

Constant Final Yield

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Annu. Rev. Ecol. Syst. 2010. 41:173–92

First published online as a Review in Advance on August 10, 2010

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

This article's doi:
10.1146/annurev-ecolsys-102209-144642

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1543-592X/10/1201-0173\$20.00

Key Words

biomass production, competition, crowding, density, density dependency, plant populations, self-thinning

Abstract

Constant final yield is an empirical generalization concerning the total biomass production of plant stands growing at different densities after a period of growth. Total standing biomass initially increases in proportion to density, levels off, and then remains constant as density increases further. We review the empirical basis for and mathematical formulations of this pattern, and we clarify the relationship of constant final yield to density-dependent mortality (self-thinning). There are several mechanisms that can explain the pattern, and it has a clear evolutionary basis. Constant final yield is a key to understanding population- and community-level phenomena. Establishing whether or not a plant community is at or close to constant final yield is important for understanding and predicting its behavior. It represents the maximum biomass for a genotype in an environment after a period of growth and, as such, can serve as a baseline for the measurement of disturbance in plant communities.

1. INTRODUCTION

1.1. Biomass-Density Relationships

The study of competition among plants starts with the study of how plant performance changes with density (Bleasdale 1967, Shinozaki & Kira 1956, Yoda et al. 1963). Three basic types of biomass-density relationships have been described. (1) In some studies population density (usually a single species or genotype) is varied and the relationship between density and mean performance is analyzed after a given period of time (“density as the dependent variable”; Weiner & Thomas 1986). (2) In another type of study, changes in density and performance are investigated over time as crowded (usually monospecific) stands grow and undergo density-dependent mortality (self-thinning; “time as the independent variable”; e.g., Franco & Kelly 1998, Weller 1987, Westoby 1984). (3) A third type of study is descriptive and correlative, looking at density and performance at different sites, which vary in many different ways and are often composed of numerous species, without any experimental treatments (“no independent variable”; e.g., Enquist et al. 1998, White et al. 2007).

Researchers have not always realized that these three types of biomass-density relationships are fundamentally different and address different questions (Weller 1989), and their conflation has been the source of much confusion in the literature. This confusion has arisen, in part, because the variables analyzed in all three cases appear to be identical: plant density (x) and mean (or total) plant biomass (y). But similarity of axes labels on graphs does not always mean similarity of the data represented or their interpretation. Students of population biology are expected to understand the difference between a life table and a survivorship curve, even though plots of both often have the same labels on their axes. Similarly, there are several different types of data addressing very different questions that have plant biomass as the y -axis and plant density as the x -axis, and these include both intra- and interspecific relationships (White et al. 2007).

Although patterns of self-thinning (type 2 above) and interspecific scaling (type 3 above) have received much attention recently (e.g., Enquist et al. 1998, Wang et al. 2004), the importance of simple density-yield relationships at one point in time (type 1 above) has not been fully appreciated. This is unfortunate, because such relationships give us one of the most compelling patterns in plant ecology: constant final yield (CFY; Shinozaki & Kira 1956). Simply put, in a density series ranging from very low to very high density of a single species and harvested at a single point in time, the total biomass produced increases linearly with density at very low densities and then levels out at higher densities. Although this pattern has most often been observed in annuals or other short-lived plants, examples from longer-lived plants do exist (e.g., Xue & Hagihara 1998). As we argue below, this pattern has important consequences for our general understanding of the ways that plants compete for resources and for modeling and predicting population behavior.

To date, there has been no systematic review of CFY, other than textbook overviews (e.g., Harper 1977, Radosevich et al. 2007, Silvertown & Charlesworth 2001). Below, we review the history, mathematical models, potential mechanisms, and implications of CFY, and we argue that it is one of the keys to understanding plant population and community behavior.

1.2. Definition of Constant Final Yield

In a series from low to high densities, the relationship between total stand biomass per unit area and density is initially linear, but eventually levels off at a constant biomass that does not increase further (Harper 1977, Shinozaki & Kira 1956) **Figure 1**). In **Figure 1a**, the x -axis is the density of plants (the number of individuals per unit area) and the y -axis is the total biomass of the stand

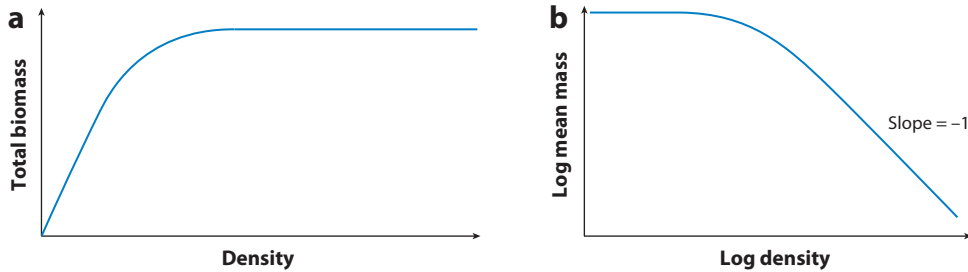


Figure 1

(a) Total biomass produced by a stand (mass per unit area) versus density; and (b) log mean mass per individual versus log density for populations grown at different densities and harvested at one point in time.

per unit area (with units of mass per unit area). In **Figure 1b** the y-axis is the mean mass per plant (the total biomass of the population per unit area divided by density, having units of mass per individual). These are two visualizations of the same relationship, both forms being used in the literature.

The term constant final yield, often referred to as the law of constant final yield, is generally attributed to Shinozaki & Kira (1956), but the first use of the term appears to be by Farazdaghi & Harris (1968). Ambiguity in the meaning of all three words—“constant,” “final,” and “yield,”—has been a source of confusion for many students and even some researchers in plant ecology and agronomy. The words “constant” and “final” suggest that the pattern concerns the development of stands over time, but here it means final with increasing density at a single point in time; that is, final refers to a maximum attainable stand biomass at a single point in time. This maximum (final) yield increases over time as plants grow and the stand accumulates mass, as we discuss below. If that were not confusing enough, “yield” usually means harvestable yield (seeds, fruits, or storage organs of crops) in agronomy, whereas here yield refers to total biomass (sometimes called biomass yield). Constant final yield applies to total biomass, but not necessarily to harvestable yield, in crop populations.

It can be useful to divide the density-yield curve into three or four parts in which different plant responses dominate (**Figure 2**). At very low densities there is no competition, which means there is a linear increase in total biomass with density starting from the origin: total biomass is proportional to density. At higher densities, the rate of increase in yield with density decreases as mean plant mass declines at higher densities; thus, the increase in total biomass is less than proportionate to the increase in density. This is *prima facie* evidence of competition. Finally, maximum biomass yield occurs when increases in density are exactly matched by decreases in mean plant weight (slope = -1 on **Figure 1b**). Although there are many advantages to using a simple mathematical formulation for this relationship along its complete range, the changes in the shape of the relationship as densities increase reflect the following changes in the processes operating to determine individual and population biomass: individual plant growth without competition at very low densities, growth constrained by resource competition at higher densities, and density-dependent mortality (self-thinning) at even higher densities.

2. HISTORY OF THE CONCEPT OF CONSTANT FINAL YIELD

Although there have been previous reviews discussing yield-density relationships (e.g., Bleasdale & Nelder 1960, Park et al. 2003, Watkinson 1980), we take a somewhat different perspective

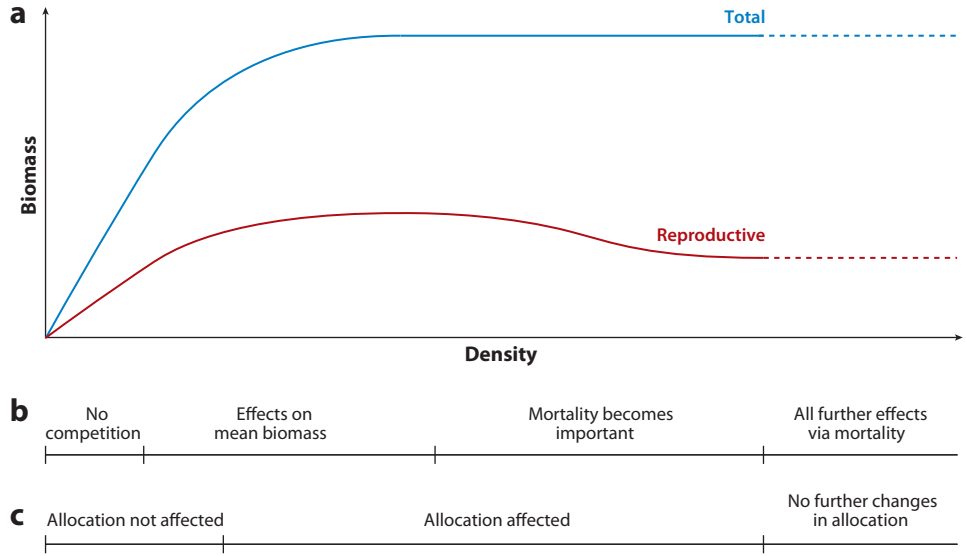


Figure 2

(a) Biomass-density relationship according to constant final yield, divided into (b) four regions with respect to competition and (c) three regions with respect to biomass components.

here by focusing on total biomass production. It was recognized early in the twentieth century that biomass yield in plant monocultures became independent of density as densities increased (Montgomery 1912). The first proposed mathematical descriptor of the effects of plant competition corresponding to CFY appears to have come from Mitscherlich (1919). He proposed that individual plant mass (w) could be related to density (N) according to the function

$$w = w_m(1 - e^{-c/N}). \quad 1.$$

This is a hyperbolic function in which w_m is plant mass in the absence of competition and c is a competition parameter: An increase in c means an increase in the negative effect of competition on plant mass. Equation 1 predicts that total stand yield is asymptotic at high densities. This function received some attention between the 1930s and 1950s (Donald 1951, Redecker 1930, Willcox 1950) and is similar to models proposed subsequently.

Mathematical modeling of the effects of density on plants became a focus for Japanese plant ecologists in the 1950s. The culmination of this was a study linking responses of plant performance to density with a model of plant growth. Kira and coworkers (Kira et al. 1953, 1954; Shinozaki & Kira 1956) started by defining a competition-density (C-D) effect at time point t , with w varying through time as plants grow:

$$w_t = d_t N^{-\alpha_t}. \quad 2.$$

α is a dimensionless scaling constant that describes the effects of density on competition, and is assumed to vary from 0 at the onset of growth (sowing or emergence, $t = 0$) to 1 at the completion of growth. d_t is a growth parameter defined as the mass of an isolated plant. The yield-density effect was a direct extension of Equation 2 to total stand yield, Y_t , at time t :

$$Y_t = d_t N^{1-\alpha_t}. \quad 3.$$

α was assumed to vary between zero at time 0 and 1 as t approaches the cessation of growth. In this growth model, total biomass is constant only with increasing density when growth has stopped. In Equation 3, the exponent $1 - \alpha_t$ implies that total yield increases with density for values of $\alpha < 1$.

Assuming a logistic model of individual plant growth, Shinozaki & Kira (1956) showed that total biomass becomes constant as plants approach the point at which they cease growth. Equations 2 and 3 could be modified such that w and Y are determined at the end of growth:

$$w^{-1} = A + BN \quad 4.1.$$

$$Y = \frac{N}{A + BN}. \quad 4.2.$$

A and B are growth parameters, and in this formulation of the model, they are essentially phenomenological; but later reparameterization of this model produced ecological interpretable parameters (see below). The model's key features are (a) it is implicitly a model for growth as a function of both time and density, whereas most subsequent analyses of competition have been static, that is, based on a single point in time (Gibson et al. 1999); (b) it only predicts final yield to be constant when growth ceases, that is, "final" here refers to time; and (c) it predicts the existence of a density that would give the same biomass at all points in time. Although the work of Shinozaki & Kira was groundbreaking, in retrospect their model is too restrictive, particularly because we know that CFY is observed at all, or almost all, stages of growth.

Several other models were proposed for yield-density relationships during the 1960s [(Bleasdale & Nelder 1960, Bleasdale & Thompson 1966, Farzadaghi & Harris 1968, Holliday 1960); reviewed by Willey & Heath (1969)]. Based on the results of plant spacing experiments, Bleasdale & Nelder (1960) proposed a relationship of the form

$$\frac{1}{w^\theta} = A + BN^\phi, \quad 5.$$

where ϕ and θ are dimensionless scaling constants, which allow for nonlinearity in the relationship between the reciprocal of mass and density. This contrasts with Equation 4.1 in which the relationship is always linear. Without supplying the details in their paper, Bleasdale & Nelder apparently derived this model by replacing the logistic growth model assumed by Shinozaki & Kira (1956) with the Richard's equation (Richards 1959). Equation 5 is a departure from previous models, because if ϕ and θ are not equal, yield may not be constant with at high densities, so the model could also be applied to biomass components that may not be constant at higher densities (**Figure 2**).

Constant final yield was subsequently extended to describe the relationship between plant density at harvest and sowing density, as well as between biomass yield and existing plant density, by Yoda et al. (1963):

$$N_s = N_i(1 + mN_i)^{-1}, \quad 6.$$

where N_i is sowing density and N_s is the density of survivors. This equation is of the same form as Equation 4.2 and predicts that there exists an asymptotic density of survivors: m^{-1} in Equation 6 is this asymptotic density, with m having units of area.

In summary, CFY was an assumption of the models developed by Shinozaki, Kira, and coworkers. They referred to final biomass yield in terms of a constant yield irrespective of density at the cessation of growth, but not necessarily before. Subsequent analyses generated a family of empirical models that produce CFY as a special case, but largely ignored the time course of yield-density relationships.

3. EMPIRICAL SYNTHESIS

The suite of empirical models described above has been synthesized into one or two formulations that are now commonly used. Watkinson (1980) reparameterized the models of Bleasdale & Nelder (1960) to yield

$$w = w_m(1 + aN)^{-b}. \quad 7.$$

The difference between this formulation and earlier ones lies in the biological interpretability of the parameters. As above, w_m is the mass of an isolated plant in the absence of competition. Parameter a is defined as the ecological neighborhood of the species (in units of area), which is essentially the area an individual requires to achieve W_m , and b is a dimensionless scaling parameter that produces CFY when it equals 1. Equation 7 assumes that the response to density is an allometric effect: The scaling of biomass accumulated as a function of resource removed (Firbank & Watkinson 1985, Vandermeer 1984, Vandermeer & Goldberg 2003, Watkinson 1980).

Vandermeer (1984) proposed a slightly different equation,

$$w = w_m(1 + aN^b)^{-1}. \quad 8.$$

The parameters of Equation 8 are defined in the same way as those of Equation 7. Vandermeer argued that Equation 8 results from a decrease in the amount of space taken by each individual with increasing density and that the parameters in this equation have a much clearer biological interpretation than those in Equation 7. The difference in behavior between the models is mainly at intermediate densities, whereas the qualitative behavior of the models is very similar at high and low densities. The important development in these two models is that their parameters are interpretable in terms of the neighborhoods within which individuals compete for resources. However, these models remain essentially phenomenological: They describe the outcome of competition. The mechanisms of competition must be compatible with these observed patterns, but that is all the models tell us about these mechanisms.

3.1. One Example

There are numerous examples of CFY in the scientific literature (Silvertown & Charlesworth 2001). Many come from experiments on agricultural crops or weeds. Relatively few studies show the development of biomass-density relationships over time (e.g., Kays & Harper 1974, Li et al. 1996, Lonsdale & Watkinson 1983, Shinozaki & Kira 1956, Watson 1984).

Data from Kays & Harper (1974) (see **Figure 3**) demonstrate both the CFY and density-dependent mortality. The grass *Lolium perenne* was grown in a density series from 320 to 10,000 plants m^{-2} under three light intensities and with four harvest dates. Constant final yield was achieved only at the highest light intensity (**Figure 3**). At the lower light intensities (not shown), total biomass is still increasing with density at all harvest dates. In the case of the relationship between numbers surviving and density (**Figure 3b**), it is clear that self-thinning is occurring at all but the first harvest.

3.2. What Determines the Parameters in Models of Constant Final Yield?

As noted above, Equations 7 and 8 are useful because they put CFY in an ecological context, and their parameters have ecological interpretations. But it is not clear which factors determine the values of the two parameters and, therefore, how we might expect these parameters to vary across species or with environmental conditions.

A rigorous answer to the question of what determines the parameters in a model of CFY requires that we be able to answer at least two of the following three questions: (a) What is the

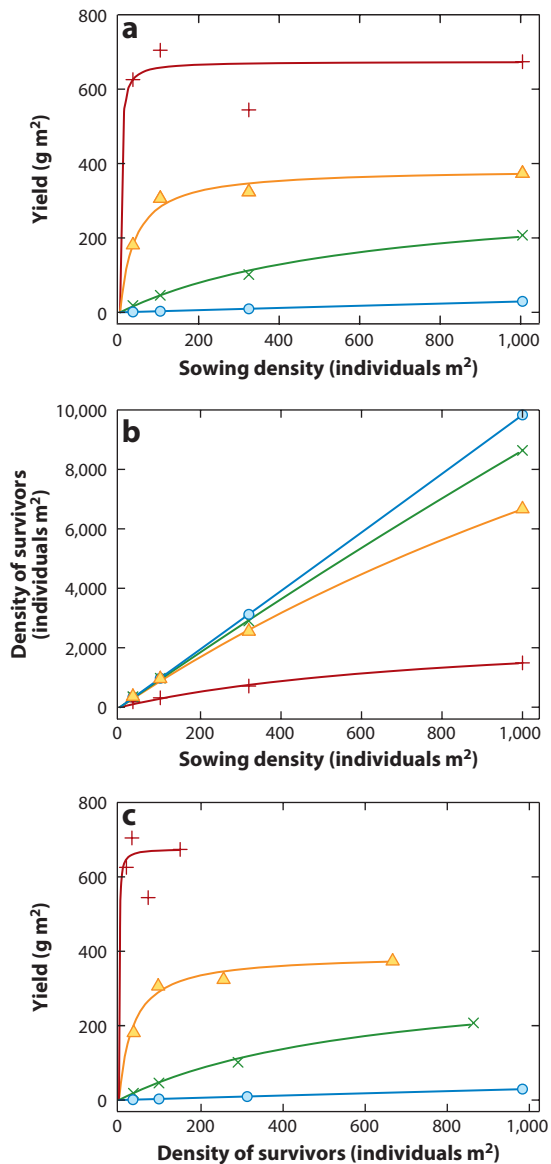


Figure 3

Constant final yield in experimental data from Kays & Harper (1974). (a) Relationship between stand biomass and density; (b) relationship between the density of survivors (individuals m⁻²) and initial density (individuals m⁻²); (c) relationship between stand biomass (g m⁻²) and survivor density (individuals m⁻²). The different symbols represent different harvest dates. In panel c the curves have been truncated at the maximum densities observed.

maximum size of an individual plant after a given period of growth (w_m)? (b) What is the maximum yield of a high-density stand (w_m/a) at this same point in time? (c) What is the area within which plants interfere with each other (parameter a)? These questions have not been considered within the context of CFY.

Early in growth, a plant's size is a function of its initial size, its initial growth rate, and the time it has had to grow. Later, internal and external limits on growth, such as increased maintenance, internal transport and biomechanical costs, and allocation to reproductive structures, play an increasing role. If we want to understand competition mechanistically, the question becomes how is the growth of an isolated plant changed by competition from neighbors through their reduction in resource availability. Although progress has been made (e.g., Berntson & Wayne 2000, Enquist et al. 2009), we are still far from such an understanding.

The resources for which plants are competing, the maximum size of an individual plant, and area over which these resources are depleted determine the size of the ecological neighborhood (parameter a). Several models have assumed that plants compete in areas of overlapping local neighborhoods of influence (Firbank & Watkinson 1985, Weiner et al. 2001, Wyszomirski 1983), and this approach has some empirical support (Benjamin 1993). Larger plants would be expected to have larger neighborhoods, especially when competition is for light. Also, neighborhood size can be expected to increase as plants grow. Plant size is both an influence on, and a result of, competition among individuals.

4. TIME COURSE OF CONSTANT FINAL YIELD

Constant final yield refers to the relationship between biomass and density at one point in time. Yet the pattern appears to hold along the whole course of growth, except before there has been any growth at all or after growth has ceased. As stands of plants of different densities develop, (a) the maximum biomass yield increases, (b) the density at which CFY is achieved is reduced, and therefore (c) the initial increase in biomass with density becomes steeper (**Figure 4**).

To accurately describe growth under competition, it is necessary to characterize the effect of contested, limiting resources on growth. Competition can start as soon as plants are large enough to contest resources, and this can be very soon at high plant density. Therefore CFY occurs at any time after there has been sufficient growth for competition to occur.

It is not meaningful to talk about density-yield relationships before there has been any growth. If a plant's initial mass is defined as its seed mass, then biomass before growth, that is, before

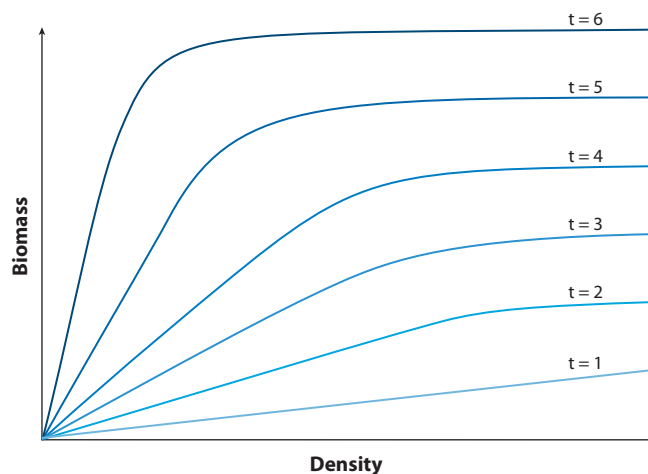


Figure 4

Illustration of time course of biomass density relationships showing constant final yield.

or immediately after germination, is proportional to density: Yield is the density at which seeds are sown multiplied by average seed mass. Early in growth, initial size composes a significant proportion of current size. The more that standing biomass is achieved through growth rather than initial propagule size, the more meaningful biomass-density relationships are.

5. CONSTANT FINAL YIELD AND SELF-THINNING

As discussed above, the relationship between plant mass and density has been studied in the context of high-density stands undergoing density-dependent mortality over time, as well as a density series harvested at one point in time. The two patterns are not independent because they occur simultaneously, and a comprehensive theory of stand development must encompass both. There is a great deal of confusion about the relationship between these two types of studies, and it has even been argued the two patterns are incompatible (Crawley 1997).

The intraspecific self-thinning relationships represent a total biomass-density boundary condition as some individuals in crowded stands of plants grow while others die (Yoda et al. 1963). There has been much debate about the slope of the log total biomass versus log plant-density relationship during self-thinning (Lonsdale 1990; Weller 1989, 1990; Zeide 1991). The question is beyond the scope of this review, and its resolution is not necessary here. We assume only that self-thinning occurs and that its trajectory on a log density versus log total (or log mean) biomass graph is close to linear.

If CFY is formulated as a function of the density of survivors (N_s) rather than the initial density (N_i), then we can depict both patterns simultaneously (**Figure 5**). When expressed this way, the thinning boundary defines a limit beyond which the yield density relationship may not pass.

Constant final yield can be used to address these problems (Xue & Hagihara 1998), because the pattern can be used to estimate, at any point in time, both Y_{\max} , the maximum yield per unit area, and N_{\max} , the maximum density per unit area. If the data obtained are at densities too low to have achieved either of these limits, then extrapolation may be used to estimate them.

We used this approach to estimate these quantities, using data from Kays & Harper (1974). One can plot the estimated mean weight per individual at the maximum density plotted against that maximum density (**Figure 6**). This approach is preferable in this case because it is clear that in most cases the observed densities and maximum yields at final harvest were not near the asymptotic values predicted by CFY; the consequence is that the observed thinning boundaries are likely to underestimate the true value. Although using CFY to estimate a thinning boundary requires extrapolation of the relationships beyond the range of densities used in the experiment, it is clearly preferable to inferring a thinning boundary from stands that may be far from it.

6. POSSIBLE MECHANISMS

What mechanisms result in CFY? Below we describe four possibilities: (a) modularity of plant growth, (b) plasticity in allometric growth, (c) size-asymmetric competition among individuals, and (d) density as limiting factor in the conversion of resources into biomass.

6.1. Modularity of Plant Growth

It has been argued that plant growth can be described in terms of the iteration of modules (individual leaves, stems, shoots, roots, etc.; de Kroon et al. 2005, Watkinson & White 1985). In this view, a stand of plants can be considered as a collection of modules or ramets, and the number of individual plants (genets) may be relatively unimportant for biomass production. Constant final

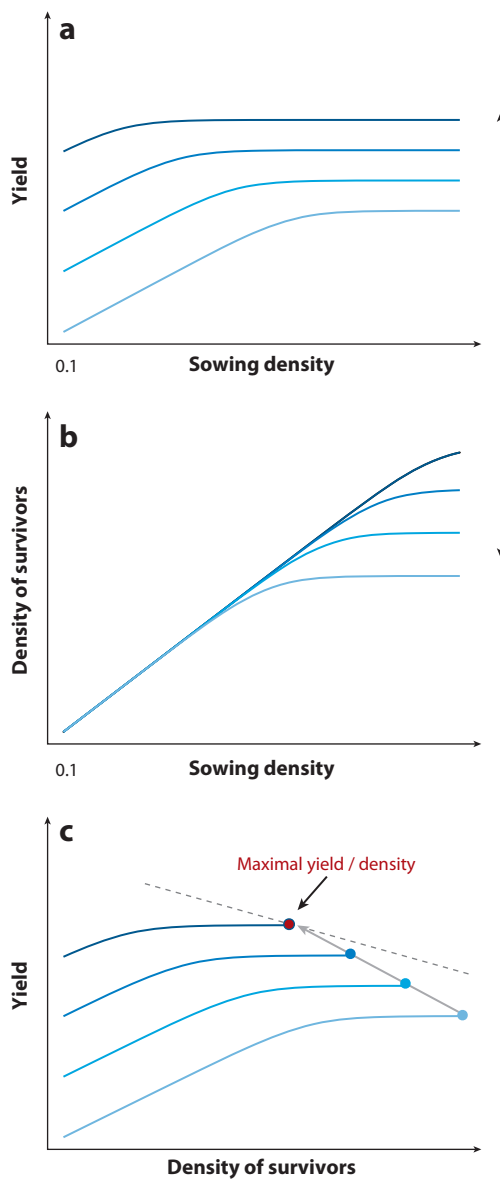


Figure 5

Relating the law of constant final yield and the thinning boundary. The thinning boundary relates the maximum yield of a stand and its maximum density during the course of growth. (a) Maximum yield as predicted by the law of constant final yield; (b) maximum density as predicted by Equation 6. (c) The thinning boundary (*dashed line*) illustrated in terms of these two quantities.

yield can result from a limit on the number of plant modules that can be supported per unit area. A simple example of this would be a lawn. If one sows a turf grass and there are no weeds, then tillering eventually gives us a continuous turf in which the whole area is covered with tillers. If we sow at higher density, this occurs sooner and the lawn will consist of many different genets (Harper 1977). If we sow at low density (and control weeds), then the establishment of the lawn

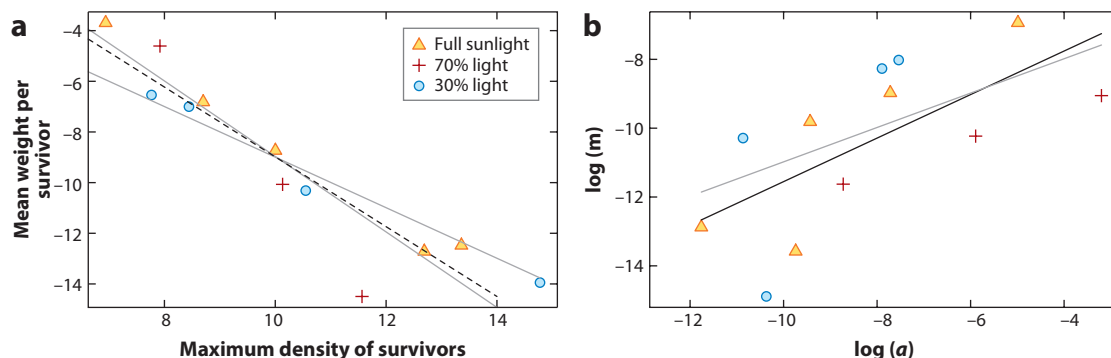


Figure 6

Relationship between the thinning law and law of constant final yield in the data of Kays & Harper (1974). (a) The relationship between log maximum density (m^2) of survivors and log mean weight per survivor (g); (b) The relationship between m (from Equation 6) and a (from Equation 7), the parameters of the density responses relating to density and yield, respectively. The different points represent successive harvests: in panel *a* early harvests are shown at the lower right, whereas late harvests are shown at the top left; in panel *b*, early harvests are shown at lower left, and late harvests are shown at top right. Note that the data in **Figure 6** are taken from full light intensity. In panel *a*, the upper gray line shows a slope of $-3/2$, whereas the lower gray line shows a slope of -1 and the dashed line is the line of best fit for the data. In panel *b* the solid line is the line of best fit, and the gray line shows a slope of 0.5.

takes longer and consists of relatively few genets. In most cases, the results will be indistinguishable in appearance and total biomass after the lawn has been established. In this case CFY is determined by tiller (ramet) density, not genet density. This explanation seems quite convincing for clonal plants that spread in two dimensions. But as we discuss below, there are problems with applying this explanation to plants that grow in height as well as horizontally.

6.2. Allometric Growth and Plasticity

Most plants do not grow by proliferating modules in only two dimensions, but in three. It is the three-dimensional growth of most plants that makes CFY nontrivial and even counterintuitive in some cases. Let us assume that plants are simple, isometric three-dimensional objects such as cones or cylinders. If the area occupied is proportional to a linear measurement, l (e.g., diameter or height) to the power of 2, while mass is proportional to l^3 , then covering an area with fewer large objects will give more mass than the same area covered by many smaller ones. This is a geometric paradox of CFY: Plants are three-dimensional objects, but packing of simple isometric objects does not result in CFY.

If we temporarily ignore the question of mortality (which is reasonable because CFY is reached at densities below those resulting in significant density-dependent mortality), then, for the packing of three-dimensional plants on a two-dimensional space to result in CFY, they must change their shape (e.g., height/diameter) as they grow: Growth has to be allometric, not isometric. But even this is not sufficient: There must be plasticity in the pattern of allometric growth (Weiner 2004), such that plants growing at higher densities are “thinner” at a given height than they would be at lower density. We know that competition changes the shape (the ratio of different dimensions) of plants (e.g., Weiner & Thomas 1992), but it seems unlikely that this plasticity in allometric growth alone would be sufficient to produce CFY over such a wide range of densities as is observed. Plants cannot be thinner and thinner at higher and higher densities without limit—this would lead to biomechanical instability, resulting in the lodging of many individuals and, therefore, a reduction

of standing biomass at very high densities. Thus, plasticity in allometric growth must play a role in the mechanisms producing CFY in species that grow in three dimensions. However, as we discuss below, even this is not sufficient. Size-asymmetric competition is necessary to produce CFY at very high densities.

6.3. Size-Asymmetric Competition

When plants grow at high density, the effects of competition are not shared equally among all individuals. Usually, larger individuals obtain a disproportionate share of contested resources and suppress the growth of smaller individuals (Cannell et al. 1984); this is a phenomenon called size-asymmetric competition (Begon 1984, Schwinning & Weiner 1998, Weiner 1990). Size-asymmetric competition seems to be primarily, if not solely, due to competition for light because higher leaves shade lower leaves but not vice versa, whereas competition below ground appears to be more size symmetric (Berntson & Wayne 2000, Weiner 1990): Larger plants have an advantage, but their advantage is not overproportional.

In neighborhood models of plant competition, it has been shown that the degree of asymmetry of competition as well as the spatial distribution of plants can influence size distributions and mean yields (Freckleton & Watkinson 2001; Stoll et al. 2002; Weiner et al. 2001; Wyszomirski 1983, 1986; Wyszomirski et al. 1999). Variation in the degree of asymmetry of resource removal at the individual level, for example, should influence the parameters of a model of CFY because it affects the rate at which the asymptotic yield is approached as density increases (e.g., Firbank & Watkinson 1985, Freckleton & Watkinson 2001).

In the extreme case, it is easy to see how the asymmetric capture of resources can lead to CFY: Under completely size-asymmetric competition, a single plant might obtain all resources within a given neighborhood while all others obtain none. Consequently, the total yield per unit area will be constant, irrespective of initial density, or even the form of the underlying function describing competition among individual plants (Pacala & Weiner 1991). Asymmetric competition generates CFY in this way in a recently developed model of forest growth (Strigul et al. 2008).

Size-asymmetric competition is necessary if total biomass production is not to decrease at very high densities. Size-symmetric competition reduces the growth rate of all plants, resulting in stand stagnation, not density-dependent mortality of the smallest individuals, as observed, and this mortality is essential for CFY at very high densities. If competition is highly size asymmetric, total yield of the population is largely unaffected by extensive mortality because it is the very smallest individuals that die. This is strong evidence for the importance of size-asymmetric competition for CFY at very high densities. The degree of size-asymmetry increases with density (Schwinning & Weiner 1998), and at some point, further increases in density result only in additional mortality, not further change in the size distribution of the survivors (**Figure 2b**). Consequently, most models that produce CFY at very high densities assume size-asymmetric competition (e.g., Aikman & Watkinson 1980), although it is perhaps premature to conclude that size-asymmetric competition is necessary for CFY at lower densities.

6.4. Density as a Limiting Factor in the Conversion of Resources into Biomass

One of the simplest ways of looking at CFY is to postulate that resources are converted into biomass in a simple linear fashion. The amount of resources in the environment determines CFY for a given species or genotype, and this yield will be achieved if density is high enough. According to this view, density itself can be regarded as a potentially limiting factor, just as meristem limitation has been considered an important factor in the growth of clonal plants (Watson 1984).

Indeed, a graph of the effect of a limiting factor on a process behaving according to Liebig's Law of the Minimum resembles the biomass-density relationship: an initial linear increase from the origin, which levels off to a maximum value. Population density is a factor that can limit resource uptake and population growth alongside mineral nutrients, water, and light. Population density limits biomass production at low densities because there are more resources available than can be consumed; the remaining resources could support more individuals (Enquist et al. 2009) and, thus, produce more biomass. According to this view, at high densities the rate of uptake of resources and their conversion into biomass is independent of density.

We can rewrite the Michaelis-Menten equation for enzyme kinetics in terms of CFY in the simplest possible way, with total biomass (Y) corresponding to the velocity of a reaction and density as a substrate concentration:

$$Y = Y_m \left(\frac{N}{N + k} \right), \quad 9.$$

where Y_m is the maximum total biomass ($N \times w$ at densities at or above CFY), k is the density giving one-half of the maximum total biomass, and N is the density. Because $T = N \times w$, we get

$$wN = Y_m \left(\frac{N}{N + k} \right). \quad 10.$$

If we divide by N , we get

$$w = \frac{Y_m}{N + k}. \quad 11.$$

According to this model, the size of an isolated plant is determined by the amount of resources an individual converts into biomass over a given period of time in the absence of competition. In contrast to the traditional view in which the size of an individual in the absence of competition is an independent parameter, here the independent parameter is the maximum population biomass production, which can be limited by low population density.

This approach turns the concept of density-dependency around, in that density is most important when it is limiting, not when competition is intense. In a given environment over a given period of time, genotypes differ in (a) the maximum biomass that can be achieved at high density and (b) the steepness with which they achieve this maximum over increasing densities. If we reparameterize by defining $w_m = Y_m/k$ and $a = 1/k$, we get $w = w_m/(1 + aN)$, which is the simplest and most common version of Equation 8. The point here is not that we should go so far as to consider the plant populations as catalysts for biomass conversion, but simply that CFY can be thought of as a reflection of processes of resource uptake, which can be limited by population density as well as by other factors (Enquist et al. 2009).

The hypothesis that density itself can be a limiting factor is similar in some ways to the modular growth hypothesis. If we grow single-celled algae in a chemostat at different starting densities, the populations will quickly converge on the same total biomass, determined by the resource renewal rate and the algal species' growth rate (Titman 1976). If each algal cell is considered a module, then conversion of resources to biomass is identical to modularity, and then we have a three-dimensional, cellular version of our lawn example (Section 6.1 above).

In the case of higher plants, however, the hypotheses of modularity and simple biomass conversion are somewhat different. In the modularity hypothesis, the emphasis is on plant structure and space. If, rather, we think of plants as machines that convert resources into biomass, then plant growth form is an aspect of the machinery, but not necessarily the dominant aspect. Several very different types of power stations can produce electricity from oil or coal. Although the power stations may be very different in their design and their efficiencies, the basic processes involved are

the same. This is analogous to different species or genotypes in the resource–biomass conversion hypothesis. A better analogy for the modularity hypothesis would be factories making different products from the same resources. Although there will be large differences in the total mass of objects produced by different “plants,” the most important difference is the nature of the objects being produced.

7. EVOLUTIONARY BASIS FOR AND EXCEPTIONS TO CONSTANT FINAL YIELD

In addition to the proximal mechanisms, we can ask why natural selection gives rise to CFY. The answer appears to be straightforward. It is in the evolutionary interest of individual organisms to obtain and utilize limiting resources. If there are unused resources, and these resources are limiting the performance of individuals, those individuals that are better at obtaining and utilizing these resources will have a selective advantage over those that are not as good at doing so. For plants, using resources means using them to produce biomass and then offspring. CFY is one of the emergent properties of populations that can be clearly understood evolutionarily. Therefore, we can expect to see CFY whenever competition for resources is the primary form of plant–plant interaction. Despite recent emphases on nonresource-based interactions among plants and facilitation in extreme environments, there is still much evidence that resource competition is the primary interaction among plants in natural as well as human-influenced ecosystems.

The few documented exceptions to CFY occur when plant–plant interactions other than resource competition predominate. For example, nonresource-mediated mechanisms such as allelopathy can act to reduce biomass to levels below that which resources would allow. When the allelopathic grass *Aristida oligantha* appears in old-field succession in Oklahoma (Rice 1984), community biomass decreases, suggesting that biomass production is not limited by resources but by allelochemicals. Other forms of interference competition, such as the overproduction of roots in response to neighbors (Gersani et al. 2001), could result in decreased biomass production at higher densities, but such effects have not yet been convincingly documented. In competition among animals, aggressive interactions can result in a decrease in resource uptake and conversion at high densities (Sutherland 1996), but such effects have not been demonstrated in plants.

Facilitation among plants, which is important in extreme environments (Brooker et al. 2008), can alter biomass density relationships. In a recent study on *Elymus nutans* grown at different densities on the Tibetan plateau, the greatest biomass was observed at intermediate density, and mean plant mass actually increased with density at low densities (Chu et al. 2008).

The fact that exceptions to CFY are so rare proves the rule while simultaneously demonstrating that CFY is not a law of nature. CFY occurs because of resource utilization and competition, and resources mediate by far most, but not all, plant–plant interactions.

8. CHANGES IN SIZE DISTRIBUTIONS AND ALLOCATION WITH DENSITY

The effects of density on size distributions and on allocation to different structures are beyond the scope of this review, so we limit ourselves to outlining the general patterns. Although total biomass production does not change at densities above the lowest density giving CFY, there are changes in the size distribution of individuals and in biomass allocation. These two effects are closely related. At higher densities, individuals are smaller. Because allocation to different structures is allometric in the broad sense—that is, it changes with size—allocation across the population will change. Within a population, smaller plants often have a lower reproductive effort or harvest

index, defined as the fraction of their total biomass in reproductive structures (Crawley 1983, Samson & Werk 1986, Weiner 1988, Weiner et al. 2009). At higher densities, the mean size of plants is smaller, so the reproductive fraction of the total population biomass decreases. However, in many annual, weedy species, reproductive biomass is simply a fraction of total plant biomass (e.g., Rees & Crawley 1989, Weiner et al. 2009). In such cases seed production as well as biomass should show CFY.

Crowding changes the shape of the size distribution as well as its mean. Size inequality (measured by the Gini Coefficient or the Coefficient of Variation) increases at higher densities (Weiner & Thomas 1986), and competition is an important contributor to the size hierarchies commonly observed in plant populations. At very high densities, self-thinning becomes important and, since mortality is concentrated among the smallest individuals, this can truncate the distribution and result in reduced size variation among survivors (Weiner & Thomas 1986). If we include all individuals in the original population, considering dead individuals as having either the size they achieved before dying or a size of zero, then inequality increases monotonically with density at all densities above those in which competition is unimportant.

9. THE IMPORTANCE OF CONSTANT FINAL YIELD FOR PLANT COMMUNITIES

We argue that CFY has enormous consequences for understanding plant population and community processes, and it can be a valuable tool in community ecology, both in the design of experiments and the interpretation of the behavior of plant communities in the field.

9.1. Constant Final Yield and Multispecies Competition Experiments

Constant final yield for the species and environment under investigation has important implications for the design of interspecific competition experiments. For example, many studies compare the performance of plants grown in monocultures and mixtures. According to the argument above, it is important that the monoculture treatments are at a density producing CFY. If this is not done, the intraspecific treatments will not measure maximum yield and performance for each species. One way to do this is to use a density series to demonstrate CFY, rather than use a single density and assume that CFY is attained, but sometimes familiarity with the species and the environment gives the researcher enough information about CFY to select an appropriate density.

9.2. Defining Constant Final Yield for Plant Communities

If we grow a pure stand of a small plant such as *Arabidopsis thaliana* at different densities and harvest all the biomass after a period of growth, it will show a typical biomass–density relationship with CFY, as illustrated in **Figure 1**. If we grow a larger plant, e.g., *Chenopodium album*, at different densities, it will behave similarly. But the biomass at CFY, and the density at which it is achieved at a given point in time, will be very different. CFY is clearly a function of the plant species/genotype as well as resource levels. In theoretical terms, the genotype in question, as well as resource levels and time, affects the parameters of any model of density–biomass relationships, such as Equations 6 and 7 above. This means that applying the concept of CFY to a plant community comprised of species of different sizes, growth forms, or growth rates is problematic. But it is worth attempting because the benefits for plant community ecology are substantial.

Even though the design and analysis of multispecies competition experiments is still hotly debated and there is as yet no consensus on the best design for specific questions (Connolly 1986,

Connolly et al. 2001, Inouye 2001, Jolliffe 2000), resolution of this debate is not necessary before we can begin to address the fundamental issue of CFY at the community level. We can start by extending the idea of the replacement series (De Wit 1960, Silvertown & Charlesworth 2001) to a multispecies community: Given a specific plant community species composition, if we vary the density of all species together, keeping the proportions the same, we can ask whether community biomass is at CFY (He et al. 2005).

We claim that the question of whether or not a plant community is at or close to CFY is essential for understanding and predicting its behavior. There is reason to expect that the behavior of plant communities at or close to CFY is much more predictable than at lower densities. Evidence for this comes from replacement series experiments that have varied density as well as species proportions. Although the replacement series has been criticized in part because its behavior can change with density (Inouye 2001, Inouye & Schaffer 1981), there is evidence that its behavior is relatively independent of density at densities at or above those giving CFY (Cousens & O'Neil 1993, Taylor & Aarssen 1989). At CFY, the community is using all available resources. This acts as a constraint on plant community dynamics, increasing predictability (Kerkhoff & Enquist 2007). Lower densities represent transient dynamics in which initial conditions and external factors play a very large role. When CFY is reached, internal process become more dominant. We maintain that most, but by no means all, natural plant communities are at CFY.

A recent study on diversity-productivity relationships (He et al. 2005) demonstrates these issues in the context of current debates about diversity and productivity in plant communities. He and colleagues varied both plant species richness and overall density, and found that while biomass increased significantly with species richness and community density, the effects of species diversity for productivity were much smaller at high density. Density compensated to some degree for low diversity. He and colleagues conclude, as we do, that CFY needs to be extended to the community level to address these issues.

9.3. Addressing Constant Final Yield in the Field

One could argue that field experiments in which propagules or plants are added to plant communities ask, among other questions, whether the community is at CFY. If the addition of propagules results in a significant increase in biomass compared to controls, then we can conclude that the community was at a density below CFY. If the propagules being added experimentally are of a species not already present, then the issue of CFY is somewhat more complex; but if we add propagules of a species that is present, it is reasonable to interpret the result in terms of community CFY. Similarly, whether or not an invading species increases community biomass can be an important question for understanding the invasion process (Vilà & Weiner 2004). If the invading species is much larger than those present, then the interpretation of increased biomass may be ambiguous, but if the invading species is similar in size and growth rate to those already present in the community, then an increase in total community biomass due to the invasion suggests that the preinvasion community was not at CFY. This leads to the hypothesis that communities at or close to CFY are more resistant to invasions than those that are not. The observation that communities with a high leaf area index are more resistant to invasion than those with less cover (Burke & Grime 1996) is consistent with this hypothesis.

Why might a community not be at CFY? One explanation could be dispersal limitation, and such a case makes one of our major points: If a population/community biomass is highly limited by dispersal, then it is dispersal, not competition, that drives the community dynamics and limits biomass production. Another possible reason why a community may not be at CFY is simply that the plants have not had enough time to grow. The community that is present will reach CFY at the

current density and composition at a later point in time. This becomes important in the context of disturbance. Disturbance results in biomass removal and keeps the community below CFY. Disturbance has been a central concept in ecology, but a definition of disturbance has proved to be elusive. We propose that the biomass of a community relative to its CFY biomass can be used to define and measure the degree of disturbance, thus making the concept of disturbance more operational.

10. CONCLUDING REMARKS

Constant final yield appears to be among the most robust patterns in ecology, and it is based primarily on experimental data. Because a range of mechanisms could produce density responses that would not result in CFY, it is neither trivial nor inevitable, although examples of observed yield-density responses that do not conform to the pattern appear to be rare. It can be a very useful tool in plant ecology because it represents a constraint within which plant populations and communities must operate, and as such it can help us to understand and predict their behavior. It can be especially useful in developing and testing hypotheses. For example, models of plant competition and stand development that do not produce CFY should be treated with suspicion. Looking toward higher levels of organization, the CFY of individual species components can be a starting point in modeling plant community processes. Finally, by describing the maximum biomass production of a genotype in an environment after a period of growth, CFY can serve as a basis for defining and quantifying disturbance in plant communities.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

Thanks to Bill Sutherland and Mark Rees for suggestions and references, and Andrew Watkinson, Brian Enquist, and an anonymous reviewer for helpful comments on earlier versions of this review. This research was supported, in part, by grants from the Danish National Research Council (21-04-0421) and the University of Copenhagen Program of Excellence.

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