



## Control of CNP Homeostasis in Herbivore Consumers Through Differential Assimilation

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Stoichiometric analysis recognizes that a herbivore is a mixture of multiple chemical elements, especially C, N, and P, that are fixed in various proportions. In the face of a variable quality food supply, herbivores must regulate ingested nutrients to maintain a homeostatic state. We develop a dynamic mathematical model, based on differential assimilation, that controls the C:N and C:P ratios in a herbivore within given tolerance ranges; the actual mathematical mechanism is to define the absorption coefficients to be dependent on these elemental ratios. The model inputs variable, time-dependent food and grazing rates and calculates the net dynamic consumer production (growth) of C, N, and P. It shows that total growth is equally sensitive to variations in both food quality and in assimilation rates, and it shows quantitatively how C-, N-, or P-limited growth could occur at different periods during the development period. The analysis generalizes earlier work limited to just two elements.

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## 1. INTRODUCTION

A single autotroph varies widely in its nutrient content and thus its C:N:P ratios. In contrast, herbivore consumers are much less variable and stay within a restricted homeostatic range. This stoichiometric imbalance between herbivores and their food greatly affects consumer growth and activity. A basic issue is to understand and model the strategies a consumer can adopt to maintain homeostasis in its elemental ratios in the face of such a variable food supply. There are two major views regarding how an organism balances its intake and assimilation. One is based upon regulatory physiology, and the other is based upon ecological stoichiometry. On one hand, in terms of regulatory physiology, organisms ingest proteins, fats, and carbohydrates, which are then broken down in highly regulated biochemical pathways during digestion; they are assimilated across the gut wall as nutrients, like amino acids, sugars, and phosphorus containing molecules. These nutrients pass across the gut wall in definite proportions and are ultimately used in metabolism in smaller units to drive the organism's energy budget requirements. These molecules have repeatedly been shown to influence feeding and digestion (Brett, 1993; Anderson and Hessen, 1995; Tang and Dam, 1999). Studies in insects have shown the importance of regulating protein and carbohydrate levels with corresponding consequences for individual performance (Simpson and Raubenheimer, 1993, 2000; Raubenheimer and Simpson, 1997). For example, at the level of food intake, many organisms have sensory devices that regulate feeding based on these nutrients. Therefore, at the individual level, one can validly argue that through feeding behavior and post-ingestive physiology, animals regulate their nutritional status, and therefore assimilation and homeostasis are nutrient-based. On the other hand, ecological stoichiometry focuses upon the elements themselves, e.g., C, P, and N. These elements represent an index of food quality rather than representing the full scope of processes determining dietary limitation. Ultimately, however, it is the mass of each element that is conserved and ecological stoichiometry seeks to resolve elemental concentrations by keeping track of the mass flow through the entire ecosystem, as it relates to both primary and secondary production. This is a view expressed originally by Lotka (1925), and more recently by Sterner and Elser (2002) who give further support for an elemental approach; it is this tack we take in this paper. Resolving mechanistic relationships that link elemental use (this paper) and digestion of macromolecules containing these elements could be an important next step in further research.

A mathematical model for the individual could be based on either approach, and there are much data on both the nutritional and elemental composition of plants and herbivores. The general approach we take is to observe that organisms themselves, and the food they consume, are made up of elements. Using a mass balance approach, we are able to account for these elements and formulate a tractable set of differential equations that model the mass fluxes through the system, where we

treat the individual organism as a type of chemical reactor. It is less obvious how to resolve nutrient fluxes of the many complex macromolecules that make up the diet and the composition of the herbivore itself; e.g., a given ingested protein eventually disappears through its specific metabolic pathway. The elemental approach also complements an experimental program where basic chemical elements (C, N, and P) of the food, the organism, and the egesta are being measured, and therefore our approach allows us to more effectively link models at other levels of biological organization, e.g., nutrient cycling in ecosystems. We follow the idea that in all the complexity of digestion, it is ultimately mass that is conserved. Other theoretical models have focused upon elemental, stoichiometric constraints as well, especially in predator–prey interactions and how elemental imbalances significantly affect the underlying dynamics (Sturner and Hessen, 1994; Shindler and Eby, 1997; Loladze *et al.*, 2000; Mueller *et al.*, 2001; Loladze *et al.*, 2004).

Herein we examine a three-nutrient system (C, N, P) and develop a model that controls consumer homeostasis through differential assimilation. A nondynamic, two-nutrient case (e.g., C and P) was studied by Sturner (1997) and Frost and Elser (2002). They show that the assumption of strict consumer homeostasis (constant C:P ratio) leads to an algebraic model of diet constraint relating food quantity and quality, and they define a homeostasis curve in food quality–quantity space that separates regions where consumer growth is C-limited (too little carbon) and where it is P-limited (too little phosphorus). To maintain a constant consumer C:P ratio, the consumer's diet must be confined to the curve. A dynamic two-dimensional model developed by Logan *et al.* (2003b) uses differential assimilation to control assimilation of elements to maintain the consumer C:P or C:N ratio within a tolerance envelope, even when the food supply is variable and time-dependent. In the present work we show how this analysis can be carried out simultaneously for three elements, C, N, and P, both for the nondynamic and the dynamic cases. In the static case we define a strict homeostatic curve in food CNP space relating food quantity, measured by carbon content times ingestion rate, and two quality variables defined by food C:P and C:N ratios. Our model gives an alternative visualization to three-element homeostasis representations given by Thingstad (1987), whose static model for bacteria relaxes the condition of strict homeostasis and elemental ratio homeostasis is represented by regions in a two-dimensional space with axes C:N and C:P, both relating to the food supply. Also see Sturner and Elser (2002, p. 195). The static model we present directly generalizes the two-nutrient curve of Sturner (1997). Secondly, and most importantly, we introduce the dynamic notion of differential assimilation control to maintain consumer C:P and C:N ratios within a set tolerance range, even when the food quality and quantity leave the homeostasis curve and are time-dependent. When food has an extreme imbalance, control of elemental assimilation shuts down absorption of the over-abundant element(s) and subsequently restricts growth in C-, P-, or N-limited regimes. The model is based upon a dynamic environment and dynamic responses by the consumer while relaxing the condition of strict homeostasis. In the model

we are mostly considering some insect herbivores, although the analysis may apply to other taxa.

An important related issue is where and how homeostasis is maintained in a herbivore? The answer to this question is not known completely. Three tactics that have been conjectured and studied are: selecting different foods when available, regulating assimilation of a given element or nutrient, and excreting excess elements through metabolism. Our model focuses on one mechanism for the post-ingestive response, namely differential assimilation of elements. We interpret ‘differential assimilation’ for an individual consumer in a broad sense, meaning assimilation in its entire system. We build a conceptual framework for homeostasis maintenance in the classical approach of mathematical modeling, where we ignore many of the intermediate details of the exact biochemical processes.

## 2. STRICT CNP HOMEOSTASIS

In this section we show how to adapt the analysis of [Sterner \(1997\)](#) and [Frost and Elser \(2002\)](#) [see also [Sterner and Elser \(2002\)](#), p. 198ff] to a static three-element system (C, N, P). In [Section 3](#) we formulate a dynamic control problem in three-dimensional phase space to model differential absorption for herbivore consumers who must maintain homeostasis of both C : N and C : P.

Nutrient acquisition and use in many consumers can be described as follows. After consumption, complex substrates are broken down into nutrient products; the fraction of these not egested is transported across the gut boundaries into the consumer’s system (e.g., for insects, into the hemolymph). There, these nutrients are broken down further and distributed to metabolic activities such as respiration and excretion, growth, reproduction, and storage, via the animal’s energy budget [e.g., see [Gurney and Nisbet \(1998\)](#), [Lika and Nisbet \(2000\)](#), [Kooijman \(2000\)](#)]. In our model we greatly simplify the underlying processes by ignoring intermediate bio-chemical kinetics; we assume that elemental nutrients are directly ingested and ultimately assimilated across the gut wall and into the organism’s system. We do not include processes like pH or water control, both of which may play a role in insect digestion modulation. Also, we assume that the herbivore is in stages prior to maturity, and so we ignore energy currency explicitly allocated to reproduction (although one could consider some allocation to reproduction as built into production). We also do not consider storage. By considering elemental flow, we can apply mass balance laws to obtain the governing dynamics.

In many insect herbivores (as well as many other taxa) there are three nutrients (C, P, and N) that affect growth, metabolism, and the maintenance of homeostasis. The structure of the model is shown in [Fig. 1](#). The herbivore ingests food consisting of specific C : N and C : P ratios; some nutrients are egested, and some are assimilated across the gut wall for growth (production) and basal maintenance

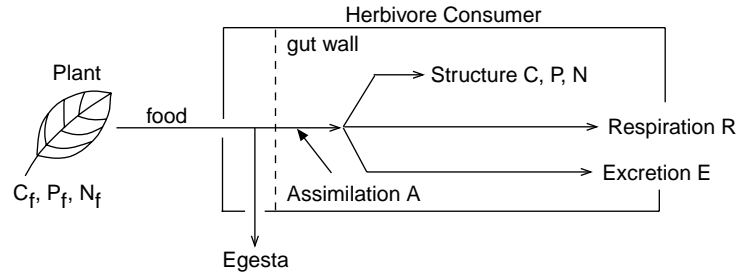


Figure 1. Schematic showing the elemental fluxes (C, P, and N) in a herbivore consumer and its energy budget allocation. Each element is ingested and a fraction is assimilated across the gut wall, the remaining being egested. The assimilated elements are ultimately allocated to structure (total biomass) and maintenance (respiration and excretion).

(respiration and excretion). For each element, we have the following balance law for the fluxes, or rates:

$$\text{Per capita production} = \text{assimilation} - \text{respiration} - \text{excretion}.$$

The model deals with three specific elements in the food and in the herbivore. The carbon biomass of the consumer is used to determine the per capita amount of C, N, and P required in the production and metabolism processes. Carbon from the plants is used by consumers for both growth and maintenance (e.g., respiration through the loss of  $\text{CO}_2$ ), while phosphorus is used only for production. Although phosphorus is required in the biochemical pathways for metabolism, it is not generally lost through either excretion or respiration. Nitrogen is used for production and it is often excreted as a by-product of metabolism, but not lost in respiration. Indigestible cellulose in the food is accounted for in the fraction of food not assimilated, and hence egested.

To formulate the model equations, we use upper case italic letters to denote the elemental amounts of C, N, and P; thus  $C = C(t)$ ,  $N = N(t)$ , and  $P = P(t)$  denote consumer elemental biomasses (in moles); the subscript  $f$  on these quantities, e.g.,  $C_f = C_f(t)$ , denotes the density (moles per volume) of the element in the food. We take  $g$  as the constant grazing rate (volume per moles of C per time), and we let  $a_c$ ,  $a_p$ , and  $a_n$  denote the constant (for present), dimensionless assimilations of the elements. The assumption of a constant feeding rate  $g$  is part of the steady-state analysis; in [Section 3](#) where we discuss the dynamic case, the feeding rate can be time dependent. Some herbivores do maintain constant rates, but others exhibit compensatory feeding and increase feeding when food quality decreases. Finally, we let  $m$  denote the constant respiration rate of C, and  $k$  the constant excretion rate for N; both rates are given in  $\text{time}^{-1}$ . An obvious deficiency in the model we formulate is that  $m$  and  $k$  do not depend upon the food densities [see [Gurney and Nisbet \(1998\)](#)]; however, the model can be extended to cover this case by letting  $m$  and  $k$  depend upon food intake. Another simplifying mathematical

assumption is that the N excretion rate is constant and does not depend upon total C biomass; over long times, where there is significant growth, our assumption may need revision.

The basic CNP model can be written as

$$\frac{1}{C} \frac{dC}{dt} = gC_f a_c - m, \quad \frac{1}{C} \frac{dP}{dt} = gP_f a_p, \quad \frac{1}{C} \frac{dN}{dt} = gN_f a_n - k \frac{N}{C}. \quad (1)$$

The first two equations coincide with those in the two-dimensional model of Sterner (1997) and Frost and Elser (2002) extended that model by replacing the ingestion rates  $gC_f a_c$  and  $gP_f a_p$  by saturating functions (Holling type II responses) of food densities to take into account handling time. In (1) we have added a third equation for N, which will complicate the homeostasis analysis.

In the sequel the term *homeostasis* is used in the sense defined by Kooijman (1995), i.e., the composition of the consumer is constant, regardless of the composition of the ingested food. We shall call this *strict* homeostasis; later we relax the constancy condition and only require homeostasis within a restricted tolerance range. At present, for the herbivore consumer we assume  $C/P = \beta$  and  $C/N = \gamma$ . Generally,  $\beta > \gamma$  because herbivores contain much more N than P. Eliminating P and N from (1) yields two conditions for homeostasis,

$$gC_f a_c - m = \beta_g P_f a_p = \gamma_g N_f a_n - k. \quad (2)$$

We introduce two food qualities,  $Q_p = P_f/C_f$  and  $Q_N = N_f/C_f$ , which are the P:C and N:C ratios in the food. Equation (2) defines a homeostasis curve in three-dimensional  $Q_p Q_N C_f$ -space that we can represent as the intersection of two cylindrical surfaces  $S_p$  and  $S_N$  defined by

$$S_p: Q_p = \frac{gC_f a_c - m}{\beta_g C_f a_p}, \quad S_N: Q_N = \frac{gC_f a_n + k - m}{\gamma_g C_f a_n}. \quad (3)$$

The (generic) surfaces and the strict homeostasis curve are sketched in Fig. 2. The quantity  $gC_f$  on the right sides of (3) is a measure of the total quantity of food ingested, so that equation (3) represents quality vs. quantity surfaces of the ingested food. The present discussion refers to Fig. 2. A consumer must have a diet that lies on the curve AB to be in strict homeostasis. Toward point B on the curve the food quantity is high and growth is high; toward point A, the lower end of the curve, growth is less. Observe that point A is limiting for growth since the homeostasis curve must lie in the positive octant, and this lower limitation depends upon the nonexcreted mineral P, since  $x > w$  (i.e.,  $m - k < m$ ), and since A lies on the intersection of the  $S_p$  surface with the coordinate plane. This conclusion is consistent with intuition; if a mineral is excreted (in this case N), then less C is required in the food to maintain homeostasis because that mineral is lost to production. So growth limitation will depend on the nonexcreted mineral, where

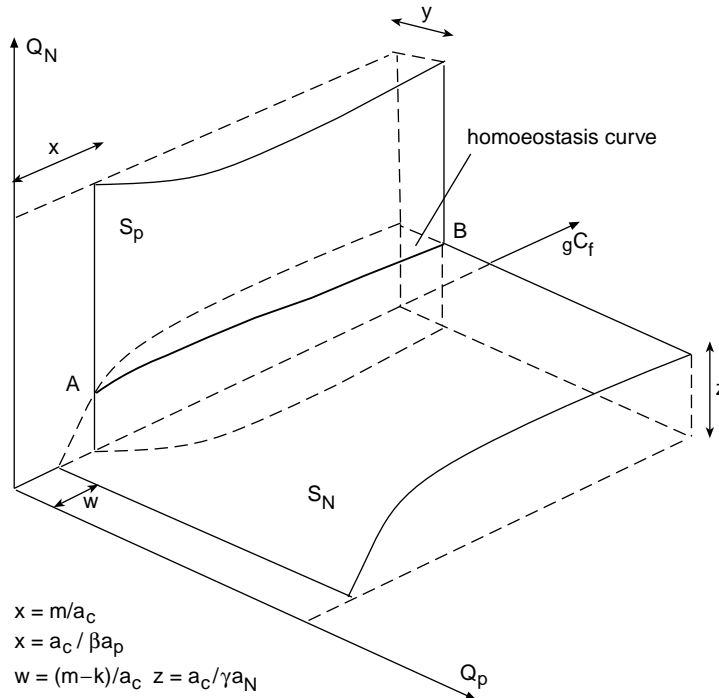


Figure 2. Homeostasis curve for a three-element system represented as the intersection of the quality vs. quantity surfaces  $S_N$  and  $S_P$ . Quantity is measured by  $gC_f$  and qualities are the P:C and N:C ratios in the food. To maintain strict homeostasis the consumer's diet must lie on the curve.

more C will be required to maintain homeostasis. Below each surface, respectively (between the surface and the coordinate plane), the food is limited in that mineral, P or N. In the intersection that lies below both surfaces, both minerals are limited. Above the surfaces C is limiting (the food is high quality but the quantity, measured in the currency C, is small).

### 3. DIFFERENTIAL ELEMENTAL ASSIMILATION

The model described in the last section is static and does not indicate what will occur under variable environmental conditions, or what the response of the consumer is. There are many strategies a consumer can adopt when faced with food scarcity or low food quality. It often compensates by altering digestive tactics to meet its nutritional needs (Zanotto *et al.*, 1993, 2000; Raubenheimer and Simpson, 1994, 1997; Karasov and Hume, 1997; Woods and Kingsolver, 1999; Whelan and Schmidt, 2003). Such tactics may include changing its morphology (e.g., gut size), changing the residence time of the food to maximize total uptake,

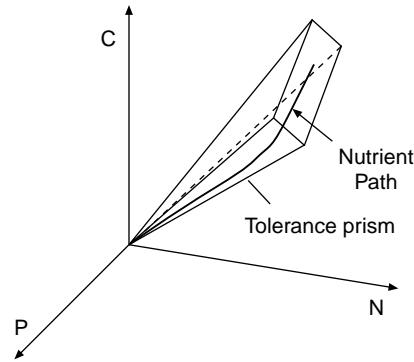


Figure 3. Schematic showing a typical herbivore response to a variable food supply in the CNP space. Differential assimilation confines the response  $C(t)$ ,  $N(t)$ ,  $P(t)$  to a tolerance prism near strict homeostasis. In the interior of the prism C, N, and P are assimilated at maximum rates. On a boundary (a side or an edge) of the prism one or more elements are limited.

or modifying absorption rates (Sibly, 1981; Dade *et al.*, 1990; Martínez del Rio and Karasov, 1990; Simpson and Raubenheimer, 1993; Yang and Joern, 1994; Jumars and Martínez del Rio, 1999; Jumars, 2000; Logan *et al.*, 2002, 2003a; Wolessky, 2002; Whelan and Schmidt, 2003; Wolessky *et al.*, 2003). However, how an animal actually regulates homeostasis is generally an open question. There is evidence that some animals modify digestive processing of food by differential assimilation across the gut wall (Zanotto *et al.*, 1993; Woods and Kingsolver, 1999), which is the response we model here.

Rather than require exact homeostasis where the C : N and C : P ratios are strict constants, the present model assumes that an organism will operate within a narrow tolerance zone defined by

$$\beta - \sigma \leq \frac{C}{P} \leq \beta + \sigma, \quad \gamma - \epsilon \leq \frac{C}{N} \leq \gamma + \epsilon, \quad (4)$$

where  $\sigma$  and  $\epsilon$  are tolerance ratios. These inequalities define a region in three-dimensional CNP space having the shape of a four-sided pointed prism (see Fig. 3). Our assumptions automatically define a homeostatic ratio for N : P; if a different N : P ratio is required by the consumer, then the tolerance zone would form a six-sided pointed prism (with an accompanying more complicated set of assimilation rules than we give below for an automatically determined N : P ratio). Initially ( $t = 0$ ) we assume the herbivore is in strict homeostasis, i.e.,

$$\frac{C(0)}{P(0)} = \beta, \quad \frac{C(0)}{N(0)} = \gamma,$$

where  $C(0)$  is the initial carbon biomass of the consumer. Then the elemental dynamics are calculated using the system (1); the calculated values  $C(t)$ ,  $N(t)$ , and

$P(t)$  define a curve in CNP space called the elemental nutrient path (or just *nutrient path*), which is the path of the consumer's stoichiometry. As long as the consumer's C:N and C:P ratios lie in the ranges defined by (4), i.e., its nutrient path lies in the tolerance prism, it assimilates all three elements at maximum constant rates,  $a_c^*$ ,  $a_p^*$ , and  $a_n^*$ , to maximize growth. However, when food imbalance forces the nutrient path to a boundary of the prism [where equality holds in one or more cases in (3)], absorption of the excess element or elements is reduced so that the ratio remains in the prism, or on its boundary. For example, when a food is high in C and low in N, it is of low quality, and the nutrient path will be driven so as to track along the upper C:N boundary where assimilation of C is restricted; this is N-limited growth. Thus the assimilation 'constants'  $a_c$ ,  $a_p$ , and  $a_n$  in the dynamic equation (1) become nonlinear functions of the carbon to mineral ratios. Rather than write out these functional relations specifically as single, complicated formulas, we define the assimilation rates piecewise in several cases. How the overall dynamic model works is the subject of the analysis below.

To determine the appropriate assimilation rates to remain in the tolerance prism when one or both ratios reach a boundary, we solve an algebraic problem that comes from specifying the vector field of (1), at any time, to lie on the boundary of the prism (either a plane, or an edge). Thus, there are eight cases to consider. The first four cases arise when the nutrient path reaches a bounding plane of the tolerance prism, and the last four cases occur when two planar boundaries are reached simultaneously, i.e., an edge is reached. We can conveniently represent the dynamics in two two-dimensional phase planes, the  $PC$  plane and the  $NC$  plane. The projection of the three-dimensional tolerance prism onto those planes gives triangular tolerance zones defined by (4).

1. Consider the case when only the upper boundary of the C:P tolerance prism is reached, i.e.,

$$\frac{C}{P} = \beta + \sigma, \quad \gamma - \epsilon < \frac{C}{N} < \gamma + \epsilon. \quad (5)$$

Here the consumer maintains the maximum P and N assimilation rates ( $a_p = a_p^*$ ,  $a_n = a_n^*$ ) and restricts its assimilation rate  $a_c$  such that the C:P ratio remains on the boundary of its tolerance zone. Using the vector field constraint  $dC/dP = \beta + \sigma$  results in the algebraic condition

$$\frac{gC_f a_c - m}{gP_f a_p^*} = \beta + \sigma, \quad (6)$$

from which we can determine the reduced carbon assimilation rate  $a_c$  given by

$$a_c = \frac{(\beta + \sigma)gP_f a_p^* + m}{gC_f}. \quad (7)$$

One can verify that  $a_c < a_c^*$ .

2. Next consider the case

$$\frac{C}{P} = \beta - \sigma, \quad \gamma - \epsilon < \frac{C}{N} < \gamma + \epsilon. \quad (8)$$

Here the lower boundary of the C : P ratio is reached, and the consumer maintains maximum C and N assimilation rates ( $a_c = a_c^*$ , and  $a_n = a_n^*$ ), while restricting  $a_p$ . We use the vector field constraint  $dC/dP = \beta - \sigma$  to obtain the condition

$$\frac{gC_f a_c^* - m}{gP_f a_p} = \beta - \sigma, \quad (9)$$

which leads to

$$a_p = \frac{gC_f a_c^* - m}{(\beta - \sigma)gP_f}. \quad (10)$$

3. When the C : N ratio reaches the upper boundary of its tolerance zone, but the C : P ratio remains within its respective zone, i.e.,

$$\beta - \sigma < \frac{C}{P} < \beta + \sigma, \quad \frac{C}{N} = \gamma + \epsilon, \quad (11)$$

the consumer maintains maximum P and N assimilation ( $a_p = a_p^*$ , and  $a_n = a_n^*$ ) and restricts  $a_c$  via

$$\frac{(gC_f a_c - m)C}{gN_f a_n^* C - kN} = \gamma + \epsilon. \quad (12)$$

That is,

$$a_c = \frac{(\gamma + \epsilon)gN_f a_n^* - k + m}{gC_f}. \quad (13)$$

4. The final single boundary case occurs when the C : N ratio reaches the lower boundary of its tolerance zone and C : P remains within its tolerance zone

$$\beta - \sigma < \frac{C}{P} < \beta + \sigma, \quad \gamma - \epsilon = \frac{C}{N}. \quad (14)$$

The maximum assimilation rates are adopted for both C and P ( $a_c = a_c^*$ ,  $a_p = a_p^*$ ) but  $a_n$  is limited via the condition

$$\frac{(gC_f a_c^* - m)C}{gN_f a_n C - kN} = \gamma - \epsilon. \quad (15)$$

Solving for  $a_n$  gives

$$a_n = \frac{gC_f a_c^* - m + k}{gN_f(\gamma - \epsilon)}. \quad (16)$$

5. The following four cases occur when both of the ratios, C:N and C:P, reach the boundaries of their envelopes simultaneously (i.e., the nutrient path reaches an edge of the prism). First consider

$$\frac{C}{P} = \beta - \sigma, \quad \frac{C}{N} = \gamma - \epsilon. \quad (17)$$

Both ratios allow maximum assimilation for carbon ( $a_c = a_c^*$ ), but N and P are limited. The conditions that determine  $a_n$  and  $a_p$  are given by (9) and (15). These two conditions are independent and yield (10) and (16) for  $a_n$  and  $a_p$ , respectively.

6. When

$$\frac{C}{P} = \beta + \sigma, \quad \frac{C}{N} = \gamma + \epsilon, \quad (18)$$

assimilation rates for P and N remain maximal ( $a_p = a_p^*$ ,  $a_n = a_n^*$ ), but the assimilation rate for C is determined by (6) and (12). For both the C:P and C:N ratios to remain in their respective tolerance zones we choose  $a_c$  to be the minimum of (7) and (13).

7. Next consider

$$\frac{C}{P} = \beta + \sigma, \quad \frac{C}{N} = \gamma - \epsilon. \quad (19)$$

These ratios permit the maximum assimilation of P ( $a_p = a_p^*$ ), but require  $a_c$  and  $a_n$  to be restricted. Using the constraints  $dC/dP = \beta + \sigma$  and  $dC/dN = \gamma - \epsilon$  we obtain the conditions

$$\frac{gC_f a_c - m}{gP_f a_p^*} = \beta + \sigma, \quad \frac{(gC_f a_c - m)C}{gN_f a_n C - kN} = \gamma - \epsilon. \quad (20)$$

The consumer can maintain elemental homeostasis by remaining on the two boundaries given in (19). The algebraic equations given in (20) uniquely determine the two assimilation rates,  $a_c$  and  $a_n$  given by

$$a_c = \frac{(\beta + \sigma)gP_f a_p^* + m}{gC_f}, \quad a_n = \frac{(\beta + \sigma)gP_f a_p^* + k}{gN_f(\gamma - \epsilon)}. \quad (21)$$

8. The final case is

$$\frac{C}{P} = \beta - \sigma, \quad \frac{C}{N} = \gamma + \epsilon. \quad (22)$$

The assimilation rate for N is unrestricted ( $a_n = a_n^*$ ) and we can proceed as in case 7. The homeostasis conditions are

$$\frac{gC_f a_c - m}{gP_f a_p} = \beta - \sigma, \quad \frac{(gC_f a_c - m)C}{gN_f a_n^* C - kN} = \gamma + \epsilon. \quad (23)$$

Again we uniquely determine assimilation rates for C and P that allow the ratios C : P and C : N to remain on the boundaries (22). Solving (23) gives

$$a_c = \frac{(\gamma + \epsilon)gN_f a_n^* - k + m}{gC_f}, \quad a_p = \frac{(\gamma + \epsilon)gN_f a_n^* - k}{(\beta - \sigma)gP_f}.$$

To summarize, the mathematical model consists of the dynamical equation (1) subject to the constraining relationships defined in cases 1–8. Reiterating, the nutrient path  $C = C(t)$ ,  $N = N(t)$ ,  $P = P(t)$  in CNP space begins at an initial homeostatic state and then moves through the tolerance prism. Within the interior of the prism all nutrients are assimilated at their maximum rates  $a_c^*$ ,  $a_p^*$ , and  $a_n^*$ . If the food supply drives the nutrient path to the boundary of the prism, then the assimilation rates are selected to align the vector field of 1 along that boundary so that it does not escape the prism. Physiologically, the herbivore differentially assimilates; when the food supply is extreme, it will operate at the edge of its tolerance range, thus limiting its production, and therefore its growth, in one or more nutrients. Maximum growth will occur when the food supply is such that the nutrient path remains near exact homeostasis, i.e., when it most matches the chemical composition of the consumer itself.

Finally, we comment on the consistency of the model with Liebig's law of the minimum, which states that a growth will be limited by whichever single resource is in lowest abundance in its environment, relative to its needs. Although this rule is normally associated with plant growth, it is also applied to consumers [e.g., Thingstad (1987), Sterner and Elser (2002, p. 190ff), and the references therein]. In our model, either *one* or *two* nutrients can be limiting. In the latter case, for example, a food supply low in N and low in P can drive the nutrient path to an edge of the tolerance region (case 6) where the consumer strongly limits its C assimilation to maintain two homeostatic ratios. Thus, for our model, Liebig's rule requires a more general interpretation to allow for multiple limiting nutrients [see Bloom *et al.* (1985)].

#### 4. NUMERICAL SIMULATIONS

It is not possible to solve the model analytically, and so we turn to simulation. We developed a Matlab program to numerically solve the differential equation (1) subject to the controls defined in cases 1–8 in Section 3. Because the model can describe many scenarios, a large number of computations could be performed to illustrate results for different food inputs (food qualities, food quantities, grazing rates), different maximum assimilation rates (depending upon taxa), and different tolerance ratios. For each variation, total growth in C, N, P, the total amount of excreta and egesta returned to the environment, as well as the nutrient paths, can be calculated. To limit space, however, we illustrate how the model performs in a specific case and we show the type of output that results.

Table 1. Parameter values.

Quantity	Name	Value
$g$	Grazing rate	$0.001 \text{ l (mol C)}^{-1} \text{ h}^{-1}$
$m$	C respiration rate	$0.002 \text{ h}^{-1}$
$k$	N excretion rate	$0.0002 \text{ h}^{-1}$
$a_c^*$	C assimilation	0.5
$a_p^*$	P assimilation	0.9
$a_n^*$	N assimilation	0.6
$\beta$	C : P biomass ratio	73.2
$\gamma$	C : N biomass ratio	6.4

Any model, of course, must be validated by empirical evidence. Unfortunately, experiments on three-element systems are lacking. In insect herbivores, for example, there is significant support of viewing N as a likely limiting nutrient [e.g., White (1993)]; but evidence for P is only now building and data are scarce (Sterner and Elser, 2002). In grasshoppers, for example, availability of excess bulk food is the norm, but the capacity to find high quality N food is limiting; the role of P is not known. Generally, C comprises the bulk dry weight of organisms, and in terrestrial organisms P is more variable than N (Sterner and Elser, 2002). Thus, the variability in the C : N ratio is much less than in the C : P ratio. Many factors, e.g., different habitats, the presence of vacuoles, etc., force plants to have larger variations in their C : P ratios as well. For our generic calculations we take median values of terrestrial invertebrate C : N and C : P ratios catalogued by Sterner and Elser (2002, p. 140ff), and typical plant ratios (p. 120 ff). As their tables show, there are large variations in all these ratios. For the herbivore consumer we take C : P = 73.2 and C : N = 6.4, which leads to an N : P ratio of 11.4, well within observations in some taxa. The tolerance ratios  $\sigma$  and  $\epsilon$  are chosen arbitrarily to be five percent of each ratio. For food we take C : P = 263 and C : N = 30. The total time of the simulation is 96 h (4 days). A typical grasshopper, for comparison, might require about three times this period to progress through one of its five instars. The remaining parameter values are given in Table 1. These average values lead to interesting dynamics and illustrate the model performance.

The nutrient path in three dimensions is difficult to visualize and thus, as discussed earlier, we illustrate it as two parametric paths in the  $PC$ -plane and the  $NC$ -plane (Fig. 4). One can compare these types of plots to the experimental plots of Simpson and Raubenheimer (2000, p. 29). At first, both C : P and C : N ratios are high because of high C concentration in the food (low quality). The nutrient path approaches both upper boundaries where C assimilation becomes reduced. Over time, however, the C limitation leads to excess P and drives the nutrient path toward the lower boundary of the C : P zone, while the C : N ratio remains in excess, causing the path to track on the boundary on the C : N zone. After a time the path

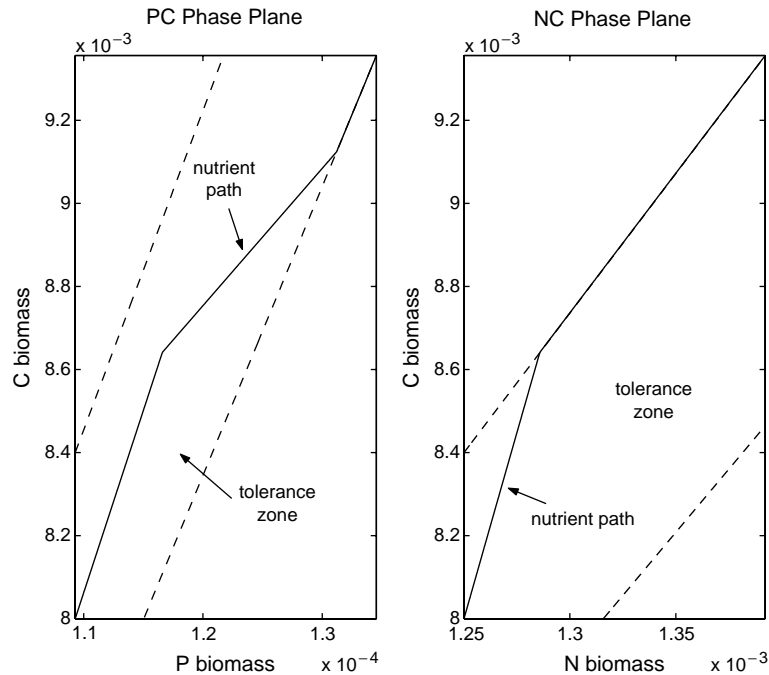


Figure 4. Numerical simulation showing the time-dependent nutrient paths in the  $PC$  and  $NC$  planes. The tolerance zones are the 2-dimensional projections of the tolerance prism onto those planes. The food supply is given by fixed with  $C_f/P_f = 10/0.038 = 263$  and  $C_f/N_f = 10/0.33 = 30$ . The total time of the simulation is 96 h, and the remaining values are given in the table.

reaches the boundary of the  $C:P$  zone and thus assimilation of  $P$  is restricted. The system continues then to track along the tolerance boundaries where both  $C$  and  $P$  are limited ( $C$  limited to maintain constant  $C:N$  and  $P$  limited to maintain constant  $C:P$ ). With regard to a regulatory physiological approach, as discussed in the introduction, one could consider identifying  $C$  with carbohydrate and  $N$  with protein and plot curves on a protein–carbohydrate plane.

In this model an organism responds to an extreme food supply by tracking along the boundaries (rather than the interior) of its nutrient thresholds. One or more elements will be limited and total production in that element will be limited, leading to restricted growth. If the food is well-matched to the herbivore, the path will track in the interior of its tolerance zones, leading to maximum assimilation of all the elements, and therefore maximum production. This model fits well, in concept, with the empirical conclusions of [Simpson and Raubenheimer \(2000\)](#). In experiments with locusts they found target ratios for different nutrients (e.g., protein vs. carbohydrate). Here, for comparison, we can associate  $N$  with protein and  $C$  with carbohydrate. This target ratio must lie in some domain in nutrient space for the organism to survive and advance to the next instar. Corresponding to a target zone there is a set of food nutrient ratios where the insect's nutrient path can reach its

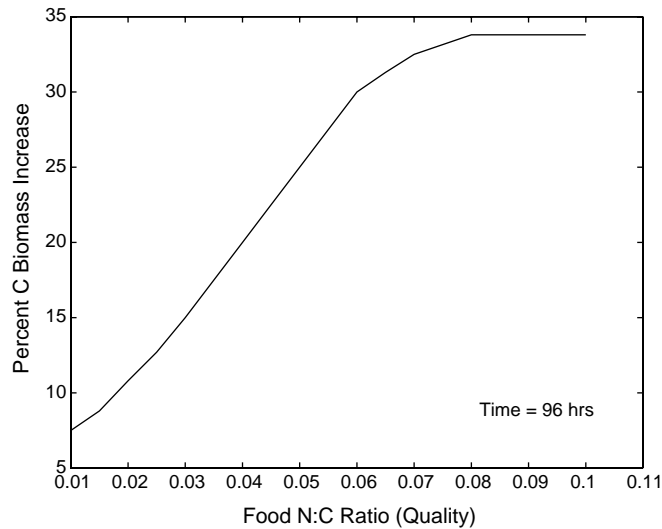


Figure 5. Calculation of the total percentage increase in carbon biomass accumulated in 96 h for different food qualities measured by the food N:C ratio; the carbon and phosphorus densities are fixed with  $C_f = 10$  and  $P_f = 0.038$ , and the remaining values are given in the table.

target zone. Although we do not pursue this here, until there is experimental data available, our model has the capability of determining the domain of food elemental ratios that force the nutrient path into a given terminal set, some subregion of the tolerance prism.

From a number of simulations, Fig. 5 shows the total percentage accumulation of C-biomass in the insect after 96 h for different food qualities measured by the ratio  $N_f/C_f$  of the food. The carbon and phosphorus contents remain unchanged. The collective simulations show that as the nitrogen content increases, i.e., as the food becomes higher quality, the final C-biomass increases up to a limiting value (33.8%) at about  $N_f/C_f = 0.07$ ; it then levels off, and no further growth occurs because at higher food quality the nutrient path remains in the interior of the tolerance prism for the 96 h duration of the simulation.

Another important issue is the time scale over which the model and its simulations are valid. We have assumed in the simulations a short-to-intermediate time length of 96 h where the food supply and ingestion rate are assumed to be constant. In reality, over this physiological time scale the food rail could be quite erratic with intervals of no ingestion and changing food composition, resulting in the animal constantly switching its nutrient path back and forth in the prism. Over long, developmental, time scales the food quality can vary significantly over a season; for example, the nitrogen content of plants can decrease dramatically over the summer, leading to an increasing C:N food ratio over time. The model can accommodate these variations by inputting  $g$ ,  $C_f$ ,  $P_f$ , and  $N_f$  as functions of time, or even including stochastic effects of weather. Yet one qualification

remains. Over developmental time scales, where growth is significant, the linearity and the density-independent assumptions in model equation (1) may lose some of their validity. Over shorter, physiological time scales, the model may perform better in predicting growth. To adapt the model as a link in the overall nutrient cycling problem in an ecosystem may require future modifications that account for these nonlinearities. For example, the N excretion rate  $k$  may depend upon total consumer C-biomass. And, the role of temperature, which is especially significant for insects, must ultimately be included in the model as a factor that affects absorption rates and metabolic activity [e.g., Wolesensky (2002), Wolesensky *et al.* (2003)].

## 5. SUMMARY

Host plants provide complex and variable concentrations of elemental nutrients. Growing herbivores face the problem of having to manage multiple and changing nutrient needs in a multidimensional and variable nutrient environment. We have incorporated differential assimilation to control elemental homeostasis in a consumer eating food of significantly different elemental ratios. The model extends the results of Sterner (1997), Frost and Elser (2002), and Logan *et al.* (2003b) to three-nutrient systems, variable food input, and variable grazing rates. By including a tolerance zone around strict homeostatic control, we show that a herbivore consumer can adjust its assimilation in response to limiting elements in its diet. As food supply ratios change, independent of the actions of the consumer, assimilation changes accordingly and relative elemental accumulation shifts. Thus, differential assimilation can effectively act as a nonlinear control mechanism permitting elemental homeostasis in consumers, as predicted by Sterner (1997). Under variable conditions the model can predict total production, or growth, and in what regimes growth is C-, P-, and N-limited.

One important conclusion that can be deduced from several simulations is that assimilation rates may play an equal role to food supply ratios in maintaining homeostasis. Even in the case where the food ratios C:N and C:P are exactly those of the homeostatic state of the consumer, the nutrient path may not track in the interior of the tolerance zone along the ideal path, but rather track on a boundary with one or more nutrients limited, thus limiting production. This limitation can be forced by changing the assimilation rates of the different elements. In insects, for example, variable assimilation rates may be the rule because digestion processes depend so strongly upon temperature. One important research question, both theoretically and experimentally, is to understand how temperature variations affect the assimilation rates of various nutrients and elements.

With appropriate qualifications we can view the model as one link in the overall nutrient cycling process in natural systems. It permits the calculation of secondary production, based on the composition of the food supply. Coupled with models for

the other components of the nutrient cycle [e.g., DeAngelis (1992), Daufresne and Loreau (2001)], this model could form another piece of this overall stoichiometric process.

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