



Effects of local density of clonal plants on their sexual and vegetative propagation strategies in a lattice structure model

Makihiko Ikegami^{a,b,*}, Dennis F. Whigham^{b,c}, Marinus J.A. Werger^{a,b}

^a Department of Plant Ecology & Biodiversity, Utrecht University, P.O. Box 80084, 3508 TB Utrecht, The Netherlands

^b SERC, P.O. Box 28, 647 Contees Wharf Road, Edgewater, MD 21037, USA

^c Department of Landscape Ecology, Utrecht University, P.O. Box 80084, 3508 TB Utrecht, The Netherlands

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ABSTRACT

Clonal plants can propagate both sexually and vegetatively and the balance between the efforts of sexual and vegetative propagation can be determined by inter- and intra-specific competition. This raises the question of whether sexual propagation becomes more suitable than vegetative propagation or vice versa. Some studies suggest seed production is positively correlated with plant density, and others, negatively. To evaluate the effects of local density of ramets on plant propagation strategy, we developed a lattice model where two strategies compete with each other. In the model, a plant changes its strategy based on local density as defined by the proportion of neighboring lattice cells containing plants. One strategy produces seeds at high local density (SEEDING at HLD) and produces ramets at low local density, and the other strategy produces ramets at high local density (RAMETING at HLD) and seeds at low local density. Seeds can spread all cells while ramets can reach only adjacent cells, and if an individual from a seed competes with an individual from a vegetative propagule, the latter always wins. Each plant has different thresholds to change its strategy from sexual to vegetative, or vice versa, along with local density. In the model, a realized density depends on both reproductive rate and mortality; thus, we evaluate the performance of each strategy under different mortalities.

When mortality is high, a realized density becomes low. Under this condition, plants reproduce mainly by seeds (either the SEEDING at HLD plants with lower threshold values, or RAMETING at HLD plants with higher threshold values) and show high performance. High mortality results in many vacant lattice cells that do not have neighboring plants. Since vegetative propagules cannot reach these isolated vacant lattice cells while seeds can, plants that propagate mostly or exclusively by seed become dominant. When mortality is low, the local density becomes high and few cells are available for new individuals. Under this condition, SEEDING at HLD becomes dominant. SEEDING at HLD plants with a high threshold value almost always reproduce ramets, but they also produce seeds when neighboring cells are completely occupied. Although SEEDING at HLD plants with a high threshold value and RAMETING at HLD plants have an equal chance to get established by vegetative propagation, SEEDING at HLD plants also produce seeds when there are no vacant neighboring cells (i.e., high density), and those seeds can, although rarely, establish new individuals. In conclusion, the production of ramets at lower densities and the production of seeds at higher densities seem to be a proper strategy in our model.

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1. Introduction

Clonal plants can spread by vegetative and sexual propagation. Through vegetative propagation, fewer but initially larger individuals with a lower mortality rate are produced, while through sexual propagation by seeds, more but initially smaller individuals with

higher mortality are produced. Vegetatively produced ramets have lower mortality rates because mother ramets support the daughter ramets with carbohydrates, water and minerals (Slade and Hutchings, 1987; Marshall, 1996; Stuefer et al., 1996). Individuals originating from seeds are, on the other hand, smaller than clonal ramets at birth and they receive no support other than resources supplied to the seed from mother plants. Seeds are more vagile than clonal ramets because they can be dispersed over a larger area. Thus, the balance between sexual and vegetative propagation is an important evolutionary and ecological feature of the life history strategies among clonal plants.

In Ikegami, 2004, we described how *Scirpus olneyi* produced more flowering shoots and seeds in patches with higher shoot

* Corresponding author. Present address: Donald Bren School of Environmental Science & Management, University of California, Santa Barbara, CA 93106-5131, USA. Tel.: +1 805 893 7044.

E-mail addresses: makihiko@mbox.kyoto-inet.or.jp, mikegami@bren.ucsb.edu (M. Ikegami).

densities, both in a field study and a garden experiment. Under field conditions, where resources are often patchily distributed, the result of our study would be expected because patches with more resources would be exploited by *S. olneyi* via the production of ramets that occupy the space, and resources would be sufficient to invest in seed production. In our garden experiment, however, the increase in seed production at higher shoot densities was not expected. The quantity of resources (i.e., nutrients) in the tubs that were used in the experiment was similar in both high- and low-density treatments. Thus, the resources per ramet were fewer in the tubs with high shoot densities compared to the resources available to ramets in the tubs with low shoot densities. Moreover, competition for light would also have been higher in the tubs with high shoot densities. Even though competitive stresses are greater at high densities (Winn and Pitelka, 1981) we would expect that the resources per ramet would have been less in the high-density treatment and available resources would have limited seed production. Results from other studies would also suggest that plants growing in relatively poor environmental conditions (i.e., our high density treatment) would increase their allocation to clonal propagation (Raven et al., 1981; Callaghan, 1988). Abrahamson (1980) theorized that even with uniformly distributed resources, vegetative propagation would be advantageous at low plant density as it facilitates local spread and occupation, while seed propagation is advantageous at high plant density as it enables dispersal to new and perhaps more favorable sites. On the other hand, some research yielded opposite results. At high shoot density, since competition between ramets is severe, clonally growing ramets have a higher chance of establishment than seedlings. Thus, in dense patches, clonal propagation is to be expected (Williams et al., 1977) and seed production can decrease (Law et al., 1979).

To explain the results of the field and garden experiments, we developed a spatially explicit simulation model to evaluate competition between clonal plants that have different reproductive strategies in response to variation in ramet density. We use a lattice model that is commonly used to describe interactions between adjacent individuals in space. Lattice models are used in various biological and ecological studies (Nakamura, 2006) such as Lotka-Volterra system (Tainaka, 1989; Wilson et al., 1993), epidemiology (Sato et al., 1994) or forest dynamics (Kubo et al., 1996). For clonal plants, Oborny et al. (2000) and Kun and Oborny (2003) studied the effect of clonal integration in space and Harada and Iwasa (1994) and Harada (1999) studied the balance between long versus short distance propagation strategies.

In clonal plants, mother plants produce ramets only in neighboring patches, so that ramet performance may be expected to be highly regulated by local density (LD) rather than the whole population density (Global density; GD). Seed dispersal tends to take place in the whole habitat of a population, and thus seed performance may be highly regulated by GD rather than LD. For this reason, we used a lattice model in the simulation which allows us to explore spatially explicit interactions at a small scale (Pacala and Silander, 1990). We compare two strategies: One strategy is the SEEDING at HLD strategy in which plants produce seeds at higher local density, and the other is the RAMETING at HLD strategy in which plants produce ramets at higher local density. In the simulation we evaluate which strategy is better under various conditions.

2. Model

Lattice models consist of numerous cells that correspond to a small site where an individual can occupy or stay vacant, and most processes/interactions occur among nearest neighboring cells

(Fig. 1). In each time step, those interactions decide the status of individual cell in the next time step (Fig. 1). We use a two-dimensional regular square lattice model with 100×100 cells. To avoid boundary effects, we assume a periodic boundary condition that allows us to connect all cells in the model across all boundaries. Each lattice cell has two states, occupied or unoccupied, and only one plant can occupy a cell at a time. Each cell is surrounded by 8 cells and plant interactions take place among neighboring cells. We measure two densities in the model; global density (GD) is defined as the ratio of the number of individual plants in the lattice to the total number of lattice cells (total number of individuals/10,000), and local density (LD) is defined as the ratio of the number of occupied cells to all cells within the neighboring field (3×3 cells) for each plant.

In the model, plants can propagate vegetatively by producing new ramets and sexually by producing seeds. At each time step in the model, each plant propagates sexually or asexually, depending on its life history strategy and LD. Individuals cannot produce both seeds and asexual ramets at one time step. Individuals are assigned one of two life history strategies in the model: SEEDING at HLD and RAMETING at HLD. SEEDING at HLD plants produce seeds at higher densities and ramets at lower densities (symbol Sh in Fig. 1). RAMETING at HLD plants produces ramets at higher densities and seeds at lower densities (symbol Rh in Fig. 1). An individual is able to switch between SEEDING at HLD and RAMETING at HLD, depending on threshold values of LD. If LD exceeds the threshold value, SEEDING at HLD individuals switches from vegetative to sexual propagation and RAMETING at HLD plants switch from sexual to vegetative propagation. For convenience, we use as threshold values the number of occupied cells around each plant. Thus, the threshold value varies from 0 to 8. In the model, individual plants are not able to identify the reproduction strategy of a neighboring plant and are only sensitive to the number of occupied neighboring cells. Each strategy has a fixed genotype, thus offspring ramets have the same characteristics as their mother plant.

New clonal individuals can only occupy adjacent vacant cells. Mother plants can only propagate ramets into the 8 adjacent cells; thus, if a vacant cell is surrounded by occupied cells, an individual can be established within by vegetative propagation from one of the surrounding cells. For each occupied cell, the model checks the propagation mode of the occupying plant and if the plant is in the vegetative propagation mode, then the model determines whether the plant propagates a new individual into the vacant cell or not, depending on its ramet production probability (RPP), the probability that the plant produces a new individual into a neighboring cell. If more than one ramet invades a vacant cell, the model randomly chooses which one is successful.

Seeds are assumed to be produced and dispersed in sufficient numbers to potentially reach every cell independent of the number of flowering individuals in the lattice. Seeds are dispersed to vacant cells if these cells do not have any occupied neighboring cells, or if no individual produces an asexual ramet into these cells. Seedlings are established in a vacant cell depending on a seed establishment probability (SEP), defined as the probability of seed establishment in every cell of the lattice. For convenience, SEP is fixed and independent of the total number of seeds produced within each time increment. If a seedling successfully establishes in a cell then the model determines which life history strategy it is assigned, depending on the seed proportion of the two strategies at each time increment. During each time step in the model, each individual in the lattice ran the risk of death based on a fixed death rate. At the end of each time step, each plant is examined to determine whether it survives or not. If a plant dies, the cell that it occupied becomes vacant for the next time step in the model. Death rates are independent of whether an individual was produced by sexual or vegetative propagation. Although the realized densities

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