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Module 775

The Resilience of Grassland Ecosystems

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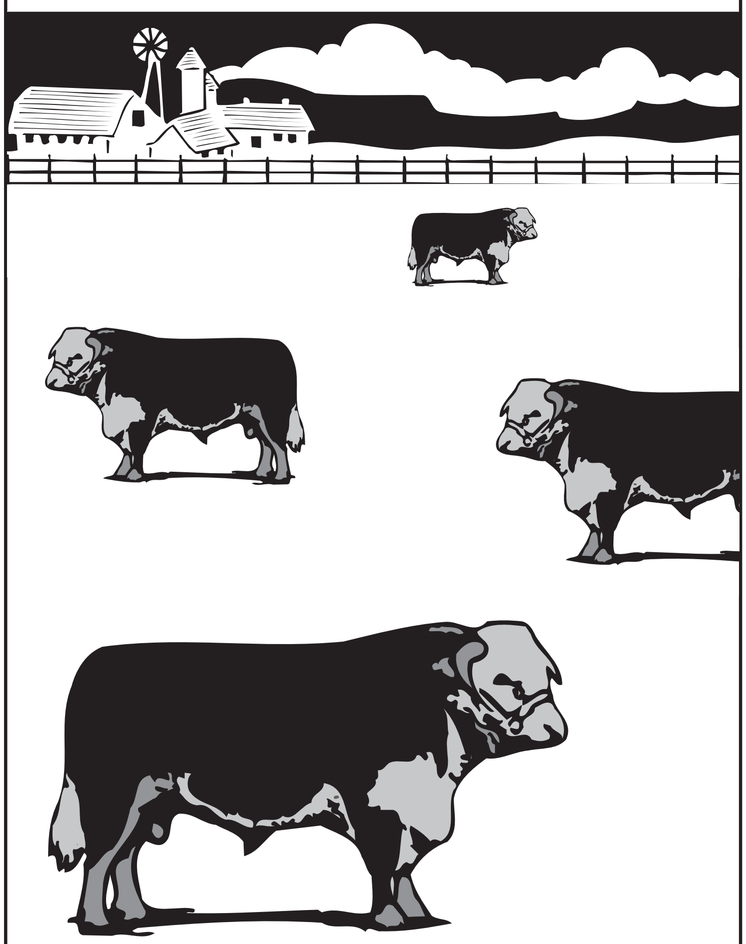

Applications of Differential Equations to Biology and Ecology

INTERMODULAR DESCRIPTION SHEET: UMAP Unit 775

TITLE: The Resilience of Grassland Ecosystems

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MATHEMATICAL FIELD: Differential equations

APPLICATION FIELD: Biology, ecology

TARGET AUDIENCE: Students in a course in differential equations

ABSTRACT: This Module introduces students to the *state-and-transition theory* explaining the succession of plant species on grassland and to the concept of *successional thresholds* partitioning plant states into those gravitating toward socially desirable or socially undesirable plant compositions over time. Students are shown how the state-and-transition theory is formulated in the mathematical ecology literature as a system of two autonomous differential equations, and how a successional threshold is defined by the stable manifold to an interior saddle-point equilibrium. A series of exercises directs students toward a qualitative phase-plane solution of the system and an analytical approximation of the stable manifold. Students also gain experience working with the numerical phase-plane plotter Dynasys, which can be downloaded from the World Wide Web. A discussion section applies the approximated stable manifold to the real-world problem of controlling livestock numbers on public grazing land to reestablish more socially desirable plant varieties. The Module is within the capabilities of students having had basic calculus and an introductory course in ordinary differential equations covering phase-plane solutions.

PREREQUISITES: Introduction to ordinary differential equations covering phase-plane solutions.

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Modules and Monographs in Undergraduate Mathematics and its Applications (UMAP) Project

The goal of UMAP is to develop, through a community of users and developers, a system of instructional modules in undergraduate mathematics and its applications, to be used to supplement existing courses and from which complete courses may eventually be built.

The Project was guided by a National Advisory Board of mathematicians, scientists, and educators. UMAP was funded by a grant from the National Science Foundation and now is supported by the Consortium for Mathematics and Its Applications (COMAP), Inc., a nonprofit corporation engaged in research and development in mathematics education.

Paul J. Campbell	Editor
Solomon Garfunkel	Executive Director, COMAP

1. Introduction

Grass varieties compete with one another for habitat in grassland ecosystems. Native grasslands in the intermountain region of the United States are dominated by highly competitive perennial grasses (e.g., bluestem, grama, and bunch grasses) as understory species to sagebrush. However, historic overgrazing of these native grasses by domestic livestock has reduced the grasses' vigor, and consequently their ability to withstand the invasion of highly competitive alien annual grasses introduced inadvertently by settlers, principally cheatgrass (*Bromus tectorum L.*) [Evans and Young 1972]. Cheatgrass has competed so strongly that it currently dominates millions of acres of native grasslands in the intermountain West [Evans and Young 1972]. It is not valueless in livestock production, but livestock do significantly less well on it than they do on native species. Cheatgrass also promotes several environmental problems. It is more superficially rooted than the relatively large fibrous root systems of perennials, and thus is not well suited for binding soil. This promotes soil erosion that, among other problems, harms riparian habitat for fish and wildlife [Stewart and Hull 1949].

The competitive dominance of cheatgrass in the intermountain West, and other alien grasses in other regions of the world, has led grassland ecologists to question the extent to which the underlying competitive forces can be reversed so that more beneficial native grasses again dominate. The conventional *plant-succession theory* contends that the variety of possible plant compositions of a grassland ecosystem is a hierarchy of *successional states*. An intervening factor such as livestock grazing can cause a retrogression in successional states from a *climax state* including only native plant varieties to lower successional states including less desirable alien varieties. When the intervening factor is removed, the grassland ecosystem is claimed to undergo a *secondary succession*, wherein the system reverses along the same pathway of successional states toward the stable climax state.

The plant-succession theory has begun to lose ground to the recently introduced *state-and-transition theory* due to empirical evidence that grassland ecosystems are not so resilient after the removal of an intervening factor. The state-and-transition theory predicts less optimistically that an intervening factor may result in plant compositions that are locked into *basins of attraction* compelling them toward stable lower successional states over time [Westoby et al. 1989; Laycock 1991]. The state-and-transition theory implies that the success of livestock reductions in promoting secondary succession depends on whether grassland conditions can be pushed across thresholds of environmental change to more socially desirable stable plant states. Thus, successional thresholds become the key analytical tool in characterizing the resilience of grassland ecosystems.

Boyd [1991] formulated the state-and-transition theory as a special case of Gause's interspecies competition equations (see. e.g., Hastings [1996]) to study, among other things, how selective grazing by wildlife on perennial grasses is linked to the long-term successional change in the plant composition of grassland. This Module contains a series of exercises deriving the necessary and sufficient ecological conditions under which Boyd's formulation results in a stable manifold partitioning phase space into basins of attraction to equilibria that represent desirable and less-desirable plant compositions. The stable manifold is composed of the convergent separatrices associated with an interior saddle-point equilibrium and represents the successional threshold of the grassland ecosystem in recovering from historic overgrazing. Further exercises demonstrate how the successional threshold can be approximated analytically using the theory of eigenvalues and eigenvectors and how the approximation can be analyzed for its mathematical accuracy.

2. Mathematical Formulation of the State-and-Transition Theory

Let Ω denote an area in which perennial and annual grasses are in competition. Let the variable $0 < g < 1$ denote the fraction of Ω colonized by grasses (i.e., perennial grasses) and the variable $0 < w < 1$ denote the fraction colonized by weeds (i.e., annual grasses). Portions of Ω may be barren or have overlapping vegetation, thus the sum of g and w need not equal one. The equations describing their competitive dynamics through time (t) are

$$g' = \{r_g\,[1 - g - q_w(g,E)w]\}\,g \qquad \textbf{(1a)}$$

$$w' = \{r_w\,[1 - g - q_g(g,E)g]\}\,w. \qquad \textbf{(1b)}$$

The bracketed terms multiplying g on the right-hand side (RHS) of **(1a)** and w on the RHS of **(1b)** measure the net per capita colonization rates of grasses and weeds, respectively. Parameters r_g and r_w (both with dimension $1/t$) measure the intrinsic colonization rates of g and w as each approaches zero, and $q_g(g,E)$ and $q_w(g,E)$ are nonnegative unitless competition rates that vary with g and a parameter E. The competition rates are discussed below.

Assume momentarily that q_g and q_w are zero (i.e., that grasses and weeds are not competitive). Equations **(1a)** and **(1b)** collapse to

$$g' = r_g g(1-g) \qquad \textbf{(2a)}$$

$$w' = r_w w(1-w), \qquad \textbf{(2b)}$$

which are basic logistic growth functions.

Exercise

1. Equations **(2a)** and **(2b)** are essentially alike, so we can examine the behavior of just one of them. Graph **(2b)** and use the graph to determine equilibrium colonization levels (i.e., values w^e for which w' equals zero). Solve the equation and graph its solution over $0 < w < 1$. What is the behavior of the solution around the equilibrium colonization levels w^e?

Positive competition rates q_g and q_w in **(1a)** and **(1b)** relate the colonization rate of one plant group to the other's competitive loss of habitat and have the impact of decreasing the loser's net per capita colonization rate. Each competition rate is a function of g because the density of grasses is assumed to determine its ability to compete with weeds for habitat. Grasses compete more favorably when g increases, forcing q_g toward an upper bound q_g^u and q_w toward a lower bound q_w^l. Boyd [1991] models the direct (inverse) bounded relationship between g and q_g (q_w) with the following *Michaelis-Menten functions*:

$$q_g = q_g^u \left(\frac{BE + g}{E + g} \right) \tag{3a}$$

$$q_w = q_w^l \left(\frac{E + g}{BE + g} \right). \tag{3b}$$

The parameter B is the ratio between the lower and upper bounds on q_g and q_w, that is, $B = q_g^l / q_g^u = q_w^l / q_w^u$. To simplify the model, Boyd assumes that B is the same for both grasses and weeds. As g increases, **(3a)** increases q_g from its lower bound ($q_g^l = Bq_g^u$ when $g = 0$) asymptotically toward its upper bound (q_g^u as $g \to \infty$). Conversely, as g increases, **(3b)** decreases q_w from its upper bound ($q_w^u = q_w^l / B$ when $g = 0$) asymptotically toward its lower bound (q_w^l as $g \to \infty$). The competition rates respond more rapidly to increases in g (i.e., q_g and q_w approach their maximum and minimum values, respectively, at lower levels of g) for small levels of the parameter E.

Exercise

2. Graph **(3a) and (3b)** to verify the above properties.

Because the competitiveness of grasses is inversely related to E, we can account for the adverse impact of livestock grazing on the competitiveness of grasses indirectly by fixing E at a relatively high level when the number of livestock preferentially grazing grasses in area Ω is relatively large. Alternatively, we can fix E at a relatively low level when the grazing pressure exerted on Ω is relatively small.

3. Solution Analysis

Inserting **(3a)** and **(3b)** into **(1a)** and **(1b)** yields:

$$g' = r_g g \left(1 - g - q_w^l \; \frac{E + g}{BE + g} \; w \right) \tag{4a}$$

$$g' = r_w w \left(1 - w - q_g^u \; \frac{BE + g}{E + g} \; g \right). \tag{4b}$$

We will solve this system using conventional phase diagram techniques, and begin by deriving the *nullcline functions* found by setting $g' = w' = 0$ in (g, w)-space.

Exercises

3. Each of the equations **(4a)** and **(4b)** yields a pair of nullclines. One of the nullclines from setting $g' = 0$ is the w-axis and one of the nullclines from setting $w' = 0$ is the g-axis. Analytically solve for the other two interior nullclines. Denote the interior nullcline from setting $g' = 0$ as $N_g(g)$, and that from setting $w' = 0$ as $N_w(g)$.

4. Verify that $N_g(g)$ has a g-axis intercept at 1, where grasses are 100% colonized and weeds are extinct, and a w-axis intercept at critical level $w_c = 1/q_w^u$. Also verify that $N_w(g)$ has a w-axis intercept at 1, where weeds are 100% colonized and grasses are extinct, and a g-axis intercept at critical level

$$g_c = \frac{1 - EBq_g^u + \sqrt{\left(EBq_g^u - 1\right)^2 + 4Eq_g^u}}{2q_g^u}. \qquad \textbf{(5)}$$

Use **(5)** to solve for the critical value of parameter $E = E_c$ that sets $g_c = 1$. Observe that g_c is less (greater) than one when E is set at a value less (greater) than E_c.

The number of steady-state solutions and their stability properties turn out to depend largely on the relative magnitudes of critical levels w_c and g_c to one. We will study the configurations leading to the existence of thresholds partitioning phase space into basins of attraction gravitating toward equilibrium plant states of differing desirability.

Exercise

5. Assume the following parameter values:

$$r_g = 0.27, \quad r_w = 0.35, \quad q_w^l = 0.6, \quad q_g^u = 1.07, \quad \text{and} \quad B = 0.3.$$

Plot $N_g(g)$ and $N_w(g)$ on the same graph for each of the following three cases:

a) $E = 0.4$;

b) $E = 0.172$; and

c) $E = 0.06$.

Recall that the parameter E is inversely related to the competitiveness of grasses, so that the impact of decreasing E over the three cases is to make grasses increasingly competitive. Identify the steady-state solutions on the axes and in the interior of the three plots. Use **(4a)** and **(4b)** to determine the directions of motion of w and g over time in the various areas partitioned by the nullclines and draw in the requisite trajectories. Comment on the observed stability of each steady-state solution.

Your work in **Exercise 5** should show that the phase-diagram solution for each of the three cases has an unstable node equilibrium at the origin ($w = g = 0$), an all-weeds equilibrium along the w-axis ($g = 0$, $w = 1$), and an all-grasses equilibrium along the g-axis ($g = 1$, $w = 0$). Stability of the all-weeds equilibrium depends completely on critical level w_c (w-axis intercept of the grasses nullcline N_g), which is inversely related to the upper bound on the competitive ability of weeds, that is, $w_c = 1/q_w^u$. When $w_c < 1$ ($q_w^u > 1$), as in all three cases above, weeds are a relatively strong competitor and the all-weeds equilibrium is a stable node attracting all initial plant states, including some level of grasses. Stability of the all-grasses equilibrium depends completely on critical level g_c (g-axis intercept of the weeds nullcline N_w, equation **(5)**), which in turn depends on the magnitude of the parameter E with respect to critical level E_c (see **Exercise 4**). For the parameter values in **Exercise 5**, $E_c = 0.103093$. When $g_c > 1$ ($E > E_c$), as in cases **(a)** and **(b)** in **Exercise 5**, grasses are a relatively weak competitor and the all-grasses equilibrium is a saddle point, repelling all plant states including some level of weeds in the positive quadrant. Alternatively, when $g_c < 1$ ($E < E_c$), as in case **c)** in **Exercise 5**, grasses are a relatively strong competitor and the all-grasses equilibrium is a stable node attracting a range of initial plant states.

Exercise

6. Use a computer program to generate numerically the phase diagrams associated with the three cases in **Exercise 5**. One such program that you can download from the World Wide Web is DynaSys at `http://www.sci.wsu.edu/idea/software.html` .

4. Successional Thresholds

Cases **(b)** and **(c)** in **Exercise 5** generate an interior saddle-point equilibrium sandwiched between two exterior stable nodes. One exterior stable node is always the all-weeds equilibrium. The other exterior stable node is the all-grasses equilibrium when $N_g(g)$ and $N_w(g)$ intersect once in the positive quadrant (case **(c)**), or an equilibrium with some level of weeds when $N_g(g)$ and $N_w(g)$ intersect twice in the positive quadrant (case **(b)**).

Exercise

7. Using the parameter values from **Exercise 5** with E fixed at 0.172, choose a set of initial conditions resting on the line $w = 0.2$ in the phase plane. Use a computer program to plot the phase trajectories passing through these initial conditions. What happens to the trajectories as the initial conditions move to the left? Try to find a curve that divides the set of initial conditions on trajectories approaching the undesirable all-weeds equilibrium at $(0, 1)$ from those on trajectories approaching an equilibrium with some level of grasses. How did you get the program to draw that curve?

The curve that separates the regions of different behavior in the phase plane is called a *separatrix*. One separatrix joining the interior saddle point emanates upward from the unstable node at the origin. Another separatrix converges downward to join the interior saddle point. Both separatrices taken together comprise the *stable manifold* of the saddle-point equilibrium [Hale and Koçak 1991]. The stable manifold partitions plant states into two disjoint groups. All plant states to the left of the manifold gravitate over time toward the undesirable all-weeds equilibrium, and thus are said to be in its basin-of-attraction. The plant states to the right are in the basin of attraction associated with a more desirable interior equilibrium including some level of grasses (case **(b)**), or the all-grasses equilibrium (case **(c)**). The stable manifold represents the threshold of environmental change referred to in the state-and-transition theory. The two conditions guaranteeing the existence of a threshold are:

- $q_w^u = q_w^l / B > 1$ (i.e., the all-weeds equilibrium is stable), and
- $N_g(g)$ and $N_w(g)$ intersect at least once in the phase plane.

5. Analytical Approximation of the Stable Manifold

In order to determine the environmental threshold for a given grassland ecosystem, the stable manifold of the interior saddle-point equilibrium must be approximated with some accuracy. First, we know that the lower portion of the stable manifold has endpoints at the origin and the interior saddle point (call it X), whose coordinates depend on the choice of parameters. These endpoints allow us to make a first approximation to the stable manifold.

Exercise

8. Draw the line from the origin to equilibrium X on the computer-generated phase diagram from **Exercise 7**. How does this line compare to the curve you plotted earlier as an approximation to the stable manifold?

There is more information useful in this approximation. If the stable manifold is described as a curve in the g-w plane, that is, $w = W(g)$, then we know the value of $W(g)$ and its derivative at the equilibrium point X. In particular, let $X = (\gamma, \omega)$ and M be the matrix in the linearization of the system of equations **(4a)** and **(4b)** about the point X:

$$\begin{bmatrix} (g-\gamma)' \\ (w-\omega)' \end{bmatrix} = M \begin{bmatrix} (g-\gamma) \\ (w-\omega) \end{bmatrix}. \qquad \textbf{(6)}$$

The matrix M has real eigenvalues of opposite sign, since X is a saddle point. Let the eigenvector associated with the negative eigenvalue be denoted (u, v), and assume that $u \neq 0$. Because the stable manifold is parallel to this eigenvector at the point X, it must have slope v/u there. Consequently, the second approximation to the stable manifold has the form $W(g) = ag + bg^2$, where a and b are chosen to satisfy the following conditions:

- $W(\gamma) = \omega$ (i.e., X must rest on the stable manifold); and
- $W'(\gamma) = v/u$ (i.e., the stable manifold must be tangent to the eigenvector at X).

This second approximation is a quadratic polynomial. One could, if necessary, obtain coefficients for an approximating polynomial of higher degree for the stable manifold. However, such a procedure is complicated and of limited effectiveness.

Exercise

9. Write the two equations allowing you to solve for the coefficients a and b in the approximation to the stable manifold. Using the same parameters as in **Exercise 7**, plot this curve on the same phase portrait from **Exercises 7** and **8**, and again compare it with a numerically computed approximation to the stable manifold. Now redo the exercise after changing the value of r_g to 0.4 and the value of r_w to 0.27. How does the approximation to the stable manifold for these new values compare with the numerically computed approximation?

Exercise 9 demonstrates that there is a problem with our approximation at the origin. The behavior of the stable manifold varies there according to the values for r_g and r_w. Whenever $r_w/r_g \neq 1$, there is a dominant direction for trajectories to leave a neighborhood of the origin. Specifically, when $r_w/r_g > 1$, trajectories tend to leave the origin tangent to the g-axis. Alternatively, when $r_w/r_g < 1$, trajectories tend to leave the origin tangent to the w-axis. It turns out that the stable manifold may be expanded in a series of the form:

$$W(g) = g^p \left[a_0 + a_1(g-\gamma) + a_2(g-\gamma)^2 + \cdots\right], \qquad \textbf{(7)}$$

where $p = r_w/r_g$ determines the behavior of the approximation as $g \to 0$. Our final approximation truncates this series after the first two terms:

$$W(g) = g^p \left[a_0 + a_1(g-\gamma)\right]. \qquad \textbf{(8)}$$

We continue to use the same conditions specified above to solve for the coefficients a_0 and a_1, that is, $W(\gamma) = \omega$ and $W'(\gamma) = v/u$.

Exercise

10. Write the two equations allowing you to solve for the coefficients a_0 and a_1 in the approximation to the stable manifold. Using the parameter values underlying **Exercise 7**, plot the approximation for the stable manifold given by **(8)** on the phase portrait from **Exercise 9**. How well does it agree with the curves that you computed earlier to approximate the separatrix? How do you expect the error in the approximation to behave?

6. Discussion

We have applied Boyd's [1991] competition model of grassland ecosystems to develop a method for analytically approximating *successional thresholds*. Successional thresholds are stable manifolds in phase space that partition grassland conditions into basins of attraction gravitating toward socially desirable or socially undesirable plant states over time. A necessary condition for the existence of a successional threshold is that undesirable plant species are relatively strong competitors in colonizing grassland.

Successional thresholds provide a valuable management tool for monitoring the long-term resiliency of grassland in response to various human activities, principally livestock production. For example, overgrazing—of the native perennial grasses that livestock prefer—is generally identified as the culprit behind the successful invasion by less desirable annual grass species of millions of acres of grassland in the intermountain region of the United States. Much of this grassland is publicly owned by the United States and available to private citizens with public grazing leases. Federal land managers have had the responsibility of setting limits on the number of livestock grazing public land to ensure the land's *sustained yield* over time [Federal Land Policy and Management Act 43 U.S.C. §1732(a) (1982)]. Given that past grazing limits set by public managers have not arrested the invasion of less desirable grass species, managers are under increasing public pressure to impose further grazing reductions to reestablish the more desirable grass species.

Further reductions in grazing decrease the consumption of the perennial grasses, thereby increasing their competitive vigor vis-à-vis invading annual varieties. Our model indirectly accounts for this by reducing the value of the parameter E, since it is inversely related to the competitiveness of perennial grasses. Reducing the value of E tends to shift the successional threshold upward and to the left in the phase plane and consequently increases the size of the basin-of-attraction, leading to a successional plant state with some positive proportion of desirable perennial grasses. If the current plant state faced by the public manager is included in the increased portion of this basin of attraction, then further grazing restrictions should prove successful in redirecting grassland to a more desirable plant state (all other things being equal).

Exercise

11. Use the same parameters from **Exercise 7** and the approximated threshold from **Exercise 10**. Assume that the public grazing manager oversees grassland that is colonized 10% by perennial grasses and 70% by invading annual varieties, that is, $(g, w) = (0.1, 0.7)$. To which equilibrium will this plant state gravitate toward over time? Should the manager reduce the number of grazing livestock? What is the impact of a grazing reduction decreasing the value of E from 0.172 to 0.1?

7. Solutions to the Exercises

1. The equilibrium values w^e are 0 and 1. **Figure 1** gives a graph of w' vs. w. The solution to **2b)** is

$$w(t) = \frac{1}{1 + c_w e^{-rt}},$$

where c_w is a constant depending on initial conditions.

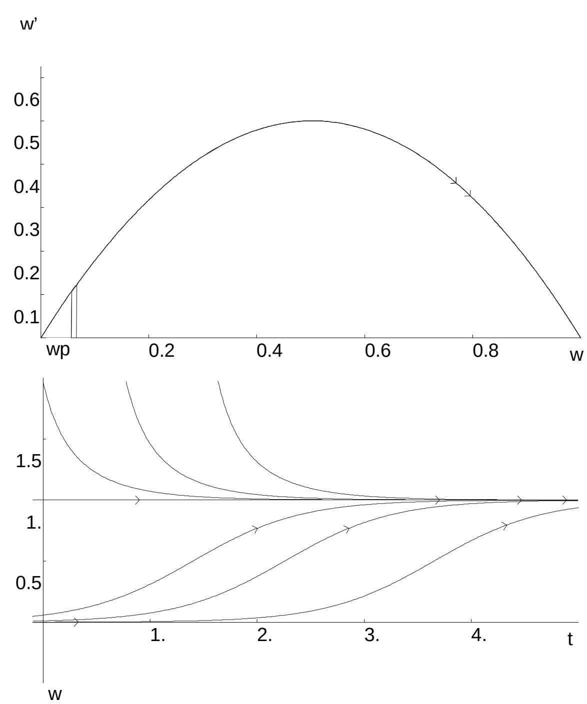


Figure 1. Plots of w' vs. w and of w vs. t for **Exercise 1**.

2. See **Figure 2**. The graph for q_g vs. g is qualitatively the same.

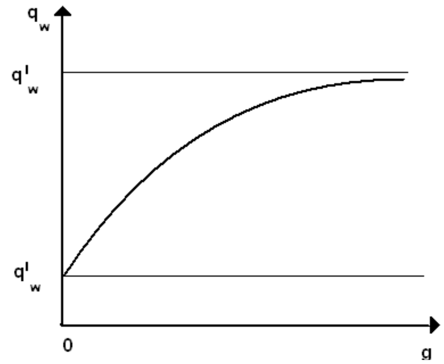


Figure 2. Solution for **Exercise 2**.

3.

$$N_g(g) = -\frac{g^2 + (BE-1)g - BE}{q_w^l(E+g)},$$

$$N_w(g) = -\frac{q_g^u g^2 + \left(q_g^u BE - 1\right) g - E}{E+g}.$$

4. $E_c = \dfrac{q_g^u - 1}{1 - q_g^u B}$.

5. See **Figure 3**.

9.

$$a = \frac{1}{\gamma^2}\left(2\gamma\omega - \frac{v\gamma^2}{u}\right), \qquad b = \frac{1}{\gamma^2}\left(\frac{\gamma v}{u} - \omega\right).$$

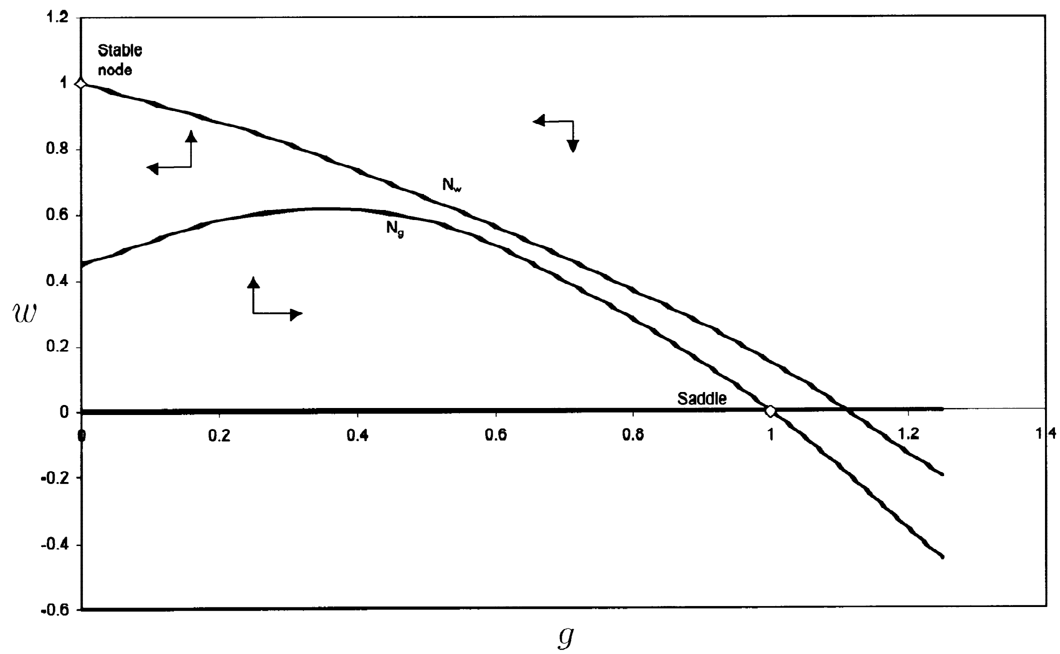
For the parameters from **Exercise 7**, we have $a = 2.28033$, $b = 20.9499$. For $r_g = 0.4$ and $r_w = 0.27$, we have $a = 6.05082$, $b = -2.77078$.

10.

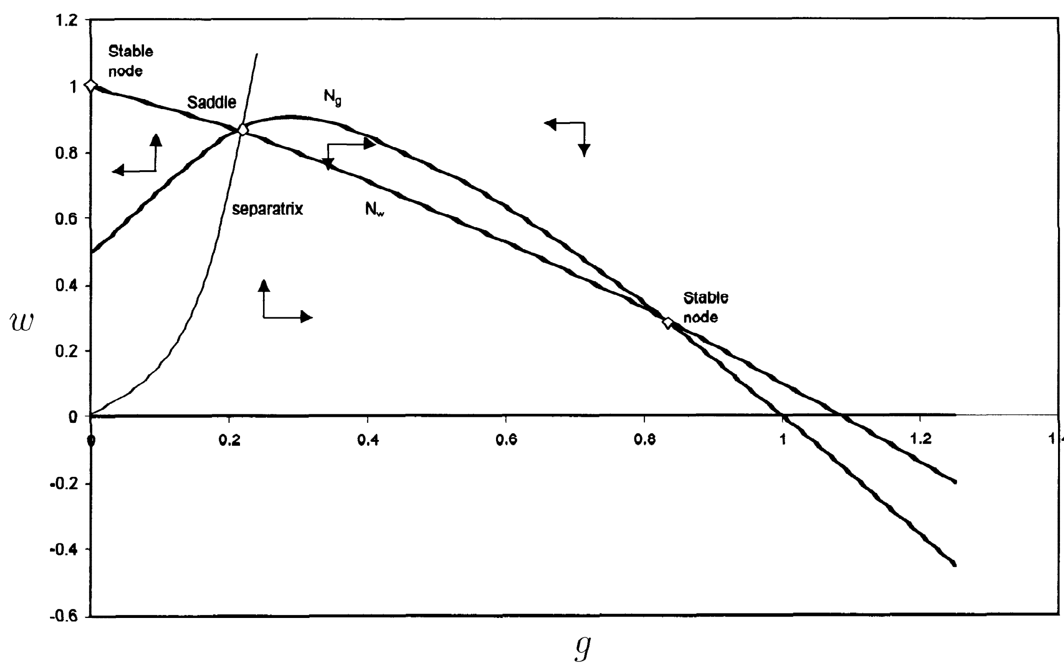
$$a_0 = \frac{\omega}{\gamma^p}, \qquad a_1 = \frac{1}{\gamma^p}\left(\frac{v}{u} - \frac{p\omega}{\gamma}\right).$$

For the parameters from **Exercise 7**, we have $a_0 = 9.67505$, $a_1 = 8.13708$.

The error in approximation obtained by truncating the series after the a_1 term is given by $a_2 g^p (g-\gamma)^2$, where a_2 is in fact given as $W''(\alpha)/2$ at some point α between g and γ. While the second derivative of W is difficult to compute, the implications of this error term for the approximation are easily understood. First, it indicates that the approximation will be at its best near γ and near 0. One expects the approximation to be at its worst as g moves far to the right of γ. The approximation will be better as the power p increases, so that when the ratio r_w/r_g of intrinsic growth rates is small, the error in the approximation will be larger. It turns out that the second derivative of W is small, since most of the curvature is due to the term g^p. Thus, the error in the approximation is very small when $p > 1$ and is will within acceptable tolerances when $p < 1$.

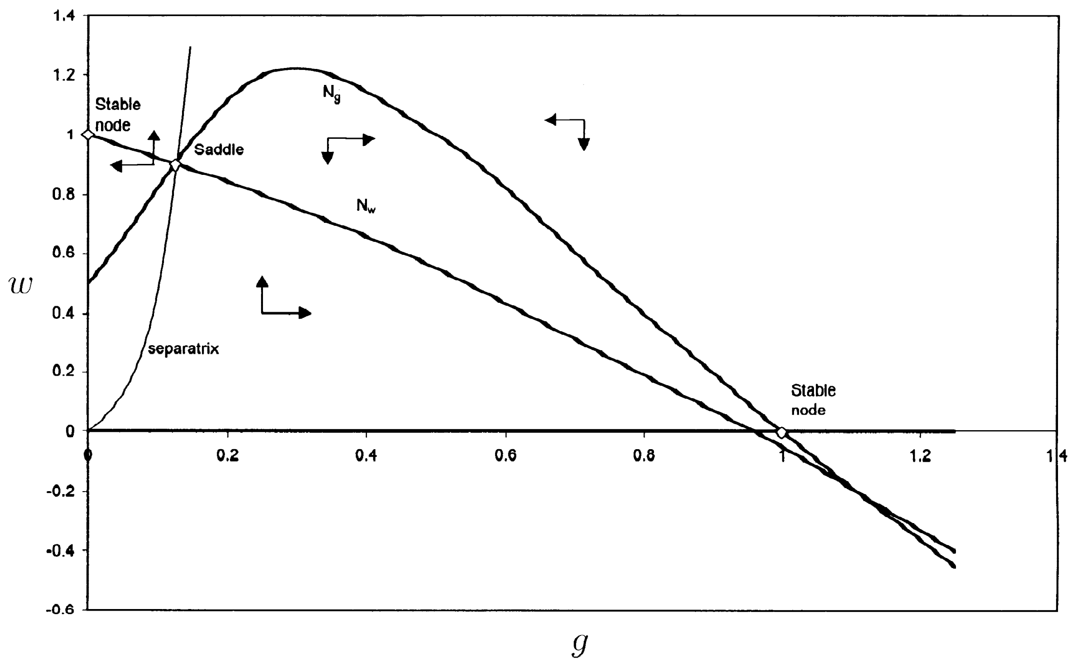


a. $E = 0.4.$



b. $E = 0.172.$

Figure 3ab. Solution for **Exercise 5ab**.



c. $E = 0.06$.

Figure 3c. Solution for **Exercise 5c**.

11. The initial plant state $(g, w) = (0.1, 0.7)$ is in the basin of attraction to the all-weeds equilibrium. If the grazing manager reduces the number of livestock so that the value of E declines from 0.172 to 0.1, the approximated threshold shifts upward and to the left (where $a_0 = 23.62$, $a_1 = 82.7589$). The initial plant state is now in the basin of attraction to a more desirable equilibrium containing some portion of native perennial grasses.

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