

# Spatial Coupling of Plant and Herbivore Dynamics: The Contribution of Herbivore Dispersal to Transient and Persistent "Waves" of Damage

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Spatial variations in the abundance of insect herbivores and in herbivore damage are both striking and commonplace. The standard explanations for heterogeneity in herbivore attack emphasize spatial variations in plant genotype, soils, or physical environment. Here I examine an alternative hypothesis—that heterogeneity arises in plant-herbivore systems, even in homogeneous environments, as a result of the direct coupling of herbivore movement to herbivore density and plant quality. Using a mathematical model for plant quality and herbivore growth and dispersal, I demonstrate how spatial instabilities about homogeneous steady state values result in both transient and stationary waves of damage to the plant. Key herbivore movement behaviors include the tendency for herbivores to aggregate over a range of spatial scales for increased feeding efficiency and the tendency for herbivores to move up gradients in plant quality (herbivory-taxis). My approach translates the biased "random walk" behavior of individual herbivores into a continuum partial differential equation model. Analytical and numerical methods are used to demonstrate the nature of the spatio-temporal variations in plant quality and herbivore density. © 1994 Academic Press, Inc.

## 1. INTRODUCTION

Most experimental investigations of variation in herbivore density concentrate on external forces such as plant genotype and environmental stress as the ultimate cause of such variation. The assumption is that there must be an underlying template of variation among plants or in the physical environment before one would expect herbivores to end up in highly uneven spatial distributions. Alternatively, abstract mathematical theory has indicated that spatial patterning is possible in many model ecological systems in homogeneous environments. (For an overview of this theory see Okubo (1980).) I examine whether an initially homogeneous distribution of

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plants, all identical in character and quality, and all in a spatially uniform environment could generate spatial patterning in herbivore densities.

First suggested by Turing (1952) to explain morphogenic patterns, and subsequently applied to ecological problems, the classical mathematical approach to modelling biological patterns is based upon the idea of a "diffusion-driven instability." In an ecological context, when there are differential dispersal rates for two species (such as predator and prey), one can determine sufficient conditions upon birth and death dynamics of the two species to ensure growth of spatial patterns via linear instabilities away from a spatially homogeneous steady state solution (Okubo, 1980). Typically, such instabilities occur only for certain modes of a given wavelength. This wavelength characteristically dominates the final patterns that evolve (Murray, 1989). Dispersal is assumed to be random and thus is modelled by a diffusion process. However, a *necessary* condition for the generation of spatial patterns is that *both species disperse*.

Although many herbivores are mobile, plants remain stationary over the length of time that it takes for patterns to evolve. For example, aphids introduced to plants commonly form high density clumps after one or two days. Thus, classical pattern formation theory cannot simply be re-applied in this new context of plant-herbivore interactions since only one species (the herbivore) is dispersing.

My alternative approach to modelling the growth of plant-herbivore spatial patterns depends upon a detailed description of the herbivore movement. As well as moving randomly, herbivores are assumed to move in response both to variations in the quality of the plants they are consuming and to variations in the population density of conspecifics. I show that, under this assumption, and with appropriate dynamics for the plant and herbivore growth, both persistent (stationary) and transient (dynamic) patterns can evolve spontaneously from a homogeneous environment.

In this paper I employ a mathematical partial differential equation approach to studying spatial dynamics in plant herbivore systems. I introduce the concept of plant quality as a relevant plant feature for the interacting herbivores (Edelstein-Keshet, 1986). Key elements of plant and herbivore dynamics are then considered. These include the regulation of herbivore abundance (through density-dependent and plant quality-dependent herbivore birth and death), the response of plants to herbivory (through plant damage, and possibly inducible defenses and compensatory growth), and the movement of herbivores (Section 2). Equations for herbivore movement are derived from first principles using a random walk with a bias towards locally increasing plant quality (Section 3.3) and with short- and long-range biases towards increased herbivore density (Section 3.4). Coupling the plant and herbivore dynamics (Section 3.2) with the herbivore movement terms, I derive a system of partial differential

equations (Sections 3.1 and 3.5), the analysis of which (Sections 3.6–5) reveals that spatially heterogeneous patterns can arise naturally, even in completely homogeneous environments. Numerical solutions of the full partial differential equation model are used to illustrate the rich variety of spatial patterns possible in plausible plant–herbivore systems (Section 5.1). I thus demonstrate that patchiness in plant quality and herbivore density need not actually be linked to external environmental variations; spatial coupling of the plant and herbivore dynamics is by itself sufficient to produce patchiness.

## 2. PLANT AND HERBIVORE DYNAMICS

### 2.1. *Plant Quality, Inducible Defenses, and Compensatory Growth*

Early attempts to model plant–herbivore systems adopted a Lotka–Volterra approach that essentially represented slightly modified predator–prey theory (Rosenzweig and MacArthur, 1963; Hassel and May, 1973; May, 1973; Noy-Meir, 1975; Caughley and Laughton, 1976; Crawley, 1983). Recently, the inadequacies of this approach have been made clear. In particular, it is evident that any robust theory of herbivory should include factors that affect herbivore sustenance but are independent of plant biomass (see Edelman-Keshet (1986) for a discussion).

Many plants exhibit mechanical, physiological, and chemical changes in response to herbivory. In some cases these changes may actually take the form of an active induced defense. Whatever the cause, as a result of feeding on plants, herbivores often alter plants such that their subsequent survivorship, growth rate, and fecundity are reduced (Rhoades, 1982; Karban and Carey, 1984; Maddox and Root, 1987; Edelman-Keshet and Rausher, 1989). Alternatively, some herbivores actually seem to improve their subsequent prospects by changes wrought by their feeding. For instance, groups of sucking insects (such as aphids) on a leaf may actually act as physiological “sinks” that divert nutrients from distant parts of the plant (Thrower and Thrower, 1966; Way and Banks, 1967; Way and Cammel, 1970; Wu and Thrower, 1973; Dixon, 1975; Veen, 1985; Hawkins *et al.*, 1985, 1986a, 1986b, 1987). This physiological “sink” effect is an example of a *compensatory* mechanism whereby local plant quality can actually *increase* in response to herbivory (see also Ghent, 1960; Crawley, 1983; McNaughton, 1983, 1992; Edelman-Keshet, 1986). In summary, herbivores may affect plant quality in opposing manners, either depressing it (in the case of damage, or possibly inducible defenses), or enhancing it (in the case of aphids and compensatory plant responses) (Fig. 1).

Because plant responses to herbivory determine herbivore demography but typically are independent of plant biomass, *plant quality*, rather than

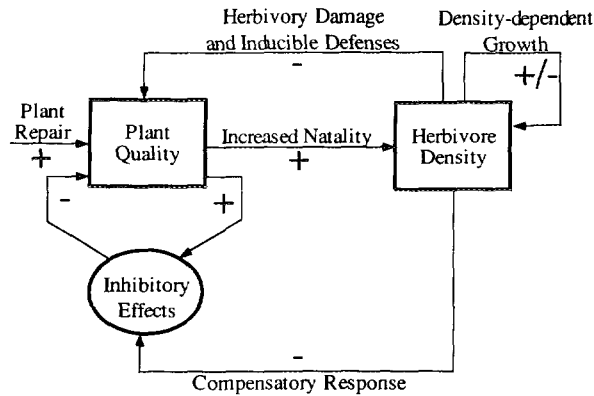


FIG. 1. Dynamical relationships between plant quality and herbivore density. The + and - signs adjacent to the arrows indicate positive and negative feedbacks.

*plant abundance*, is the relevant measure for models of plant-herbivore dynamics. I adopt the plant quality definition proposed by Edelman-Keshet (1986) (see also Edelman-Keshet and Rausher, 1989): plant quality,  $v(x, t)$ , is an index of how the foodplant might be "rated" by a herbivore on a purely arbitrary scale. Included in any consideration is a composite of properties such as internal nitrogen, concentrations of noxious defence substances, succulence of foliage, toughness of stems, amount of resin, and size or function of the plant. Plant quality is specific to each plant-herbivore relationship; a different herbivore species may have a different physiological effect upon the plant and may have different nutritional needs (Hawkins *et al.*, 1987; Mattson and Addy, 1975; Myers and Post, 1981; Kraft and Denno, 1982; Lincoln *et al.*, 1982; Rhoades, 1982; Crawley, 1983; Denno and McLure, 1983; Strong *et al.*, 1984). By using plant quality as a state variable in my model, I treat the vegetation as a *physiologically structured* population.

## 2.2. Regulation of Herbivore Abundance and Distribution

Herbivore abundance and distribution are regulated by birth and death processes and by herbivore movement. These, in turn, depend upon factors such as the plant quality and the herbivore density. Other factors such as predation (Kareiva and Odell, 1987), parasitism (Price, 1980), and age structure (Hastings, 1992) may also be significant but add an extra level of complexity to any model. In the interest of focusing upon the plant-herbivore interaction I do not include these other factors in the models I examine.

Exact details of plant-herbivore interactions often depend upon the particular herbivore and plant species. To develop models connected to the

real world, I use the example of aphid populations, while noting that many of the behaviors and processes that apply to aphids can also be found in other plant-herbivore interactions.

Very high potential reproductive rates, based upon parthenogenesis, viviparity, and telescoping of generations, permit aphid populations to exploit plants over short seasons when the conditions are right for growth. However, experimental evidence indicates that reproductive rates are controlled by two factors: (1) population density and (2) plant quality (Dixon, 1985). Jostling movements from developing larvae seem to slow reproduction even when nutrition appears to be adequate (density-dependent natality), and, at the same time, feeding on the opposing side of the leaf from *highly* crowded aggregates (lower plant quality) reduces the reproductive rate of solitary aphids (Way and Cammel, 1970).

Aphids are believed to feed more effectively in groups because they may divert food to the colonized leaf from other parts of the plant (Way and Cammel, 1970; Hawkins *et al.*, 1986a). Thus, although highly crowded aggregates of aphids typically *reduce* plant quality, low levels of aggregation may actually *enhance* it. For example, mean adult sizes of single aphids have been found to be significantly higher when a moderately crowded aggregate of aphids was experimentally placed on the other side of the leaf from the single aphids (Way and Cammel, 1970). In addition experiments indicate that aphids often aggregate actively, using tactile and possibly chemical mechanism (Ibbotson and Kennedy, 1951; Way and Cammel, 1980; Turchin and Kaveira, 1989). By acting as local "sinks" for nutrients, aggregations can compete successfully against the natural "sinks," namely, growing parts of the plants (Dixon, 1975) and storage organs (Hawkins *et al.*, 1987). Aphid aggregation also has the advantage of reducing the per capita predation pressure in dense patches (Cappuccino, 1987; Turchin and Kareiva, 1989).

Experimental evidence indicates that aphids are sensitive to variations in the quality of their food plants. Vail (1990) showed that aphids respond to experimentally manipulated variations in quality of *Brassica* plants by moving to the higher quality areas.

In the remainder of this paper I consider a plant-herbivore model that captures the following essential features: (1) density-dependent and plant quality-dependent herbivore growth dynamics (see Fig. 1), (2) inducible defenses, herbivory damage, inhibitory effects, compensatory mechanisms, and plant repair for controlling the plant quality (see Fig. 1), and (3) herbivore movement up gradients in plant quality and dependent on conspecific density.

### 3. MODEL FORMULATION

#### 3.1. Overview of the Mathematical Model

To build a model that encompasses the key elements of a wide variety of plant-herbivore interactions, I need to include terms that describe the coupling between herbivores and plant quality in the absence of movement, and then I need to describe the movement process, itself. For the movement process I will include three types of motion (with the relative importance of each controlled by parameters that can be adjusted depending on the biological system in question): random motion, motion towards regions of high plant quality and away from low plant quality (herbivore-taxis), and motion towards conspecifics (aggregation). The local population density of herbivores is represented by the variable  $u(x, t)$ ,  $x$  denoting space and  $t$  denoting time, and the local plant quality is represented by the variable  $v(x, t)$ . The resulting system of equations takes the form

$$\frac{\partial u}{\partial t} = f(u, v) + \text{Movement Term} \quad (1)$$

$$\frac{\partial v}{\partial t} = g(u, v), \quad (2)$$

where  $f(u, v)$  describes herbivore birth and death processes and  $g(u, v)$  describes plant quality dynamics.

#### 3.2. Modelling the Dynamics

Prior to formulating a *specific* model for the dynamics  $f(u, v)$  and  $g(u, v)$  in Eq. (1) and (2), respectively, it is instructive to determine general rules which we expect the dynamics to obey. The rules, based upon the discussion in Section 2, are also shown diagrammatically in Fig. 1.

1. Reproduction and survival of herbivores will correlate positively with plant quality. An increase in plant quality ( $v$ ) thus causes a corresponding increase in the population growth rate for herbivores ( $f(u, v)$ ).

2. Herbivores will regulate themselves through density-dependent death. At high herbivore densities ( $u$ ), a further increase in  $u$  results in a decrease in  $f(u, v)$ .

3. Herbivores will damage plants (and possibly induce defences in plants), thereby reducing the plant quality. An increase in  $u$  results in a corresponding decrease in the plant quality growth rate ( $g(u, v)$ ).

4. Plant quality will self-regulate through inhibitory effects. In the absence of herbivory, the quality of plants will self-regulate and eventually

plateau at some high value. In other words, when  $u=0$  and  $v$  is high, a further increase in  $v$  results in a decrease in  $g(u, v)$ . When herbivores are present  $u > 0$ , the situation may become more complex (Fig. 1); inhibitory effects may be reduced by a competing compensatory response of the plants to the herbivores.

5. I assume that, for large  $u$ , herbivory damage and inducible defenses (item 3) eventually dominate compensatory mechanisms (second half of item 4). Otherwise the possibility of a biologically unrealistic positive feedback loop exists, where herbivore density and plant quality increase unboundedly (see Fig. 1).

These rules are sufficient to determine the general shapes for null clines of  $f(u, v)$  and  $g(u, v)$ ; the shape of the null cline  $f(u, v)=0$  is determined by items (1) and (2) and the shape of the null cline  $g(u, v)=0$  is determined by items (3) through (5). These rules indicate that the function  $f(u, v)$  is positive for small  $u$  and large  $v$  and is negative for large  $u$  and small  $v$ , and that the function  $g(u, v)$  is positive for small  $u$  and small  $v$  and negative for large  $u$  and large  $v$ . Null clines that assume a shape similar to that shown in Fig. 3.

The following is a *specific* model for the growth dynamics ( $u \geq 0$  and  $v > 0$ ) which satisfies the above rules (see also Fig. 1),

$$\begin{array}{rcccl}
 f = & \text{Natality} & + & \text{Natality} & - & \text{Density-dependent} \\
 & \text{independent of} & & \text{dependent on} & & \text{death and} \\
 & \text{plant quality} & & \text{plant quality} & & \text{natality reduction} \\
 & \rho u & + & \gamma uv & - & \delta u^2
 \end{array} \quad (3)$$

$$\begin{array}{rcccl}
 g = & \text{Improvement} & - & \text{Inhibitory} & - & \text{Herbivory} \\
 & \text{due to plant} & & \text{effects (which} & & \text{damage and} \\
 & \text{maintenance} & & \text{may be reduced} & & \text{inducible} \\
 & \text{and repair} & & \text{by herbivory)} & & \text{defenses} \\
 & \mu & - & sv/(1 + mu) & - & \phi u
 \end{array} \quad (4)$$

where  $\rho, \gamma, \delta, \mu, s, h,$  and  $\phi$  are non-negative.

### 3.3. Modelling "Herbivory-Taxis"

It is natural to expect that mobile herbivores will orient and move towards stimuli that signal increased plant quality. These behaviors of orientation and taxis have, indeed, been widely studied and documented for herbivores such as phytophagous insects (Ahmad, 1983). Field observations indicate, however, that not all herbivore movements are directed up

gradients of plant quality; typically there is a balance between random and directed motion (Morris and Kareiva, 1991).

In this section I mathematically derive movement terms that describe the random and directed components of herbivore movement in relation to plant quality. Temporarily ignoring birth, death, and aggregative movement, I assume that individuals within a population can be described by motion with two components: (1) a completely random component and (2) a tendency to move up gradients of plant quality ( $v(x, t)$ ). My approach is to describe the behavior of an individual organism with a random walk which exhibits bias toward regions of superior plant quality. This gives rise to a partial differential equation describing spatial fluxes in the population density of herbivores ( $u(x, t)$ ).

Equations for modelling such random and directed movement components are well established in the mathematical biology literature. Such equations can be used to describe chemotaxis (Keller and Segel, 1971) and prey-taxis (Kareiva and Odell, 1987) as well as herbivory-taxis (Gueron and Liron, 1989; Morris and Kareiva, 1991). My brief derivation for the movement terms thus has a secondary purpose—to introduce the framework for a biased random walk which can be used in deriving more complex aggregative movement terms in Section 3.4.

Let the variable  $p(x, t)$  be defined as the probability of a randomly chosen individual being found on the interval  $(x - \lambda/2, x + \lambda/2)$  at the time  $t$ , where  $\lambda$  is a small space interval. Thus, for a population size  $N$ ,

$$p(x, t) = \frac{1}{N} \int_{x - \lambda/2}^{x + \lambda/2} u(\xi, t) d\xi \rightarrow \frac{\lambda u(x, t)}{N} \quad \text{as } \lambda \rightarrow 0. \quad (5)$$

I discretize time ( $0 < t < \infty$ ) into short intervals of size  $\tau$ , and space ( $-\infty < x < \infty$ ) into small intervals of length  $\lambda$  and model the movement of individuals as follows: during the time interval  $\tau$  an individual may move  $\lambda$  to the right with probability  $R(x, t)$ ,  $\lambda$  to the left with probability  $L(x, t)$ , and may remain stationary with the probability  $N(x, t) = 1 - R(x, t) - L(x, t)$ .

I assume that herbivores can sense plant quality on the space intervals directly to the right and left and that the probability of the herbivore moving in a given direction depends linearly upon the ensuing increment in plant quality. Thus the probability of moving to the right is given by

$$\begin{aligned} R(x, t) &= \text{random component of motion} \\ &+ \alpha \times \text{increase in quality to the right} \\ &= \frac{1}{2}r(x, t) + \alpha[v(x + \lambda, t) - v(x, t)] \end{aligned}$$



and the probability of moving to the left is given by

$$\begin{aligned}
 L(x, t) &= \text{random component of motion} \\
 &+ \alpha \times \text{increase in quality to the left} \\
 &= \frac{1}{2}r(x, t) + \alpha[v(x - \lambda, t) - v(x, t)],
 \end{aligned}$$

where  $0 < r(x, t) < 1$  is the random component of the movement and  $\alpha$  relates the probability of moving to the increase in plant quality. Provided  $\partial v/\partial x$  is bounded,  $R$  and  $L$  converge to  $r/2$  as  $\lambda \rightarrow 0$ . Thus  $R, L > 0$  and  $R + L < 1$  for sufficiently small  $\lambda$ . If there are no births and deaths then  $p(x, t)$  satisfies

$$\begin{aligned}
 p(x, t) &= N(x, t - \tau) p(x, t - \tau) \\
 &+ R(x - \lambda, t - \tau) p(x - \lambda, t - \tau) \\
 &+ L(x + \lambda, t - \tau) p(x + \lambda, t - \tau).
 \end{aligned}$$

Expanding all the above terms about the point  $(x, t)$  yields

$$\begin{aligned}
 \tau \frac{\partial p}{\partial t}(x, t) &= -\lambda \frac{\partial}{\partial x} \{ (R(x, t) - L(x, t)) p(x, t) \} \\
 &+ \frac{\lambda^2}{2} \frac{\partial^2}{\partial x^2} \{ (R(x, t) + L(x, t)) p(x, t) \} + \mathcal{O}(\lambda^3), \quad (6)
 \end{aligned}$$

where the bias,  $R(x, t) - L(x, t)$ , and the motility,  $R(x, t) + L(x, t)$ , are given by

$$R(x, t) - L(x, t) = \alpha[v(x + \lambda, t) - v(x - \lambda, t)] \quad (7)$$

$$= 2\alpha\lambda \frac{\partial v}{\partial x}(x, t) + \mathcal{O}(\lambda^3) \quad (8)$$

and

$$\begin{aligned}
 R(x, t) + L(x, t) &= r(x, t) + \alpha[v(x + \lambda, t) - 2v(x, t) + v(x - \lambda, t)] \\
 &= r(x, t) + \alpha\lambda^2 \frac{\partial^2 v}{\partial x^2}(x, t) + \mathcal{O}(\lambda^4). \quad (9)
 \end{aligned}$$

Substituting (9) and (8) into (6), taking the appropriate limit as  $\lambda$  and  $\tau$  converge to zero ( $\lambda, \tau \rightarrow 0$  so that  $\lambda^2/(2\tau) \rightarrow D$ ) (see, for example, Okubo (1980)), and using (5) gives

$$\frac{\partial u}{\partial t} = D \frac{\partial}{\partial x} \left[ r \frac{\partial u}{\partial x} - 4\alpha u \frac{\partial v}{\partial x} \right]. \quad (10)$$

The first term inside the square brackets in this equation describes the flux due to random movement of individuals and the second terms describes the flux due to herbivory-taxis, or movement up gradients in plant quality.

### 3.4. *Modelling Aggregative Movement*

Because many herbivores respond positively to one another, either because they can enhance one another's feeding efficiency or because the presence of a fellow feeder might signal a good food source, it is worth developing a way of describing such aggregation. Previous mathematical descriptions of aggregation have simply emphasized the effects of neighbors in the immediate vicinity (see, for example, Turchin (1989)). For greater flexibility, I envisage aggregation that represents a weighted response to conspecifics as a function of their distance from the individual herbivore. I will show that this weighted response model is really a natural extension of the previous "local aggregation" models; it can be simplified to such a local aggregation model by choosing the appropriate weighted response function.

Temporarily ignoring birth, death, and movement by herbivory-taxis, I assume that individuals within a population can be described by motion with two components: (1) a completely random component and (2) a tendency to move toward groups of conspecifics. To date, models for this latter component have assumed movement up *local* gradients of conspecific density. This kind of movement up local gradients is restrictive; individuals can only respond to the conditions precisely at their own location. Conspecifics sensed a short distance away are ignored completely. Such local aggregation models typically result in ill-posed equations from a mathematical perspective (see the discussion in Section 3.4.2).

I derive an alternative method for modelling movement toward groups of conspecifics by assuming that the aggregative movement of an individual depends not only upon the density of conspecifics at the individual's precise location, but also upon the density of conspecifics short distances away. The relevant quantity for determining aggregative movement is thus a spatial average of the conspecific density, weighted according to the distance between the location of the individual and the location of conspecifics. Using this approach, individuals are assumed to move up gradients in the *non-local*, spatially averaged, density of conspecifics. Typically, conspecifics that are far away have little influence upon an individual's movement behavior, while conspecifics that are nearby may influence movement behavior strongly; the weighting function is thus assumed to be monotonically non-increasing with distance and to be equal to zero for large distances. With such a non-local aggregation model the problem of ill-posedness, encountered by local aggregation models, is typically avoided.

Similar non-local aggregation models have been formulated independently by researchers employing a generalized flux in continuum conservation laws (see Section 3.4.2 for a discussion). However, my approach for deriving the model equation is new in the context of non-local aggregation—that of a biased random walk. Interestingly, the resulting equations are subtly different from typical generalized flux models. This is discussed in more detail in Section 3.4.2.

In Sections 3.4.1 and 3.4.2 I formulate the non-local aggregation model and analyse its potential to generate spatial patterns, or “clumps” of individuals. I show that, in the absence of any other interactions, aggregating populations form regular patterns, with a wavelength which is determined approximately by three factors: (1) the average density of individuals, (2) the magnitude of aggregation tendencies relative to random movement tendencies, and (3) the variance of the spatial weighting function. I define each of these components precisely and derive the relationship describing the wavelength of resulting aggregation patterns.

### 3.4.1. Derivation of the Aggregation Model

I envisage herbivores sensing their conspecifics through a weighted spatial average of the surrounding population density, given by

$$A(x, t) = \int_{-\infty}^{\infty} w(y) u(x + y, t) dy, \quad (11)$$

where  $w(y)$  is the weighting function, or kernel. This general formulation assumes only that the information is linearly related to the density of conspecifics. (An even more general formulation might replace  $u$  by some function  $f(u)$  in (11).) For the purpose of our model, we normalize the weighting kernel so that

$$\int_{-\infty}^{\infty} w(y) dy = 1.$$

Some typical shapes for the kernel  $w(y)$  are shown in Fig. 2. A normally distributed kernel, shown by the dashed line, uses

$$w(y) = \sqrt{\frac{b}{\pi}} \exp(-bx^2). \quad (12)$$

Two simple forms for  $w(y)$ , shown by the solid and dotted lines, assume that individuals cannot sense conspecifics beyond a certain radius. The kernel denoted by a solid line assumes that individuals have perfect

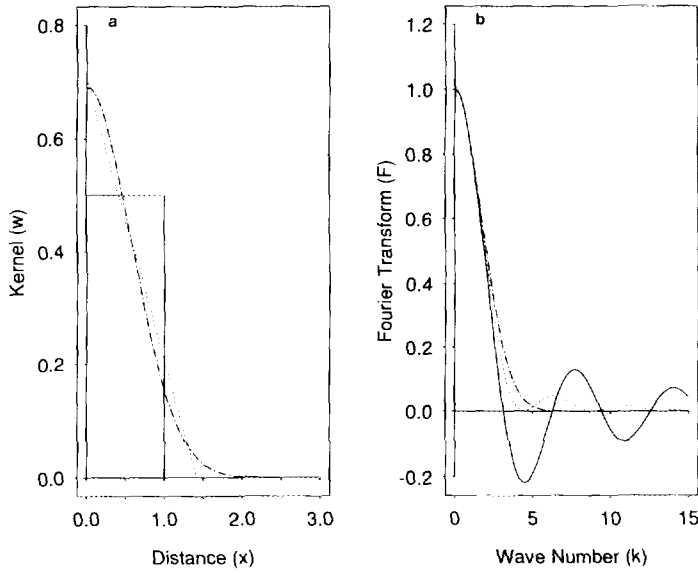


FIG. 2. The aggregation kernel,  $w(y)$ . The kernel is assumed to be symmetric about the point  $y=0$ , and thus only the right half of the kernel is shown. A normally distributed kernel, denoted by the dashed line in (a), is described by (12) with  $b$  chosen as 1.5. Two alternate descriptions for the kernel, denoted by the solid and dotted lines in (a), are described by Eqs. (13) ( $l_1 = 1$ ) and (14) ( $l_2 = \sqrt{2}$ ). All three of these kernels have identical second moments  $w_2 = \frac{1}{6}$  (see (21)–(23)). Fourier transforms of the kernels are shown in (b).

perception within the radius,  $l_1$ , and treat all conspecifics within this radius as having equal weight,

$$w(y) = \begin{cases} 0 & \text{if } |y| > l_1 \\ \frac{1}{2l_1} & \text{if } |y| \leq l_1. \end{cases} \quad (13)$$

If perception decreases linearly with distance or the weight accorded to a conspecific decreases linearly with distance then the following kernel, denoted by a dotted line, may be appropriate:

$$w(y) = \begin{cases} 0 & \text{if } |y| > l_2 \\ \frac{l_2 - |y|}{l_2^2} & \text{if } |y| \leq l_2. \end{cases} \quad (14)$$

Employing (11) it is observed that the net increase in  $A(x, t)$  incurred by moving from the point  $x_0$  to the point  $x_1$  at time  $t$  is

$$A(x_1, t) - A(x_0, t) = \int_{-\infty}^{\infty} w(y)[u(x_1 + y, t) - u(x_0 + y, t)] dy \quad (15)$$

This change in the weighted spatial average of the population density is used to determine the direction of aggregative movement. When (15) is positive then individuals at point  $x_0$  will tend to move to  $x_1$  and when (15) is negative then the converse is true. Using this simple idea, I model the movement of an individual herbivore by a random walk with bias towards regions of increasing  $A(x, t)$ .

As in the previous section I define the variable  $p(x, t)$  to be the probability of a randomly chosen individual being found on the interval  $(x - \lambda/2, x + \lambda/2)$  at the time  $t$ , where  $\lambda$  is a small space interval (see also Eq. (5)). I discretize time  $(0 < t < \infty)$  into short intervals of size  $\tau$  and space  $(-\infty < x < \infty)$  into small intervals of length  $\lambda$  and model the movement of individuals as follows: during the time interval  $\tau$  an individual may move  $\lambda$  to the right with probability  $R(x, t)$ ,  $\lambda$  to the left with probability  $L(x, t)$ .

The probability  $R(x, t)$  is given by

$$\begin{aligned}
 R(x, t) &= \text{random component of motion} \\
 &+ m \times \text{net increase in } A(x, t) \text{ incurred by moving to the right} \\
 &= \frac{1}{2}r(x, t) + mN \sum_{-\infty < j < \infty} w(j\lambda)[p(x + (j + 1)\lambda, t) - p(x + j\lambda, t)],
 \end{aligned}
 \tag{16}$$

where  $0 < r(x, t) < 1$  is the random component of the movement and  $m$  relates the probability of moving to the net increase in  $A(x, t)$  incurred by moving. This increase in  $A(x, t)$  is expressed as a discrete formulation of (15) which is exactly correct as  $\lambda \rightarrow 0$  and is approximately correct for small  $\lambda$  (see also Eq. (5)). The probability  $L(x, t)$  is given by

$$\begin{aligned}
 L(x, t) &= \text{random component of motion} \\
 &+ m \times \text{net increase in } A(x, t) \text{ incurred by moving to the left} \\
 &= \frac{1}{2}r(x, t) + mN \sum_{-\infty < j < \infty} w(j\lambda)[p(x + (j - 1)\lambda, t) - p(x + j\lambda, t)].
 \end{aligned}
 \tag{17}$$

Provided  $\partial p/\partial x$  is bounded, the infinite sum in Eq. (16) converges to zero as  $\lambda \rightarrow 0$ . Thus  $R, L > 0$  and  $R + L < 1$  provided  $\lambda$  is sufficiently small. It is shown in Appendix A that, using these probabilities for individual movements, and constraining  $\lambda$  and  $\tau$  to converge to zero in the usual manner ( $\lambda, \tau \rightarrow 0$  so that  $\lambda^2/(2\tau) \rightarrow D$ ), a partial differential equation can be derived that describes spatio-temporal changes in the population density,

$$\frac{\partial u}{\partial t} = D \frac{\partial}{\partial x} \left[ r \frac{\partial u}{\partial x} - 4mu \int_{-\infty}^{\infty} w(y) \frac{\partial u}{\partial x}(x + y, t) dy \right],
 \tag{18}$$

and, alternatively, the integro-partial differential equation (18) can be reduced to a partial differential equation with higher order derivatives,

$$\frac{\partial u}{\partial t} = D \frac{\partial}{\partial x} \left[ r \frac{\partial u}{\partial x} - 4mu \sum_{j>0} w_{j-1} \frac{\partial^j u}{\partial x^j} \right], \quad (19)$$

where

$$w_j = \frac{1}{j!} \int_{-\infty}^{\infty} y^j w(y) dy, \quad j = 0, 1, 2, \dots, \quad (20)$$

defines the moments of the kernel  $w(y)$ .

Implicit in the derivation of the diffusion limit ( $\lambda, \tau \rightarrow 0$  so that  $\lambda^2/(2\tau) \rightarrow D$ ) are assumptions of infinite speed of motion ( $\lambda/\tau \rightarrow \infty$ ) and frequent ( $\mathcal{O}(\tau^{-1})$ ) changes in movement direction. A consequence of this limit is that the net displacement of an individual over a given time interval is much less than the total distance that the individual travels in that time interval. Lin and Segel (1988) provide further discussion of this limiting process. In the context of herbivore movement, I am assuming that the herbivores are highly mobile and that they can frequently change movement direction.

The first term in Eq. (18) and (19) describes the flux due to random movement of individuals, and the second term describes the flux due to the aggregation of individuals. The alternate formulation (19) is often simpler to study mathematically than (18), especially when the infinite series in equation (19) is truncated after a number of terms. Such a truncation is valid (provided the solution to (18) is not singular) because the higher order moments,  $w_j$  converge to zero. Note that the normalization of  $w(y)$ , established earlier, ensures that  $w_0 = 1$ .

### 3.4.2. Discussion and Analysis of Aggregation Model

Equation (18) can be viewed as a very general model for random motion; by employing appropriate kernel functions,  $w(y)$ , it can be reduced to various classical random walk models. For example, if  $w(y) = 0$  the simple random motion equation (see, for example, Okubo (1980)) is obtained; if  $w(y) = -\delta(y)$  the biased random motion of Gurney and Nisbet (1975) is obtained; and if  $w(y) = \delta(y)$  the aggregative movement model of Turchin (1989) is obtained (see also Aronson, 1985). (Substitution of these kernel functions into the alternative formulation (19) produces identical results.) None of these classical models, however, incorporate the responses to nonlocal populations density, described in (18) and (19).

For kernels such as those described in (12)–(14) and shown in Fig. 2a, all odd moments are zero (due to symmetry of  $w(y)$ ) and higher moments get progressively smaller. When these kernels are employed, the moments

$$w_j = \begin{cases} \left(\frac{1}{2bj}\right)^{j/2} & \text{if } j \text{ is even} \\ 0 & \text{if } j \text{ is odd,} \end{cases} \quad (21)$$

$$w_j = \begin{cases} \frac{l_1^j}{(j+1)!} & \text{if } j \text{ is even} \\ 0 & \text{if } j \text{ is odd,} \end{cases} \quad (22)$$

and

$$w_j = \begin{cases} \frac{2l_2^j}{(j+2)!} & \text{if } j \text{ is even} \\ 0 & \text{if } j \text{ is odd} \end{cases} \quad (23)$$

are calculated for (12), (13), (14) respectively.

For the purpose of analytically and numerically studying aggregation dynamics, I truncate the infinite series in (19), retaining only the significant lower order terms. When terms containing the 4th moment ( $w_4$ ) and higher are excluded from (19), one obtains the following more tractable equation:

$$\frac{\partial u}{\partial t} = D \frac{\partial}{\partial x} \left[ (r - 4mw_0u) \frac{\partial u}{\partial x} - 4mw_2u \frac{\partial^3 u}{\partial x^3} \right]. \quad (24)$$

In Appendix B, I show that Eq. (24) can act as a useful caricature of the more complex equation (18). In this appendix each equation is linearized about a constant solution  $u = u_0$  and behaviors of these linear equations are compared for each of three different spatial averaging kernels (12)–(14). The caricature model (24) predicts that when  $r/(4mu_0) < 1$  aggregate patterns form with wavelength of approximately  $2\pi/k_m$ , where  $k_m$  satisfies

$$k_m^2 = \frac{1 - r/(4mu_0)}{\sigma^2}, \quad (25)$$

and  $\sigma^2$  is the variance of the kernel  $w(y)$  (see Appendix B). This prediction is shown to be approximately true for (18) with each of the three different kernels. Based upon these results, it seems highly likely that the result holds true for most biologically relevant spatial averaging kernels. In that case, given (1) an unknown spatial averaging kernel  $w(y)$  with known variance  $\sigma^2$ , (2) an average density  $u_0$ , and (3) an estimate of the magnitude of the random component of motion relative to the aggregative component  $r/m$ , one can predict approximately the wavelength of resulting aggregations as  $2\pi/k_m$ , where  $k_m$  satisfies (25). This caricature is particularly useful because it reduces the problem to one for which all parameters are experimentally

accessible. Alternatively, a given population with a fairly constant density will start to aggregate into clumps once the density exceeds  $r/(4m)$ . Results also indicate that in order for (24) to be an appropriate caricature for (18),  $r/(4mu_0)$  cannot approach zero (Appendix B).

The derivation of (24) from a random walk approach relates the partial differential model directly to individual behavioral rules. This is particularly useful in ecological applications, where overall population patterns are clearly a result of individual behaviors. An alternative approach to describing generalized dispersal in a population derives the relevant partial differential equation model directly from a continuum conservation law,

$$\frac{\partial u}{\partial t} = -\nabla \cdot \mathbf{J},$$

where  $\mathbf{J}$  represents the population flux (see, for example, Murray, 1989). While classical simple diffusion models employ Fick's law for  $\mathbf{J}$ , formulations for a generalized flux arise from a variety of other models. These include Landau-Ginzburg free energy models (Cohen and Murray, 1981; Ochoa, 1984), integral models which use weighted spatial averaging (Murray, 1989), and random walk models with integral formulations (Kawasaki, 1978; Appendix I of Turchin, 1989). As in Eq. (24), many of the generalized flux formulations have high order spatial derivatives (such as biharmonic terms), although in contrast to Eq. (24), their terms are typically non-degenerate as  $u \rightarrow 0$  (but see Alt, 1985). The degeneracy property evident in (24) and also in (18) and (19) causes the equations to reduce to simple diffusion models as  $u \rightarrow 0$ . It can be shown that the related non-degenerate version of (24) can have negative solutions; it appears that the degeneracy is crucial for ensuring that solutions remain non-negative and thus biologically realistic. This is a subject of ongoing research by the author.

Discussion of the aggregation model formulated here would be incomplete without a brief mention of how it fits in with previous theoretical models. A model for population redistribution according to attractive and repulsive interactions between organisms, termed a " $\mathcal{A}$ -model", was proposed by Taylor and Taylor (1977, 1978). Partly in response to criticisms regarding the logical structure and predictions of this  $\mathcal{A}$ -model (see, for example, Thorarinsson, 1986, and Turchin, 1989), Turchin (1989) developed an alternative "aggregative movement" model, based on a random walk approach with local bias towards increasing densities. The aggregative movement Eq. (24) extends Turchin's model to cover the case in which organisms respond to both local conspecifics and conspecifics that are at a distance. As discussed earlier in this section, Turchin's model can be recovered from Eq. (24) if  $w(y) = \delta(y)$ .



Turchin also chose to let the constant  $m$  in (24) depend on herbivore density so that  $m = m(u)$ . This is biologically reasonable; it is quite possible that organisms may attract each other at low densities but repel each other at higher densities and thus the sign of  $m$  would change with  $u$ . I do not incorporate this additional detail into the model because a rich variety of aggregative patterns are evident in the simplest case where  $m$  is constant.

The aggregative movement model presented in this paper overcomes two limitations of Turchin's (1989) model (which were pointed out in his paper):

1. Local aggregative movement models using initial boundary value problems with negative diffusivity are ill-posed (for discussion see Alt, 1985; Aronson, 1985); small perturbations in initial conditions cause major qualitative changes in the solution to Turchin's equation. This problem does not arise with Eq. (24). The higher order term acts to stabilize growth of aggregations and the final solution is not sensitive to initial conditions.

2. Turchin's model has no "characteristic" clump size for aggregations; the density profile at equilibrium may be broken into discontinuous clumps of any size, from very wide to very narrow. In contrast, my model yields a wave number defining the characteristic clump size, whose wave number can be calculated explicitly (see Eq. (25)).

A model that shares many features with the one presented here is given by Roughgarden (1974); a more mathematical presentation and some elaboration can be found in Gurney and Nisbet (1976). This model considers a resource/plant or resource/plant/consumer system in which the plant draws resource from a finite neighborhood and the consumer's feeding rate and movement are determined by appropriate average plant density over a locally averaged neighborhoods. The papers look at spatial pattern caused, not by true local instability of the spatially homogeneous steady state, but by the amplification of small local inhomogeneities in the carrying capacity.

### 3.5. *Incorporating Random Motion, "Herbivory-taxis," and Aggregative Motion into the Movement Flux Term*

I now incorporate the descriptions of random motion, herbivory-taxis (Section 3.3), and aggregative motion (Section 3.4) into the movement term for Eq. (1):

Movement Term

Random Motion + “Herbivory-taxis” + Aggregative Motion

$$\begin{aligned}
 &= D \frac{\partial^2}{\partial x^2} [ru] - 4D \frac{\partial}{\partial x} \left( \alpha u \frac{\partial v}{\partial x} \right) - 4D \frac{\partial}{\partial x} \left( mw_0 u \frac{\partial u}{\partial x} + mw_2 u \frac{\partial^3 u}{\partial x^3} \right) \\
 &= D \frac{\partial}{\partial x} \left[ (r - 4mw_0 u) \frac{\partial u}{\partial x} - 4mw_2 u \frac{\partial^3 u}{\partial x^3} - 4\alpha u \frac{\partial v}{\partial x} \right]. \tag{26}
 \end{aligned}$$

The mathematical model for plant-herbivore interactions is thus given by (1)-(4) and (26).

3.6. Nondimensional Model

I nondimensionalize the plant-herbivore model (1)-(4) and (26) to reduce the number of parameters and facilitate an assessment of the essential ecological processes. The new variables are

$$\begin{aligned}
 u^* &= 4mw_0 u, & v^* &= 4mw_0 v, & x^* &= \frac{x}{\sqrt{D/\rho}}, & t^* &= \rho t, & \alpha^* &= \frac{\alpha}{mw_0}, \\
 \gamma^* &= \frac{\gamma}{4mw_0 \rho}, & \delta^* &= \frac{\delta}{4mw_0 \rho}, & \mu^* &= \frac{4mw_0 \mu}{\rho}, & h^* &= \frac{h}{4mw_0}, \\
 s^* &= \frac{s}{\rho}, & \phi^* &= \frac{\phi}{\rho}, & \omega^* &= \frac{w_2 \rho}{w_0 D}, & f^* &= \frac{4mw_0 f}{\rho}, & g^* &= \frac{4mw_0 g}{\rho}.
 \end{aligned}$$

Dropping the asterisks for notational simplicity, (1)-(4) and (26) are rewritten as

$$\frac{\partial u}{\partial t} = f(u, v) + \frac{\partial}{\partial x} \left[ (r - u) \frac{\partial u}{\partial x} - \omega u \frac{\partial^3 u}{\partial x^3} - \alpha u \frac{\partial v}{\partial x} \right] \tag{27}$$

$$\frac{\partial v}{\partial t} = g(u, v), \tag{28}$$

where

$$f(u, v) = u + \gamma uv - \delta u^2$$

$$g(u, v) = \mu - \frac{sv}{1 + hu} - \phi u.$$

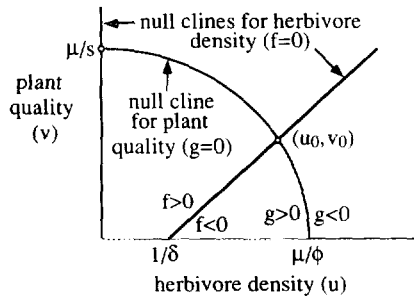


FIG. 3. Null clines for the nondimensionalized herbivore-plant equation (27)–(28).

3.7. Steady States

I now consider spatially homogeneous steady state solutions to (27)–(28). The null clines for (27), given by  $f = 0$ , are

$$u = 0 \quad \text{and} \quad v = \frac{1}{\gamma} (\delta u - 1)$$

and the null cline for (28), given by  $g = 0$ , is

$$v = \frac{1}{s} (\mu - \phi u)(1 + hu)$$

(Fig. 3). Note that there is a steady state solution  $(u_0, v_0)$  in the first quadrant provided that  $\phi < \phi_c$ , where

$$\phi_c = \delta\mu \tag{29}$$

(Fig. 3). The steady state value  $u_0$  is the larger root satisfying

$$\gamma h \phi u^2 + (s\delta + \gamma(\phi - h\mu))u - \gamma\mu - s = 0, \tag{30}$$

and  $v_0$  is given by  $(\delta u_0 - 1)/\gamma$ . A second steady state solution is given by  $(u, v) = (0, \mu/s)$  (Fig. 3).

3.8. Boundary and Initial Conditions

In a typical field environment a variety of different boundary conditions may apply. For example, herbivores may or may not enter and leave the system. In this paper I do not attempt rigorous derivation of boundary conditions from first principles for a physically isolated patch; such a derivation must by necessity take into account the higher order moments (see (20)) which are not included in the model (27)–(28). Instead, I consider a patch of length  $L$  which is located in the interior of a field and prescribe values surrounding the perimeter of the patch. I consider two possible cases:

1. Steady state values at the perimeter,

$$u(0, t) = u(L, t) = u_0, \quad v(0, t) = v(L, t) = v_0, \quad (31)$$

which have been supplemented by the additional constraint

$$\frac{\partial^2 u}{\partial x^2}(0, t) = \frac{\partial^2 u}{\partial x^2}(L, t) = 0 \quad (32)$$

(see Ochoa (1984) for similar boundary conditions).

2. Zero flux for the herbivore across the perimeter. This is achieved when the flux terms in (27) vanish at the perimeter and thus

$$\frac{\partial u}{\partial x}(0, t) = \frac{\partial u}{\partial x}(L, t) = \frac{\partial v}{\partial x}(0, t) = \frac{\partial v}{\partial x}(L, t) \quad (33)$$

and

$$\frac{\partial^3 u}{\partial x^3}(0, t) = \frac{\partial^3 u}{\partial x^3}(L, t) = 0. \quad (34)$$

Biologically these conditions indicate that there will be no net flux of herbivores across the perimeter if (i) the plant quality does not vary at the perimeter and (ii) there is local symmetry of herbivore density with respect to the perimeter.

Because I am specifically interested in the potential that (1)–(2) has for spontaneous formation of spatial patterns, I will assume that that state variables are initially very close to the unique spatially homogeneous positive steady state solution  $(u_0, v_0)$  which is given in Section 3.7. Thus a linear analysis about this steady state solution can be used to determine whether perturbations with a given wave number will grow.

#### 4. LINEAR STABILITY ANALYSIS

Linearization of (27)–(28) reveals the stability of this steady state to spatially uniform perturbations; the inequalities for the partial derivatives

$$\frac{\partial f}{\partial u}(u_0, v_0) < 0, \quad \frac{\partial f}{\partial v}(u_0, v_0) > 0, \quad \frac{\partial g}{\partial u}(u_0, v_0) < 0, \quad \frac{\partial g}{\partial v}(u_0, v_0) < 0$$

ensure that the eigenvalues for the linearized system have negative real parts. The other biologically relevant steady state solution, given by  $(u, v) = (0, \mu/s)$  (Fig. 3), corresponds to healthy plants with no herbivores.

This is a saddle point; it is *stable* to spatially uniform perturbations in  $v$ , but is *unstable* to spatially uniform perturbations in  $u$ . In other words, plant quality will regulate itself in the absence of herbivory but herbivore density will grow when herbivores are introduced at a uniform low level.

I consider the behavior of small spatially heterogeneous perturbations of the state variables away from  $(u_0, v_0)$ . Linearization of (27)–(28) gives rise to a homogeneous system of linear equations describing the behavior of these small disturbances. Non-trivial solutions to this system satisfy a dispersion relation between the temporal and spatial components of the perturbations and the parameters in the model. Thus I determine when and how the steady state can become linearly unstable.

The linearized form of (27)–(28) is

$$\begin{pmatrix} -\frac{\partial}{\partial t} + f_u + \frac{\partial^2}{\partial x^2}(r - u_0) - \omega u_0 \frac{\partial^4}{\partial x^4} & f_v - \alpha u_0 \frac{\partial^2}{\partial x^2} \\ g_u & -\frac{\partial}{\partial t} + g_v \end{pmatrix} \begin{pmatrix} u - u_0 \\ v - v_0 \end{pmatrix} = \mathbf{0}, \quad (35)$$

where

$$f_u = \frac{\partial f}{\partial u}(u_0, v_0)$$

and similarly for  $f_v$ ,  $g_u$ , and  $g_v$ . I use the principle of superposition and look for solutions of the form

$$u - u_0, \quad v - v_0 \propto \exp(\sigma t + ikx). \quad (36)$$

Substitution into (35) gives a dispersion relation between  $\sigma$  and  $k^2$  that must be satisfied for non-trivial solutions. This relation is

$$\sigma^2 + B(k^2)\sigma + C(k^2) = 0, \quad (37)$$

where

$$B(k^2) = \omega u_0 k^4 + [r - u_0] k^2 - f_u - g_v \quad (38)$$

$$C(k^2) = -g_v \omega u_0 k^4 - [g_v(r - u_0) k^2 + g_u \alpha u_0] k^2 + f_u g_v - g_u f_v. \quad (39)$$

For the uniform steady state to be stable to perturbations with a spatial component, it is required that the roots of (37) have a negative real part for all positive  $k^2$ . If there is a root with a positive real part for some  $k^2$ , then the linear theory predicts that small random perturbations away from the steady state will grow exponentially with a spatial wavelength of  $2\pi/k$ .

#### 4.1. Conditions for Bifurcation to Spatial Patterns

Necessary and sufficient conditions for the roots of (37) to have negative real parts are

$$B(k^2) > 0 \quad \text{and} \quad C(k^2) > 0 \quad (40)$$

for all positive  $k^2$ .

If the spatial pattern bifurcations have finite wave numbers,  $k$ , where  $0 < k^2 < \infty$ , Eq. (40) must be met for very large and very small  $k^2$ . The case  $k^2 \rightarrow 0$ , describing spatially homogeneous perturbations, was shown to be stable earlier in Section 4. Perturbations with large wave numbers are also stable because the leading order terms in (38) and (39) are positive and thus (40) is satisfied as ( $k^2 \rightarrow \infty$ ).

Consider the case where either condition in (40) is not met over some range  $k_- < k < k_+$ . Then the linear analysis predicts that modes with wave numbers in this range will grow exponentially according to (36) providing the boundary conditions ((31)–(32) or (33)–(34)) are met. In other words, a mode will grow providing

$$k_- < \frac{n\pi}{L} < k_+ \quad (41)$$

for some integer  $n$ , where  $L$  is the length of the solution domain,  $0 \leq x \leq L$ . The special case

$$k_- = \frac{n\pi}{L} = k_+ \quad (42)$$

describes a neutrally stable mode, which neither grows nor decays.

I now consider the point at which there is a bifurcation to linear instability for a critical wave number,  $0 < k_c < \infty$ , as the real part of an eigenvalue of the linear system increases through zero. According to (42) this mode will be neutrally stable provided  $k_- = k_+ = k_c$  and thus  $L = n\pi/k_c$ . For the purpose of simplifying the linear analysis I assume that this  $L$  satisfies this constraint, while noting that the more general case given by (41) is

$$\frac{n\pi}{k_+} < L < \frac{n\pi}{k_-}$$

The bifurcation to linear instability can be described by

$$\max_{1,2} \Re\{\sigma_i\} \begin{cases} = 0 & \text{if } k = k_c \\ < 0 & \text{if } k \neq k_c. \end{cases}$$

This bifurcation occurs through a pure imaginary eigenvalue (Hopf bifurcation) when the first constraint in (40) is violated, and at a zero eigenvalue when the second constraint in (40) is violated. For notational convenience, I denote the critical wave number for a Hopf bifurcation as  $k_c = k_H$  and the critical number for a zero bifurcation as  $k_c = k_R$ . Thus the condition

$$B(k^2) \begin{cases} = 0 & \text{for } k = k_H \\ > 0 & \text{for } k \neq k_H \end{cases} \quad \text{and} \quad C(k^2) > 0 \quad \text{for all } k \quad (43)$$

leads to a Hopf bifurcation through  $\sigma = \pm i\sigma_H$  and

$$B(k^2) > 0 \quad \text{for all } k \quad \text{and} \quad C(k^2) \begin{cases} = 0 & \text{for } k \neq k_R \\ > 0 & \text{for } k \neq k_R \end{cases} \quad (44)$$

leads to a bifurcation through  $\sigma = 0$ .

Examination of (38) and (39) reveals that a necessary condition for either of the above bifurcations is that  $r < u_0$ . In ecological terms this means that the tendency for the herbivores to aggregate over short distances dominates the tendency for the herbivores to make random movements. Thus the short-range movement term in (27) ( $[(r - u)u_x]_x$ ) is destabilizing. This contrasts with the two other movement terms; both the long-range movement term ( $[-\omega uu_{xxx}]_x$  describes how the herbivores aggregate over further distances) and the herbivory-taxis term ( $[xuv_x]_x$  describes how the herbivores move up gradients in plant quality) are stabilizing.

I now find necessary constraints on the model parameters for the Hopf and real bifurcations described above. For the Hopf bifurcation (43), setting  $B(k_H^2) = B'(k_H^2) = 0$  yields

$$k_H^2 = \frac{u_0 - r}{2\omega u_0} \quad (45)$$

when

$$(u_0 - r)^2 + \omega u_0(f_u + g_v) = 0. \quad (46)$$

For the real bifurcation (44), setting  $C(k_R^2) = C'(k_R^2) = 0$  yields

$$k_R^2 = \frac{u_0 - r}{2\omega u_0} - \frac{\alpha g_u}{2g_v \omega} \quad (47)$$

when

$$[g_v(r - u_0) + \alpha g_u u_0]^2 + 4\omega g_v u_0[f_u g_v - g_u f_v] = 0. \quad (48)$$

If both the Hopf and real bifurcations were to occur simultaneously then (46) and (48) would both be met and the ratio of critical wave numbers would satisfy

$$\left(\frac{k_R}{k_H}\right)^2 = \frac{g_v(u_0 - r) - \alpha g_u u_0}{g_v(u_0 - r)}.$$

Employing (46) and (48), it is observed that this ratio must also satisfy

$$\left(\frac{k_R}{k_H}\right)^4 = \frac{f_u g_v - g_u f_v}{g_v(f_u + g_v)}. \quad (49)$$

## 5. DYNAMIC AND STATIONARY PATTERNS

Given a *particular* plant-herbivore system one might determine a *specific* set of parameter values for Eq. (27) and (28). However, rather than modelling a specific system, my primary purpose is to investigate the rich potential that (27)-(28) has for pattern formation. This is achieved by considering the effect of varying parameter values near a doubly critical bifurcation point that satisfies (46) and (48).

By way of an example I choose the reaction dynamics to be given by

$$\gamma = 0.297, \quad \delta = 1.25, \quad \mu = 17.0, \quad s = 19.0, \quad h = 0, \quad \phi = 1.0 \quad (50)$$

and movement terms to be given by

$$\omega = 0.01, \quad r = r_c = 0.1, \quad \alpha = \alpha_c = 12.825. \quad (51)$$

Thus at the steady state solution  $(u_0, v_0) = (1.0, 0.842)$  partial derivatives for the reaction dynamics are

$$f_u = -1.25, \quad f_v = 0.297, \quad g_u = -1.0, \quad g_v = -19.0$$

and the critical wave numbers satisfy

$$k_H^2 = 45.0, \quad k_R^2 = 11.25$$

(Fig. 4).

I now determine the effect of small changes in the random motion parameter ( $r$ ) and herbivory-taxis parameter ( $\alpha$ ) upon the dispersion relation (37)-(39). The effect that these two parameters exert upon the dispersion relation describes how small changes in herbivore movement behavior (measured through changes  $r$  and  $\alpha$ ) manifest themselves as dramatic changes in patterns of herbivore density.



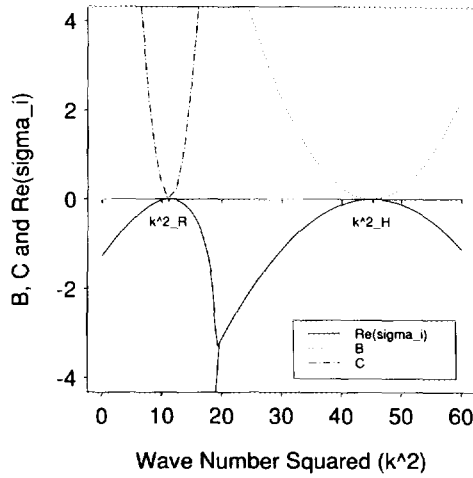


FIG. 4. Dispersion relation for a doubly critical bifurcation satisfying (46) and (48). Parameters are given by (50)–(51).

1.  $r = r_c - 0.01$ ,  $\alpha = \alpha_c + 0.5$ : Hopf bifurcation (Fig. 5). Linear analysis predicts an exponentially growing oscillatory mode with wavelength approximately  $2\pi/k_H = 0.94$ .
2.  $r = r_c + 0.01$ ,  $\alpha = \alpha_c - 0.5$ : real bifurcation (Fig. 6). Linear analysis predicts an exponentially growing stationary mode with wavelength approximately  $2\pi/k_R = 1.87$ .

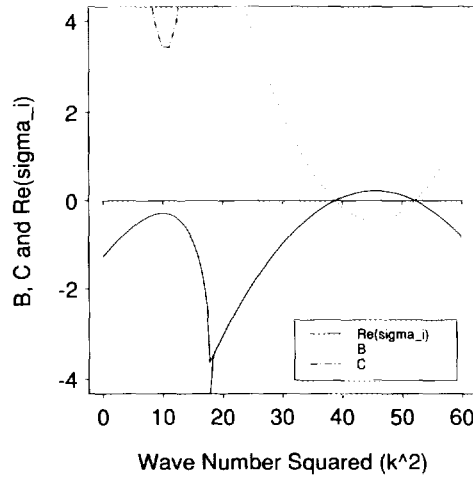


FIG. 5. Supercritical dispersion relation near a Hopf bifurcation. Parameters are given by (50)–(51) except  $r = r_c - 0.01$  and  $\alpha = \alpha_c + 0.5$ .

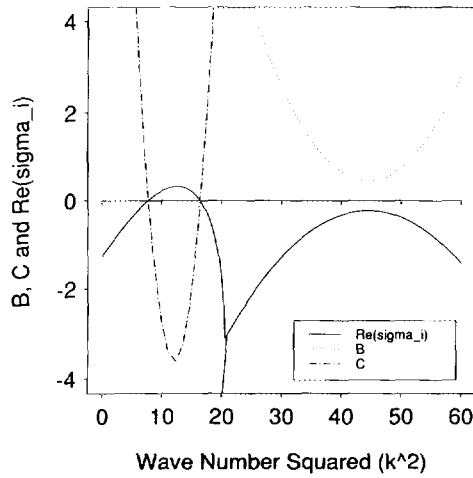


FIG. 6. Supercritical dispersion relation near a real bifurcation. Parameters are given by (50)–(51) except  $r = r_c + 0.01$  and  $\alpha = \alpha_c - 0.5$ .

3.  $r = r_c - 0.01$ : simultaneous Hopf and real bifurcations (Fig. 7). Linear analysis predicts simultaneous growth of the two modes described above.

From this example it is observed that a decrease in  $r$  may lead to the growth of both stationary and oscillatory modes and a decrease in  $\alpha$  may lead to the growth of stationary modes. Analysis of the bifurcations

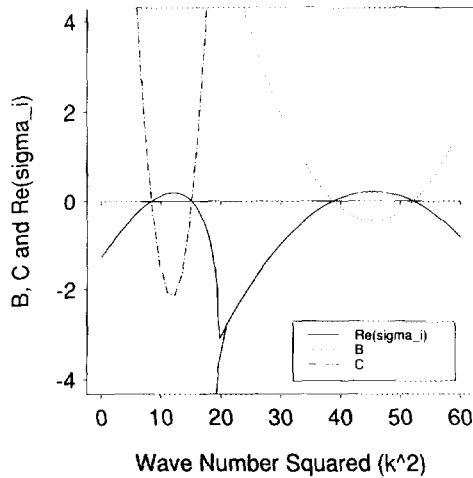


FIG. 7. Supercritical dispersion relation near Hopf and real bifurcations. Parameters are given by (50)–(51) except  $r = r_c - 0.01$ .

conditions (43)–(44) and the dispersion relation coefficients (38)–(39) indicates that this is indeed the case in general.

### 5.1. Numerical Solutions

Linear analysis indicates that for critical parameter sets spatial patterns may arise as the homogeneous steady state becomes linearly unstable to perturbations with a spatial component. This analysis is valid only for small time and infinitesimal perturbations; over long periods the exponential growth predicted by the linear analysis may be dominated by other non-linear terms. If these non-linear terms damp and eventually balance the growth rate predicted by linear analysis, then a new, bounded, spatially heterogeneous solution may result (much in the same way that a limit cycle can arise from a Hopf bifurcation). A classical analytical method for analyzing the contribution of higher order terms is through weakly non-linear analysis (see, for example, Matkowski (1970)). For the purpose of this paper, however, I restrict myself to a numerical approach. This has the added advantage of illustrating graphically the resulting spatial patterns of herbivore density and plant quality.

For each of the three cases discussed above I solved the full non-linear system (27)–(28) with the boundary conditions (33)–(34) numerically by using finite differences for the space terms (Smith, 1985) and solving the resulting system of ordinary differential equations. Results are shown in Fig. 8 through 10. In each of the three cases, growth of the modes remained bounded. Note that for the third case (where linear analysis predicts

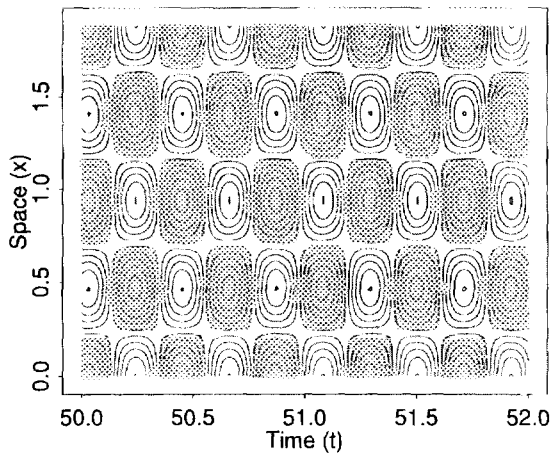


FIG. 8. Numerical solution to (27)–(28) with boundary conditions (33)–(34) and parameter values are given in Fig. 5. The method of lines and Gear's method were used to calculate the herbivore density ( $u(x, t)$ ) and plant quality ( $v(x, t)$ ) through time. Isoclines for herbivore density are shown for  $t \in [50, 52]$ . Shaded areas mark the regions where  $u > u_0 = 1.0$ .

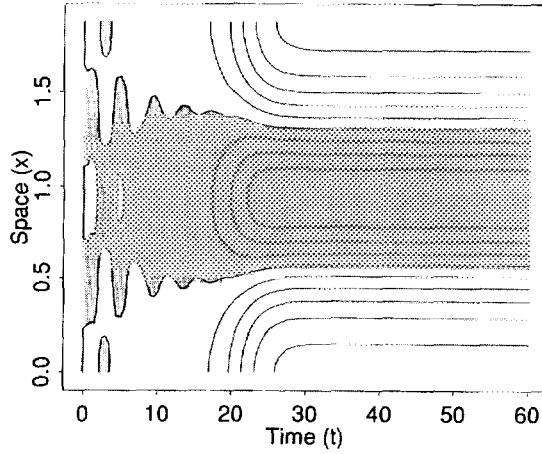


FIG. 9. Numerical solution to (27)–(28) with boundary conditions (33)–(34) and parameter values are given in Fig. 6. The method of lines and Gear's method were used to calculate the herbivore density ( $u(x, t)$ ) and plant quality ( $v(x, t)$ ) through time. Isoclines for herbivore density are shown for  $t \in [0, 60]$ . Shaded areas mark the regions where  $u > u_0 = 1.0$ .

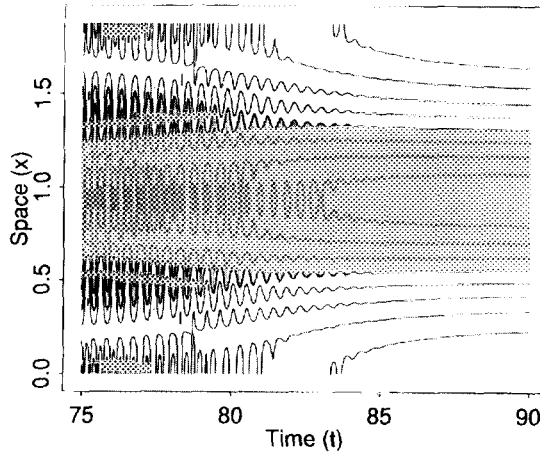


FIG. 10. Numerical solution to (27)–(28) with boundary conditions (33)–(34) and parameter values are given in Fig. 7. The method of lines and Gear's method were used to calculate the herbivore density ( $u(x, t)$ ) and plant quality ( $v(x, t)$ ) through time. Isoclines for herbivore density are shown for  $t \in [75, 90]$ . Shaded areas mark the regions where  $u > u_0 = 1.0$ .

simultaneous growth of oscillatory and stationary modes) it is the stationary pattern that dominates over a long time period although both modes grow initially. This transformation to stationary pattern is shown in Fig. 10. The transformation may arise from interactions between higher order nonlinear terms in (27)–(28) and would be an interesting subject for further detailed mathematical analysis.

## 6. DISCUSSION

The purpose of this paper is to illustrate how, in a spatially homogeneous environment, the spatial coupling of herbivore dispersal with plant and herbivore dynamics can give rise to dynamic and stationary waves of herbivore density and thus of plant damage. The growth and propagation of such patterns also depends critically upon the interplay between random (i.e., diffusive) and non-random (i.e., herbivory-taxis and aggregative) elements of herbivore dispersal.

Several general conclusions can be drawn from the analysis:

1. The generation of spatial patterns (both stationary and dynamic) depends upon the herbivores aggregating toward surrounding conspecifics ( $\omega > 0$  in (38) and (39) so that the bifurcation conditions (43) and (44) can be satisfied). If herbivores were merely to respond to conditions precisely at their own locations, no patterns will form. Patterns form by the growth of linearly unstable modes about a positive steady state solution ( $u_0, v_0$ ). Such a steady state solution can be shown to exist providing some very general rules about plant–herbivore dynamics are satisfied (see Section 3.2).

2. When herbivores aggregate towards surrounding conspecifics ( $\omega > 0$ ), stationary aggregative patterns may form, even when plant quality and birth and death dynamics are ignored completely. The wavelength for such a pattern, calculated in Section 3.4.1, is shown to be approximately  $2\pi/k_m$ , where  $k_m$ , expressed in Eq. (25), is a function of the variance of spatial averaging kernel ( $\sigma^2$ ), an average density ( $u_0$ ), and a ratio of random movement to aggregative movement ( $r/m$ ).

3. The introduction of herbivory-taxis ( $\alpha > 0$ ) tends to reduce the likelihood of the formation of stationary aggregative patterns (note that  $C(k^2)$  increases in (39) and thus it is more difficult to achieve a bifurcation as described by (44)). If stationary aggregative patterns do none the less occur they will have a reduced wavelength. (This can be seen by evaluating  $2\pi/k_R$ , where  $k_R$  satisfies (47)). However, herbivory-taxis introduces the possibility of dynamic spatial waves. Mathematically, these arise through a Hopf bifurcation with a spatial component, as described in (43). Furthermore, it can be shown that dynamic spatial waves cannot arise unless there

is a herbivory-taxis component to herbivore movement: when  $\alpha = 0$ , Eq. (38) and (39) yield

$$C(k^2) + g_v B(k^2) = g_u f_v - g_v^2 < 0$$

and thus (43) can never be satisfied.

4. Stationary and dynamic patterns in herbivore abundance/plant quality can both grow simultaneously, with different wavelengths. Numerical solutions indicate that the resulting patterns can evolve and change slowly over long time periods (see Section 5.1) providing a complex spatio-temporal progression of patterns. This is an interesting subject for further detailed mathematical analysis.

5. The other major possibility for pattern formation in plant-herbivore systems may arise through coupling the plant-herbivore system to a third trophic level (i.e., predators or parasites). Possibly classical models for diffusion-driven instabilities would apply here. This remains an open question.

Moving to the wider context of modelling spatial movement in ecology, I suggest that for many populations simple diffusion provides an inadequate description of the dispersal process, particularly when individuals respond actively to environmental gradients and to conspecifics. This paper demonstrates that the detailed analysis of other movement components (such as herbivory-taxis and aggregation) can be instrumental in revealing new mechanisms that are capable of generating spatial patterns.

#### APPENDIX A: BIAS AND MOTILITY TERMS FOR RANDOM WALK WITH AGGREGATION

The bias,  $R(x, t) - L(x, t)$ , and the motility,  $R(x, t) + L(x, t)$ , are given by

$$\begin{aligned} R(x, t) - L(x, t) &= 2mN\lambda \sum_{-\infty < j < \infty} w(j\lambda) \left( \frac{\partial p}{\partial x}(x + j\lambda, t) + \mathcal{O}(\lambda^2) \right) \\ &= 2mN \left[ \frac{\partial p}{\partial x}(x, t) \sum_{-\infty < j < \infty} w(j\lambda)\lambda \right. \\ &\quad + \frac{\partial^2 p}{\partial x^2}(x, t) \sum_{-\infty < j < \infty} j\lambda w(j\lambda)\lambda \\ &\quad \left. + \frac{\partial^3 p}{\partial x^3}(x, t) \frac{1}{2} \sum_{-\infty < j < \infty} (j\lambda)^2 w(j\lambda)\lambda + \dots + \mathcal{O}(\lambda^2) \right] \end{aligned} \quad (52)$$

and

$$\begin{aligned}
 &R(x, t) + L(x, t) \\
 &= r(x, t) + mN \sum_{-\infty < j < \infty} w(j\lambda) [p(x + (j-1)\lambda, t) \\
 &\quad - 2p(x + j\lambda, t) + p(x + (j+1)\lambda, t)]. \\
 &= r(x, t) + mN\lambda^2 \sum_{-\infty < j < \infty} w(j\lambda) \frac{\partial^2 p}{\partial x^2}(x + j\lambda, t) + \mathcal{O}(\lambda^4), \quad (53)
 \end{aligned}$$

respectively. Substituting (52) and (53) into (6), taking the limit as  $\lambda$  and  $\tau$  approach zero so that  $\lambda^2/(2\tau) \rightarrow D$ , and using (5) I obtain

$$\frac{\partial u}{\partial t} = D \frac{\partial}{\partial x} \left[ r \frac{\partial u}{\partial x} - 4mu \int_{-\infty}^{\infty} w(y) \frac{\partial u}{\partial x}(x + y, t) dy \right]; \quad (54)$$

or, alternatively, Eq. (52) yields

$$\frac{\partial u}{\partial t} = D \frac{\partial}{\partial x} \left[ r \frac{\partial u}{\partial x} - 4mu \sum_{j>0} w_{j-1} \frac{\partial^j u}{\partial x^j} \right], \quad (55)$$

where

$$w_j = \frac{1}{j!} \int_{-\infty}^{\infty} y^j w(y) dy, \quad j = 0, 1, 2, \dots \quad (56)$$

defines the moments of the kernel  $w(y)$ .

#### APPENDIX B: LINEAR BEHAVIOR FOR EQUATIONS FOR AGGREGATIVE MOVEMENT

In this appendix the linear behaviors of Eqs. (18) and (24) are compared about a constant solution,  $u = u_0$ .

Linearizing (18) about the constant solution,  $u = u_0$ , and transforming the resulting linear equation yields

$$\dot{U} = DUK^2 [4mu_0 \mathcal{F}\{w(x)\} - r], \quad (57)$$

where  $U(k, t)$  is the Fourier transform  $\mathcal{F}\{u(x, t) - u_0\}$ . Alternatively, the same procedure when applied to (24) yields

$$\dot{U} = DUK^2 [4mu_0(w_0 - w_2 k^2) - r]. \quad (58)$$

These two equations are identical except for the fact that  $\mathcal{F}\{w(x)\}$  in Eq. (57) has been replaced by  $w_0 - w_2 k^2$  in (58).

How close are stability prediction for these two equations when the three different kernels (12)–(14) are used? Transforms ( $\mathcal{F}\{w(x)\}$ ) for these three kernels, given by

$$\frac{1}{2} \exp(-k^2/(4b)), \quad \frac{\sin(kl_1)}{kl_1}, \quad \text{and} \quad \frac{2}{k^2 l_2^2} (1 - \cos(kl_2)), \quad (59)$$

respectively, are shown in Fig. 2b. The choice of  $l_1 = 1$ ,  $l_2 = \sqrt{2}$ , and  $b = 1.5$  (Fig. 2) yields kernels with identical second moments ( $w_2 = \frac{1}{6}$ ) and thus identical variances ( $\sigma^2 = 2w_2 = \frac{1}{3}$ ). The linearized caricature equation (58) is thus identical for all three kernels. Equations (57) and (58) can be rewritten in the form

$$\dot{U} = 4Dmu_0 G(k) U,$$

where  $G(k)$  is proportional to the growth rate for modes with wave number  $k$ . Figure 11 shows the growth rate  $G = k^2(\mathcal{F}\{w(x)\} - r/(4mu_0))$ , for each of the three kernels and the growth rate  $G = k^2(w_0 - w_2 k^2 - r/(4mu_0))$  for the linearized caricature equation. (For this sample calculation the value

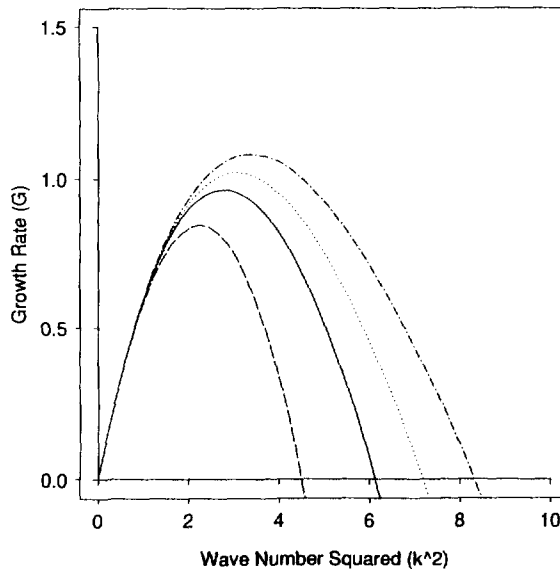


FIG. 11. Plot of the growth rate ( $G$ ) versus the wave number squared ( $k^2$ ) (see Appendix B). Curves are shown for  $G = k^2(w_0 - w_2 k^2 - r/(4mu_0))$  (inner) and  $G = k^2(\mathcal{F}\{w(x)\} - r/(4mu_0))$  with  $w(x)$  given by (14), (13), and (12) (outer). Parameter values for (12)–(14) were chosen as  $l_1 = 1$ ,  $l_2 = \sqrt{2}$ , and  $b = 1.5$ . The Fourier transforms ( $\mathcal{F}\{w(x)\}$ ) are given by (59).



for  $r/(4\mu u_0)$  was chosen to be 0.25.) These *dispersion* relations between the growth rate and wave number indicate that the linearized caricature equation successfully captures the qualitative dynamics of the more complex models (Fig. 11).

We expect that, when the linear approximation is valid ( $u$  near  $u_0$ ), wave numbers with the largest growth rates, shown in Fig. 11, will grow fastest and dominate the solution. In other words, linear analysis predicts that the wavelength of resulting aggregations is approximately  $2\pi/k_m$ , where, for each kernel,  $k_m$  is the square root of the maximum value of  $k^2$  attained on the relevant curve in Fig. 11. For the caricature model

$$k_m^2 = \frac{w_0 - r/(4\mu u_0)}{2w_2} = \frac{1 - r/(4\mu u_0)}{\sigma^2}, \quad (60)$$

where  $\sigma^2 = 2w_2$  is the variance of the kernels. This relationship (60), which is exactly true for the caricature model, holds approximately true for specific kernels, as shown in Fig. 11.

However, Eq. (24) may be a poor caricature for the integral equation model (18) when the quantity  $r/(4\mu u_0)$  approaches zero. For example, observing Fig. 2b we note that, for  $r/(4\mu u_0)$  sufficiently small, the linear growth rate,  $k^2(\mathcal{F}\{w(x)\} - r/(4\mu u_0))$ , may possibly have two or more local maxima at different  $k$ . This feature would not be reflected by the growth rate of the caricature model.

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