Chapter 1: General introduction

Functional specialization of ramets in heterogeneous environments

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Functional Specialization of ramets

Clonal plants are one of the most successful growing strategies in the plant world and they are found in almost all terrestrial and aquatic plant habitats. By repeatedly producing new individuals (ramets), clonal plants can efficiently occupy habitats and exploit resources. By placing new ramets further away from the mother plants, they can explore the environment and reach better spots. Clonal reproduction allows plants to occupy space, sometimes at the exclusion of other species, and the areas that individual genets occupy can be quite large, *e.g.* *Populus tremuloides* (Mitton and Grant, 1996) or *Pteridium aquilinum* (Oinonen, 1967). Thus, it is important to study the behavior of clonal plants and how they survive in plant communities.

Over the past few decades, a considerable number of studies have been made on clonal plants. Ramets are potentially independent units of clonal plants and can show different forms and work differently under various conditions. Since clonal plants can spread horizontally by vegetative growth, they have the potential to grow across a heterogeneous environment. Thus local functional specialization of ramets and co-operation between interconnected ramets in heterogeneous environments has received the attention of researchers recently.

Ramets can functionally specialize in many different ways. For instance, in an environment with favorable or poor patches, some clonal plants produce different types of ramets: long ramets that can explore better spots, or short ramets that can exploit a specific patch (specialization in vegetative spreading). Or, clonal plants can change the production of sexual ramets under different conditions (specialization in propagation). Sometimes interconnected ramets which grow across a contrasting environment show specialization in capturing the local resources (specialization in resource capturing).

Since clonal plants can grow across heterogeneous environments, these functional specializations of ramets in different patches allow plants to utilize or exploit different types of habitats efficiently. Thus studying the specialization of ramets is important to understand the life history strategy of clonal plants.

At Utrecht University and the Smithsonian Environmental Research Center in the USA, I have studied ramet development and specialization of the clonal plant *Scirpus olneyi*. I studied this plant from the following aspects;

1. Ramet specialization in different communities and seasons
2. Ramet specialization at different plant densities
3. Ramet specialization in environments where resources are inversely distributed
1. Ramet specialization in different communities and seasons

Clonal plants build a variety of architectural forms by modifying the lengths of spacers (rhizomes or stolons), branching frequencies and branching angles (Hartnett and Bazzaz, 1983; Salzman and Parker, 1985; Slade and Hutchings, 1987a; Slade and Hutchings, 1987b; Slade and Hutchings, 1987c). These architectures differ among plant species or within a species in different environments (Bell, 1980; de Kroon and Knops, 1990; Hutchings and De Kroon, 1994; Lovett Doust, 1981). Thus plasticity in clonal architecture may be an adaptive plant trait (Hartnett and Bazzaz, 1983). One typical example is the Phalanx and Guerrilla strategy (Lovett Doust, 1981). Clonal plants with the Phalanx strategy produce frequently branched ramets with short spacers and occupy local resources patches in dense populations while plants with the Guerrilla strategy produce less frequently branched ramets with longer spacers and grow out of a patch to explore adjacent patches (de Kroon and Knops, 1990; de Kroon et al., 1994; Dong and De Kroon, 1994). The Phalanx strategy can be associated with the exploitation of local patches while the Guerrilla strategy can be associated with the exploration of new patches. In an evolutionary context, differences in clonal architectures might represent differences in foraging strategies of clonal plants (de Kroon and Knops, 1990; Dong, 1996; Harper, 1985; Hutchings and De Kroon, 1994; Lovett Doust, 1981). It means that, each ramet can specialize to perform different tasks in clonal spreading strategies.

*Scirpus olneyi* grows and dominates under a rather wide range of environmental conditions, and shows architectural plasticity by producing two types of ramets within one genet. Some ramets have long or very long rhizomes (Long Rhizome Ramet: LRR) while others have very short rhizomes (Short Rhizome Ramet: SRR). In the field, we found that *S. olneyi* shows a different development pattern of its ramets both in space (ramet architecture) and in time (phenology), and this may result from differences in foraging strategies of this species in different environments.

2. Ramet specialization at different plant densities

Units of vegetative offspring are larger than seedlings and have a lower mortality because mother ramets provide daughter ramets with carbohydrates, water and minerals. Clonal growth can cause, however, local crowdedness within a genet, and inter-genet competition becomes higher. Thus vegetative propagation may have less benefit at high density patches. On the other hand, since seeds can spread over wide ranges whereas vegetative propagules can not, sexual propagation can have a higher benefit at high density patches.

According to Abrahamson, the balance between vegetative and sexual propagation is affected by inter- and intraspecific competition (Abrahamson, 1980). As plant density increases, competitive stress also increases (Winn and Pitelka, 1981) and several authors have found that seed production is positively correlated with plant density (Abrahamson, 1975; Abrahamson, 1980; Giroux and Bedard, 1995). On the other hand, several studies expected that sexual propagation should decrease as density increased (Loehle, 1987), or when site conditions become less favorable (Abrahamson, 1980) or due to a stronger competitive stress (Eriksson, 1989; Newell and Tramer, 1978). Thus it is important to evaluate the density effects on propagation strategies of clonal plants. Plant density also can affect patterns of vegetative propagation as ramet production has been shown to be negatively correlated with plant density (Briske and Butler, 1989;
Hartnett and Bazzaz, 1985; Lapham and Drennan, 1987). In addition, plant density is also affected by ramet architecture. Repeated production of ramets with short spacers can cause a higher plant density, while ramets with longer spacers may not. Thus, if a clonal plant can control its ramet density through changing the architectural elements of their morphology (e.g., shorten or lengthen their spacers), then clonal plants can persist at sites with favorable resource conditions or emigrate from one resource state to explore adjacent environments (de Kroon and Knops, 1990; Dong, 1996; Hutchings et al., 1997; Slade and Hutchings, 1987a). This has hardly been studied in a quantitative way but important to understand foraging strategies of plants and ramet specialization.

3. Functional specialization of ramets in environments where resources are inversely distributed

Non-clonal plants tend to allocate proportionally larger amounts of biomass to the organ which experiences the severest shortage of resources because that limiting resource controls the rate of photosynthesis (Aung, 1974; Chapin, 1980; Hutchings and De Kroon, 1994). For example, plants will allocate proportionally more biomass to the belowground organs in patches with high light and low water availability, and allocate proportionally more biomass to the aboveground organs in patches with low light and high water availability (Brouwer, 1983; Iwasa and Roughgarden, 1984; Werger, 1983). This is functional specialization in resource capturing in individual plants to compensate local resource shortage. On the other hand, clonal plant can specialize differently if interconnected ramets grow across different environmental patches. Due to physiological integration, ramets can functionally specialize to capture locally abundant resources and exchange these among ramets to clone parts where resources can be used best. A consequence of clonal integration is that the clone performs significantly better in spatially heterogeneous than in homogeneous environments (Alpert and Stuefer, 1997; Hutchings and Wijesinghe, 1997). Stuefer et al. (1996) referred to this allocation pattern as spatial Division of Labor (DoL).

DoL is a rather new finding and has not been thoroughly studied, and one of its interesting topics is the degree of specialization. Garden experiments showed that each ramet specializes in capturing either water or light by allocating more biomass to roots or leaves, respectively, but nevertheless each ramet also allocates biomass to leaves in patches with a low light availability and to roots in patches with a low availability of water (Stuefer et al., 1996). Intuitively, however, it seems more profitable if the plants locally allocate all biomass to those organs that capture the locally abundant resource, but the full specialization of ramets has not been a common characteristic of clonal plants under experimental or field conditions (Jonsdottir and Callaghan, 1989; Stuefer et al., 1998). Thus it can be interesting to study ecological features behind the specialization of resource capturing in clonal plants to fill the gap between the results from experimental gardens and theoretical studies.

Outline of this thesis

In Chapter 2 and Chapter 3, functional specialization in vegetative spreading is considered. The clonal architecture in community types of the target species, Scirpus
olneyi, is described Chapter 2. In Chapter 3, the main focus is the development pattern of this species both in space and in time under different conditions. We test the hypothesis that plants produce differently specialized ramets in different proportions and in different time schedules in response to varying environmental conditions by conducting a garden experiment and field observations.

In Chapter 4 and 5, the density effect on the propagation strategy of clonal plants and functional specialization in sexual or asexual propagation are discussed. The hypotheses behind Chapters 4 are 1) that seed production will be greatest in habitats where shoot densities are high and 2) plants will branch more frequently and produce more ramets with shorter spacers at low density to exploit local resources while less branching and more ramets with longer spacers are produced at high density patches to escape severe competition and explore new patches.

In Chapter 5, a simulation model is developed to evaluate the outcome of competition among clonal plants that have different patterns of reproduction. Two strategies are presented in this Chapter: One strategy is the Density Dependent Seed Strategy (DDSS) in which plants produce seeds at higher density, and the other is the Density Dependent Ramet Strategy (DDRS) in which plants produce ramets at higher density. To evaluate the outcome of competition between the two strategies at different densities, a lattice model is used.

In Chapter 6 and 7, functional specialization in resource capturing is considered. In Chapter 6, a garden experiment is described. The objective of the experiment was to evaluate the degree of specialization and contrast in resource availability, with Scirpus olneyi growing in environments in which the availability of two resources is negatively correlated. In Chapter 7, a theoretical model is developed to evaluate the degree of specialization in plants growing according to a DoL program under various environmental conditions. The model is designed to determine optimal shoot and root investment, and water transport patterns, to maximize the total biomass acquired at the end of the growing season, in sets of two interconnected ramets growing in different environments. This model is designed to verify the results of the garden experiments in Chapter 6.

References


