

Markovian spatial-inhibition models for established clonal populations

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Keywords: *Aralia nudicaulis*, Density-dependence, Local interaction, Ramet, Second-order spatial analysis, Self-thinning, Spatial pattern.

Abstract: While a number of experimental studies and models have examined the foraging behaviour of single clonal genets, very few investigations have focussed on the dynamics of ramet recruitment in established clonal monocultures. This contribution discusses modelling the spatial structure of density-dependent clonal populations using Markovian spatial-inhibition rules. Markovian dependence refers to situations where local conditions (interactions with neighbours) determine the outcome of a process. An example is presented in which the Markov spatial-inhibition model is successfully fitted to observed ramet spatial patterns in the clonal herb *Aralia nudicaulis* L. (wild sarsaparilla).

Introduction

A large number of clonal plant growth models have been described in the literature (Waller & Steingraeber 1985, Cook 1985). Deterministic, stationary models are generally based on averaged values of field-measured divergence angles, internode lengths, and daughter module fates (e.g. Smith & Palmer 1976, Bell & Tomlinson 1980). Because such models focus on idealized clonal growth designs, they implicitly assume that genet architecture is adaptive, and that selection favours precise clonal organization. However, field studies indicate that natural variation and stochastic processes can produce ramet patterns that cannot be predicted by simple architectural rules. While clonal growth rules are under developmental control (making the description of modular branching relatively straightforward), the modelling of ramet interaction is considerably more problematic (Bell 1986).

More realistic clonal growth models can be obtained by using so-called 'non-stationary' rules (Waller & Steingraeber 1985). In non-stationary models, ramet initiation is a function of the local environment encountered, as well as internal factors such as branch order and apical dominance (Sutherland & Stillman 1990; compare the 'sighted' models of Bell 1986). By varying growth rules independently, these models can

produce a variety of potential clonal growth forms (Callaghan et al. 1990). Mechanistically, clonal plant architecture is under physiological control: important factors include apical meristem longevity, the position, abundance and activity of lateral meristems, branching angles and phenotypic plasticity. It has been suggested that morphological (developmental) plasticity in clonal plants is highly adaptive (e.g. Waller & Steingraeber 1985; Hutchings & Mogie 1990).

Clonal growth models have also been used in simulations of foraging behaviour in clonal plants (recently reviewed by Hutchings & de Kroon 1994). Foraging models investigate the effects of parameters such as spacer length and branching intensity on the placement of ramets within simulated 'patchy' environments. These iterative simulations generally follow a single clone through time (e.g. Oborny 1994). Unfortunately, very few of these clonal growth models have been tested against real populations. The flourishing clonal growth observed in simulation models (and controlled experiments) is generally not seen in well-established (density-dependent) clonal populations (Sutherland & Stillman 1990).

Many clonal species form extensive, persistent monocultures in which ramet production is density-dependent. The most obvious are 'consolidating'

species such as *Phragmites australis*, *Typha latifolia*, *Solidago canadensis* (de Kroon & Schieving 1990), but the potential to form dense monocultures is by no means restricted to this group. It has often been observed that clonal plants develop a more branched structure, and a high density of ramets, in favourable habitats (Hutchings & Mogie 1990). In such situations, the '-3/2 self-thinning rule' operates to effectively regulate ramet density (Hutchings 1979). Pitelka (1984) hypothesized that most clonal populations avoid self-thinning by controlling meristematic activity. A likely mechanism is a decrease in bud activity in response to decreased light quantity and changes in light quality; such a mechanism operates regardless of whether the population consists of a single genet, or many genets (de Kroon & Schieving 1990). Such control ensures that ramet density in a population is high enough to effectively exploit the space (and to prevent other species from invading), while remaining low enough to minimize inter-ramet interactions.

In dense clonal monocultures, the spatial arrangement and packing of ramets determine the overall efficiency of resource capture (Harper 1985). In order to respond quickly and efficiently to changes in resource space (e.g. death of a ramet), clonal growth must be highly dynamic. Localized or Markovian inter-ramet interactions are critical in this regard (Waller & Steingraeber 1985); sensitivity to local conditions (neighbours) ensures that daughter ramets are placed outside the 'resource depletion zones' of existing ramets. Consequently, a locally regular spatial pattern of ramets (the result of ramet-to-ramet inhibitory interactions) should develop and be maintained. However, very few studies have examined the spatial pattern of natural clonal populations for evidence of spatial regularity.

In this paper, I discuss the importance of localized (Markovian) ramet interactions in modelling clonal growth. In particular, I discuss the utility of Markov spatial inhibition processes for modelling the spatial structure and dynamics of established, density-dependent clonal populations. An example of fitting the model to observed spatial patterns of the clonal herb *Aralia nudicaulis* L. (wild sarsaparilla) is presented.

Spatial Inhibition Processes

Matérn (1960) developed a series of spatial inhibition process models based on the simple rule that no two individuals (ramets) can be less than a distance δ apart. Such processes, which are collectively referred to as 'hard-core' models (Ripley 1977), produce patterns of high local spatial regularity. Matérn process models assume that there is complete inhibition up to a distance δ , and no interaction outside this bound. Given

that organisms are morphologically and physiologically plastic, such 'hard-core' models are probably too restrictive (Cormack 1979). A more realistic alternative makes it unlikely, but not impossible, for two (or more) individuals to occur in close proximity (Cormack 1979, Diggle 1983). Markov point processes (Strauss 1975, Ripley & Kelly 1977) are spatial-inhibition models that quantify spatial interactions in this 'non-strict' way. Markovian dependence is implied whenever local conditions (e.g. resource depletion zones) determine the outcome of a process at a given location.

Biologists are most familiar with Markov processes in the context of Markov chains, which are formally defined as stochastic processes for which the conditional distribution of event X_n , given a set of past events, depends only on the last observation in the set (Bhat 1982). A similar property for random fields (in our case, stochastic processes in the plane) requires definition of an analogue of the local dependence condition (ideas of 'past' and 'future') that underlies the one-dimensional case (Adler 1982). Ripley & Kelly (1977) define local conditionality in terms of 'neighbourhoods', where individuals (ramets) are 'neighbours' if they are less than a distance δ apart. Markovian dependence is implied since the probability density of a ramet occurring at location X depends only on local conditions. Since conditional intensity depends only on the configuration in the 'neighbourhood' of X , the process is said to be 'Markov of range δ ' (Diggle 1983). The basic Markovian model generates an entire process of locally regular point patterns.

The Strauss Process

The basic Markovian process model was developed by Strauss (1975) and modified by Ripley and Kelly (1977). The conditional density of the process is given by:

$$f(X) = \alpha \beta^n \gamma^s \quad (1)$$

α = normalizing constant.

β = indicator of intensity of the process ($\beta > 0$).

γ = descriptor of interaction between neighbours ($0 \leq \gamma \leq 1$).

s = number of ramets in population X less than a distance δ apart.

n = total number of ramets.

Varying the interaction parameter γ results in a spatial process. Specifically, $\gamma = 0$ produces a Matérn 'hard-core' process of range δ , while $\gamma = 1$ results in a Poisson random pattern. Intermediate values ($0 < \gamma < 1$) produce a continuum of 'non-strict' inhibition processes; the larger the value of γ , the less 'strict' the

process. Examples of resulting point patterns are given in Upton & Fingleton (1985: 21), Diggle (1983: 66) and Baddeley & Møller (1989: 92).

Generating Strauss Processes

A straightforward point-deletion algorithm for generating the Strauss process is described by Ripley (1979). One begins with an initial (say, random) configuration of n points (ramets). A randomly-selected point X_1 is then deleted, retaining X_{n-1} points. For the neighbourhood model described above, new random coordinates for X_1 are produced and this 'replacement' ramet is accepted with probability $p(X_1) = \gamma^s$, where s is the number of ramets within a distance δ of ramet X_1 (Kenkel 1993). Repeating the deletion-replacement step many times results in convergence to a Strauss process; Ripley (1979) suggests that $4n$ such steps are adequate in practice. A toroidal correction should be implemented to account for edge effects.

Alternative definitions of the Strauss replacement probability $p(X_1)$ are possible. Diggle (1983: 65) suggested models in which the replacement probability is a function of local inter-ramet distances. Baddeley & Møller (1989) develop models in which the concept of 'neighbourhood' is context-dependent (rather than being a fixed distance δ). Of particular interest to biologists is a model that defines interactions between nearest neighbours, where 'neighbours' are defined using the Dirichlet tessellation (see Kenkel et al. 1989 for an application of tessellation analysis to biological patterning).

Application to Clonal Plant Populations

Despite the acknowledged importance of localized interactions in developing clonal populations, very few studies have investigated the spatial pattern of clonal ramets. If localized spatial inhibition is indeed important, regular spatial patterns of ramets should be observed in nature. In mapping populations, it is essential to select environmentally uniform sites so as not to obscure patterns developed through biotic interactions (Hutchings & Barkham 1976, Kenkel 1988). A locally regular pattern offers strong empirical evidence, but not proof, of inhibitory biotic interactions (Antonovics & Levin 1980).

Kenkel (1993) modelled Markovian dependence in two populations of wild sarsaparilla (*Aralia nudicaulis* L., Araliaceae) growing in the understory of a mature oak-ash gallery forest in southern Manitoba, Canada. The species is a clonal, acaulescent herb with long-lived, perennating rhizomes that produce numerous dormant meristems. Ramets are produced approxi-

mately every meter or so. Each ramet is a vegetative shoot consisting of a single doubly compound leaf having a distinctive 'umbrella' shape. Natural populations are often extensive monocultures consisting of a complex interdigitation of genets.

Two populations (5 x 5 m plots) were selected (based on perceived uniformity of site conditions) and the position of each ramet mapped. One plot contained $n=533$ ramets, the other $n=580$ ramets. Second-order spatial analysis (Ripley 1977) indicated a trend toward spatial regularity at local spatial scales (10-25 cm radius range) in both plots. This is consistent with a Markovian model of inter-ramet interaction: since competitive interactions are by definition inhibitory, minimal overlap of resource depletion zones is expected, resulting in a locally regular spatial pattern of ramets. I fitted Strauss process models to the observed patterns by iteratively varying the parameters γ (the descriptor of interaction between neighbours) and δ (the interactive radius). A goodness-of-fit criterion suggested by Diggle (1983: 77) was used in fitting the model to the empirical data. For both populations, best fits to the Markov point process model were obtained for parameter values $\delta = 18$ cm and $\gamma = 0.8$. The interaction radius $\delta = 18$ cm corresponds closely to the mean horizontal radius of wild sarsaparilla leaves (ramet shoots), indicating that clonal interactions occur at the spatial scale of individual ramets. The interaction radius can therefore be interpreted as a measure of the size of a ramet's resource depletion zone. The value $\gamma = 0.8$ indicates that the degree of spatial inhibition is comparatively weak (recall that $\gamma = 1$ corresponds to complete spatial randomness, $\gamma = 0$ a Matérn 'hard-core' process). This indicates that the Matérn process is far too restrictive a model, as anticipated by Cormack (1979).

Future Directions

Ecologists have expended considerable effort developing models and undertaking controlled experiments to examine the foraging properties of single genets. By contrast, comparatively few studies have focussed on inter-ramet interactions in well-established, density-dependent clonal monocultures (Sutherland & Stillman 1990). Clonal monocultures form extensive and persistent rhizome systems (from the same or different genets) that function in the storage of photosynthates and in the acquisition of water and nutrients (Hutchings & de Kroon 1994). Excavations have revealed that a dense, persistent rhizome system is characteristic of *Aralia nudicaulis* populations (Kenkel 1993). The presence of an extensive rhizome system may be an important adaptive strategy for optimizing the acquisition of limiting resources. Specifi-

cally, the presence of numerous dormant meristems ensures that lost ramets are quickly replaced; all that is required is activation of a previously-dormant meristem (c.f. Pitelka & Ashmun 1985). In some respects this dynamic, Markovian view of clonal population dynamics is similar to the foraging of clones in spatially and temporally dynamic environments (Oborny 1994), with two important differences: (a) in dense monocultures, habitat heterogeneity is largely determined by endogenous factors; (b) the occupation of a favourable habitat (a patch created by the death of a ramet) requires only activation of a pre-existing meristem, rather than growth of a rhizome into the patch. There is clearly a need for controlled manipulative experiments to test these ideas on natural clonal populations.

Markov spatial inhibition processes can be considered mathematical formalizations of the local (neighbourhood) models of ramet interaction proposed and advocated by ecologists. In particular, 'local interaction radius' (used by statisticians) and 'resource depletion zone' (used by ecologists) are clearly analogous concepts. My work with the clonal plant *Aralia nudicaulis* (Kenkel 1993) indicates that Markovian inhibitory processes are indeed useful in modelling established clonal plant populations. Additional studies should be undertaken on other species to determine the general validity of the Markovian inhibition model. Spatial inhibition processes could also be used to model the dynamics of density-dependent clonal populations. In this regard, the spatial birth-and-death processes developed by Preston (1977) are particularly relevant. Alternative (non-Strauss) definitions of replacement probabilities, such as those advocated by Diggle (1983: 65) and Baddeley & Møller (1989), may also prove useful to ecological modellers.

Acknowledgements: I thank an anonymous reviewer for providing me with valuable comments and criticisms on an earlier draft of this manuscript. This research was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) Individual Operating Grant A-3140.

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