The plant in the labyrinth: Adaptive growth and branching in heterogeneous environments

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ABSTRACT

The "ant in the labyrinth" problem describes spatial constraints upon a moving agent in a disordered medium. In contrast with an animal-like agent (an "ant"), a clonal plant can stay in a place and move at the same time: some parts develop roots, while others continue moving by horizontal growth and branching. Hereby we present a spatially explicit, dynamic model for the study of percolation by plant growth rules in lattices that consist of open and closed sites. Growth always starts from a single seed in an open percolation cluster (patch). By increasing the proportion of open sites (p), we describe a new kind of threshold (the "tracking threshold", approximately $p_t=0.73$), which is higher than the site percolation threshold ($p_c=0.5$ in this lattice). At $p_c<p<p_t$ the habitat contains a giant component, but the plant cannot spread successfully, because the pathways are too narrow compared to the scale of growth. We demonstrate this by varying the grain of the habitat pattern relative to the distance between two branching points. We conclude that fine-grained habitats can act as "labyrinths" for the plant within a broad range of p values. Within this range, the plant individual is likely to utilize only a small fraction of the available resources, leaving gaps open for colonization by other individuals. Therefore, the "labyrinth effect" is a considerable factor in the self-organization of plant communities.

1. Introduction

Clonal plants are widespread on the Earth, and dominate the vegetation in many habitat types (Callaghan et al., 1992; Cornelissen et al., 2014). Studying their space use is crucial for understanding the diversity and stability of ecosystems (Oborny and Bartha, 1995; Zobel et al., 2010; Herben and Wildová, 2012). We present a spatially explicit, dynamic model to investigate the clones' ability to spread and fill an available habitat patch by horizontal (2D) growth.

Plant clones expand by adding new modules (ramets) to the ends of branches. New branches are initiated from discrete branching points (lateral buds; Fig. 1**a**). Ramets can take up resources from the environment (water, nutrients, and light). Typically, they are spaced by stolons, rhizomes or other organs of horizontal growth. (For simplicity, we write "stolons" throughout the paper.) The pattern of growth and branching influences the clone's access to resources in the environment. "Plant foraging" has been the subject of many experiments since the 1970s (see a review by de Kroon and Hutchings, 1995). Binary environments (resource-rich vs. poor patches) were frequently used in the experiments. Theoretical modeling progressed together with the experimental work (see reviews by Oborny and Cain, 1997; Oborny et al., 2012). The importance of modeling is underlined by the

fact that many of the interesting patterns unfold on spatial and temporal scales that are too broad for direct observation. In many species, a clone can live for hundreds of years (up to several thousands), and can cover many square meters (up to hectares; see De Witte et al., 2010 for a list of examples). The objective of our model is to investigate the long-term consequences of horizontal growth and branching in various, heterogeneous environments.

Natural habitats are often heterogeneous on the fine scale of individual ramets. For example, light quality (R/IR ratio) may vary significantly across centimeters (Silvertown and Smith, 1988). Soil resources (phosphate, potassium, etc.) have also been observed to show strong spatial patterning within a meter (Jackson and Caldwell, 1993). For a plant, adjusting the growth pattern to the habitat pattern can be highly advantageous. Several papers have discussed the evolution of plant form in this context (e.g., Bell, 1984; Novoplansky, 2002; de Kroon et al., 2005). We investigated one aspect within the broad topic. Consider a single resource patch that is suitable for colonization, and is surrounded by an unsuitable area. The shape of the patch can be simple (e.g., round-shaped) or complex (e.g., containing narrow lanes, dead ends, and loops). Starting from a single seed within the patch, we studied whether the plant clone could track along these structures, occupying the whole patch, or did it leave some regions unoccupied.
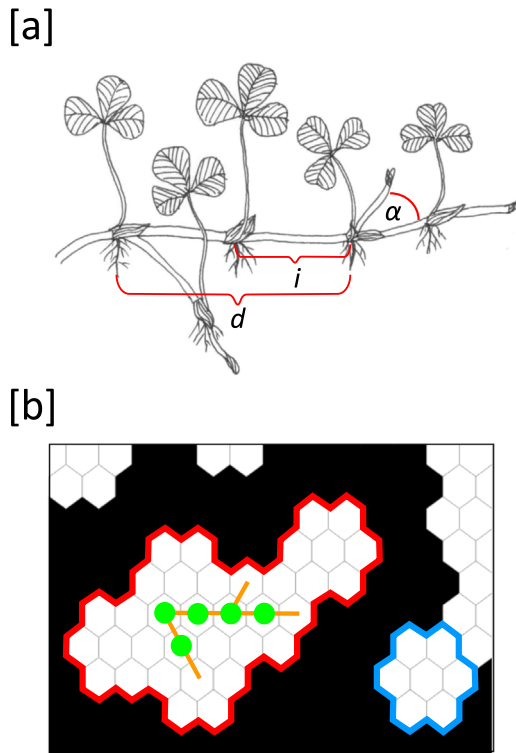
Fig. 1. A clonal plant in a heterogeneous environment. [a] An example: five rooted ramets and three growing stolon tips. α is the branching angle; *i* is the length of a fully developed stolon between two successive ramets; *d* is the distance between two branching points. [b] The same plant in our lattice model. Ramets are denoted by green dots; stolons are yellow lines. The lattice constant is *i*. In this example, the habitat pattern is coarse-grained relative to *i*. Elementary hexagons (sites) are grouped into larger hexagons (spots). All sites that belong to the same spot have the same quality: open (white) or closed (black). Adjoining open sites form percolation clusters (patches). We outlined the patch in which the plant is growing (red), and we show an example for a spot (blue) that is part of another patch. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The motion of animals in habitat patches is an intensively studied subject, especially at the landscape scale (Patterson et al., 2008). Some finer-scale phenomena have also been studied, e.g. the pathways of tenebrionid beetles, moving on bare ground among grass tussocks (Wiens and Milne, 1989). The application of percolation theory (Wiens et al., 1997), in particular, an "ant in the labyrinth" model has also been proposed for understanding the pathways of motion (With et al., 1999). The "ant in the labyrinth" model had originally been introduced in statistical physics, to describe the motion of a freely moving agent in a disordered medium (de Gennes, 1976; chapter 6.1 in Stauffer and Aharony, 1994). The simplest motion is random walk. Former studies have tested random walk, and some other rules which also assumed freely moving agents (e.g., correlated or biased random walks; Codling et al., 2008). In this paper, we extend the scope to clonal plants, which do not move freely.

The motion of clonal plants can also be described by definite spatial rules (see Oborny et al., 2012 for review). They differ from "ants" in three main characteristics. (1) A plant can stay at a place and can move on at the same time. Staying is realized by rooting; moving is achieved by growth, usually at the apices of specified shoots, e.g. stolons (Fig. 1a). (2) Consequently, a specific kind of self-avoiding motion can be observed. Rooted ramets usually act as considerable obstacles, while stolons can cross one another's way. (3) The pathway can branch.

We investigated this special motion by using a spatially explicit, dynamic model (Fig. 1b). To focus on the aforementioned three characteristics, the model contained the following simplifications: (1) We assumed that all the ramets stayed alive during the course of the simulation. This allowed us to observe the entire pathway of growth in

each run. (2) The lattice constant was chosen in such a way that one lattice cell could not contain more than one ramet. Once a site had been occupied by a ramet, no further growth could occur into that cell. (3) Each ramet developed maximally one main and one side-branch. If those branches failed to find any empty open cell, then no further trial was permitted. Rules (2) and (3) were chosen to magnify plant characteristics (2) and (3), respectively. Real plants are usually less limited (see the Discussion), although rule (3) does occur in this strict form (for example, in *Trifolium repens*; Gautier et al., 2000).

Our study focused on the efficiency of space filling. We recorded the size of the patch in which the seed had landed, and observed the occupied vs. unoccupied portion of the patch. In the simulations, we varied the resource pattern (fine vs. coarse-grained), and the growth pattern of the plant (Basic vs. Rigid).

2. The model

Space was represented by a two-dimensional, triangular lattice, which consisted of $A = 150 \times 150 = 22500$ sites (hexagons). *p* proportion of the sites was open; and $1 - p$ was closed. Only open sites could be colonized by ramets (Fig. 1b). The lattice constant was equal to the ramet size. The offspring ramets developed adjacent to their parents. Time and the states of sites were discrete variables; the model was based on a stochastic cellular automaton, with the extension that the direction of growth and the branching order within the plant were also taken into account.

2.1. The environment

In the fine-grained habitats (*r*=1), open and closed sites were distributed randomly. The proportion of open sites was *p*. In the coarse-grained habitats (*r*=2), the lattice was subdivided into larger hexagons (spots), each consisting of seven elementary hexagons, i.e., the sides of each spot were 2 units (see an example outlined in blue in Fig. 1b). The proportion of open spots was *p*, and they were randomly distributed. The area was cut to size *A*, truncating the spots at the edges. Thus, *p·A* was the exact number of open sites in the fine-grained habitats, and the average number in the coarse-grained ones. In every simulation, we recorded the size of the patch in which the seed had landed. A patch was defined as a set of adjacent open sites, i.e. a percolation cluster. For example, the patch outlined in red in Fig. 1b consists of five spots; its size is $s = 35$ sites. Figs. 2 and 3 show examples for fine and coarse-grained habitats, respectively.

2.2. The plant

The plant consisted of ramets and stolons (Fig. 1a). Stolon tips could grow and produce offspring ramets in new sites. The direction of growth was recorded. The offspring ramet always initiated a stolon tip to continue growth in that (principal) direction. In addition, it could initiate a side-branch, which diverted from the principal direction by a branching angle α, selected at random from the four possible directions ($\pm 60°$ and $\pm 120°$). In the Basic growth form, the branching probability was 1, thus the distance between two branching points was exactly *d*=1 unit (Fig. 3a). In the Rigid form, the branching probability was 0.5, thus the expected distance between two branching points was $\bar{d}$=2 (Fig. 3b). Consequently, it was more difficult for the Rigid plant to turn when the pathway turned.

2.3. Initial conditions and updating

Every growth process started from a single seed near the center of the field, in order to let the plant develop undisturbed by the boundaries for a period of time. The boundaries were closed, i.e., could not be crossed by the stolons. In the simulations that produced the results (Figs. 4–6), the initial site was at position (75, 75); while in