DYNAMICS OF SELF–ORGANIZATION OF RAMIFIED PATTERNS IN AN ELECTROMECHANICAL SYSTEM.

BY

JOSEPH JUN

B.A. New York University, 1997

THESIS

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We study the dynamical self-organization of conducting particles into ramified tree networks when subjected to strong electric fields. We find that for a general class of initial configurations of particles that the trees grow in three stages: (I) strand formation, (II) boundary connection, and (III) geometric expansion. We show that graph theoretical measures like the average adjacency of particles clearly delineate the three growth stages. Additionally, we find that each particle becomes one of three species of particles, depending on the number of connections each particle makes with neighboring; this process occurs on a relatively short time scale. We find that the numbers of each kind of species is statistically robust across different experiments that have similar numbers of particles. We numerically explore the electrodynamic properties of the system, including the overall resistance; we find that this quantity scales non-linearly with the number of particles in the network. We qualitatively investigate the effects of the initial configuration of particles, and we find that the initial conditions strongly influence the final form of the networks, e.g. their topological structure.

To understand how the geometrical arrangement of particles influences the steady-state topology of the system, we generate artificial trees using experimental data to seed our algorithms. By applying graph theory to the system, we attempt to predict the topological structure of the experimental trees. To accomplish this, we use three algorithms: 1) random, 2) minimal spanning, and 3) propagating front. We compare the results of the different algorithms and find that the minimal spanning tree algorithm reproduces the best match to the statistics of the experimental trees.

In the experiments described above, we explore the dynamics of how tree struc-
tures self-organize in the system. We are also interested, more generally, in how the detailed structure of ramified patterns affects the properties of systems that use them for transportation. Therefore, in collaboration with researchers at the Santa Fe Institute, we theoretically explore a biological system: ant foraging colonies. These are commonly known to forage along ramified trunk trail networks. We show that the structure of these foraging patterns has consequences on the net energy collection rate of the ant colony. From this, we predict that there should exist both an optimal and maximal colony size.
To Annie
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Chapter 1

Introduction

Pattern formation, loosely speaking, is the study of order in open dissipative systems; this includes dynamic self–organization, characteristic of fluid and chemical systems (Swinney (1996)), and inhomogeneous growth, characteristic of some physical (Witten and Sander (1981); Niemeyer et al. (1984); Rinaldo et al. (1993)) and biological (Matsushita and Fukiwara (1991); Tsimring et al. (1995)) systems¹. Of more recent interest, not generally categorized under pattern formation, is the evolution of complex networks characteristic of economic, sociological, and ecological systems (Albert and Barabási (2002)). Though this latter study has so far focused on abstract topological questions, it may soon make important connections with some of the former studies, especially as it pertains to branched—what we shall refer to as ramified—patterns used for transportation throughout nature. Indeed, several researchers have attempted to include either spatial (i Cancho and Solé (2001); Gastner and Newman (2004)) or flow (Toroczkai and Bassler (2004)) constraints to the study of complex networks. Meanwhile, efficient transportation of resources through real fractal networks and especially the topologies of those networks were an important insight into understanding the allometric scaling of all organisms (West et al. (1997); Banavar et al. (1999)).

¹An excellent popularized account can be found in Ball (1999)
An example of a non-biological transportation network was studied theoretically and experimentally in an electromechanical system where conducting particles self-organize into dendritic patterns under the influence of an electric field (Merté et al. (1988); Hadwich et al. (1990); Dueweke (1997)); figure 1 shows the dendrites produced in experiments by Merté et al. The black strands are the dendrites which actually consist of discrete macroscopic conducting spheres submerged in a castor oil medium; figure 1 (a) shows an experiment consisting of 1000 particles, and (b) shows one for 400 particles. The ring surrounding the dendrites is also conducting and is connected to the negative terminal of a power source; the positive terminal is not shown but hovers above the rest of the experiment; the power source fixes the potential difference $V$ between the two; typical values for $V$ range from 15 kV–25 kV. The particles started the experiment in a random configuration; when the steady-state structures shown in fig. 1 form in the system, the particles are now electrically connected to the ring and hence the negative terminal of the battery. We shall henceforth refer to the ring as the boundary electrode (BE) and the positive electrode as the source electrode (SE).

![Figure 1.1](image)

**Figure 1.1**: Figure reproduced from Merté et al. (1988). The dendrites (black strands) formed by the electromechanical system for (a) 1000 particles and (b) 400 particles. The ring surrounding the dendrites is electrically connected to the negative terminal of the power source. Figure (c) is the same as (b) except all the endpoints observed to point toward the source electrode are highlighted.

The first papers studying this phenomenon were concerned with the variational principle that governs open-dissipative systems; the authors’ view was that the system minimizes the dissipation due to ohmic resistance. In this thesis, we focus away
from the minimal properties of the limiting state of the system, and instead shift to studying the dynamics of the system. This has several key advantages. One, because the variational methods focus on the steady-state properties of the system, it is not predictive of the structure of the dendrites. By looking at the dynamics, we can hope to examine the conditions that lead to particular structures, and attempt to predict them. Two, it allows us to explore a far greater range of initial conditions than those studied by previous authors, who used only random initial conditions. Indeed, we find an entirely new phenomenon when the particles are initially arranged far away from the boundary electrode; they move as strands that “inch” their way to connect to the boundary. At this point, the rest of the particles can join the boundary by connecting to neighboring particles, and they do so by forming a ramified network. After this connection period, the particles expand to fill the available space in the dish. We classify these three growth periods into stages: (I) strand formation, (II) boundary connection, and (III) geometric expansion. By applying graph theory to the system, the transitions between the stages are clearly visible. We also examine the steady-state structure of the networks using graph theory. We classify three different species of particles depending on the number of other particles to which they are connected: 1) a terminus connects to only one other particle, 2) a trunk connects to exactly two particles, and 3) a branching point connects to three or more particles. We find that the relative proportion of these particles is statistically robust across different experiments; they increase linearly with increasing particle number. We also qualitatively explore different initial conditions and find that the symmetry of the initial state persists in the final state. To study perimeter effects, we perform a set of cheat experiments where we bypass growth stage I. We find that these experiments produce more termini than the natural case.

We also explore the electrodynamic properties of the system, especially the overall resistance; we show that this quantity scales nonlinearly with the number of particles.
in the network. We find, in contrast to previous work, that the number of termini does not necessarily correlate with a decrease in the overall resistance of the system. We demonstrate an extreme case of this by producing an artificial spiral that has a resistance of nearly one-third of that of a comparably sized network. Even for real experimental structures, comparing the cheat experiments to the natural experiments, we find that the latter set are consistently lower in resistance than the former despite the fact that the cheat experiments contain more termini.

To understand how the geometrical arrangement of particles influences the topological structure of the system, we use graph theory to predict the structure of the trees. To do this, we generate artificial trees using experimental information of the positions of particles. We take as input a snapshot of the state of the experiment directly preceding the initiation of stage II. We then implement different algorithms on that snapshot to find ways to connect the particles together such that they form a tree. The three algorithms are: 1) random, 2) minimal spanning, and 3) propagating front. We compare the results of the different algorithms and find that the minimal spanning tree algorithm reproduces the best match to the statistics of the experimental trees.

Finally, in the experiments described above, we explore the dynamics of how tree structures self-organize in the system. We are also interested, more generally however, in the ways in which the detailed structure of ramified patterns can affect the properties of systems that use them for transportation. Therefore, in collaboration with researchers at the Santa Fe Institute, we theoretically explore ant foraging. Many species of ants are known to forage along ramified trunk trail networks. We show that the structure of these foraging patterns has consequences on the net energy collection rate of the ant colony. From this, we predict that there should exist both an optimal and maximal colony size.

In the remainder of this section, I will give a comprehensive review of the previous
experiments and theory relevant for the electromechanical system.

1.1 Dendritic structures in an electromechanical system—a review

1.1.1 Merté et al. (1988)

The first papers were concerned with the variational principle that governs open-dissipative systems in general. Merté et al. made the first attempt at a variational calculation of the electromechanical system that is the topic of this thesis. They claimed that a dendritic structure minimized the dissipation in the system. They showed this by stating, without proof, that the potential energy of the system, $U$, is a Lyapunov\(^2\) function and therefore must be minimal. Thus, the dissipation given by

$$D = \int \int (\nabla \varphi(r))^2 / \rho_{oil} \, dA = \frac{U}{\rho_{oil} \varepsilon_{oil}}, \quad (1.1)$$

must also be minimal for the structures to be stable. The integral in 1.1 is performed over the oil surface; $\varphi(r)$ is the electric potential as a function of position $r$ on the oil surface, $\rho_{oil}$ is the resistivity of the castor oil medium, and $\varepsilon_{oil}$ is the dielectric constant of the oil.

The authors did not prove that the structures must be dendritic for the dissipation to be minimal. Instead, their proof is generic; any structure that is stable under the conditions of their theory must be minimal in dissipation. Since dendrites are observed in the experiment, the authors (implicitly) conclude that the dendritic structures formed by the system have minimal dissipation. This fact severely limits the scope of

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\(^2\)A Lyapunov function, call it $L(x)$, is a potential-like function. If one can be constructed (if it exists) in a system, then the system dynamics has no closed orbits; the fixed point is globally asymptotically stable. Lyapunov functions must have the following three properties: 1) $L(x) > 0$ for all $x \neq x^*$; 2) $L(x^*) = 0$; and 3) $\dot{L}(x) < 0$, for all $x \neq x^*$. See Strogatz (1994) for details.
their calculation. It is not predictive, therefore any breakdown in assumptions implies that the observed dendrites may not belong to a minimal state.

The authors also experimentally studied the total resistance, \( R_{\text{total}} \), as a function of the number of particles, \( N \), in the dendrites. They did so by digitizing the positions of the particles and numerically solving the Poisson equation,

\[
\nabla^2 \varphi(r, t) = S(r, t) / \sigma_{\text{oil}},
\]

for the potential with a numerical relaxation method. \( \sigma_{\text{oil}} = 1 / \rho_{\text{oil}} \) is the conductivity of the oil; \( S(r, t) \) is the strength of the source as a function of space and time, which is assumed constant in time and uniform in space, \( S(r, t) = S_0 \). The boundary conditions used for 1.2 is that the boundary electrode, all particles electrically connected to it, and everything outside of it are fixed at zero potential, \( \varphi = 0 \). Using this method, the authors found that the resistance scales with the number of particles as \( R_{\text{total}} \sim N^\xi \) with \( \xi_{\text{Me}} = 0.73 \pm 0.03 \); this reported value of the scaling exponent must have been an error as their graph clearly shows \( R_{\text{total}} \) decreasing with the value of \( N \) (see fig. 1.1.1), so that \( \xi \) has to be less than zero. Even if the minus sign was omitted due to a typo, the absolute value of their \( \xi \) differs from other reported values by a factor of three. Also, it is not clear whether the assumption of space independence of the source holds in the system. The charge in the system conducts through the air, presumably by ionization of gas molecules in the air, and perhaps impurities like dust. Let us follow one such ionized particle. We assume that it is stripped on an electron near the positive source electrode. Positively charged, it is now attracted to the boundary electrode and connected particles, and it is repelled from the source electrode. As it scatters downward toward the dish, it well tend to move toward connected particles or the boundary electrode. There is a balance to this since there are other ionized particles in the air that tend to repel each other. This will push the charge particles out to a cone. The charge density distribution within the cone need not be uniform, and their in lies the issue of whether the source is independent
Figure 1.2: Figure reproduced from Merté et al. (1988). The scaling as a function of (a) the number of connected particles $N$ and (b) the number of endpoints. The scaling exponent for graph (a) was reported by Merté et al. as $\xi_{Me} = 0.73 \pm 0.03$

of space.

The authors also measured the change in resistance as a function of the number of endpoints—defined as the number of particles that touch only one other connected particle. Because the resistance decreases with increasing number of endpoints, the authors concluded that loops, or cycles, in the network are unstable. A loop can be broken into two endpoints; if the resistance decreases as the number of endpoints increases and if the resistance is minimal in the system, it follows that any loop should be unstable to forming two additional endpoints. It is not clear whether the authors found a relationship with the number of endpoints for fixed number of particles or whether they simply scaled the resistance with the number of endpoints while simultaneously increasing $N$. This is an essential point since, regardless of the number of endpoints, having more connected particles reduces the overall dissipation. This is due to being able to write the overall resistance from the dissipation 1.1 as $R_{total} = D/I_0^2$ where $I_0$ is the total current flowing through the system; increasing the number of connected particles will increase the charge collection rate of the system and hence increase $I_0$ thereby decreasing $R_{total}$. The authors did not address this issue, or present results on the scaling of the number of endpoints with number of total particles, or even report the scaling exponent of $R_{total}$ with the number of
Figure 1.3: Figure reproduced from Dueweke (1997). (a) Two endpoints initially apart from one another are (b) artificially placed into a closed loop. (c) after some time the loop breaks apart and the two endpoints return to the original state.

endpoints—they only showed it decreasing, see fig. 1.1.1 (b).

Reporting the scaling exponents would clarify the issue. Let us assume that the resistance scales with the number of endpoints $M$ as $R \sim M^{-\mu}$ and with the number of particles $N$ as $R \sim N^{-\xi}$, with $\mu, \xi \geq 0$. If endpoints are truly preferred due to minimal resistance arguments, then $\mu > \xi$. We could also infer the relationship by knowing how the number of endpoints scales with the number of particles. Say $M \sim N^\eta$, then $\eta \mu = \xi$. If endpoints are preferred, then $\eta = \xi/\mu > 1$. In other words, the relative proportion of endpoints should grow with increasing particle number. Though the instability of loop structures has indeed been observed by Dueweke (1997), see fig. 1.3, the argument that two tips are preferred over a loop due to minimal resistance requirements needs reexamination.

1.1.2 Hadwich et al. (1990)

The second paper written on the subject (Hadwich et al. (1990)) was also interested in the variational principles governing open–dissipative structures. Using the same electromechanical system described in the first paper, the authors reproduced the proof that the system must be in a state of minimal dissipation in greater detail.
Namely, to derive the Poisson equation 1.2, one starts with the continuity equation

\[ \dot{p} = -\vec{\nabla} \cdot \vec{J} + S_0 \]  

(1.3)

where \( p \) is the charge density, \( \dot{p} \equiv dp/dt \), and \( \vec{J} \) is the current density. Combining 1.3 with Ohm’s law

\[ \vec{J} = \sigma_{oil} \vec{\nabla} \varphi; \]  

(1.4)

one obtains 1.2 in the steady-state. In the experiment, however, charge can move when a particle moves. The second paper made explicit the assumption that the mechanical relaxation time scale \( \tau_m \) is far greater than the electrical relaxation time scale \( \tau_e; \tau_m \gg \tau_e \); thus they justified the adiabatic elimination (Haken (1978)) of the fast variable \( \dot{p} \approx 0 \). In other words, by the time a particle can move an appreciable distance so as to effect the flow of charge, the electric potential has already relaxed to a quasi-steady state value; at least on the time scale of the motion of a particle.

Solving 1.2 gives the steady-state value of the electric potential \( \varphi \) everywhere on the surface of the oil—all connected particles are considered in the boundary conditions. By writing the total potential energy of the system as

\[ U = \frac{\hbar \epsilon_{oil}}{2} \iint (\vec{\nabla} \varphi)^2 dA, \]

where \( h \) is the height of the oil, the authors assumed that the equation of motion of each particle is given by

\[ -\gamma \dot{q}_i - \vec{\nabla}_{q_i} U = 0 \]  

(1.5)

where \( q_i \) is the position of particle \( i \) and \( \dot{q}_i \equiv dq_i/dt \). In order for the system to reach a stationary state, \( \dot{q}_i = 0 \), therefore \( \vec{\nabla}_{q_i} U = 0 \); hence, the total potential energy \( U \) must be extremal in order to satisfy 1.5. To show that the stationary state is stable, the authors again invoked the fact that \( U \) is a Lyapunov function of the system; consequently, since \( U \) is related to the dissipation by 1.1, the dissipation \( D \) is also minimal for the stationary state to be stable.

Again there is no prediction in this analysis of the structure of the networks. It is only because they observe dendrites in the system that they claim dendrites are of
Figure 1.4: Graphs reproduced from Hadwich et al. (1990). (a) The number of endpoints \( M \) as a function of time for several values of the potential difference, \( 12.5 \text{kV} \leq V \leq 25.0 \text{kV} \). (b) The strong correlation between the fractal dimension, number of endpoints, and number of connected particles all as a function of time. (c) The fast convergence of the dissipation as a function of time. (d) The scaling of the dissipation as a function of \( N \), the scaling exponent is reported as \( \xi_H = -2.35 \pm 0.4 \).
minimal dissipation. For this to be true, the conditions of their variational principle must hold, but Hadwich does not list the range of validity of his calculation, i.e. for what ratios of physical constants.

Hadwich et al. also reported experimental results on the system; see fig. 1.4 for a synopsis of their results. Like Merté et al., they measured the dissipation as a function of the number of connected particles, except Hadwich et al. reports a scaling exponent \( \xi_H = -2.35 \pm 0.4 \) (fig. 1.4 (d)), a factor of three larger in magnitude than that reported by Merté. Though the two papers share some of the same authors, this discrepancy in the scaling exponents is not discussed.

Hadwich also reports the resistance as a function of time, which falls steeply initially and levels off to the steady–state value, fig. 1.4(c). This behavior correlates well with their measurements of the number of endpoints as a function of time; it increases rapidly and tops off near the same time as the resistance bottoms out. Their result suggests a strong inverse relationship between the number of endpoints and the resistance as argued by Merté; except, the resistance and the number of endpoints versus time also correlate strongly with the total number of connected particles. Indeed, citing his own thesis (Hadwich (1989)), Hadwich reports that the number of endpoints \( M \) scales with the number of grounded particles \( N \) linearly, \( M \sim N \); thus \( D \sim N^\xi \sim M^\xi \). Therefore, for reasons stated earlier, it is difficult to draw concrete conclusions about the true relationship between the number of endpoints and the total resistance of the dendrites, especially as it pertains to the stability of loops. Besides, Hadwich et al. and Merté et al. omit their method of calculating the resistance. Presumably there are ungrounded particles in the dish; though they are not fixed at a potential like the grounded particles, they may alter \( \vec{\nabla} \varphi \) since the surface of the conducting particles must be an equipotential. Presumably, both studies worked at a level of discretization where one particle fills only one grid point; thus eliminating the need to consider unconnected particles. The limitations of this
method are unknown.

Hadwich et al. used a box–counting algorithm to measure the fractal dimension \( d_f \) of the dendrites; this quantity is defined as

\[
d_f \equiv \lim_{\lambda \to 0} \frac{\ln N_b(\lambda)}{\ln(1/\lambda)}
\]  

(1.6)

where \( N_b(\lambda) \) is the number of boxes of linear size \( \lambda \) required to completely cover the dendrite. Their value, as a function of time, saturates near 1.6—they do not report the exact number. The dimension also correlates strongly with the number of connected particles and endpoints, fig. 1.4(b); Hadwich notes \( d_f \sim M \sim N \). Their reported value of \( d_f \) is shown only for a single combination of the potential difference \( V = 15 \text{ kV} \) and of the number of particles in the dish.

Though Hadwich does include a few temporal measurements of the system, he does not provide an account of the dynamics of the system. It is still unclear how the system develops into dendrites, other than that it converges rapidly to the steady–state structure.

### 1.1.3 Dueweke (1997)

Both early papers on the experiment were brief reports. Dueweke in his Ph.D. thesis (Dueweke (1997)) devoted two chapters (chapters 5 & 6) to the system, the former devoted to experimental measurements, the latter to theoretical results. Keeping with the pattern of earlier discussions, I will first review the theory in chapter 6.

Beginning with a brief review of dendrites throughout different branches of science. He brings up an interesting point about the various kinds:

An essential difference between biological systems and the physical dendritic structures which have been investigated up to now is the type of nonequilibrium, in particular the time dependence of the flux through the
surface of the dendrite. For example, a blood vessel system needs to provide a constant supply of nutrients. Therefore the flux of nutrients through the system is approximately constant, whereas the flux of heat through the interface of an [sic] dendrite growing in an undercooled melt, or the electric current in dielectric breakdown, is peaked in time. Furthermore, the volume of the blood vessel and other biological dendritic structures is constrained through efficiency considerations. (Dueweke (1997), p. 68)

Dueweke further claims that dendritic structures are stationary and stable in systems when “at least the space dependence of the imposed flux is fixed.” He proceeds to show that this is true for the electromechanical system discussed thus far by using a variational calculation, where the resistance is the extremal property. I will summarize Dueweke’s proof.

Dueweke’s analysis differs from those of Hadwich and Merté’s on several points. First, he considers a full three–dimensional model of the electric charges—he maintains the constraint that the particles move in two–dimensions. Second, he uses as his equation of motion:

\[-\gamma \dot{q}_i - \vec{\nabla} q_i (U(q_i, t) - W_B(q_i, t)) = 0\]  

(1.7)

The most noticeable difference in 1.7 from 1.5 is Dueweke’s inclusion of the work performed by the battery \(W_B(q_i, t)\). To estimate both \(U\) and \(W_B\), Dueweke calculated the free charge that resides on the interfaces between differing media; he notes that this free charge will reside on connected particles—on both the particle–air interface (p–air) and the particle–oil interface (p–oil), on the positively charged source electrode–air interface (se) that is above the experiment, and on the oil–air interface (oil–air). To get the free charge density \(\Lambda_f\) between media \(a\) and media \(b\), one notes Gauss’ law concerning the boundary conditions for the electric field between differing media

\[(\varepsilon_b \mathbf{E}_b - \varepsilon_a \mathbf{E}_a) \cdot \mathbf{n} = \Lambda_f\]  

(1.8)
together with Ohm’s law eq. 1.4, the free charge density becomes

\[ \Lambda_f = \left( \frac{\varepsilon_b - \varepsilon_a}{\sigma_b - \sigma_a} \right) J_n \]  

(1.9)

where \( J_n \) is the component of the current density that is normal to the surface of the interface.

It is then possible to write the free charge \( Q_{b-a} \) that resides on the interface of media \( a \) and \( b \) as

\[ Q_{b-a} = \int_{A_{b-a}} \Lambda_{f_{b-a}}(r, q_i, t) \, da = \int_{A_{b-a}} \left( \frac{\varepsilon_b - \varepsilon_a}{\sigma_b - \sigma_a} \right) J(r, q_i, t) \cdot da \]

\[ = \left( \frac{\varepsilon_b - \varepsilon_a}{\sigma_b - \sigma_a} \right) I_{b-a} \]

(1.10)

where \( I_{b-a} \) is the total current between the two media. The charge on each interface is given by:

\[ Q_{se} = \left( \frac{\varepsilon_{air}}{\sigma_{air}} \right) I_{se} \]  

(1.11)

\[ Q_{oil-air} = \left( \frac{\varepsilon_{oil} - \varepsilon_{air}}{\sigma_{oil} - \sigma_{air}} \right) I_{oil} \]  

(1.12)

\[ Q_{p-air} = - \left( \frac{\varepsilon_{air}}{\sigma_{air}} \right) I_{p-air} \]  

(1.13)

\[ Q_{p-oil} = - \left( \frac{\varepsilon_{oil}}{\sigma_{oil}} \right) I_{oil} \]  

(1.14)

Because of charge conservation, all of the charge that originates at the source electrode must flow through to the boundary electrode (assuming no leakage of charge in the system). According to Dueweke this can happen in two ways: 1) charge flows through the air directly to the connected particles or 2) charge flows through the oil to the connected particles. This means \( I_{total} = I_{tip} = I_{p-air} + I_{oil} \); which gives the following relationship for the charges in eqs. 1.11–1.14:

\[ Q_{se} = \frac{\varepsilon_{air}}{\sigma_{air}} (I_{oil} + I_{p-air}) \]

\[ = \frac{\varepsilon_{air}}{\sigma_{air}} (I_{oil} + I_{p-air}) + \frac{\varepsilon_{oil}}{\sigma_{oil}} I_{oil} - \frac{\varepsilon_{oil}}{\sigma_{oil}} I_{oil} \]

\[ = - \left( \frac{\varepsilon_{oil} - \varepsilon_{air}}{\sigma_{oil} - \sigma_{air}} \right) I_{oil} + \frac{\varepsilon_{air}}{\sigma_{air}} I_{p-air} + \frac{\varepsilon_{oil}}{\sigma_{oil}} I_{oil} \]

\[ = -Q_{oil-air} - Q_{p-air} - Q_{p-oil} \]

(1.15)
There are a few worthwhile remarks about eqs. 1.11–1.14. First, in eqs. 1.11, 1.13, and 1.14, the source electrode and the particles are made of stainless steel and therefore have a far greater conductivity than any other media in the experiment; therefore, it is assumed to be infinite, \( \varepsilon_p / \sigma_p \approx 0 \). Second, note from eqs. 1.12 and 1.14 that Dueweke implicitly assumes that the current between the oil-air interface flows completely through the particle-oil interface—Dueweke writes \( I_{\text{oil}} \) for both 1.12 and 1.14, i.e. \( \int_{\text{oil surf.}} J(r, q_i, t) \cdot dA = \int_{p-oil} J(r, q_i, t) \cdot dA \), rather than \( I_{\text{oil-air}} \) and \( I_{p-oil} \) respectively. This neglects the ability of the charge to flow from the oil straight to the boundary electrode; indeed, it also neglects the air-boundary electrode interface. The former omission will not effect Dueweke’s proof much, since in the end he approximates \( \sigma_{air} \gg \sigma_{oil} \); in other words, any charge moving through the oil is not considered to effect the system much, rather the connected particles collect most of the charge directly from the air. This approximation is supported by the observation that the oil moves away from the surface of the particles—there is enough oil in the dish for them to be submerged—and that the endpoints of the dendrites lift off of the dish and point toward the SE. The latter omission is also justified so long as the current density between the boundary electrode and the air is independent of the positions of individual particles (because the variational principle is performed over the positions of the particles); one can only presume that this is reasonable.

Once the charge distributions are known, it is possible to write both the potential energy and the work performed by the battery in terms of them. The potential energy is

\[
U(q, t) = \frac{1}{2} \varphi^+ Q_{se}(r, t) + \frac{1}{2} \varphi^- Q_{p-air}(r, t) + \frac{1}{2} \varphi^- Q_{p-oil}(r, t) + \frac{1}{2} \int_{\text{oil surf.}} \varphi(r, t) \Lambda(r, t) dA
\]

(1.16)

where \( \varphi^+ \) is the fixed potential of the source electrode and \( \varphi^- \) is the fixed potential of the boundary electrode. The term \( \varphi(r, t) \) is the potential at a point on the oil surface; it can, in principle, be determined by solving 1.2. Using 1.15 and the fact that
\( \varphi^+ - \varphi^- = V \) is the potential difference imposed by the battery, we can rewrite 1.16 as

\[
U(q, t) = -\frac{1}{2}(Q_{p-air} + Q_{p-oil})V - \frac{1}{2}Q_{o} \varphi^+ + \frac{1}{2} \int_{oil\ surf.} \varphi(r, t) \Lambda(r, t) dA \tag{1.17}
\]

The work done by the battery is given by:

\[
W(q, t) = Q_p(\varphi_{high} - \varphi_{low}) = -(Q_{p-air} + Q_{p-oil})V - \int_{oil\ surf.} (\varphi^+ - \varphi(r, q_i, t)) \Lambda_{o} \varphi(r, q_i, t) dA = Q_{o} \varphi^+ + \int_{oil\ surf.} \varphi(r, q_i, t) \Lambda_{o} dA \tag{1.18}
\]

which is the work needed to move charge through the relevant change in electric potential—\( V \) for charge sitting on the particle, \( \varphi^+ - \varphi(r, q_i, t) \) for charge sitting on the surface of the oil at position \( r \). Equation 1.18 neglects the work done by the battery in keeping a steady current, which is the energy needed to push the charge through ohmic dissipation. Dueweke argues that this work does not effect the movement of the particles, and is therefore omitted from the present discussion.

Now that the work and potential energy are established, it is possible to rewrite the particle equation of motion\(^3\), eq. 1.7, in terms of the electric potential and the charge distribution.

\[
\gamma \dot{q}_i = -\frac{1}{2}V \nabla_{q_i} (Q_{p-air} + Q_{p-oil}) - \frac{1}{2} \varphi^+ \nabla_{q_i} Q_{o} \varphi^+ + \frac{1}{2} \int_{oil\ surf.} \varphi(r, q_i, t) \Lambda_{o} \varphi(r, q_i, t) dA + \frac{1}{2} \int_{oil\ surf.} \Lambda_{o} \varphi(r, q_i, t) \nabla_{q_i} \varphi(r, q_i, t) dA \tag{1.19}
\]

By adding and subtracting a term \( \frac{1}{2} \varphi^- Q_{o} \varphi^+ = \frac{1}{2} \int_{oil\ surf.} \varphi^- \Lambda_{o} dA \)

---

\(^3\)Dueweke and I differ on this equation by a factor of a minus sign in the last term. In taking the gradient of the work in 1.18, Dueweke appears to have neglected to take the gradient of \( \varphi(r, q_i, t) \).
into 1.19, we write:

\[ \gamma \dot{q}_i = -\frac{1}{2} V \nabla_{q_i} (Q_{p-air} + Q_{p-oil} + Q_{oil-air}) \]

\[ + \frac{1}{2} \int_{oil \ surf.} \left( \varphi(r, q_i, t) - \varphi^- \right) \nabla_{q_i} \Lambda_{oil-air}(r, q_i, t)dA \]

\[ + \frac{1}{2} \int_{oil \ surf.} \Lambda_{oil-air}(r, q_i, t) \nabla_{q_i} \varphi(r, q_i, t)dA \]

(1.20)

The charge in the first term of eq. 1.20 can be related to the total current in the system from 1.15 and 1.11,

\[ Q_{p-air} + Q_{p-oil} + Q_{oil-air} = -Q_{se} = -\frac{\varepsilon_{air}}{\sigma_{air}} I_{total} \]

Therefore the equation of motion reduces to

\[ \gamma \dot{q}_i = \frac{1}{2} \frac{\varepsilon_{air}}{\sigma_{air}} \nabla_{q_i} I_{total} + \frac{1}{2} \int_{oil \ surf.} \nabla_{q_i} \left( (\varphi(r, q_i, t) - \varphi^-) \Lambda_{oil-air} \right) dA \]

(1.21)

If we now consider the relationship between the total current and the total resistance as \( R_{total} = V/I_{total} \), and if we rewrite the charge density in terms of the current density from 1.9, then we may rewrite 1.21 as

\[ \gamma \dot{q}_i = -\frac{1}{2} I_{total}^2 \frac{\varepsilon_{air}}{\sigma_{air}} \nabla_{q_i} R_{total} \]

\[ + \frac{1}{2} \left( \frac{\varepsilon_{oil}}{\sigma_{oil}} - \frac{\varepsilon_{air}}{\sigma_{air}} \right) \int_{oil \ surf.} \nabla_{q_i} \left( (\varphi(r, q_i, t) - \varphi^-) J_{n,oil-air}(r, q_i, t) \right) dA \]

(1.22)

where \( J_{n,oil-air} \) is the current density normal to the oil-air interface. As mentioned earlier, Dueweke argues that because \( \sigma_{oil} \ll \sigma_{air} \) that the majority of charge will collect on the particle–air interface, especially at the dendrite endpoints which lift off the dish floor. Provided this argument holds, then \( J_{n,oil-air} \) should be small and the second term in eq. 1.22 can be neglected and we are left with Dueweke’s main result

\[ \gamma \dot{q}_i = -\frac{1}{2} I_{total}^2 \frac{\varepsilon_{air}}{\sigma_{air}} \nabla_{q_i} R_{total} \]

(1.23)

In other words, particles in the system are pushed toward regions where the overall resistance decreases. Again, Dueweke invokes the argument that \( R_{total} - R_{min} = L \),

\[ 4 \text{Again, because of the sign difference in eq. 1.19, Dueweke and I differ on the second term of this equation as well. It will not effect the results critically, as Dueweke neglects this term in his final analysis, but it may alter the arguments needed to eliminate it.} \]
where $L$ is a Lyapunov function for the dynamics of the system, which requires that $dL/dt \leq 0$ and $L(t \to \infty) = 0$, meaning the system approaches a state of minimum total resistance. I assume that Dueweke means a local minimum, as the global minimal state is argued by Marani et al. (1998) to be a lattice. I will discuss that paper in a later section.

All of the variational principles neglect the inertial term in their analyses, i.e. $m\ddot{\mathbf{q}}_i$. None of them discuss the range of validity of this approximation. Another problem: The variational principle indicates that the velocity of all the particles are zero in the minimal state. In the experiment, however, it is observed that the particles can sway significantly and do not remain stationary in the dendrites. Nevertheless, the topology of the dendrites does not change as a result of this motion; the particles maintain their connection structure.

Dueweke also admits that the inclusion of static friction may keep the system from reaching a truly optimal state. Of course, this kind of dynamical consideration is completely left out of a variational calculation—this criticism applies to all the above authors’ work. Indeed, the variational calculation only determines a property of the system in the steady-state. It does not predict how the network should look in order for it to meet this criterion; it merely shows that under the constraints of the calculations the system will tend toward a state of minimal resistance. Indeed, the landscape over which the system navigates is a $2^N$-dimensional space, of which we know very little; perhaps, a variational principle is trivially met in such a space. Regardless, it is entirely impossible to match the state of minimal resistance to the structures found in the system. Moreover, if there exist multiple degenerate minima, how does the system break the symmetry? How far across the landscape can the system see? Particles typically join the boundary a few at a time, how does this temporal sequence effect the trajectory through the landscape? None of this is addressed in any of the variational calculations reviewed here.
Moreover, the variational calculation relies on the fact that the potential energy $U$ will also be minimized by the system. Therefore, there is no calculational gain, nor deeper insight offered by formulating a variational principle in terms of the resistance. It is not clear from their calculations that their results should be general for other open–dissipative systems.

To conclude my discussion of Dueweke’s work, I will summarize some of his experimental findings. Dueweke repeated many of the measurements performed by both Merté et al. (1988) and Hadwich et al. (1990), confirming and expanding some, and contradicting others. For example, his value for the scaling exponent of the total resistance as a function of the number of connected particles was reported as $\xi_D = -2.33 \pm 0.13$, in agreement with Hadwich. But whereas Hadwich reported that the scaling exponent of the total resistance with the number of connected particles was the same as the scaling exponent with the number of endpoints $M$ or $R_{\text{total}} \sim N^{\xi_H} \sim M^{\xi_H}$, Dueweke reports that the scaling exponent with the number of endpoints is $\xi_{M,D} = -1.85 \pm 0.13$, implying that the number of endpoints do not scale linearly with $N$ as reported by Hadwich. Dueweke does not describe the reason for the discrepancy; furthermore, Dueweke does not show a plot of $M$ vs $N$. One can infer the relationship from their scaling relationships with the total resistance, $M \sim N^{\xi_D/\xi_{M,D}} = N^{1.26}$. This would mean that the relative proportion of endpoints increases with increasing particle number; thus Dueweke’s results suggest that endpoints are preferred in the system. The discrepant results from all three authors makes it difficult to determine.

As a side note, Dueweke estimated $R_{\text{total}}$ by numerically solving a discretized version of Poisson’s equation, 1.2, for $\varphi(r)$. He then used the steady–state value of $\varphi$ to numerically integrate eq. 1.1 for the dissipation $D = I_{\text{total}}^2 R_{\text{total}}$, written as

$$R_{\text{total}} = \frac{\hbar \sigma_{\text{oil}}}{I_{\text{total}}^2} \sum_{i=1}^{L} \sum_{j=1}^{L} \left( (\varphi_{i+1,j} - \varphi_{i,j})^2 + (\varphi_{i,j+1} - \varphi_{i,j})^2 \right)$$  \hspace{1cm} (1.24)

where $L$ is the linear size of the square lattice used to discretize the dish and particles.
and $\varphi_{i,j}$ is the electric potential at lattice site $(i, j)$.

Dueweke also expanded previous measurements of the fractal dimension using the same box–counting method that Hadwich employed. Dueweke measured the fractal dimension $d_f$ as a function of $N$, rather than for a single value as Hadwich did. He found that $1.3 \leq d_f \leq 1.54$ for $300 \leq N \leq 1200$. It is difficult to gauge the form of the plot (see fig. 1.5); it is monotonic, but it may be weakly nonlinear or linear with a lower roll off. Regardless, Dueweke does not discuss the relationship between the fractal dimension and the total resistance. Ostensibly the fractal dimension derives from the spatial arrangement of the particles which should effect the overall resistance of the system; figure 1.6 shows the different dendrites formed for varying numbers of connected particles.

There are less than two orders of magnitude between the smallest and largest scale in the system. Applying a fractal measure like the box–covering dimension means little here. A more useful measure would be the mass dimension which would at least offer a description of the distribution of particles in the dish. Again, Dueweke offers only a few temporal measurements which show that the properties of the system converge rapidly. He does not, however, provide an overall picture of the growth of dendrites.

### 1.1.4 Marani et al. (1998)

Marani et al. were not concerned with a variational principle as the previous authors were. Instead, they wanted to discover a dynamical rule that gives rise to fractals (Marani et al. (1998)). Accordingly, they simulated the experiment discussed by the previous authors. Their simulation rules can be summarized as follows: place $N$ particles on a 2–D, $L \times L$ lattice; solve for the electric potential of all sites $\varphi_{i,j}$ by a relaxation method, again all boundary points and all particles connected to the boundary are set to $\varphi = 0$ (initially no particles are connected), non–connected
particles are treated the same way as unoccupied sites; calculate the value of $\nabla \varphi$ at every occupied site in all eight lattice directions; select the site and direction with the highest value of the gradient, and move the associated particle in that direction—multiple occupancy of a site is disallowed, the site and direction with the second highest gradient in potential is chosen, and so forth as required; particles continue to move in this fashion until one of them eventually reaches a site which neighbors either a boundary site or a site occupied by a particle already connected to the boundary; in this case, the potential must be recalculated everywhere with the new boundary conditions; all non-connected particles are then moved again with the same maximum gradient rule described already, particles that are connected no longer move; the simulation ends when all particles connect to the boundary. The authors claim that variations of this dynamical rule—ones that include simultaneous movement of all particles—produce qualitatively similar results.

The above algorithm does indeed produce fractal structures that resemble a cross between diffusion-limited aggregation clusters (Witten and Sander (1981)) and polymers, see fig. 1.7. The scaling dimensions they found are: box-counting dimension
Figure 1.6: Reproduced from Dueweke (1997). The different dendrites formed for different numbers of particles. (a) $N = 1260$, (b) $N = 1151$, (c) $N = 1047$, (d) $N = 939$, (e) $N = 901$, (f) $N = 750$. 
Figure 1.7: Figure reproduced from Marani et al. (1998). A typical dendrite formed by the algorithm of Marani et al. described in the text. The number of particles is 2048 and the grid size is 128 × 128.

d_{f} = 1.30 \text{ (for all values of } N), \text{ mass dimension } d_{m} = 1.63, \text{ and resistance scaling } \xi_{Ma} = 2.00; \ d_{f} \text{ is defined by } 1.6, \text{ the mass dimension is obtained by integrating the density of particles } n_{p}(r) \text{ as a function of the radius } r \text{ about some arbitrary point } P \ i.e. \int n_{p}(r)dr \sim r^{d_{m}}, \text{ the point } P \text{ is usually chosen near the center of mass, the discrete version replaces the integral with a sum. The authors admit that the values obtained through the simulation are not to be compared with the values observed in the experiment because of the stark simplifications of their model. However, they do note that their simulations provide statistically robust results for the estimated potential energy } U \text{ of each dynamically obtained configuration given the same boundary conditions and number of particles. They also note that their model produces fractals using non–stochastic rules, a departure from models such as the dielectric breakdown model (Niemeyer et al. (1984)) and the aforementioned diffusion–limited aggregation. It should be noted, however, that the fractalness of the structure can be due more to the sticking rule than the movement rule; fractals were found in the diffusion limited aggregation model where particles move randomly and stick to the existing cluster. There it is the shielding effect that create the fractal structures; particles are unlikely to navigate down into narrow ravines without bumping into the existing cluster. In this way, empty areas of the cluster are protected from filling with particles, which produces a fractal rather than compact structure. The same sticking rule applies to}
the algorithm of Marani et al.; it is no surprise, therefore, that their rule produces fractal structures.

**Figure 1.8:** Figure reproduced from Marani et al. (1998). The electric potential field $\varphi_{i,j}$ on the grid for the dendrite shown in fig. 1.7. The potential energy of this configuration can be estimated by using a discrete version of eq. 1.1. Compare this potential field with that shown in fig. 1.9

The authors raise an important point concerning the optimality of the structures. They claim, but do not show, that all dynamically produced configurations correspond to a local minimum in the potential energy. Their point is that this system is similar to other physical processes (Rodriguez-Iturbe and Rinaldo (1997)) where short-sighted searches for optimality produce structures that are within local optima, although it is not clear in what way the system is in a local optima from their paper. The potential energy is related to the electric potential by eq. 1.1, and the electric potential will be a function of the positions of all particles; thus, the local minimum resides in a $2^N$–dimensional space. Nevertheless, in support of their claim, the authors report that they performed a refined annealing procedure over dynamically established aggregates, however, they do not show the results of their procedure; they only mention that it produces aggregates that “show significant departures from the features of the initial structure.” The gist of the refined annealing procedure is to
Figure 1.9: Figure reproduced from Marani et al. (1998). An artificially produced lattice configuration (top right corner) and its associated electric potential field (below) for the same number of particles and the same grid size as in figures 1.7 and 1.8. Marani et al. argue that this is the globally minimum potential energy state.
stochastically rearrange the structure in order to escape from local minima, accept changes that produce an overall decrease in the desired goal function, in this case the potential energy. As changes are added to the structure, the noise level of the annealing procedure is lowered (akin to lowering the temperature, hence the nomenclature); the procedure is known to place goal functions near the ground state. The authors do not report the salient features of the obtained ground states for their system—do they share the robust statistical properties that their “parent” aggregates possess? By what fraction does the annealing procedure reduce the potential energy? Do the annealed structures retain fractal properties? Reputedly, the absolute global minimum of the potential energy is obtained for a given set of particles when they are arranged in a lattice, see fig. 1.9. The argument that Marani et al. offer is that for the one-dimensional case the optimal arrangement of particles is when they are uniformly separated from each other. By adding the condition that particles must be connected to the boundary either directly or through other connected particles, extending the one-dimensional argument to two-dimensions produces a lattice structure; it is not clear whether this extension to two-dimensions holds—the authors do not reproduce the proof. The authors artificially generated a lattice for a given particle number and found that the potential energy reduced by nearly a factor of three, well outside the error bars of the dynamically produced aggregates. Yet, questions remain. Why does the refined annealing procedure fail to place the system into the global minimum? Why is this configuration barred in the experimental system as well as the simulations? Even considering the argument that dissipation on the particles due to friction bar the system from obtaining the true optimal state (Dueweke (1997)), there is the fact that in the real system closed loops tend to break apart, disallowing lattices. If the variational principles discussed thus far are true, then the true global minimum state—the lattice—must be very narrow and surrounded by many strong local minima or by very steep walls leading out of it that in practice bar the system
from ever reaching the minimum, even if the perturbation from it is only within some tiny neighborhood \( \epsilon \) away from it in the \( 2^N \)-dimensional space.

To conclude my review of the relevant literature, I will quote a portion of the conclusion section from Marani et al. (1998), which summarizes quite neatly, besides their own work, the general state of research in this system.

Whether or not dynamical rules necessarily obey a variational principle, and thus whether fractal forms in nature are or are not metastable states of a dynamical search for optimality, our results suggest that one ingredient for the emergence of fractality is the existence of a set of stationary or recursive states satisfying a global constraint. In this case the constraint is the dissipation of the injected charge through the boundaries. It is thus possible that, in some cases, local interactions may yield a globally felt constraint through boundary conditions. The system studied here is analogous to glasses. There, the ground state is known to be a crystal but on rapid quenching of a liquid, the dynamics inhibit crystallization and a glassy structure (which is not fractal) is obtained. The key difference here is that the boundaries impose a global constraint which results in the metastable states becoming scale free over a certain range of length scales.

1.2 Research Summary

In this section I will summarize my research perspective at several points contrasting it to the work done by the previous authors. These points of contrast can be broadly summarized as follows: 1) all the previous research focused on the steady–state properties of the system, I study many of the dynamical aspects of the system; 2) rather than focusing on variational principles and dynamical rules, and hence the detailed
electrodynamics, I will attempt to abstract the system into a topological description, namely in how particles connect to other particles in the network; 3) whereas all of the previous authors considered one class of initial conditions for the particles, random initial conditions, I will explore general initial conditions.

By studying the dynamics of the system, it opens the possibility of making predictions of the final structure, as opposed to making an untestable statement about the steady–state properties of the system. Whereas past researchers only cared to show that the system be in some minimal state—one that is not verifiable experimentally, we want to discover how it is that the final state comes about. While Marani et al. did make such an attempt in simulation, they focused on the fractal properties of the system. Considering that there are less than two orders of magnitude between the smallest and largest scale, the fractal dimension is not a robust measure of the system.

Indeed, this leads us to the reason for changing from the physical electromagnetic description to the more abstract topological description. The topology of the network is both statistically robust across experiments and structurally stable in a single experiment—the particles will sway together while maintaining the connection structure. In this paper we will attempt to model this aspect of the system, how the particles choose to connect to one another. We do so through simulation by trying different algorithms to link particles together into a tree. In doing so, we will require a few ideas from graph theory, especially the notion of adjacency. We find that the quantity of various topological species and the average adjacency are good observables in the system in that they capture both the steady–state aspects and the dynamical properties of the system.

In studying general initial conditions, I will focus on those that are tightly compact, meaning that particles are connected together in some initial shape, but as a whole are far from the boundaries of the system. Under these kinds of initial con-
ditions, we find a new behavior: strand formation of the particles to connect to the boundary. Additionally, we find in this case that the system makes a rapid transformation into its final topological form, with the remainder of its evolution being guided only by its expansion into unoccupied space in the dish. We classify these different phenomena into stages, I will describe all of the stages in detail in chapter 2.

Finally, in the above studies, we focus on the dynamics of how tree structures self-organize in the system. We also wish to explore, more generally, how the detailed structure of ramified patterns effects the properties of systems that use them for transportation. Therefore, in collaboration with researchers at the Santa Fe Institute, we will model how ant colonies forage for food. Many ant colonies are commonly known to forage along ramified trunk trail networks. We will show that the structure of these foraging patterns has consequences on the net energy collection rate of the ant colony. From this, we predict that there should exist both an optimal and maximal colony size.

1.3 Thesis Overview

In Chapter 2, I describe in detail the experimental setup and illustrate the physical aspects of the system. I also present all of the experimental results from the system. I describe the dynamical formation of the network by showing details of each stage of growth in the experiment. I define the different topological species that each particle can be, and I show that the relative numbers of each type is statistically robust across experiments. I qualitatively explore the effects of the initial conditions by trying different shapes for the initial conditions. I test to see how particles on the perimeter effect the final topology of the system by testing a few special initial conditions. For comparison with previous studies, I also look at the electrodynamics of the system especially the overall resistance; I also test a few artificial cases.
In Chapter 3, I apply graph theory to the system in an attempt to make predictions on the topology of the trees. I artificially grow networks in computer simulation by using real data from the experiments. I apply three different algorithms on the system: random, minimum spanning tree, and propagating front model. I compare the statistical attributes of each of these three algorithms to those of the experimental trees.

In Chapter 4, I describe a model of how ant colonies forage for food. We find that the structure of how ants forage for resources places constraints on the net energy that they can intake. We find that this constraint predicts the existence of both a maximal and optimal colony size.
Chapter 2

Experiments in the dynamics of self-organization of ramified patterns

In this chapter, I will describe: 1) the experimental setup, 2) basic physical picture, 3) the dynamics of the self-organization, 4) the effects of the initial conditions, 5) the topological properties in the steady-state, 6) the electrodynamic properties in the steady-state, and finally 7) I will summarize my results.

2.1 Experimental setup

A schematic of the experimental setup is shown in figure (2). It consists of an insulating cylindrical dish (glass or acrylic) containing \( N \) (400–1200) nonmagnetic stainless steel ball bearings of radius \( r \approx 1.5 \text{ mm} \) and mass \( m \approx 0.016 \text{ g} \) completely immersed in a layer of castor oil. The dish has a radius \( R \approx 12 \text{ cm} \) and the layer of oil has a height \( h_{\text{oil}} \approx 3.5 \text{ mm} \). Two counter electrodes are set up: the source electrode (SE) is placed above the oil surface at a height of \( h_{\text{se}} \approx 5 \text{ cm} \); the boundary electrode (BE) lines the perimeter of the dish and is immersed in the oil. The SE and BE are
Figure 2.1: A schematic diagram of the experimental setup.

held at a fixed potential difference, $\Delta V \approx 20$ kV, by a high voltage power source. The entire experiment is encased in a glass enclosure to avoid convection currents in the air from disturbing it. The experiment is run at room temperature $T \approx 23^\circ$ and atmospheric pressure $P \sim 10^5$ Pa. Another important environmental variable is the relative humidity which effects the electrical conductivity of the oil surface, the experiments presented here were performed in a range of conditions varying from 18%-39% relative humidity.

We choose castor oil for the medium because it is a good insulator, has high viscosity, and the ohmic heating is low. Without the castor oil as medium, the particles are not sufficiently damped; instead of forming stationary patterns, the particles bounce against each other and the boundary. The height of the oil is chosen to be high enough to cover the particles, but low enough to allow the particles to feel the electric field.

The SE is so called because the change is viewed as being sprayed in a cone shape whose base rests on the oil surface and whose tip emanates from the SE; the charge carriers are electrons, therefore the charge originates from whichever electrode is attached to the negative terminal of the power source. We label the top electrode as
the source because it is located at the tip of the charge cone, not necessarily because the electrons originate from it. Switching polarity of the electrodes does not effect the formation of patterns. As a side note, if the lab is dark enough it is possible to see this cone of charge as a bluish tinge near the tip of the SE. The charge conducts through the air by ionizing gas molecules. The conductivity of the oil is theoretically quite small, but the presence of surfactants may it; their effect has not been studied in this thesis.

The BE is a thin cylindrical shell made of stainless steel. It lines the interior wall of the dish, surrounding the particles and the oil.

The stainless steel particles are spherical in shape. They are denser than the oil medium ($\rho_s = 7.68 \text{ g/cc}$, $\rho_{oil} = 0.96 \text{ g/cc}$), and therefore sink to the bottom of the dish. Before beginning an experiment, the particles can be set into an initial configuration (IC). The IC can be of arbitrary shape and density (compactness) on the plane. In this thesis, I will be primarily interested in studying the self–organization of particles that start from initially compact, circular distributions; in other words, the particles are initially arranged in a circle with a radius close to the minimum value possible for a given number of particles.

The particles interact through electrostatic forces with the SE, the BE, and each other. The SE is positively charged and produces a radial field along the dish. The BE is negatively charged and also produces a radial electric field. The particles, before connection, can carry charge by distributing charge amongst themselves and collecting charge that conducts through the air to the oil and finally to the particles. They also will interact with nearby particles via induced electric dipoles; these are induced from both electrodes, charged particles, and nearby particles that have dipoles.
2.2 Physical picture

The system can be described by Poisson’s equation:

$$\nabla^2 \varphi(\vec{r}, t) = S(\vec{r}, t)/\sigma_{\text{oil}}$$  \hspace{1cm} (2.1)

where $\varphi(\vec{r}, t)$ is the electric potential as a function of both space and time, $S(\vec{r}, t)$ is a source term, and $\sigma_{\text{oil}}$ is the specific conductivity of the oil medium. For simplification, we assume that the source sprays charge over the surface of the oil uniformly in space and at a constant rate in time. Therefore equation (2.1) simplifies to:

$$\nabla^2 \varphi(\vec{r}, t) = S_0/\sigma_{\text{oil}}$$  \hspace{1cm} (2.2)

Equation (2.2) holds with the following boundary conditions:

i. The BE is held at fixed potential

ii. Any particle connected to the BE either by direct contact or through contact to a chain of particles that touches the BE are held at the same fixed potential as the BE.

For convenience we consider the BE to be at zero potential, and we will often refer to particles that are in electrical contact with the BE as being grounded. Condition ii implies that the boundary conditions of the system are adjustable via the positions of the particles.

2.3 Dynamics of Network Self–Organization

There are three stages to the growth of the pattern: (I) strand formation, (II) boundary formation, and (III) geometric expansion. I will describe the phenomenology of the three stages below.

In stage I, the particles act coherently toward connecting to the boundary. This can best be seen in the single particle width strands that grow toward the outer
Figure 2.2: Time sequence for single experimental run. The number of particles in the final network is 784. (a) Circular initial condition, $t = 0s$ (b) After the voltage is applied bumps form along the perimeter of the distribution, $t = 10s$ (c) Bumps self-organize into chains, $t = 847s$ (d) One chain connects, the rest wither and form into outer termini, interior particles begin to form inner network, $t = 854s$ (e) Network unfolds from the outside in with little change in network structure, $t = 928s$ (f) Final state of network, the box indicates the area of detail shown in Fig. 2.8, $t = 4647s$. 
Figure 2.3: The growth of the six largest strands vs. time from an experiment containing 784 particles; the distance has been scaled by the diameter of a particle. The dashed line is the path of the average speed of the winning strand. The insets show that the distance that the lead particle moves correlates well with the number of particles in the strand, meaning that a lead particle of a strand moves by recruiting particles in its trail. The dashed lines in the insets are again the paths of the average speed for each strand.
Figure 2.4: The strand growth for an experiment containing 1044 particles. The coherence of the strands is much weaker than in the case shown for figure 2.3.

electrode, depicted in figs. 2.2 (b) and (c). The growth of individual strands vs. time for a typical experiment is shown in fig. 2.3. The graph plots the distance that the lead particle of a strand moves from its starting position as a function of time. The insets show that the distance of the lead particle matches well with the number of particles in a strand, defined as the number of particles that have moved more than one particle radius from their starting positions to join the strand. This means that the lead particle recruits particles behind it as it moves toward the boundary. The first noticeable feature from fig. 2.3 is that each strand grows in spurts, with periods of movement and rest. The second, more remarkable, feature is that there is some correlation between the spurts; strands tend to move and rest together. Looking at different numbers of particles, we see that the correlation still persists in higher numbers of particles, but that it is less pronounced, see figure 2.4. For smaller number of particles, the correlation is seemingly sharper, but in this case it is mostly due to the fact that very few strands move after a point, see figure 2.5. We have also found that the terminal velocity of the lead particle is \( v_t \approx 0.4 \text{mm/s} \).

In stage II, the particles connect together to form the network and establish its
Figure 2.5: The strand growth for an experiment containing 591 particles. The coherence of the strands is more pronounced, but this is simply because very few strands move beyond a point.

topology. The lead particle of the “winning” strand connects to the boundary; we shall refer to this particle as the root particle. Successive particles connect to neighbors that are already connected. The cascade of connections runs through all the particles in a short time, on the order of fractions of a second\(^1\). The key aspect of the connections is that the network topology sets during this time. In other words, each particle becomes one of three species: (i) is a trunk which connects to only two other particles; (ii) is a branching point which connects to three or more particles; (iii) is a terminus which connects to only one other particle (see fig. 2.8 for a detailed look at each kind of particle). Each particle that binds to the network chooses its species in stage II depending on how many neighboring particles it binds to, and therefore the topology of the network is largely determined during this stage. Reconfiguration of the frozen topology may occur during stage III, but because the particles are tightly bound to the network, the final structure is mostly determined in stage II. Figure 2.6

\(^1\)Video recordings taken at 30 frames per second do not capture the detailed dynamics of the cascade.
shows a measure of the connectedness of the particles as a function of time. The graph shows the average number of neighbors that each particle has surrounding it; we refer to this quantity as the average adjacency, \( \langle c \rangle \), mathematically defined as

\[
\langle c \rangle = \frac{1}{N} \sum_{i=1}^{N} c_i = \frac{1}{N} \sum_{i=1}^{N} \sum_{j \neq i}^{N} \Theta(l_c - |\vec{r}_i - \vec{r}_j|).
\]

Where the sums are over the total number of particles \( N \), and where \( c_i \) and \( \vec{r}_i \) are the adjacency and position of particle \( i \), and \( l_c \) is a cutoff length that would ideally be set very close to a particle diameter \( d \); \( l_c \) is set to be 1.21 \( \cdot d \) in fig. 2.6. Stage II is indicated in the plot, note the drastic change in slope of \( \langle c \rangle \) as a function of time after that point. The top dashed line is an estimate of the initial adjacency by considering the relative number of perimeter particles to volume particles, \( \langle c \rangle_0 \approx 6 - \frac{2\pi}{\sqrt{N}} \sqrt{\frac{(8\sqrt{3}+12)}{(7\pi)}} \). The bottom dashed line represents an estimate of the steady–state value of the adjacency that is derived purely from topological conservation; this value is given by \( \langle c \rangle_f = 2(1 - 1/N) \). Appendix A describes the methods and tools used here, and shows the derivation of the initial and steady–state adjacencies. Figure 2.7 shows the plot of the adjacency versus time, but with several experiments of differing numbers of particles plotted together. The dramatic drop in adjacency exists for all experiments. Greater numbers of particles produce a shorter stage I duration and also smooth out the transition to the steady–state adjacency.

In stage III, the network expands into the available space, while maintaining its network topology. Particles located nearest the boundary are the first to spread. The unfolding then proceeds to the inner particles until the entire network spreads to its maximum size. At this point, the network moves only slightly, which neither effects its topology nor its average spatial properties. The movement is mostly in the outer termini, where long terminal strands sway to and fro. Figures 2.2(d)-(f) depict the unfolding process. Figure 2.9 shows the radial distribution of particles at different times for a single experiment starting with the initial distribution (square points). At \( t = 847s \) (circular points), the particles are just about to hit stage II; most particles
**Figure 2.6:** Graph showing the adjacency $\langle c \rangle$, as a function of time for one experiment containing 513 particles. The various growth stages are indicated. The top dashed line is an approximation to the value of the initial adjacency $\langle c \rangle_0$ using geometric considerations. The bottom dotted line is the steady–state value of the adjacency $\langle c \rangle_f$, given by $2(1 - 1/N) \approx 1.996$. The inset shows the average adjacency for several values of the cutoff; the sharp transition is observed for all three values.

**Figure 2.7:** Graph showing the adjacency $\langle c \rangle$, as a function of time for several experiments with different numbers of particles. The sharp transition exists for all experiments. Experiments with higher numbers of particles have a shorter stage I and also have a smoother transition to the steady–state adjacency.
Figure 2.8: Detail of the final network from Fig. 2.2(f). The network is characterized by the three species of particles shown in the figure. Termini touch only one other particle; trunk particles touch exactly two other particles; branching points touch three or more particles.

have not moved except at larger radii at the perimeter where many have moved into strands. The other four sets of data show how the unfolding of stage III increases the spacing of the particles until the steady-state is reached; note that the distributions for $t = 1208s$ (diamond points) and $t = 4647s$ (sideways isosceles triangles) are nearly identical. Figure 2.10 shows the steady-state radial distribution of particles from different experiments containing similar numbers of particles. The mass dimension, defined as the exponent obtained from $\sum \rho(r) = N \sim r^{\zeta_m}$, was fitted from the data shown in figure 2.10. The obtained values of the dimension were $\zeta_m \simeq 1.74–1.91$.

It is also possible to observe the radial distribution of termini. Figure 2.11 shows a plot of this for the same set of experiments shown in figure 2.10. Again, the distributions are similar for experiments with similar numbers of particles. One can also compare the distribution of termini across experiments with different numbers of particles; this is shown in figure 2.12. If, however, we normalize both the radial distribution of all particles and the radial distribution of termini by the total number of each respectively, then the distributions are as shown in figure 2.13. For each experiment the normalized number of termini collapses over the normalized number
of particles indicating that the termini are evenly distributed throughout the network.

![Figure 2.9](image)

**Figure 2.9:** The radial distribution of particles as a function of time shown for a single experiment; the dashed lines are fits to the data shown to guide the eye. Between the start of the experiment and \( t = 847 \text{s} \), the time directly preceding stage II, there is only a change at the perimeter of the initial distribution. After that point, the particles spread rapidly until they settle into the steady–state distribution.

### 2.4 Steady–state properties of the networks

Successive experiments produce different networks; nevertheless, statistical features of the topology are robust. For example, the number of termini, \( T \), and branches, \( B \), will be similar for the same number of particles that comprise the network, \( N \). Further, \( T \) varies linearly with \( N \). Figure 2.4 shows a plot of \( T \) as a function of \( N \).

It bears mentioning that the network rarely forms closed loops–every terminus in the network has a distinct path to the boundary; only when the number of particles becomes too high (\( \sim 1400 \)) do they appear. Indeed, loops are unstable in the network. The inset of fig. 2.15 shows a pair of particles artificially placed in a loop; within a few moments the two particles separate from each other. Figure 2.15 also shows the separation of the two particles as a function of time.
Figure 2.10: The integrated number of particles as a function of the radius from the center of mass of the network for several different experiments with similar number of particles.

Figure 2.11: The distribution of termini for the same experiments shown in figure 2.10.
Figure 2.12: The distribution of termini for experiments with different numbers of particles.

Figure 2.13: A combination plot showing the distribution of all particles and termini normalized to the total number of each respectively. For each experiment the normalized distribution of all particles and termini collapse indicating that the termini are distributed evenly throughout the network.
Figure 2.14: The number of termini (above) and the number of branches (below) plotted against the number of particles in the network. Experiments were run with circular initial states.
Figure 2.15: The insets on the left show three snapshots of two particles (indicated by the two arrows in each photo) who were artificially placed in a loop (top). After less than a second the two particles separate from one another (middle). At that point, the particles return to a steady state (bottom). The colors on the photos have been digitally inverted for better visibility. The graph on the right shows the separation of the two particles (scaled by the size of one particle radius) as a function of time; the unfilled boxes represent the data points depicted by the inset photos on the left. The dashed line is a linear fit to the initial movement of the particles; this gives a relative speed of 1.92 mm/s.
Another interesting note, branching points mostly connect to three other particles. Connecting to four is possible, but much rarer; connecting to five or six never happens, and beyond six is not possible in two dimensions for particles of the same size. Because the network is a tree there is a topological “conservation” equation for the tree (derived in Appendix A):

\[ T = B_3 + 2B_4 + 3B_5 + 4B_6 - 1 \]  \hspace{1cm} (2.3)

where \( B_n \) is the number of particles that connect to \( n \) other particles. Here, \( B_5 = B_6 = 0 \), therefore from 2.3 we know how many branching points connect to four other particles:

\[ B_4 = T - B + 1 \]  \hspace{1cm} (2.4)

Figure 2.16 shows the percentage of branch points that have four–way connections as opposed to 3–way connections. There appears to be no trend as a function of the number of particles in the network, and the scatter of the data is large suggesting that the formation of the \( B_4 \) sub–species is not tied to a desired state of the system.
2.5 Effects from initial conditions

The narration of the dynamics of section 2.3 describes a typical formation of the network, and fig. 2.2 shows snapshots of the formation with timestamps. It should be noted that deviations from the typical case are dependent upon the initial state of the system. First, if many particles start sufficiently close to the boundary in the initial state, then it is possible that several networks form simultaneously, each competing for ungrounded particles to recruit into itself; the steady-state properties for these conditions are contained in references Merté et al. (1988); Hadwich et al. (1990); Dueweke (1997). Second, the time to complete stage I and stage III depends on three factors: 1) the number of particles in the dish, 2) how diffusely distributed the particles are in the initial state, and 3) the geometry of the initial state. Having more particles, more diffuse initial states, and less symmetry decreases the distance of the particles from the boundary, and therefore speeds up stage I because of shorter traveling distances and increased induced dipole interactions; these three effects set a lower limit (about 400) to the number of particles that will still produce a network from a centered, circular, and compact (all particles touching) initial state. Having less particles and more diffuse initial states decrease the time for stage III because it is easier to unfold as a network into empty space.

The geometry of the initial state can effect the topology of the network. Because the binding of particles to the boundary is strong, the network does not reconfigure easily; therefore, the way the particles are distributed during stage II largely determines how the particles connect to one another. This sets the relative number of trunks, branches, and termini that the network forms. Figure 2.17 shows how different initial states lead to different final networks. In the language of the variational principle, the initial conditions places a severe constraint on the accessible regions of phase space.

Another interesting qualitative case is shown in figure 2.18. Here we have started
the particles in a spiral configuration. This should predispose the particles to linking into a spiral; nevertheless, the system persists in forming a tree structure, as shown in figure 2.18 (b). Evidently, there is an instability into forming ramified structures in the system, and there appear to be limits on the rapid topological freezing described earlier.

As a last initial condition, we explore how the unconnected strands at the perimeter of the main body of particles effect the final topology of the system. Since, in the original experiments, only one strand connects to the boundary, the remainder are constrained to join the network as long termini. We therefore performed a set of “cheat” experiments, where a single strand was artificially set in place before turning on the voltage. In this situation, instead of many long strands forming at the perimeter of the initial distribution of particles, the one cheat strand connects rapidly to the main body of particles and the network goes directly into stage II, bypassing
Figure 2.18: (a) Spiral initial configuration. (b) Ramified network that forms from spiral initial configuration.

Figure 2.19: Photos of a typical (a) initial configuration for cheat experiments and (b) final configuration from it.

stage I. Figures 2.19 show the initial configuration and the resulting tree that forms from it for one of these experiments. Figures 2.20 and 2.21 shows a comparison of the number of termini and branching points between the regular and cheat experiments. The greater slope in the fit for the cheat experiments is unsurprising since for larger numbers of particles more strands can form at the perimeter of the initial configuration; strands in Stage I that do not reach the boundary typically join the network as long terminus strands, which consists of several particles locked into being trunks and one particle as a termini. In the cheat experiments, there are no prominent losing strands; consequently, perimeter particles can more freely choose their topological species.
Figure 2.20: Comparison plot of the number of termini between the natural and cheat experiments.

Figure 2.21: Comparison plot of the number of branching points between the natural and cheat experiments.
2.6 Electrodynamic properties of the steady–state network

For comparison with previous studies, we examine the resistance of the network using the same method of those authors (Merté et al. (1988); Hadwich et al. (1990); Dueweke (1997)). This consists of discretizing the positions of all the connected particles, the BE, and everything outside of it; all these points are in the boundary conditions and are fixed at zero potential. Then, the electric potential on the rest of the points is found by running a standard relaxation algorithm to solve eq. 2.2; this updates the potential at a randomly selected lattice site by averaging over its neighboring lattice sites. The relaxation terminates when a target number (usually 100000) of the randomly selected sites is updated from its previous value by less than a threshold percentage (usually 1%); figure 2.22 shows the potential field for a single experiment. Once the potential everywhere is known, we applied 1.24 to find \( R_{\text{total}} \); we set all constants to 1, thus our units of resistance will be arbitrary. Note that the resistance is proportional to \( \int_{\text{oil surface}} (\nabla \phi)^2 dA \); thus steep regions of the potential contribute significantly to the resistance. In figure 2.22 (a), the steep regions of the potential lie is the area between the particles and the boundary electrode. Our analysis, in keeping with previous work, assumes that the source is uniform throughout the dish. The steep walls in the buffer areas represent charge from the source that is trapped between the network and the boundary electrode. Why the particles are repelled from this region is still an issue for discussion, but most likely it is safe to assume that the source is not completely independent of space, rather it depends on what is happening in the dish.

Figure 2.23 shows a log–log plot of the resistances as a function of the particle number for the natural experiments; the scaling exponent is \(-1.35\). The figure also indicates the values for two artificial structures, a lattice and a spiral; these will be
Figure 2.22: Two different plots of the potential for an experiment containing 784 particles. The unit for the potential is arbitrary. (a) A 3–D rendering of the potential landscape, the flat area around the high potential walls is a discretization of the BE and everything outside of it. (b) a contour plot showing the equipotential lines.

discussed later in the text. For comparison, the resistances for the cheat experiments is plotted log–log in figure 2.24; the scaling exponent is $-1.34$, similar to that of the natural experiments. Figure 2.25 shows a comparison of the two experiments on linear axes. The cheat experiments have a higher resistance than the natural experiments, despite the fact that they have more termini (see fig. 2.20). This may indicate a few things. One, by allowing strand formation in the natural experiments, the system can access regions of phase space that are not accessible to the cheat experiments—allowing it to explore other minima in the landscape. Two, there may be no simple direct connection between the topological species and the state of minimal resistance as claimed by Merté et al. (1988).

As an example of this, consider a lattice and a spiral; figure 2.26 shows the potential fields due to each with the same boundaries as for the experimental structures. Both of these artificial configurations have lower resistances than the experimental networks, but they contain zero and one termini respectively. The spiral has a lower resistance than that of the lattice; this, despite the report of Marani et al. (1998) who claim that the lattice should be the ground state in potential energy, and hence the resistance as well. Figure 2.27 shows a comparison of the potential fields for (a) a square lattice, (b) a diamond lattice, and (c) a spiral on a 100 by 100 square lattice.
Figure 2.23: The resistance, in arbitrary units, as a function of the number of particles for the natural experiments. For reference, the resistance of two artificial structures, a lattice and a spiral are shown. The resistance of the spiral is significantly lower than that of the trees.

Figure 2.24: The resistance as a function of the number of particles for the cheat experiments.
Figure 2.25: A comparison of the natural and cheat sets of experiments. The cheat experiments are typically at a higher resistance than the natural experiments.

Figure 2.26: The potential fields for (a) a lattice and (b) a spiral. Both configurations contain 703 particles, and have resistances significantly lower than the experimental structures. In arbitrary units, the lattice has a resistance of 9930, the spiral 5330, and a tree with 697 particles has a resistance of 13000.

without the BE and its surrounding area. Case (b) is the same case as in Marani et al.; it has the most particles at 2658 of the three configurations, but it has the highest resistance 2120 in arbitrary units. The square lattice has the second most particles, 2379, and the second highest resistance of 1920. The spiral has the fewest particles at 2377, but it has the lowest resistance of 1370.
2.7 Summary of experimental results

In this chapter, I have given an overview of the experimental setup and phenomenology of the experiment. We found that there are three stages to the growth of the network: (I) strand formation, (II) boundary connection, and (III) geometric expansion. In stage I, particles on the perimeter of the initial configuration line up to form strands; the strands tend to grow and rest in a correlated fashion. In stage II, the particles electrically connect to the boundary electrode. In stage III, the network expands to fill unoccupied space in the dish. Both stage II and stage III determine the topology of the network; in these stages particles become one of three species of particles depending on how many particles they connect to. Termini are the endpoints and connect to only one other particle; trunks connect to exactly two other particles, and branching points connect to three or more particles, except that we have never observed a particle linking to 5 or more particles in the experiment. We used the average adjacency as a measure of how the topology is set during the different stages, and found that it falls steeply to the steady–state value. We also observed that the relative number of each type of species of particle is statistically robust for increasing number of particles in the network. We explored how the relative proportion changes due to surface effects from unconnected strands in stage I. To do this, we performed a
set of cheat experiments, where a single strand was artificially placed to connect the main body of particles to the boundary. Unsurprisingly, the relative number of termini increased. We also examined the resistances of both the experimental structures as well as a few artificial ones. We found that the resistance of the networks scales with the number of particles with a dimension $\xi \approx -1.35$. Additionally, we found that the artificial structures had lower resistances than the experimental structures. We note, however, that our results suggest that the space independence of the source needs further examination.
Chapter 3

Artificially Generated Networks

As we already explored in Chapter 2, the final topology of the network is largely determined in a short amount of time. Particles connect to the network before they have moved very far from the position they are in immediately before stage II. We also know that the final form of the network is a tree, meaning that there are no closed loops in the system. Therefore, we would like to explore how the positions of the particles, directly preceding the time that the lead strand connects to the boundary, effects the type of trees that can ultimately arise. In other words, we are trying to apply the language of graph theory into the system to try to predict the topology of the real networks. In order to do this, we look at every experiment, from each we choose an appropriate photo which shows the state of the system directly preceding stage II; figure 3.1 shows an example of this kind of photo. We then generate from each photo a neighborhood graph which shows how particles sit adjacent from one another in each picture for a given cutoff length (see Appendix A for a complete description); figure 3.2 shows the neighborhood for the experimental photo of figure 3.1—the cutoff length is three times a particle diameter. Next, we apply an algorithm to each of the adjacency graphs; the algorithms choose links in the neighborhood graph in such a way that the particles become connected to one another in a tree, meaning that there are no cycles allowed in the graph.
Figure 3.1: Photo from an experiment which shows the position of all the particles at a time directly preceding stage II. The positions of the particles are digitized from the photo; these are used to seed the algorithms that artificially generate networks. This process is done for each experiment.

Figure 3.2: The neighborhood for the experimental photo shown figure 3.1. Appendix A defines the procedure used to obtain this neighborhood. The cutoff value used here is three times a particle diameter. One can think of this neighborhood graph as being the potential connections between particles, meaning that the algorithms will never connect any pair of particles that lack a link in figure 3.2. In other words, the effect (but not the process) of the algorithms is to prune connections in the neighborhood graph until a minimum number of trees remain. In this case there would be three “trees,” one from the main body of particles, and the two loners that cannot connect to anyone else.
Figure 3.3: An example of a connection configuration chosen by the random network algorithm described in the text. The connections are randomly chosen from the available ones shown in figure 3.2; a connection is kept only if it does not violate the network from forming a tree. Figure (a) shows both the particles and the links. Figure (b) removes the particles to show the skeleton connections between the particles. Figure (c) was produced using a spring embedding algorithm available in the Combinatorica package of Mathematica; it spreads out the tree structure to make it more readily visible.

In the remainder of this chapter, I will describe three algorithms we implemented, summarizing the results for each. The three algorithms are 1) random (RAN), 2) minimum spanning tree (MST), and 3) propagating front model (PFM). In the final section, I will compare the results of the three algorithms and contrast them to the topologies of the real networks.

3.1 Random Trees

The random connection algorithm is the simplest, and it serves as our zero model of how the particles can connect. The basic function of the algorithm is to randomly pick an available connection between a pair of particles from the neighborhood list, accepting the connection if it maintains a tree structure, rejecting the connection if it violates a tree structure by producing a loop—also known as a cycle—in the graph. In practice, this is accomplished by labeling every connected particle by which tree it belongs to. There are then three cases to examine: 1) either particle or both particles is/are unconnected—accept the connection, 2) particle 1 is connected to
Table 3.1: The decision table which shows the possible states of a pair of particles and the outcome chosen by the algorithm based on those states.

<table>
<thead>
<tr>
<th>Particle 1:</th>
<th>Particle 2:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Particle state</td>
<td><em>unconnected</em></td>
</tr>
<tr>
<td><em>unconnected</em></td>
<td>accept</td>
</tr>
<tr>
<td><em>connected to tree</em> j</td>
<td>accept</td>
</tr>
</tbody>
</table>

Tree i and particle 2 is connected to tree j—accept the connection and merge tree j into tree i, 3) particle 1 and particle 2 are both connected to tree i—reject the connection; table 3.1 summarizes these choices. These steps are repeated until every particle joins a tree. Figure 3.3 shows one configuration of connections produced by the algorithm; (a) shows the particles and the links together, figure (b) skeletonizes (a) so that the connection structure is clearly visible, figure (c) shows the network after it has been run through a spring embedding algorithm in the Combinatorica package for Mathematica. The spring embedding attaches a linear spring between every node in the network, and moves each one based on Hooke's law; this spreads the tree into a more visible representation while maintaining its topology.

In the end there may exist multiple trees because one tree does not have any particles that are close enough to interact with particles from the other trees—all particles of one tree are at a distance greater than the cutoff length of all particles in all other trees. These only account for a few loners or possibly a small strand of particles that dwell outside the main tree. They are commonly observed in the experiment as well.

We run the above algorithm through one-hundred thousand permutations of pair selection ordering for each experiment. For each of these one hundred thousand, the number of each species of topological particle, as defined in Chapter 2, is recorded. The network shown in figure 3.3 was chosen as representative because it produced
Figure 3.4: The distribution of the number of termini generated by 100000 permutations of the random algorithm on one experimental photo.

a tree that had a number of termini that matches the mean for the sampling of random configurations. Figure 3.4 shows the frequency of different values of the number of termini or endpoints—particles that connect to only one other particle. The distribution shown in figure 3.4 is the fit to a Gaussian. This procedure is done for all experiments, and the value of the mean and the standard deviation is then plotted as a function of the number of particles in the network; the same is done for the number of branches (not shown individually for each algorithm; see figures 3.18 and 3.19 to see a comparison of all algorithms). Figure 3.5 shows the number of termini produced by the RAN algorithm for all natural experiments.

3.2 Minimum Spanning Trees

Minimum spanning trees were originally defined in the context of graph theory. If given a set of nodes and weighted links, where each node is accessible by every other node by traversing some set of links, a minimum spanning tree would have a) a unique path connecting any pair of nodes (no cycles) and b) a minimum total weight.
Figure 3.5: The plot of the number of termini as a function of the number of particles in the network.

for all the paths. Figures 3.6–3.8 shows a simple example of a graph, a non–minimum spanning tree of the graph, and the minimum spanning tree of the graph respectively.

The procedure to generate a minimum spanning tree is relatively simple, and requires only one key difference from the random algorithm. Instead of randomly selecting a possible link, sort all available links by weight, in this case we use the euclidean distance between a pair of particles, then select links based on their rank, shortest links are selected first. The same rejection/acceptance criteria of the random case, as summarized in table 3.1, applies to the minimum spanning tree algorithm. Figure 3.9 shows a representative connection configuration generated by the minimum spanning tree algorithm for the neighborhood defined in figure 3.2; the panels are the same as in the random case.

The minimum spanning tree procedure is deterministic, however many of the links will have the same weight. Therefore, we run the algorithm through one hundred thousand different permutations of ordering the degenerate links. Figure 3.10 shows the distribution of the number of termini for all the different permutations. The
**Figure 3.6:** A simple graph, the circles represent the nodes and the lines the links or vertexes. The length of each link represents its weight.

**Figure 3.7:** By removing some of the links, the graph becomes a tree but not a minimal one.

**Figure 3.8:** By removing the correct links, the graph becomes a minimal spanning tree; the sum of all weights is minimized.
Figure 3.9: One possible configuration generated by the minimum spanning tree algorithm, chosen because the number of its termini matches the mean value of the 100000 permutations. (a) shows the particles and the links. (b) the skeletal connection structure. (c) the skeletal connection structure shown in a spring embedding.

A gaussian fit to the data shown in figure 3.10 gives the mean and the standard deviation used for figure 3.11 which shows the number of termini for all experiments.

### 3.3 Propagating Front Model

The above two algorithms can create a link between a pair of particles regardless of the location of the pair—they may be at the edge or in the center. In the experiments, however, we know that the boundary forms from a particular direction; it starts with the lead particle of the winning strand and proceeds to the next particle in line and so forth. At some point it will reach the main body of particles, and the boundary will have to propagate through it in some fashion.

In an attempt to capture the motion of the front, we created the propagating front model, where particles connect to the growing boundary only if they are in proximity to it. Thus, particles far from the connection point join the network much later than particles near it. To do this, the first step is to pick a connection point; here, we simply pick the point that is farthest from the center of mass of all particles. The connection point is the seed particle; it is the first to join the boundary. Each time a particle is added to the boundary, a list of particles that are allowed to connect is
**Figure 3.10:** The distribution of the number of termini generated by one hundred thousand permutations of degeneracies of the minimum spanning tree algorithm.

**Figure 3.11:** Plot showing the variation of the number of termini as a function of the number of particles in the network.
Figure 3.12: Schematic diagram of the propagating front model algorithm after many iterations, but before all particles have joined the network. The grey cross-thatched particles have already joined the network; the lines show how they have connected. The white particles are available to connect to the boundary because they are adjacent to it. Red dotted particles are unavailable to connect to the boundary because they do not neighbor a particle already in the network. (a) The state of the particles prior to choosing the next particle to connect. (b) Now that a white particle has been randomly selected (the grey-filled particle), it must now choose to connect randomly to one of its neighbors that are already in the network (blue arrows). (c) Once the chosen particle is established in the network, any previously unavailable particles neighboring it (blue checkered particles) change their colors to white and become available for connection. (d) The system is in the pre-choose state again, as in (a), except one particle has been added to the network and several new particles have become available for connection.
Figure 3.13: An example of a tree produced by the propagating front algorithm, representative of the mean number of termini generated by different permutations run on the same experiment. (a) shows the particles and the links. (b) shows the skeletal connection structure. (c) shows the connection structure in a spring embedding. Note the direction of propagation is visible in the tree structure.

updated. The particles in this list are neighbors to particles that already exist in the boundary. From this list, a particle is randomly selected to join the boundary; it then randomly selects which of its neighbors already in the boundary it will connect to; figure 3.12 shows the basic steps of the algorithm for one particle connection. Each particle in the list has equal probability to join the boundary, there are no multiple entries for a single particle in the list. In practice, this possibility could be explored, but as a matter of principle one rule appears as good as another. The above procedure is run until all particles connect to the network. Note, unlike previous models where a potential connection could be rejected by the algorithm to maintain a tree structure, here, we only connect unconnected particles to already connected particles; thus, the tree structure is never violated by any connection. Figure 3.13 shows a representative tree created by the PFM.

Again, we run the algorithm through one–hundred thousand permutations of connection ordering, but keep the seed connection point the same for all one–hundred thousand. Figure 3.14 shows the distribution of termini for all permutations of a single experimental photo. The gaussian fit gives us the mean and the standard deviation for figure 3.15 which plots the number of termini as a function of the number
Figure 3.14: The distribution of the number of termini for one hundred thousand permutations of the propagating front model from a single experimental photo.

3.4 Comparison of the algorithms with experiments

Figures 3.16 and 3.17 show a plot of the number of termini produced for all algorithms and experiments for the natural and cheat case respectively. The experimental results derive from the properties of the steady–state networks of each experiment used to feed all of the algorithms—they are the same results shown in chapter 2. For both cases the MST algorithm most closely matches the properties of the experimental system. The other two algorithms consistently overestimate the number of termini. This can happen in two ways: 1) the number of branching points increases and 2) the connectivity of branching points increases, meaning more particles attach to four, five, or six particles rather than just three. Figures 3.18 and 3.19 show the increase in the number of branching points as a function of particle number for all algorithms and experiments for the natural and cheat case respectively. The difference in the number of branching points between the different algorithms and the experiment is

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Figure 3.15: The number of termini as a function of the number of particles for the propagating front model algorithm.

not quite as pronounced as it is for the number of termini. This suggests that both the PFM and RAN algorithms are producing more branching points of higher adjacency, and not just increasing the abundance of lower order branching points. For instance, because of topological conservation (see appendix A), the number of termini in the network must be given by

$$T = 1 + B_3 + 2B_4 + 3B_5 + 4B_6$$  \hspace{1cm} (3.1)

where \(B_n\) is the abundance of branching points of adjacency \(n\). Since the number of branching points is given by the sum of all \(B_n\), the difference between the number of termini and branching points is given by

$$T - B = 1 + B_4 + 2B_5 + 3B_6$$  \hspace{1cm} (3.2)

This means that the difference in the number of termini and the number of branching points is independent of the relative number of branching points of adjacency three—the type most commonly found in the experiment. By looking at the difference between the number of termini and the number of branching points, figures 3.20
Figure 3.16: A comparison of the number of termini for all algorithms and the experiment in the natural case.

Figure 3.17: A comparison of the number of termini for all algorithms and the experiment in the cheat case.
Figure 3.18: A comparison of the number of branching points for all algorithms and the experiment in the natural case.

Figure 3.19: A comparison of the number of branching points for all algorithms and the experiment in the cheat case.
and 3.21, it is evident that both the PFM and RAN algorithms are generating many more higher order branches than both the experiments and the MST algorithm.

In this section, we have explored several algorithms to build trees from experimental conditions. We find that the algorithm which connects particles together minimally, best reproduces the statistics of the experimental system. We note that this is not necessarily a true model concerning how the particles connect in the real system. Nevertheless, our results suggest two things. One, the direction of propagation of the front might not be a determining factor in the creation of the topology; the MST algorithm is independent of direction—it determines the structure based only on relative distances between particles. Two, in chapter 2 we showed that the gross features of the initial conditions persuade the final configurations of the network; here our results suggest that even at level of interparticle spacing the initial conditions of the system affect the final topology. The discrepancy between the RAN and MST algorithm evinces this fact; the RAN algorithm ignores the interparticle spacing information, whereas MST completely depends on it. One might argue that the differences between the two algorithms are due mostly to interactions between strands and bulk particles, and therefore depend on the cutoff length. We purposefully chose a high cutoff length of three particle diameters to ensure that a good portion of the particles will be contiguously set by the neighborhood generating algorithm. In figure 3.2, one can see how there are potential connections that are unlikely to exist in the real experiment. The MST algorithm is more likely to weed out such possibilities since by the time all the shorter connections have been filled, the longer connections will no longer be viable in maintaining a tree structure. The RAN algorithm, however, treats these possibilities with equal probability as the shorter connections. Despite this argument, it is still possible to observe a significant difference in the number of termini in the simulations run on the cheat experiments, where the interactions between perimeter particles and the boundary are minimized. Indeed, figure 3.22
Figure 3.20: A comparison of the difference in termini and branching points for all algorithms and the experiment in the natural case. The significant differences between the PFM and RAN algorithms versus the MST algorithm and the experiments suggest that the former two contain higher order branching points, something not observed in the experiments.

Figure 3.21: The same as figure 3.18 except for the cheat case.
Figure 3.22: The number of termini created by the RAN algorithm for two different values of the cutoff length. Both values produce similar results, indicating that the differences between the RAN algorithm and the experiments (green triangles) are not entirely dependent upon the chosen cutoff length.

shows a comparison of the RAN algorithm run with two different cutoff lengths used to create the neighborhood graph; the filled boxes are the original values that were shown in figure 3.5, which were produced with a cutoff length $l_c = 3d$, where $d$ is a particle diameter; the unfilled boxes show the results for a few of the experiments using $l_c = 1.5d$. The reduced cutoff length only marginally reduces the number of termini; therefore, our results indicate that the information stored in the interparticle spacing directly preceding stage II is somehow preserved in the limiting form of the experimental networks.
Chapter 4

Theory of the allometric scaling of ant foraging colonies

In previous chapters, we studied the dynamical formation of ramified structures in an experiment, and we attempted to predict those structures using graph theory. In this chapter, we turn our attention to how the structure itself can affect the transport properties of the system. To accomplish this, we attempt to model a biological system where ramified structures are used to collect and transport resources: ant foraging colonies.

4.1 Introduction

Aggregation of individuals into colonies raises important questions about scaling of structure and function. We model the metabolic benefits and costs of two-dimensional, fractal-like foraging trails, such as those used by ant colonies. Total area foraged by the colony, and consequently resource flow to the nest and rate of colony metabolism, increase non-linearly with number of foragers \( F \) as \( F^{2/3} \). Since the cost of foraging increases linearly with \( F \), the model predicts an optimal number of foragers and therefore total foraging area that maximize colony fitness or energy allocation to
reproduction. The scaling of foraging may influence evolution of coloniality.

A major transition in organic evolution is the association of individual organisms to form colonies Buss (1987); Maynard-Smith and Szathmary (1995). By remaining together and coordinating their activities, individuals create a new level of biological organization that has its own emergent informational and metabolic properties. Allometric scaling laws for individual organisms describe how body size influences structure and function Schmidt-Nielsen (1984); Brown et al. (2000). Additional problems of scaling arise as individuals aggregate into colonies. How do critical structures and functions vary with colony size, and how do these scaling relations affect the ecology and evolution of colonial organisms?

Social insects have provided seminal insights into the causes and consequences of coloniality with respect to both information, including genetics and communication, and metabolism, including energetics of foraging, growth, maintenance, and reproduction Wilson (1971); Bourke and Franks (1995); Pasteels and Deneubourg (1987); Lighton (1989); Hölldobler and Wilson (1990); Seeley (1995). Important questions concern how resource acquisition and allocation scale with colony size, how foraging activities are organized for efficient resource uptake, and what limits the size of colonies and the areas that they forage.

Here we address questions about scaling of energetics and metabolism of colonies by modeling the foraging of ants. Large ant colonies typically forage along trunk trails that have a fractal-like branching structure (Fig. 4.2a); they can be semi-permanent structures that extend hundreds of meters Hölldobler and Wilson (1990). Recent models that describe the metabolic scaling of individual organisms base themselves on special features of hierarchically branched distribution networks, such as plant and animal vascular systems West et al. (1997, 1999). A similar model for ant foraging trails leads to quantitative predictions of how resource uptake and foraging area scales with the number of foragers. The model also implies that there is an optimal colony.
size that maximizes the rate of resource allocation to reproduction.

4.2 The Network Model for Ant Foraging Trails

The model considers a colony containing worker ants of a single species in a given environment. Each individual forager travels along trails between the nest and a foraging zone, where it searches for food items. These types of networks are believed to arise as adaptations that enhance collection of certain kinds of food resources, defense against predators and parasites, communication by chemical and tactile signals, and other benefits Hölldobler (1976); Hölldobler and Lumsden (1980); Acosta et al. (1995). The trails form a hierarchical branching network that originates in a single trunk at the nest, at branching level \( k = 0 \). Each branch splits into \( n \) branches at each of \( T \) branching levels, and the network terminates in \( n^T \) foraging zones (Fig. 4.2b). Each branching level has a characteristic length, \( l_k \), and density (per unit length) of foragers, \( \lambda_k \).

We make several assumptions to characterize the geometry and dynamics of the network:
a. There is a constant rate of resource supply per unit area per unit time.

b. Resources are harvested, transported to the nest, and consumed with minimal time lags. Consequently, transient, non-steady-state dynamics, such as temporary resource depletion (overharvesting) and storage of resources in the colony are ignored.

c. The metabolic rate of the ant colony, $B$, is proportional to the resource intake rate, which in turn is proportional to the rate of resource supply, $\dot{R}$, so that $B \propto \dot{R}$. Losses of resources are ignored: all resources available in the environment are harvested, and all harvested resources are consumed. $B$ includes all energy use by the colony. Net gains from foraging are allocated to some combination of growth (production of additional foragers) and reproduction (production of alates).

d. Individual foragers are equivalent. They travel at constant speed, $v$, and are similar in size and behavior.

e. The smallest branches end at foraging zones of fixed area, and have invariant flow rates.

f. The non-overlapping foraging zones of the trail termini are densely packed; they completely fill the colony foraging area.

g. The trail network is hierarchical and fractal-like. It can be characterized by scale factors, Fig. 4.2b):

\[
\text{length ratio: } \gamma_k \equiv \frac{l_{k+1}}{l_k} \quad (4.1)
\]
\[
\text{forager density ratio: } \beta_k \equiv \frac{\lambda_{k+1}}{\lambda_k} \quad (4.2)
\]
h. The branching ratio of the paths, $n$, remains constant, which means that there are a total of $n^T$ terminal branches and foraging zones. Assumptions (g) and (h) can be relaxed to permit asymmetrical space-filling branching without affecting our results Turcotte et al. (1998).

i. We assume that all ants leaving the colony complete a circuit to a foraging zone and back. (i.e., that deaths and incomplete forays have a negligible effect on the flux of foragers.) Together with assumption (d) and time-averaging to smooth out stochastic fluctuations, this means that the flux of foragers through the trail network is conserved.

These assumptions lead to two important properties of the model:

1. Space-filling: each level of branching divides the total foraging area into non-overlapping sub-areas whose sizes are determined by the branch lengths at level $k$. Following the model of West et al. West et al. (1997), but for two dimensions, this leads to the following relationship for sizes and numbers of branches as a function of $k$:

   $$n^k l_k^2 = n^{k+1} l_{k+1}^2$$  \hspace{1cm} (4.3)

   $$\gamma_k \equiv \frac{1}{\gamma} = \frac{l_{k+1}}{l_k} = n^{-\frac{1}{2}}$$  \hspace{1cm} (4.4)

2. Flux-preserving: since the flux of foragers is conserved across branching levels, we can relate the total flux of foragers returning to the nest, $\dot{Q}_0$, to the flux at each level:

   $$\dot{Q}_0 = \lambda_0 v = n^k \lambda_k v = n^{k+1} \lambda_{k+1} v = n^T \lambda_T v$$  \hspace{1cm} (4.5)

   $$\beta_k \equiv \beta = \frac{\lambda_{k+1}}{\lambda_k} = \frac{1}{n}$$  \hspace{1cm} (4.6)
Using these properties, we derive the scaling exponent, which relates the total number of foragers, $F$, to the properties of the network:

\[
F = \sum_{k=0}^{T} \lambda_k l^k n^k = n^T \lambda_T l_T \frac{1 - (n\beta\gamma)^{-T+1}}{1 - (n\beta\gamma)^{-1}} \quad (4.7)
\]

Since $n\beta\gamma < 1$ and $T \gg 1$, equation (4.7) is closely approximated by:

\[
F \approx l_T \lambda_T \frac{(\beta\gamma)^{-T}}{1 - n\beta\gamma} = l_T \lambda_T \frac{n^{\frac{4T}{T}}}{1 - n^{-\frac{T}{2}}} \quad (4.8)
\]

By assumptions (d) and (e), $\lambda_T$ and $\nu$ are constants, so equation (4.5) implies that $\dot{Q}_0$ is proportional to the total number of foraging sites, $n^T$. Further, by equation (4.8) and assumptions (e) and (h), $n^T$ scales as $F^{\frac{4}{3}}$, and therefore, by assumption (c) resource acquisition and metabolic rate scales as $B \propto \dot{Q}_0 \propto n^T \propto F^{\frac{4}{3}}$. This implies that colony metabolism is given by $B(F) = B_0 F^{\frac{4}{3}}$, where $B_0$ is a normalization factor. $B_0$ will vary with characteristics of the ant species, such as forager size, and of the environment, such as resource availability.

### 4.3 Optimal Colony Size: Energetic Constraints and Predictions

The scaling of the trail network, net resource uptake, and colony metabolism as a function of forager number leads to predictions for maximal and optimal colony size (Fig. 4.3). The net rate of energy gain, $\dot{G}$, from foraging is simply $\dot{G} = B - \dot{C}$, where $\dot{C}$ is the rate cost of foraging. Therefore, $\dot{C}$ is the cost of collecting food, and the total metabolic rate of the colony minus this cost of foraging represents the rate of energy accumulation that can be allocated to growth and reproduction. From assumption (d) it follows that this cost, $\dot{C}$, increases linearly with the number of foragers. From this assumption and equation (8), which implies that $B \propto F^{2/3}$, we can derive an expression for the net rate of energy gain

\[
\dot{G} = \dot{E}_0 F^{\frac{2}{3}} - \dot{C}_0 F \quad (4.9)
\]
Figure 4.1: The scaling of the colony metabolism $B$ and the total foraging cost $\dot{C}$ with the number of foragers $F$. The net rate of energy gain, $\dot{G} = B - \dot{C}$, is maximized at $F = F_{\text{opt}}$ and is zero at $F = F_{\text{max}}$.

where both $B_0$ and $\dot{C}_0$ are normalization constants.

Therefore, gross energy intake rate per forager decreases with increasing number of foragers, $\frac{B}{F} \propto F^{-1/3}$. Consequently, there is an optimal number of foragers, $F_{\text{opt}} = \left(\frac{\dot{B}_0}{\dot{C}_0}\right)^{3/2}$, which maximizes the net rate of energy gain so that $\dot{G} = \dot{G}_{\text{max}}$ (Fig. 4.3). Since $\dot{G}$ represents the rate at which energy can be allocated to other components of fitness such as colony growth (production of sterile castes) and reproduction (production of alates), the colony should grow until it reaches optimal size, and then all further net energy intake should be allocated to production of reproductives. This means that the optimal colony size is substantially smaller than the maximum possible colony size at which all incoming energy would be allocated to maintenance and none would be available for reproduction. Although our model is expressed in terms of the number of foragers, if the energetic costs of producing and maintaining other castes are known, it should be possible to develop expressions for optimal numbers of other castes and hence for total colony size. This model has features in common with previous attempts to understand energetic consequences of
4.4 Results and Discussion

The model offers insight into the metabolism of ant colonies, such as how energetics constrain colony growth and result in optimal and maximal colony size. Previous qualitative cost-benefit models predict an optimal colony size Oster and Wilson (1978), but our allometric model makes explicit quantitative predictions for how the number of foragers determines the income of energy available for colony growth and reproduction. Figure 4.3 can also be interpreted in terms of colony foraging area, which corresponds to rate of energy intake. Foraging area grows slower than linearly with increasing numbers of foragers, as $F^\frac{2}{3}$. This is a fundamental constraint of the network: as larger colonies use larger areas, each forager spends proportionately more time traveling between the nest and its foraging zone, and the colony has a greater proportion of its foragers in transit as opposed to searching for food. This scaling limits colony metabolism and affects the allocation of energy and resources to growth and reproduction similarly to the way that constraints of vascular supply limit metabolic rate and allocation to growth and reproduction in individual organisms.

We are well aware that many ant species do not exactly conform to all assumptions of our model. For example, workers may vary in size, travel speed, and size of food particles transported. Like any model, ours is a deliberate oversimplification of a more complex reality. Some of the assumptions, which were made for simplicity, can be relaxed without changing the predicted scalings. For example, assumption (a), that there are equal rates of resource supply per unit area, can be relaxed average rate of supply to the colony foraging area is constant with respect to the total number of foragers in the colony. Assumption (c), that all available resources are harvested.
and then consumed could be relaxed by incorporating terms for losses. If a model is useful it should capture the fundamental essence of pattern and process and lead to increased understanding of how nature—in this case an ant colony—works. We believe that our model does help to explain and to ask new questions about the functional organization and scaling relations of ant colonies.

Our model makes predictions about foraging efficiency, net energy return from foraging, and colony foraging area as functions of the number of foragers. We are unaware of studies of ant colonies that provide data of sufficient precision to test these predictions quantitatively. What is known about ants that use trunk trails for foraging is consistent with the model. The geometry of foraging trails is often fractal-like (Fig. 4.2a) Hölldobler and Wilson (1990). For the desert harvester ant, *Pogonomyrmex barbatus*, there tend to be approximately four trunk trails leaving a colony entrance Gordon and Kulig (1996). Our model considers only one trunk trail so that a multiplicative constant is necessary to describe colonies with multiple trunks.

Information that colonies grow logistically to some approximately constant size Hölldobler and Wilson (1990) is consistent with there being an optimal number of foragers. For example, in *P. barbatus* the number of foragers and total colony foraging area increase rapidly after colony founding, reach relatively stable levels after 3-5 years, and then maintain these values for the life of the colony, which may be 15-20 years Gordon (1992, 1995); Gordon and Kulig (1996). According to Lighton (1989), cost of foraging (total energy expenditure by foragers) apparently does increase linearly with the number of foragers, as the model assumes (e.g., Fig. 4.3). Additionally, one cost of foraging that has been measured, mortality of foragers due to fighting with neighboring colonies, varies linearly with number of foragers Gordon and Kulig (1996), which is again consistent with the assumption of our model.

This study raises interesting questions about how the metabolic and informational
systems of colonies are integrated. Our model does not explain why ants should use trunk trails in the first place. An alternative foraging strategy would have each forager traveling directly to and from its foraging site by the straightest path. Honeybees and some ants that maintain small colonies use such individual foraging. Advantages of using fractal-like trunk trails include: i) the space-filling property facilitates efficient harvesting of resources throughout the colony foraging area; ii) the pheromone and tactile cues used to mark the trails transmit information that facilitates navigation to and from the nest and recruitment to resources; iii) maintenance of semi-permanent major trunks promotes rapid, efficient travel; iv) trunk trails help avoid competition for strictly central-place foraging Hölldobler (1976); Hölldobler and Lumsden (1980); Acosta et al. (1995).

The model and this allometric approach to the costs and benefits of coloniality raises further questions about how the colony obtains, processes, and uses information to regulate its size and allocate its resources to growth, maintenance, and reproduction. The existence of an optimal number of foragers provides a quantitative measure of one advantage of coloniality because net energy gain, $\dot{G}$, is maximized when $F > 1$. This, in turn, raises questions about how natural selection operates to control and integrate the activities of the individuals for the metabolic welfare and evolutionary fitness of the colony. Perspectives from allometric scaling offer potentially valuable insights into other evolutionary transitions such as those that produced multicellular organisms, colonial animals, and human societies.
Chapter 5

Conclusions

We studied the dynamics of self-organization of conducting particles into ramified tree networks when subjected to strong electric fields. We found, for initial configurations where particles are initially far from the boundary electrode, that the trees grow in three stages: (I) strand formation, (II) boundary connection, and (III) geometric expansion. The strand formation was previously unobserved in past experiments, where random initial conditions were used. We also found that the strands tend to grow in a correlated fashion, moving and resting together.

We applied graph theoretical measures like the average adjacency of particles on the system; this measure clearly delineates the three growth stages, since the adjacency drops sharply at the initiation of stage II and into stage III. Additionally, during this relatively short time period, we discovered that each particle becomes one of three species of particles depending on the number of neighboring particles each connects to. We showed that the numbers of each kind of species is statistically robust across different experiments with similar numbers of particles. We also investigated the effects of the initial configuration of particles, and we found that the initial conditions strongly influence the final form of the networks, e.g. their geometric symmetry and their topological structure. In particular, we found that by eliminating stage I in a set of cheat experiments, where a strand to the boundary was artificially set in
place, the experiments formed more termini than in the natural case.

We explored the electrodynamic properties of the system, especially the overall resistance; we showed that this quantity scales nonlinearly with the number of particles in the network. We found, in contrast to previous work, that the number of termini does not necessarily correlate with a decrease in the overall resistance of the system. This was acutely shown in the case of an artificial spiral that had a resistance of nearly one-third of that of a comparably sized network. Even for real experimental structures, comparing the cheat experiments to the natural experiments, we found that the latter set are consistently lower in resistance than the former despite the fact that the cheat experiments contain more termini.

To understand how the geometrical arrangement of particles influences the topological structure of the system, we generated artificial trees by applying graph theory into simulations of tree growth. We implemented three algorithms to generate trees: 1) random, 2) minimal spanning, and 3) propagating front. We compared the results of the different algorithms and found that the minimal spanning tree algorithm reproduces the best match to the statistics of the experimental trees. We concluded from this that a) the direction of propagation of the front may be unimportant to the topology of the tree and b) somewhat paradoxically, the detailed information contained in the interparticle spacing may somehow be preserved in the final networks.

Finally, in collaboration with researchers at the Santa Fe Institute, we theoretically explored a biological system: ant foraging colonies. We showed that the structure of the foraging patterns has consequences on the net energy collection rate of the ant colony. From this, we predicted that there should exist both an optimal and maximal colony size.
5.1 Future Studies

Experimentally, there are still many open questions yet to be answered and many tools yet to be implemented. First and foremost of these is to automate the digitization of particle positions. It is too exhausting and time consuming to track all the positions of the particles manually to do thorough detailed studies of the system dynamics. This process is the single greatest bottleneck to doing all the different experiments one can imagine; these would include changing the shape of the boundary, arranging different sets of source electrodes, and adding multiple particle sizes. A great challenge to automation is the photography of the experiment. Currently, the source electrode rests above the dish and the camera sits below it. Once the experiment connects the oil will shift and bend on the surface causing anything above the oil to refract; this pollutes the photograph, and makes it difficult to distinguish particle from shadow, even for the human eye. With a better lighting arrangement and a better color for the background and source electrode, it may be possible to have the computer program eliminate everything but the particles; this can be accomplished using a combination of color and high-pass filters.

If the automation could be done, then the correlation between strand movement could be more thoroughly investigated. In particular, one could look at the velocity–velocity correlations in more detail. From this, one could try to determine the physical conditions that lead to correlated movement between strands.

Another interesting case would be to try a continuous system. One could try the experiment with mercury and observe the structure that emerges. Will the system still form branches? Under what conditions? What would be the characteristic width and length in the branches? One potential difficulty would be to slow the mercury down enough so that the trees would be stable. In our experiments, without the oil the particles do not form trees. Instead, they transport charge mechanically by bouncing back and forth from the boundary of the dish to the center of the dish. If we
could continuously change the viscosity of the medium without changing its dielectric properties, could we see a phase transition from this behavior to the stationary rami-fied patterns? What would the transition look like? Changing the viscosity of the oil can be achieved by changing its temperature; it has a sensitive viscosity profile near room temperature.

Now that the system has been abstracted to a topological level, it is important to bring that back into the physical level, and tie the two together. The algorithms we explored thus far have only used geographic locations of particles as a parameter. It would therefore be interesting to see how adding in the electrodynamics will effect the output of the algorithms.
Appendix A

Elementary definitions for graph theory

In this appendix, I introduce some graph theory and the relevant measures for the system that is the topic of this thesis. I also describe the methods and tools developed to analyze the graph theoretical measures. I estimate the initial adjacency as a function of $N$ the number of particles in the experiment. I derive the topological conservation equation. Finally, I derive the steady-state value of the adjacency.

A.1 Elementary concepts and definitions

Here I will present a brief outline of the graph theory vocabulary necessary for this thesis. For a more detailed but still introductory discussion, I refer the reader to Chartrand (1977).

A graph is an abstract representation of the topology of discrete elements, in other words, how nodes are connected to one another through links. A node is usually represented as a circle, and a link is usually represented as a line that connects a pair of nodes. Links and nodes can symbolize just about anything. For example, each node can be an airport where links between pairs of nodes represent the presence of
a direct flight between the two airports\textsuperscript{1}. The graph is independent of the placement of the nodes; graphs are equivalent so long as the topology is preserved. In the case of airports, it may be inconvenient to represent the nodes other than where they geographically sit; nevertheless, it is possible to retain the important information in the form of weights on each link. The obvious choice for airports is the flight distance, but it could be any measure relevant to both nodes like flight traffic or number of shared airlines. Certain measures may require a different topology. For example, whereas volume of flight traffic between cities can be represented by the same graph as the direct flight distances, number of shared airlines may require additional links—an airline may operate in two different cities, but choose not to offer a direct flight between them. Figures A.1 and A.2 show a fictitious direct flight graph for several major cities. Figure A.1 maintains the relative geographical locations of the cities while figure A.2 places the cities in a circle making it easier to draw the connections.

One of the properties of a node is its adjacency, or how connected it is; this quantity is also often referred to as a node’s degree, we shall stick to adjacency here since it evokes spatial proximity. The adjacency of a node is simply measured by counting the number of links it has. Looking at the graph of figure A.1, we see that LA has an adjacency of two—it is connected to every other node—whereas Santa Fe has an adjacency of two—it is connected only to LA and HOU. From the individual measure of each node’s adjacency, it is possible to determine the overall connectedness of a graph. We can do this by finding the average adjacency $\langle c \rangle$ of all the nodes. For figure A.1, this value is $32/7 \approx 4.57$. Since there are only seven nodes in this graph, it can be called dense, and one can determine that there is a good chance of having a direct flight between any two cities with this measure. If, however, there were 200 cities in the graph with the same average adjacency, then one could conclude that

\textsuperscript{1}Sometimes a pair of cities may have a direct flight in one direction, but not in the opposite direction; graphs can handle this by using directed links—links with arrows on them. We will not need the concept of directed graphs here, so I will not make any further mention of it.
Figure A.1: A graph that shows the direct flights available between the cities shown.

Figure A.2: Topologically equivalent graph to figure A.1. The sense of relative locations of cities is lost, but the connections are easier to follow. The numbers are the weights of the respective links, in this case the flight distances.
finding a direct flight between any two cities would be relatively uncommon, and the
graph would could be called sparse.

A.2 Graph Theoretical Measures

For the system discussed in this thesis, we are interested in two different graphs: 1) the
preconnection neighborhood graph and 2) the postconnection tree graph—these
occur directly preceding and following stage II respectively. The second graph is
a subset of the first. The reason for this was discussed in chapters 2 and 3; the
essential point is that the boundary propagates to all the particles rapidly in stage
II, therefore the connections freeze before the particles have time to move far from
each other. Consequently, we approximate the connections as occurring only between
desparticles that neighbor one another just before the initiation of stage II.

In our experiment, we treat each particle as a node, each particle shares a link
with every other particle that it neighbors; each link receives a weight based on the
distance between the two particles. Ideally, two particles are connected if they are
separated by exactly one particle diameter, \(d\). For this ideal case, the number of
connections (henceforth referred to as the adjacency) for an individual particle \(i\), \(c_i\)
would be given by:

\[
c_i = \sum_{j \neq i}^{N} \delta(|\vec{r}_i - \vec{r}_j| - d)
\]  
(A.1)

And the average adjacency would be given by:

\[
\langle c \rangle = \frac{1}{N} \sum_{i=1}^{N} \sum_{j \neq i}^{N} \delta(|\vec{r}_i - \vec{r}_j| - d)
\]  
(A.2)

Where \(\vec{r}_i, \vec{r}_j\) are the positions of particle \(i\) and \(j\); and \(N\) is the total number of particles.

This ideal case is broken by the noise inherent in digitizing the positions of the
particles. Therefore, it is necessary to allow for a range of distances in counting the
adjacency. We do this by replacing the delta functions in eqs. (A.1) and (A.2) with
Figure A.3: Graph showing the sensitivity of $\langle c \rangle$ on the cutoff length $d_c$, measured in particle diameters, $d$. The value saturates at a value $\approx 1.6 \cdot d$. The inset shows a detail of the saturation region.

Step functions and use a more tolerant cutoff length:

$$c_i = \sum_{j \neq i}^N \Theta(|\vec{r}_i - \vec{r}_j| - l_c) \quad (A.3)$$

$$\langle c \rangle = \frac{1}{N} \sum_{i=1}^N = \frac{1}{N} \sum_{i=1}^N \sum_{j \neq i}^N \Theta(|\vec{r}_i - \vec{r}_j| - l_c) \quad (A.4)$$

Here, $\Theta$ is the Heaviside step function and $l_c$ is a cutoff length that includes some measure of the digitization noise. If we were to assume that the noise is Gaussian and independent of systematic effects of photographing the particles, then one would hope that $l_c$ could be chosen so that $l_c - d = 3\sigma$, where $\sigma$ would be the width of the Gaussian for every experiment. Generally speaking, we have found that $1.16 \cdot d \leq l_c \leq 1.28 \cdot d$ to be sufficient. The sensitivity of $\langle c \rangle$ on the cutoff length $l_c$ is depicted in figure A.2 for the initial configurations of several experiments.
A.3 Tools and methods

We want to measure the average adjacency, $\langle c \rangle$, from each experimental photograph. We do this by digitizing the positions of the particles. We then apply an algorithm to parse through the list of positions. The algorithm computes the distances between all pairs of particles and then compares them to the cutoff length, $l_c$, described above. Each pair that has a distance below the cutoff is considered an adjacent set of particles. Since $l_c$ is higher than the ideal value, $d$, the algorithm searches for any particles that may obstruct the view of a pair of particles; any obstructed pair are considered not to be adjacent. Also, because the particles are spherical and of the same size and because the spheres rest on a plane, the densest packing possible is hexagonal cells; thus, each particle is limited to a maximum of six nearest neighbors. The algorithm outputs an adjacency list, and the network is visualized by using a specialized graph software package Combinatorica for Mathematica.

Figures A.3 and A.3 show typical results of the algorithm on an initial state and a final state of one experiment. The left panels show the experimental photographs; the right panels show the digitization of the particles and the links generated by the adjacency finding algorithm. Figure A.3(a) shows that the algorithm is picking out grain boundaries and holes that are in the photographed initial distribution. Figure A.3 shows that the algorithm is able to determine the correct network structure, with a few links either missing or generated where they should not be.

A.4 Estimating the initial adjacency

To estimate the initial value of the adjacency $\langle c \rangle_{t=0}$ we assume that the particles that are within the bulk of the initial state have six neighbors each $c_b = 6$, and that particles on the perimeter have four particles each $c_p = 4$; both of these assumptions will clearly overestimate the adjacency of the initial state, and will basically set an
Figure A.4: Typical results of the adjacency algorithm on a circular initial distribution. (a) experimental photo (b) the digitized positions of the particles and the links generated by the adjacency algorithm using a cutoff length $l_c = 1.23 \cdot d$. The algorithm can detect grain boundaries and holes that are found in the photo. Figure (b) was produced using the Combinatorica package in Mathematica.

Figure A.5: Typical results of the adjacency algorithm on the steady-state network. (a) experimental photo (b) the digitized positions of the particles and the links generated by the adjacency algorithm using a cutoff length $l_c = 1.23 \cdot d$. The algorithm is generally good at picking up the network structure, with the exceptions of a few missing and extra links.
upper bound for $\langle c \rangle_{t=0}$. Using these assumptions, the initial average adjacency will be

$$\langle c \rangle_{t=0} \simeq \frac{6 \cdot N_b + 4 \cdot N_p}{N} \quad (A.5)$$

where $N_b$ is the number of bulk particles and $N_p$ is the number of perimeter particles.

It remains to find the relative proportion of bulk particles to perimeter particles with the constraint that $N_b + N_p = N$, the total number of particles. The number of perimeter particles scales linearly with the circumference of the circle of the initial state: $N_p \sim 2\pi R/d$, where $R$ is the radius of the circle and $d$ is the diameter of a single particle. To estimate the radius of the initial circle, we approximate the area of the larger circle as the sum of the individual circles that comprise it, $A_{\text{total}} \simeq N\alpha \pi \left(\frac{d}{2}\right)^2$, where $\alpha > 1$ is a measure of the excluded space between particles; I will estimate $\alpha$ later in the section. The radius of the initial circle will be $R \simeq \sqrt{N\alpha d}/2$. Which means the number of perimeter particles will be $N_p \sim \pi \sqrt{N\alpha}$ and the number of bulk particles will be $N_b = N - N_p \sim N - \pi \sqrt{N\alpha}$. Pulling everything together, the initial adjacency can be approximated as

$$\langle c \rangle_{t=0} \simeq 6 - \frac{2\pi \sqrt{\alpha}}{\sqrt{N}} \quad (A.6)$$

To calculate an estimate of $\alpha$, we assume that the basic unit of area is a hexagonal cell that contains seven particles tightly packed within it, see fig. A.4 for a depiction of the the unit cell. The total area is then $A_{\text{total}} \simeq N\alpha A_p \simeq A_{\text{hex}} \frac{N}{7}$, where $A_p = \pi \left(\frac{d}{2}\right)^2$ is the cross-sectional area of an individual particle and $A_h = \frac{3\sqrt{3}}{2}l^2$ is the area of the minimal equilateral hexagon of side $l$ that encloses all seven particles. It remains to find the $l$ in terms of $d$. As shown is fig. A.4, we note that we can draw a regular trapezoid whose top side is of length $d$ and whose base is of length $d + 2b$, where $b$ is the base of the triangle that forms each “wing” of the trapezoid. This base has length $b = (d/2) \tan 30$. Therefore, $l = d(1 + 1/\sqrt{3})$ and the area of the hexagon in terms of $d$ is $A_h = (2\sqrt{3} + 3)d^2$. We then find an approximate value for $\alpha \approx \frac{(8\sqrt{3} + 12)}{7\pi}$. 

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Figure A.6: The hexagonal packing pattern of seven particles that form the unit cell used to estimate \( \alpha \).

Therefore, eq. A.6 becomes:

\[
\langle c \rangle_{t=0} \approx 6 - \frac{2\pi \sqrt{(8\sqrt{3} + 12)/(7\pi)}}{\sqrt{N}} = 6 - \frac{6.813 \ldots}{\sqrt{N}} 
\]  

(A.7)

A.5 Topological conservation

Consider a simple line, with no branching points. Regardless of its length, it has two endpoints. The length is determined by constituents that are connected to two other constituents, like trunk particles. Evidently, two-way connection constituents add no new termini. If, however, we consider a Y-shaped string, then there must exist exactly one constituent with a three-way connection. There are now three endpoints, one more than the straight line. We can continue to add three-way connection points, each one removes a terminus and replaces it with two. We can do this for any \( n \)-way junction point, each one takes a terminus in and splits it into \( n - 1 \) termini; thus,
the net gain in termini is $n - 2$. Therefore, in general the number of termini is the original two plus the additional termini generated by all branch points:

$$T = 1 + \sum_{n=3}^{\infty} (n - 2) \cdot B_n$$  \hspace{1cm} (A.8)

where $B_n$ is the number of $n$–way branching points. One of the termini must connect to the boundary electrode, we therefore refer to this particle as a trunk since it has two connections; we have already considered the subtraction of this termini in eq. A.8. For the system in this thesis, all the particles are all the same size. Thus, the packing in 2–dimensions constrains the branching points to a maximum of six–way connections; in the experiment we only observe three and four–way connections however.

### A.6 Steady–state adjacency

The steady–state adjacency is easily obtained by noting that the number of connections in a tree must be exactly one less than the total number of particles, $N - 1$. But in
Figure A.8: The adjacency values output by the adjacency finding algorithm that are closest to the theoretical value. The boxed inset shows a detail with the associated value of the cutoff used by the algorithm to obtain the best value for each data point. The second inset shows a frequency count of the cutoff values, which provides a notion of the best ranges to use for the cutoff value.

Considering the average adjacency for each particle, every link is counted twice, therefore the steady state value of the average adjacency is simply \( 2(N-1)/N = 2(1-1/N) \); this value holds so long as the network is a tree. Figure A.6 shows the values that the adjacency algorithm outputs that are nearest to the theoretical values. The boxed inset shows a detail of this with each point labeled by the value of the cutoff used to obtain the best value. The frequency count of these cutoff values is shown in the second inset. This provides a range of valid values for the cutoff length, which is between 1.16 and 1.28 times the size of a particle diameter.


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Vita

Joseph Kee Wook Jun was born on March 11, 1975 in Seoul, Korea. He came to the States in the Fall of 1979. Upon his arrival, he vowed to return to Korea after ten days. Twenty-five years later, he admits that he miscalculated his return date. In the meantime, he received his bachelors degree in physics from New York University in 1997 and his Ph.D. in physics from the University of Illinois in 2004. His first postdoctoral appointment began in October 2004 in the physics department at Pennsylvania State University, where Joseph started work in theoretical neuroscience.