Appendix B 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)

Grazer Competition with Explicit Quota Dynamics (Modification 3)

The model system considered in the "Modification 3" section is

$$\frac{dA}{dt} = u\left(1 - \frac{k_Q}{Q}\right)\left(\frac{L}{b+L}\right)A - A\sum_j f_j G_j, \tag{B1a}$$

$$\frac{dQ}{dt} = v(R) - u\beta\left(1 - \frac{k_Q}{Q}\right)Q, \tag{B1b}$$

$$\frac{dG_j}{dt} = \min\left(e_j f_j A - r_j, e_j f_j A \frac{Q}{q_j}\right)G_j - \delta_j G_j, \tag{B1c}$$

where $v(R)$ and R follow equations (16). Like in the other models, separate equilibria emerge for a single species of grazer when nutrient or carbon limited. When the grazer is nutrient limited, this single-grazer equilibrium becomes

$$Q^* = \begin{cases} \frac{1}{2}\left[k_Q + \left(\frac{S}{u\beta} - QA_j^*\right)\left(\frac{u}{v}\right) + \frac{q_j v}{f_j h} + C_{NL}\right] & R \leq h \\ k_Q + \frac{v}{u\beta} & R > h \end{cases}, \tag{B2a}$$

$$A^* = QA_j^*\left(\frac{1}{Q^*}\right), \tag{B2b}$$

$$G^* = \frac{u\beta}{f_j}\left(1 - \frac{1}{Q^*}\right), \tag{B2c}$$

where

$$C_{NL} = \left\{4u^2B^2e_j^2 f_j hk_Q q_j v + \left[e_j f_j Sv - \delta_j q_j v + u\beta e_j\left(f_j hk_Q - q_j v\right)\right]^2\right\}^{0.5}, \tag{B2}$$

and where A_j^* and QA_j^* represent the minimal sequestered carbon and nutrient requirements of the grazer, respectively (following eq. [10]). With a nutrient-limited grazer, the plant's nutrient uptake rate, $v(R)$, saturates when $R^* = h$ or when

$$S = h + QA_j^* + \frac{e_j q_j}{f_j}\left(\frac{u\beta}{u\beta k_Q + v}\right). \tag{B3}$$

When the grazer is carbon limited, the single-grazer equilibrium becomes

$$A^* = A_j^*, \tag{B4a}$$

$$G^* = \begin{cases} \frac{1}{2}\left(\frac{S}{q_j} + \frac{u\beta k_Q h}{q_j v} + \frac{u\beta}{f_j} + C_{CL}\right) & R \le h \\ \frac{u\beta v}{f_j(u\beta k_Q + v)} & R > h \end{cases}, \tag{B4b}$$

$$Q^* = \begin{cases} \frac{e_j f_j S v + u\beta e_j\left(f_j k_Q h - q_j v + C_{CL}\right)}{2\left[u\beta e_j f_j h + v\left(\delta_j + r_j\right)\right]} & R \le h \\ k_Q + \frac{v}{u\beta} & R > h \end{cases}, \tag{B4c}$$

where

$$C_{CL} = \left(e_j\left\{4u\beta k_Q q_j v\left[u\beta e_j f_j h + v\left(\delta_j + r_j\right)\right]\right\} + e_j\left[f_j v S + u\beta\left(f_j k_Q h - q_j v\right)\right]^2\right)^{0.5}. \tag{B5}$$

With a carbon-limited grazer, the plant's nutrient uptake rate, $v(R)$, becomes saturated when

$$S = h + A_j^*\left(k_Q + \frac{v}{u\beta}\right) + \frac{u\beta q_j}{f_j}\left(1 - \frac{u\beta k_Q}{u\beta k_Q + v}\right). \tag{B6}$$

The resource limitation threshold becomes

$$S = QA_j^* + u\beta\left\{k_Q\left(\frac{h}{v} + \frac{\delta_j + r_j}{\delta_j f_j}\right) - q_j\left[\frac{\delta_j h}{v\left(\delta_j + r_j\right)} - \frac{1}{f_j}\right]\right\}. \tag{B7}$$

Nutrient uptake of plants coexisting with a nutrient-limited grazer can become saturated if light supply, L, exceeds

$$L = b\left[\frac{\delta_j q_j u}{\left(\delta_j + r_j\right)v} - \frac{u}{v}k_Q - 1\right]^{-1} > 0. \tag{B8}$$

Like in the simpler models, resource supply determines these thresholds, but a slightly more complex situation arises now. The nutrient-limited grazer can invade the ecosystem if nutrient supply (S) exceeds the grazer's minimal sequestered nutrient demands (QA_j^*; feasibility criterion *a* in fig. 5*A*, 5*B*). The grazer is nutrient limited (*gray region*, fig. 5*A*, 5*B*) until the resource limitation threshold (eq. [B7]) is reached (at threshold *b* in fig. 5*A*, 5*B*). Afterward, the grazer becomes carbon limited (*white region*, fig. 5*A*, 5*B*). Incidentally, the example system parameterized with just G_1, and the plant, G_1, becomes carbon limited before the nutrient-limited saturation threshold (eq. [B3]) is reached; thus, that nutrient-limited saturation threshold does not apply (see fig. 5*A*; table 1). Once G_1 becomes carbon limited, nutrient uptake rate of the plant will eventually become saturated (at eq. [B6]; threshold *c* in fig. 5*A*, 5*B*). In contrast, given the parameters used (table 1), nutrient uptake rate by the plant does become saturated at high light supply when G_2 is nutrient limited (at threshold *d* in fig. 5*B*).

As in the previous more simple models, this version permits grazer coexistence assuming a $QA_j^* - A_j^*$ trade-off. As long as $R^* < h$, the two-grazer equilibrium becomes

$$A^* = A_1^*, \tag{B9a}$$

$$Q^* = \frac{QA_2^*}{A_1^*}, \tag{B9b}$$

$$R^* = \frac{u\beta h}{v}\left(\frac{QA_2^*}{A_1^*} - k_Q\right), \tag{B9c}$$

$$G_1^* = \frac{1}{f_2 q_1 - f_1 q_2}\left[f_2(S - QA_2^* - R^*) + u\beta q_2\left(1 - \frac{A_1^*}{QA_2^*}k_Q\right)\right], \tag{B9d}$$

$$G_2^* = \frac{1}{f_2 q_1 - f_1 q_2}\left[-f_1(S - QA_2^* - R^*) + u\beta q_1\left(1 - \frac{A_1^*}{QA_2^*}k_Q\right)\right]. \tag{B9e}$$

Here, nutrient uptake of plants becomes saturated ($R^* = h$) when

$$\beta = \frac{1}{\frac{u}{v}\left(k_Q - \frac{QA_2^*}{A_1^*}\right)}. \tag{B10}$$

Only a negative degree of light saturation meets this nutrient saturation threshold (because the term in parentheses in the denominator of eq. [B10] is always negative). Thus, the plant's uptake rate cannot saturate at a feasible two-grazer equilibrium.

Resource supply again delineates the major thresholds governing potential coexistence of the grazers. (Here, we assume a stable two-grazer equilibrium). At a given light supply, the superior nutrient competitor (G_1) can outcompete the superior carbon competitor (G_2) at low nutrient supply (fig. 5*C*). This grazer must become carbon limited (eq. [B7]; limitation threshold b in fig. 5*C*) before G_2 can invade. Then, G_2 invades when nutrient supply, S, exceeds

$$S = QA_2^* + R^* + u\beta\frac{q_1}{f_1}\left(1 - \frac{A_1^*}{QA_2^*}k_Q\right) \tag{B11a}$$

(feasibility threshold c in fig. 5*C*) and competitively displaces G_1 when S exceeds

$$S = QA_2^* + R^* + u\beta\frac{q_2}{f_2}\left(1 - \frac{A_1^*}{QA_2^*}k_Q\right) \tag{B11b}$$

(feasibility threshold d in fig. 5*C*). G_2 is again nutrient limited once it displaces the superior nutrient competitor but eventually becomes carbon limited (limitation threshold e in fig. 5*C*). The plant's nutrient uptake may be saturated after displacement of G_1, whether G_2 is nutrient limited or carbon limited (saturation thresholds f and g in fig. 5*C*, respectively).

Stability analysis of the two-grazer equilibrium is more complex. First, substitutions $F_1 \equiv dA/dt$, $F_2 \equiv dQ/dt$, $F_3 \equiv dG_1/dt$, and $F_4 \equiv dG_2/dt$ are made. The four-dimension Jacobian matrix (**J**) of F_1–F_4 with respect to A, Q, G_1, and G_2 yields

$$\mathbf{J} = \begin{bmatrix} 0 & \frac{u\beta k_Q A^*}{Q^*} & -f_1 A^* & -f_2 A^* \\ -\frac{vQ^*}{h} & -u\beta + \frac{v}{h}A^* & -\frac{q_1 v}{h} & -\frac{q_2 v}{h} \\ e_1 f_1 G_1 & 0 & 0 & 0 \\ \frac{e_2 f_2 G_2^* Q^*}{q_2} & \frac{e_2 f_2 A^* G_2^*}{q_2} & 0 & 0 \end{bmatrix} \tag{B12}$$

when evaluated at the two-grazer equilibrium. **J** has a characteristic polynomial $\lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4$. The Routh-Hurwitz criteria for stability require that $A_1 > 0$, $A_3 > 0$, $A_4 > 0$, and $A_1 A_2 A_3 > A_3^2 + A_1^2 A_4$. At the two-grazer equilibrium, $A_1 > 0$ always (because $A_1 = -J_{22}$). One can show that the second criterion, $A_3 > 0$, is always met (but the expression for it is too complex to be informative here). The third criterion, $A_4 > 0$, is not always met because

$$A_4 = \frac{(A^*)^2 e_1 e_2 f_1 f_2^2 G_1^* G_2^* (q_2 - q_1) Q^*}{h q_2} \tag{B13}$$

can be either positive (if $q_2 > q_1$) or negative (if $q_2 < q_1$). Here, nutrient content q_j is grazer j's impact vector on plant nutrient content. Thus, if G_2 has higher nutrient content than G_1, the equilibrium is stable. If not, it is unstable (a saddle). The fourth criterion is challenging to evaluate analytically. The term A_2,

$$A_2 = A^* f_2\left(e_2 f_2 G_2^* \frac{Q^*}{q_2} + e_1 f_1 G_1^*\right) + A^* v\left[\frac{e_2 f_2 G_2^*}{h} + \frac{u\beta}{h}\left(\frac{k_Q}{Q^*}\right)\right], \tag{B14}$$

is always positive, but it is difficult to determine algebraically under which circumstances $A_1 A_2 A_3 > A_3^2 + A_1^2 A_4$. Therefore, the fourth criterion may place additional requirements for stability of the two-grazer equilibrium. Suffice it here to say that when evaluated numerically, the parameter set used, and slight deviations from it, meets this criterion (as long as $q_2 > q_1$).