precision of the predictions. On the other hand, April 24 really does represent the best prediction we have, based on available data. It may not be a very good prediction, but it is in fact the only one available. It may seem quite counterintuitive that, having taken five full weeks to arrive at only 14 aphids per plant, in only 2 more days the critical figure of 40 aphids per plant will be reached, but such is the nature of exponential processes. A simple model like this could help the farmer plan pest control strategies.

### **Density Dependence: Intraspecific Competition**

In the above section, we showed that any population reproducing at a constant per capita rate will grow according to the exponential law. Indeed, that is the very essence of the exponential law; each individual reproduces at a constant rate. However, the air we breathe and the water we drink are not completely packed with bacteria or fungi or insects; as they would be if populations grew exponentially forever. Something else must happen. That something else is usually referred to as intraspecific competition, which means that the performance of the individuals in the population depends on how many individuals are in it; this concept is commonly known as density dependence. Density dependence is a complicated issue, one that has inspired much debate and acrimony in the past and one that still forms an important base for more modern developments in ecology.

The idea of density dependence was originally associated with the human population and was brought to public attention as early as the

eighteenth century by Sir Thomas Malthus (1830). Verhulst (1838) first formulated it mathematically as the “true law of population,” better known today as the logistic equation (see below). Later, Pearl and Reed (1920), in attempting to project the human population size of the United States, independently derived the same equation. While this mathematical formulation was being developed, Gause (1934) and other biologists initiated a series of laboratory studies with microorganisms in which population growth was studied from the point of view of competition, both intra- and interspecific.

In the early part of the twentieth century a variety of terms appeared, all of which essentially referred to the same phenomenon: a population approached some sort of carrying capacity through a differential response of per capita population growth rate to different densities. Chapman (1928) formulated the idea in terms of “environmental resistance.” In 1928, Thompson redefined Chapman’s formulation as “general” and “independent” of density versus “individualized” and “dependent” on density, and later Smith (1935) proposed the density-independent–density-dependent gradient. Thus, by the 1930s the dichotomy of density independence versus density dependence had taken firm root, after having been sown not long after the turn of the twentieth century.

In the 1930s Nicholson and Bailey (1935) first formalized the concept of regulation through density-dependent factors and clearly identified the idea of intraspecific competition with density dependence (see also Nicholson 1957). In Nicholson and Bailey’s conceptualization of density dependence, four points were proposed: (1) population regulation must be density dependent; (2) predators and parasites may function as density-dependent forces; (3) more than density dependence alone may function to regulate population density; and (4) density dependence did not always function to regulate population density.

In contrast to Nicholson and Bailey (and especially their later followers), Andrewartha and Birch (1954) held that the environment was not divisible into density-dependent versus density-independent forces. Andrewartha and Birch argued that, although resources could limit populations, they rarely do so because some aspect of the physical environment (usually collectively referred to as the weather) almost always reduces the population before it becomes stressed by lowered resources. They furthermore noted that the mathematical models that presume equilibrium and persistence were not really necessary if there

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was no “balance” in nature (density dependence strongly implies some sort of balance of nature). Most data sets failed to support the idea of density dependence, and Andrewartha and Birch suggested that the idea was possibly untestable. Rather, they argued, the regulation of populations was frequently taken as an article of faith. The problem was, How long could a population persist without regulation? Their recognition of the fact that local populations would frequently go extinct but would be refounded from other population centers anticipated ideas of metapopulations that would become popular some 20 years later.

Milne (1961) modified both versions of population regulation (the density-dependent and density-independent schools) and noted that perfect density dependence, if it ever exists, does so only at very high densities. Rather, what most characterizes populations in nature is what might be referred to as imperfect density dependence (similar to what Strong [1986] referred to as “density vagueness”); predators and parasites plus density-independent effects usually held populations below levels at which intraspecific competition could become important.

Finally, several variations on the basic theme have recently emerged. Levins (1974) introduced the notion of positive and negative feedback loops for analyzing the dynamics of a population. Dempster (1983) suggested that density independence could be operative within limits, such that an upper ceiling would be imposed upon the population and a lower limit would prevent the population from going extinct. Almost all of these variations are fundamentally in the density-dependence camp but with strong notions of nonlinearities and the importance of spatial distribution, topics discussed in later chapters.

In the end, it would seem that the entire debate about density-dependent versus density-independent control of populations was focused on a false dichotomy. In a variety of guises (e.g., metapopulations, as discussed in chapter 5), modern ecology has come to acknowledge that density-dependent and density-independent forces may function together to regulate populations in nature. But more important, there is general agreement that the rate of growth or decline of a population relative to its size does not necessarily suggest any particular mechanism of regulation. However, there is a recent burgeoning literature, beyond the intended scope of this text, that seeks to use advanced methods of analysis of long-term data sets to determine

whether density dependence operates (Hastings et al. 1993). Part of this later literature is associated with the possibility that many populations under density-dependent control actually may be chaotic (discussed more fully in chapter 3). Chaotic populations can easily be confused with random populations. One way of resolving some of the earlier debates about density dependence was to acknowledge that extreme density dependence (which would promote chaos) could easily produce population behavior that looked quite density independent (i.e., chaotic) (Gukenheimer et al. 1977).

As one can see from the previous paragraphs, the literature on density dependence is enormous. Yet much of it can be divided conceptually into three categories. First, the effect of density on the growth rate of the population (be it through declining reproduction or increased mortality) is simply added to the exponential equation to form the famous logistic equation (as discussed below). Traditionally, the logistic equation is expressed in continuous time as a differential equation, but recently a large literature has been generated by consideration of the special properties of the logistic idea expressed in discrete time, the logistic map. The logistic equation, either its continuous or discrete form, treats the population growth rate as a single constant, even though we understand it actually represents birth rate minus death rate. Other approaches treat each of these rates separately.

Decomposing the population growth rate into its two components, the second category focuses on the relationship between density and reproduction (i.e., density modifies birth rate). We guess that the first acknowledgment of density dependence in nature was by the world's earliest farmers. When one is planting crops, it soon becomes apparent that higher planting densities provide higher yields (which, in principle, are correlated with reproductive output), but only to a point. Once you reach a high enough density, further increases in density fail to provide further increases in yields. This general relationship is referred to as the yield–density relationship and is, in some respects, the most elementary form of density dependence. Originally developed mainly in the agronomy literature, the relationship between density and yield subsequently became an important theoretical baseline for general plant ecology. Yield was usually a product of reproduction, because the subject was mostly the yield of seed crops such as corn and soybeans, and thus the subject of yield and density can be thought of more generally as the relationship between density and reproduction.

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Finally, the third category examines the possibility that density affects survivorship rather than reproduction (i.e., density modifies death rate). The main literature on this topic was originally conceived by forest ecologists, but the idea has since been generalized as self-thinning laws, which are mainly used in plant ecology. The yield–density relationship, discussed in the previous paragraph, involves examining yields of different populations that have been sown at different densities. It is a static approach in this sense. Once established through sowing, the population density remains constant and the variable of interest is the yield. An alternative approach is more dynamic and follows changes in both size (biomass) and density over time in the same population. This more dynamic approach considers mortality as well as growth, and in the context of forestry, where it was originally developed, mortality is known as thinning.

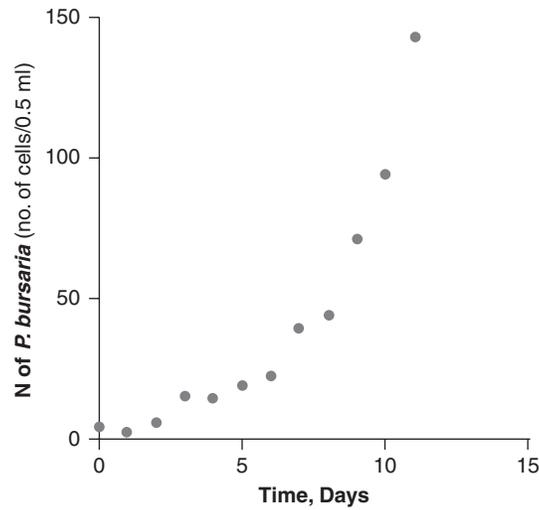
In the following three sections, we follow this basic schema: (1) the logistic equation, (2) yield–density relations, and (3) self-thinning laws.

### *The Logistic Equation*

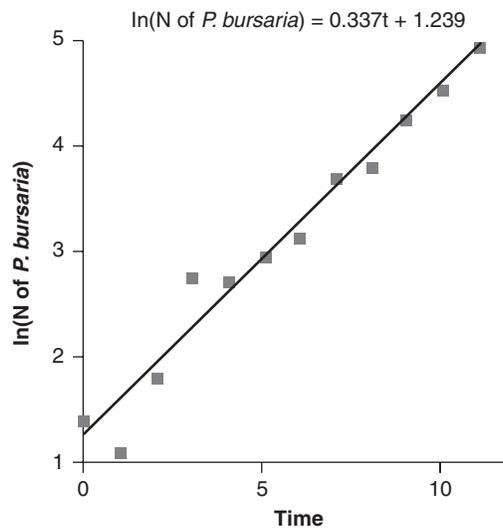
Density dependence is generally regarded as the major modifier of the exponential process in populations. Consider the data shown in figure 1.4 for example (Vandermeer 1969). The protozoan *Paramecium bursaria* was grown in bacterial culture in a test tube, and the data shown are for the first 11 days of culture (data are number of cells per 0.5 ml). In figure 1.5 those numbers are shown as a graph of  $\ln N$  versus time (recall how the intrinsic rate of natural increase was estimated in this way).

The relationship is approximately linear (see figure 1.5), and our conclusion would be that the population is growing according to an exponential law. If this equation were followed into the future, we would have a very large population of *Paramecium*. Indeed, considering the size of *P. bursaria*, there could be about 3000 individuals in 0.5 ml if you stacked them like sardines. Thus, the 3001st individual would cause all the animals to be squeezed to death, and we can compute exactly when this event will happen.

$$\ln(3001) = 0.337t + 1.239$$



**Figure 1.4.** Growth of a culture of *Paramecium bursaria* in a test tube (Vandermeer 1969).



**Figure 1.5.** Logarithmic plot of the data of figure 1.4.

which can be arranged to read,

$$t = [\ln(3001) - 1.239] / 0.337 = 20.80$$

Thus, on the basis of an 11-day experiment, we can conclude that after about 20 days, the test tube will be jam-packed with *P. bursaria* such that all the individuals will suddenly die when that 3001st individual is produced. The actual data for the experiment carried out beyond the 20-day expected protozoan Armageddon is shown in figure 1.6. These data suggest that something else happened. As the density of the *Paramecium* increased, the rate of increase declined, and eventually the number of *Paramecium* reached a relatively constant number. The theory of exponential growth must be modified to correspond to such real-world data.

Begin with the exponential equation, but assume that the intrinsic rate of growth is directly proportional to how much resource is available in the environment. Thus, we have,

$$dN/dt = rN \tag{12}$$

the classical exponential equation discussed earlier in this chapter. But here we presume that  $r$  is directly proportional to  $F$  ( $r = bF$ ), where  $F$  is the amount of resource ( $F$  for food) in the system that is available for the population and the constant  $b$  represents the efficiency of converting food to babies. Thus, equation 12 becomes,

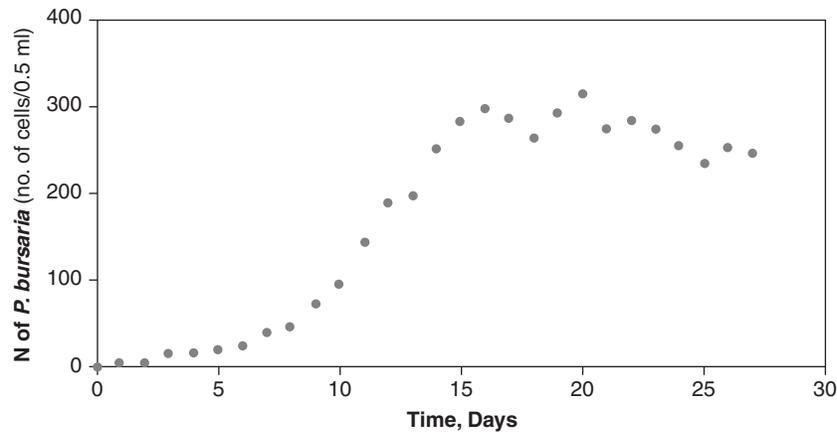
$$dN/dt = bFN \tag{13}$$

But now we assume that there is no inflow of resource into the system so that the total amount of resource is constant and is divided up into that part that is useable by the population and that part that has already been used. That is,

$$F_T = F + cN \tag{14}$$

where  $F_T$  is the total amount of resource in the system and  $c$  is the amount of  $F$  held within each individual in the population. Equation 14 can be manipulated to read,

$$F = F_T - cN \tag{15}$$



**Figure 1.6.** Long-term data for the same population of *Paramecium bursaria* (data from time = 0 to time = 12 are the same as in figure 1.4).

Substituting equation 15 into equation 13, we have,

$$dN/dt = b(F_T - cN)N \quad (16)$$

whence we see that equation 16 is a quadratic equation. Finding the equilibrium point, that is, the point at which the population neither increases nor decreases, is done by setting the population growth rate equal to zero, thus obtaining,

$$0 = b(F_T - cN)N$$

which has two solutions. The first solution is at  $N=0$ , which simply says the rate of change of the population is zero when there are no individuals in the population. The second solution is at  $F_T/c$ , which is the maximum value that  $N$  can have. This is the value of  $N$  for which  $F=0$ , when all the resource in the system is contained within the bodies of the individuals in the population. Because the limitations of the environment are more or less stipulated by the value of  $F_T$ , and the maximum number of individuals that that environment can contain is  $F_T/c$ , the value  $F_T/c$  is frequently referred to as the carrying capacity of the environment (the capacity the environment has for carrying individuals). The traditional symbol to use for carrying capacity is  $K$ , so we

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write  $K = F_T/c$ . We also note that as the population approaches zero (as  $N$  becomes very small but not exactly at zero), the rate of increase of the original exponential equation will be  $bF_T$  (since the general equation is  $bF$  and when  $N$  is near to zero  $F$  is almost the same as  $F_T$ ). After some manipulation of equation 16 we can write,

$$dN/dt = bF_T N [(F_T/c) - N] / (F_T/c)$$

and now substituting  $r = bF_T$  and  $K = F_T/c$  we obtain

$$\frac{dN}{dt} = rN \frac{(K - N)}{K} \quad (17)$$

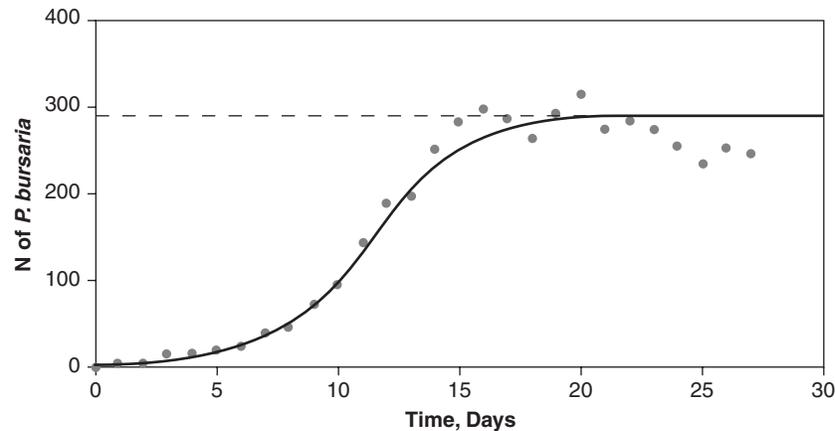
which is the classic form of the logistic equation. Note the form of the equation. It has a very simple biological interpretation. The quantity  $(K - N)/K$  is the fraction of total available resource that remains available: that is, the fraction of the carrying capacity that has not yet been taken up by the individuals in the population. As shorthand we might refer to this quantity—the fraction of the carrying capacity or the fraction of total available resource—as the available niche space. Then the logistic equation is obtained by multiplying the original intrinsic rate of increase,  $r$ , by the available niche space.

Returning to the earlier example of *Paramecium bursaria*, a glance at the data suggests that the carrying capacity is around 290 individuals (average all the points after the data have leveled off). The original estimate of  $r$  as 0.337 was probably too low (since the effects of density dependence were probably effective even during the time of the initial growth) so taking a slightly larger value, let  $r = 0.5$ . The logistic equation for these data then becomes,

$$\frac{dN}{dt} = 0.5N \left( \frac{290 - N}{290} \right)$$

which is plotted in figure 1.7, along with the original data. This example represents a reasonably good fit to the logistic equation.

The existence of density dependence also calls into question the extrapolations that one is tempted to make from a process that seems inexorably exponential. The example earlier in this chapter of the aphids in the milpa agroecosystem is a case in point. Concluding that the



**Figure 1.7.** Fit of logistic equation to the *Paramecium bursaria* data.

farmer had only 2 days before disaster struck may have been correct, but it also could have been grossly in error, depending on the strength of the density dependence. Indeed, with strong density dependence, the field's carrying capacity for the herbivore could have been below the threshold where the farmer needed to take action, in which case no action at all would have been necessary.

In some management applications (e.g., fisheries), it is desirable to maximize the production of a population, which is to say maximize the rate of increase, not the actual population. The logistic equation can provide a useful guideline for such a goal because it is reasonably simple to show that the maximum rate of increase of the population will occur when the population is equal to  $K/2$ . Thus, once the carrying capacity is known, the population density at which the rate of growth will be maximized is automatically known. In actual practice this so-called maximum sustained yield has some severe problems associated with it, largely stemming from the simplifying assumptions that go into its formulation (these issues are more fully discussed in chapter 4).

Using much of the same reasoning as above, we can formulate density dependence in discrete time rather than continuous time. Rather than asking how a population grows instantaneously, we can ask how many individuals will be in the population next year (or some other time unit in the future) as a function of how many are here now. Recall equation 3 from the section on the exponential equation,

$$N_{t+1} = RN_t$$

which is a statement of population growth in discrete time. Now, rather than proceed with a generalization about what numbers will be in a future time (which was the development taken earlier), we remain in the realm of discrete time and ask what might be the necessary modifications to make this equation density dependent. In other words, what do we come up with if we use the same rationale we used in developing the logistic equation, but this time do it in discrete time?

It seems reasonable to suppose that the population will grow slowly if the population is near its carrying capacity ( $K$ ) and will grow more rapidly if it is far below its carrying capacity. This is the same as saying that  $R$  varies with population density. If we simply allow  $R$  to vary with density (the same conceptual approach we took with the logistic equation), we could write,

$$R = r(K - N_t)/K$$

which would make the original equation

$$N_{t+1} = r[(K - N_t)/K]N_t$$

Frequently, the carrying capacity is set equal to 1.0, a transformation that does not change the qualitative behavior of the equation and makes it easier to work with. Thus we have,

$$N_{t+1} = rN_t(1 - N_t)$$

(Note that the parameter  $r$  here refers to discrete population growth, whereas earlier it refers to continuous growth.) This equation is usually referred to as the logistic map (map, because it maps  $N_1$  into  $N_2$ ) or the logistic difference equation. It has some remarkable features that will be explored in more detail in chapter 4. We add a small technical note here. The logistic map is not what you get when you integrate the logistic differential equation and then solve for  $N_{t+1}$  in terms of  $N_t$ , although the perceptive reader might be excused for thinking it so since both equations are called logistic. The logistic map is derived directly from first principles (as above). Integrating the logistic differential equation gives a different time interval map.

### *The Yield–Density Relationship*

The process of intraspecific competition (density dependence) is certainly ubiquitous and thus legitimately calls for a theoretical framework, the most common and general of which is the logistic equation. However, for many applications it is not sufficient to consider only population growth rate. We also want to decompose that rate into its component parts, birth rate and death rate. In this section we consider the effect of density on birth rate. This theory developed from work on plants, especially in agroecosystems. Farmers need to know the relationship between planting density and the yield of a crop (which is frequently the seed output). This relationship is known as the yield–density relationship and is the basis of much agronomic planning as well as a springboard for much general plant ecology. For our purposes here, the yield–density relationship provides the most elementary form of the effect of intraspecific competition on reproduction and lays bare its essential elements. We thus give considerable space to the development of the principles of intraspecific competition as reflected in the yield–density relationship (Vandermeer 1984).

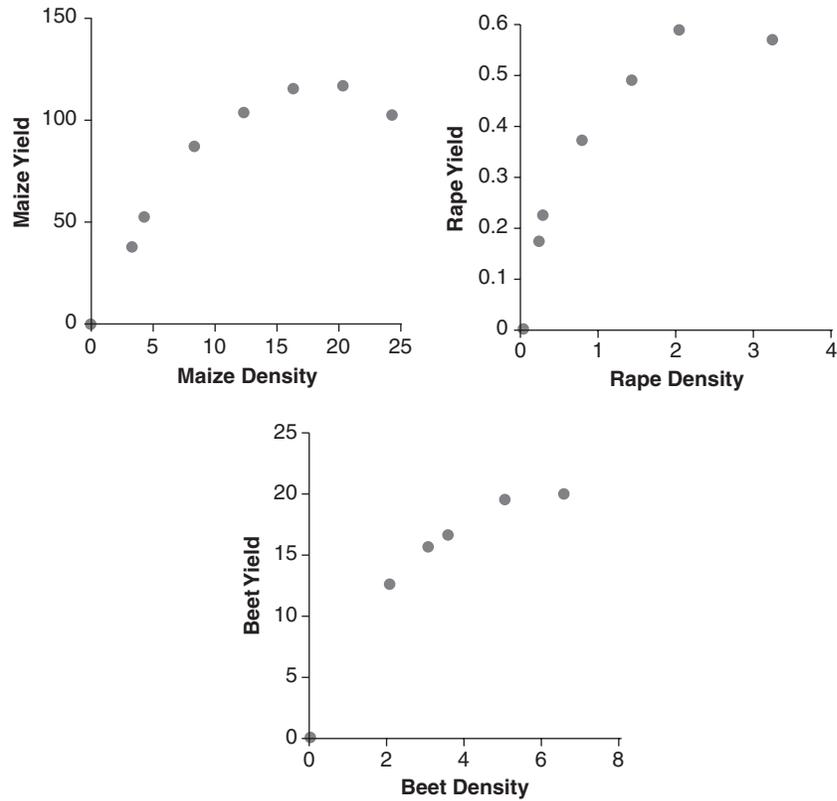
The formal elaboration of yield–density relationships first appeared in 1956 with Shinozaki and Kira’s work. Shinozaki and Kira noted, as had many workers before them, that plotting yield versus density for various plant species usually results in a characteristic form. Several examples are shown in figure 1.8.

Shinozaki and Kira suggested a simple hyperbolic form:

$$Y = Dw_{max} / (1 + aD)$$

where  $D$  is population density,  $Y$  is yield,  $w_{max}$  is the unencumbered (i.e., without competitive effects) yield of an individual plant, and  $a$  is an arbitrary constant. This equation asymptotes as  $D$  becomes very large and thus corresponds to another well-known empirical observation in plant ecology known as the law of constant final yield (which actually is not always true as discussed below). Figure 1.9 shows Shinozaki and Kira’s equation in comparison with the rape data of figure 1.8.

Much of this empirical curve fitting can be rationalized with some simple plant competition theory. We begin by considering what might happen with individual plants and later accumulate those plants into a

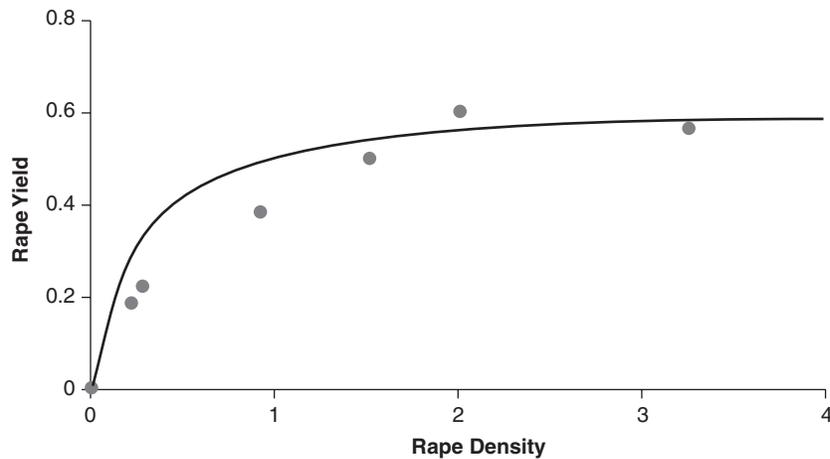


**Figure 1.8.** Exemplary yield versus density data (from Willey and Heath 1969).

population so as to examine the effect of density. Consider a single corn plant in a pot. When provided with all necessary light, water, and nutrients, it will grow to some specified height with some specified biomass. If two corn plants are planted in a pot of the same size and provided with the same amount of light, water, and nutrients, each of the corn plants will attain a biomass smaller than the corn plant grown alone, because the same amount of resources is being used by two individuals rather than one. If we symbolize the biomass attained when a plant is growing alone as  $k$ , we can write the simple relationship,

$$w_1 = k - \alpha w_2 \quad (18)$$

where  $w_1$  refers to the biomass (usually estimated as dry weight) of the first plant,  $w_2$  to the biomass of the second plant, and  $\alpha$  is the propor-



**Figure 1.9.** Equation of Shinozaki and Kira superimposed on the rape data from figure 1.8.

tionality constant that relates the decrease in biomass of the first individual as a proportion of the biomass of the second individual. Rearranging equation 18, we see that

$$\alpha = (k - w_1) / w_2 \quad (19)$$

This same development could be applied to three plants growing in a single pot, in which case the equation describing the results would be,

$$w_1 = k - \alpha_{1,2}w_2 - \alpha_{1,3}w_3 \quad (20)$$

where  $\alpha_{1,2}$  is the effect of a unit of biomass of individual 2 on the biomass of individual 1 and  $\alpha_{1,3}$  is the effect of a unit of biomass of individual 3 on the biomass of individual 1. The parameter  $\alpha$  is frequently referred to as a competition coefficient because it represents the effect of one individual on another. The calculation of  $\alpha$  from real data is quite easy when we have only two plants: Grow a single plant in a pot and measure its biomass after some specified time, giving the value of  $k$ ; then grow two plants in a pot and measure their biomasses, giving the values of  $w_1$  and  $w_2$ ; then apply equation 18 to determine the value of  $\alpha$ . The estimation of the competition coefficients when there are more than two individuals is somewhat more complicated but need not concern us at this point. For now it is important only to understand

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the logic of the thinking that went into the construction of equation 19. We now proceed to generalize equation 20.

Let us suppose that instead of just two or three individuals planted in a pot, we plant a large number of individuals. If the total number planted is  $n$ , we can expand equation 19 by simply adding more terms until we have added all  $n$  individuals to the calculation. That is, equation 20 for  $n$  individuals becomes,

$$w_1 = k - \alpha_{1,2}w_2 - \alpha_{1,3}w_3 - \dots - \alpha_{1,n}w_n$$

or, more compactly,

$$w_1 = k - \sum \alpha_{i,j}w_j \quad (21)$$

where the summation is taken from  $j=2$  to  $j=n$ . If all the individuals are exactly the same, it might be argued that all the  $\alpha_{i,j}$  values are equal. As a first approximation this is probably a good assumption. However, there is a crucial way in which the competition coefficients differ from one another, as becomes evident when we try to elaborate this same example from the level of a pot to the level of a field, below.

For now assume (a bit unrealistically) that all individuals produce the same biomass and the competition between any two pairs of individuals is identical from pair to pair (or assume we can substitute the mean values for biomass and competition). The summation over  $i$  and  $j$  now represents the summation of two constants exactly  $D$  (density of the population) times, so we can thus write,

$$w' = k - D\alpha'w' \quad (22)$$

where  $D$  is the population density, and the primes in this case indicate mean values. Equation 22 can be rearranged as follows:

$$w' + D\alpha'w' = k$$

or

$$w' (1 + \alpha'D) = k$$

and finally,

$$w' = \frac{k}{(1 + \alpha D)} \quad (23)$$

If  $w'$  is the biomass of an average individual in the population, the total population yield must be,

$$Y = w'D$$

and substituting from equation 23 for  $w'$ , we obtain,

$$Y = \frac{Dk}{(1 + \alpha D)} \quad (24)$$

which is identical to the empirical equation of Shinozaki and Kira (we have eliminated the prime from the competition coefficient to make the notation less messy). The advantage of equation 24 is that, because the derivation is based on plant competition theory, the parameters in the equation have obvious meaning,  $k$  being the unencumbered yield of an average individual plant and  $\alpha$  being the mean competition coefficient between two individual plants.

An additional complication arises when we have data like the maize data of figure 1.8, where at high densities the yield actually falls. To accommodate data such as these, Bleasdale and Nelder (1960) suggested modifying the basic Shinozaki and Kira equation with an exponent, citing either,

$$Y = \frac{kD}{(1 + \alpha D)^b}$$

or

$$Y = \frac{kD}{(1 + \alpha D^b)}$$

as reasonable approximations to data that are shaped parabolically. The constant  $b$  is, in the context of Bleasdale and Nelder's derivation, a fitted constant that they presume is related to an allometric effect (i.e., the harvested material is produced proportionally less at higher densi-

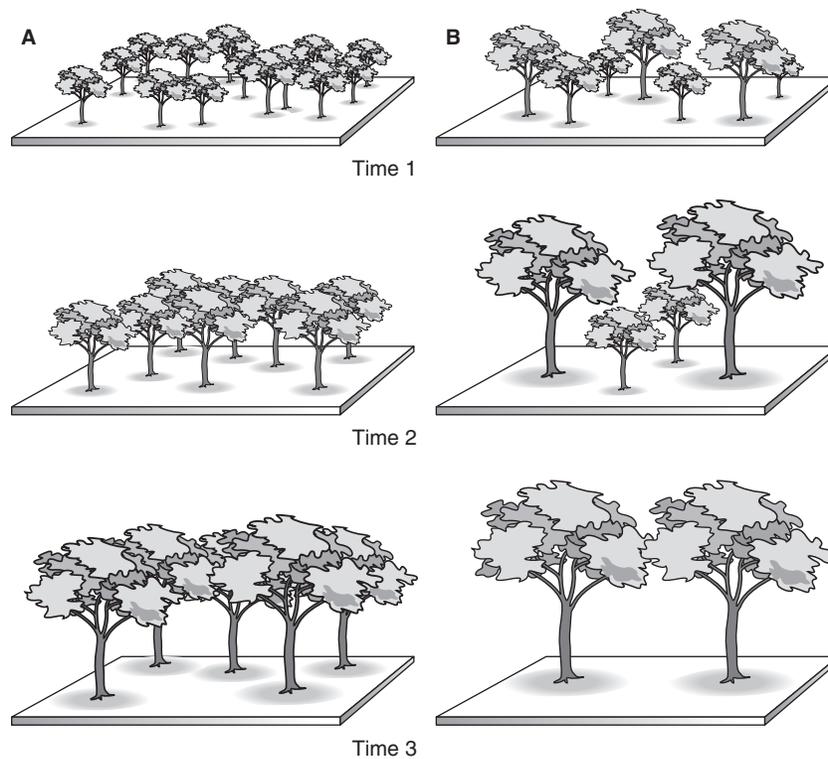
ties of the plant). Either equation reduces to Shinzaki and Kira's equation when  $b=1.0$ . Bleasdale and Nelder chose the first of those two equations arbitrarily, and it has become a standard in the plant ecology literature. It is worth noting that it is not only the allometric effect that can produce a yield density curve that descends at high densities. An increase in competitive intensity as individuals get closer to one another also will create the effect of declining yield with high density (Vandermeer 1984).

Either of Bleasdale and Nelder's equations can be viewed as a discrete map, much like the logistic map, although with slightly different properties. If we think of yield as the number of organisms that will be found in the population in the next generation, this equation becomes equivalent to an iterative map (like the logistic map). The properties of these sorts of maps will be discussed in detail in chapter 4.

### *Density Dependence and Mortality: Thinning Laws*

In the above developments, we assumed that density dependence acts in such a way that the growth of individuals is slowed by a larger population and that a decline in individual growth rate leads to a lower birth rate that eventually stabilizes the population at some particular number. In our development of the logistic equation, no explicit assumption was made about birth or mortality, and the derivation revolved around the intrinsic rate of natural increase, which includes both death and birth rates. However, implicitly in the section on the logistic and explicitly in the above section on the yield–density relationship, the assumption was that we were dealing exclusively or mainly with birth rate modifications rather than death rate modifications.

There are times where the distinction between birth rate and death rate modifications can be crucially important. For example, the growth in biomass of a plantation of trees is usually approximately logistic in form, but the same logistic equation could account for the pattern in either figure 1.10A or 1.10B. And the difference between the two figures is not trivial from a forester's point of view. In figure 1.10A there are large numbers of very small trees, none of which is harvestable; in figure 1.10B there are a smaller number of larger trees. The point is that in figure 1.10A there has been a great deal of intraspecific competition, but it took the form of each individual's growing slowly and almost no mortality, whereas in figure 1.10B one of the main responses to in-



**Figure 1.10.** Diagrammatic representation of the process of thinning.

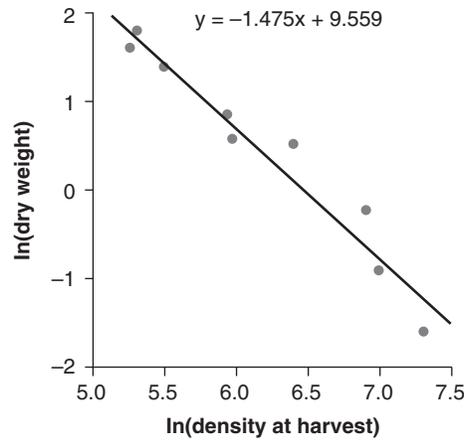
traspecific competition was for some individuals to die while others continued growing rapidly. The biomass of the forests in the two figures is the same (that is the way the example was constructed), but one will be useful for harvest, the other not. Similar examples could be given for any organism with indeterminate growth. For example, many fish become stunted when in very dense populations and thus represent less of an attraction for sport or commercial fishing.

Reflect for a moment on the pattern of growth and mortality in a densely planted tree plantation or in a natural forest when large numbers of seeds germinate more or less simultaneously. First, seedlings are established at a very high density. Walking through a beech-maple forest, for example, one is struck by the carpet of maple seedlings in almost every light gap one encounters. As the seedlings grow, the increase in biomass of each individual treelet is limited by intraspecific

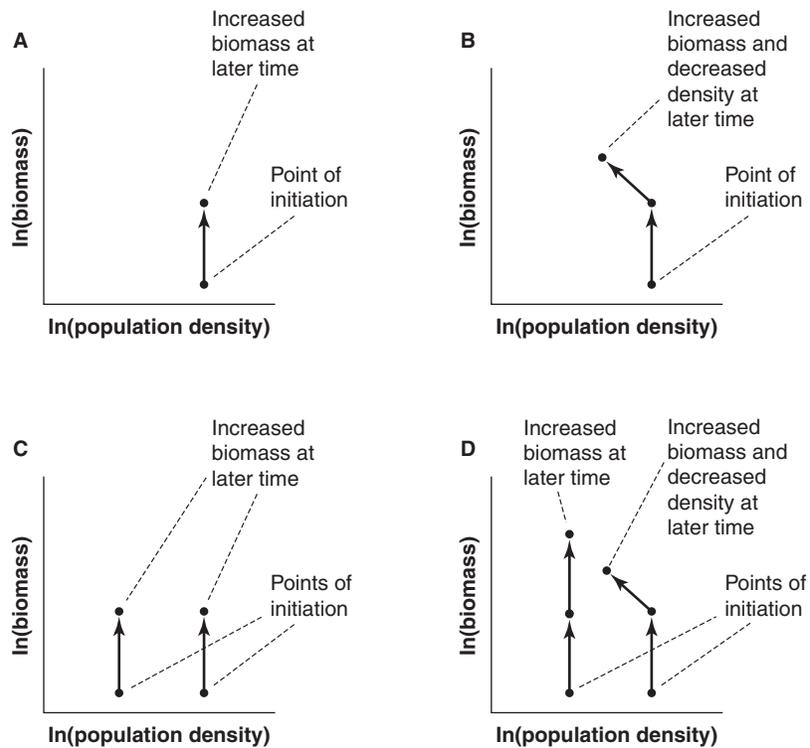
competition. But when populations are sufficiently dense, inevitably some individuals come to “dominate” (grow larger) while others become “suppressed” (remain small owing to competition from their neighbors). Eventually, the suppressed individuals die, and we say that the population has been thinned. But then the trees keep on growing and the process repeats itself; some trees are suppressed, others dominate. In this way, a population of plants that began at a very high density is thinned to the point that the adults are at some sort of carrying capacity. In some ways, this process seems to be the reverse of what was described in the development of the logistic equation. Here, we begin with a number larger than  $K$ , and through the process of thinning the population is reduced to  $K$ , rather than beginning with a small population and increasing to the value of  $K$ . On the other hand, remember that biomass is increasing throughout the process.

This phenomenon is most easily seen as a graph of log of biomass versus log of density at harvest time, as shown with the data in figure 1.11 and more schematically in figure 1.12. But the whole idea is much more dynamic. To look at the dynamics, take a single starting density and observe changes in biomass (or some related variable). If no mortality occurs, we expect a straight vertical line; that is, the per plant biomass increases, but the population density remains constant (see figure 1.12A). But if there is mortality, over time, the curve will shift to the left, to lower densities, while at the same time the per plant biomass will have increased (see figure 1.12B). If, on the other hand, we had begun with two different populations at slightly different densities we would see that plants of both populations would increase biomass. Assuming that densities were such that this increase in biomass happened without competition, the two populations will grow in biomass the same amount (see figure 1.12C). Now if we let both of these populations continue to grow, we expect some thinning (mortality) to occur, especially in the denser population (figure 1.12D).

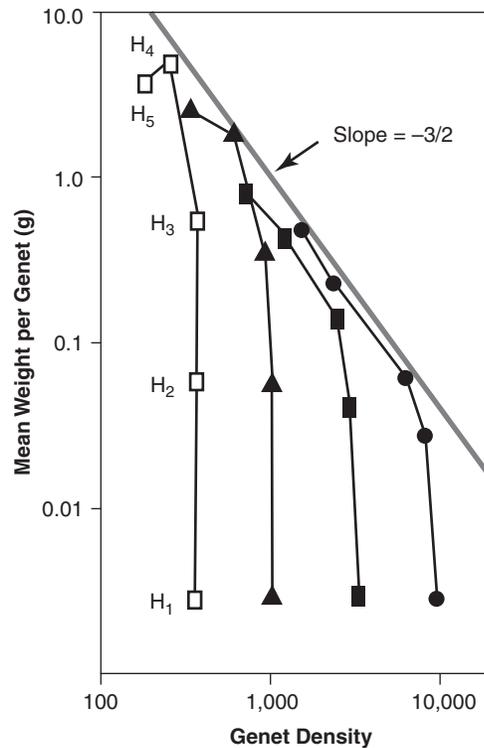
Here, we can see both a plastic effect on growth and a mortality effect. The plastic effect is a smaller biomass increase at larger densities, as shown in figure 1.12D. The mortality effect is seen as a decrease in density at higher densities, as shown in figure 1.12D. If we continue the pattern of development illustrated in figure 1.12 through time, we see that each population begins its process of thinning as it approaches a theoretical thinning line, as can be seen in the data shown in figure 1.13. Once mortality starts, the population tends to follow a straight



**Figure 1.11.** Typical relationship between log density of surviving plants and natural log (ln) dry weight per plant. Example is of *Helianthus annuus* (Hiroi and Monsi 1966).



**Figure 1.12.** Expected pattern of growth and mortality as the thinning process and growth in biomass interact. Log of biomass refers to the logarithm of the biomass of an average individual in the population.



**Figure 1.13.** Relationship between the density of genets and the mean weight per genet in populations of *Lolium perenne*. H<sub>1</sub>, H<sub>2</sub> etc. are successive harvests (Kays and Harper 1974).

line on a log-log scale. This kind of relationship has been shown many times—most often in herbaceous plants over time or in comparisons of woody plant plantations at different densities.

This self-thinning law (called *self* because no forester or agronomist is there doing it) was first developed for plants but many animals show a similar pattern. This is a very nice way of showing growth and mortality effects of density on the same graph. But it also provides an elegant way of looking at density-dependent mortality that can be easily compared among species on very different time scales because time is not explicit. Furthermore, some time ago plant ecologists noticed that this process of self-thinning always seemed to take on a particular pattern. In plots of the logarithm of the biomass of an average individual plant versus the population density at the time

the biomass was measured, the points in a thinning population appeared linear, and the slope of the line always appeared to be nearly  $-3/2$  (as in figures 1.11 and 1.13), providing the population was undergoing thinning. This phenomenon is known as the three-halves thinning law.

Yoda and colleagues (1963) provided an elegant theory explaining the origin of the law. Suppose that each plant is a cube. If each side of the cube is  $x$ , the area of one of the cube's faces is  $x^2$  and the volume of the cube is  $x^3$ . Now we imagine that the plantation is made up of a large number of these cubes and they begin growing and thinning through intraspecific competition. The overall process is illustrated in figure 1.14. The area of the plantation is  $A$ . The population density will be the total area divided by the surface area occupied by a single plant (that is, a single cube). Thus,  $D$ , the population density, is equal to  $A/x^2$ . We now presume that the biomass,  $w$ , of an individual plant is approximately equal to the volume of the cube representing it, so that  $w = x^3$ . So we have the pair of equations,

$$D = A/x^2$$

and

$$w = x^3$$

Rearranging these equations we write,

$$x = A^{1/2}D^{-1/2}$$

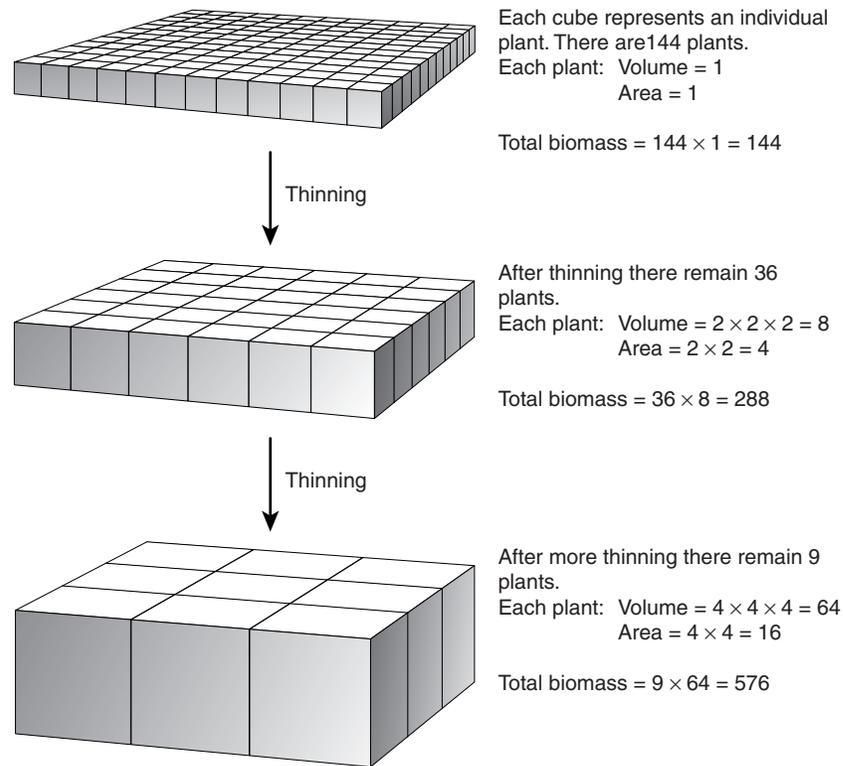
and

$$x = w^{1/3}$$

Since the left-hand side of both equations is equal to  $x$ , we can set the right-hand sides of the two equal to each other, giving,

$$A^{1/2}D^{-1/2} = w^{1/3}$$

which simplifies to,



**Figure 1.14.** Yoda and colleagues's interpretation of the origin of the  $3/2$  thinning law.

$$w = A^{3/2}D^{-3/2}$$

which can be put in the more standard form,

$$\ln(w) = (3/2)\ln(A) - (3/2)\ln(D)$$

which represents a straight line with a slope of  $-3/2$  on a graph of  $\ln(w)$  versus  $\ln(D)$ .

Thus we see from very simple reasoning that it is not unusual to expect the three-halves thinning law. On the other hand, the basic empirical base of the "law" has been persistently questioned (e.g., Westoby 1984). In fact only a few data sets conform convincingly exactly to a  $-3/2$  slope, and many ecologists feel that data such as those shown in

figures 1.12 and 1.13 are actually exceptions to a rule that is something other than  $-3/2$ . It is worth noting that, alongside this general consensus that the three-halves thinning law is not correct, its theoretical basis is quite shaky to start with. Plants are not, after all, cubes, and the fact that their thinning pattern does not follow the  $3/2$  thinning law exactly is not all that surprising. But the basic idea still seems sound. We should expect a linear relationship between the log of the biomass and the log of the density, and that appears to be almost always true. While we expect the slope of that line to be  $-3/2$  in the case of plants shaped like cubes, most plants are not shaped like that. It is perhaps best to treat the  $3/2$  thinning law something like the Hardy-Weinberg law (Futuyma 1979), something that ought to be true under ideal conditions but rarely happens in fact because those ideal conditions are hardly ever met.

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