

MODELING MARKOVIAN DEPENDENCE IN POPULATIONS OF *ARALIA NUDICAULIS*¹

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Abstract. I examined spatial patterns of two populations of the clonal herb *Aralia nudicaulis* for evidence of spatial inhibition among neighboring ramets. Second-order spatial analysis revealed that ramet patterns of both populations were regular at local spatial scales, a result consistent with the proposition that localized, inter-ramet interactions are important in reducing spatial overlap. Localized ramet interactions suggest Markovian dependence, which is defined when an event (e.g., occurrence of a ramet) at X is dependent solely on the existence or otherwise of an event within a distance δ of X . Evidence of Markovian dependence in the populations was tested by fitting Markov point-process models to the observed ramet patterns. The populations conformed well to the Markov model, the results indicating that both ramet spatial patterns were Markov of range $\delta = 18$ cm. This inhibition distance corresponds closely to the mean horizontal radius of an *A. nudicaulis* ramet, indicating that interactions occur at the spatial scale of the individual. I suggest that a likely mechanism for the development of locally regular spatial patterns in these populations is inter-ramet competition for a limiting resource, probably light.

Key words: *Aralia nudicaulis*; clonal plant; local interaction; Manitoba, Canada; Markov point process; modeling; second-order spatial analysis; spatial pattern; spatial scale; ramet.

INTRODUCTION

Because plants are sessile organisms, an individual's performance is determined in part by the size and proximity of its immediate neighbors (Mack and Harper 1977, Kenkel 1991). This local dependence of events will also affect a population's spatial pattern (Cormack 1979). Since local dependence implies spatial inhibition, both dynamic models incorporating local interactions (Lepš and Kindlmann 1987) and the simpler spatial-inhibition models (e.g., Matérn 1960) will always produce regular spatial patterns of individuals. The presence of a regular spatial pattern in a population thus offers strong inferential evidence for resource competition between individuals (Pielou 1962, Antonovics and Levin 1980). While environmental heterogeneity and disturbance often mask the development of regular spatial patterns in natural plant populations (Antonovics and Levin 1980), regular patterns have been described (e.g., Laessle 1965, Kenkel 1988). Few attempts have been made to model observed regular spatial patterns, however. This is due in part to the paucity, until recently, of biologically meaningful spatial-inhibition models (Ripley and Kelly 1977).

Early spatial-inhibition models have been criticized as being biologically unrealistic. Matérn's (1960) models, for example, are based on an inhibition rule specifying that any two individuals cannot be less than a distance δ apart. Such an inhibition rule is probably too restrictive for most biological situations; a more realistic model would make it unlikely, but not im-

possible, for two (or more) individuals to occur in close proximity to one another (Cormack 1979, Diggle 1983). Markov point processes (Ripley and Kelly 1977) are point-inhibition models which quantify spatial interactions in such a "non-strict" manner. Biologists are most familiar with Markov processes in the context of Markov chains, which have been used to model successional and spatial sequences (Facelli and Pickett 1990). The formal definition of a Markov process is a stochastic process in 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 (stochastic processes in > 1 dimension, Adler 1982) requires definition of an analogue of the local dependence condition (ideas of "past" and "future") that underlies the one-dimensional case. Ripley and Kelly (1977) define local conditionality in terms of "neighborhoods," where pairs of points are neighbors if they are less than a distance δ apart. Such processes are said to display Markovian dependence, since the probability density of a point occurring at location X depends only on local conditions—specifically, the process within the neighborhood of X (Ripley 1981). Thus Markov inhibition models generate locally regular spatial point patterns (Kelly and Ripley 1976). Although Cormack (1979) and others have advocated the use of flexible Markov inhibition processes in modeling biological systems, the present study is the first to use Markov point-process models in this way.

One area in which Markovian dependence can be applied is in the modeling of inter-ramet interactions in clonal plant populations. Resource capture efficiency in clonal plants is increased by positioning ramets so

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as to minimize their spatial overlap (Harper 1985). Many ramet positioning models are architectural, and based on averages of field-observed branching angles, inter-node length, and bud and meristem fates (e.g., Smith and Palmer 1976, Bell and Tomlinson 1980). In these models it is assumed that genet architecture is adaptive, with selection favoring precise clonal organization. However, observations of natural populations (see Cook 1985) have revealed that natural variation and stochastic processes produce ramet patterns that cannot be predicted by simple architectural models; developmental plasticity is apparently of greater adaptive significance. Clonal growth models based on module-by-module interactions produce more realistic results (Waller and Steingraeber 1985), suggesting that the mechanisms determining aboveground clonal patterns operate at the level of the individual ramet. This will be especially true when interactions are mainly between ramets that are not physiologically integrated, as would occur in a population consisting of a number of genets having a "runner" (Bell 1984) architecture. If inter-ramet interactions are important in minimizing spatial overlap, a locally regular spatial pattern of ramets is expected of clonal populations growing in homogeneous environments.

In this study I describe and model observed spatial patterns of ramets in two populations of the clonal herb *Aralia nudicaulis*. I demonstrate that the observed patterns are consistent with a Markov point-process model, and discuss possible mechanisms for the development and maintenance of locally regular spatial patterns in the populations.

MATERIALS AND METHODS

Aralia nudicaulis

Aralia nudicaulis L. (Araliaceae; wild sarsaparilla) is a clonal acaulescent herb of wide distribution in North America, occurring from British Columbia to Newfoundland, and from Georgia to the southern Yukon (Flanagan and Bain 1988). The species produces a long-lived, perennating rhizome with small dormant axillary buds (\approx every 5 cm) that have the potential to develop into rhizome branches. As the rhizome grows, it produces a short, thick caudex or "spur shoot" \approx every 1 m, which may or may not be active in a given growing season. When a spur shoot forms, the dormant bud behind it grows to maintain a repetitive production of shoots and rhizome regeneration. Proliferative branching occurs when the terminal shoot is replaced by two renewal shoots; dormant lateral buds are also released if the terminal erect shoot dies (Bawa et al. 1982). A preformed caudex bud typically produces a vegetative shoot consisting of a single doubly compound leaf having a distinctive "umbrella" shape (Fig. 1). Most leaves have a petiole length of 25–30 cm and a leaf area of 500–1000 cm². Leaf scars can be counted to determine caudex age; a mean age of 20 yr has been

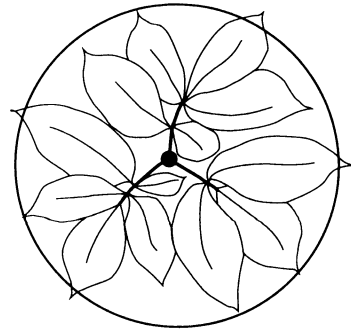


FIG. 1. Aerial view of a typical *Aralia nudicaulis* leaf. An 18-cm radius circle, centered on the petiole (●), is superimposed on the image.

recorded from natural populations (Strong and La Roi 1983, Flanagan and Bain 1988). Reproductive shoots are uncommon, particularly at high clonal densities and in shaded habitats (Barrett and Thomson 1982). The clones themselves are extensive; rhizome excavations indicate that genets may occupy 10 × 10 m areas or larger, although rhizome fragmentation makes the exact determination of clone size difficult (Barrett and Thomson 1982). Established populations may consist of a complex interdigitation of genets, with the result that spatially adjacent ramets rarely belong to the same genet (Edwards 1984).

Study area

I examined populations of *Aralia nudicaulis* in a gallery forest at the University of Manitoba Field Station, Delta Marsh, Manitoba, Canada (50°11' N, 98°23' W). The forest is \approx 2 km south of Lake Manitoba along an oxbow of the Assiniboine River. It is dominated by mature *Quercus macrocarpa* and *Fraxinus pennsylvanica*, with *Acer negundo* occurring at low abundance. The understory is dominated by *A. nudicaulis*. *Carex assiniboinensis* also occurs as a lower layer (rarely higher than 15 cm), but is not abundant where *A. nudicaulis* is present. Other species occasionally encountered were *Rhus radicans*, *Osmorhiza longistylis*, *Actaea rubra*, and *Rudbeckia laciniata*.

The climate is sub-humid continental, with short warm summers and long cold winters. Mean annual temperature is 1.5°C. The warmest month is July (mean = 19.1°C), and the coldest is January (mean = -19.8°C). Precipitation averages 49.9 cm/yr, \approx 75% of which falls as rain. The mean number of degree-days (temperature above 5°C) is 1600, and there are 125 frost-free days (Environment Canada 1981).

Soil cores ($n = 24$) were taken to a depth of 10 cm in a rich clay-loam. Soil was dried at 60°C, ground, and mixed with distilled water at a 1:5 ratio. Mixtures were shaken for 1 h and gravity filtered. Average values of 6.6 ± 0.2 for pH, and 0.542 ± 0.05 mS for conductivity, were obtained (means \pm 1 SD). Percentage

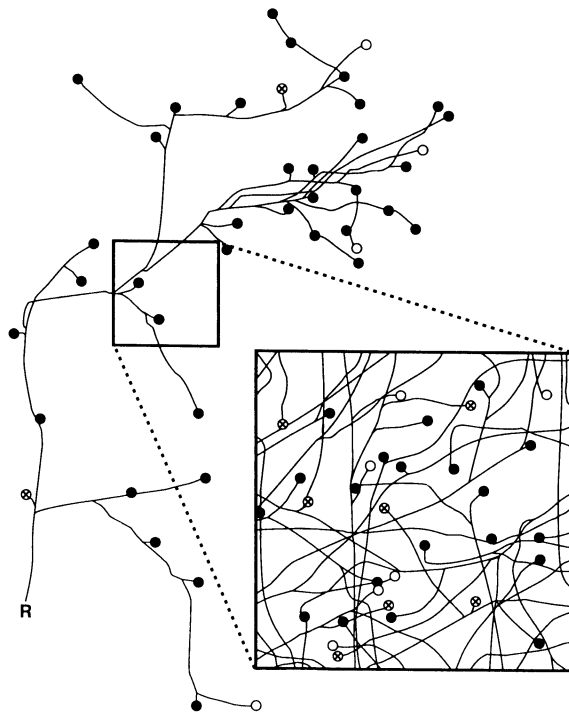


FIG. 2. Map of an excavated genet (total rhizome length ≈ 29 m), and detail of 1×1 m area of excavated rhizomes. Symbols code: R = rotted end of rhizome; ● = ramet shoot; ○ = newly formed caudex bud; ⊗ = dead caudex bud.

of organic matter (by ignition, 12 h at 430°C) averaged $17 \pm 2.6\%$.

Site selection and field mapping

The two stands of *Aralia nudicaulis* were selected based on perceived uniformity of site conditions. Thus regions containing trees, tall shrubs, or other understorey species were avoided in favor of those with uniform ramet densities and light conditions. This minimized site heterogeneity problems that would otherwise mask patterns resulting from biotic interactions and lead to a violation of the homogeneity and isotropy assumptions of second-order spatial analysis. Each 5×5 m plot was shaded by a single large *Quercus macrocarpa* tree.

The two 5×5 m plots were gridded into 25 1×1 m subunits. Within each subunit, ramets were marked, and distances (± 1 cm) to each of the four corner posts of the plot recorded. The law of cosines was then used to obtain the spatial coordinates for each ramet (see Kenkel 1988). One plot contained $n = 533$ ramets, the other $n = 580$ ramets.

After ramet mapping was completed, excavations were undertaken to examine the population's rhizome system. A map of one of the genets excavated, together with a representative 1×1 m area of the rhizome system, is shown in Fig. 2. These results confirm previous studies indicating that ramets are generally wide-

ly spaced along rhizomes, and that populations of *A. nudicaulis* consist of a complex of many interdigitated genets. Thus the majority of localized interactions in the population occur between ramets that are not interconnected.

Statistical analysis

Second-order spatial analysis.—The spatial pattern of ramets was analyzed using second-order spatial analysis, which is derived through a reduction of second moments under assumptions of homogeneity and isotropy of a point configuration (Ripley 1977). Consider n points (individuals) distributed within a region of area A ; the intensity (mean number of individuals per unit area) is $\lambda = n/A$. In second-order spatial analysis, a circle of radius t is centered on each individual, and the number of neighboring individuals (those within the circle) determined. Spatial pattern can be examined at various spatial scales simply by varying t .

The function $\lambda K(t)$ is defined as the expected number of individuals within distance t of an arbitrarily selected individual; $K(t) = \pi t^2$ (the area of a circle of radius t) if the spatial pattern is Poisson random. The empirical function $\lambda \hat{K}(t)$, which is the observed number of individuals within distance t of a randomly selected individual, is biased unless an edge correction is implemented. Ripley (1977) suggested a toroidal edge correction, defining:

$$\hat{K}(t) = n^{-2} A \sum k(x, y),$$

where $k(x, y)$ is a weighting (specified for each ordered pair of points x, y) that is inversely proportional to the circumference of a circle, centered on point (individual) x and passing through point (individual) y , that lies within the bounds of the study area. Summation is over all ordered pairs of points less than t apart. Thus $k(x, y)$ is inversely proportional to the probability of observing an individual at a distance y from individual x (Ripley 1981:159).

In practice, the analysis of point pattern involves plotting $\hat{L}(t)$ against t , where:

$$\hat{L}(t) = t - \sqrt{\frac{\hat{K}(t)}{\pi}}.$$

Like $K(t)$, the function $L(t)$ has zero expectation when the spatial pattern is Poisson random. The square root serves to both linearize the plot and stabilize the variance (see Besag, in Ripley 1977: discussion section following article). For a given radius t , the degree to which $\hat{K}(t)$ deviates from πt^2 offers insight into the observed pattern of individuals at that spatial scale. Positive values of $\hat{L}(t)$ indicate spatial regularity, while negative values indicate clumping. Applications of the method to ecological pattern analysis include Kenkel (1988), Rebertus et al. (1989) and Andersen (1992).

Monte Carlo simulation is used to test the significance of departures of $\hat{L}(t)$ from random expectation

(Diggle 1983:7). The following method was used to generate confidence envelopes in this study: (1) generate a random configuration of n individuals within an area A , using a high-quality congruential random number generator (Arnason 1977); (2) determine $\widehat{L}(t)$ vs. t for this random configuration; (3) repeat steps 1 and 2 $m = 99$ times, and use the maximum and minimum values of the m simulations to define a confidence envelope (see Diggle 1983, Kenkel 1988). The generation of a confidence envelope using $m = 99$ random simulations is adequate for tests at the conventional 5% level (Besag and Diggle 1977, Marriotti 1979). Portions of the observed function $\widehat{L}(t)$ vs. t exceeding the confidence envelope limits indicate the spatial scales at which the observed spatial pattern shows significant deviation from statistical randomness.

Markov point processes.—Markovian dependence among events occurs when the conditional intensity of an event at a given point (individual) X is dependent solely on the existence or otherwise of an event within a distance δ of X (Diggle 1983). Markov point processes (Ripley and Kelly 1977) are spatial inhibition models in which the conditional intensity of X for a given spatial configuration depends only on the configuration in the “neighborhood” of X . Since points are “neighbors” if they are closer than δ apart, the point process is said to be Markov of range δ . An extreme example is the Matérn (1960) process, in which no two points in the process are less than δ apart. Flexibility in the degree of local dependence is achieved using the Strauss (1975) process, the conditional density of which is given by:

$$f(\mathbf{X}) = \alpha \beta^n \gamma^s \quad \beta > 0, 0 \leq \gamma \leq 1.$$

Here α is a normalizing constant, β reflects the intensity of the spatial process, γ describes the interaction between neighbors, s is the number of point pairs in configuration \mathbf{X} less than δ apart, and n is the number of points (Diggle 1983). A value of $\gamma = 1$ produces a Poisson random pattern, while $\gamma = 0$ produces a Matérn “hard-core” (simple inhibition) process of range δ (Ripley 1977). Intermediate values of γ produce an entire family of “non-strict” inhibition processes. Ripley (1988) and Cressie (1991) summarize the theory of Markov point processes, and demonstrate the relationship between Markov processes and the Gibbs process of statistical physics.

Strauss processes can be generated using a point deletion–replacement algorithm (Ripley 1979). One begins with an initial configuration of n points in the plane. A point X_1 is selected at random and deleted, retaining $\{X_2, \dots, X_n\}$. A replacement point X_1 is then chosen according to the conditional density:

$$p(X_1) = \prod_{i=2}^n h(d\{X_i, X_1\}),$$

where $d\{X_i, X_1\}$ is the Euclidean distance between points

X_i and X_1 , and $h(d) \leq 1$. For the Strauss process, $h(d) = 1$ if $d\{X_i, X_1\} > \delta$, while $h(d) = \gamma$ whenever $d\{X_i, X_1\} < \delta$. It follows that the replacement point X_1 is accepted with probability $p(X_1) = \gamma^s$. Repeating the deletion–replacement step many times results in convergence to the Strauss process. Ripley (1979) suggests that $4n$ steps are adequate in practice. I used a toroidal correction to overcome the edge effect problem in generating the process.

Fitting a Strauss process model to an observed pattern is done iteratively by changing the parameters γ (the descriptor of interaction between neighbors) and δ (the interactive radius). I used the goodness-of-fit criterion suggested by Diggle (1983:77), in which the discrepancy (D) between the Strauss model and the observed pattern is measured as:

$$D(\theta) = \int_0^1 [\sqrt{\widehat{K}(t)} - \sqrt{K(t; \theta)}]^2 dt,$$

where $K(t; \theta)$ is the K function for a point pattern generated by the Strauss process, and $\widehat{K}(t)$ is the estimator calculated from the observed pattern. Once I found the parameters γ and δ that minimized $D(\theta)$, the upper and lower limits from $m = 99$ simulations of the Strauss process were used to define a confidence envelope for the model.

RESULTS

Second-order spatial analysis of the two ramet spatial patterns (Fig. 3) indicates a trend toward spatial regularity at low spatial scales (10–25 cm radius range). This is consistent with a model of spatial inhibition between neighboring ramets.

For both populations the best fits to the Markov point process were obtained for parameter values in the range $16 \text{ cm} < \delta < 19 \text{ cm}$ and $0.775 < \gamma < 0.825$. Strauss process models were fitted using $\delta = 18 \text{ cm}$ and $\gamma = 0.8$ (Fig. 4). Both simulation envelopes completely included the observed second-order analysis results, indicating a good model fit within the range $0 \text{ dm} < t < 10 \text{ dm}$.

The results indicate an interaction radius δ of $\approx 18 \text{ cm}$ for the two populations of *Aralia nudicaulis*. However, the value $\gamma = 0.8$ indicates that the degree of inhibition is comparatively weak (recall that $\gamma = 1$ indicates complete spatial randomness, $\gamma = 0$ indicates the Matérn complete-inhibition process). Thus although the spatial pattern of ramets is regular at local spatial scales, a Matérn process (completely non-overlapping circles of radius δ) would be far too restrictive a model for the data. The fitted model indicates that the probability of ramet “survival” is $\approx 0.8^s$, where s is the number of neighbors within 18 cm of the ramet.

DISCUSSION

The observed ramet spatial patterns in the two *Aralia nudicaulis* populations are consistent with a Markov-

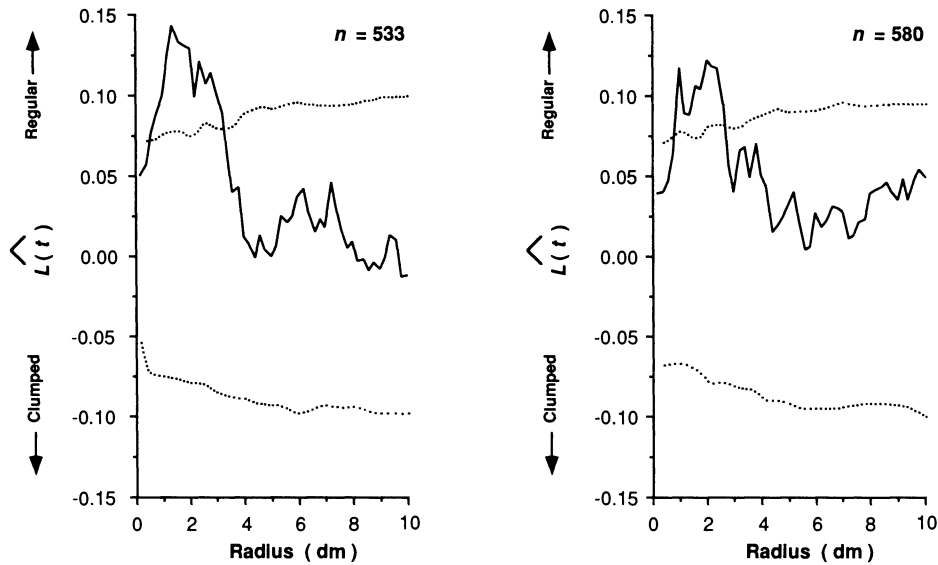


FIG. 3. Second-order spatial analysis of the two *Aralia nudicaulis* ramet maps. — = observed pattern; ···· = confidence envelope for the 99 random simulations. $\hat{L}(t)$ measures the intensity of pattern at various spatial scales.

ian model of inter-ramet interaction. The spatial interactions are inhibitory in nature, since the probability of ramet establishment decreases as local density (number of neighbor ramets) increases. This results in a regular pattern of ramets at local spatial scales.

The horizontal plane architecture of *Aralia nudicaulis* ramets (Fig. 1) is characteristic of a species maximizing its photosynthetic capacity in severely shaded environments (Niklas and Kershner 1984), suggesting that light is a limiting resource. The success of a given

ramet at intercepting light depends on the supply rate in its immediate neighborhood, which in turn depends on local ramet density. The fitted Markovian models indicate that the “survival” probability of a given ramet decreases as ramet density within an 18-cm radius increases. Since the mean horizontal radius of *A. nudicaulis* leaves is ≈ 18 cm (Fig. 1), I infer that interactions occur at the spatial scale of an individual ramet.

A spatiotemporal model of differential ramet production, based on competition for light, can be invoked

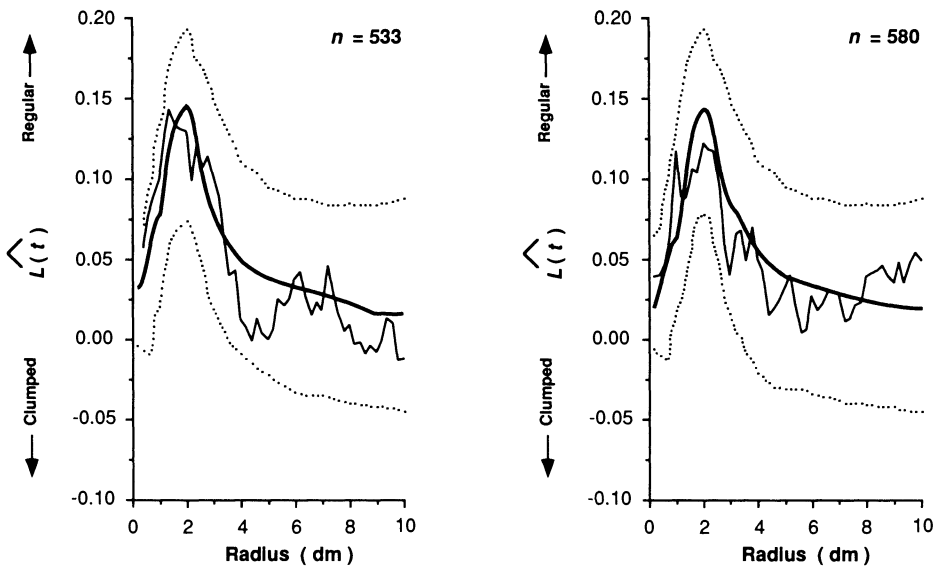


FIG. 4. Second-order spatial analysis of Markov point process models for the two *Aralia nudicaulis* ramet maps. — = observed pattern; — = mean fit of 99 random simulations of the Strauss process with $\gamma = 0.8$, $\delta = 18$ cm; ···· = confidence envelope for the 99 simulations of the Strauss process. $\hat{L}(t)$ measures the intensity of pattern at various spatial scales.

to explain the creation and perpetuation of locally regular patterns in these populations. Begin with an initial homogeneous substrate colonized by one or more *A. nudicaulis* seedlings. At low initial densities, the ramets will rarely interact. As ramet density increases, however, local high-density areas will develop and ramets will begin to shade one another. In high-density areas light levels will be insufficient to support new ramets, with the result that new ramets will tend to succeed only in areas of lower local density. It is possible that control of ramet production in high-density areas is achieved through bud activity inhibition in response to both low light levels and a decrease in the red-to-far red light ratio (de Kroon and Kwant 1991). In clonal species there is some evidence to support the idea that such a mechanism operates at fine spatial scales (e.g., Briske and Butler 1989). One expected result of such a mechanism is to prevent ramet overproduction in clonal populations (Pitelka 1984, de Kroon and Kwant 1991). Another is the development of a locally regular spatial pattern in accordance with Markovian rules, as I found in this study.

It has been suggested that the maintenance of rhizome connections, as occurs in *Aralia nudicaulis*, allows new ramets to draw resources from older parts of the clone in overcoming the "competitive superiority" of established neighbors (Cook 1985). However, a study of C^{14} assimilate distribution in *A. nudicaulis* (Flanagan and Moser 1985) found only limited evidence for the physiological integration of ramets; the majority of exported carbon was translocated basipetally to the adjacent rhizome section. This indicates that individual ramets function as physiologically independent subunits (Watson 1986). Given that a given caudex of *A. nudicaulis* is long-lived (Flanagan and Bain 1988), one would expect photosynthate transport to and storage in adjacent rhizome sections for use in the following growing season. Thus rhizome retention in the species may simply be an adaptation for survival in temperate climates. Rhizome retention may also allow rapid reestablishment of ramets in areas where they have been removed through herbivory, disturbance, or natural death of caudex shoots. Specifically, gaps created in the *A. nudicaulis* canopy could be quickly filled by development of axillary buds from an extensive, established rhizome system (Fig. 2).

Markovian dependence may prove to be a characteristic feature of interactions in sessile organisms. For example, the demonstration that individual plant performance is determined in part by the proximity of neighbors is consistent with the idea of "local" or Markovian dependence of events. The same may be true of interactions between plant metamers, since it is known that the occurrence of a leaf at a given position on a tree branch, or the location and growth of the branch itself, is largely determined by prevailing "local" conditions (Honda et al. 1981). Additional studies should be undertaken to determine the general validity

of Markovian dependence in modeling spatial interactions in plants and other sessile organisms.

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