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From virtual plants to real communities: A review of modelling clonal growth

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ABSTRACT

Clonal plants grow by the production of semi-autonomous modules (ramets), and form complex branching structures which may provide communication/resource flow channels between the units. These characteristic features have made clonal plants a challenging subject for spatial modelling. We review the advance of ideas and new directions in theoretical research since the last review (Oborny and Cain, 1997). We place clonal growth models into a general framework of spatial population dynamic models, comparing individual ramets of a clone with individuals in a non-clonal population. We discuss three specificities of clonal spreading: (1) ramets can be physiologically integrated through the network of branching structures; (2) formation of new ramets occurs by the growth of these branching structures which can be directional, following architectural rules; and (3) formation of new ramets can be adjusted to the environment by phenotypic plasticity. We review methods by which these traits have been implemented into models. We summarize model predictions, for the spatial structure and fitness of clonal plants, and link these predictions with existing empirical data. Emphasis is given to the contributions that theoretical studies could provide for experimental studies in the field.

We emphasize the following recent major developments: (i) a much better understanding of emergent consequences of various clonal growth rules over broad spatial and temporal scales has been reached. (ii) Links have been found to other complex systems. For example, a key problem of integration vs. splitting of connecting structures has been shown to be closely related to a problem in percolation theory. (iii) Interactions between physiological integration, architectural growth and plastic responses have been demonstrated; research on these interactions has generally shown a large degree of contingency in the effects of these traits. Finally, we outline some areas for future research.

1. Introduction

The study of pattern formation and population growth in space has been an attractive research area throughout the history of mathematical modelling in ecology. Although the topic concerns all organisms, modelling sedentary modular organisms (multicellular plants, corals, sponges, etc.) has some interesting specificities. First, there is an inherent discreteness in the system: growth proceeds by the re-iteration of finite developmental programs (White, 1979; Harper, 1985; Tuomi and Vuorisalo, 1989). For example, in the case of plant shoots, a single developmental step produces a metamer; this is the smallest, elementary unit (Harper and Bell, 1979). Second, the elementary units are organized into ranks of a hierarchy. For example, a consecutive sequence of plant metamers makes a branch, and branches form branching systems. If these elements are to be captured by models, it is necessary to go beyond the general approaches to pattern formation that have been used to model simple sedentary organisms.

Clonal plants are an excellent example of modular organisms; they are specific among plants in the sense that the modules can become autonomous. Thus, the genetic individual (genet) can consist of multiple physiological individuals (ramets), each possessing potentially all the organs that are needed for an individual life. It is noteworthy, however, that the definition of clonality does not require the actual occurrence of full independence; a potential is sufficient. Indeed, the degree of autonomy/physiological integration among ramets exhibits large variation among clonal species and environments (Jónsdóttir and Watson, 1997), and, in some species, the potential for autonomy is utilized only after injury or other traumatic event (Harper, 1985).

Historically, clonal species were an attractive subject for modelling research, namely for spatially explicit modelling. One reason was an exciting regularity of clonal growth forms, which can

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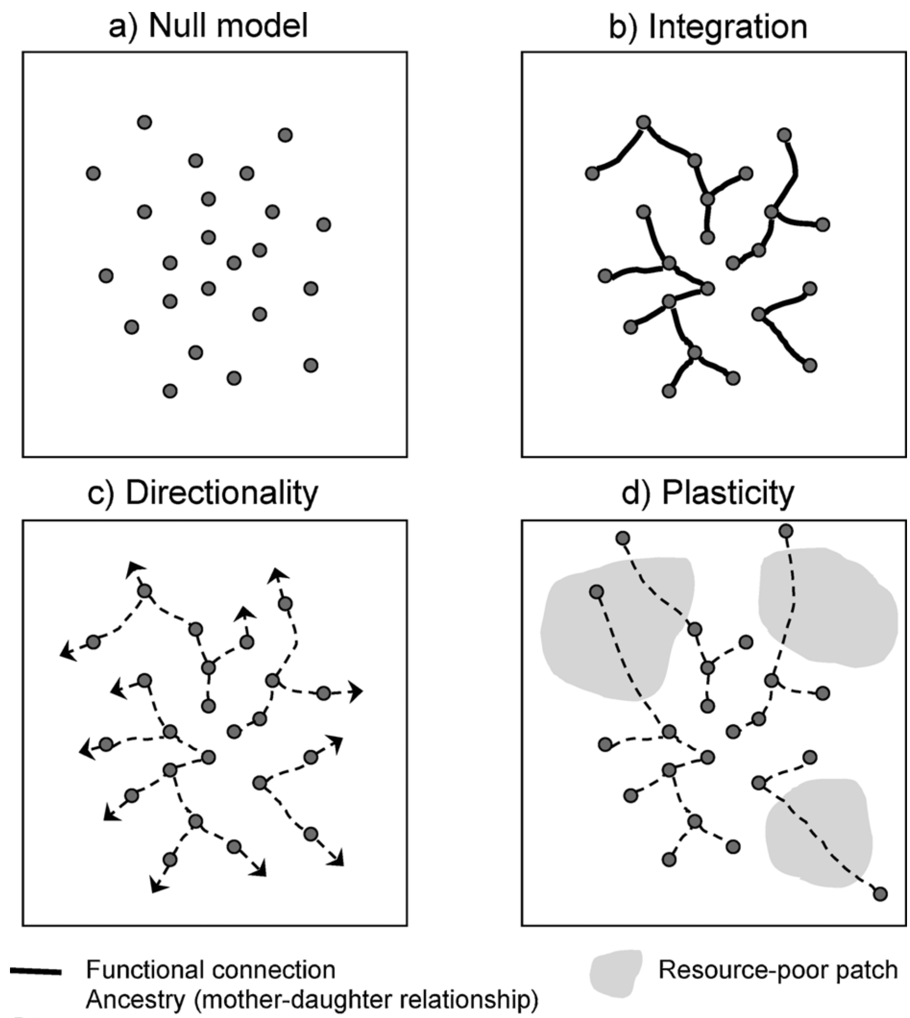

Fig. 1. Three major features of clonal growth models (b)–(d) compared to spatial models of population dynamics in non-clonal plants (a).

be easily captured by two-dimensional spatial models (Bell and Tomlinson, 1980). The other, perhaps even more important, was a demand on the side of empirical research. After clonal growth in plants and its implications became a coherent research subject in the early 1980s, researchers identified two questions that called for a combination of empirical and modelling approaches. First of them was the issue of foraging, i.e., a process through which a set of ramets searches for a spatially heterogeneous resource and exploits it. (Hutchings and Slade, 1988; Sutherland and Stillman, 1990; Hutchings and De Kroon, 1994; Stuefer, 1996; Oborny and Cain, 1997; Novoplansky, 2002; De Kroon et al., 2005). Many experimental data were available about growth responses to the environment within short periods of time, on a scale which ranged from single ramets to small groups of ramets. Theoretical modelling was required to extrapolate over longer periods of time, up to the scale of large genets, in order to understand the potentials and limitations of foraging under natural conditions. Theoretical results, in turn, motivated new experiments (e.g., Wijesinghe and Hutchings, 1997; Piqueras and Klimeš, 1998; Alpert and Simms, 2002). The second issue was research on clonal integration, i.e., on the flow of matter (photosynthate, nutrient) through physical connections between ramets (Pitelka and Ashmun, 1985; Kelly, 1995; Jónsdóttir and Watson, 1997). Theoretical research was required for clarifying the effect of integration on the performance of the whole clone.

Strong links between modelling and experimentation have made research on clonal plants a rather unique field. In the present paper, we provide a conceptual review of clonal plant modelling since the last published review (Oborny and Cain, 1997; see also earlier reviews by Waller and Steingraeber, 1985; Sutherland and Stillman, 1990).

The aim of the current review is threefold. In Section 2, we identify the key features of clonal plants that make their modelling a separate subfield, distinct from general individual-based spatially explicit models. In Section 3, we review questions and concepts that have appeared in the past 15 years in modelling clonal plants, and link these to already existing concepts. We review the specific outcomes/predictions of such studies, and their value for research on clonal plants and for plant ecology in general. In Section 4, we review how theoretical research may complement experimental field research. In doing so, we hope to add to the existing collaboration between modelling and empirical research that have characterized research on clonal plants, and identify possible further areas for collaboration.

2. Capturing special features of clonal plants: challenges for modelling

For a null model, consider a population that consists of nonclonal individuals spatially dispersed in a particular pattern (Fig. 1a). The elementary events that can occur to the individuals include reproduction, death, and motion, either by active or passive means. This setting is a typical subject of spatial population