Appendix A from S. R. Hall, "Stoichiometrically Explicit Competition between Grazers: Species Replacement, Coexistence, and Priority Effects along Resource Supply Gradients"

(Am. Nat., vol. 164, no. 2, p. 157)

Invasion/Feasibility Criteria and Stability Analysis of Base Model

In the base model, four equilibria emerge in scenarios with just one grazer: a trivial equilibrium, a plant-only equilibrium, and equilibria with a single nutrient- or carbon-limited grazer. The plant can always invade the trivial equilibrium,

$$A^* = 0,\ G_j^* = 0 \tag{A1}$$

(i.e., the invading plant has a positive per capita growth rate when rare at the trivial equilibrium, $(1/A)(dA/dt) > 0$) if $u\beta > 0$. After it invades, a plant-only equilibrium arises:

$$A^* = \frac{S}{k_Q},\ G_j^* = 0. \tag{A2}$$

Without grazers (i.e., in a lower dimensional system with only eq. [1a] and [1c] and where $G_j = 0$), this equilibrium would be stable because of its negative eigenvalue, $-2u\beta$. At this plant-only equilibrium, producers have incorporated all available ecosystem nutrients in their tissues, and producer nutrient content sits at its minimum (i.e., $Q^* = k_Q$). Herbivores can invade this stable, plant-only equilibrium (A2) when rare if $(1/G_j)(dG_j/dt) > 0$.

When herbivores invade this plant-only equilibrium, they will often be nutrient limited (unless $q_j \le k_Q$). In the unlikely event that the invading grazer is carbon limited (i.e., $q_j \le k_Q$), the ecosystem must satisfy

$$S > \frac{d_j k_Q}{e_j f_j} \tag{A3}$$

for it to invade successfully. This threshold equals the feasibility criterion for the equilibrium with a single carbon-limited grazer (eqq. [6]). In the more likely case, a nutrient-limited herbivore can invade the plant-only equilibrium if $S > QA_j^*$. Once the nutrient-limited herbivore invades, a feasibility criterion (derived from the A^*) requires that S must not exceed

$$S = \frac{q_j\left(e_j u\beta + d_j\right)}{e_j f_j}, \tag{A4}$$

but the herbivore becomes carbon limited before nutrient supply reaches this criterion.

Local, linearized stability analysis of the two-dimension "linear" food chain model systems considered in cases 1 and 2 below is a straightforward endeavor (Gurney and Nisbet 1998). Each analysis follows similar logic. First, imagine each case as a lower-dimension subset of the full model, where the plant coexists with only one grazer (i.e., the other equals 0). Second, the substitutions $F_1 \equiv dA/dt$ and $F_2 \equiv dG_j/dt$ are made. One then calculates the Jacobian matrix (**J**) by taking the partial derivatives of F_1 and F_2 with respect to A and G_j. Stability of **J** depends on the coefficients of its characteristic equation $\lambda^2 + A_1\lambda + A_2$ and the Routh-Hurwitz criteria. These criteria require that $A_1 = -(J_{11} + J_{22}) > 0$ and $A_2 = J_{11}J_{22} + J_{12}J_{21} > 0$ (where λ's are eigenvalues and J_{ik}'s are the elements of matrix **J**). Thus, the trace of **J**, evaluated at equilibrium, must be negative, while its determinant must be positive.

Case 1: One Nutrient-Limited Grazer Only

At equilibrium with a single nutrient-limited herbivore (eqq. [4]), **J** becomes:

$$\mathbf{J} = \begin{bmatrix} \frac{fS}{q} - \frac{d}{e} - u\beta & -\frac{(dq + equ\beta - efS)(2dq + equ\beta - efS)}{e^2 k_Q qu\beta} \\ 0 & d - \frac{efS}{q} \end{bmatrix}, \tag{A5}$$

where the subscript j has been dropped on grazer parameters for clarity. Note that **J** has a zero J_{21} element but a negative J_{22} element (because $S > QA_j^*$ for a feasible equilibrium). A feasible equilibrium guarantees negative elements J_{11} and J_{12}. Thus, despite the relatively unusual architecture of its Jacobian matrix, this equilibrium is stable because the trace ($J_{11} + J_{12}$) is negative and the determinant ($J_{11}J_{22}$) is positive. Consequently, stoichiometric feedbacks onto the nutrient-limited herbivore stabilize this system in the one-grazer subspace.

Case 2: One Carbon-Limited Grazer Only

At the carbon-limited, single-grazer equilibrium (eqq. [6]), **J** becomes

$$\mathbf{J} = \begin{bmatrix} -\frac{2k_Q du\beta}{e(fS - qu\beta + C_2)} & -\frac{d}{e^2}\left[e + \frac{4k_Q qu\beta}{(qu\beta - fS + C_2)^2}\right] \\ \frac{e(fS + qu\beta - C_2)}{2q} & 0 \end{bmatrix}, \tag{A6}$$

where

$$C_2 = \sqrt{(qu\beta - fS)^2 + \frac{4dk_Q qu\beta}{e}}. \tag{A7}$$

A feasible equilibrium yields negative elements J_{11} and J_{12} and positive element J_{21}. As a result, a feasible carbon-limited, single-grazer equilibrium is always stable in the one-grazer subspace because the trace, J_{11}, is always negative and the determinant, $-J_{12}J_{21}$, is always positive.

Case 3: Two-Grazer Equilibrium

The behavior and stability of the two-grazer competition model depend on five thresholds and the relative slopes of the grazers' impact vectors, f_j/q_j. As shown in the stability analysis below, the two-grazer equilibrium is stable when each grazer more strongly impacts the resource limiting, implying $f_1/q_1 > f_2/q_2$. This case is considered first. Along a gradient of nutrient supply (S), the minimal sequestered nutrient requirement (QA_1^*) of the superior nutrient competitor, G_1 (criterion a in fig. 3), must be exceeded for G_1 to invade the plant-only equilibrium. As nutrient supply increases, G_1 becomes carbon limited (at a resource limitation threshold b in fig. 3A) when

$$S = QA_1^* + u\beta\frac{q_1}{f_1}\left(1 - \frac{1}{q_1}k_Q\right). \tag{A8}$$

Then, the next threshold permits the superior carbon competitor, G_2, to invade the $G_1^* - A^*$ equilibrium; this interior invasion/feasibility criterion (threshold c in fig. 3A) becomes

$$S = QA_2^* + u\beta\frac{q_1}{f_1}\left(1 - \frac{A_1^*}{QA_2^*}k_Q\right). \tag{A9}$$

This threshold requires higher nutrient supply than G_1's resource limitation threshold (eq. [A8] because $Q^* > q_1$), but once S meets it, the two-grazer equilibrium becomes feasible. G_1 eventually displaces its competitor as S increases further. Thus, an additional criterion

$$S = QA_2^* + u\beta\frac{q_2}{f_2}\left(1 - \frac{A_1^*}{QA_2^*}k_Q\right) \tag{A10}$$

places an upper resource-supply limit on grazer coexistence (criterion d in fig. 3A). When exceeded, this threshold prohibits G_1 from invading the $G_2^* - A^*$ equilibrium. When G_2 displaces G_1, G_2 remains nutrient limited. Therefore, G_2 becomes carbon limited at a second resource limitation threshold (criterion e in fig. 3A) when S exceeds

$$S = QA_2^* + u\beta\frac{q_2}{f_2}\left(1 - \frac{1}{q_2}k_Q\right). \tag{A11}$$

Notably, the invasion/feasibility criteria for the two-grazer equilibrium approached an asymptote. The lower and upper asymptotes (from eqq. [A9], [A10], respectively) are

$$S = QA_2^* + u\frac{q_1}{f_1}\left(1 - \frac{A_1^*}{QA_2^*}k_Q\right) \tag{A12a}$$

$$S = QA_2^* + u\frac{q_2}{f_2}\left(1 - \frac{A_1^*}{QA_2^*}k_Q\right) \tag{A12b}$$

(because as $L \to \infty$, $\beta \to 1$). Thus, if nutrient supply exceeds the upper asymptote (eq. [A12a]), the superior nutrient competitor cannot competitively displace the superior carbon competitor, regardless of light supply. This result could be relaxed if light extinction is explicitly modeled, perhaps following Huisman and Weissing's (1995) approach.

When $f_1/q_1 < f_2/q_2$, the two-grazer equilibrium is unstable (see stability analysis below) because each grazer most strongly impacts the resource most limiting its competitor. These different ratios affect the progression of thresholds past G_1 's boundary invasion and resource limitation thresholds. Most important, the interior/feasibility thresholds of G_2 (eq. [A9]) and G_1 (eq. [A10]) are encountered in reverse order as nutrient supply increases (because now $q_1/f_1 > q_2/f_2$). In the example presented (fig. 3B, 3D), the resource limitation threshold for G_2 is encountered between the resource limitation threshold for G_1 and the invasion/feasibility threshold of G_1. This result occurs because at the unstable two-grazer equilibrium, nutrient content of the plant (QA_2^*/A_1^*) exceeds nutrient content of G_2 (q_2). (Remember that the superior carbon competitor must be nutrient limited when coexistence is feasible.) Between the two grazers' resource limitation thresholds, either G_1 or G_2 exists alone with the plant, depending on initial conditions.

To consider stability of the two-grazer equilibrium, the system's Jacobian matrix (**J**) expands to three dimensions. With substitutions $F_1 \equiv dA/dt$, $F_2 \equiv dG_1/dt$ (where G_1 is carbon limited), and $F_3 \equiv dG_2/dt$ (where G_2 is nutrient limited), **J** becomes

$$\mathbf{J} = \begin{bmatrix} -u\beta\left(\frac{A_1^*}{QA_2^*}\right) & -A_1^* f_1 - u\beta k_Q q_1\left(\frac{A_1^*}{QA_2^*}\right)^2 & -A_1^* f_2 - u\beta k_Q q_2\left(\frac{A_1^*}{QA_2^*}\right)^2 \\ e_1 f_1 G_1^* & 0 & 0 \\ 0 & -\frac{e_2 f_2 q_1}{q_2}G_2^* & J_{33} \end{bmatrix} \tag{A13}$$

when evaluated at the two-grazer equilibrium (eqq. [7]) and where

$$J_{33} = \frac{e_2 f_2}{f_1 q_2 - f_2 q_1}\left[f_1(QA_2^* - S) + u\beta q_1\left(1 - \frac{A_1^*}{QA_2^*}k_Q\right)\right]. \tag{A14}$$

When the two-grazer equilibrium is feasible, J_{33} is always negative if $f_1/q_1 > f_2/q_2$ but is positive otherwise. When $f_1/q_1 > f_2/q_2$, the two-grazer equilibrium is stable. In this case, **J**'s elements have the signs

$$\begin{bmatrix} - & - & - \\ + & 0 & 0 \\ 0 & - & - \end{bmatrix}. \tag{A15}$$

The characteristic polynomial of **J** is $\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3$, where λ's are the eigenvalues, $A_1 = -(J_{11} + J_{33})$, $A_2 = J_{11}J_{33} - J_{12}J_{21}$, and $A_3 = J_{21}(J_{12}J_{33} - J_{13}J_{32})$. The Routh-Hurwitz criteria for stability of a three-dimension system demand that $A_1 > 0$, $A_3 > 0$, and $A_1 A_2 > A_3$. Given the signs of **J** in this case, obviously $A_1 > 0$ always because J_{11} and J_{33} are both negative. It can be shown that $A_3 > 0$ always as well because the term in parentheses, $(J_{12}J_{33} - J_{13}J_{32})$, is positive assuming a feasible two-grazer equilibrium. Then, because J_{21} is always positive, A_3 is guaranteed to be positive. With some manipulation, the third criterion becomes

$$-J_{11}^2 J_{33} - J_{11}J_{33}^2 + J_{11}J_{12}J_{21} > -J_{13}J_{21}J_{32}. \tag{A16}$$

Because of the sign structure of **J** in this case, the left-hand side of this condition is always positive. Meanwhile, the right-hand side is always negative. Thus, the equilibrium meets the third Routh-Hurwitz criterion, and a stable two-grazer equilibrium arises.

When $f_1/q_1 < f_2/q_2$, J_{33} becomes positive. Stability analysis with this change might typically become more complex, but this analysis terminates at the first criterion because $A_1 < 0$. In this case, criterion A_1 is negative when

$$S < QA_2^* + u\beta\left\{\frac{A_1^*}{QA_2^*}\left[\frac{q_1}{f_1}\left(k_Q - \frac{1}{e_2}\right) + \frac{q_2}{e_2 f_2}\right] + \frac{q_1}{f_2}\right\}. \tag{A17}$$

The upper invasion/feasibility criterion (eq. [A10]) is always smaller than the right-hand side of stability criterion A_1 because their difference (right-hand side of eq. [A17] minus the right-hand side of eq. [A10])

$$\frac{u\beta(f_2 q_1 - f_1 q_2)\left[A_1^*\left(1 - e_2 k_Q\right) + e_2 QA_2^*\right]}{e_2 f_1 f_2 QA_2^*} \tag{A18}$$

is always positive (because $1 - e_2 k_Q > 0$, because $e_2 < 1$ and $k_Q < 1$, and $f_2/q_2 - f_1/q_1 > 0$). Thus, when $f_1/q_1 < f_2/q_2$, this two-grazer equilibrium is unstable (a saddle).