Spatial Patterns in Plant Populations with Male Sterile Individuals

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Abstract
A integro-differential equation model of a gynodioecious plant population is constructed and analyzed. Linear stability analysis is performed about a spatially constant solution, and conditions are derived under which spatial patterns may form. It is shown that there are two necessary conditions, a difference in the length scales at which pollen and seed are dispersed, and a platykurtic pollen dispersal kernel. We also numerically solve the integro-differential equation and simulate a related individual based stochastic model. In each case we observe similar results.

Introduction

Flowering plants exhibit a large diversity of breeding systems. The most common system is one in which plants are hermaphrodites, that is, flowers carry both male and female parts. About 80% of angiosperms are hermaphrodites [12].

About 10% of angiosperms exhibit a variation of this breeding system named gynodioecy in which some individuals produce flowers without functional pollen, thus rendering these individuals male sterile, or female [6]. In gynodioecious populations, both hermaphrodite and female individuals coexist. Examples of gynodioecious plants are the wild thyme (*Thymus polytrichus*), the buckhorn plantain (*Plantago lanceolata*), and the meadow saxifrage (*Saxifraga granulata*) [12].

Gynodioecy is commercially exploited in agricultural systems, such as wheat or maize, when plant breeders wish to have control over the genetic make-up of seeds; male sterility is typically achieved through interspecies crossing [13], [15]. Because of its commercial importance, gynodioecy has

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been studied extensively. Recently, the molecular basis of gynodioecy has been discovered [14].

The study of gynodioecy is of particular interest from an evolutionary point of view. Gynodioecy is thought of as a precursor to dioecy [2]. It is therefore of interest to study how gynodioecy can evolve and be maintained in a natural population.

Studies in wild populations indicate that in most species male sterile individuals are rare. There are, however, some species in which the fraction of plants that are males sterile varies over a wide range in different populations.

One interesting observation is the fact that in some species, the male sterile plants of a gynodioecious population cluster together [5], [9]. For example in [20], van Damme showed that in a particular population of Plantago lanceolata the total fraction of male sterile plants was small, only on the order of 5%. However, the male steriles clustered together. In the center of these clusters, the male sterile plants made up to 60% of the present plants. Clustering of male sterile plants is also observed in Beta vulgaris.

Clustering of plants must be due to their “movement”; in other words, due to the way in which they disperse pollen and seed. In this paper, we ask what qualities of seed and pollen dispersal lead to clustering of male sterile plants. We approach this problem by building a mathematical model of a gynodioecious population. This model is a pair of integrodifferential equations. Analysis of the model yields a condition which the functions describing seed and pollen dispersal must satisfy in order for spatial patterns to arise. We have also numerically solved the model, and simulated a related interacting particle system. The numerical results and the simulations are consistent with the analysis of the model.

Hermaphrodites are not pollen limited

Non-Spatial Model

The main model is a mixture of male sterile and hermaphroditic plants in which male sterility is maternally inherited and the hermaphrodites are not limited by pollen (that is hermaphrodite pollination is not density dependent).

In order to describe clustering behavior, we will need a model in which spatial interactions are described, but to gain a basic understanding of the population dynamics, we first concentrate on a non-spatial model. This will take the form of the following ordinary differential equations:

\[ \dot{u} = r_1 u v (1 - u - v) - u, \]  \hspace{1cm} (1) 
\[ \dot{v} = r_2 v (1 - u - v) - v, \]  \hspace{1cm} (2) 

where \(u\) is the fraction of female (male-sterile) plants, \(v\) is the fraction of hermaphrodites, and total population has been scaled in such a way that the per capita death rate is 1. We assume that females, who need hermaphrodites as a pollen source, grow at a rate proportional to their own density, to the density of hermaphrodites, and to the amount of
open space available. Hermaphrodites grow proportionally to their own density and to the amount of open space. Both populations have the same constant per capita death rates.

This system has three equilibrium solutions:

1. \[ u = 0 \quad v = 0, \]
2. \[ u = 0 \quad v = 1 - \frac{1}{r_2}, \]
3. \[ u = 1 - \frac{1}{r_2} - \frac{r_2}{r_1}, \quad v = \frac{r_2}{r_1}. \]

Case 1 describes the situation in which both types are absent; case 2 is the monoculture equilibrium of hermaphrodites; case 3 is referred to as the nontrivial equilibrium. It is clear from the dynamics that male steriles cannot survive in the absence of hermaphrodite individuals; hence there is no equilibrium in which \( u > 0 \) and \( v = 0. \)

We are interested in the situation when the nontrivial equilibrium (that is, the equilibrium in which both the female and hermaphrodite populations are positive) exists and is stable. It is straightforward to show that this will be the case if

\[ r_2 > 1 \quad \text{and if} \quad r_1 > \frac{r_2^2}{r_2 - 1}. \quad (3) \]

The first condition, \( r_2 > 1 \), ensures survival of hermaphrodites in the absence of male sterile plants.

If the second condition, \( r_1 > \frac{r_2^2}{r_2 - 1} \), holds, then male sterile plants can invade a monoculture of hermaphrodites.

In Figure (1) we see that in order for coexistence of the two types the fecundity of male sterile plants needs to exceed the fecundity of the hermaphrodites by a positive amount to compensate for the loss of fecundity due to male sterility in the absence of hermaphrodite neighbors.

**FIGURE ONE HERE**

**Spatial Model**

Next, we include a spatially explicit component into our model. This will result in a pair of one dimensional integro-differential equations. In order to do this, we introduce two additional processes: pollen dispersal and seed dispersal; they will both be described by dispersal kernels, \( k_p(x) \) and \( k_o(x) \) respectively.

Assume that \( k_p(x) \) and \( k_o(x) \) are symmetric, positive, and integrate to 1. These kernels work in the following manner: in a small region of size \( \Delta z \) about \( z \), if \( v(z) \Delta z \) is the number of hermaphrodite plants, then the amount of pollen that arrives at \( x \) due to these plants at \( z \) is proportional to

\[ k_p(x - z) v(z) \Delta z \]

The total amount of hermaphrodite pollen which arrives at \( x \) is then proportional to

\[ [k_p * v](x) = \int k_p(x - z) v(z) dz \]

(5)
Since the number of male sterile plants in an infinitesimal interval of size $dz$ about $z$ is $u(z)dz$, we find that the number of seeds at $x$ is proportional to

$$ [k_s * u(p * v)](x) = \int k_s(x - z) u(z) \int k_p(z - y) v(y) dy dz $$  \hspace{1cm} (6)$$

Similarly, the amount of male sterile seed which falls at $x$ is

$$ [k_s * u](x) = \int k_s(x - z) u(z) dz $$  \hspace{1cm} (7)$$

The spatial model will have the following form

$$ \frac{\partial}{\partial t} u = r_1 [1 - u - v] [k_s * u [k_p * v]] - u $$  \hspace{1cm} (8)$$

$$ \frac{\partial}{\partial t} v = r_2 [1 - u - v] [k_s * v] - v $$  \hspace{1cm} (9)$$

The model is defined on a finite interval $[a, b]$. Periodic boundary conditions are imposed on both $u(x)$ and $v(x)$ so that $u(a) = u(b), v(a) = v(b)$.

Assuming that $r_1$ and $r_2$ satisfy (3), the system will have the spatially constant nontrivial equilibrium solution $(u, v)$ with

$$ u(x) = 1 - \frac{1}{r_2} - \frac{r_2}{r_1}, \quad v(x) = \frac{r_2}{r_1} $$  \hspace{1cm} (10)$$

We are interested in whether or not this equilibrium is stable under spatial perturbations. If it is, we will observe the system in the spatially homogeneous state. If not, there is the possibility of spatial pattern formation.

For notational simplicity, we call the values of $u$ and $v$ at this spatially constant equilibrium $f'$ and $h'$ respectively. Substituting $f = u - f'$, $h = v - h'$ into (8) and (9) gives the system

$$ \frac{\partial}{\partial t} f = r_1 (1 - f - f' - h - h') [k_s * (f + f') [k_p * (h + h')]] - (f + f') $$  \hspace{1cm} (11)$$

$$ \frac{\partial}{\partial t} h = r_2 (1 - f - f' - h - h') [k_s * (h + h')] - (h + h') $$

While we have used notational shorthand here, it is important to remember that $f$ and $h$ are functions of space and time, $k_p$ and $k_s$ are functions of space, but not time, and $f'$ and $h'$ are constant in both space and time.

Now we linearize the system about the new equilibrium, $f = 0$ and $h = 0$. $f$ and $h$ represent deviation from the the equilibrium solutions, $f'$ and $h'$. The details of this calculation are given in Appendix A. Linearization yields

$$ \frac{\partial}{\partial t} f = -r_2 f' (f + h) + (f' / h') [k_s * [k_p * h]] + [k_s * f] - f $$  \hspace{1cm} (13)$$

$$ \frac{\partial}{\partial t} h = -r_2 h' (f + h) + [k_s * h] - h $$  \hspace{1cm} (14)$$

In order to analyze the stability of the equilibrium, we Fourier transform these equations. Using the fact that the Fourier transform of a convolution
is the product of the Fourier transforms gives us the following system of ordinary differential equations, which hold for each $\omega$:

$$
\begin{bmatrix}
\frac{\partial}{\partial t} f(\omega) \\
\frac{\partial}{\partial t} h(\omega)
\end{bmatrix} =
\begin{bmatrix}
-r_2 f' + \dot{k}_s(\omega) - 1 & -r_2 f' + \frac{1}{k_p} \dot{k}_p(\omega) \dot{k}_s(\omega) \\
-r_2 h' & -r_2 h' + \dot{k}_s(\omega) - 1
\end{bmatrix}
\begin{bmatrix}
f(\omega) \\
h(\omega)
\end{bmatrix}.
$$

(15)

This system is of the form

$$
\frac{\partial}{\partial t} \begin{bmatrix}
f(\omega) \\
h(\omega)
\end{bmatrix} =
\begin{bmatrix}
a_1(\omega) & a_2(\omega) \\
A(\omega)
\end{bmatrix}
\begin{bmatrix}
f(\omega) \\
h(\omega)
\end{bmatrix}.
$$

(16)

We wish to know if the solution $f(0) = 0, \dot{h}(0) = 0$ is stable. In general, this system will have solutions

$$
\begin{bmatrix}
f(\omega) \\
h(\omega)
\end{bmatrix} =
\begin{bmatrix}
\xi_1 \\
\xi_2
\end{bmatrix} e^{\lambda_1 t} +
\begin{bmatrix}
\xi_3 \\
\xi_4
\end{bmatrix} e^{\lambda_2 t}
$$

(17)

where $\xi_1, \xi_2, \lambda_1,$ and $\lambda_2$ are the eigenvectors and eigenvalues of the matrix

$$
A =
\begin{bmatrix}
a_1(\omega) & a_2(\omega) \\
a_3(\omega) & a_4(\omega)
\end{bmatrix},
$$

(18)

as defined in equation (16), and depend on $\omega$. To understand stability, we investigate

$$
\lambda(\omega) \equiv \max\{\text{Re}(\lambda_1(\omega)), \text{Re}(\lambda_2(\omega))\}.
$$

(19)

If $\lambda(\omega)$ is negative for all $\omega$, the spatially constant solution is stable for perturbations of all wave numbers. On the other hand, if $\lambda(\omega) > 0$ for some $\omega$, perturbations of this wave number will be unstable, and lead to spatial patterns.

**The sign of $\lambda(\omega)$**

Because both dispersal kernels are probability densities we see that

$$
|\dot{k}_s| \leq \int k_s(z) |e^{iz\omega}| dz \leq 1.
$$

(20)

and the same is true for $|\dot{k}_p|$. Thus it is only necessary to consider $-1 \leq \dot{k}_p, \dot{k}_s \leq 1$. We want to find conditions on $k_s(\omega)$ and $k_p(\omega)$ such that $\lambda(\omega)$ is positive, and thus the spatially constant equilibrium solution to (8) and (9) is unstable. These conditions are summarized in the following theorem.

**Theorem:**

Let $\lambda(\omega) = \max\{\lambda_1(\omega), \lambda_2(\omega)\}$, where $\lambda_1(\omega)$ and $\lambda_2(\omega)$ are the eigenvalues of the matrix $A$ defined in (15). For $r_2 > 1$ and $r_1 > r_2^2/(r_2 - 1)$, $\lambda(\omega) > 0$ if and only if $k_p(\omega) < 0$ and

$$
\dot{k}_s(\omega) > \frac{(1 + r_2 - r_2 f \dot{k}_p(\omega)) - \sqrt{(1 + r_2 - r_2 f \dot{k}_p(\omega))^2 - 4r_2}}{2}.
$$

(21)
Proof: To prove this we show, first, that the sum of eigenvalues of $A$, i.e. trace($A$), is negative. Thus, the real part of at least one eigenvalue is always negative. In order to have one positive and one negative eigenvalue it must be the case that the product of the eigenvalues, det($A$), is negative. First we show that if $k_p(\omega) > 0$ this is never the case, and then that if $k_p(\omega) < 0$ it will be the case under the additional condition given in the theorem.

If we look at the matrix $A$, we have

$$\text{Trace}(A) = 2k_0 - r_2 - 1 \quad (22)$$

Because $|\hat{k}_0(\omega)| \leq 1$ and $r_2 > 1$, we know that Trace($A$) < 0. Thus, there will be an eigenvalue with positive real part if and only if det($A$) < 0. The determinant is

$$k_0^2 + (r_2 f' \hat{k}_p - r_2 - 1) \hat{k}_0 + r_2 \quad (23)$$

First, consider the case where $k_p > 0$. We consider det($A$) a function of $\hat{k}_0$. If we differentiate det($A$) with respect to $\hat{k}_0$, and set this equal to zero, we see that it will be minimized when

$$\hat{k}_0 = \frac{1 + r_2 - r_2 f' \hat{k}_p}{2} \quad (24)$$

which is greater than zero. Furthermore, when $\hat{k}_0 = 0$, det($A$) = $r_2$, and when $\hat{k}_0 = 1$, det($A$) = $r_2 f' \hat{k}_p$. These are both positive, and so the determinant will always be positive for $\hat{k}_0 \in [-1, 1]$ unless the minimum value of the determinant is negative. This minimum value will be

$$\left(- \left( \frac{r_2 f' \hat{k}_p - r_2 - 1}{2} \right) \right)^2 + r_2 \quad (25)$$

However, because $r_2 > 1$, comparison of (24) and (25) shows that it is impossible to have the minimum occur when $\hat{k}_0 < 1$, and to have the minimum be less than 0. That is, if $k_p > 0$, the determinant is always positive, and the there is no positive eigenvalue.

Next, consider the case $k_p < 0$. If $\hat{k}_0 = 1$, the determinant is equal to $r_2 f' \hat{k}_p$, which is negative. Thus, for large enough $\hat{k}_0 = 1$ it is possible to have a positive eigenvalue. To find the the minimum value of $\hat{k}_0$ for which the positive eigenvalue exist, we set equation (23) equal to zero and solve. We see that if

$$\hat{k}_0 > \left( \frac{1 + r_2 - r_2 f' \hat{k}_p}{2} - \sqrt{(1 + r_2 - r_2 f' \hat{k}_p)^2 - 4r_2} \right)$$

then we have a positive eigenvalue, and the spatial constant solution will be linearly unstable to spatial perturbations. □

The relationship between $\hat{k}_0(\omega)$, $\hat{k}_0(\omega)$, and $\lambda$ is shown in Figure 2. For this graph, we choose $r_1 = 2$ and $r_2 = 8$. The dark region corresponds to values of $\hat{k}_0(\omega)$ and $\hat{k}_0(\omega)$ for which $\lambda > 0$. The light region corresponds to values for which $\lambda < 0$.  

6
FIGURE TWO HERE

**Corollary 1:**
If seed dispersal and pollen dispersal are the same, i.e. if $k_s(x) = k_p(x)$, then spatial patterns will not develop.

This follows from the theorem since if $k_s(x) = k_p(x)$, then either $k_s(\omega) = k_p(\omega) > 0$ in which case the first necessary condition of the theorem is violated, or $k_p(\omega) = k_s(\omega) < 0$ in which case the second condition is violated.

This corollary is illustrated in the following numerical simulations of the original system. We choose both $k_s(x)$ and $k_p(x)$ to be uniform distributions on the interval $[2, 2]$, and initial conditions are the equilibrium values of $u(x)$ and $v(x)$ perturbed with a small amount of “white noise.” As we see, both populations decay back to the equilibrium.

FIGURE THREE HERE

Though no spatial pattern develops if the dispersal kernel of seed and pollen are the same, spatial heterogeneity may develop spontaneously if they are sufficiently different. This can be justified when dispersal of both seed and pollen is uniform.

**Corollary 2:**
If $k_p = \text{Uniform}(-p, p)$ and $k_s = \text{Uniform}(-s, s)$, then for fixed $p$, and sufficiently small $s$, the spatially constant solution will be unstable.

To see why this is the case, it is easiest to consider a graph of $k_s(x)$ and $k_p(x)$, and a graph of $\tilde{k}_s(x)$ and $\tilde{k}_p(x)$ as shown in Figure (4).

FIGURE FOUR HERE

If $k_p(x) = \text{Uniform}(-p, p)$, then $\tilde{k}_p(\omega) = \sin(\omega p) / \omega p$, and so for certain $\omega$, $\tilde{k}_p(\omega)$ will be negative. In order for the eigenvalue to be positive, the distance between the two transforms must be sufficiently large. In order to guarantee this, we make $s$ small which keeps $\tilde{k}_s(\omega)$ close to 1 for small $\omega$. Thus, the spatially homogeneous solution is unstable if $\tilde{k}_p(\omega) < 0$ and if the seed dispersal distance is much smaller than the pollen dispersal distance.

Numerical simulations show this instability as well: In Figure (5) we graphed the abundance of the female population with the same initial conditions as in the previous simulations, and dispersal kernels as shown in the above graphs, $k_s(x) = U[-2, 2]$, $k_p(x) = U[-20, 20]$.

FIGURE FIVE HERE

The populations converge to an equilibrium which is spatially heterogeneous. In this equilibrium, peaks of high female density alternate with peaks of high hermaphrodite density. This is shown in the Figure 6.

FIGURE SIX HERE

Another interesting question is, what determines the wavelength of these oscillations? In other words, we wish to know what determines
the size of plant clusters. In the specific case of uniform seed and pollen dispersal, this question is answered by the following corollary.

**Corollary 2'**

In the case of $k_p(x) = \text{Uniform}(-p, p)$, $k_s(x) = \text{Uniform}(-s, s)$, with $p$ and $s$ so that the spatially constant solution is unstable, the wave number which grows the fastest satisfies $\omega \propto \frac{p}{s}$.

The selected $\omega$ will be that which maximizes $\lambda$. From the graph of $\hat{k}_s$ and $\hat{k}_p$ we see that the this will be such that the equation

$$\frac{\partial}{\partial \omega} \hat{k}_p = 0$$

is satisfied. Thus, $\omega p$ will be the first positive, nonzero solution of

$$\omega p = \tan(\omega p),$$

which implies that $\omega p$ is a constant. Clusters of male steriles will grow to a size proportional to the pollen dispersal length. This is intuitive: clusters cannot grow to a size larger than this length because it would leave some male sterile plants in a position where they could not be pollinated by hermaphrodites.

**Results of the analysis**

This analysis has shown that there are two components necessary to produce clustering. The first is that pollen must be dispersed further than seed, second is the condition $\hat{k}_p(\omega) < 0$ for some $\omega$.

In order to understand the second condition, we ask, what sort of pollen dispersal kernels will have a Fourier transform which is negative for some values of $\omega$. What is required of these kernels is a sharp transition between the area upon which a plant's pollen falls and the area upon which it does not fall. In our numerical calculations we used the kernel $k_p(x) = \text{Uniform}(-p, p)$. In this case, all pollen falls within $p$ units of the plant, and no pollen falls outside that area. It does not allow “leakage” of pollen into the male sterile clusters.

A good counter-example is provided by a Gaussian kernel. In this case, enough pollen reaches into male sterile clusters to maintain these plants. This limits clustering because male steriles are competitively superior due to their higher fecundity as long as they can receive pollen. If pollen cannot reach into the center of the male sterile clusters, the male sterile plants die, and the hermaphrodites can invade. In terms of our theorem, the long range pollen dispersal is reflected by the fact that the Gaussian dispersal kernel has fatter tails, and thus its Fourier transform is positive (it is, in fact, itself a Gaussian).

This is not to say that the dispersal kernel need to be compactly supported. It is possible to construct “big shouldered” kernels, which disperse the majority of there pollen in a finite area, but have thin tails which decay rapidly to zero at infinity.

The second requirement is that the scale upon which pollen is dispersed must be much larger then the scale upon which seed is dispersed. If these
requirements are satisfied, then we expect the constant equilibrium to be
unstable, and patterns on the order of the pollen dispersal length to be
observed.

This analysis was done for a model in one spatial dimension, but this
was for ease of explanation. It is straightforward to do the same analysis
in two dimensions. The conditions now involve $k_x(\omega_x, \omega_y)$ and $k_y(\omega_x, \omega_y)$,
the Fourier transforms of the two dimensional pollen and seed dispersal
kernels, but otherwise they are the same as described by the above theo-
rem. We have also done two dimensional numerical simulations which
show that in the case where the constant solution is unstable, the final
two dimensional distribution of male sterile and hermaphroditic plants
depends heavily on the form of the dispersal kernels.

**Interacting Particle System Models**

Integro-differential equations can be thought of as a long-range limit of
individual based, spatially explicit particle systems [10], which are called
interacting particle systems. Such interacting particle systems can be
used to model individual plants, and thus allow us to study short range
interactions. We asked whether an individual based model with short
range interaction would show different results.

We modeled the system on a two dimensional regular grid $\mathbb{Z}^2$, using
an interacting particle system. Each point on the grid is either vacant
(white), or occupied by a female (black) or hermaphroditic (grey) plant.
All individuals die at rate 1. Hermaphrodites give birth onto vacant sites
within their seed dispersal neighborhood, $r_f$, at rate $\beta_h$. Male steriles give
birth onto vacant sites within their seed dispersal neighborhood, $r_f$, at
rate proportional to the number of hermaphrodites within whose dispersal
neighborhood, $r_p$, they reside. The constant of proportionality is $\beta_s$.
Initial conditions are product measure with equal frequencies.

We simulated this system on the stochastic simulator, S3. The results,
which we show in Figure (7), are qualitatively equivalent to the results
we derived from the differential-integral equations. Specifically, what we
observe is first, in order for both species to coexist, the female birth rate
must be significantly higher then the hermaphroditic birth rate. Second,
clustering occurs only if the pollen dispersal neighborhood is much larger
then the seed dispersal neighborhood.

**FIGURE SEVEN HERE**

**Hermaphrodites are pollen limited**

Finally, we ask whether our results are due to the assumption that hermaphroditic
are not limited by pollen. In order to test this, we assume that a fraction,
$\epsilon$, of the hermaphroditic plants are pollinated in a density independent
manner, and the remaining fraction, $1 - \epsilon$, are pollinated in a density
dependent manner. This leads to a non-spatial model of the form.

$$ \frac{d u}{dt} = r_1 (1 - u - v)uv - u $$

(29)
\[
\frac{d}{dt} v = r_2 (1 - u - v)(\epsilon v + (1 - \epsilon) v^2) - v \quad (30)
\]

Note that in the special case \( \epsilon = 1 \), the system is the same as that studied above. This has the nontrivial equilibrium solution

\[
u = 1 - \frac{r_2 \epsilon}{r_1 - r_2 (1 - \epsilon)} - \frac{1 - \epsilon}{r_1} \quad (31)
\]

We will only consider values of \( r_1 \) and \( r_2 \) so that this equilibrium exists and is stable. Again we will transform this to a spatial model by the introduction of seed and pollen dispersal kernels, \( k_s(x) \) and \( k_p(x) \). This gives us the following system.

\[
\frac{\partial}{\partial t} u = r_1(1 - u - v)[k_s * u[k_p * v]] - u \quad (32)
\]

\[
\frac{\partial}{\partial t} v = r_2(1 - u - v)[k_s * (\epsilon v + (1 - \epsilon) v[k_p * v])] - v \quad (33)
\]

We will follow the same program as we used to analyze the original spatial system. Thus we first switch to a coordinate system in which the spatially constant equilibrium is \( f(x) = 0, h(x) = 0 \). The system becomes

\[
\frac{\partial}{\partial t} f = r_1 (1 - f - f' - h - h')[k_s * (f + f')][k_p * (h + h')] - (f + f') \quad (34)
\]

\[
\frac{\partial}{\partial t} h = r_2 (1 - f - f' - h - h')[k_s * (\epsilon (h + h') + (1 - \epsilon)(h + h'))] - (h + h') \quad (35)
\]

Next we linearize about this equilibrium. The linear system is

\[
\frac{\partial}{\partial t} f = -r_2 f' (f + h) + (f'/h')(k_s * [k_p * h]) + [k_s * f] - f \quad (36)
\]

\[
\frac{\partial}{\partial t} h = -r_2 h'(\epsilon + (1 - \epsilon)h')(f + h) + [k_s * h] + \frac{r_2}{r_1} (1 - \epsilon)[k_s * [k_p * h]] - h \quad (37)
\]

In order to study the stability of the equilibrium state, we Fourier transform these equations to get the ordinary differential equations

\[
\frac{\partial}{\partial t} \tilde{f} = [-r_2 f' + \tilde{k}_s - 1] \tilde{f} + [-r_3 f' + (f'/h')\tilde{k}_s\tilde{k}_p] \tilde{h} \quad (38)
\]

\[
\frac{\partial}{\partial t} \tilde{h} = [-r_2 h'(\epsilon + (1 - \epsilon)h')] \tilde{f} + \tilde{h} \quad (39)
\]

Analysis of the eigenvalues of this system is algebraically quite complicated, and we restrict ourselves to studying the eigenvalues numerically. In Figure (8), we have choose \( r_1 = 8, \ r_2 = 2, \) and \( \epsilon = 0.25 \). The dark area corresponds to values of \( \tilde{k}_s(\omega) \) and \( \tilde{k}_p(\omega) \) for which one of the eigenvalues is positive. The lighter area corresponds to values for which both eigenvalues are negative.

**FIGURE EIGHT HERE**
Thus, we see that qualitatively the situation is the same as the case where pollination of hermaphrodites is not density dependent; in order to have a positive eigenvalue (and thus a unstable spatially constant equilibrium), \( \hat{k}_p(\omega) \) must be negative, and \( \hat{k}_r(\omega) \) must be positive and close to 1. We have tested this for a different values of \( \epsilon > 0 \), as well as different values of \( r_1, r_2 \). Note that the condition on \( \epsilon \) is necessary in order for the nontrivial equilibrium to be stable. This picture is typical of these results as long as parameters are chosen in such a way that the nontrivial equilibrium to the ordinary differential equation system exists and is stable.

Conclusion

In this paper we derived conditions which must be satisfied by seed and pollen dispersal in order for spatial patterns to arise in a gynodioecious plant population. We show that two things must be true. First, pollen dispersal must be longer range than seed dispersal. Second, pollen dispersal must be such that there is a clear transition between the area where a plant’s pollen falls, and the region where it does not fall. Mathematically, this corresponds to the statement that the Fourier transform of the pollen dispersal kernel must be negative for some wavelengths.

These conditions were derived using linear stability analysis. We have also numerically solved the integro-differential equations, and simulated a related interacting particle system. These results agree with the stability analysis.

There are other interesting questions which might be asked in further modeling studies of gynodioecious populations. As mentioned above, two-dimensional simulations of the integro-differential equations show that the topology of the stable, non-constant spatial pattern of plants depends on the form of the dispersal kernels. It would be interesting to find conditions on the dispersal kernels which lead to realistic spatial patterns.

Another interesting avenue for future research would be to incorporate a third species, one which carried a “restorer” gene. These genes have been shown to offset the mutations which cause male sterility.

Finally, it would be very interesting to know if the specific predictions of this model, for example, that the size of male sterile clusters is proportional to pollen dispersal length, are consistent with field observations.
References


Appendix A

We wish to linearize the system

\[
\frac{\partial}{\partial t} f = r_1(1 - f - f' - h - h')[k_a \ast (f + f')[k_p \ast (h + h')]] - (f + f')
\]

\[
\frac{\partial}{\partial t} h = r_2(1 - f - f' - h - h')[k_a \ast (h + h')] - (h + h')
\]

(40)

about the equilibrium, \( f(x) = 0, h(x) = 0 \). We will be using the fact that the convolution of the constants \( f' \) and \( h' \) with the dispersal kernel \( k_p \) and \( k_a \) leaves the constants unchanged. We will also use the fact that \( f' \) and \( h' \) are equilibrium solutions of the ordinary differential equations (2), and thus

\[ r_1 h(1 - h - f) = r_2(1 - h' - f') = 1. \]

First we rewrite the system

\[
\frac{\partial}{\partial t} f = -r_1(f + h)[k_a \ast (f + f')[k_p \ast (h + h')]]
\]

\[ + r_1(1 - f' - h')[k_a \ast (f + f')[k_p \ast (h + h')]] - (f + f') \]

\[
\frac{\partial}{\partial t} h = -r_2(f + h)[k_a \ast (h + h')]
\]

\[ + r_2(1 - f' - h')[k_a \ast (h + h')] - (h + h'). \]

(41)

This is equivalent to

\[
\frac{\partial}{\partial t} f = -r_1(f + h)[k_a \ast (f[k_p \ast h] + f'[k_p \ast h] + f h' + f' h')]
\]

\[ + (1/h')[k_a \ast (f[k_p \ast h] + f'[k_p \ast h] + f h' + f' h')] - (f + f') \]

\[
\frac{\partial}{\partial t} h = -r_2(f + h)[(k_a \ast [h + h']) + (k_a \ast h)] + h' - (h + h')
\]

(42)

Next, we discard the quadratic terms and perform algebraic manipulations involving the definitions of \( f' \) and \( h' \). We now have the system

\[
\frac{\partial}{\partial t} f = -r_2 f'(f + h) + (f' / h')[k_a \ast [k_p \ast h]] + [k_a \ast f] - f
\]

\[
\frac{\partial}{\partial t} h = -r_2 h'(f + h) + [k_a \ast h] - h
\]

(43)
Figure 1: A graphical representation of the conditions which must be satisfied by $r_1$ and $r_2$ in order for hermaphrodite and male-sterile coexistence.
Figure 2: The dark region corresponds to values of $\hat{k}_x(\omega)$ and $\hat{k}_y(\omega)$ for which the spatially constant solutions are unstable in the spatial model in which hermaphrodites are not pollen limited with $r_1 = 8$ and $r_2 = 2$.

Figure 3: A simulation in which the spatially constant solution is stable. Initial conditions are equal to the constant equilibrium plus noise.
Figure 4: On the left, seed and pollen dispersal kernels corresponding to the Fourier transforms on the right. The pollen dispersal kernel, $k_p(x)$, is much broader than the seed dispersal kernel, $k_s(x)$.

Figure 5: A simulation of the model with the seed and pollen dispersal kernels as in Figure 4. We see the female population. Initial conditions are as in Figure 3.
Figure 6: This is the stable, non-constant equilibrium to which the simulation is Figure 5 evolve. This shows both the female and hermaphrodite populations.

Figure 7: Interacting particle system simulation. Black represents females, grey represents hermaphrodites, and white represents empty space. On the left, seed dispersal is longer than pollen dispersal, and we see a well mixed population. On the right pollen dispersal is longer than seed dispersal and we see clustering of females.
Figure 8: The dark region corresponds to values of $\hat{k}_n(\omega)$ and $\hat{k}_p(\omega)$ for which the spatially constant solutions are unstable in the spatial model in which hermaphrodites are pollen limited with $\epsilon = .25$, $r_1 = 8$ and $r_2 = 2$. 