Mathematical Model of Consumer Homeostasis Control in Plant-Herbivore Dynamics

J. DAVID LOGAN[*], ANTHONY JOERN[†], & WILLIAM WOLESENSKY[‡]

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Abstract

Consumers must regulate the elemental composition of body tissue at ratios that differ from those of their food. This problem of elemental homeostasis is especially acute for herbivores for which elemental composition of food does not equal that of the consumer and changes widely throughout the lifespan. We extend work of Sterner [1] and Frost & Elser [2] using a dynamic model of homeostatic control within tolerance limits by consumers feeding on unbalanced diets based on nonlinear assimilation as a primary mechanism. Differential assimilation provides a suitable, if incomplete, mechanism for homeostasis where the limiting element defines the accumulation trajectory of nutrients incorporated into the consumer.

Keywords: mathematical ecology, homeostasis, digestion control, nutrient cycling, food quality and quantity.

AMS Classification: 92D40

1 Introduction and Motivation

The chemical makeup of food plants eaten by herbivores differs dramatically from the chemical makeup of their own tissue, where nutrient consumption is often unbalanced relative to needs (Bernays & Chapman [3], Sterner [4], Elser & Urabe [5], Elser et al. [6], Simpson & Raubenheimer [7]). In natural environments, food quality fluctuates dramatically as well, where an herbivore is faced with limitation for different nutrients or elements to varying degrees that may vary unpredictably (Schindler & Eby [8], Frost & Elser [2]). Herbivores typically adjust feeding decisions and postingestive processing to maintain stoichiometric homeostasis in the face of this imbalance (Zanotto et al. [9], [10], Yang & Joern [11], Sterner & Hessen [12], Elser et al [13], Karasov & Hume [14], Simpson &

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[*] Department of Mathematics, University of Nebraska, Lincoln NE 68588-0323.

[†] School of Biological Sciences, University of Nebraska, Lincoln NE 68588.

[‡] Program in Mathematics, College of St. Mary, Omaha NE 68134

Rabenheimer [15]). We develop dynamic models of plant-herbivore interactions under the assumption of elemental homeostasis of the herbivore consumer to examine the effects of variable food quality and quantity on consumer growth patterns. This paper assumes that the herbivore maintains constant elemental ratios (carbon-to-nitrogen, or carbon-to-phosphorus), at least in the abstract, and it introduces a control mechanism, namely differential assimilation, to regulate homeostasis within acceptable tolerance ranges. These models extend the work of Sterner [1], Shindler and Eby [8], and Frost and Elser [2] to a dynamic food environment. The recent book by Sterner & Elser [16] reviews work on ecological stoichiometry and homeostasis in plants and consumers.

A challenge to the herbivore is to maintain its homeostatic balance in the midst of environmentally-driven stoichiometric imbalance, which changes in direction and degree throughout the season. In accordance with mechanisms underlying ecological stoichiometry, consumers preferentially consume and retain specific elements in the diet depending on which element is most limiting, leading to highly dynamic feeding, digestion and growth (Simpson & Raubenheimer [7], Whelan & Schmidt [17]). Differential absorption and/or excretion of elements in the diet may regulate elemental homeostasis and growth in consumers (Zanotto et al [10], Woods & Kingsolver [18], Whelan & Schmidt [17]), ultimately affecting the chemical composition of excreta, and possibly nutrient redistribution and cycling to the entire ecosystem (Sterner & Hessen [12], Elser & Urabe [5]).

Mathematical models have played an important role in developing an understanding of ecological stoichiometry in natural systems (Anderson [19], Andersen [20], Sterner [1], Loladze, Kuang, & Elser [21]), but much remains to be done to understand consumer regulation based on individual responses to food C:N:P. Our goal in this paper is to model the degree to which variable food quality and the dissimilarities in C:P or C:N ratios between food and consumers act to constrain digestion, growth, and contributions to secondary production and nutrient cycling. We assume that stoichiometric regulation is a major principle underlying secondary production in climatically variable ecosystems regulated by multiple limiting factors. The level of imbalance between food and consumers alters performance accordingly, and individual consumers may alternate between energy (measured by carbon biomass) versus mineral limitation. Some basic questions are: When and where are nutritional constraints important and how are they manifested? And, how does energy limitation interact with mineral limitation, if at all? Available theoretical and empirical analysis (Schindler & Eby [8], Sterner [1], Frost & Elser [2]) conclude that food quality and quantity interact to limit consumer production. Their steady-state models indicate that thresholds may exist between C-limitation (energy) vs. mineral-limitation (N or P), and consumers may exist in either of these states depending on environmental conditions affecting both food quality and consumption by consumers. There is significant support for viewing N as a likely limiting mineral nutrient in many insect herbivores (Slansky & Feeny [22], White [23]), and P may also be important (Frost & Elser [2]). For insect herbivores such as grasshoppers, availability of excess bulk food is the norm, but the capacity to find high quality food and to digest food may be rate limiting.

2 The C:P System

The basis of our models for consumer homeostasis is a dynamic energy budget that defines how they allocate ingested nutrients to growth, storage, reproduction, respiration, and excretion (Gurney & Nisbet [24], Kooijman [25], Lika & Nisbet [26], Nisbet et al [27]). Ignoring reproduction, we view bioenergetics in a simple manner by noting that consumers have two main needs from their food: energy for metabolism and structural material for biomass. The basic balance equation for each nutrient is

$$\text{Rate of change of structural biomass} = A - R - E,$$

where A is its assimilation rate, R is its respiration rate, and E is its excretion rate (Fig. 1). All of these quantities are given in rates per capita of carbon biomass, which is a measure of the size of the consumer. Typically, food is variable and the consumer must adapt its metabolic processes to maintain homeostasis.

We first adapt the Sterner C:P model, which focuses on zooplankton, to a dynamic case. Our analysis takes the simplified view that the total energy available for metabolism is proportional to the total food quantity, measured by the carbon density C_f of the food times the ingestion rate. Carbon is essential for both energy and biomass, and it is lost through respiration as CO_2. Phosphorus, which is ingested at a rate proportional to the carbon biomass of the herbivore, has an important role in the organism's metabolic processes as well as a role in structure, but it is not lost through respiration or excretion. Letting $C = C(t)$ and $P = P(t)$ denote the structural biomasses, $C_f = C_f(t)$ and $P_f = P_f(t)$ the variable food densities, a_c and a_p the constant (for present) assimilation rates, m the constant, per capita, respiration rate of carbon, and g the constant grazing rate, the nutrient balance equations for C and P are

$$\frac{1}{C}\frac{dC}{dt} = gC_f a_c - m, \qquad \frac{1}{C}\frac{dP}{dt} = gP_f a_p. \tag{1}$$

The quantities have typical dimensions:

$$\begin{aligned}
[a_c] &= [a_p] = 1, \quad [t] = \text{time}, \quad [C] = \text{mol C}, \quad [P] = \text{mol P},\\
[P_f] &= \frac{\text{mol P}}{\text{vol}}, \quad [C_f] = \frac{\text{mol C}}{\text{vol}}, \quad [g] = \frac{\text{vol}}{\text{mol C}\cdot\text{time}}, \quad [m] = \text{time}^{-1}.
\end{aligned}$$

A clear deficiency in this simple model is that the respiration rate does not depend upon the food density, as seen in many organisms (Gurney & Nisbet [24], Sterner [1]). The homeostasis hypothesis is that the C:P ratio of the consumer is constant, or $C/P = \beta$. It easily follows from (1) that

$$\frac{gC_f a_c - m}{gP_f a_p} = \beta, \tag{2}$$

Introducing the time-dependent food quality $Q = P_f/C_f$, the homeostasis condition becomes

$$Q = \frac{gC_f a_c - m}{\beta g C_f a_p}. \qquad \text{(C:P homeostasis)} \tag{3}$$

Further, (1) is easily solved in this simple model to obtain exponential growth of the carbon structural biomass at time t,

$$C(t) = C(0) \exp\left(\int_0^t (gC_f(s)a_c - m) ds \right). \tag{4}$$

If C_f is constant, this represents simple exponential growth with growth rate $r = gC_f a_c - m$.

Figure 2 is a schematic of the consumer's diet and shows the homeostasis curve (3), where Q plotted as a function of gC_f , which is a measure of the total quantity ingested. In the present case both quantities are time-dependent. When the food supply is time-dependent and the other quantities constant, this homeostasis model requires the quality and quantity to change so as to always lie on this curve; i.e., the diet must adapt to the organism. Although consumers are often selective in their food choice (Stephens & Krebs [28]), it is unlikely that the environment and the diet can always be controlled. Thus, in the face of variable food supply (e.g., Fig. 2) the organism must adapt either its assimilation rate or excretion rate to remain on the homeostasis curve.

Observe that the homeostasis curve in Figure 2 is represented differently from Sterner [1] and Frost & Elsner [2]. They plot the food quantity C_f versus the inverse of food quality $(1/Q)$. Thus, one of their limiting asymptotes , where the assimilated C is exactly equal to metabolic requirements, is represented by the single point where $Q = 0$ in figure 2. Notice that the homeostasis curve separates the diet into two regimes, a C-limited region where growth is limited by too little carbon, and a P-limited region where growth is limited by too little phosphorus.

3 Differential Assimilation

When a consumer is faced with limited options to select food, through food scarcity or low food quality, it may compensate by altering it digestive tactics to meet its nutritional needs (Zanotto et al [9],[10], Raubenheimer and Simpson [29], Karasov & Hume [14], Woods & Kingsolver [18], Whelan & Schmidt [17]). Such strategies might include changing its morphology (e.g., gut size), changing its throughput rate or residence time, changing its absorption rates, or maximizing its total uptake (Sibly [30], Dade et al [31], Martínez del Rio & Karasov [32], Simpson & Raubenheimer [15]; Yang & Joern [11]; Jumars & Martínez del Rio [33], Jumars [34], Whelen & Schmidt [17], Logan et al [35], [36]; Wolesensky [37]). However, how an animal 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 [10], Woods & Kingsolver [18]).

There are many strategies a herbivore can follow to regulate elemental homeostasis. One possibility is to maintain homeostasis is through excretion or respiration control. If the assimilation rates are constant, the herbivore could regulate by taking

$$m = m(t) = gC_f(t)(a_c - \beta a_p Q(t)).$$

This model is consistent with dynamic energy budget theory and with some empirical evidence showing that excretion and respiration rates are food dependent. Another possibility having an empirical basis is that the herbivore will select a different, more suitable food source, provided it is available. Also, some consumers may control their throughput rate g to get maximum absorption. Another tactic, which we investigate here, is differential assimilation or absorption control, under the assumption of constant respiration and excretion rates. The model assumes that the herbivore institutes feedback controls on its assimilation rates based upon its instantaneous internal chemical state.

Rather than restrict the homeostasis condition to an absolute, constant C:P ratio β, it seems more plausible that the herbivore will operate within a tolerance range $\beta - \sigma$ to $\beta + \sigma$, where σ is the tolerance ratio. This tolerance envelope is shown schematically in figure 3 in a PC phase plane. We remark that the tolerance envelope widens as the organism grows, which is again plausible. Between these two tolerance limits, the herbivore operates with maximum assimilation rates. That is, if the herbivore's C:P ratio C/P lies in the envelope, then we set a_c and a_p to their constant maximum values a_c^* and a_p^*. If C/P exceeds the upper limit (P-limited growth) $\beta + \sigma$ then carbon assimilation is decreased to meet the constraint that the C:P ratio track along the carbon side of the tolerance envelope, i.e., $dC/dP = \beta + \sigma$; when C/P is under the lower limit $\beta - \sigma$ (C-limited growth), then P assimilation is decreased to meet the constraint that the C:P ratio track along the phosphorus side of the tolerance envelope, or $dC/dp = \beta - \sigma$ (Fig. 3). This strategy of operating under a single nutrient limititation at any one time is consistent with Leibig's rule (Bloom et al [38]).

Along the upper boundary of the tolerance envelope we maintain the same maximum P assimilation, $a_p = a_p^*$; then the constraint $dC/dP = \beta + \sigma$ can be written

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

from which we can obtain the reduced carbon assimilation rate a_c. Similarly, along the lower boundary we maintain the maximum C assimilation, $a_c = a_c^*$. The lower boundary constraint then becomes

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

which determines the reduced phosphorus assimilation a_p. A schematic showing a typical consumer response is shown in figure 3 where the path $P = P(t)$,

$C = C(t)$ remains in the envelope, but may wander from boundary-to-boundary due to a variable food source.

In summary, the differential assimilation model is

$$\left.\begin{aligned} \tfrac{dC}{dt} &= gC_f a_c^* C - mC \\ \tfrac{dP}{dt} &= gP_f a_p^* C \end{aligned}\right\} \quad \text{if } \beta - \sigma < \frac{C}{P} < \beta + \sigma, \tag{5}$$

and

$$\left.\begin{aligned} \tfrac{dC}{dt} &= (\beta + \sigma) gP_f a_p^* C \\ \tfrac{dP}{dt} &= gP_f a_p^* C \end{aligned}\right\} \quad \text{if } \frac{C}{P} \geq \beta + \sigma, \tag{6}$$

and

$$\left.\begin{aligned} \tfrac{dC}{dt} &= gC_f a_c^* C - mC \\ \tfrac{dP}{dt} &= (\beta - \sigma)^{-1}(gC_f a_c^* - m)C \end{aligned}\right\} \quad \text{if } \frac{C}{P} \leq \beta - \sigma, \tag{7}$$

This model predicts the following behavior. At time $t = 0$ the herbivore is assumed to be in a homeostatic state $C(0) = C_0$, $P(0) = C_0/\beta$. As time advances the C:P ratio will track into the tolerance envelope in a direction depending upon the time-dependent food supply ratio C_f/P_f and the magnitude of the assimilation rates. When the path encounters a boundary it remains there unless there is a shift in the food supply to cause it to return to the interior of the envelope. The total growth in carbon biomass of the consumer is still given by the equation (4) with $a_c = a_c(t)$. A food supply that never constrains the carbon assimilation rate will lead to greater growth in carbon biomass.

Assuming the food supply is constant, some insight into the important parameter ratios can be gained by scaling problem (1) (e.g., Logan [39]). Introducing new variables

$$c = \frac{C}{C_f}, \quad p = \frac{P}{C_f/b}, \quad \tau = gC_f a_c t,$$

equations (1) can be written

$$\frac{dc}{d\tau} = (1 - \mu)c, \quad \frac{dp}{d\tau} = \nu c,$$

where μ and ν are dimensionless constants

$$\mu = \frac{m}{gC_f a_c}, \quad \nu = \frac{\beta P_f}{C_f}\frac{a_p}{a_c} = \beta Q r.$$

The homeostasis envelope is now given by

$$1 - \theta < \frac{c}{p} < 1 + \theta, \qquad \theta = \frac{\sigma}{\beta}.$$

Note that $100\times\theta$ is the percentage tolerance. So there are only two degrees of freedom in the Sterner model. The parameter μ is the ratio of the respiration rate (loss) to the consumption rate, and the parameter ν involves two ratios, the quality of food Q and the ratio $r = \frac{a_p}{a_c}$ of the absorption rates. This shows that deviations from exact homeostasis depend equally on the absorption ratios as on the quality of food. Either r or Q can drive the C:P ratio toward the upper tolerance boundary (P-limited growth) or the the lower tolerance boundary (C-limited growth). For example, the C:P ratio is driven toward the upper limiting boundary when $dc/dp > 1$ or $(1-\mu)/\nu > 1$. This condition will hold when, for example, when ν is small, which can be accomplished by decreasing the quality of food or decreasing the ratio of P to C. Thus differential assimilation *and* food quality play a role in homeostatic growth.

Numerical simulations of (5)–(7) confirm the preceding observations. We adapt data from Sterner [1] based on published values for an algae-*Daphnia* system. For all the simulations we fix the parameters: $m = 0.002$ hr^{-1}, $g = 0.001$ l$\cdot\mu$mol^{-1}hr, $\beta = 90$, $\sigma = 4.5$ (5%), $a_c = 0.5$, $a_p = 0.9$. For the simulations we vary the food quality and calculate (Figs. 4 and 5) how the C:P ratio varies with time ($0 \le t \le 10$) in the PC phase plane. In Figure 4 the food quantity is $C_f = 48$ μ mols C$\cdot$ l^{-1}with (low) quality $Q = 1/400$. In this case the C:P ratio approaches, reaches, and then tracks along the upper tolerance boundary; along that boundary C assimilation is limited, which limits C biomass (this is P-limited in the food supply). Figure 5 shows the path when the food supply is changed from low quality ($Q = 1/400$) to high quality ($Q = 1/75$) at $t = 2.5$, part way through the time interval. Here the C:P ratio approaches the carbon-limiting boundary, but then changes directions and ultimately tracks along the P-limiting boundary. In this case the carbon assimilation is never reduced and there is no limitation of carbon biomass, only P biomass.

It is straightforward to calculate the C:P ratio for any time-dependent food supply. Under an ideal food ratio lying in the envelope, e.g., $C_f = 48$ μmols C$\cdot$ l^{-1}, $Q = 1/170$, the path remains in the envelope close to homeostasis. As stated above, the approach to tolerance boundaries can also be controlled by changing the ratio of the assimilation rates a_c and a_p.

3.1 Saturating Food Supply and C:N ratios

The two dimensional model can be extended in other directions, such as a saturating food supply and to a carbon-nitrogen system. The Sterner model (1) was modified for mayflies (larvae) to include a saturating food supply given by a Holling type II functional response (Frost & Elser [2]):

$$\frac{1}{C}\frac{dC}{dt} = \frac{gC_f}{1+g\tau C_f}a_c - m, \qquad \frac{1}{C}\frac{dP}{dt} = \frac{gP_f}{1+g\tau C_f}a_p,$$

where τ is the handling time, and where the food densities and assimililation rates are constant. In this case the homeostasis hypothesis $C/P = \beta$ forces the condition

$$Q = \frac{g(a_c C_f - \tau m) - m}{\beta g a_p C_f},$$

which can be analyzed as in Figure 2. In the same way, a tolerance envelope $\beta - \sigma < \frac{C}{P} < \beta + \sigma$ can be defined and assimilation rates can be introduced that constrain the C:P ratio to remain in the envelope or track along its upper or lower boundary.

A carbon-nitrogen (C:N) system can be treated in a similar manner. However, nitrogen is generally excreted (e.g., in urine). If we modify the N equation by including a per capita excretion rate proportional to the N/C ratio, then the model becomes

$$\frac{1}{C}\frac{dC}{dt} = gC_f a_c - m, \qquad \frac{1}{C}\frac{dN}{dt} = gN_f a_N - k\frac{N}{C}.$$

The homestasis condition is, in terms of quality $Q = N_f/C_f$ and quantity,

$$Q = \frac{gC_f a_c + k - m}{\gamma g a_N C_f}, \qquad \text{(C:N homeostasis)}$$

where $C/N = \gamma$ is the homeostasis hypothesis. The main qualitative difference between this homeostasis curve (not plotted) and the C:P homeostasis curve in Figure 2 is that the limiting point where the minimum growth occurs is shifted to the left, i.e., $Q = 0$ when $gC_f = (m-k)/a_c$ versus $gC_f = m/a_c$ for carbon-phosphorus. Further, because most herbivores have significantly more nitrogen than phosphorus, we have $\gamma < \beta$. The limiting asymptote as C_f gets large is also higher in the C:N case and the C:N homeostasis curve generally lies entirely above the C:P homeostasis curve. Consequently, when a mineral is excreted, the herbivore can survive on a lower quantity of food and maintain homeostasis with respect to that mineral. This conclusion seems reasonable since more mineral is lost and thus lower levels of carbon are required to keep the body ratio constant. At the same time, for a given quantity of food, a higher quality of C:N food is required for homeostasis. For a fixed quality, the C:N ratio will limit growth more than the C:P ratio. We can adapt differential assimilation or control of a_N and a_c to maintain ratios in a tolerance envelope exactly as in the C:P system described in Section 2.

4 Summary

In this paper, we explicitly incorporate differential assimilation with a variable food supply to examine control of the maintenance of elemental homeostasis in a consumer eating food composed of significantly different elemental ratios. Our model extends those of Sterner [1] and Frost & Elser [2] (see also Sterner & Elser [16]). By including a tolerance envelope around exact homeostatic control, we show that a consumer can adjust assimilation in response to food the most limiting element. The limiting nutrient defines the trajectory of elemental accumulation constrained by the tolerance envelope, allowing one to predict the biomass accumulation of critical elements (e.g., C, P) depending on the relative abundance of these elements in the food supply. As the food supply ratio changes independent of the action of consumers, assimilation changes accordingly and relative elemental accumulation shifts. In this sense, differential assimilation can effectively act as a nonlinear control mechanism permitting elemental homeostasis in consumers as predicted by Sterner [1]. Finally, this work has further application to the overall nutrient cycling problem in ecosystems, being one essential component in the process (DeAngelis [40], Daufresne & Loreau [41], Mueller et al [42]).

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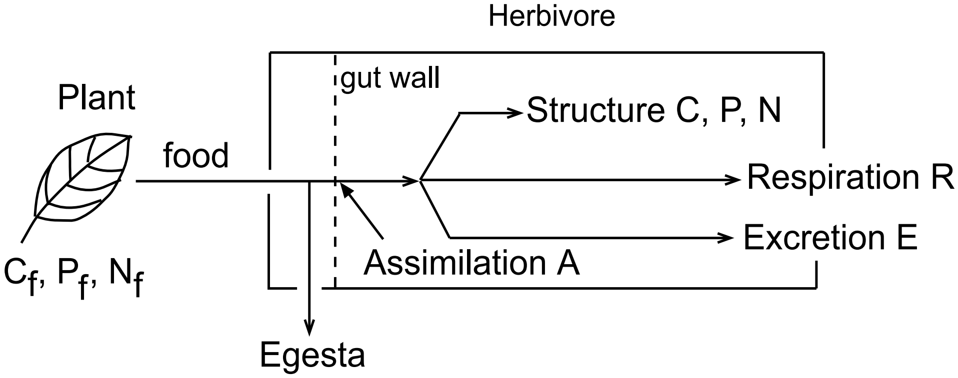

Figure 1: Schematic showing the elemental fluxes (nutrients C, P, or N) in a herbivore consumer and its energy budget. Each nutrient is ingested and a fraction is assimilated across the gut wall, the remaining being egested. The assimilated nutrients are distributed to structure (total biomass) and maintenance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

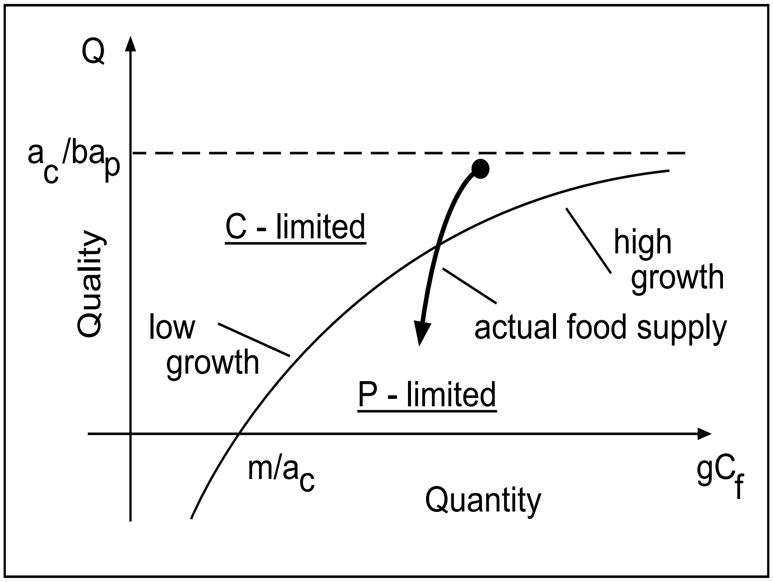

Figure 2: Schematic showing the herbivore diet and the C:P homeostasis curve (quality vs. quantity of food).

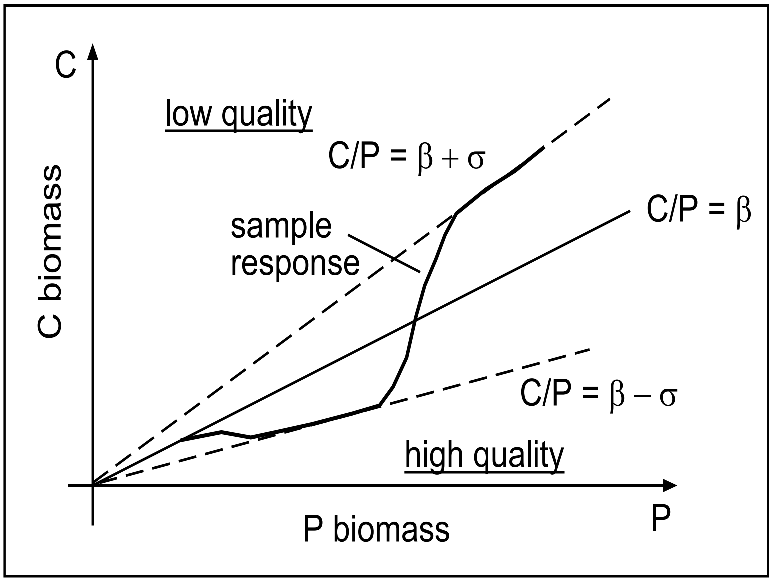

Figure 3: Schematic showing a typical herbivore response to a variable food supply in the PC- phase plane. Differentiated assimilation confines the response to a tolerance envelope near exact homeostasis.

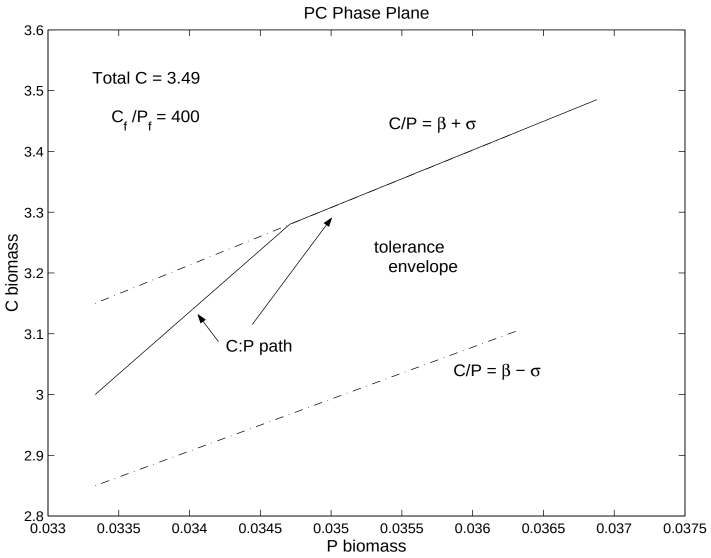

Figure 4: Calculated C:P biomass ratio for $0 \leq t \leq 10$ with a low quality food supply: $C_f = 48$, $Q = 1/400$. The remaining parameters are defined in the text. The total growth is $C(10) = 3.485$.

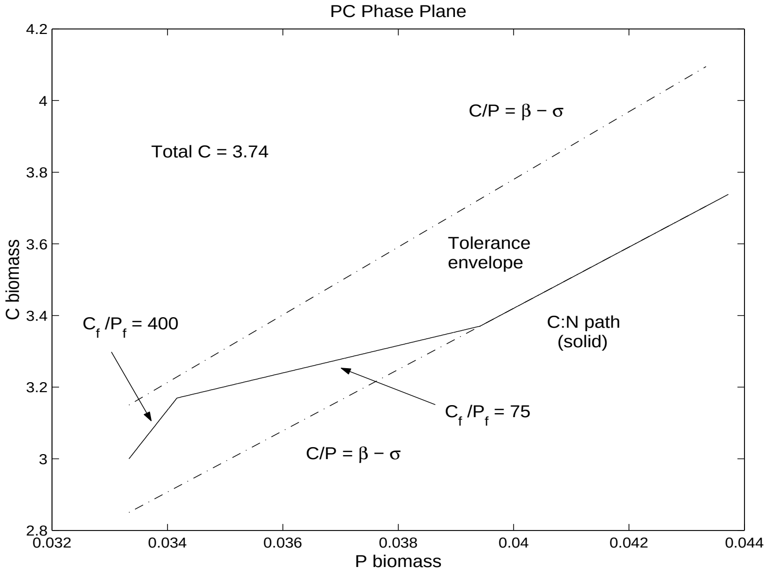

Figure 5: Calculated C:P biomass ratio in $0 \leq t \leq 10$ with a changing food supply: a low quality food supply $C_f = 48$, $Q = 1/400$ in $0 \leq t \leq 2.5$,and high quality $C_f = 48$, $Q = 1/75$ in $2.5 \leq t \leq 10$. The total growth is $C(10) = 3.738$.