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Mathematical theory for plant–herbivore systems

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Abstract. The interactions of host plants with herbivores can be mediated by factors other than population sizes or biomass alone. Recent evidence indicates that features of the vegetation (loosely termed "plant quality") may change in response to herbivory and may, in turn, influence the performance of herbivores (i.e. by affecting survivorship, fecundity, or growth rates). A model which incorporates the effect of plant quality is presented. First it is shown that the frequency distribution of plant quality in the vegetation ($p(q, t)$) satisfies an equation of conservation. Then, qualitative aspects of the system are discussed in three situations: (1) mobile herbivores interacting with all plants; (2) sessile herbivores feeding exclusively on single plants; (3) intermediate situations in which mobility is moderate to low.

I show that depending on the plant quality response, $f(q, h)$, and the herbivore response, $g(q, h)$, it is possible to obtain stable equilibria as well as stable periodic oscillations. In the former case the populations tend to lose their heterogeneity. In the latter case, oscillations are accompanied by alternate narrowing *and* broadening of the distribution. Empirical testing and further research are suggested.

Key words: Plant-herbivore systems — Plant quality — Structured populations — Conservation laws — Mathematical models

1. Introduction

Classical approaches to modeling plant-herbivore systems are based on an analogy to predator-prey systems (see for example, Caughley and Lawton 1981; Crawley 1983; May 1973). There are limitations to this analogy. One distinction is that plants can be infested without being killed; this places the association more within the class of host-parasite systems. A more subtle but equally important aspect recently discovered is that some plants can exhibit an "immune response" which limits the effectiveness of their attackers.

It is generally recognized that many aspects of the vegetation can change in response to herbivory. One example of this situation occurs in the interactions of the larch budmoth with larch. Defoliation by the larch budmoth causes an increase in the "raw fiber" content of larch needles. this then results in an increased mortality and lowered fecundity of the herbivore (Fischlin and Baltensweiler 1979).

The abundance of plant and arthropod species in our world and the amazingly complex ways that they have adapted to each other means that attempts at generalities are at best feeble. Nevertheless, carefully understanding certain simplified prototypes can be illuminating if only for the empirical questions these suggest. For this reason I have attempted to study several models which incorporate the effect of change in *aspects* of the vegetation on herbivory. This paper outlines the approach and several examples to which it can be applied.

2. A simplified view

Abstracting from the properties of numerous examples, I will refer to the feature or aspect through which the plant most closely interacts with its herbivores as *the plant quality* (q). Since this concept is potentially confusing, a word of explanation is called for. In the theory, q is simply an index which conveys how a given part of the vegetation might be "rated" by a herbivore on a purely arbitrary scale (for example $q=0$ might be totally repulsive or non-nutritious, whereas $q=1$ might be exceedingly appealing). This variable is clearly correlated to the physiological state of the vegetation, which both affects and is affected by herbivory. Since a plant's physiological state would consist of a multitude of factors, q is simply a means of lumping together such factors into a single independent variable. (A common technique in modeling is thereby used to get a preliminary appreciation of a system before getting enmeshed in all of its details).

In a given situation, the aspect or attribute which we call "plant quality" would have to be empirically determined, possibly using a set of bioassays (see Sect. 10). It should be emphasized that a plant may be of different quality to different herbivores. Quality could, in specific instances, be correlated to physical or chemical properties (e.g. internal nitrogen, concentrations of noxious defence substances, succulence of foliage, toughness of stems, amount of resin, and/or size or business of the plant). A given plant may be heterogeneous (see Whitham et al., 1984) so that the natural unit of vegetation might be a single leaf or branch rather than a whole plant.

Good summaries of recent biological findings on the role of plant quality may be found in Rhoades (1982); Mattson and Addy (1975); Lincoln et al. (1982); Myers and Post (1981); Kraft and Denno (1982); Crawley (1983); Denno and McLure (1983); Strong et al. (1984).

In the proposed model, a basic starting step is to represent the vegetation as a heterogeneous population in which individual components have different qualities. A frequency distribution of plant quality is defined in the following way

$$p(q, t) = \text{frequency of plants whose quality is } q \text{ at time } t.$$

More precisely, the integral

$$\int_q^{q+\Delta q} p(q, t)\, dq$$

is the number of plants (or equivalently the vegetation biomass) whose quality falls within the range $(q, q+\Delta q)$. Note that $p(q, t)$ of this definition can be used to describe the vegetation whether its components are whole plants, single leaves of one plant, stems or flowers, etc.). Dyer (1975) and Whitham (1980, Fig. 2) give frequency distributions of corn ear size and of leaf size which can be used to convey the general idea of $p(q, t)$ (at a fixed time t).

The first step in formulating the theory will be to make a statement describing the effects of herbivory on the plant quality distribution $p(q, t)$. Once this is accomplished, the goal will be to investigate what qualitative outcomes may be expected when plant and herbivore populations interact.

3. The single plant model

Let us start with the response of a single component of the vegetation to the herbivores that consume it. From empirical observations of the system at different host quality and at different intensities of herbivory it should be possible to reconstruct functions f and g that depict the mutual effects of the two species. More explicitly, given a particular vegetation quality index q and herbivore density h, I assume that one can predict changes in q and h based on the equations

$$\left\{\begin{aligned} \frac{dq}{dt} &= f(q, h), && \text{(1a)} \\ \frac{dh}{dt} &= g(q, h). && \text{(1b)} \end{aligned}\right.$$

The functions f, g above are, respectively, the rates of change of the plant quality and of the herbivore population. Both functions may depend on q and on h; they are specific to a particular plant and herbivore system, and must be determined or conjectured based on biological information. Given this empirical knowledge of single plant components, the goal will be to deduce what happens to the plant population as a whole.

Implicit in Eq. (1a) is a statement that herbivory causes changes in the physiological state of a plant. (These changes are then reflected in the quality of the plant as perceived by the herbivore.) Note that the function f can also encompass physiological changes which take place in a plant as it matures (e.g. in the absence of herbivores, $f(q, 0)$). Such processes as relocation of energy reserves within the vegetation could make some of its components less attractive to herbivores as the season advances.

In the above, I have assumed that two ordinary differential equations describe a single plant and herbivores interacting with it in isolation. This means that the model applies to situations where plant quality and herbivore load vary in a continuous way (as for example, during a single season). The accuracy of this assumption would depend on the system and the time-scale of observation.

For plant-herbivore systems in which quality changes abruptly in all all-or-none effect (e.g. the induction of chemical defenses (Rhoades 1982)) or in which many nonoverlapping herbivore generations are implicated, a better starting model of the single vegetation component would be

$$\left\{\begin{aligned} q^{n+1} &= F(q^n, h^n), \\ h^{n+1} &= G(q^n, h^n). \end{aligned}\right. \qquad \text{(2a)}$$

for q^n, h^n respectively the plant quality and herbivore population during the nth generation. A model of type (2a) has been discussed by Fischlin and Baltensweiler (1979). Models of type (1) have been described by Caughley and Lawton (1981).

While the applicability of the models given by Eqs. (1a, b) or (2a, b) depends on the particular case, the availability of the analytical techniques for ordinary differential equations makes the first model an attractive first step in gaining a preliminary understanding of general effects. Thus, in this paper, analysis will be restricted to the case of plant-herbivore systems in which the processes are continuous ones.

4. Herbivory-induced changes in the vegetation

Given a particular view of what happens to a single plant (or to a single vegetation unit), equations will now be written to describe changes in the populations as a whole. The way in which this transition from the level of the individual to that of the population is made will form the key new concept of the model.

The equation for the vegetation (represented by $p(q, t)$) can be derived in a rigorous way by discretizing q and making a statement of balance for plants which enter or leave a given quality class (e.g. the class of plants whose quality is in the interval q to $q+\Delta q$). A more amusing method is to employ the physical analogy below:

The vegetation $p(q, t)$ is a collection of individual plants displayed along a scale of quality q. Each plant shifts along this scale at the rate prescribed by $dq/dt=f$ (f an empirically determined function). Now consider an analogous collection $c(x, t)$ of particles displayed along a scale of distance, x. If these particles move collectively at the rate $dx/dt=v$ they form a "convective fluid," described by the standard equation of conservation

$$\frac{\partial c}{\partial t}=-\frac{\partial cv}{\partial x}\pm\sigma$$

(cv is their flux and σ is a rate of local production or degradation of particles).

By making a correspondence between variables in the two situations above one can deduce an appropriate equation for the vegetation. Replace location in physical space by location on the quality scale ($x\to q$), the density of particles by the vegetation density ($c(x, t)\to p(x, t)$) and physical velocity by rate of shift in quality ($v=dx/dt\to f=dq/dt$). The result is

$$\frac{\partial p}{\partial t}=-\frac{\partial pf}{\partial q}-\sigma, \tag{3}$$

where σ is a term which accounts for death of plants.

Many previous models for plant-herbivore systems have focused primarily on quantitative changes in the vegetation which stem from removal of plants or herbivory-induced mortality. While this is easily included by selecting appropriate terms for σ in Eq. (3), I purposely omit this term in order to focus attention on effects which arise purely from quality changes. Taking $\sigma=0$ means that one neglects plant mortality over the timescale of observation. The case $\sigma\neq 0$ is briefly discussed in Sect. 9.

To place the above analogy into a somewhat broader perspective, one should mention that conservation laws appear widely in applied mathematics. Other biological problems have previously been tackled with similar equations. The most well-known example stems from a continuous model for populations distributed into age classes. In that context such equations have been studied by Von Foerster (1959), Rubinow (1968), and others. Another example, that of size distributions of growing organisms, has been described by Thompson (1983) and by Edelstein and Hadar (1983).

To go further in assembling the model it is necessary to make several assumptions about how mobile herbivores are as they feed on the vegetation. Two extreme cases will be discussed in some depth: (a) the herbivore visits many plants in its foraging, (b) the herbivore is intimately associated with a single plant. A grazing grasshopper would exemplify type (a) (see Parker and Root 1981) whereas a scale insect would exemplify type (b) (see Edmunds and Alstad 1978). An intermediate case in which an herbivore migrates occasionally from plant to plant will be outlined in Sects. 7-8.

5. Mobile herbivores

First consider the case of a highly mobile herbivore which feeds on many different plants and responds only to an average of the quality index in the vegetation. Define h as the average herbivore load per plant. If the total plant population is constant, a differential equation for h can be written as follows:

$$\frac{dh}{dt} = g(\bar{Q}, h), \tag{4}$$

where $\bar{Q}$ = average plant quality. The average quality is something that can be obtained directly from the frequency distribution of plant quality $p(q, t)$, since for Q = total quality, P = total number of plants,

$$Q(t) = \int_0^\infty qp(q, t)\, dq, \tag{5}$$

$$P(t) = \int_0^\infty p(q, t)\, dq, \tag{6}$$

and $\bar{Q} = Q/P$. Q and P are the first and second moments of the distribution $p(q, t)$.

Thus, in the case of the mobile herbivore, Eqs. (3) and (4) would completely describe the plant-herbivore population. Supplemented by particular forms for the empirical functions f and g, as well as initial conditions and assumptions about $p(0, t)$, these equations would make up the mathematical problem to be studied.

a. Example 1: low herbivory increases food quality of the plant

In the following hypothetical example, I select the two functions, f for the plant's response to herbivores and g for the herbivore's response to plant quality. The particular choices are made only in order to illustrate the method — not as a claim to a general theory.

Let us consider the situation in which a low to moderate level of herbivory increases the quality of the plant as a potential food source for the herbivore. Several examples of this type are given by Crawley (1983, pp. 123-124) under the general term "group feeding". For instance, aggregations of sawfly larvae can more readily penetrate the tough exterior of pine needles and thus stand a greater chance of survival than solitary individuals (Ghent 1960). McNaughton (1983) also discusses the potential stimulation of a plant at low herbivore densities which would tend to increase food availability to the herbivore. The choices of f and g were made with this general situation in mind.

More particularly, I assumed that the plant quality index (e.g. the amount of accumulated internal reserves of the plant) increases at some constant rate K_1 when herbivores are absent, and is further increased when h is small. Thus, f, the rate of increase of quality, was taken to be

$$f(q, h) = K_1 + K_2 q h (h_0 - h). \tag{7}$$

Note that for $h < h_0$, f will always be positive. For $h > h_0$, f will be positive for low q, and negative for sufficiently large q. The dependence of f on q might reflect a dependence of plant sensitivity on the current state of the plant. (Low q plants produce lower responses than high q plants.) This dependence means that when herbivores abound ($h > h_0$), the quality of high-q plants will dwindle while that of the low-q plants will continue to increase.

For the rate of change of the herbivore population, $g(q, h)$, consider

$$g(q, h) = K_3 h(1 - K_4 h / \bar{Q}). \tag{8}$$

This represents a standard assumption that eventually population growth is density-limited. Here I have assumed that the carrying capacity of the vegetation for the herbivore population is proportional to the average quality of the vegetation.

The model consisting of Eqs. (3), (4), (7), and (8) will now be discussed. It has been assumed that the total number of plants, P, remains constant. In particular, it will be assumed that σ in Eq. (3) is zero. This assumption does not alter the basic character of the equations. (See comments in the previous section.)

b. Integrating Eq. (3) for f linear in q

The special form chosen for f allows, in this one instance, a reduction of the model to a set of ordinary differential equations. Note that f is linear as a function of q, i.e.

$$f = f_1(h) + q f_2(h). \tag{9}$$

Using the definition of total plant quality, Q, and carrying out an integration by parts, yields

$$\frac{dQ}{dt} = \frac{d}{dt}\int_0^\infty qp\,dq = \int_0^\infty q\frac{\partial p}{\partial t}\,dq$$

$$= -\int_0^\infty q\frac{\partial (pf)}{\partial q}\,dq = -(qpf)\Big|_0^\infty + \int_0^\infty pf\,dq.$$

The first term in the resulting expression would be zero in any practical situation since there are no plants of infinitely high quality. (It is assumed $p(q, t)$ has compact support.) Now substituting the special form of f in the above, one obtains

$$\begin{aligned}\frac{dQ}{dt} &= \int_0^\infty (pf_1(h) + pqf_2(h))\, dq,\\ &= f_1(h) \int_0^\infty p\, dq + f_2(h) \int_0^\infty pq\, dq,\\ &= f_1(h)P + f_2(h)Q. \qquad (10)\end{aligned}$$

Thus, if the total number of plants P is constant, one can investigate fluctuations in the average plant quality and total herbivore density by studying the set of ordinary differential equations:

$$\begin{cases} \dfrac{dQ}{dt} = f_1(h)P + f_2(h)Q, & (11a)\\[2ex] \dfrac{dh}{dt} = g(h, Q/P). & (11b)\end{cases}$$

c. *Predictions of the model*

The steps of the previous section, applied to Eqs. (7) and (8) lead to

$$\begin{cases} \dfrac{dQ}{dt} = K_1P + K_2Qh(h_0 - h),\\[2ex] \dfrac{dh}{dt} = K_3h(1 - K_4h/\bar{Q}). \end{cases} \qquad (12)$$

Since P is constant, the above can be written in terms of the total herbivore population $H = hP$,

$$\begin{cases} \dfrac{dQ}{dt} = \hat{K}_1 + \hat{K}_2QH(H_0 - H),\\[2ex] \dfrac{dH}{dt} = K_3H(1 - K_4H/Q), \end{cases} \qquad (13)$$

where $\hat{K}_1 = K_1P$, $\hat{K}_2 = K_2/P^2$, $H_0 = h_0P$. To investigate the behavior of the equations it is convenient to rewrite them in the dimensionless form below:

$$\begin{cases} \dfrac{dQ}{dt} = 1 + KQH(1 - H),\\[2ex] \dfrac{dH}{dt} = \alpha H(1 - H/Q), \end{cases} \qquad (14)$$

with $K = (K_2K_4/K_1)h_0^3$, $\alpha = (K_3K_4/K_1)h_0$ (see Appendix for further details).

It may be verified by a combination of linear stability theory and phase plane analysis that these equations admit a single steady state (H_s, Q_s) at the intersection of the null clines given by $Q=1/(KH(H-1))$ and $Q=H$. The steady state is stable (either a node or a focus) and, has the property that $H_s>1$.

Translating this into a biological prediction, the herbivore attack will lead to decaying oscillations in the average plant quality index as well as in the total herbivore population; both variables eventually settle into a stable equilibrium in which a limiting herbivore density persists on vegetation whose average quality is constant.

d. The distribution of plant quality

To predict how the distribution of quality in the vegetation changes due to herbivory one needs to solve the full model (Eqs. 3 and 4, given 7 and 8), not just the simplified system of ordinary differential equations. To prepare the way it is helpful to notice that by results of the previous section, the system will settle into a stable equilibrium with a level of herbivores H_s greater than 1. The herbivore density per plant at equilibrium, h_s, thus exceeds the value h_0 (in Eq. 7). From this it follows that after some possibly transient response, $f(q, h)$ viewed as a function of q will converge to a straight line with negative slope $-K_2h_s(h_s-h_0)$, and $f(0, \cdot)$ will be a positive number (see Fig. 1(b)).

An important feature of the example is the fact that f eventually has a negative slope. Below it is shown that this attribute guarantees that the diversity of the vegetation will *decrease*.

Lemma. *Let* $p(q, 0)$ *be a function of compact support on some interval* $(0, q_{\max})$. *Let* $f: R^1 \to R^1$ *be a continuous function satisfying the following properties*:

(a) $f(q^*)=0$ *for some* $q^* \in (0, q_{\max})$, $f(0)>0$,

(b) $f'(q)<0$, $\forall q \in (0, q_{\max})$.

Then for $p(q, t)$ *the solution of*

$$\frac{\partial p}{\partial t}=-\frac{\partial pf}{\partial q} \tag{15}$$

with boundary conditions $p(0, t)=0$, $p(q, t)=0$ *for all* $q \geq q_{\max}$ *we have*

$$p(q, t) \to \delta(q^*) \quad \text{as } t \to \infty.$$

Proof. The characteristic equations to (15) are

$$\begin{cases} \dfrac{dq}{dt}=f \\[2ex] \dfrac{dp}{dt}=-f'p. \end{cases}$$

Combining (a) and (b) note that $f(q)>0$ for $q<q^*$ while $f(q)<0$ for $q>q^*$. Thus the slope of the characteristic curves is positive for $q<q^*$, negative for $q>q^*$, and approaches zero as $q \to q^*$ from both directions. For $t \to \infty$, these curves therefore converge to the line $q=q^*$.

Note that since $f' < 0$, $p(q, t)$ will increase along characteristic curves whenever $p(q, 0) \neq 0$. The conclusion is that q^* is a point of accumulation for the distribution.

Biocorollary. *If vegetation of high quality tends to decline in quality whereas vegetation of low quality tends to improve then all parts of the vegetation will eventually acquire some intermediate quality* q^* *(for which* $f(q^*, \cdot) = 0$*).*

The preceding lemma and its corollary suggest that in certain cases herbivory can have a homogenizing influence — i.e. cause a decline in the diversity of the

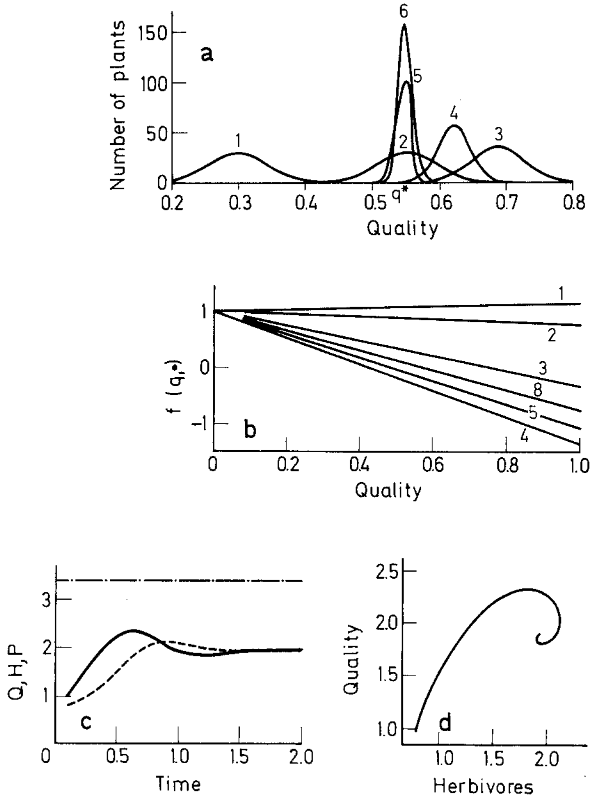


Fig. 1. (a) Quality distributions of plants over the course of the herbivore attack in Example 1. For low pest populations all plants are increasing in quality (1, 2, 3). As the herbivore load gets heavier, damage to plants forces a decrease in the mean quality (4). Damped oscillations eventually result in a nearly homogeneous vegetation in which the predominant quality is q^* (5, 6). Equations (3), (4), (7), (8) were integrated numerically with parameter values $\alpha = 5.0$, $K = 1.0$, an initial quality distribution $p(q, 0) = 30.0 \exp(-(q - 0.3)^2/0.004)$, and an initial herbivore load $h(0) = 0.8$ (dimensionless units). Shown are six successive distributions at intervals of $\Delta t = 0.25$ dimensionless time units starting with $t = 0$.

(b) Graphs of the rate of change of quality, f, as a function of quality, q. The slope of the line depends on the herbivore population level, and changes during the course of the outbreak. Note that the lines are converging to line 8 which intersects the $f = 0$ axis at $q^* \approx 0.55$. Δt same as in (a).

(c) Total plant quality, Q (*solid curve*), total herbivore population, H (*dashed*) and total number of plants, P (*dot-dashed*) as functions of time. Note that while P stays constant, Q and H undergo damped oscillation.

(d) Q plotted against H reveals the phase plane trajectory traced out by the system for this example vegetation. The particular features of the example which lead to this conclusion were (a) deterioration in the quality of the high-quality vegetation, (b) the fact that response to herbivory is not uniform at all qualities, but greater (and more negative) at high qualities.

In general if the response function f considered as a function of q is positive at $q=0$ and has a negative slope ($\partial f/\partial q<0$) there is a tendency for the distribution of plant qualities to *narrow*. The opposite conclusion (i.e. widening) follows if f satisfies $\partial f/\partial q>0$. In summary, for $f(q=0)>0$

$$\begin{aligned} \partial f/\partial q<0 \quad &\Rightarrow \quad p(q,t) \text{ narrows,} \\ \partial f/\partial q>0 \quad &\Rightarrow \quad p(q,t) \text{ widens.} \end{aligned}$$

e. *Predictions of the model*

Equations (3), (4), (7), (8) were integrated numerically using a method of characteristics (i.e. integrating an o.d.e. along characteristic curves of the hyperbolic Eq. 3). Figure 1(a) displays $p(q,t)$, the frequency distribution of plant quality in a time sequence at various stages of herbivory. As the analytical results predicted, a sequence of decaying oscillations accompany a general overall tendency of narrowing in the distribution. The total plant quality and herbivore populations are depicted in Figs. 1(c) and (d). In addition, several plots of f as a function of q are also displayed to illustrate its convergence to a line with negative slope.

To underscore the message of this example, properties of the plant's response function, f (independent of the herbivore function, g) can influence qualitative changes in $p(q,t)$ such as narrowing or widening over certain intervals of q. However, f and g acting in concert determine the overall stability properties of the system, including presence or absence of oscillations.

While f in (7) is not based on any one real-life situation, data from Dyer (1975) indicates that this type of response function is characteristic of red-winged blackbirds and the size of corn ears. Dyer noted that corn tends to overcompensate for damage due to bird pecking by increasing in size faster than the natural rate. Dyer further claims that birds preferentially attack larger corn ears. Identifying the size of a corn ear as the feature of the vegetation which determines its quality as a food source for red-winged blackbirds, one obtains the formula (7) as a representation for the plant response to herbivory, f. It is interesting to observe that the sort of narrowing size distribution which was predicted by the model is in fact observed in some of Dyer's data.

6. Sedentary herbivores

The single major difference between sedentary and mobile herbivores is that in the former, individuals interact largely with a single host plant; thus they affect and are in turn affected by the plant quality of one plant, not of the whole plant population. While herbivore species could characteristically have varying degrees of mobility, in this section the limiting case of totally sessile herbivorous insects will be discussed.

The new feature to be included in the model is the fact that herbivores are not identical. Those sitting on plants of favorable quality may reproduce rapidly or have a low mortality. Others may suffer higher mortalities and low reproductive rates if their hosts are of unfavorable quality. Lack of mobility effectively subdivides the population of herbivores into classes that will be successful to different degrees depending on their distribution among hosts of different qualities. Moreover, the effect of herbivory on a plant will no longer be related to the total population of pests, but rather to the relative proportion of the herbivores on the plant. In modeling this type of plant–herbivore system, the letter b ("bugs") will be used in place of the previous variable h ("herbivore") to emphasize that the model applies to sessile herbivorous insects.

Several approaches were used in developing a model to describe this situation. In the first, the sessile herbivores were described by the variable

$b(q, t)$ = density of herbivores per plant on plants whose quality is q at time t.

The problem with this definition is that it presupposes a correlation between the quality of the plant and its herbivore load. That this assumption is faulty emerges from the equation for b derived by straightforward considerations: the equation

$$\frac{\partial b}{\partial t} = -f\frac{\partial b}{\partial q} + g$$

(L. Edelstein-Keshet, unpublished observations) is a nonlinear hyperbolic equation (since f depends on both b and q). It is well known that such equations admit solutions in which a given q value does not have a unique b ("shocks" in the terminology of applied mathematics).

In a more valid second approach to the problem of sessile herbivores the extent of herbivory is considered an additional independent variable, along with plant quality. The motivation for this approach is to some extent derived from a discussion of herbivore attack patterns in Crawley (1983), who defines $p(i)$ as the proportion of plants with i herbivores. Crawley assumes that $p(i)$

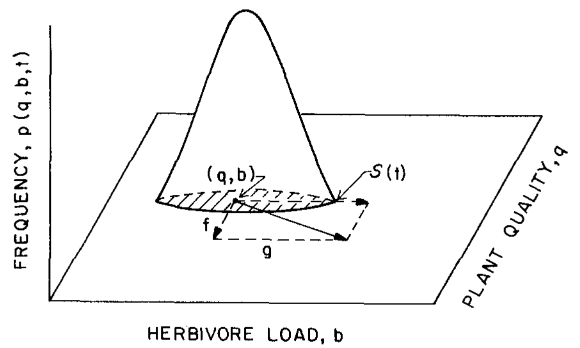


Fig. 2. In the case of sessile herbivores, b and q are both viewed as attributes of the plant. The set S consisting of pairs (q, b) represents a collection of plants, with $p(q, b, t)$ a frequency distribution with support S. The vector (f, g) defines the motion at each point in the plane

does not change with time. More realistically, since some plants provide more hospitable conditions than others, the pattern of herbivore attack could gradually shift during the course of herbivory.

To incorporate this more general situation, a new distribution is defined to simultaneously describe the plant quality and herbivore load of plants. What makes this possible is the fact that an herbivore load can be viewed as an additional attribute of the plant, particularly in the case of sessile herbivores. I then define $p(q, b, t)$ to be the frequency distribution of plants of quality q and herbivore load b at time t.

That is,

$$\int_{q}^{q+\Delta q}\int_{b}^{b+\Delta b} p(q, b, t)\, dq\, dp,$$

is the number of plants (or biomass of the vegetation) whose quality is between q and $q+\Delta q$ and whose herbivore load is between b and $b+\Delta b$.

This definition proves useful for several reasons. First, it leads to a rather natural generalization of a previous plant equation which condenses information about the two interacting populations into a single statement. Second, it applies to a situation in which plants may have few or many herbivore units, regardless of the current plant quality, i.e. it eliminates problems which arise if one assumes that herbivore loads are correlated to the quality of the plant.

The derivation of an equation for $p(q, b, t)$ again follows by analogy with a physical situation, but one of a higher dimensionality. Each plant is now associated with a pair of coordinates, (q, b), i.e. (plant quality, herbivore load of plant). These coordinates change with time as before in accordance with the equations

$$\begin{cases} \dfrac{dq}{dt}=f(q, b), & \text{(19a)} \\[2ex] \dfrac{db}{dt}=g(q, b), & \text{(19b)} \end{cases}$$

which summarize the mutual effects of plant quality and herbivory on one another. Now identify the plant coordinates $(q(t), b(t))$ with a position (in a two-dimensional "state-space"), and the vector (f, g) with a velocity (i.e. rate of change of (q, b) with time). Then, by an identical analogy with a distribution of particles moving over a plane, one finds the equations for $p(q, b, t)$ to be

$$\frac{\partial p}{\partial t}=-\frac{\partial pf}{\partial q}-\frac{\partial pg}{\partial b}. \tag{20}$$

Note that the RHS is equivalent to $\operatorname{div}(J)$ where $J=(pf, pg)=$ flux of plants and div is the operator $(\partial/\partial q, \partial/\partial b)$; i.e. the equation is again in the form of a standard conservation equation, $\partial c/\partial t=-\operatorname{div}(J)$.

Equation (20) is written for a constant total plant population. One can include a death of part of this population by using a term of the form $(-dp)$ in the RHS of the equation. For the purpose of this analysis it will again be assumed that plants do not die.

a. The mathematical problem

The mathematical problem consists of Eq. (20), together with initial conditions, such as $p(q, b, 0) = p_0(q, b)$ and boundary conditions. The precise boundary conditions depend further on details of the specific situation, and in particular, on the functions f and g. It should be clear from Eq. (19b) that $g(q, 0) = 0$, i.e. that if there are no herbivores, the herbivore population cannot increase. This is equivalent to a no-flux boundary condition at the boundary $b = 0$, i.e. there are no initially herbivore-free plants which later become colonized by pests. If $f(0, b) = 0$ or else $p_0(0, b) = 0$, one has an additional no-flux condition at the boundary $q = 0$ which ensures that no plants of initially "zero quality" eventually become part of the population.

About the initial conditions one can generally assume that the distribution $p(q, b, 0)$ has compact support (i.e. is identically zero outside some interval). (Under reasonable assumptions about f and g this will imply that $p(q, b, t)$ will always have compact support, although the support may grow as $t \to \infty$ in some instances.)

Harvesting or other biological manipulations such as removal of heavily infested plants can be accommodated in the problem by setting $p = 0$ for $q \geqslant q_1$ or $b \geqslant b_1$ for b_1, q_1 fixed. This means that all plants attaining or exceeding a quality q_1 are removed and/or all plants which are infested by b_1 or more herbivores are eliminated. (One can calculate the biomass which has been removed by integrating the flux at $q = q_1$ or $b = b_1$ over the timescale of the process.)

b. A qualitative interpretation

Suppose the plant population consists of a number of plants, n. At starting time $t = 0$ each plant i could be represented by a pair of values (q_i, b_i), its plant quality and herbivore load. The whole population can be thus depicted by a collection of points in the qb-plane. (These points will *move* as a result of herbivory.) The frequency distribution $p(q_0, b_0, 0)$ can be identified with the probability of finding a plant whose initial state is (q_0, b_0). Then, for the ith plant,

$$\left\{\begin{aligned} \frac{dq_i}{dt} &= f(q_i, b_i), && \text{(21a)} \\ \frac{db_i}{dt} &= g(q_i, b_i). && \text{(21b)} \end{aligned}\right.$$

These are the characteristic equations associated with (20), which describe the population from the standpoint of cohorts (following a group of plants that had a specified initial state). Writing n systems of equations (with two equations each) for the n plants in a sample population appears to complicate the problem. However, an equivalent point of view is to consider Eqs. (21a, b) as a dynamical system equipped with a *set of initial data* $s = \{(q_1, b_1) \cdots (q_n, b_n)\}$, and a probability function $p(q, b, t)$ defined on this set. More generally, a large population of plants could be characterized by any compact subset $S(t)$ of the qb-plane, where $S(t) = sp\{p(q, b, t)\}$ is the set on which p is non-zero. This leads to a qualitative theory for the effects of herbivory on the plant–herbivore population to be outlined below.

c. *Qualitative outcome of herbivory*

With the interpretation given in the previous section, the problem can be restated in the following way: given a dynamical system in the qb-plane and a compact set S of initial data, how will S evolve with time? The answer to this type of question would depend on the set $S(0)$ and the functions f and g. Typically, the set S may shrink, expand, or distort as it undergoes motions governed by the dynamical system. This is related to a phenomenon observed in example 1 where it was demonstrated that assumptions about the quality-response function f lead to a narrowing or broadening plant quality distribution. In this section, I demonstrate analogous properties for the case of sedentary herbivores. To be more precise, conditions will be obtained which guarantee that plants represented by points of the set S will become more (or less) similar in their properties.

Starting with two initially similar plants (q_0, b_0) and $(q_0+\varepsilon, b_0+\delta)$, where ε and δ are, respectively, their differences in quality and herbivore load, the first outcome is equivalent to $\varepsilon, \delta \to 0$ as $t \to \infty$. Using Eqs. (21a, b) and substituting for the coordinates of the second plant, one gets

$$\begin{aligned} \frac{d(q_0+\varepsilon)}{dt} &= f(q_0+\varepsilon, b_0+\delta), \\ \frac{d(b_0+\delta)}{dt} &= g(q_0+\varepsilon, b_0+\delta). \end{aligned} \tag{22}$$

For ε and δ small, upon expanding the LHS, rewriting the RHS in a Taylor series in ε, δ, one obtains

$$\begin{aligned} \frac{d\varepsilon}{dt} &= \varepsilon \left.\frac{\partial f}{\partial q}\right|_{(q_0,b_0)} + \delta \left.\frac{\partial f}{\partial b}\right|_{(q_0,b_0)} + \cdots, \\ \frac{d\delta}{dt} &= \varepsilon \left.\frac{\partial g}{\partial q}\right|_{(q_0,b_0)} + \delta \left.\frac{\partial g}{\partial b}\right|_{(q_0,b_0)} + \cdots, \end{aligned} \tag{23}$$

in which all quadratic and higher order terms in ε, δ have been omitted.

Using a shorthand notation in future references to the above set of equations, we write

$$\frac{d}{dt}\begin{pmatrix} \varepsilon \\ \delta \end{pmatrix} = A \begin{pmatrix} \varepsilon \\ \delta \end{pmatrix}, \tag{24}$$

where

$$A = \begin{pmatrix} \partial f/\partial q & \partial f/\partial b \\ \partial g/\partial q & \partial g/\partial b \end{pmatrix} \tag{25}$$

is the Jacobian of the mapping associated with the dynamical system (19).

The deviations ε and δ will decay, i.e. two plants whose initial states were (q_0, b_0) and $(q_0+\varepsilon, b_0+\delta)$ will become more similar when $(0, 0)$ is stable steady state of (24), the linearized version of the equations. By linear stability theory two prerequisites are necessary for such stability:

$$\text{(a)} \quad \operatorname{Tr} A<0, \qquad \text{and} \qquad \text{(b)} \quad \det A>0. \tag{26}$$

Given f and g, conditions (a) and (b) are inequalities, ($f_q+g_b<0$ and $f_q g_b+f_b g_q>0$) which define certain regions (open sets in the set-theoretic sense) in the qb-plane. When two nearby points representing two plants fall within a region satisfying (26) they will get closer with time. Equivalently, as long as the set $S(t)$ is completely contained in this region it will contract.

For example, a somewhat obvious result is obtained when the system described by Eqs. (19) has a single stable equilibrium, (q^*, b^*). Since (q^*, b^*) must itself satisfy a) and b) to be stable, it must be contained in the interior of a region which contracts the distribution. All points in the plane will converge to (q^*, b^*), simultaneously growing arbitrarily close to each other (see Fig. 3). More complex outcomes may ensue for systems in which f and g admit multiple steady states with various stability properties.

d. Stable oscillations and the plant population

Given that the underlying structure of a sessile herbivore-plant system is that of a dynamical system in the plane, it is reasonable to anticipate the possibility of sustained stable oscillations. That is, for particular f and g which lead to stable limit cycles in q and b one should perceive periodic oscillations in the herbivore load and plant quality of each plant. This phenomenon has been observed in empirical situations (see Haukioja 1981, Fischin and Baltensweiler 1979). The following result addresses the nature of the plant population in situations where stable oscillations occur.

Claim. Sustained periodic oscillations in a (sessile) herbivore-plant system must be accompanied by *both* narrowing (at some phases) *and* broadening (at other phases) in the distribution of plant quality and herbivore load, $p(q, b, t)$.

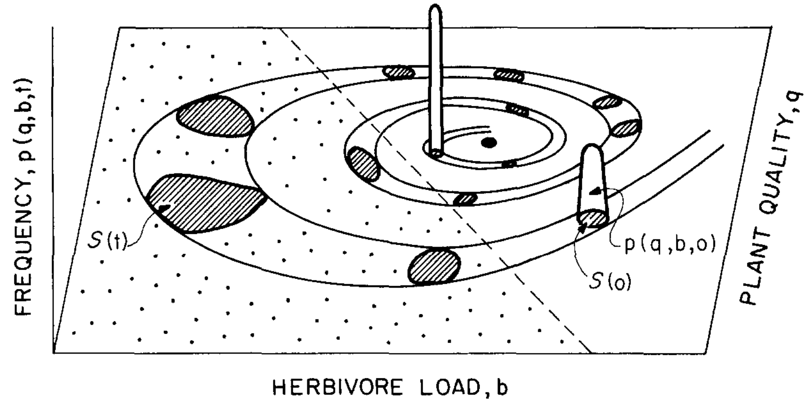


Fig. 3. In the sessile-herbivore case, the nature of the populations can be partly deduced by observing the qualitative features of the set S in the phase plane. When the set S enters a region (shown white) satisfying (26), it shrinks. This corresponds to a peaking or narrowing of the distribution $p(q, b, t)$ which means that there is a tendency towards uniformity of quality and herbivore load in the vegetation

Proof. Verification of the claim follows from Bendixson's negative criterion. (For the system (19) it may be paraphased as follows: in order for a region D in the qb phase plane to contain a closed trajectory it is necessary that the quantity $(\partial f/\partial q + \partial g/\partial b)$ vanish identically or change its sign in the region.) Thus, it is impossible for a region characterized by $(\partial f/\partial q + \partial g/\partial b) < 0$ to completely contain a limit cycle. The closed trajectory must dip outside this region, forcing the expansion of the set characterizing the plant population. On the other hand, assuming that *only* expansion takes place as the cycle is traversed leads to a contradiction since, by assumption, the limit cycle is stable and attracts neighboring trajectories.

Biocorollaries. (1) *In plant-herbivore systems in which sustained oscillations are present, herbivory cannot lead to a homogenizing effect on the vegetation.*

(2) *In the presence of sustained oscillations, the vegetation will alternate between a disperse (broad) quality distribution, and a focused (narrow) quality distribution during every cycle.*

Example 2: periodic oscillations in plant–herbivore systems

To demonstrate how the model for sessile herbivores would be applied, consider the following particular case, again chosen only for the purposes of illustration. Let the response functions f and g be given by

$$\begin{cases} \dfrac{dq}{dt} = f(q, b) = q(1-q)(\alpha(1-b)+q), & \text{(27a)} \\[2ex] \dfrac{db}{dt} = g(q, b) = \beta b(Kq - b). & \text{(27b)} \end{cases}$$

For the purposes of this example, the plant quality response, f was constructed with the following properties: $f = 0$ for $q = 0$ and for $q = 1$, so that plant quality initially in the range $0 < q < 1$ is forever confined to that interval. Further, there is a critical quality q^* such that $f(q^*) = 0$ and $\partial f/\partial q(q^*) > 0$. (Note that q^* depends on herbivore-load, $q^* = \alpha(b-1)$, and is in fact in the interval of interest provided $\alpha(b-1) < 1$, i.e. $1 < b < 1 + 1/\alpha$).

For a fixed b, if q^* is in the (0, 1) interval, the plant population is effectively divided into two groups. Depending on the intensity of herbivory, plants whose quality is lower that the threshold level (q^*) will deteriorate in quality whereas those above the threshold q^* will increase in quality (up to a maximum quality $q = 1$). For high herbivore loads the "breakeven" point, q^*, is large, meaning that *most* quality levels are not adequate to prevent deterioration.

One interpretation is that fitness or hardiness of a plant is correlated with the index which determines its attractiveness from the standpoint of the herbivore. This means that low q values also mean low tolerance to herbivory. Depending on the herbivore pressure, this situation would imply that weak plants grow yet weaker and loose their attractiveness for herbivores, whereas hardy plants are either unaffected (if close to $q = 1$) or else continue to increase in attractiveness. Note that for very large herbivore intensities, f is always negative (all plants succumb) whereas for very low herbivore pressure f is always positive (all plants flourish).

The function g was chosen as before, with the idea that the quality of the plant is a feature that at high levels, enhances herbivore growth rates. Thus the carrying capacity of the plant for its inhabitant pests is again assumed to be proportional to plant quality. Note the duality in the mutual effects of the herbivore on the plant and vice versa. On one hand, the herbivore load determines the threshold level of quality, q^*, that determines whether plant quality will then increase or decrease. On the other hand, plant quality determines the threshold level of herbivore density on plant beyond which overcrowding implies a net mortality.

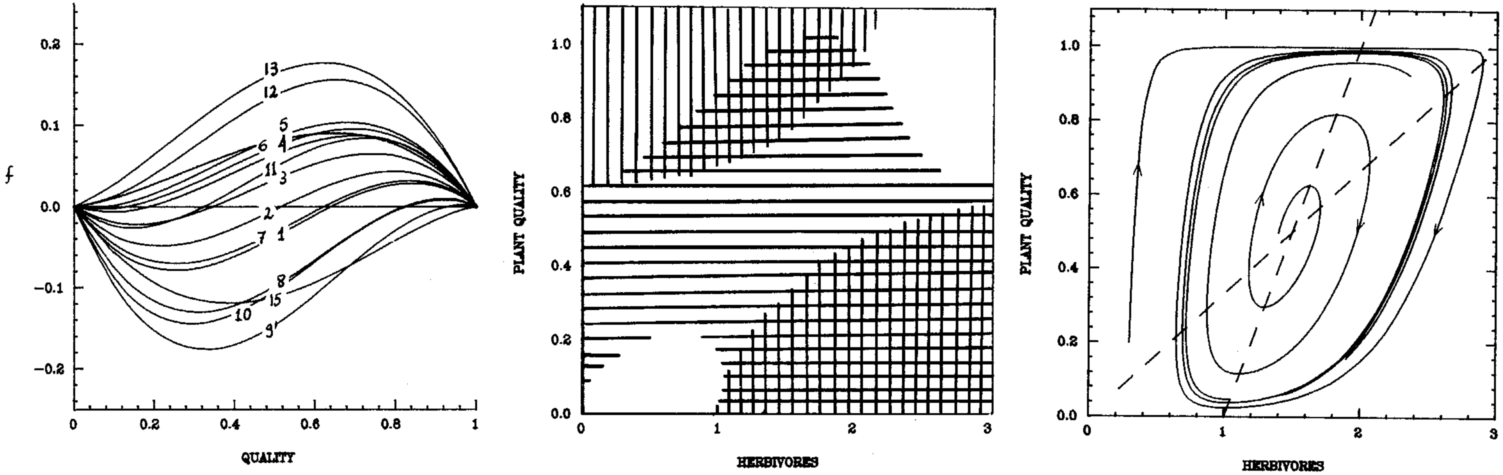
To avoid potential misunderstanding, it is again stressed that the interpretation given to the terms in Eqs. (27) are somewhat arbitrary, and are not to be viewed as a claim for a general theory, only as an illustrative example.

The above model will now be analyzed for predictions about the population of plants. Since f and g are both nonlinear functions, an attempt to extract meaningful equations for mean plant quality and total herbivore population using (20) is unsuccessful. (Failure stems from the fact that integration by parts results in higher moments of the distribution being introduced into the equations.) However, we study the dynamical system given by (27) with the idea that it describes individual plants represented by points (q, b) and thus a set consisting of many such points which represents the whole population.

It is readily verified that the system (27) admits four steady states, at $(0, 0)$, $(1, 0)$, $(1, K)$ and $(\gamma, K\gamma)$ for $\gamma = \alpha/(\alpha K - 1)$. The first two are saddle points. Stability of the latter two depends on γ and β. If $\gamma > 1$, then $(1, K)$ is a stable node and $(\gamma, K\gamma)$ is a saddle. If $\gamma < 1$, then $(1, K)$ is a saddle and $(\gamma, K\gamma)$ is a focus. In the latter case, stability of $(\gamma, K\gamma)$ hinges on the value of β, i.e., for large β this point is a stable focus which, as β decreases, gives rise to a Hopf bifurcation resulting in the birth of a stable limit cycle and an unstable focus at $(\gamma, K\gamma)$. Figure 4(b) illustrates the appearance of a stable limit cycle.

Turning attention to the whole plant population, we examine what happens to a set $S(t)$ whose points $(q(t)b(t))$ satisfy (27). The conditions 26(a) and 26(b) are shown in Fig. 4(c). In the intersection of regions where these inequalities are satisfied, plants which are of similar qualities and herbivore laods should become nearly identical. They then diverge and grow dissimilar as the set S leaves the above regions. A repetition of this process occurs each time the limit cycle (not explicitly shown here) is traversed.

Figure 5 gives one example of the actual evolution of an initial population of plants, marked by 1. Eleven points (along a straight line segment) represent the initial states of 11 hypothetical plants. It can be seen that the flow in the qb phase plane causes the line-segment to distort, bend and twist, so that these points are at times closer to each other, and at times further separated. The example also reinforces a remark made previously, namely that one may not presuppose any correlation between the level of quality and the herbivore density on a given plant. (While the initial distribution, 1, has a unique b for each q, this property breaks down later, e.g. in the 10th step.)



(a) (b) (c)

Fig. 4. (**a**) The function f given by Eq. (27a) is displayed as a function of q for several values of the herbivore load b. Numbers correspond to those labeling Fig. 5. Parameters used in the simulation are $\alpha = 1.0$, $K = 3.0$ and $\beta = 0.1$.

(**b**) Phase plane behavior for the dynamical system given by (27). For the parameter values $\alpha = 1.0$, $K = 3.0$ and $\beta = 0.1$, a stable limit cycle is obtained.

(**c**) *Shaded areas* represent regions in the (q, b) plane for which (26) is satisfied in the example given by (27). In the *crosshatched* regions, the plants would tend to become more uniform in quality and herbivore loads

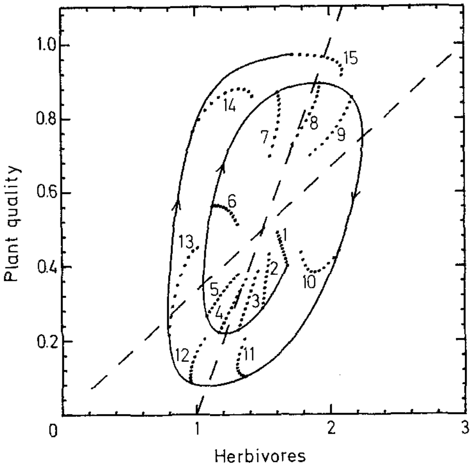


Fig. 5. An initial set of 11 points (marked 1) was chosen to represent 11 plants in a population. (S would consist of these points.) With time, the points shift in the (q, b) plane under the influence of the flow governed by Eqs. (27). The trajectory of one of the plants is explicitly shown

On a more abstract note, the problem of sessile herbivores appears to be equivalent to the problem of determining the asymptotic behavior of compact set(s) in the phase plane given an underlying dynamical system. Given general properties of such dynamical systems (e.g. the numbers and stability properties of steady states and closed orbits) one would like to make general predictions about how such sets evolve, and whether or not their volume shrinks or contracts.

7. Herbivores with partial mobility: foraging and the pattern of herbivore attack

When herbivores have a moderate degree of mobility, their distribution in the vegetation may be affected by a number of factors. Such factors may include attractiveness or apparancy of plants (i.e. "plant quality," q), the degree to which herbivores tend to aggregate or to avoid high densities of their kind, as well as predetermined effects such as interplant spacing and geometry.

Models which have dealt with spatial herbivore movements have been described by Kareiva (1982), and Cain (1984). Continuous models for population dispersal over space are reviewed by Okubo (1980). While formulating a model which includes spatial distributions is relatively straightforward, the gain in realism is somewhat offset by a loss in analytical insight. At this stage, the plant-herbivore system is already being described by a function of three independent variables $p(q, b, t)$; it therefore seems prudent to restrict attention to the spatially homogeneous situation before turning to a more detailed description which would include spatial variations.

Ignoring the spatial distribution of plants means that one is describing a system for which interplant spacing is small compared to herbivore movelength so that the host plant selection is not strictly correlated to the physical location of a plant. With this qualification in mind, a generalization of the theory in Sects. 1-6 is given and used to understand the steady state herbivore distributions in an unchanging vegetation.

After deriving a set of equations to describe the process of herbivore mingling a somewhat accessible special case will be examined with the following question in mind: Given particular assumptions about how herbivores select or reject a host plant, what is the resultant effect on the distribution of herbivores in the vegetation? To use current biological phrasing the purpose is to derive the *herbivore attack pattern* (Crawley 1983) and its relation to the vegetation quality distribution. It is also possible to treat a fuller problem which encompasses both the plant response *and* the herbivore reproduction/migration and growth, though here the equations are sufficiently complicated to warrant a numerical approach, not abstract analysis.

As before, the distribution of herbivores *and* quality in the vegetation will be described by the double frequency distribution $p(q, b, t)$ (as defined in Sect. 6) which relates the probability of finding a plant of quality q with a population of b herbivores on it at time t. In particular, the focus is on how *herbivore mobility* affects a steady state distribution p_{ss}. It will be assumed that while finding a plant is largely a matter of chance, the decision to leave a plant may depend on two factors: the current herbivore load, and the quality of the plant. Initially taking plant qualities fixed, two equations are derived to describe the *redistribution* of herbivores in the vegetation. The first is an equation for herbivores on plants written from the standpoint of the plant, i.e. in terms of $p(q, b, t)$. It is derived by considering the possible transitions which take place when a plant is found or rejected by one herbivore (see Fig. 6). Being a continuous approximation to a discrete process, the equation applies primarily to cases in which the average herbivore load of a plant is large (e.g. aphids). A second equation will keep a

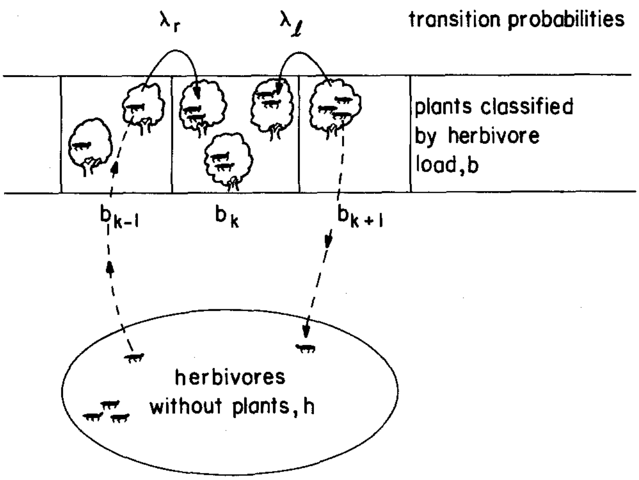


Fig. 6. In the case of partly mobile herbivores, plants of a given quality are classified according to their herbivore loads. Transition to the left, with probability λ_l, is identified with loss of a herbivore, whereas transition to the right, with probability λ_r signifies the addition of a herbivore

count of the herbivores which are not on plants, $h(t)$ with the assumption that a herbivore which rejects one host plant must temporarily join this population.

a. The distribution of herbivores in the vegetation

Figure 6 summarizes the idea behind the derivation of an appropriate set of equations. First, consider a classification of plants according to their herbivore loads. If $B_{\max}$ is the largest number of herbivores that could be present on a given plant, it is convenient to define

$$b^* = b/B_{\max},$$

$$\Delta b = 1/B_{\max}.$$

Then b^* is a dimensionless number (smaller than unity) and Δb is the dimensionless equivalent of a single herbivore. (Thus, the distribution $p(q, b^*, t)$ will be nonzero only for $0 \leq b^* \leq 1$.) The loss (or gain) of 1 herbivore will result in *a shift of the state of a plant* from (b^*, q) to $(b^* - \Delta b, q)$ [or to $(b^* + \Delta b, q)$, respectively]. Now consider a timescale T over which interactions between herbivores and their hosts occur and let τ^* be the fraction of that time for which an average of one herbivore leaves or finds a plant. The likelihood of leaving a plant may depend on its quality, q as well as on the degree of crowding on the plant, b^*. The likelihood of finding a plant may depend on plant quality (e.g. in the case of aromatic or physically more apparent plants) and on the pressure of searching herbivores (those not currently on plants, h). Define

$\lambda_l = \lambda_l(b^*, q) =$ probability that a plant of quality q infested with b^* herbivores loses one herbivore during the dimensionless time τ,

$\lambda_r = \lambda_r(h, q) =$ probability that a plant of quality q gains one herbivore during τ^*.

Note that the above transition probabilities are defined from the standpoint of the plants, not the herbivores (i.e. they represent the likelihood that a plant *changes its state* from (b^*, q) to $(b^* - \Delta b, q)$ or to $(b^* + \Delta b, q)$ during the time τ^*).

By keeping track of the transitions into and out of a given herbivore load class ($b_k = k\Delta b$ for fixed q) one arrives at the following discrete equation (in which *'s have been dropped for convenience of notation):

$$p(b_k, q, t+\tau) - p(b_k, q, t) = \lambda_r\{p(b_{k-1}, q, t) - p(b_k, q, t)\} \\ + \{\lambda_l(b_{k+1}, q)p(b_{k+1}, q, t) - \lambda_l(b_k, q)p(b_k, q, t)\}. \tag{28}$$

A standard diffusion approximation (Karlin and Taylor 1981) then leads to the continuous version

$$\frac{\partial p}{\partial t} = -\frac{\partial}{\partial b}\{pu\} + \frac{\partial^2}{\partial b^2}\{p\mathscr{D}\}, \tag{29a}$$

for

$$u=(\lambda_r-\lambda_l)\frac{\Delta b}{\tau}, \tag{29b}$$

$$\mathscr{D}=(\lambda_r+\lambda_l)\frac{\Delta^2 b}{2\tau}, \tag{29c}$$

or an equivalent equation,

$$\frac{\partial p}{\partial t}=-\frac{\partial}{\partial b}\{pw\}+\frac{\partial}{\partial b}\mathscr{D}\frac{\partial p}{\partial b} \tag{30}$$

where

$$w=\left(u-\frac{\partial \mathscr{D}}{\partial b}\right). \tag{30a}$$

Several comments are called for: first, note that u, w, and $\mathscr{D}$ may be functions of the variables b, q and h (as will presently be demonstrated). Also, it is of interest to point out that the equation resembles a diffusion-convection equation (not in physical space but in the abstract state space of herbivore loads). In particular, this means that tendency to form sharp peaks in the $p(q, b, t)$ distribution will be tempered by the smoothing effect of the "random motion". Technical discussions of other biased random walk equations and their continuous approximations are also given in Patlak (1953) and Okubo (1980).

While Eq. (30) depicts *only* the process of redistribution of herbivores in the vegetation, it is easy to include herbivore growth, mortality or plant quality changes as before: one would obtain, by direct superposition of flows in the qb-plane

$$\frac{\partial p}{\partial t}(b, q, t)=-\nabla\cdot J=-\frac{\partial J_b}{\partial b}-\frac{\partial J_q}{\partial q}, \tag{31}$$

where

$$J_b=\left\{p\left(u-\frac{\partial \mathscr{D}}{\partial b}+g\right)-\mathscr{D}\frac{\partial p}{\partial b}\right\}, \tag{32a}$$

$$J_q=\{pf\}, \tag{32b}$$

with f and g having their previous meanings, as in (19a, b).

b. Herbivores searching for plants

To now complete the model for mobile herbivores let us write an equation to keep track of herbivores which are not currently on plants. Here one could include terms for higher mortality from starvation or aggravated risk of falling prey due to greater exposure. Typically such an equation would be

$$\frac{dh}{dt}=\mathscr{L}(t)-\mu h+e, \tag{33a}$$

where

$$\mathscr{L}(t)=\iint(\lambda_l-\lambda_r)p(b, q, t)\,db\,dq. \tag{33b}$$

The first term, $\mathscr{L}$ represents the sum of net herbivore loss from all plants, the second term, μh is net mortality while searching and the last term, e includes net migration into the patch. The equation is written in dimensionless variables as before. In a steady state situation it can be assumed that $\mathscr{L}(t)=\mathscr{L}$ is some constant. Then $h_{ss}=(\mathscr{L}+e)/\mu$, i.e. the size of the steady state herbivore population off plants depends on the relative magnitude of the mortality while searching and the sum of the arrival rates, $\mathscr{L}$ and e. In a limiting case taken in the next section it will be assumed that the migration pressure e is much larger than the term $\mathscr{L}$ so that the steady state $h=e/\mu$ is virtually independent of the transition probabilities.

A "complete" model would be composed of Eqs. (33), (31), (32), and (19). In addition, one needs some empirical information governing the transition probabilities λ_l and λ_r which would then make u and $\mathscr{D}$ known functions of q, b and h. A steady state analysis of this model is used for describing the pattern of herbivore attack in the next section.

8a. *Steady state herbivore attack patterns*

In this section it is shown that assumptions about the way that herbivores select and reject a host plant lead to predictions about the steady state distribution of herbivore loads in the vegetation $(p(\cdot, b, \infty))$. In the biological literature (e.g. Crawley 1983) this distribution is called the *herbivore attack pattern* and is often assigned a purely phenomenological functional description, without derivation from underlying mechanisms.

Below I examine three possible situations.

Case I: The probability that an herbivore leaves its plant is constant, regardless of the current herbivore load on the plant.

Case II: Crowded conditions increase the likelihood that an herbivore will reject the plant.

Case III: A large herbivore load tends to lower the likelihood that an herbivore will leave; i.e. the herbivores are gregarious or cooperative.

To simplify analysis I consider only the steady distributions when $dh/dt=0$, $dp/dt=0$. Setting the derivative equal to zero in Eq. (30) leads to

$$0=-\frac{\partial}{\partial b}\left(wp-\mathscr{D}\frac{\partial p}{\partial b}\right). \tag{34}$$

After integrating once with respect to b one arrives at

$$wp-\mathscr{D}\frac{\partial p}{\partial b}=C_1. \tag{35}$$

The general solution of (35) is

$$p_{ss}(b)=e^{-\int s\,db}\left[\int \frac{C_1}{\mathscr{D}}\,e^{\int s\,db}+C_2\right], \tag{36a}$$

for

$$s=\frac{1}{\mathscr{D}}\left(\frac{\partial \mathscr{D}}{\partial b}-u\right). \tag{36b}$$

The quantity C_1 is a flux which would be zero if there are no new plants introduced at $b=0$ and no loss of plants at $b=1$. Consider the case when the problem consists of Eqs. (29) with zero-flux boundary conditions at $b=0$ and $b=B_{\max}$. Taking $C_1=0$, using Eqs. (29b) and (29c) and simplifying the expression leads to

$$p_{ss}(b)=\frac{C_2}{\mathscr{D}}\exp\left(-\frac{b}{\varepsilon}+\frac{2I}{\varepsilon}\right), \tag{37a}$$

where $\varepsilon=\Delta b/2$, C_2 is a constant of integration, and

$$I=\int\frac{\lambda_r}{\lambda_r+\lambda_l}\,db. \tag{37b}$$

While the proof of stability of the above steady state may be mathematically nontrivial, physical arguments would tend to support the notion that this steady state is a stable one which is established asymptotically as a result of the underlying physical processes. Now we introduce assumptions about what governs the departure and arrival of an herbivore to or from a plant.

Let us examine the definitions of λ_l and λ_r in more detail. Recall that these are defined as probabilities of transition of the state of a plant. Thus, given a plant whose herbivore load is b, if K is the probability per herbivore that the plant will be rejected, then $\lambda_l=Kb$. Depending on whether herbivores are aggregative or avoid overcrowding and whether they make choices based on plant quality, K could itself depend on b and on q. On the other hand, λ_r the likelihood that a plant is found is generally independent of its current herbivore load but is proportional to the size of the subpopulation h which is searching for plants, $\lambda_r=k_2h$. In some cases, particularly where olfactory or visual stimuli guide herbivore searching, k_2 could depend on plant quality. For example, plants which are bushier or give off volatile substances could be more apparent and thus more easily detected by herbivorous insects.

By the arguments presented above, in the idealized situation it can be assumed that

$$\lambda_l=K(q,b)b, \tag{39a}$$

$$\lambda_r=k_2h. \tag{38b}$$

I now examine the three cases previously outlined:

Case I: $K(q,b)=k_1$;
(Each herbivore has a *constant* probability of rejecting a plant.)

Case II: $K(q,b)=k_3b$;
The probability of leaving per herbivore increases with the herbivore load.

Case III: $K(q,b)=k_4/(k_5+b)$;
The probability of leaving per herbivore declines as the herbivore load increases.

By performing an integration of Eq. (37b) in each of these cases and substituting the result into Eq. (37a) one obtains a functional description of the steady state herbivore attack pattern. The quantities $\mathscr{D}$, w, and u can also be given as functions of b. A summary of the results is given in Table 1 in terms of dimensionless parameters. In Cases I and II a single parameter θ, the ratio of (departure rate of last herbivore inhabitant) to (arrival rate) governs the solution, whereas in Case III an additional parameter is involved (ϕ = number of herbivores which result in half-maximal departure rate from a plant).

Figure 7 is an example of the three types of steady state attack patterns $p_{ss}(x;\, \theta)$ for several values of θ. The graph generally has a maximum, representing the *most probable herbivore load* which occurs when $u = \partial\mathscr{D}/\partial b$ (see Eq. 30a). The location of the peak shifts to higher herbivore loads when θ decreases, since there is then a greater propensity to *gain* herbivores than to loose a remaining few. In Case III a peak is present only when $\theta > 1$, i.e. when the maximal departure rate K_4 is bigger than the constant arrival rate, k_2h, and the solution is extremely sensitive to slight changes in $(\theta - 1)$ (see γ in Case III of Table 1).

The following are general trends displayed in these graphs. (Some of these can be anticipated, to some degree, from the assumptions.) For comparable θ values, most plants have lower herbivore loads in Case II than in Case I since herbivores tend to leave crowded plants more frequently. In Case III the attack

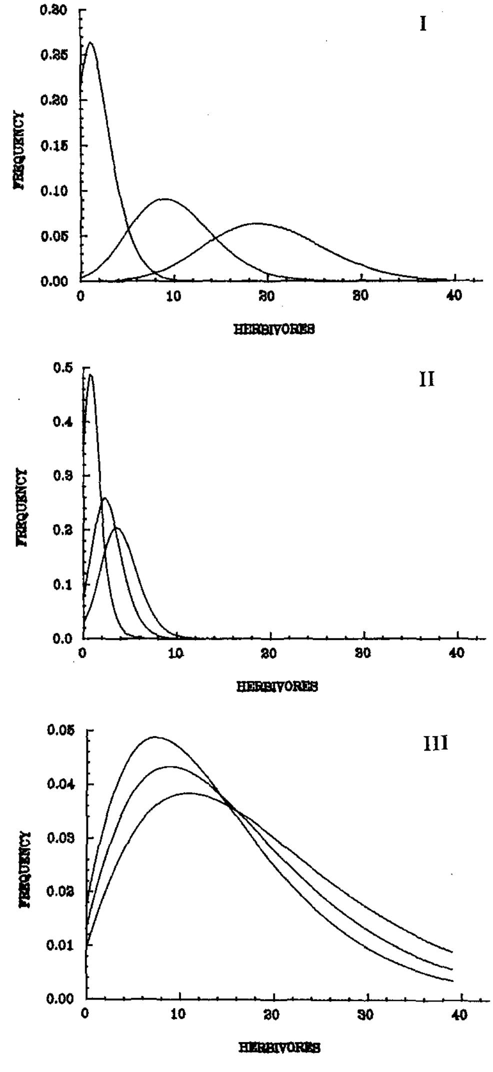


Fig. 7. Examples of typical herbivore attack patterns for mobile herbivores which reject a host plant at a rate dependent on herbivore load. For plant quality fixed, the steady state frequency distribution $p_{ss}(b, .)$ of herbivore loads is shown in three distinct cases: (I) constant rejection rate; (II) higher rejection when host plant has many herbivores on it; and (III) lower rejection rate if other herbivores are present (cooperativity). The distributions are shown for three different values of θ (see Table 1) in each case. From *right* to *left*: (I) 0.05, 0.1, 0.5; (II) 0.05, 0.1, 0.5; (III) 1.25, 1.3, 1.35. In case III, $\phi = 3.0$ (see Table 1)

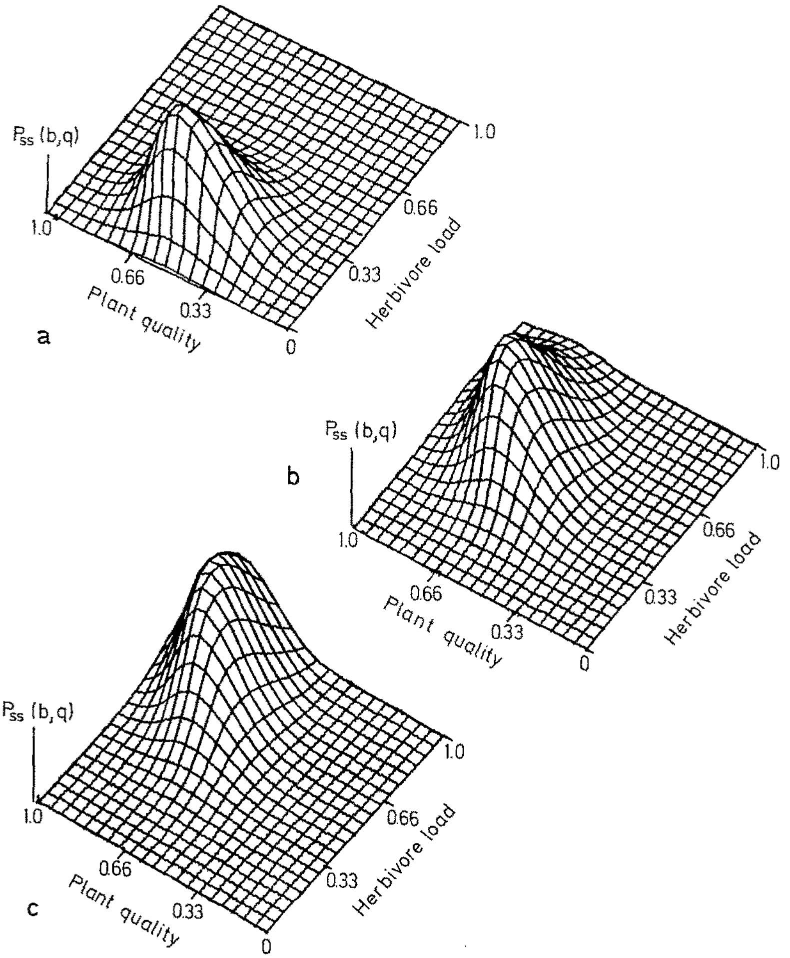


Fig. 8a–c. Steady state herbivore attack patterns $p_{ss}(b, q)$ for vegetation of heterogeneous quality. A herbivore leaves its plant at a rate k_1 and finds a plant at rate k_2. (**a**) k_1, k_2 constant; (**b**) $k_1 = 2/(q+0.5)$, k_2 constant; (**c**) k_1 constant, $k_2 = 2(0.5+q)$. When plant quality is a cue for the herbivore's rejection or detection of a host, the attack pattern reveals a tendency to aggregate on higher quality plants

pattern is more disperse even when its maximum is at low values. This stems from the fact that high herbivore densities are self-sustaining in that they result in lowered likelihood of departure.

b. Plant quality dependent herbivore attack pattern

More generally, an herbivore's selection of a suitable host plant may depend on plant quality. If the vegetation has some quality distribution, assumed fixed momentarily, then high densities of herbivores and high quality vegetation may well be correlated. I give two examples of this relationship below.

One can proceed in several ways. A typical plausible assumption is that herbivores tend to exhibit a lower rejection rate when host quality is high. This

Table 1. The steady state herbivore attack pattern, p_{ss} (as well as the terms for apparent diffusion and convection in state space) is given above in dimensionless form. C is a normalization constant and $x = b/\varepsilon$

Case #	$K(q, b)$	$u, \mathscr{D}, w$	Dimensionless parameters	$P_{ss}(x)$	Comments
I	k_1	$u = 1 - \theta x$ $\mathscr{D} = 1 + \theta x$ $w = 1 - \theta x - \theta$	$\theta = k_1/k_2 h$ $r = 2/\theta$	$\dfrac{Ce^{-x}}{\mathscr{D}(x)}(1+\theta x)^r$	maximum at $x = 1 + 1/\theta$
II	$k_3 b$	$u = k - \theta x^2$ $\mathscr{D} = 1 + \theta x^2$ $w = 1 - \theta^2 - 2\theta x$	$\theta = k_3 \varepsilon^2/k_2 h$	$\dfrac{C}{\mathscr{D}(x)} \exp\left\{-x + \dfrac{2}{\sqrt{\theta}} \arctan(\sqrt{\theta} x)\right\}$	max p_{ss} at $x = -1 + \sqrt{1 + 1/\theta}$
III	$\dfrac{k_4}{(k_5 + b)}$	$u = 1 - \dfrac{\theta x}{\phi + x}$ $\mathscr{D} = 1 + \dfrac{\theta x}{\phi + x}$	$\theta = k_4/k_2 h$ $\phi = k_3/\varepsilon$ $r = \dfrac{2\phi\theta}{(1+\theta)^2}$ $\gamma = \dfrac{(\theta - 1)}{(\theta + 1)}$	$\dfrac{C}{\mathscr{D}(x)} e^{-\gamma x}(\phi + x(\theta + 1))^r$	p_{ss} has max if $\theta > 1$

would mean that $K(q, b)$ is a decreasing function of q. Because Eq. (30) only explicitly involves b as an independent variable, all the previous calculations carry through and one finds that in the solutions given in Table 1, the parameter θ is a function of quality. A second assumption could be that plants of higher quality are more apparent, or more easily found that those of low quality. This means that the parameter k_2 of Eq. (38b) increases with q. Again the result is the same, so that one could in principle select some representative dependence $\theta(q)$ and plot p_{ss} as a function of two variables, b and q.

In Fig. 8(a) through (c) I have assumed that plant quality is normally distributed with mean $q = 0.5$ and standard deviation $\sigma = 0.2$, that herbivores are of type I, and that $k_1 = 2/(q + 0.5)$. (This is equivalent to $\theta = (0.5/q + 0.5)$ for $e = 0.025$; see Table 1.) The distribution is significantly shifted towards higher quality plants. In a second example, assuming that the arrival rate $k_2 = 2(0.5 + q)$ has an analogous effect.

In this section I have dealt only with the "easy cases" in which the herbivores are not changing the quality of their plants and are at some steady state population density. (The functions $f(q, b)$ and $g(q, b)$ which depict changes in plant quality and in herbivore population are zero in Eqs. (29) and (30).) However, it is not difficult to visualize what happens when these responses are incorporated, as in Eqs. (31)-(32). Typically, the distributions shown in Fig. 8 may undergo some distortion, their peaks may shift gradually, and there may be a narrowing or a widening, depending on the nature of the functions f and g. The exact dynamical process would depend, among other things on the relative timescales of herbivore mingling and changes in plant quality and herbivore numbers.

9. Discussion

Some previous theoretical work on plant-herbivore systems will be briefly described in this section and compared with the model presented in this paper.

Earlier plant-herbivore models (Caughley and Lawton 1981; Crawley 1983) were phrased in terms of total vegetation biomass and total herbivore population, assumed to vary continuously. This would lead to a system of coupled ordinary differential equations to describe changes in densities or biomass. Most of these models do not address the changes in vegetation quality to which recent empirical work has drawn attention (see Rhoades 1982).

The catch-phrase "plant quality" has appeared in several previous models, although the emphasis is often quite different. For example, Moran and Hamilton (1979) discuss the effectiveness of low nutritive quality as a defense for plants against insect attackers by showing that low plant quality can, under particular assumptions, minimize the damage to a plant. (Damage is represented by a variable, D, which stands for the total consumption of plant material by herbivores.) In their model, larval growth rate is proportional to plant quality, a fixed parameter which is not changed or affected by herbivory. In this sense, the duality of plant-herbivore interactions is not fully explored in their model.

In a classic model for the spruce budworm, the health or condition of the forest plays a role analogous to that of plant quality. Ludwig et al. (1978), give a set of three ordinary differential equations for B, the budworm population, S the average three size, and E the "condition" of the forest. The growth rate of budmoth is coupled to S and E; the condition of the forest in turn depends on the average herbivore load per unit tree size (B/S) as well as on E. The average size of the trees, S, increases at a rate which depends on the average tree condition E. Data for outbreaks of budworm in previous decades is used to estimate values of twelve parameters, three of which determine the qualitative properties of the system. The authors note that while qualitative behavior similar to a typical outbreak cycle is obtained, there are differences which probably stem from lumping 75 tree age classes into a single variable, S. On this point, the difference between our models emerges. The present author would probably have treated E as an independent variable and looked at a partial differential equation version for $S(E, t)$.

While the above models all treat herbivory as a continuous process, it is more realistic to use difference equations for cases where herbivores or plants have nonoverlapping generalizations. Fischlin and Baltensweiler (1979) have given a model for the larch budmoth in which plant quality is identified as raw fiber content of larch needles. Experimental data is used to fit functional forms for the effect of raw fiber content on larval mortality and fecundity and also for the annual recruitment of raw fiber based on previous defoliation. (Note that these are analogous to f and g in Eqs. (1).) In emphasizing the dual effects of herbivores and plants on one another, the Fischlin-Baltensweiler model bears a parallel to the present one. It differs considerably in detail, being a discrete model which does not deal with the way that herbivory or plant attributes are distributed in the vegetation.

A model due to Wang et al. (1977) for the Boll weevil on cotton uses several equations mathematically related to Eq. (3). However, similarity in appearance is misleading, since emphasis is placed on another phenomenon, that of herbivore-dependent vegetation mortality. The authors follow age distributions of herbivores and of vegetation components with von-Foerster McKendrick equations coupled via the mortality terms.

To contrast the new model with the above, the following points might be emphasized: (a) properties of the vegetation other than quantity or biomass are accommodated in its relationship to herbivores. (This follows from the definition of the variable q for plant quality.) (b) On the level of the individual, the herbivores and the vegetation exert mutual effects. (These are depicted by the two response functions, f and g, which are in principle empirically measurable; see Sect. 10.) (c) Information at the level of the individual is used in following collective changes in the populations as a whole. (This is done by the conservation equation for the distribution $p(q, t)$ or $p(q, b, t)$; see Eqs. (3) and (20).)

To paraphrase the results, conclusions depend somewhat on the degree of intimacy shared by the two species. If herbivores are committed to a single plant (sessile), the mathematical problem consists of a single partial differential equation for both populations. This case can be partially analyzed by phase plane arguments, but the object of interest is a set S which evolves with time, not a single trajectory. (The set contains information about the structure of the plant-herbivore system, i.e., about the distribution of the herbivores and the plant quality in the vegetation.)

For philandering (i.e. highly mobile) herbivores it is necessary to use separate equations for the plants and their visitors. At present, this leads to a coupled

ODE-PDE system which under a very restrictive assumption (linearity of $f(q, \cdot)$) can be replaced by a pair of ODE's.

The model at present can be applied to real specific cases provided that (a) the plant-herbivore interactions are continuous or graded over the timescale of observation; (b) the spatial distribution of the vegetation is not a major determinant of the pattern of herbivory in the vegetation (i.e. spatially homogeneous vegetation or small inter-plant spacing relative to movelength for mobile herbivores, or else sessile herbivores); (c) the response functions f and g can be conjectured or experimentally ascertained (see Sect. 10).

The model can readily be accommodated to incorporate plant mortality by including σ (a negative term) in Eqs. (3) and (20). Presumably, mortality depends on the combination of herbivory damage and the current physiological state of the plant, i.e. $\sigma = \sigma(q, h)$ is correlated to the quality variable and herbivore load of the vegetation. The effect of this term will be to selectively decrease the proportion of the vegetation at a particular range of q (for which the magnitude of σ is large). This sort of mortality term parallels the presence of a "sink" in the description of physical fluids in that it tends to make particles "vanish" locally rather than causing a shift in their state. For example, a typical term for mortality, e.g. $\sigma(q, h) = ph/(k+q)$ might represent the fact that loss rate is proportional to the rate of encounter between plants and herbivores (ph), but that plants of higher quality are more resistant ($1/(k+q)$). Other examples (of age-dependent mortality) can be found in Wang et al. (1977).

The next major step in extending the model to more realistic situations will be to deal with spatially heterogeneous vegetation and herbivore movement. Some work in this direction has been done by Kareiva (1982) who considered situations in which the spatial distribution of the vegetation and its quality were empirically predetermined.

The model can be readily generalized to cases where two or more uncorrelated attributes of the plant play equally important roles in mediating its relationship with its herbivores. It is similarly possible to consider larger systems with multiple plant or herbivore species. While the underlying ideas would be the same, the complexity of these multi-dimensional problems would clearly increase rapidly with their size.

Another divergent approach would be to modify the model to deal with discrete, nonoverlapping generations (e.g. annual plants, annual herbivorous insects). Some of the mathematical methods suitable for this approach appear in the work of May et al. (1974). The perhaps unfortunate aspect is that relatively simple difference equation models frequently produce exotic dynamic behavior which, at present, defies mathematical analysis (e.g. approach to chaos in the Henon equations). This might tend to detract from ease with which such systems can be understood from a theoretical point of view.

10. Possible empirical approaches

Two key ideas emerge from the general theory. First, one perceives the importance of determining the responses of the vegetation and the herbivores *simultaneously*. A second, somewhat more subtle point, is that changes in the heterogeneity of the vegetation may reveal important features of the plant-herbivore system. The vegetation may be better described by a frequency distribution of some attribute than by its biomass or average quality.

Below, I have attempted to give a rough indication of empirical approaches that might be adopted in connection with the theory. Since the details will clearly differ vastly from system to system, this is meant to be a sketchy outline, at best.

a. Setting up a quality gradient. A collection of initially "identical" plants are subdivided into herbivory groups (A, $B, \dots, N$). Each group is subjected to a controlled intensity of herbivory (e.g. $A =$ low, $\dots$, $N =$ high). This will presumably *induce* the physiological changes that result in plant qualities $q_A, q_B, \dots, q_N$ respectively in each of these groups.

b. Chemical or physical quality assays. By methods detailed in the literature, one might assay for nitrogen, water content, presence of secondary chemicals, physical toughness or fiber content. One or several of these may be readily correlated to the intensity of herbivory and could thus serve as a "chemical marker" for the state of the plant.

c. Herbivore "taste" tests. Where feasible, portions of the vegetation could be presented to herbivores in N-way preference tests. If herbivores are selective, such tests could provide a second biological marker for the variable called "plant quality".

d. Plant quality bioassay. For each of plant groups (A, $B, \dots, N$) which result from (a) above, remove "old" herbivores and apply "fresh" ones (reared on identical plants) at two levels, low and high. On the resulting groups of plants ($A_{\text{low}}, B_{\text{low}}, \dots, N_{\text{low}}$) and ($A_{\text{high}}, B_{\text{high}}, \dots, N_{\text{high}}$) determine the herbivore mortalities, fecundities, and growth rates. If these responses differ over the plant types A-N, they can in future be used as a bioassay for the plant quality variable. If no difference is perceived, the plant-quality theory must be rejected for the particular system studied.

e. Identifying the plant's response. Cross an initial quality gradient (established in a) with a second application of herbivores at levels ($a, b, .. m$) for a time duration Δt (Δt should be small on the natural timescale of interactions, but large enough to detect changes in plant quality). The above procedure leads to an array of plant groups, p_{Kj}, where $K = A, \dots, N$ and $j = a, m$. Assay for plant quality before and after herbivory. The plant response function, f would then be given by

$$f(q_K, h_j) \approx (q_{\text{initial}} - q_{\text{final}})/\Delta t.$$

(Note that it may be necessary to replace herbivores which fall off or die to keep the herbivore intensity h_j constant within a given vegetation group.)

f. Identifying the herbivore's response. This would be determined in a cross similar to the above, but with focus on changes such as growth rates, mortalities, etc., in the herbivores. The time interval Δt would be chosen with the idea of detecting small changes in the herbivore density or biomass. The herbivore's response to a given vegetation type would then be:

$$g(q_K, h_j) \approx (h_{\text{initial}} - h_{\text{final}})/\Delta t.$$

(Note that it may be necessary to contrive to fix the quality of the vegetation by continually presenting the herbivore with "fresh" vegetation whose quality q_K has been predetermined.)

While certain of these suggestions undoubtedly present problems in many systems, it is to be hoped that some particularly convenient experimental systems might allow for the above or similar manipulations which could then be used to test the theory.

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Appendix A1

B. Dimensional analysis, Eqs. (13)

In Eqs. (13) set

$$Q = Q^* \tilde{Q}, \qquad t = t^* \tau, \qquad H = H^* \tilde{H}.$$

Then,

$$\frac{dQ^*}{dt^*} = \hat{K}_1(\tau/\tilde{Q}) - \hat{K}_2(\tau \tilde{H}) Q^* H^* (\tilde{H} H^* - H_0)$$

$$\frac{dH^*}{dt^*} = K_3(\tau) H^* (1 - K_4 \tilde{H} H^* / \tilde{Q} Q^*). \tag{A1}$$

Choose

$$\tau = \tilde{Q}/\hat{K}_1, \qquad \tilde{H} = H_0, \qquad \tilde{Q} = K_4 \tilde{H}.$$

After dropping stars, the equations are given by (14) with

$$K = \hat{K}_2 \tilde{H}^2 = \hat{K}_2 K_4 H_0^3 / \hat{K}_1 = \frac{K_2 K_4}{K_1} h_0^3$$

$$\alpha = K_3 \tau = K_3 K_4 H_0 / \hat{K}_1 = \frac{K_3 K_4 h_0}{K_1}. \tag{A2}$$

Appendix A2

C. Phase plane analysis, Eqs. (14)

Letting $W = 1 - KQH(H-1)$, $V = \alpha H(1 - H/Q)$, coefficients of the Jacobian matrix for Eqs. (14)

consist of

$$\begin{aligned} a_{11} &= \left.\frac{\partial W}{\partial Q}\right|_{ss} = -KH(H-1)\Big|_{ss} \\ a_{11} &= \left.\frac{\partial W}{\partial I}\right|_{ss} = -KQ(2H-1)\Big|_{ss} \\ a_{21} &= \left.\frac{\partial V}{\partial Q}\right|_{ss} = \alpha H^2/Q^2\Big|_{ss} = \alpha \\ a_{22} &= \left.\frac{\partial V}{\partial I}\right|_{ss} = \alpha(1-2H/Q)\Big|_{ss} = -\alpha. \end{aligned} \tag{A3}$$

(Where the above quantities are evaluated at the steady state.) Then

$$a_{11}+a_{22} = -KH(H-1)-\alpha|_{ss} \quad \text{is negative } (H_{ss}>1)$$

$$a_{11}a_{22}-a_{12}a_{21} = \gamma = K\alpha H(3H-2)|_{ss} \quad \text{is positive so that } (Q_{ss}, H_{ss})$$

is stable. Oscillations would occur if

$$\{(KH(H-1)+\alpha)^2-4K\alpha H(3H-2)\}|_{ss}<0. \tag{A4}$$

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