



# The analysis of an effect of seed propagation on defense strategy against pathogen transmission within clonal plant population using lattice model



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## ABSTRACT

Many clonal plants have two breeding systems, vegetative and seed propagation. In vegetative propagation, plants reproduce genetically identical offspring that have lower mortality rates. By contrast, the seed propagated offspring has higher mortality rate, however, the seed propagation acts an important role in maintaining the genetic diversity and reproduce widely. According to the experimental studies, the balance between the breeding systems, vegetative and seed propagation, is determined by several functions, such as resource allocation. The infection and spread of systemic pathogen also affect the optimal balance of the breeding systems.

Thus, we examine the effect of invasion of systemic pathogen on the optimal balance of the breeding systems of clonal plant using lattice model in two cases, single population and mixed population. In the analysis, the equilibrium and its local stability were derived using approximation method and numerical simulation in single population. Additionally, two situations were assumed in mixed population, infected and uninfected populations, and the efficacy of seed propagation on the suppression of epidemic infections was examined by comparing the results in the two situations.

As a result, seed propagation is an effective defensive behavior against systemic pathogens. In the single population, the plants increase their population by increasing the proportion of seed propagation when the epidemic pathogen has highly infective. In mixed population, the increasing proportion of seed propagation is the optimal breeding strategy to defend against the spread of a systemic pathogen.

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## 1. Introduction

Approximately 70% of terrestrial plants (van Groenendael and Kroon, 1990) and most aquatic plants, such as sea grass Berković et al., are clonal. Many clonal plants have two breeding systems, vegetative and seed propagation. In vegetative propagation, plants reproduce genetically identical offspring that have lower mortality rates because resources are supplied to the offspring from other individuals through interconnected ramets (Marshall, 1996; Slade and Hutchings, 1987). By contrast, plants maintain the genetic diversity and reproduce widely in seed propagation although the seedling has higher mortality.

The balance between the breeding systems, vegetative and seed propagation, has been studied experimentally (Boedeltje et al., 2008; Chu et al., 2011; Hegazy, 1994; Kleunen et al., 2001). Ac-

ording to these studies, the balance is determined by several functions, such as resource allocation, competitive ability and colonization capacity. For instance, if the resource is distributed heterogeneously in space, then vegetative propagation has an advantage over seed propagation because the vegetative propagules can be supplied resources from local colonies of clones (Sakai, 1995). On the contrary, if the resource is distributed homogeneously, then seed propagation has an advantage over vegetative propagation because seed propagation can spread the offspring long distances and distribute them over an entire habitat (Abrahamson et al., 1980).

The infection and spread of systemic pathogen also affect the optimal balance of the breeding systems. According to Stuefer et al. (2004), systemic pathogens have diverse negative effects on plants, which result in severe damage or death. For example, they can lead to leaf deformations (Gibbs and Harrison, 1976), growth rate reductions (Jones, 1992; Piqueras and Klimeš, 1998; Potter, 1993), growth-form changes (Piqueras, 1999; Wennstrom and Ericson, 1992) and reduced reproduction

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(García-Guzmán and Burdon, 1997; Groppe et al., 1999; Pan and Clay, 2002). Thus, the plant population suffers serious damage through effect of a pathogen. Plants have diverse defense responses to systemic pathogens (Koubek and Herben, 2008), such as (i) deliberately detaching the infected ramets or tissues (McCrea and Abrahamson, 1985), (ii) increasing their clonal growth rate (Frantzen, 1994; Piqueras, 1999; Van Groenendael et al., 2012; Wennstrom and Ericson, 1992), and (iii) limiting the infection risk and pathogen spread by severing the physical connections of ramets (Eriksson, 1993; Piqueras and Klimeš, 1998) or by long-distance dispersal through seed propagation. The detaching action blocks the spread of the pathogen in a population, although the benefits of vegetative propagules decrease due to the reduction in the genet size. The increase in the growth rate of vegetative propagation is an effective escape behavior from the pathogen's spread. However, vegetative propagation assists the pathogen's spread because the vascular system in the ramets acts as a transmission pathway to other ramets. Thus, the disease becomes epidemic in a colony of vegetative propagules (Stuefer et al., 2004). Increasing seed propagation is an effective defensive behavior against the spread of pathogens because the plants will reproduce in areas distant from the infection site.

Several mathematical models, such as transition matrix model (Takada and Nakajima, 1996), reaction-diffusion equation model (Hamidi et al., 2012), lattice model (Boots et al., 2000; Ellner, 2001; Harada, 1999; Harada and Iwasa, 1994; Harada et al., 1997; Hiebeler, 2000; 2007; Liao et al., 2013; 2015; 2016; Ying et al., 2014) and individual-based model (Fischer and Van Kleunen, 2001; Herben and Suzuki, 2002; Ikegami et al., 2012; Oborny and Kun, 2003; Winkler and Fischer, 2002), are used to express the plant reproductive process. We adopted the lattice model among them because the spatial structure has an impact on above phenomena. Actually, the interactions between a plant and a pathogen depend on the spatiotemporal dynamics, such as pathogen dispersal and the spatial positioning of ramets (Koubek and Herben, 2008; van Mölken and Stuefer, 2008). According to Koubek and Herben (2008), features of the host assist local pathogen transmission and the evolution of the pathogen towards lower virulence levels (Gandon et al., 2001) because clonal growth increases the probability of finding susceptible hosts in the vicinity of the initially infected host. Additionally, the analyzing the model on lattice space is suited to express plant reproduction processes. The model creates discrete spaces, and the framework (the configurations of sites and distances between each site) of the lattice does not change. Plants are distributed discretely in space and plants cannot move from the established place during their lifetime.

There are many approaches that use the lattice model to analyze the breeding dynamics of clonal plants (Harada, 1999; Harada and Iwasa, 1994; Harada et al., 1997; Ikegami et al., 2012; Liao et al., 2013; 2016), as well as pathogen transmission dynamics (Haraguchi and Sasaki, 2000; Sakai and Takada, 2016; Satō et al., 1994). Among them, studies of breeding dynamics examined the effects of spatial structures on the reproductive strategy, represented in plants by the competition between vegetative and seed propagation. Harada and Iwasa (1994), Harada et al. (1997) and Harada (1999) considered two types of plants and considered the model based on multitype contact process (Neuhauser, 1992). One type reproduces through both seed and vegetative propagation (mixed strategy), and the other one reproduces through only vegetative propagation (pure strategy). Additionally, they assumed that the proportion of both breeding propagation systems in the mixed strategy depends on the distance from the parents, and they examined the ESS of the balance between vegetative and seed propagation. Ikegami et al. (2012) considered the effects of plant density and mortality on the adoption of breeding systems. They assumed that each individual switches between seed and vegetative propa-

gation depending on the local density of the individuals and that the switching threshold of the reproductive pattern is affected by mortality. They analyzed the optimal switching strategy based on local density and mortality. These studies did not consider the effects of pathogens on the reproductive strategy.

However, studies of pathogen transmission dynamics examined the transition threshold of the equilibrium phase (mainly extinction, disease-free and epidemic phases). Sato et al. (1994) analyzed in particular the phase transition in the TCP using the PA. Haraguchi and Sasaki (2000) assumed that multiple pathogens have different virulence levels. They examined the ESS of the infection rate using a numerical simulation. Their simulation suggested that pathogens evolve to an intermediate infection rate. Sakai and Takada (2016) examined the effects of superinfection on the evolution of plants and pathogens. However, it is necessary to modify their models to describe both the plant reproduction process, including seed propagation, and the pathogen propagation process because their models could not express the seed propagation process.

We, in the present paper, examined the dynamics of plant reproduction and pathogen propagation, and the effects of seed propagation on the defense responses to pathogen spread in single and mixed (coexistence of several plant types) plant populations. Thus, the change of relative merit in the breeding system caused by the invasion of a plant population by systemic pathogens was expressed. In the analysis, the equilibrium and its local stability were derived using approximation methods in the case of single populations. Additionally, using the Monte Carlo simulation, the effects of spatial structure through a comparison with approximately solution was examined, and the case of a mixed population was analyzed. In mixed populations, two situations were assumed, infected and uninfected populations, and they were analyzed using only the MCS because other analyses of the model are too complex to obtain analytical results, having too many variables. The efficacy of seed propagation on the suppression of epidemic infections was examined by comparing the results in the two situations.

## 2. Model

A model that included the plant reproductive process (both vegetative and seed propagation) and the pathogen transmission process was constructed. The dynamics of the model is a continuous Markov process on a lattice space. The states of each site are presented as empty ("0"), susceptible (healthy) individual ("S"), infected individual ("I"), the intrinsic reproduction rate of the plant by  $m_s$ , the intrinsic transmission rate of the pathogen by  $m_i$ , the proportion of vegetative propagation by  $\alpha$ , and the mortality rate of individuals of each state by 1. Additionally,  $\rho_\sigma(t)$  ( $\sigma \in \{0, S, I\}$ ) is the probability that a randomly chosen site has state  $\sigma$  at time  $t$ . Thus,  $\rho_\sigma(t)$  indicates the global density of the site with state  $\sigma$ .

Four demographic processes were configured: (i) seed propagation (SP); (ii) vegetative propagation (VP); (iii) infection (IP); and (iv) death (DP). The plant reproductive processes (SP and VP) are represented by transitions from state "0" to "S", which indicates that plants reproduce offspring by either breeding system into an open area (an empty site is then occupied by a healthy individual). IP is represented by the transition from state "S" to "I", which indicates that healthy individuals are infected by pathogens. DP is represented by the transition from "S" or "I" to "0", which represents the death of healthy or infected individuals, respectively, from natural causes and the virulence of the pathogen, respectively. In addition, infected individuals can not return to health and reproduce their offspring.

The model was constructed based on two stage contact process (TCP) (Krone, 1999; Li and Han, 2013), which is modification of basic contact process (Harris et al., 1974), in mathematical mod-

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