

*Functional
Specialization
of Ramets
in a Clonal
Plant
Network*

Functional Specialization of Ramets in a Clonal Plant Network

*Funtionele specialisatie in het rametnetwerk
van een clonale plant*

(met een samenvatting in het Nederlands)

Proefschrift

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to my friends

*"Voici est mon secret. Il est tres simple: on ne voit bien qu'avec
la coeur. L'essentiel est invisible pour les yeux."*

(What is essential is invisible to the eye)

Antoine de Saint-Exupéry, Le petit prince

"Unless you dig up"

Maki

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Preface:

The Rules of the Game

-Variety is the spice of life-

I am interested in differences among things. Each plant and animal, each human culture and the tools we use are the result of evolution and cultural history. Through their evolution and historical paths, all things have changed their shapes and functions, to reach the condition in which we find them today. Some features are common to many organisms and objects while others share few similarities. What accounts for the differences and similarities through evolutionary paths?

In forests, for example, there are many plant species, some are shrubs, some are trees and, under the shrub layer, there is a wide diversity of herbaceous species. They are all plants that live in the same forest, almost all of them photosynthesize, obtain resources through roots and have almost the same basic structure, yet their life strategies are often quite different. In forest, some species reproduce by seeds while other produce new plants by vegetative reproduction. What accounts for these types of differences? Why is diversity so high among plants whereas they share the same origin, live in the same places, and many share the same evolutionary paths? How are species able to adapt themselves to specific habitats? Natural selection is clearly important but how does selection operate at the level of individual species within a complex habitat? What are “the rules” for the evolutionary game?

Many plant species respond morphologically and physiologically along habitat gradients. My research aim is to understand “the rules” that lead to such differences. In this thesis, I examine functional specialization of ramets of a clonal species "*Scirpus olneyi*" a common species in brackish wetlands in eastern North America. The research is part of my Ph.D. program at Utrecht University which is a part of a collaborate program between Utrecht University and the Smithsonian Institution. *Scirpus olneyi* shows highly plastic growth patterns in brackish wetlands. In some habitats genets produce short rhizomes that result in a clumped distribution of shoots and most of the shoots produce seeds. In others, genets produce long rhizomes resulting in lower shoot density in patches and few shoots produce seeds. Plants in patches with a high shoot density produce more seeds than plants in patches with a low shoot density. In shaded patches, plants allocate proportionally more biomass to aboveground parts and ramet production continues throughout the entire growing season. In habitats without any overhanging canopy, plants allocate proportionally more biomass to belowground and ramet production stops early in the growing season. What factors account for these differences among habitats? What benefits do the plants receive by varying their patterns of ramet architecture and resource allocation? I have been addressing these questions by conducting field observations, controlled experiments and computer simulations.

Chapter 1:

General introduction

Functional specialization of ramets in heterogeneous environments

IKEGAMI Makihiko

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.

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Chapter 2:

Description of Scirpus olneyi A. Gray in salt marshes in East Coast of the U.S.A.

- study site, features of species, clonal architectures and community types -

IKEGAMI Makihiko

Site description and climate

This research was conducted in brackish tidal marshes at the Smithsonian Environmental Research Center (SERC). SERC is located 40 km east of Washington, D.C. and 16 km south of Annapolis, Maryland, on the western shore of the Chesapeake Bay in the United States (Fig. 1) (MicrosoftEncarta, 2001). The SERC property includes ownership of approximately 3000 ha of the Rhode River (38°53'N, 76°33'W). The studies described in this thesis were conducted in brackish tidal wetlands within the subestuarine portion of the Rhode River system (Fig. 2).



Figure 1. Map showing the location of the research site, the SERC in Maryland, in the USA. The SERC is 16 km south of Annapolis.

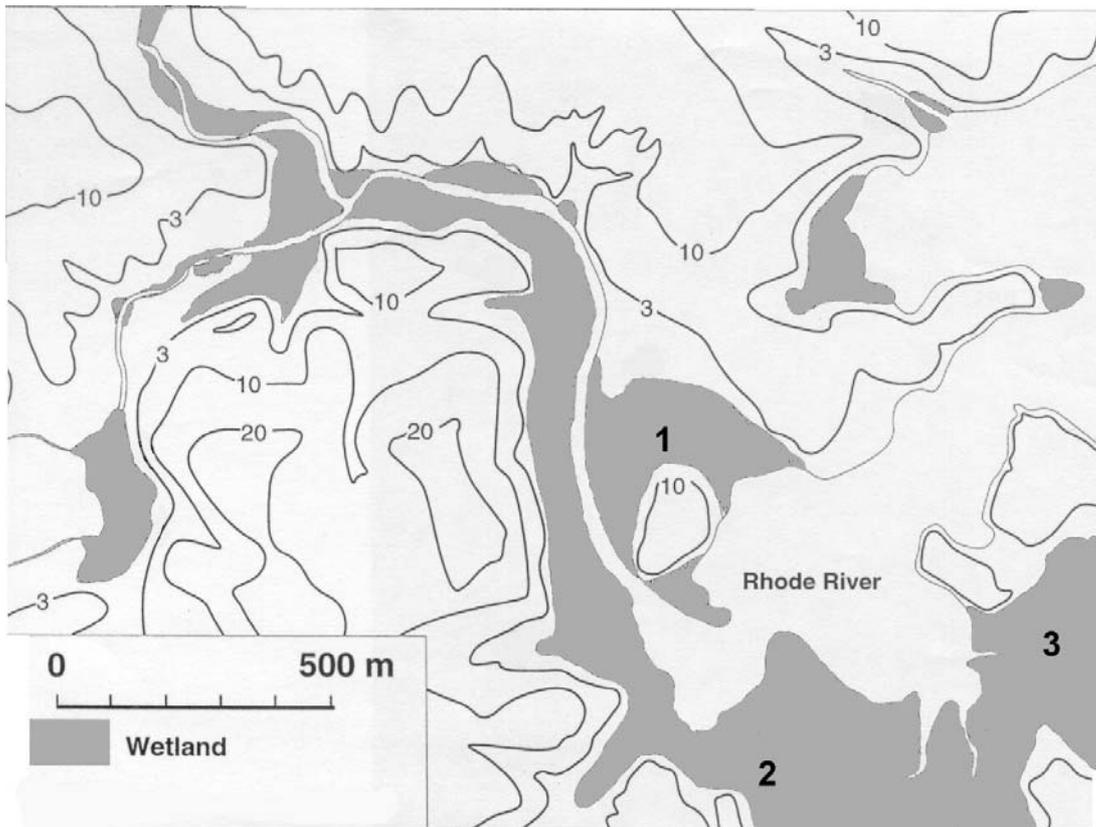


Figure 2. Map showing the location of 3 study sites (dotted) in the research area. Contours in the map indicate altitude above sea level (m). Site 1 is called Hog Island Marsh, site 2 is called Kirkpatrick Marsh and site 3 is called Corn Island Marsh.

Specifically, the studies were conducted in three brackish tidal marshes locally known as the Hog Island Marsh, the Kirkpatrick Marsh and the Corn Island Marsh (Fig. 2). The region has a temperate rainy climate (Fig. 3) (Walter and Lieth, 1967), characterized by generally hot humid summers and cool winters. July temperatures in Baltimore (62 km north of the SERC) average a high of 31°C and a low of 19°C. January temperatures in Baltimore average highs of 5°C and lows of -5°C. The plant growing season, or period from the last killing frost in spring to the first killing frost in fall, is around 240 days. The first major frost in fall usually occurs in early November. The last major spring frost can be expected in early March

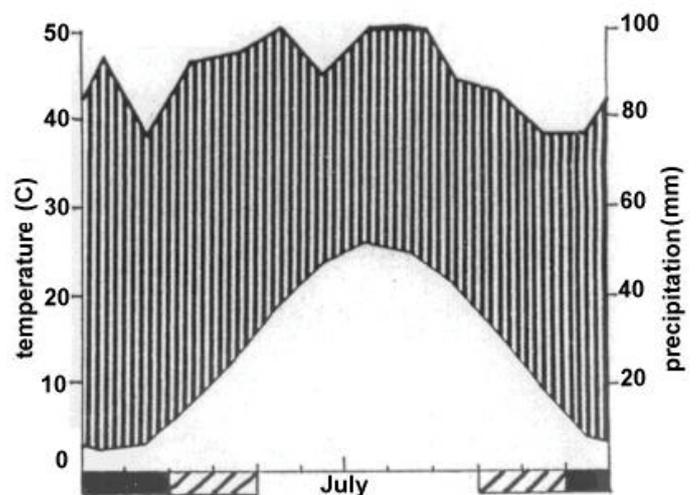


Figure 3. Annual pattern of rainfall and temperature at Baltimore (after Walter & Lieth 1967).

(Microsoft Encarta, 2001; Walter and Lieth, 1967).

The 160-year average annual precipitation (rainfall and snowfall) is 1080 mm. The long-term average precipitation by season is 280 mm (December to February), 314 mm (March to May), 245 mm (June to August), and 246 mm (September to November). Most precipitation is in the form of rain. In the winter, snow is common but usually does not persist for more than several days. Thunderstorms are the common source of precipitation in the summer months and hurricanes periodically impact the area in the late summer and early autumn (Microsoft Encarta, 2001; Walter and Lieth, 1967).

The Plant

Scirpus olneyi A. Gray, (Olney Threesquare, Olney's Bulrush, Three Square Grass, Salt Marsh Sedge, etc), a member of the sedge family Cyperaceae. The currently accepted scientific name of this species is *Schoenoplectus americanus* (Pers.) Volk. ex Schinz & R. Keller. Schuyler (1974) pointed out, however, the difficulties associated with the application of this name (Schuyler, 1974). A number of taxonomists regard *Scirpus olneyi* Gray as a younger synonym of *Scirpus americanus* Pers. Some taxonomist, however, consider *Scirpus americanus* Pers. as a synonym of another species, *Scirpus pungens* (partly?). Since these two species, *Scirpus pungens* and *Scirpus olneyi*, are clearly different species but have the same name, *Scirpus americanus*, using "americanus" causes confusion. Moreover, several taxonomists distinguish this section of the genus *Scirpus* as a genus of its own, *Schoenoplectus*, thus resulting in the name *Schoenoplectus americanus* (Pers.) Volk. ex Schinz & R. Keller. Although these changes are incorporated into recently published floras to various extents, the names are still confusing throughout the scientific literature.

If we reject "*Scirpus americanus*", we can use *Scirpus olneyi* and *Scirpus pungens* without any confusion. Because of the nomenclatural complexity associated with the study species, I have chosen to refer to it as *Scirpus olneyi*, the name that is most widely used.

Scirpus olneyi occurs in a broad range of salt marsh communities in both North and South America. In the USA, it occurs in almost all coastal states except New Hampshire and Maine in the northeast. It also is found in non-coastal states, especially in the intermontane west where the climate is drier and saline wetlands occur.

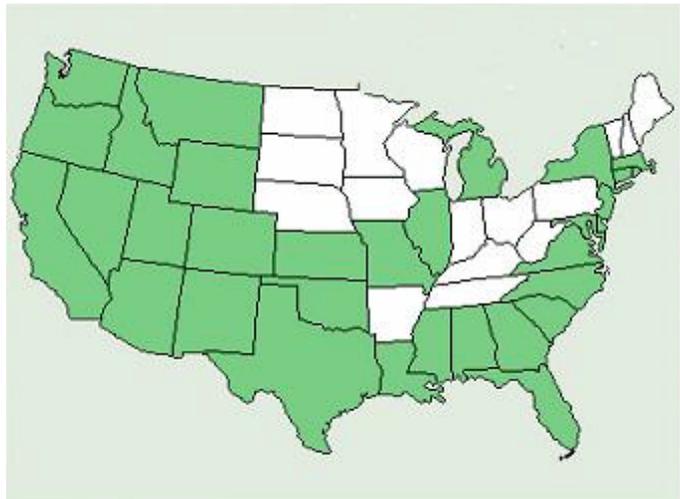


Figure 4. Map showing the current distribution of *Scirpus olneyi* in the USA. *S. olneyi* occurs in the shaded states (after Natural Resources Conservation Service copyright by Image generated using gd 1.8).

The species also occurs in two states (Missouri, Michigan) in the Mississippi drainage (Fig. 4). In Maryland, *S. olneyi* occurs in brackish tidal marshes where it forms dense monospecific stands or it occurs in mixed stands with other plant species (McCormick and Somes, 1982; Tiner and Burke, 1995).

Scirpus olneyi is an emergent, rhizomatous, perennial macrophyte. An individual ramet consists of a shoot, roots and a tuber with or without a rhizome (Fig. 5). An individual ramet produces from one to three new ramets throughout the growing season. Clonal propagation allows *S. olneyi* to spread rapidly and form patches of interconnected ramets.

a) Long Rhizome Ramets



b) Short Rhizome Ramet



Figure 5. The clonal architecture of *Scirpus olneyi*. (a) Long Rhizome Ramets (LRR) and (b) Short Rhizome Ramets (SRR).

Below ground plasticity is a characteristic of this species. Tubers and rhizomes are located within 15 cm of the soil surface and persist for several years. Individuals form two types of ramets. One type of ramet includes a tuber and a rhizome, hereafter called a “Long rhizome ramet”. The second type of ramet includes the tuber and no rhizome or a very short rhizome, hereafter called a “Short rhizome ramet” (Fig. 5). Genets that produce Short rhizome ramets form patches with high shoot densities that are monospecific and apparently occupy areas for long periods of time. Shoot densities are lower in areas where plants primarily produce long rhizome ramets. The placement of ramets at the end of long rhizomes allows the species to occupy new areas. The Short rhizome ramet type follows a “Phalanx growth strategy” and individuals that produce Long rhizome ramets follow the “Guerilla growth strategy” (Lovett Doust, 1981).

Above ground shoots are erect, sharply triangular, and needle-like. Above ground shoots are composed of short leaves, up to 10cm long, that are closely adpressed to the shoot and emerge from the lower part of the culm. Total culm height ranges from approximately 50 to 200 cm. Green shoots appear above ground in April at our study sites and green shoots persists well into the winter (*i.e.*, December) the most shoots senesce during the autumn months following the onset of freezing temperatures. New ramets produced near the end of a growing season do not include an above ground shoot.

Flowering occurs in May and June in Maryland. Not all shoots flower, and the flowering ratio (the ratio of flowering shoots to all shoots) varies within and among communities. Seeds mature and are shed in September. Seed yields range from 0 to 27 kg/ha

(Palmisano and Newsom, 1968). The seeds remain dormant as long as they are submerged in water and thus become a component of the marsh seed bank. Germination and seedling establishment potentially occurs on exposed mudflats following marsh drawdown. The seed germination of this species is strongly regulated by salinity. At a salinity of 4 ‰ germination is reduced by 50 % and above 13 ‰ no germination at all (Palmisano and Newsom, 1968). Thus, due to high salinity, seed germination is quite rare in salt marshes.

Habitat

Scirpus olneyi occurs in mesohaline brackish tidal marshes at SERC. Brackish tidal marshes are transitional between salt marshes and tidal and non-tidal freshwater marshes (McCormick and Somes, 1982; Tiner and Burke, 1995). Interstitial salinity varies within individual marshes and seasonally but typically mesohaline brackish marshes are defined as having interstitial salinities that range from 5 parts per thousand to 18 parts per thousand (Tiner and Burke, 1995; Whigham *et al.*, 1989). Brackish marshes at SERC are found in two habitats. Areas that are only infrequently inundated by tides are called High Marsh habitats (Jordan *et al.*, 1984). Brackish marshes also occur in areas that flood more frequently because the marsh surface elevation is lower in the intertidal zone and are referred to as Low Marshes habitats (Jordan *et al.*, 1984). The tidal range in the Rhode River subestuary is approximately 50 cm. High marsh habitats typically have higher interstitial salinity than Low marsh habitats because they are inundated less frequently. Variations in flooding regime and salinity create a variety of environmental conditions resulting in a vegetation mosaic that is also spatially variable. *Scirpus olneyi* occurs in both Low and High marsh habitats but it is most abundant on the High marsh. Other dominant species in brackish marshes associated with High marsh habitats are *Distichlis spicata*, *Hibiscus palustris*, *Iva frutescens*, *Phragmites communis*, *Scirpus olneyi*, *Spartina patens*, *Scirpus cynosuroides* and *Typha angustifolia*.

McCormick and Somes (1982) listed 10 different plant communities that are associated with brackish marshes in Maryland. At the SERC, I studied *S. olneyi* in 4 of the communities described by McCormick and Somes: 1) Typha marsh (Cattail), 2) Hibiscus marsh (Rosemallow) 3) Spartina marsh (Meadow Cordgrass/Spikegrass), and 4) Scirpus marsh (Threesquare) community.

In this project, I further recognize three categories of the Scirpus marsh community: Scirpus High marsh, Scirpus Low marsh and Scirpus Shaded marsh community. Although *S. olneyi* is a dominant species in all three categories, there are differences, described below, in the physical environments and differences in shoot and rhizome characteristics of *S. olneyi*.

Methods

In 1999, 5 observation plots (each 50cm X 50cm) were established in 6 communities (Typha, Spartina, Hibiscus, Scirpus High marsh, Scirpus Low marsh and Scirpus Shaded marsh in the Hog Island Marsh area). I recorded the number of shoots, and ramet status (sexual or vegetative) in each observation plot. Salinity, light availability and soil compactness were measured in each plot. Salinity of the interstitial water was measured by collecting interstitial water from a depth of 10 cm deep. Water samples were collected with piezometers made of PVC pipe that was sealed at the base and had holes drilled into them near the base. Salinity of the interstitial water was measured in the field with a hand-held refractometer. Light levels were measured under clear sky in late July, between 11:00 through 15:00 (EST). I measured light levels three times and took the intermediate value. The light levels were measured at the surface of the substrate and at three heights (50 cm, 100 cm, 150 cm) in the center of each plot using a Licor Quantum Radiometer, Photometer Model LI-185A. Soil compactness was measured at 9 points in each observation plot with a hand-held penetrometer (Eijkelkamp, Hand Penetrometer, Type 1B).

To characterize the morphological features of *Scirpus olneyi*, sods (25 cm X 25 cm X 20 cm) were excavated from Hog Island Marsh. I excavated one sample from each community in September and two samples in December. Data on shoot morphology and biomass allocation, shoot heights, shoot diameter, the weight of underground ramets (roots, rhizomes and tubers) and shoot weight were obtained from the September samples. To analyze ramet architecture, types of ramets (long rhizome or short rhizome) and the lengths of rhizomes that connected ramets, the September and December samples were used. Sods excavated in the field were brought back to the laboratory, and the entire ramet system, including tubers, rhizomes, roots and shoots was then extracted from the sediment. Each ramet was classified into one of two categories, a short rhizome ramet (a tuber without a rhizome) and a long rhizome ramet (a tuber with a rhizome) (Fig. 5). After measurements of rhizome length and branching, ramets were separated into 3 other categories, current year's ramets, older than one-year ramets and dead ramets. Ramets were then dried for 72 hours at 68°C for dry weight determination.

In mid-September, inflorescences were collected to evaluate sexual reproductive effort. *S. olneyi* did not produce flowers in the Shade Marsh community thus reproductive shoots we only collected in the Spartina community and the Scirpus High Marsh community. Inflorescences were collected from flowering shoots in each observation plot, and dried at room temperature for 1 week and weighed.

Plants Community descriptions

1) Typha community (Cattail marsh community)

Typha angustifolia (Cattail) was the dominant species in this community. This community was mainly located close to the land (Fig. 6), next to the Scirpus Shaded marsh community. Salinity was low (Table 1), probably because of fresh water runoff

from adjacent uplands. The substrate consisted of organic matter, mainly dead rhizomes and leaves of *T. angustifolia*, and soil compactness was very low (Table 1). Because shoots and leaves of *T. angustifolia* were taller than those of *Scirpus olneyi*, light levels were low (Table 1).

The number of *S. olneyi* shoots was lowest and shoots height was high in this community (Table 2). The shoot/root ratio was high (Table 3) due to lower light availability. In this community, *S. olneyi* produced long and short rhizome ramets in equal numbers and the number of branchings per ramet was intermediate (Table 4). Flowering was rare. (Table 5).

2) *Spartina* community (Meadow Cordgrass/Spikegrass marsh community)

Spartina patens (Meadow Cordgrass) was a major component and *Scirpus olneyi* appears to invade this community from the margins. This community was located in the high marsh, typically near the center of a marsh (Fig. 6). The salinity was low but varied among observation plots (Table 1). The sediment was highly organic and consisted of thick rhizomes and roots of *S. patens*, and thus was compact (Table 1). Light availability for *S. olneyi* was high, because shoots of *S. patens* are horizontal during much of the growing season (Turitzin and Drake 1981) (Table 1).

Shoot density was low (Table 2) and shoot height and average shoot weight were the lowest in this community (Table 2), perhaps because there were no other taller plants and thus no competition for light. *S. olneyi* allocated more resources to below ground biomass in this community resulting in a shoot/root ratio that was the lowest of any of the communities (Table 3). Ramets mainly consisted of current year ramets (Table 3). *S. olneyi* produced mostly long rhizome ramets and few short rhizome ramets in this community and ramets did not branch very often (Table 4). No flowering shoots were found in this community (Table 5).

3) Hibiscus community (Rosemallow marsh community)

S. olneyi was co-dominant in this community with *Hibiscus palustris* (Rosemallow), *Iva frutescens* (Marshelder) and, to a lesser degree, with *Spartina patens* (Meadow Cordgrass). This community was located at the edge of the high marsh, and relatively close to lower elevation marshes (Fig. 6). Salinity was low (Table 1) and the sediment was composed mostly of dead *S. olneyi* roots and rhizomes (tubers). Soil compactness was low (Table 1).

The number of *S. olneyi* shoots was high, shoots were the tallest, and shoot weight was greatest in this community (Table 2). Plants had a low shoot/root ratio and underground plant parts consists of many rhizomes and tubers that were more than one year old (Table 3). Plants produced heavier but shorter rhizomes (Table 3,4). *S. olneyi* produced many reproductive shoot and seeds in this community (Table 5).

4) *Scirpus* High marsh community (Threesquare marsh community)

S. olneyi was a major component of this community and it was associated with *Spartina patens* (Meadow Cordgrass) and *Distichlis spicata* (Spikegrass). This community occupied the largest part of the high marsh at SERC (Fig. 6). Interstitial salinity was the highest in this community. Due to the accumulation of Meadow Cordgrass and/or Spikegrass ramets, soil compactness was high (Table 1).

S. olneyi produced the largest number of smaller shoots in this community (Table 2).

S. olneyi had many old rhizomes (Table 3) and had the shortest rhizomes in this community (Table 4). *S. olneyi* produced the largest number of flowering shoots in this community (Table 5).

5) Scirpus Patchy marsh community (Threesquare marsh community)

S. olneyi was a major component of this community, and was associated with *Spartina patens* (Meadow Cordgrass), *Hibiscus palustris* (Rosemallow), and *Iva frutescens* (Marshelder). This community was located in the Low marsh habitat (Fig. 6). Because of the tide, most part of this habitat is flooded twice a day, and plant occurred on hummocks. Thus, *S. olneyi* in this community had a clumped distribution. Salinity was relatively high (Table 1) and, soil compactness varied, since the sediment between the hummocks was highly organic and very soft whereas the sediment in a hummock was hard and consisted of thick rhizomes and roots of *S. patens* and *S. olneyi* (Table 1). Light availability was low on the hummocks (Table 1), but higher in the open areas between the hummocks.

Shoot density was high and shoots formed dense patches (Table 2). Shoot height and weight was intermediate (Table 2). *Scirpus olneyi* produced many short rhizome ramets and these short rhizome ramets branched frequently (Table 4). As a result, ramets formed dense clumps. *S. olneyi* produced an intermediate number of reproductive shoots and seeds in this community (Table 5).

6) Scirpus Shaded marsh community (Threesquare marsh community)

Only a few species, mainly *S. olneyi* and *Phragmites communis* (Common Reed), occurred in this community. This community was located on the edge between land and marsh (Fig. 6). A feature of this community was the low light availability from overhanging tree branches (Table 1). Fresh water input from the adjacent upland mixed with tidal waters, resulting in intermediate salinity (Table 1). The sediment consisted of decomposed leaves from the trees, and was too soft to be measured with the penetrometer (Table 1).

In this community, shoot density was the lowest (Table 2). Due to low light availability, *S. olneyi* made taller shoots (Table 2) and had higher shoot/root ratios (Table 3). Ramets had longer rhizomes and frequently branched (Table 4). *S. olneyi* did not reproduce sexually in this community.

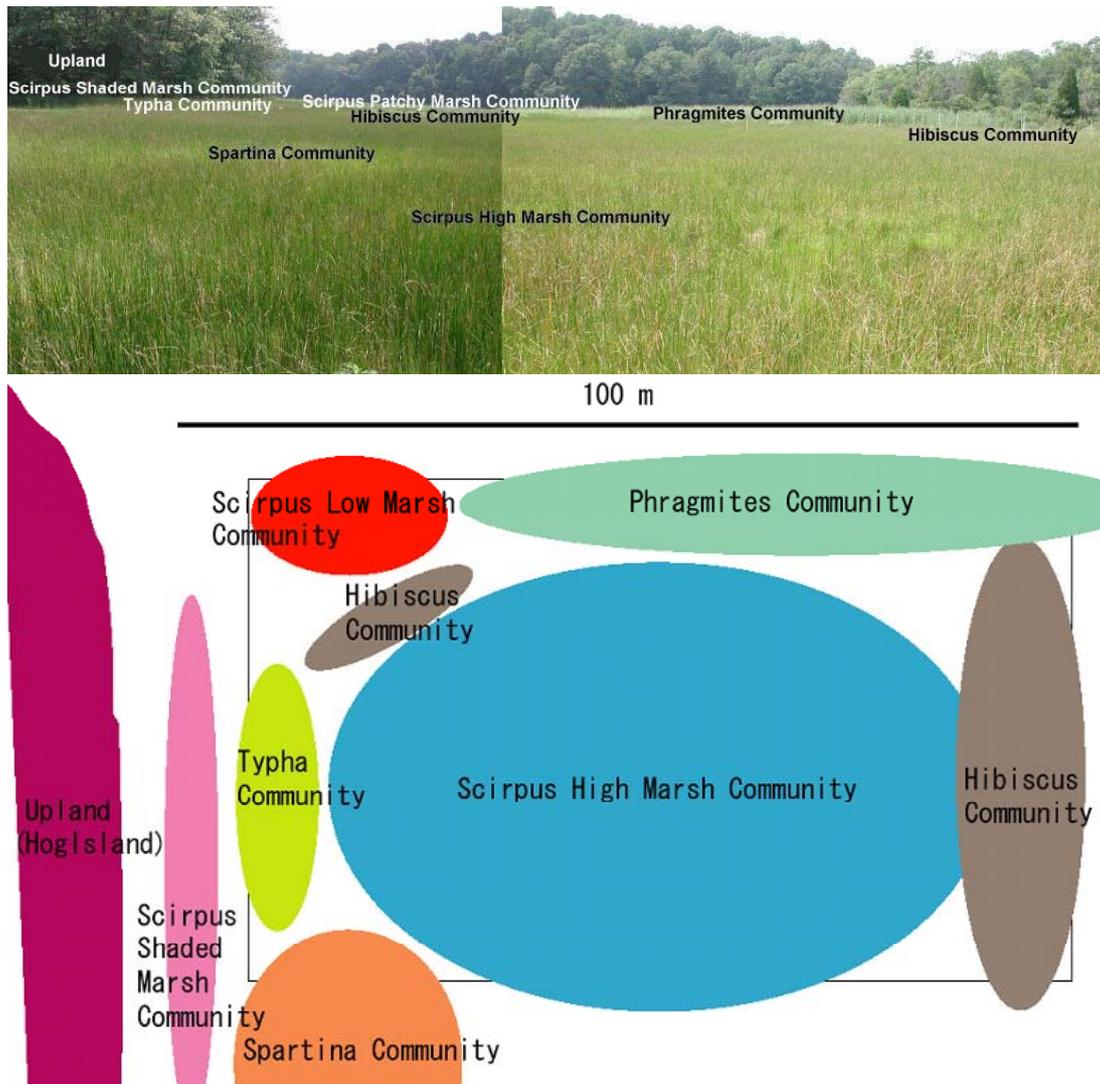


Figure 6. The distribution of plant communities in one study site, “Hog Island Marsh”. No *Scirpus olneyi* occurs in the Phragmites community.

Table 1. Salinity, soil compactness and light availability in the 6 habitats described in the text. Data were measured in 5 observation plots in Sept. 1999. Interstitial salinity was measured at two points in each habitat, compactness at 9 points and light at the center of each plot at 4 different heights. Light was measured as $\mu\text{mol s}^{-1} \text{m}^{-2}$. Data are mean values ± 1 SD. Different letters indicate significant differences between values ($P < 0.05$) in one-way ANOVA.

	salinity (ppt)	compactness (kg/cm ²)			
Typha (Cattail)	9.60 \pm 0.8a	59.80 \pm 19.6a			
Spartina (Meadow Cordgrass)	8.30 \pm 2.5b	122.90 \pm 39.5b			
Hibiscus (Rosemallow)	8.50 \pm 1.2b	66.86 \pm 49.8ac			
High Marsh (Threesquare)	13.70 \pm 1.3c	146.70 \pm 38.9d			
Patchy Marsh (Threesquare)	11.50 \pm 1.1bc	26.43 \pm 21.5e			
Shaded Marsh (Threesquare)	9.30 \pm 1.2a	N/O			

	light level at 150cm ($\mu\text{mol s}^{-1} \text{m}^{-2}$)	light level at 100cm ($\mu\text{mol s}^{-1} \text{m}^{-2}$)	light level at 50cm ($\mu\text{mol s}^{-1} \text{m}^{-2}$)	light level at 0cm ($\mu\text{mol s}^{-1} \text{m}^{-2}$)
Typha	1620 \pm 98.0a	1560 \pm 196.0a	620 \pm 116.6a	142 \pm 38.2a
Spartina	1606 \pm 90.2a	1606 \pm 90.2a	1606 \pm 90.2b	1602 \pm 90.2b
Hibiscus	1500 \pm 0a	920 \pm 204.0b	274 \pm 81.9c	57 \pm 21.4a
High Marsh	1560 \pm 49.0a	1560 \pm 49.0a	480 \pm 98.0ac	178 \pm 77.0a
Patchy Marsh	1630 \pm 107.7a	1590 \pm 111.4a	540 \pm 177.2a	118 \pm 51.9a
Shaded Marsh	151 \pm 35.8b	94 \pm 64.1c	92 \pm 30.6c	55 \pm 33.5a

Table 2. Characteristics of *Scirpus olneyi* shoots morphology in the 6 habitats described in the text. Shoots were from samples collected in Sep. 1999. Values for Height and Diameter are means (\pm SD). Different letters indicate significant differences at ($P < 0.05$) in one-way ANOVA.

	shoot number (No./m ²)	total shoot weight (g/m ²)	per shoot weight (g)	shoot height (cm)	diameter (mm)
Typha	160	267.84	1.67	109.75 \pm 17.8a	5.68 \pm 0.63a
Spartina	160	116.64	0.73	58.84 \pm 22.9b	5.07 \pm 0.57a
Hibiscus	240	573.12	2.39	126.30 \pm 22.7ac	5.20 \pm 0.56a
High Marsh	560	403.20	0.72	65.17 \pm 13.7bd	3.75 \pm 0.74b
Patchy Marsh	1168	1081.60	0.93	75.92 \pm 20.1e	3.98 \pm 0.87b
Shaded Marsh	208	197.12	0.95	99.54 \pm 11.4a	4.99 \pm 0.42a

Table 3. Biomass allocation to shoots, old rhizomes and new rhizomes. One sample was collected from each of 6 habitats in Sept. 1999. Current year's shoot biomass and current year's rhizome biomass was used to calculate the current year's shoot/root ratio. Current year's shoot and rhizome biomass, and biomass of rhizomes older than the current year were used to calculate the total shoot/root ratio.

	shoot weight (g/m ²)	current year rhizome weight (g/m ²)	older than one year rhizome weight (g/m ²)	total rhizome weight (g/m ²)
Typha	267.84	118.40	302.40	420.80
Spartina	116.64	94.40	52.80	147.20
Hibiscus	573.12	200.00	1582.40	1782.40
High Marsh	403.20	211.20	1100.80	1312.00
Patchy Marsh	1081.60	699.20	1513.60	2212.80
Shaded Marsh	197.12	80.00	67.20	147.20

	current year total S/R S/R Ratio	ratio of current/old ratio	No. of current year year rhizome	weight per current rhizomes (No./m ²)	year rhizomes
Typha	2.25	0.64	0.39	1136	0.14
Spartina	1.23	0.79	1.77	384	0.20
Hibiscus	2.87	0.32	0.13	2432	0.22
High Marsh	1.90	0.31	0.19	3520	0.08
Patchy Marsh	1.55	0.49	0.46	3712	0.15
Shaded Marsh	2.46	1.34	1.19	1120	0.15

Table 4. Below ground ramet architecture for *Scirpus olneyi* in 6 different habitats. Three samples were collected from each habitat in Sept. and Dec. 1999. The number of short and long rhizomes and the short rhizome ratio to all rhizomes are means of 3 samples, length and branching figures are mean values (\pm SD). Different letters indicate significant differences between values ($P < 0.05$) in one-way ANOVA.

	mean No. of short rhizome (No./m ²)	mean No. of long rhizome (No./m ²)	ratio of short rhizome (%)	Mean length of short rhizome (cm)
Typha	683.20	708.80	49.08	0.80 \pm 0.33a
Spartina	123.20	384.00	24.29	0.89 \pm 0.33a
Hibiscus	2971.20	2484.80	54.46	0.93 \pm 0.26a
High Marsh	3664.00	3136.00	53.88	0.81 \pm 0.30a
Patchy Marsh	2379.20	1780.80	57.19	0.82 \pm 0.30a
Shaded Marsh	288.00	308.80	48.26	0.65 \pm 0.24a

	mean length of long rhizome (cm)	short rhizome branching	long rhizome branching
Typha	5.91 \pm 3.50a	1.12 \pm 0.36a	1.70 \pm 0.70a
Spartina	5.28 \pm 2.57ab	1.00 \pm 0.00ab	1.35 \pm 0.51ab
Hibiscus	3.76 \pm 2.40c	1.12 \pm 0.33abc	1.37 \pm 0.53b
High Marsh	3.51 \pm 1.66c	1.17 \pm 0.38abc	1.40 \pm 0.52b
Patchy Marsh	4.53 \pm 2.89b	1.32 \pm 0.53bd	1.75 \pm 0.68a
Shaded Marsh	8.60 \pm 5.23d	1.47 \pm 0.78d	1.88 \pm 0.92c

Table 5. Sexual reproductive effort in 4 of 6 *Scirpus olneyi* habitats. In Sept. 1999, seeds and flowers were collected from 5 observation plots. The Spartina (Meadow Cordgrass) and Shaded Marsh (Threesquare) habitat did not produce seeds, thus those habitats were excluded from the analysis. Figures are mean values (\pm SD) of 5 observation plots. Different letters indicate significant differences between values ($P < 0.05$) in one-way ANOVA.

	No. of flowering shoots (No./m ²)	No. of all shoot (No./m ²)	Flowering shoot ratio
Typha	60.0 \pm 25.6a	94.4 \pm 24.4a	85.6 \pm 34.3a
Hibiscus	192.0 \pm 50.0b	245.6 \pm 50.0b	77.7 \pm 9.4ab
High Marsh	555.2 \pm 32.4c	652.8 \pm 70.4c	65.7 \pm 7.0abc
Patchy Marsh	140.0 \pm 75.6ab	423.2 \pm 126.8d	34.2 \pm 15.9bc

	inflorescence mass (g/m ²)	seed mass (g/m ²)	seed number (No./m ²)
Typha	1.08 \pm 0.72a	0.24 \pm 0.24a	213.6 \pm 158.4a
Hibiscus	5.24 \pm 1.60b	1.28 \pm 1.04a	923.8 \pm 719.2a
High Marsh	13.8 \pm 3.72c	6.52 \pm 2.32b	5310.7 \pm 1782.8b
Patchy Marsh	2.12 \pm 2.04ab	0.52 \pm 0.80a	479.8 \pm 674.8a

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Chapter 3:

*Ramet development of a clonal sedge
Scirpus olneyi A. Gray in time (phenology)
and in space (architecture)*

IKEGAMI Makihiko, Dennis F. WHIGHAM and Marinus J.A. WERGER

Summary

The clonal plant *Scirpus olneyi* occurs in various communities in the salt marshes and shows different growth forms. This species has two types of ramets, ramets with very long rhizomes (Long Rhizome Ramet: LRR) and ramets with very short rhizomes (Short Rhizome Ramet: SRR). In different communities, this species shows different ramet architectures in combination of the two types of ramets. We hypothesized that these two types of ramets are functionally specialized to different tasks and that they appear at different time during the growing season. We evaluated the ramet architecture and appearance of ramets through the growing season in different environments in field observations and a garden experiment.

We found that the proportion of SRRs and LRRs varied among the communities. The garden experiment showed that plants produce proportionally more SRRs in higher quality treatments. We also found that SRRs appeared early in the growing season while LRRs tended to appear over a longer period. Thus plants produce most of their shoots early in the growing season in high quality environments with a larger proportion of SRRs while they produce new shoots continuously in low quality environments with a larger proportion of LRRs. We also found that the shoot longevity is longer in shoots from SRRs than from LRRs.

These results support the notion that individual ramets are functionally specialized to perform different tasks to spread. *S. olneyi* produces SRRs as a mechanism to consolidate its occupancy and exploitation of favorable habitats while is also has the ability to produce LRRs to explore new and possibly other high-quality habitats. And for this task, producing SRRs early in the growing season is beneficial since plants need to occupy the available better patches immediately and keep their shoots there during the growing season, while for exploration or escape, the production of LRRs continuous would be beneficial, as the plants then have a higher chance to reach better environments.

Keywords: clonal plant, ramet architecture, phenology, *Scirpus olneyi*

1) Introduction

Clonal growth is one of the most successful propagation strategies in the plant world. By repeatedly producing genetically identical ramets, clonal plants develop a variety of architectural forms that result from the formation of spacers (rhizomes or stolons) of different lengths, different branching frequencies and different branching angles. The complexity of clonal architectures differs among plant species or within the same species growing in different environments (Bell, 1980; Bell, 1984; de Kroon and Knops, 1990; Hutchings and de Kroon, 1994; Lovett Doust, 1981). Clonal plants may locally change the architectural elements of their morphology, *e.g.* shorten or lengthen their spacers, and thus occupy local resource patches or grow out of a patch and explore adjacent patches (Hartnett and Bazzaz, 1983; Salzman and Parker, 1985; Slade and Hutchings, 1987a; Slade and Hutchings, 1987b; Slade and Hutchings, 1987c). In clonal plant species, this plasticity in clonal architecture may be an adaptive plant trait (Hartnett and Bazzaz, 1983). 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).

Scirpus olneyi, is a clonal species of brackish wetlands that grows and dominates under a rather wide range of environmental conditions, varying from brackish to fresh water sites, and from shady to open habitats (Drake, 1984; McCormick and Somes, 1982). The ability of *S. olneyi* to successfully colonize a wide range of habitats may be, in part, the result of plasticity in clonal architecture. *S. olneyi* maintains architectural plasticity by producing two types of ramets, often within one clone. Some ramets have very long rhizomes (Long Rhizome Ramet: LRR) while others have very short rhizomes (Short Rhizome Ramet: SRR).

We hypothesize that plants produce LRRs and SRRs in different proportions in response to different environmental conditions. Some plants would produce SRRs to occupy resource patches while others would produce LRRs to explore and subsequently colonize new resource patches. This dual clonal strategy enables *S. olneyi* to exploit resources in favorable patches while at the same time exploring the environment for other favorable patches in spatially heterogeneous ecosystems. The ability to produce spacers of variable length also enables plants to escape from less favorable patches where resource levels are low or where competition stress is high (de Kroon and Hutchings, 1995; Dong, 1996; Dong and de Kroon, 1994; Slade and Hutchings, 1987a; Slade and Hutchings, 1987b; Slade and Hutchings, 1987c).

We also hypothesize that plants will produce LRRs for a longer period of time than they will produce SRRs. The production of LRRs during the entire growing season increases the probability of encountering suitable habitat patches. In contrast, if plants produce SRRs to exploit areas already occupied, then SRRs should be produced early in the growing season to maximize the amounts of resources obtained during the growing season. We investigated these hypotheses by conducting garden and field experiments.

2) Plant and Communities

Scirpus olneyi A. Gray, a member of the sedge family Cyperaceae, occurs in different plant communities in tidal wetlands that range from brackish to fresh water along the East Coast of the USA (Drake, 1984; McCormick and Somes, 1982). The currently accepted scientific name of this species is *Schoenoplectus americanus* (Pers.) Volk. ex Schinz & R. Keller. Schuyler (1974) pointed out, however, difficulties associated with the application of this name. A number of taxonomists regard *Scirpus olneyi* Gray as a younger synonym of *Scirpus americanus* Pers. Some taxonomist, however, consider *Scirpus americanus* Pers. as a synonym of another species *Scirpus pungens* (partly?). Since these two species, *Scirpus pungens* and *Scirpus olneyi*, are clearly different species but have the same name *Scirpus americanus*, using “*americanus*” causes confusion. Moreover, several taxonomists consider this section of the genus *Scirpus* to be a separate genus, *Schoenoplectus*, and thus call this species *Schoenoplectus americanus* (Pers.) Volk. ex Schinz & R. Keller. Although these changes are incorporated into recently published floras to various extents, the names are still confusing. Because *Scirpus olneyi* is still a widely applied name for this species we have chosen to use it in this study.

The aboveground part of each ramet consists of a vegetative or reproductive shoot that is annual. Shoots are erect, sharply triangular, needle-like, with rudimentary leaves. The belowground parts of a ramet consist of roots, a tuber and a rhizome. The node of each underground ramet is a tuber from which long or short internodes emerge. A daughter tuber with a measurable rhizome is defined as a “Long Rhizome Ramet (LRR)” (Fig. 1a) and a daughter tuber with an unmeasurable rhizome (maximum of a few mm) attached to the mother tuber, is defined as a “Short Rhizome Ramet (SRR)” (Fig. 1b).

a) Long Rhizome Ramets

b) Short Rhizome Ramet



Figure 1. Figures of the clonal architecture of *Scirpus olneyi*. (a) Long Rhizome Ramets (LRR) and (b) Short Rhizome Ramets (SRR).

This research was conducted in three tidal wetlands (Hog Island Marsh, Corn Island Marsh, and Kirkpatrick Marsh) at the Smithsonian Environmental Research Center (SERC) in Maryland, USA. *S. olneyi* occurs in 4 different plant communities at the SERC: 1) *Scirpus* High marsh community, 2) *Scirpus* Patchy marsh community, 3)

Scirpus Shaded marsh community and 4) *Spartina* community. *S. olneyi* is a dominant species in the Scirpus High marsh, the Scirpus Patchy marsh and the Scirpus Shaded marsh communities, and it invades the *Spartina* community from the edge. The characteristics of each community are as follows:

In the Scirpus High marsh (SHM) community, *S. olneyi* is a dominant species along with *Spartina patens* and *Distichlis spicata* (McCormick and Somes, 1982). This community occupies the largest percentage of the high marsh habitats at the SERC. In this community, light availability drastically declines from the top to the bottom of the canopy due to high shoot densities. Living and partially decomposed shoots, roots and rhizomes of *S. patens* and/or *D. spicata* result in a hard, compact substrate. Interstitial water is brackish; usually averaging around 14‰ during the growing season.

In the Scirpus Patchy marsh (SPM) community, *S. olneyi* is a dominant species. Associated species are *Spartina patens*, *Hibiscus palustris*, and *Iva frutescens* (McCormick and Somes, 1982). The latter two species are tall suffrutescens perennial shrubs with shoots that are between 1 and 2 meters. Hummocks are a characteristic feature of this community. The hummocks are formed by vertical accretion of living and dead shoots of the dominant species. *S. olneyi* shoot density is high on the hummocks resulting in a steep light gradient from the top of the canopy to the base of the shoots. Light availability is much higher in the open areas between hummocks. Soil compactness varies, since the sediment between hummocks is highly organic and very soft whereas hummock substrates are hard due to the presence of living and dead shoots, rhizomes and roots, primarily of *S. patens* and *S. olneyi*. Salinity of interstitial water at the base of hummocks averages around 13‰ during the growing season.

In the Scirpus Shaded marsh (SSM) community, species diversity is low and the only common species are *S. olneyi* and *Phragmites communis* (McCormick and Somes, 1982). This community occurs around the edge of the wetland and forms the boundary between the wetland and adjacent upland. Because of overhanging tree branches light availability in this community is low during the growing season. The substrate consists of highly decomposed organic matter resulting in a very soft substrate. Interstitial salinity averages 11‰ during the growing season.

In the *Spartina* (SPA) community, *Spartina patens* is the dominant species and *Scirpus olneyi* appears to invade this community from the margins. Light availability is high in this community for most of the growing season because the shoots of *S. patens* become horizontal shortly after they are mature. The sediment is highly organic and consists of a dense mat of rhizomes and roots of *S. patens*. The substrate is a hard and compact and interstitial salinity averages around 13‰ during the growing season.

The SHM, SSM and the SPA communities were sampled for studies of ramet phenology and clonal architecture. The SPM community was included in the clonal architecture study.

3) Materials and Methods

To evaluate ramet phenology, on the 17th of April 2000, we established 31 plots (25 X 25 cm) in the SHM, SSM and SPA communities. The distribution of plants among sites and communities is shown in Table 1. Every two weeks we tagged all new shoots in

each plot with numbered plastic labels. The status (live or dead, sexual or asexual) of all tagged shoots was evaluated bi-weekly until the 28th of November, when the first killing frost occurred. The phenology observation period was 224 days. Phenology observations were not made on the 4th and 18th of September thus we had to estimate the number of new and dead shoots for those two dates. This was done by examining new shoots and counting the number of dead shoots on the 2nd of October. Shoot that were > 30cm were assumed to have appeared between September 4-18 and shoots that were ≤ 30cm were assumed to have appeared between September 18 and October 2. Shoots that were completely yellow on October 2 were assumed to have died before Sept 4th and shoots that still had some green color were assigned to the cohort that died by September 18th.

In late November and December 2000 we excavated 20 samples from the phenology plots (Table 1) for a study of clonal architecture. The plots were 25 X 25 cm and they were excavated to a depth of 20cm. In addition, we excavated 5 samples from the SPM community (Table 1).

The samples were washed in the laboratory to remove loose organic material from the ramet systems. Roots and rhizomes were carefully extracted to remove entire ramet systems. For every ramet we recorded the type of ramets (LRR or SRR), the age of the ramets (current-year or older-than-one-year),

the number of daughter ramets (branching) and the rhizome length for each ramet. We used the plastic tags from the phenology study to determine which ramets were produced in the current-year and to determine the date of appearance of each rhizome. The date of appearance of each rhizome was assumed to be the date of appearance of its aboveground shoot. The rhizome systems were individually weighed after drying for 72 hours at 68°C in a Grieve forced air oven.

In August 2001, we conducted a separate study to compare shoot morphology and biomass allocation patterns in the different communities. We excavated ten plots (10 X 10 X 20 cm) in each of the four communities; 4 plots at Hog Island marsh, 3 plots at Corn Island marsh and 3 plots at Kirkpatrick marsh. We measured up to 4 shoots in each plot. For shoot dimensions we measured shoot height, the width of the broadest side of the triangular shoot at about 10cm above the soil surface and the hypotenuse of the “triangle” at that point. We used these data to calculate the Green Area (GA) of the shoots, being the total surface area of the triangular pyramidal shoot. Subsequently, we measured shoot weight, current-year rhizome weight and older-than-one-year rhizome

Table 1. Number of observation plots in each of the 3 study sites (Hog Island Marsh, Corn Island Marsh and CO2 sites are locally known site names). The numbers without parentheses indicate the number of plots in which shoot phenology observations were made. The number of excavated plots is given in parentheses.

community	total plot numbers observed	Hog Island	Corn Island	CO2 Site
SHM	8 (6)	3(2)	2(2)	3(2)
SPM	0 (5)	0(2)	0(2)	0(1)
SSM	12 (7)	5(3)	6(4)	1(0)
SPA	11 (7)	6(4)	0(0)	5(3)

weight after 72 hours of drying at 68°C, and calculated the Specific Green Area (SGA), as GA divided by the shoot weight.

Growth of *Scirpus olneyi* is primarily influenced by three factors: nutrients, water (salinity) and light. To evaluate each of these factors separately, we conducted three separate experiments to evaluate the effects of nutrients, salinity, and light on clonal architecture. In May 1999, we obtained 150 genets of *S. olneyi* from a plant nursery (PINELANDS NURSERY, NJ, USA). On 1st of June, we chose 75 healthy genets and randomly assigned them in equal numbers into the following treatments.

For the nutrient experiment, plants were grown in full sun and fresh water with either 200kg-N/ha (referred to as NOR) or 20 kg-N/ha (referred to as PON) added. The nitrogen source was a commercial slow-release fertilizer (OSMOCOTE). For the salinity experiment, plants were grown in full sun and they were fertilized with 200kg-N/ha. Salinity was either 10‰ (referred to as S10) or 20‰ (referred to as S20). For the shading experiment, plants were grown in shade (referred to as SHD) or full sun. Standard shade cloth was used to reduce the amount of light to 5% of full sun. Plants in this treatment were grown in freshwater and fertilized at a rate of 200kg-N/ha. The other treatment for this experiment was NOR as described above.

In all three experiments, plants were grown in 9cm diameter X 12cm depth plastic pots filled with commercially obtained sand. Water was maintained at the soil surface level by placing pots into 25 X 32 X 15 cm tubs. Plants in the full-light experiments were kept in the open and, for the salinity experiment, water levels were adjusted regularly to maintain the appropriate salinities. On the 24th of September, we randomly chose 7 samples from each treatment. After washing sediment from the root systems of each plant we measure shoot height and quantified clonal architecture by taking the same measurements that were described for the field experiment. Belowground and aboveground biomass measurements were made after 72 hours of drying at 68°C.

4) Data analysis

We classified every ramet as either LRR or SRR and assigned each as having originated from a current-year's or an older-than-one-year's LRR or SRR. To quantify clonal architecture, for each ramet we specified the type and the age of the mother ramet, the existence of daughter ramets, and their types and numbers. We also scored the number of ramets that stopped producing daughter LRRs and SRRs and expressed that as a proportion of all ramets. The values for daughter LRRs and daughter SRRs were expressed as proportions of all daughter ramets.

From the bi-weekly monitoring of the plots we were able to calculate a rate of appearance of new shoots and a rate of shoot mortality. Data on shoot appearance and mortality were used to calculate ratios for new and dead shoots: as described above, we estimated the number of new and dead shoots on the 4th and 18th of September based on shoot heights and color as described above. To compare the phenology data among the three communities and over the growing season statistically, we separated the growing season in three phases. The spring phase was between the 17th April and 12th June (the 1st and 56th observation day); the summer phase was between 26th June and 4th

September (the 70th and 140th observation day); the autumn phase was between the 18th September and 28th November (the 154th and 224th observation day). We calculated the average values for each phase for each community for the following: new shoot appearance ratio, dead shoot ratio, green shoot ratio, flowering shoot ratio, new SRR appearance ratio, new LRR appearance ratio, rhizome length ratio, and rhizome weight ratio. We also calculated the ratio of surviving shoots at the end of the observation period. The ratios for each plot and each phase were calculated as follows:

The new shoot appearance ratio is the number of new shoots that appear in a plot during a phase divided by the total number of shoots that appeared during the growing season. The dead shoot ratio is the number of dead shoots that appear in a plot during a phase divided by the total number of shoots that appeared during the growing season. The surviving shoot ratio was the ratio of number of green shoots present in a phase to the total number of shoots present at the end of each phase. The shoot ratio in each phase in each plot was calculated as the numbers of green shoots in a phase in each plot divided by the total number of shoots that appeared during the growing season in that plot. The flowering shoot ratio is the number of flowering shoots that appeared in a phase divided by the total number of shoots present during that phase. The new SRR appearance ratio and the new LRR appearance ratio were, respectively, calculated as the number of new SRRs and LRRs that appeared during a phase divided by the total number of new SRRs and LRRs that appeared during the growing season. The rhizome length ratio and the rhizome weight ratio, respectively, in a phase were calculated as the increase in total rhizome length and total rhizome weight that appeared in a phase divided by the total rhizome length and total rhizome weight produced during the growing season.

To compare shoot longevity, rhizome weight and rhizome weight/length between SRRs and LRRs in the three communities we used the phenology data for the period 1st May and 15th May (14th and 28th observation days, respectively). We used 15th May as a cut-off date for evaluation of these variables because shoots that appeared after 15th May tended to survive until they were killed by frosts at the end of the growing season. Shoots that appeared after 15th May, therefore could not be used for longevity calculations. At the same time, we used rhizome weight data 1st and 15th May for comparison, since the mean rhizome weight and length also differ between the early growing season and the later growing season. Shoot longevity was defined as the number of days between the day of shoot appearance and the day of shoot death. If a shoot was green until the day of excavation, then the date of shoot death was set on the last observation day. Since the last observation day was after the first major frost in that growing season, we assumed every shoot was dead regardless its color. We also calculated the ratio of rhizome weight to rhizome length to evaluate the biomass investment to length growth in each community.

Fisher's exact test was used to compare the ages of mother ramets that produced current-year ramets, the types of mother ramets, the number of existent daughter rhizomes, the number of daughter LRRs and the number of daughter SRRs for all ramets. We tested these parameters between SRRs and LRRs within a community, among LRRs or SRRs in different communities, between current-year and older-than-one-year LRRs or SRRs. Since Fisher's exact test can be applied to pairs only, for multiple comparisons, we first compared every combination among communities, and tested for significance by Bonferroni-Dunn post-hoc tests.

One-way ANOVA was used to compare the mean number of current-year shoots, mean shoot height, mean total biomass, mean ratio of aboveground biomass to belowground biomass, mean ratio of current-year belowground biomass to all belowground biomass and mean branching frequency of rhizomes among the four communities, and rhizome weight and weight/length among the three communities. Because of skewed distributions, we used a logarithmic transformation for the data of rhizome weight and length. We also used two-way ANOVA to test differences in new shoot appearance ratios, dead shoot ratios, green shoot ratios, new SRR appearance ratios, new LRR appearance ratios, belowground length and weight ratios among the three phases and among the three communities followed by a Bonferroni-Dunn test for multiple comparisons. The t-test was used to test differences in shoot longevity between SRR and LRR in the three communities, to test the flowering shoot ratio between phases and between communities, and to test the branching number per ramet between LRRs and SRRs.

5) Results

Shoot Morphology

In the SHM and the SPM communities, the mean number of current-year shoots was significantly larger than in the SSM and the SPA communities (Table 2). Plants in the SHM and SPM communities had significantly higher biomass than plants in the SSM and SPA communities (Table 2). The belowground biomass of plants in the SHM community was twice that of the aboveground biomass. In contrast, plants in the other three communities had more aboveground biomass than belowground biomass (Table 2).

Table 2. Mean number or current-year shoots in 10 cm² plots, mean shoot height (cm), mean SGA (Specific Green Area, cm²g⁻¹) of shoots, mean total weight (g), mean ratio of aboveground weight to belowground weight, mean ratio of current-year rhizome biomass to all rhizome biomass. Values are means (\pm SD). Different letters indicate significant differences between values ($P < 0.0083$) in one-way ANOVA.

community	number of current-year shoot		shoot height		SGA	
SHM	10.4 \pm 3.37	a	109.35 \pm 12.95	a	72.67 \pm 18.71	a
SPM	14.1 \pm 9.12	a	104.24 \pm 23.55	a	62.36 \pm 14.42	bc
SSM	3.5 \pm 1.27	b	145.92 \pm 30.24	b	82.28 \pm 19.46	ad
SPA	3.9 \pm 1.45	b	82.43 \pm 15.46	c	68.02 \pm 13.87	ac

community	total biomass		ratio of aboveground biomass to belowground biomass		ratio of current year rhizome biomass to all rhizome biomass	
SHM	34.91 \pm 10.89	a	0.47 \pm 0.18	a	11.47 \pm 7.46	a
SPM	23.86 \pm 6.74	a	1.92 \pm 0.79	b	61.74 \pm 22.88	b
SSM	7.53 \pm 2.86	b	3.4 \pm 1.40	b	71.17 \pm 31.61	b
SPA	5.80 \pm 2.43	b	1.78 \pm 0.70	b	73.24 \pm 26.27	b

Plants in the SSM community had the highest ratio of aboveground to belowground biomass but the means were not significantly different from the SPM and the SPA communities (Table 2). Current year belowground biomass accounted for only 11% of all belowground mass in the SHM community. In the other communities, current year belowground biomass accounted for more than 60% of the total belowground biomass (Table 2). Shoot height was taller in the SSM community and shortest in the SPA community. SGA values were highest in the SSM community, but the means were not significantly different from values in the SPA and SHM communities (Table 2).

Rhizome morphology

About 80% of all ramets were SRR, in the SPM community while 28% were SRRs in the SPA community (Table 3). LRRs tended to branch more frequently than SRRs but the differences between the two types of ramets were only significant in the SHM and SPM communities. In the SPM community, SRRs and LRRs branched more frequently than ramets in the other three communities (Table 3). The LRRs lengths were greatest in the SSM community and shortest in the SHM community (Table 3).

Table 3. The number of total rhizome, the ratio of the SRR, mean of branching frequency and mean length of rhizome of Long Rhizome Ramet (LRR) and Short Rhizome Ramet (SRR). Values of branching frequency and length of rhizome (cm) are means (\pm SD). Different letters indicate significant differences between values ($P < 0.0083$) in one-way ANOVA. Significant levels are, *: $P < 0.001$ **: $p < 0.01$ ***: $p < 0.05$ ns: $p > 0.05$ significant tested by Fisher's Exact test between LRR and SRR. Different letters indicate significant differences between values ($P < 0.0083$) in one-way ANOVA, The symbols are differences between LRR and SRR, the characters are differences among habitat; small letters are differences among LRR and large letters are differences among SRR in different treatments.

community	type	Total number of rhizome	SRR ratio (%)	Branching number per ramet		Length of rhizome	
				1	2	1	2
SHM	LRR	206		1.11 \pm 0.31	a	3.91 \pm 1.84	a
	SRR	336	62.0 a	1.03 \pm 0.16	***	0.85 \pm 0.27	A
SPM	LRR	213		1.87 \pm 0.78	b	5.64 \pm 4.02	b
	SRR	804	79.1 b	1.46 \pm 0.64	*	0.82 \pm 0.27	A
SSM	LRR	103		1.44 \pm 0.74	c	9.62 \pm 6.96	c
	SRR	110	51.6 c	1.18 \pm 0.61	ns	0.80 \pm 0.26	A
SPA	LRR	182		1.27 \pm 0.5	ac	4.98 \pm 2.63	b
	SRR	70	27.8 d	1.11 \pm 0.32	ns	0.89 \pm 0.30	A

Table 4. Total ramet number, the proportion of ramets originated from a current-year ramet or an old-year ramets, the proportion of ramets originated from LRRs and SRRs, the number and proportion of ramets that stopped producing new ramets, the number of continued ramets, the number of daughter ramets types, and the proportion of daughter ramet numbers to continued ramets number in current year ramet (4a) and in old-year ramets (4b, except the age of originated ramets). Significant levels are, *: P<0.001 **: p<0.01 ***: p<0.05 ns: p> 0.05 tested by Fisher's Exact test between LRR and SRR. The symbols in column 1 are differences between LRR and SRR, the characters in column 2 are differences among habitat; small letters are differences among LRRs and large letters are differences among SRRs. The symbols in column 3 are differences between the old year rhizomes and the current year rhizomes. Different letters indicate significant differences between values (P<0.0083) in one-way ANOVA.

A

Community	type	total	age of the mother ramet (%)		type of the mother ramet (%)	of the mother ramet		1	2
			current	old		1 LRR	SRR		
SHM	LRR	186	76.1	23.9	A	76.2	23.8	a	
	SRR	330	31.5	68.5 *	A	26.2	73.8 *		A
SPM	LRR	150	83.6	16.4	A	62.9	37.1	b	
	SRR	795	81.3	18.7 ns	B	21	79 *		A
SSM	LRR	95	73.8	26.2	A	73.8	26.2	ab	
	SRR	109	61.8	38.2 ns	C	57.3	42.7 ***		B
SPA	LRR	155	84.6	15.4	A	88.5	11.5	c	
	SRR	68	55.7	44.3 *	C	61.4	38.6 *		B

Community	type	Continued ramet		1	Type of daughter ramet				1
		number	%		LRR	%	SRR	%	
SHM	LRR	131	70.4	a	120	83.9	23	16.1	a
	SRR	118	35.8 ***	A	36	30.3	83	69.7 ***	A
SPM	LRR	126	84	b	114	46.2	133	53.8	b
	SRR	412	51.8 ***	B	64	11.0	520	89.0 ***	B
SSM	LRR	75	78.9	ab	61	61.0	39	39.0	b
	SRR	38	34.9 ***	AB	15	34.1	29	65.9 **	A
SPA	LRR	115	74.2	ab	136	85.5	23	14.5	a
	SRR	27	39.7 ***	AB	18	52.9	16	47.1 ***	A

Table 4, continued

Community	type	total	type of the mother ramet (%)			continued ramet				
			LRR	SRR		No.	%			
SHM	LRR	609	74.0	26.0	a	ns	582	95.6	a	*
	SRR	1013	42.8	57.2 *		A *	734	72.5 ***	A	*
SPM	LRR	51	55.0	45.0	b	ns	51	100.0	a	**
	SRR	168	27.5	72.5 *		B ns	148	88.1 ***	A	*
SSM	LRR	60	83.6	16.4	ac	ns	42	70.0	b	ns
	SRR	75	60.5	39.5 **		B ns	46	61.3 ***	A	ns
SPA	LRR	78	90.9	9.1	c	ns	71	91.0	a	ns
	SRR	48	66.0	34.0 *		B ns	27	56.3 ***	B	ns

community	type	number of daughter LRR (%)						
		LRR	%	SRR	%	1	2	3
SHM	LRR	516	50.5	505	49.5	a		ns
	SRR	177	19.1	751	80.9 ***		A	ns
SPM	LRR	53	39.3	82	60.7	a		ns
	SRR	42	14.9	239	85.1 ***		AB	**
SSM	LRR	70	50.7	68	49.3	a		**
	SRR	23	32.4	48	67.6 ***		AC	ns
SPA	LRR	105	66.5	53	33.5	b		ns
	SRR	11	28.2	28	71.8 ***		A	ns

Rhizome connection

In each community, more than 70% of the current-year LRRs originated from current-year ramets. In contrast, 81% of the current-year SRRs originated from current-year ramets in the SPM communities while only 32 % of the current-year SRRs originated from current-year ramets in the SHM community (Table 4a).

Generally, in each community more than 60% of the current-year LRRs originated from LRRs (Table 4a). The SPA community was the only one in which current-year LRRs were significantly higher (88.5%) than in the other communities. More than 70% of the current-year SRRs originated from SRRs in the SHM and SPM communities, while less than 43% of these had the same origin in the SSM and SPA communities (Table 4a). LRRs and SRRs that were older than one year showed the same pattern as current year rhizomes. The only exception was in the SHM community where the SRRs that were older than one year originated from LRRs that were older than one year (Table 4a,b). More than 70% of the current-year LRRs produced new ramets, whereas less than 52% of the SRRs did (Table 4a). Almost 40% of the SRRs did not produce any new ramets during the following growing season in the SSM and the SPA communities. More than 90% of the LRRs ramets produced new ramets during the next growing season in the SHM, SPM and SPA communities compared to 70% in the SSM community (Table 4b). More than 70% of the SRRs that were more than a year old produced new ramets in the subsequent growing season in the SHM and SPM communities compared to 56% in the SPA community.

More than 80% of the daughter ramets of current-year LRRs were LRRs in the SHM and SPA communities, compared to 46% in the SPM community. Almost 90% of the

daughter ramets of the current-year SRRs were SRRs in the SPM communities, compared to less than 50% in the SPA community. In the SHM and SPA communities, older LRRs tended to produce more daughter SRRs than current-year LRRs did (Table 4a,b).

Shoot phenology

Plants in the three communities had similar shoot appearance patterns. Most shoots appeared in the spring and the least appeared in the autumn. There were, however, some differences in the proportion of shoot appearances in each phase (Fig. 2a).

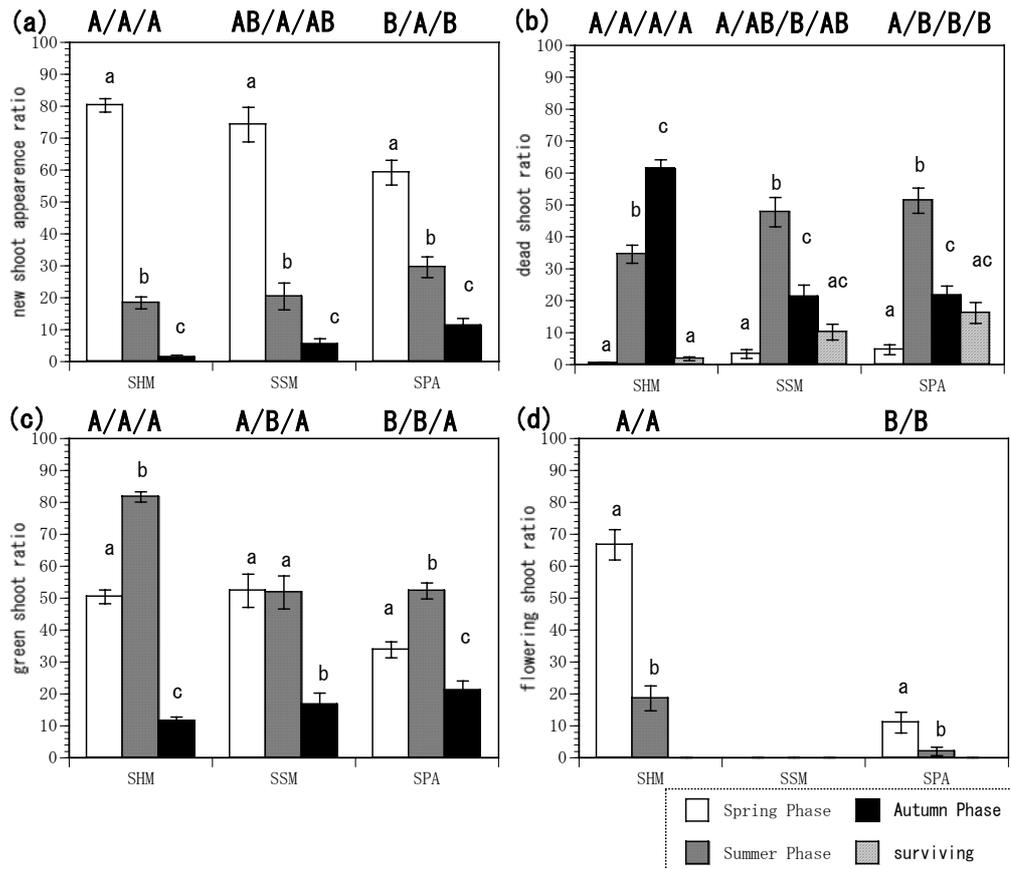


Figure 2. (a) The average new shoot appearance ratio (\pm SD), (b) the average dead shoot ratio (\pm SD), (c) the average green shoot ratio (\pm SD) and (d) the average flowering shoot ratio (\pm SD) of observation plots on each phase at three communities. Surviving means the green shoot ratio at the end of observation in (b). Different small letters above the bars indicate a significant difference between phases. Different capital letters above the graphs indicate a significant difference in phases between communities. Significance levels are $p < 0.0167$ in (a) and (c) $p < 0.0083$ among phase and $p < 0.0167$ among communities in (b) by Bonferroni-Dunn. test and $p < 0.05$ in (d) by t-test. The results and F-value of two-way-ANOVA were given in Table 7. SHM: Scirpus High marsh community, SSM: Scirpus Shaded marsh community, SPA: Spartina community.

Plants in the SHM community produced many shoots during the spring and summer phases and only produced about 1.4% of the total new shoot production in the autumn (Fig. 2a). In the SPA community, many new shoots appeared early in the growing

season, but the ratio was significantly less than in the SHM community. Shoot production continued, though at a lower level, until the end of the growing season. Plants in the SPA community produced about 11% of the shoots in the autumn phase, a value that was significantly higher than the shoot appearance ratio in the SHM community (Fig. 2a). Plants in the SSM community were intermediate between the SHM and SPA communities; plants produced many shoots during the spring and summer phases, and few in the autumn but there was no significant difference with both the SHM and SPA communities.

Patterns of shoot mortality differed among the three communities (Fig. 2b). In the SHM community, most shoots (on average 61% of all shoots) died in the autumn (Fig. 2b). On the other hand, in the SSM and the SPA communities shoots began to die earlier in the growing season and the largest number died in the summer phase (Fig. 2b). On average, 1.8% of the shoots in the SHM community, 13.5% of the shoots in the SSM community and 18.3 % of the shoots in the SPA community kept their shoots green until the last phenology observation was made (Fig. 2b). In the SHM community the green shoot ratio was 80% through the summer phase but it reached almost 0% at the end of the growing season (Fig. 2b, c). Plants in the SSM and the SPA communities kept lower green shoot ratios during the growing season and the number of live shoots gradually declined until the end of the growing season (Fig. 2b, c). Flowering shoots appeared mostly in the spring phase and few in the summer phase ($p < 0.001$ in the SHM and $p < 0.05$ in the SPA community). Plants in the SHM produced flowering shoots in a higher ratio: about 70% of shoots produced flowers compared to only 12% in the SPA community in the spring ($p < 0.001$, Fig. 2d).

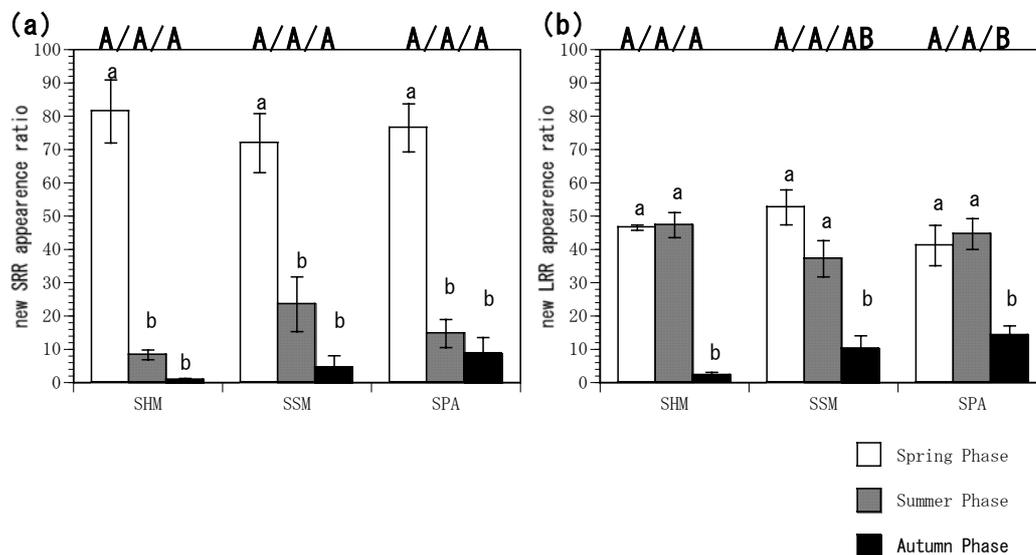


Figure 3. (a) The average new SRR appearance ratio (\pm SD) and the average new LRR (\pm SD) appearance ratio in observation plots in each phase in the three communities. Different small letters above the bars indicate a significant difference between phases. Different capital letters above the graphs indicate a significant difference in each phase between communities. Significance levels are $p < 0.0167$ by Bonferroni-Dunn Test. The results and F-value of two-way-ANOVA were given in Table 7. SHM: Scirpus High marsh community, SSM: Scirpus Shaded marsh community, SPA: Spartina community.

Rhizome phenology

In each community most SRRs appeared in the spring (Fig. 3a) while LRRs appeared mainly in the spring and summer. Plants in the SSM and SPA communities continued to produce LRRs in the autumn. In the SPA community, plants showed a significantly higher ratio of LRRs appearance; 14% of LRRs appeared in the autumn phase while 2% in the SHM community (Fig 3b). Shoots that originated from SRRs had a longer longevity than shoots from LRRs in the SHM and SPA communities (Table 5).

Table 5. Longevity (in days), mean length (in cm), mean weight (in g) and mean weight/length ratio of SRR and LRR from the 14 and the 28 observation days. Values are means (\pm SD). Different letters indicate significant differences among values ($p < 0.016$) in one-way ANOVA; small letters are differences among LRRs and large letters are differences among SRRs. Longevity are means (\pm SD) and tested by t-test. Significant levels are, *: $P < 0.001$ **: $p < 0.01$ ***: $p < 0.05$ ns: $p > 0.05$ significant tested by Fisher's Exact test between LRR and SRR.

community	type	number of total rhizome	Longevity	rhizome weight	weight/length
SHM	LRR	24	113.2 \pm 25.4 ***	0.179 \pm 0.076 a	0.08 \pm 0.037 a
	SRR	205	126.9 \pm 28.5	0.093 \pm 0.066 A	0.111 \pm 0.069 A
SSM	LRR	12	115.5 \pm 44.7 ns	0.221 \pm 0.205 a	0.027 \pm 0.015 b
	SRR	21	116 \pm 46.9	0.11 \pm 0.106 A	0.147 \pm 0.082 A
SPA	LRR	19	71.5 \pm 27.2 ***	0.187 \pm 0.108 a	0.059 \pm 0.035 a
	SRR	21	102 \pm 36.6	0.127 \pm 0.090 A	0.147 \pm 0.082 A

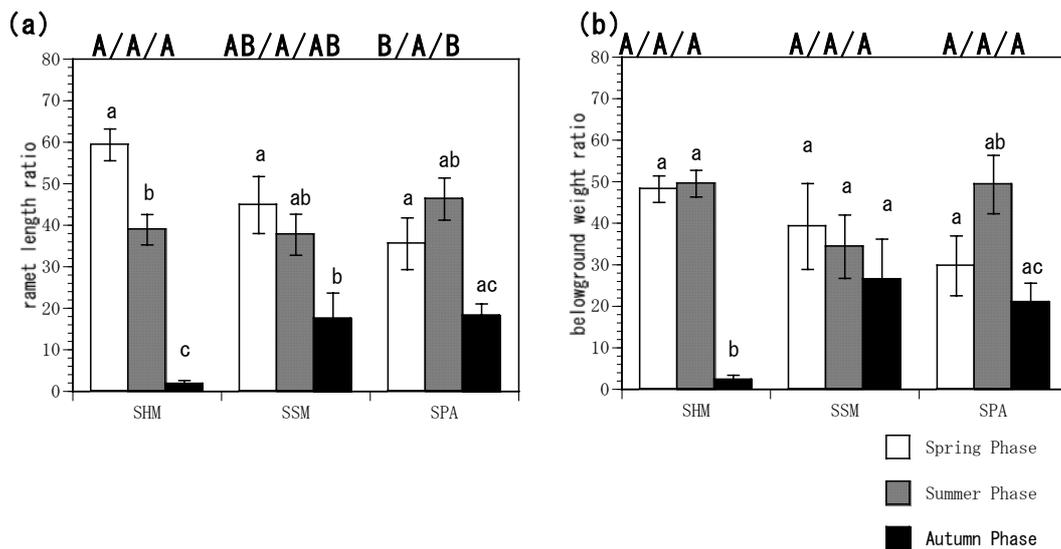


Figure 4. (a) The average total belowground ramet length ratio (\pm SD) and (b) the average total belowground ramet weight ratio (\pm SD) in observation plots in each phase in the three communities. Different small letters above the bars indicate a significant difference among phases. Different capital letters above the graphs indicate a significant difference per phase among communities. Significance levels are $p < 0.0167$ by Bonferroni-Dunn. The results and F-value of two-way-ANOVA were given in table 7. SHM: Scirpus High marsh community, SSM: Scirpus Shaded marsh community, SPA: Spartina community.

There was no difference among the three communities in the SRR weight/length ratio and plants in the SSM community had significantly lower LRR weight/length ratios (Table 5). Based on total belowground ramet length and weight ratio, the SHM community produced most of the belowground ramet growth in the spring and summer (Fig 4a, 4b). In the SSM and the SPA communities, plants continued to produce about constant amounts of belowground material, both in rhizome length and biomass, right into the autumn (Fig. 4a, 4b). Fig. 5 shows the total weight of SRRs (a), LRRs (b) and the sum of SRRs and LRRs (c) at each observation day. In the SHM community, plants showed two peaks (Fig. 5c). The first peak was on 14th and 28th observation days due to SRRs (Fig. 5a), and the second was on 70th and 84th days due to LRRs (Fig. 5b).

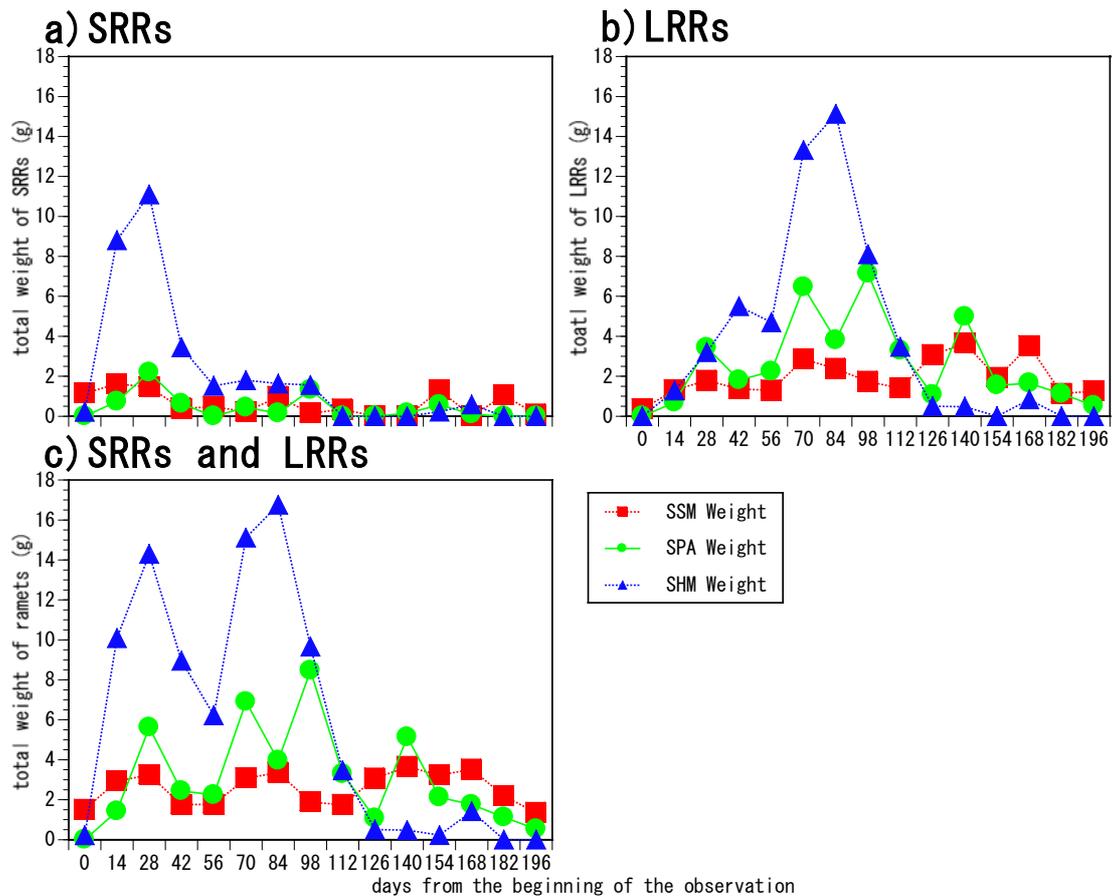


Figure 5. The total amount of SRR weight (a), LRR weight (b) and whole ramet (c) of all observation plots in each observation day in the three communities. SSM: Scirpus Shaded marsh community (■), SPA: Spartina community (●), SHM: Scirpus High marsh community (▲).

Table 6. Mean number of ramets, mean shoot height (cm), mean of total biomass (g) and shoot to root ratio in the garden experiment. Values are means (\pm SD). Different letters indicate significant differences between values ($P < 0.005$) in one-way ANOVA.

treatment	ramet number	shoot height	total biomass	S/R ratio
NOR	7 44.86 \pm 7.11 a	53.33 \pm 13.36 a	9.86 \pm 1.80 a	0.84 \pm 0.11 a
PON	7 27.29 \pm 11.00 b	34.11 \pm 8.98 b	3.55 \pm 1.32 b	0.41 \pm 0.02 b
S10	7 52.00 \pm 16.61 a	45.13 \pm 16.15 ac	11.17 \pm 2.86 a	0.63 \pm 0.10 c
S20	7 25.71 \pm 9.38 b	42.24 \pm 11.58 bc	2.90 \pm 1.67 b	0.44 \pm 0.11 bc
SHD	7 21.29 \pm 5.88 b	70.76 \pm 20.33 d	2.95 \pm 1.21 b	1.07 \pm 0.20 d

Table 7. Total ramet number, the ratio of the SRR, the proportion of ramets originated from LRRs and SRRs, the proportion of ramets that stopped or continued producing new ramets, the number of daughter ramets, and the proportion of daughter ramet types, mean of branching number per ramet and mean length of ramets. Values are means (\pm SD) for branching number per ramet and length of ramets. Significant levels are, *: $P < 0.001$ **: $p < 0.01$ ***: $p < 0.05$ ns: $p > 0.05$ tested by Fisher's Exact test between LRR and SRR. Different letters indicate significant differences between values ($P < 0.005$) in one-way ANOVA; , The symbols in column 1 are differences between LRR and SRR, the characters in column 2 are differences among habitat; small letters are differences among LRR and large letters are differences among SRR in different treatments.

treatment	type	total	SRR ratio (%)	type of mother ramet (%)		continued ramet	
				LRR	SRR	number	%
NOR	LRR	159		70.4	29.6	129	81.1
	SRR	156	49.5 a	63.3	36.7 ns	71	45.5 ***
PON	LRR	129		76.2	23.8	99	76.7
	SRR	61	32.1 b	64.9	35.1 ns	43	70.5 ns
S10	LRR	142		70.7	29.3	121	85.2
	SRR	175	55.2 ac	53.3	46.7 **	86	49.1 ***
S20	LRR	109		75.7	24.3	84	77.1
	SRR	71	39.4 ad	63.6	36.4 ns	45	63.4 ns
SHD	LRR	92		68.1	31.9	81	88
	SRR	58	38.7 ad	71.2	28.8 ns	37	63.8 **

treatment	type	type of daughter ramet				branching number per ramet	length of ramet
		LRR	%	SRR	%		
NOR	LRR	112	54.1	95	45.9	1.55 \pm 0.67	3.79 \pm 1.56
	SRR	47	46.1	55	53.9 ns	1.43 \pm 0.60	0.67 \pm 0.38
PON	LRR	96	72.2	37	27.8	1.28 \pm 0.50	3.62 \pm 1.23
	SRR	30	60	20	40.0 ns	1.14 \pm 0.35	0.72 \pm 0.40
S10	LRR	99	52.4	90	47.6	1.53 \pm 0.65	3.83 \pm 1.34
	SRR	41	34.2	79	65.8 **	1.39 \pm 0.59	0.74 \pm 0.35
S20	LRR	81	65.9	42	34.1	1.44 \pm 0.57	4.14 \pm 1.78
	SRR	26	52	24	48.0 ns	1.04 \pm 0.29	0.70 \pm 0.35
SHD	LRR	62	62.6	37	37.4	1.21 \pm 0.41	3.86 \pm 1.49
	SRR	29	65.9	15	34.1 ns	1.08 \pm 0.27	0.79 \pm 0.35

Results from the garden experiment

The number and biomass of ramets in the NOR and S10 treatments were significantly higher (Table 6). Plants in the SHD treatment also had the highest aboveground/belowground biomass ratio in all treatments produced the tallest shoots (Table 6).

The SRR ratio was highest in the S10 and significantly lower in the PON treatment (Table 7). Generally, both LRRs and SRRs originated from LRRs in most treatments (Table 7). More than 75% of the LRRs kept producing new ramets in each experiment. On the other hand there was more variability in the production of SRRs. Less than 50% of the SRRs produced new ramets in the NOR and S10 treatments, while more than 70% produced new ramets in the PON treatment (Table 7). LRRs tended to produce more LRRs than SRRs in all treatments and the average ranged from 72% in the PON treatment to less than 55% in the NOR and S10 treatments (Table 7). Sixty-six percent of the daughter ramets of SRRs were SRR in the S10 treatment, compared to less than 40% in the PON and SHD treatments (Table 7).

In the NOR, PON, S10 and SHD treatments, the number of branches per ramet did not differ among treatments. In the S20 treatment, however, the LRRs branched more frequent than SRRs. Among communities, the number of branches per ramet was significantly different and LRRs and SRRs in the NOR and S10 treatments branched more often than LRRs and SRRs in the PON and SHD. There were no differences in mean length of the LRRs among communities.

6) Discussion

Architecture

Scirpus olneyi produces two types of ramets, LRRs and SRRs, and shows variable clonal architectures within the four habitats and five treatments examined in this study. In the garden experiment, since every treatment started at the same time, the differences in biomass and the number of ramets among treatments is a response to differing habitat qualities. Results of the garden experiment indicate that biomass and the number of ramets are greatest when plants are growing in high light conditions at intermediate salinities (e.g., 10 ‰). Plant performance was lower in higher interstitial salinities, lower light levels and lower nutrient levels. Plants growing in better quality treatments also had higher SRR ratios (Table 7). The frequency of branching was also higher for plants grown in higher light, intermediate salinities, and higher nutrient levels. In the garden experiment (Table 7) we also found differences in branching patterns for the two rhizome types. LRRs tended to branch more frequently than SRRs and most of the new rhizome segments produced by the LRRs during the growing season were LRRs. LRRs in better quality treatments (i.e., high light, intermediate salinities, and higher nutrient levels) produced more SRRs than in poor quality treatments. SRRs in high quality treatments tended to propagate SRRs or stop producing new ramets while SRRs in poor quality treatments tended to propagate new LRRs. The garden experiment indicates that *Scirpus olneyi* has higher SRR ratios in the better quality habitats. And this suggests that *S. olneyi* forages in these patches or consolidates its occupancy of three patches. It has been demonstrated that some clonal plants change the length of spacers and

branching frequency in response to varying environmental conditions (De Kroon and Knops 1990, De Kroon and Hutchings 1995). The length of spacers strongly relates to the foraging behavior of plant species. Dong and de Kroon (1994) found that *Cynodon dactylon* produced shorter rhizomes under higher light conditions. Slade and Hutchings (1987) showed similar results with *Glechoma hederacea*, and similar results have been shown by others (de Kroon and Knops, 1990; Dong, 1996; Harper, 1985; Hutchings and de Kroon, 1994; Lovett Doust, 1981). These studies suggest that the production of shorter spacer ramets allows plants to occupy better quality patches while producing longer spacer allows plants to escape lower quality patches (de Kroon and Hutchings, 1995; de Kroon and Knops, 1990; Dong and de Kroon, 1994). Ramets also increase branching frequency in higher quality patches and decrease branching frequency in lower quality patches (de Kroon and Hutchings, 1995). Our experiments clearly demonstrated that, *S. olneyi* changes its clonal architecture with changing branching frequency and the ratio of SRR in response to differences in the quality of habitats. The results support the notion that individual ramets are functionally specialized to perform different tasks. *S. olneyi* produces SRRs as a mechanism to consolidate occupancy and exploit favorable habitats while also having the ability to produce LRRs to explore new and possibly other high-quality habitats.

In the field, plants showed a variety of growth patterns. Plants in the SHM community had the highest biomass, higher SRR ratios but branched less frequently. Plants in the SPM community had higher biomass and SRR ratios and a higher branching frequency. Most of the biomass was in older ramets in the SHM community and in current-year ramets in the SPM community. Based on the higher production rate of current-year ramets, we speculate that the SPM community had the best growing conditions for *S. olneyi*. These results collectively support the conclusion within the marsh habitat that *S. olneyi* exploits local conditions by producing variable numbers of LRRs and SRRs. Further studies will be required to quantify the relationships between patterns of ramet production and the spatial variability of resource conditions in the marsh.

Phenology

Our hypothesis regarding phenological differences in the production of LRRs and SRRs was confirmed. In the field, SRRs and LRRs showed different phenologies in the three communities (Fig. 3). SRRs appeared mainly in the spring and the LRRs appeared in the spring and summer. Producing SRRs at the very beginning of the growing season seems a strategy that allows individuals to increase their density in sites where plants already occupied the patches during the previous growing season, and subsequently increase their ability to exploit local resources. On the other hand, producing LRRs throughout the growing season is a useful strategy for exploring new sites.

The number of new ramets that appeared in the autumn in the SSM and SPA communities was low compared to the spring and summer. In terms of total weight and length, however, rhizomes produced in the autumn did not differ significantly from ramets produced in the spring and summer (Fig. 4a, b). We interpret this result to mean that *Scirpus olneyi* in the SSM and SPA communities continue to explore new localities throughout the growing season with fewer but heavier ramets and with longer internodes. In contrast, plants in the SHM community cease producing new ramets after the early growing season and do not explore new localities intensively, but exploit the

local habitat by producing many SRRs at the beginning of the growing season (Fig. 4a, b). The SHM community also had the highest proportion of long-lived shoots from SRRs produced early in the growing season, while the SPA community has the highest proportion of short-lived shoots from LRRs produced throughout the growing season. This suggests that the ramets in the SHM community occupy sites rapidly and exploit local resources throughout the growing season, while plants in the SPA community explore their habitat gradually throughout the growing season.

Two contrasting strategies related to foraging are suggested by our results. In the SHM community, the plants clearly show two peaks of ramet production (Fig. 5c). The first peak is due to SRR production (Fig. 5a) and the second peak is due to the production of LRRs (Fig. 5b). The other two communities also show small peaks with an intervening low period of ramet production. This result implies that the plants may benefit from the production of a large number of SRRs early in the growing season by using resources stored over winter. A high shoot density may result in increased photosynthetic gains of the genet: using that the plants produce LRRs that may reach higher quality habitats and thus increasing resource capture.

The interplay of these strategies may explain the patterns of ramet production that we found in the three communities. Plants in the SHM community, where plant density is high, the substrate density is high and where there are few areas not occupied by existing vegetation, the dominant strategy is the production of SRRs, and the plants store carbohydrates in old ramets which results in larger old ramets' biomass. In the two communities (SSM and SPA) where resources appear to be more variable, individuals produce relatively more LRRs. In the SSM community, light is limiting due to overhanging tree crowns and LRRs seem to facilitate escape to better-lit patches nearby. In the SPA community, *S. patens* is the dominant species and by mid-summer, its dense, flattened canopy captures most the light. But *S. patens* has a more shallow root system than *S. olneyi* and *S. olneyi* therefore is able to invade the SPA community by sending LRRs beneath the root system of *S. patens*. Once the shoots of *S. olneyi* break through the dense *S. patens* canopy, they have access to full sunlight and the resources of the site can be exploited. In that stage, *S. olneyi* starts to produce SRRs.

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Chapter 4:

*Density effects on Seed and Vegetative Propagation of *Scirpus olneyi* A. Gray*

IKEGAMI Makihiko, Dennis F. WHIGHAM and Marinus J.A. WERGER

Summary

It is believed that the balance between seed and vegetative propagation is affected by inter- and intra-specific competition. Some studies suggested that seed production is positively correlated, but others suggested that it is negatively correlated with plant density. Since density may correlate with other factors such as nutrient availability, it is difficult to evaluate the effects of varying density on resource allocation. Plant density can also affect the belowground architecture of clonal plants. If density is high, plants may produce longer internodes (spacers) between ramets allowing new ramets to occupy spaces that are more distant from parent plants. At low density, plants may produce short spacers resulting in a consolidation of plant biomass in areas immediately adjacent to parent plants. At the same time, density in clonal plants can also be affected by clonal architectures. The production of short internodes between parents and ramets results in high shoot density while the production of longer internodes results in lower shoot density. To further evaluate density effects on the sexual and vegetative propagation strategy of clonal plants, we conducted field observations and a garden experiment with the clonal species *Scirpus olneyi*. Field observations and garden experiment clearly showed that sexual propagation was positively correlated with plant density. As shoot density increased the ratio of flowering shoot to all shoots and the number of inflorescences increased. At the same time, plants produced taller shoots at higher density. We also found that plants tended to produce shorter internodes at higher density. If resources are patchily distributed, patches with more resources should have a larger number of individuals and also a higher production of seeds in contrast to patches with lower resources. In our garden experiment, the soil resources per ramet in the tubs were equally spread and thus the available resources per ramet in tubs with high shoot densities were much less than in tubs with low shoot densities. This result suggests that plant density affected the propagation strategy of *S. olneyi* more than nutrient availability. *S. olneyi* produced proportionally more long internodes at lower ramet density and more short internodes at higher ramet density. This result suggests that plants at high density produce SRRs to consolidate in patches which the mother ramet occupied while plants at low density produce LRRs to explore and occupy new localities. As ramet density increases, *S. olneyi* shifted its propagation strategy from exploring with LRRs to exploiting with SRRs and producing more sexual shoots.

Keywords: clonal plant, density, propagation strategy, ramet architecture, *Scirpus olneyi*

1) Introduction

Clonal plants can spread by seed and vegetative propagation. Seeds can be dispersed over large distances whereas vegetative propagules can not because vegetative propagation almost always results in the production of ramets near parent plants. Seed propagation often results in the establishment of many new individuals that have a relatively high mortality while vegetative propagation produces offspring that are larger than seedlings and have a lower mortality because mother ramets provide daughter ramets with carbohydrates, water and nutrients. Plants that primarily propagate vegetatively are often associated with resource-poor environments as vegetative propagules are better able to survive harsher environments than seedlings (Callaghan, 1988; Raven *et al.*, 1981).

According to Abrahamson (1980), the balance between seed and vegetative propagation is affected by inter- and intraspecific competition. 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). Abrahamson theorized that vegetative propagation would be advantageous at low plant density as it facilitates local spread and occupation while seed propagation is advantageous at high plant density as it enables dispersal to new and perhaps more favorable sites (Abrahamson, 1980).

However, plant density also affects 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). A number of mechanisms such as the production of dormant buds (Makita, 1996) and physiological integration between ramets (Hutchings, 1979; Pitelka, 1984) allows clonal plants to avoid intraspecific, or within genet competition. Plant density in clonal plants is also affected by clonal architecture (Chapter 3) but it has hardly been studied in a quantitative way.

In clonal plant species, which grow in a wide range of habitats, plasticity in clonal architecture may be an adaptive trait (de Kroon and Knops, 1990; Dong, 1996; Hutchings and de Kroon, 1994; Schmid, 1992; Slade and Hutchings, 1987a). Clonal plants may locally change the architectural elements of their morphology (*e.g.*, shorten or lengthen their spacers) and persist in sites with high resource conditions or emigrate from one resource state to explore adjacent environments (de Kroon and Knops, 1990; Dong, 1996; Hutchings and Wijesinghe, 1997; Slade and Hutchings, 1987a). Plasticity of clonal architecture may thus benefit clonal plants and can be adaptive in an evolutionary context.

Plant density is typically low when a plant first colonizes a site but density can increase significantly through vegetative propagation. As plant density increases, intraspecific competition for local resources increases and plants may make morphological adjustments. For example, if plasticity in the production of spacers or branching frequency may be beneficial, plants can make longer spacers to escape from crowded patches or to explore new habitats. Plants can also reduce branching and make shorter spacers to consolidate ramets in a patch or avoid competition. In a previous study (Chapter 3), we showed that the clonal plant *Scirpus olneyi* had different clonal architectures in different plant communities by changing the proportion and connection

patterns of two different types of ramets: ramets with long rhizomes (LRRs, Fig. 1a) and ramets with very short rhizomes (SRRs, Fig. 1b). In a garden experiment (Chapter 3), at a low level of nutrient supply, plants produced 31% SRRs and 69% LRRs whereas at the highest level of nutrient supply these values were 49% and 51% respectively. The differences based on responses to nutrient supply suggest that plants tend to produce SRRs to occupy resource rich patches and LRRs to explore other patches.

a) Long Rhizome Ramets



b) Short Rhizome Ramet



Figure 5. The clonal architecture of *Scirpus olneyi*. (a) Long Rhizome Ramets (LRR) and (b) Short Rhizome Ramets (SRR).

In addition, plant density is also affected by ramet architecture. Repeated production of SRRs can cause a higher plant density, while LRRs may not. Thus, if a clonal plant can control its ramet density through changing the architectural elements of their morphology (*e.g.*, length of spacers, branching frequency), 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 and Wijesinghe, 1997; Slade and Hutchings, 1987b). The control of density through changing ramet architecture has hardly been studied in a quantitative way but it is important to understand the impacts of varying foraging strategies of plants and ramet specialization.

Based on our previous studies, we hypothesize that plants would branch more frequently and produce more SRRs at low density and branch less frequently and produce more LRRs in high density patches. Based on Abrahamson (1980) we would also predict that seed production would be greatest in habitats where shoot densities were high.

In this paper we evaluate the effects of density on the propagation strategy of *Scirpus olneyi* through field observations and a garden experiment. In the field, we established line transects and measured the density of vegetative and sexual shoots. We also excavated individuals from patches with different shoot densities to characterize the belowground clonal architecture. For the garden experiment, we first collected plants from the field at sites where the density of *S. olneyi* varied. After one year of propagating the field harvested plants, we harvested the plants and then replanted rhizomes at different densities. After one year, we harvested the plants and measured belowground architecture and sexual reproduction effects as inflorescence production.

2) Material and method

Species description

Scirpus olneyi A. Gray, a member of the Cyperaceae, occurs in different plant communities on temporally flooded sites in gradients from brackish to fresh water along the East Coast of the USA (Drake, 1992; McCormick and Somes, 1982). In this study, we define the aboveground parts of a ramet as a shoot. The shoot is annual, erect, sharply triangular, needlelike, and has only rudimentary leaves. The belowground parts of a ramet consist of roots and a tuber. Individuals produce ramets that are attached to the parent plant by a long (LRR) or short (SRR) rhizome (Fig. 1). LRR rhizomes are typically 10-20 cm long. SRR rhizomes are typically too short to be measured.

Field Habitats

Field sampling of *S. olneyi* was conducted in three tidal marshes at the Smithsonian Environmental Research Center (SERC) in Maryland, USA. *S. olneyi* occurs in 4 different plant communities at SERC (see Chapter 2). In this paper, we studied *S. olneyi* in the *Scirpus* High marsh community (Drake, 1992; McCormick and Somes, 1982) where it is a dominant species along with *Spartina patens* and *Distichlis spicata*. In this community, light availability drastically declines from the top of the canopy to the litter surface, due mostly to the high density of shoots. The accumulation of *S. patens* and/or *D. spicata* roots and rhizomes results in a hard, compact substrate in the *Scirpus* High marsh community. Interstitial water is brackish with salinity averaging around 14‰ during the growing season. Shoot density varies within the *Scirpus* High marsh community, in particular, in the area where the *Scirpus* High marsh community ends and other communities begin, shoot density tends to be low, and in the interior of the *Scirpus* High marsh community, shoot density tend to be high.

Field Sampling

In July 2001, we established 51 plots along three 48m line transects in three wetland areas at SERC, locally known as Kirkpatrick Marsh, Corn Island Marsh and Hog Island Marsh. At 3m intervals, we established 50 X 50cm census plots. If a sampling plot fell in an area that had obvious signs of disturbance (e.g., muskrat burrowing) or if no vegetation was present, the census plot was moved to a randomly chosen area within a radius of 1m of the original point.

In each plot the number of flowering and non-flowering shoots was counted and every inflorescence was harvested. We then harvested all above ground *Scirpus olneyi* shoots in every plot. We randomly chose 6 mature shoots from each plot and measured height. We measured the biomass of the harvested material (shoots and inflorescences) after 72 hours drying at 68°C.

To characterize clonal architectures at different shoot densities, we excavated 12 samples in December 2001. In each of the three line transects, we randomly chose two plots from the subset of plots that had the 5 highest shoot densities. We also sampled two plots from the subset of the 5 plots that had the lowest shoot densities. We excavated a 25 X 25 X 20 cm sample from the center of each 50 X 50 cm plot. The samples were returned to the

laboratory where they were washed to remove loose organic matter and sediment. The entire rhizome system, including tubers, rhizomes and roots was extracted. Each rhizome segment, consisting of a rhizome and a node, was placed into one of two categories, LRR or SRR. We counted the number of LRR and SRR in each sample and calculated the ratio of SRR segments to all ramets. We also randomly selected 12 undamaged LRR and SRR to quantify belowground ramet length, and the number of branches per node. The length of a ramet was measured from their point of attachment to the parent tuber to the end of the tuber. After all measurements were made, we separated the rhizome segments into 3 categories: current year's rhizomes, living rhizomes older than 1 year, dead rhizomes. Biomass for each of the 3 categories was determined by drying samples for 72 hours at 68°C and weighing each one separately.

Greenhouse Experiment

In 1999, we collected rhizome segments (rhizomes and nodes) from the three SERC wetlands that were used for the field study. The plants were propagated clonally in a greenhouse in the Uithof Botanical Gardens at Utrecht University, the Netherlands. The samples that were collected were propagated together so the samples used in the experiments described below were of unknown genetic ancestry.

In March 2001, we randomly selected clonal fragments, consisting of 1 to 3 ramets, and randomly assigned them across 2 treatments. We used flat plastic tubs (43 X 40 X 6 cm) and planted one clonal fragment at the center of tubs to simulate a low density treatment and 15 clonal fragments were planted within a radius of 10 cm of the center of tubs to simulate a high density treatment. There were 10 replicates of the low density treatments and 7 replicates of the high density treatment at the beginning of the experiment. Because of poor growth, one tub was excluded from data analysis for each of the treatments. The soil mixture in each tub consisted of peat and sand at 3:1. As a N-base we added 25 kg/ha OSMOCOTE at the beginning of the experiment and in May 2002. We used the same procedures described above for the field study to characterize belowground clonal architecture.

Data Analysis

In this study, we used two measurements of density: Shoot density is defined as the shoot number per square m (Shoot No./m²) and ramet density is the number of ramets per cubic m (Ramet No./m³).

We used the ratio of flowering shoots to all shoots and the ratio of inflorescence mass to total shoot mass sampling area (field study) and tub (greenhouse study) to evaluate seed propagation efforts. We used the ratio of SRRs to all ramets, the number of branches per ramet and the mean length of LRRs to evaluate the clonal architecture.

For the field data, we used standard bivariate regression analysis on mean shoot height, the ratio of flowering shoots to all shoots and the ratio of inflorescence mass to total shoot mass against shoot density. We also used regression analysis on the ratio of SRRs to all ramets, mean length of LRRs, the ratio of current year belowground biomass to all belowground biomass and the number of branches per ramet against ramet density. We used quadratic regression analysis for shoot density and mean height of shoots and for

ramet density and mean length of LRRs, and linear regression analysis for the rest. For the garden experiment data, we used the t-test to compare shoot density, height of shoot, the ratio of flowering shoots to all shoots, the ratio of inflorescent mass to shoot mass, the ratio of SRRs to all ramets and the ratio of current year belowground biomass to all belowground biomass between high and low density treatments. Because of skewed distribution in data of the number of branches per ramet, we also used Mann-Whitney U-test for the number of branches per ramet between two treatments.

3) Results

Shoot and density

Shoot density varied along the transect in each of the marshes and, on average, density was twice as high at the Corn Island site compared to the other marshes (Fig. 2). The ratio of flowering shoots to all shoots also varied along each transect (Fig. 2).

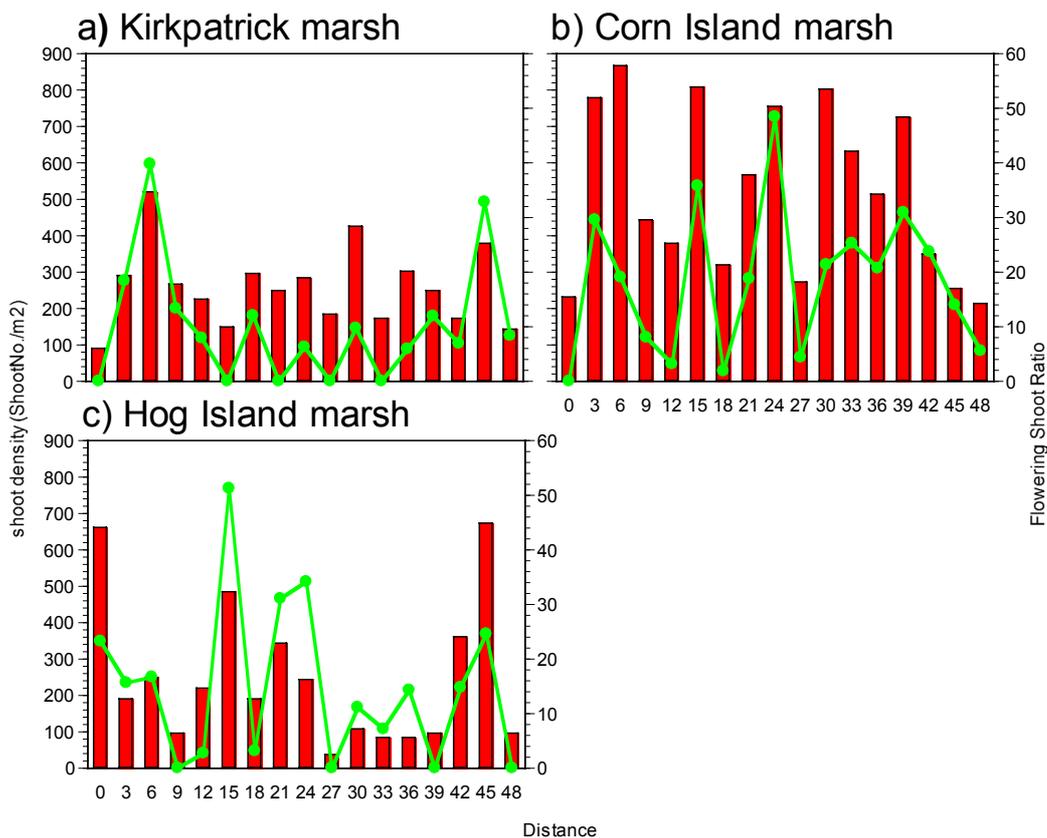


Figure 2. Spatial distribution of flowering ratio (lines) and density of current year shoot (bars) for 0.5m x 0.5m plots in a transect across the *Scirpus olneyi* high marsh community in three different marshes. a) Kirkpatrick marsh, b) Corn Island marsh and c) Hog Island marsh. X-axes plot positions along 48 m long transects. Left y-axes plots Shoot No./m² and right y-axes plots flowering shoot ratio.

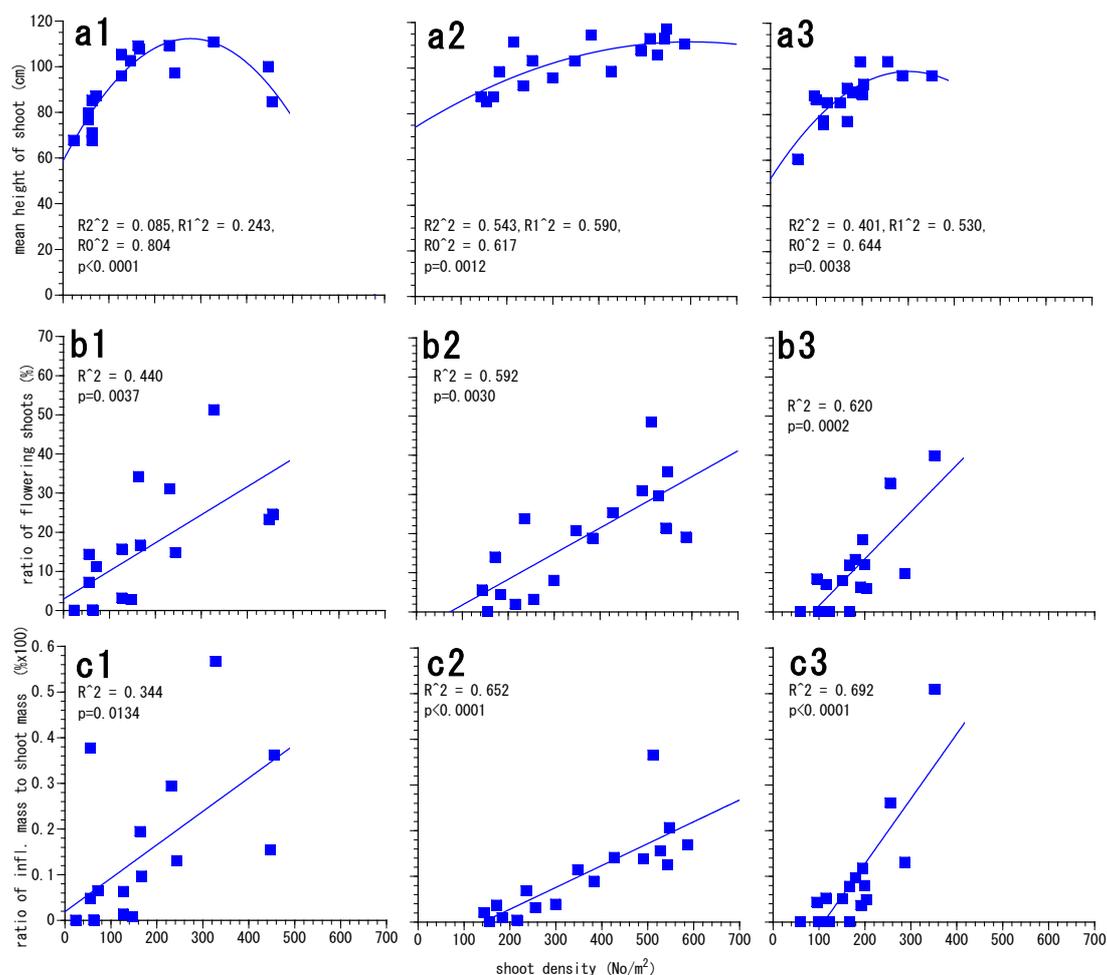


Figure 3. Relationships between shoot density and (a) mean height of shoot, (b) the ratio of flowering shoots to all shoots, and (c) the ratio of inflorescence mass to shoot mass for three *Scirpus olneyi* habitats on three different marshes. (1) Hog Island marsh, (2) Corn Island marsh and (3) Hog Island marsh. Quadratic regression analysis for mean height of shoot, and linear regression analysis for the ratio of flowering shoots and the ratio of inflorescence mass to shoot mass are given.

In the field plots, shoot height and shoot density were positively related to each other (Fig. 3a1-3) but in the Kirkpatrick and Hog Island marshes, shoot height decreased at the highest shoot densities. In the garden experiment, two treatments showed clear differences in shoot density at the end of the experiment (Fig. 4a) and plants in the high density treatments produced taller shoots ($p < 0.05$, Fig. 4b).

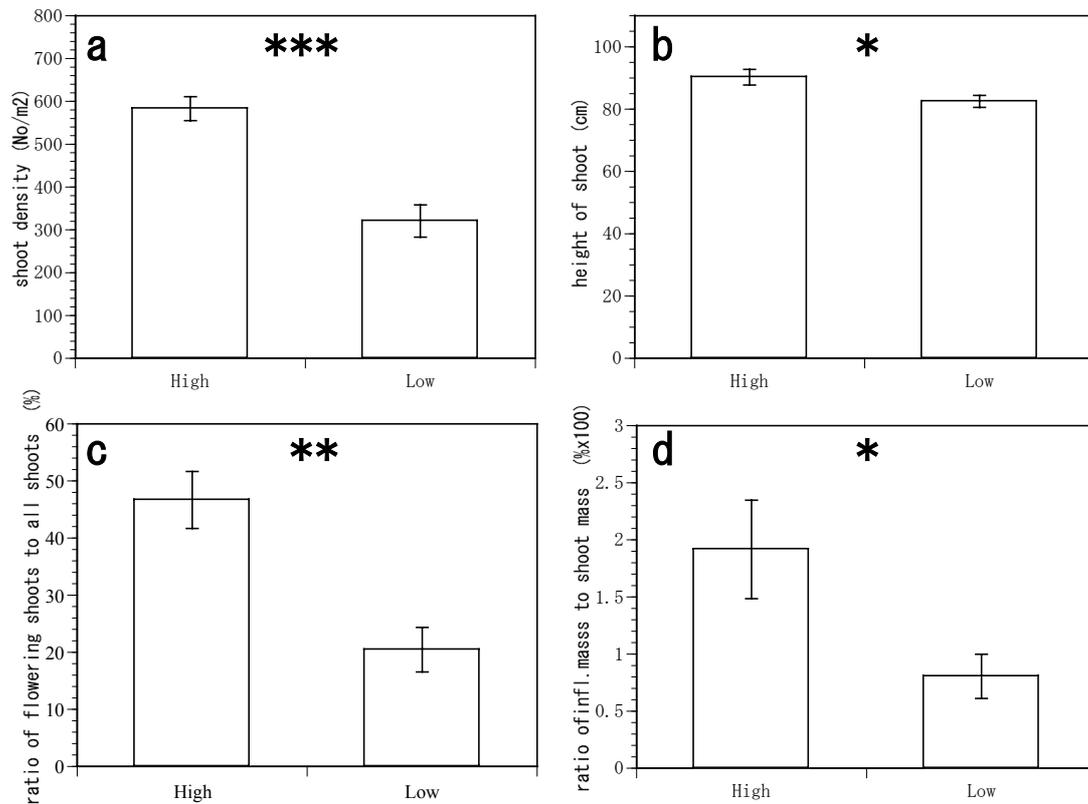


Figure 4. (a) shoot density at the harvest (mean \pm SE), (b) the height of shoots (mean \pm SE) (c) the ratio of flowering shoots to all shoots (mean \pm SE) and (d) the ratio of inflorescent mass to shoot biomass (mean \pm SE), in High and Low density treatments for the garden experiment. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns not significant.

Seed propagation and density

In the field study, the ratio of flowering shoots to all shoots increased as shoot density increased (Fig. 3b1-3). The ratio of inflorescence mass to shoot mass also increased as shoot density increased (Fig. 3c1-3). In the garden experiment, plants in the high density treatments showed the higher ratio of flowering shoots to all shoots and the higher ratio of inflorescence mass to total current shoot mass, than plants in the low density treatments (Fig. 4c, 4d). Inflorescence production was 5 times higher in the garden experiment (Fig. 3c1-3,4d).

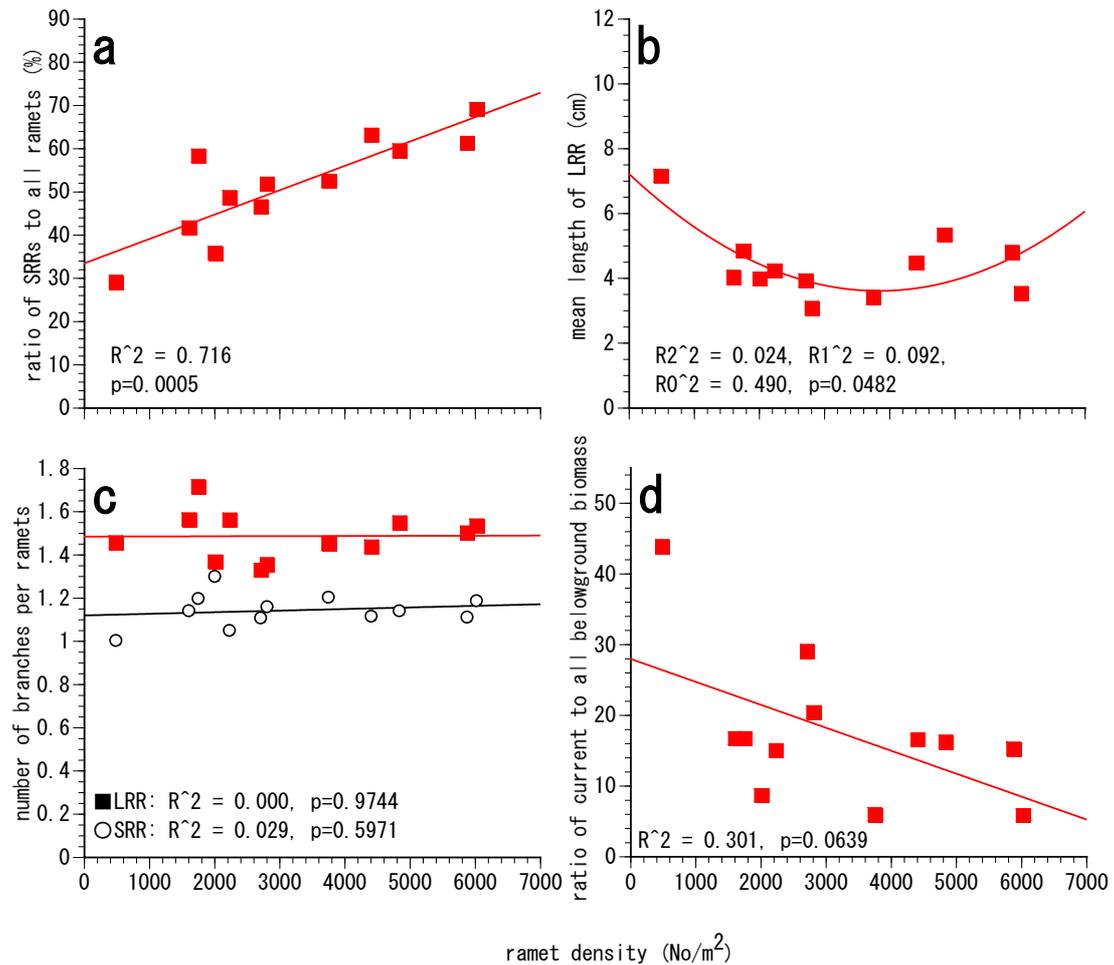


Figure 5. (a) ramet density at the beginning of the garden experiment (mean \pm SE), (b) ramet density at the harvest (mean \pm SE), (c) dry weight of total biomass (mean \pm SE), and (d) ratio of current-year to older-than-one-year belowground biomass (mean \pm SE) in High and Low density treatments for the garden experiment. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns not significant.

Biomass

In the garden experiment, plants in the low density treatments showed a higher growth rate both in ramet density and in weight than plants in the high density treatment (Fig. 5a-c). This resulted in higher ratio of current year belowground biomass to all belowground biomass in the low density treatments, however, this difference was not statistically significant ($p = 0.0502$, Fig. 5d). In the field, plants showed the same tendency, between the two parameters but there was not a statistically significant difference (Fig. 6d).

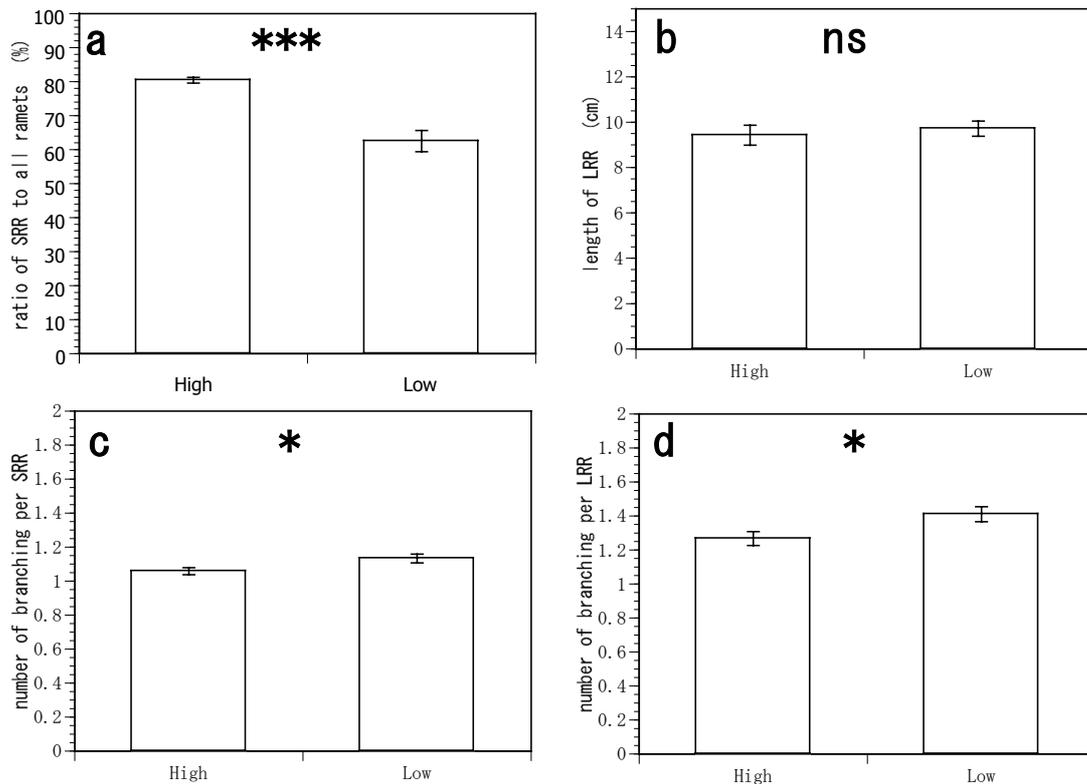


Figure 6. Relationships between ramet density and (a) the ratio of SRRs to all ramets, (b) mean length of LRRs, (c) the number of branches per LRR and SRR and (d) the ratio of current-year belowground biomass to all belowground biomass for the field. ○ represents SRR and ■ represents LRR in fig 5c.

Vegetative propagation and density

There were clear positive relationships between ramet density and the SRR ratio; as ramet density increased the ratio of SRRs to all ramets increased (Fig. 6a, 7a). Generally, plants produced higher SRR ratios in the garden experiment. In the field, the mean length of LRRs was shortest at lower ramet densities but increased at higher ramet densities (Fig. 6b, $p < 0.05$). On the other hand, in the garden experiment, the mean length of the LRRs was not different (Fig. 7b, $p = 0.6238$). There was no relationship between ramet density and the number of branches per ramet in the field (Fig. 6c). In the garden experiment, however, plants in the low density treatments tended to have more branches than plants in the high density treatments ($p < 0.05$, Fig. 4c, 4d).

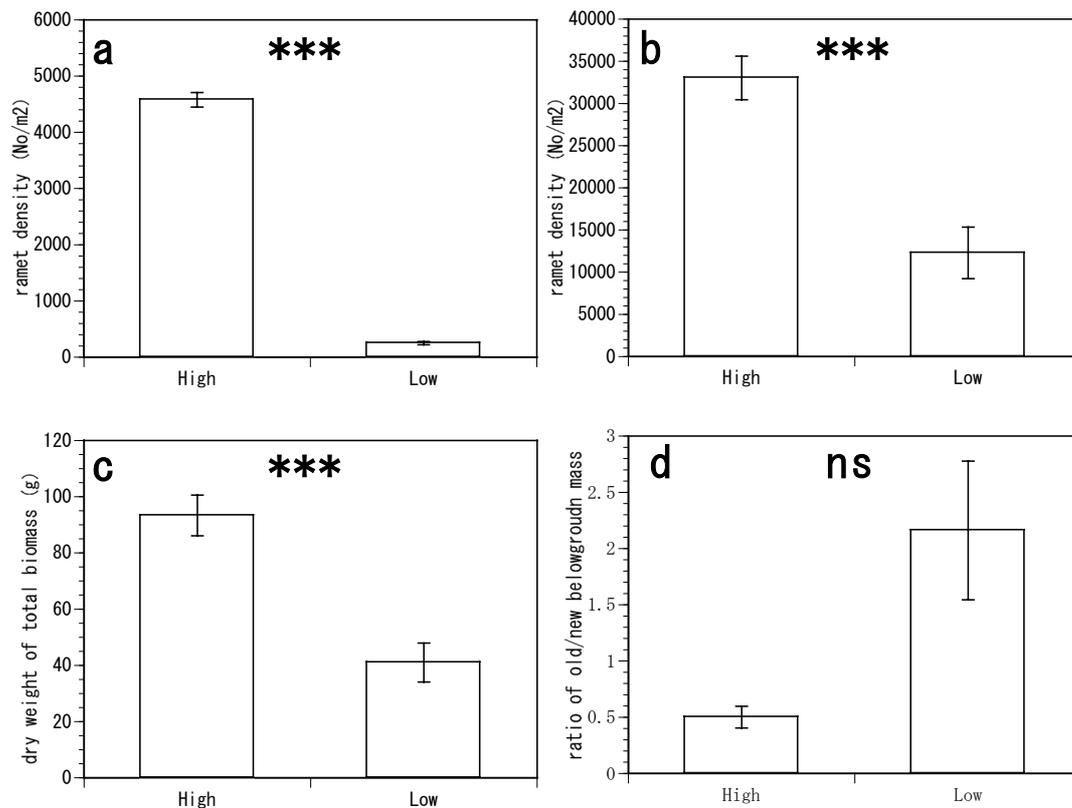


Figure 7. (a) the ratio of SRR to total ramet number (mean \pm SE), (b) the length of LRRs (mean \pm SE), (c) the number of branches per SRR (mean \pm SE) and (d) the number of branches per LRR (mean \pm SE) in High and Low density treatments for the garden experiment. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns not significant.

4) Discussion

Shoot

The height of *Scirpus olneyi* shoots increased as shoot density increased in the field and in the garden experiment (Fig. 3a1-3, 4b). This result is likely the response to increases in shoot density as a result in a stronger competition for light, and to harvest more light, plants produce taller shoots. Researchers reported similar results for *Scirpus maritimus* (Jelinski *et al.*, 2001) and *Gynerium sagittatum* (de Kroon and Kalliola, 1995). Thus, this result suggests *S. olneyi* responds to variations in light availability, especially in high density patches where light would limit growth and where competition for light would be most intense.

Seed and Vegetative Propagation

Both in the field and the garden experiment seed production increased as shoot density increased confirming our hypothesis (Fig. 3b1-3, 3c1-3, 4c, 4d). At higher shoot density, plants tended to produce flowering shoots at a higher ratio, and thus the ratio of

inflorescence mass to all shoot mass increased. Similar results have been reported for other plant species. Under high plant density, plants increased sexual reproduction in *Rubus hispidus* (dewberry) (Abrahamson, 1975), *Fragaria virginiana* (Holler and Abrahamson, 1977), *Tussilago farfara* (Ogden, 1974) and *Scirpus pungens* (Giroux and Bedard, 1995). Negative relationships were found between density and vegetative reproduction in *Mimulus primuloides* (Douglas, 1981). On the other hand, some experiments indicated that seed output decreases at high density. Law *et al.* used Turf grasses and found there were negative relations between density and seed output (Law *et al.*, 1979). *Cyperus rotundus* (purple nutsedge) also decreased sexual reproductive effort at high density (Williams *et al.*, 1977). In a field study of two forms of *Elymus lanceolatus*, Humphrey and Pyke (1998) confirmed that both forms decreased the number of flowering tillers at higher densities (Humphrey and Pyke, 1998). Loehle (1987) and Newell & Tramer (1978) expected that sexual propagation should be favored at low density where potential success of sexual propagation is higher. At our study site, however, seedling establishment of *Scirpus olneyi* is rare (Ikegami personal observation), most likely because there are few open locations for seeds to become established due to a thick litter layer and typically low light levels at the litter layer. Another explanation of decreased flowering and seed production at higher density may be that nutrients and/or light become limiting under such conditions (Loehle, 1987). The resource availability hypothesis, however, can also explain the results of our field study. Under field conditions, resources can be patchily distributed. Thus patches with more resources would be exploited by clonal plants by producing more ramets, and at the same time, plant resources within individual ramets would be sufficiently high to invest in the production of seeds, which can be used to reach and colonize other distant patches. In the garden experiment, however, the increased seed production at increased shoot densities was not expected. In the tubs the soil resources per ramet were equally spread and thus resources in the tubs with high shoot densities were much less available than in the tubs with low shoot densities. Thus, even though resources were sufficient to invest significantly in seed production in the garden experiments, plants produce more seeds in the high density treatment where nutrient availability was likely lower. It is well known that differences in density affect the sexual reproduction much stronger than nutrient availability for annual plants (Kawano *et al.*, 1990; Kawano *et al.*, 1989; Kawano and Nagai, 1986; Nagai and Kawano, 1986). These results indicate that plant density can affect the reproductive of *S. olneyi* than nutrient availability.

Our hypothesis about the production of SRRs and LRRs, however, was not confirmed. Plants produced more LRRs at lower ramet density and more SRRs at high ramet density (Fig. 5a, 6a). In the field, if the patches of high ramet density were rich in resources compared to those with low ramet density, our results are in accordance with the idea of foraging in clonal plants (de Kroon and Knops, 1990; Dong, 1995; Harper, 1985; Hutchings and de Kroon, 1994; Salzman and Parker, 1985; Schmid, 1992; Slade and Hutchings, 1987a; Slade and Hutchings, 1987b; Slade and Hutchings, 1987c). Based on the foraging theory, formation of SRRs to exploit colonized habitats in rich resources patches generally results in high ramet densities, while formation of LRRs to explore new habitats, at least initially, results in low ramet densities.

In the garden experiment, however, this reasoning is less logical because resources were equally mixed in the tubs, resulting in less N per ramet in the tubs with high shoot densities. If the resource availability hypothesis would be true, we would expect that plants in the high density plots and tubs would produce more LRRs to “escape” to better resource patches. In contrast, we would expect plants in the low density tubs to produce more SRRs to consolidate ramets in areas with greater N per ramet (*i.e.*, the better resource patches). While the results were the opposite of what would be expected based on foraging theory, foraging behavior was apparent in *S. olneyi* with a tendency to consolidate ramets at higher densities and to spread at lower densities. In addition, plants tended to produce fewer new ramets (Fig. 5d, 7a, 7b, 7d) but a larger number of sexual shoots at higher density. We conclude that ramet density of *Scirpus olneyi* regulate the clonal propagation strategy of this species.

It has been suggested that ramet density of clonal plants is regulated intracolonally to avoid inter-ramet competition (de Kroon and Kwant, 1991) possibly through physiological integration (Hutchings, 1979). As a result, Clonal plant can prevent the overproduction of ramets. Ramet architectures also potentially control ramet density, but no research had been conducted on the effects of varying density on ramet architectures. Our results show demonstrate that *S. olneyi* can control its ramet density through changing the architectural elements with the combination of two types of ramets. From foraging theory, we would expect that plants would produce LRRs at high density and SRRs at low density due to resource availability per ramet. *S. olneyi*, however, showed the opposite result, indicating that ramet density and variations in the biotic environment can affect ramet architectures differently than the abiotic environment.

5) Conclusion

When local density is low, *S. olneyi* produces LRRs to spread and occupy new localities rapidly (see Abrahamson, 1980) and start consolidating localities with SRRs. Once local density increased, fewer localities are available for plants since most places are already occupied by other ramets. Thus even if plants produce LRRs that reach further than SRRs, plants have less chance to reach available patches and can not facilitate local spread and occupation but the production of SRRs allows the species to consolidate in the same locality as the mother ramets grew and produce sexual shoots in the following season. In addition, producing SRRs may cost less than producing LRRs in terms of biomass, and plants can use saved resources for sexual propagation or storage (Chapter 3). Thus as ramet density increases, *S. olneyi* shifts its propagation strategy from exploring with LRRs to exploiting with SRRs and spreading by seeds.

6) Acknowledgment

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Chapter 5:

Density Dependent Propagation Strategy of clonal plants

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Summary

Abrahamson suggested that the balance between seed and vegetative propagation is affected by inter- and intra-specific competition. Yet, some studies indicated that seed production is positively and others negatively correlated with plant density. To evaluate the effects of local density of ramets on plant propagation strategy, we developed a lattice model where two strategies competed each other. We refer to one strategy as the Density Dependent Seed Strategy (DDSS) in which plants produce seeds at higher density. We refer to the other as the Density Dependent Ramet Strategy (DDRS) in which plants produce ramets at higher density. Each strategy has different thresholds to change from sexual to vegetative propagation or vice versa according to Local Density (LD), the number of surrounding neighboring individual (ramets).

When the death rate is high, the DDSS with lower or the DDRS with higher threshold values tend to win. At high death rate, many plants suffer mortality at every time step in the model thus there are many vacant cells in the lattice that do not have neighboring plants. Since vegetative propagules can not invade the isolated vacant cells in the lattice, those spaces can only be occupied by seeds. Consequently, sexual reproduction potentially adds a large number of offspring to the lattice and the probability increases that the lattice will be occupied by a sexually propagated individuals. Thus strategies that propagate only or nearly by seeds are suitable for surviving under high death rate. When the death rate is low, the DDSS plants with higher threshold values are the best strategy. When the death rate is low, LD is high and DDSS plants tend to propagate sexually. When there are vacant cells the lattice, LD decreases and plants with the DDSS strategy produce new ramets which may establish new individuals in adjacent cell. Thus, DDSS plants with higher threshold values has an equal chance to become established by vegetative propagation with DDRS plants since DDRS plants tend to propagate only vegetatively at higher density. In addition, DDSS plants also produce seeds when there are no or few vacant adjacent cells and those seeds can, although perhaps rarely, establish new individuals. Our result suggests that the production of ramets at lower densities and the production of seeds at higher densities seems to be a proper strategy, and the negative relations between density and sexual propagation in the field may not directly relate to the density but abiotic environments such as nutrient availability per individual.

Keywords: clonal plant, density, lattice model, sexual propagation, vegetative propagation

1) Introduction

Clonal plants can spread by vegetative and sexual propagation. Through vegetative propagation of ramets, fewer but initially larger individuals with a lower mortality rate are produced, while through sexual propagation by seeds, many but initially smaller individuals, with higher mortality are produced. Asexually produced ramets have lower mortality rates because mother ramets support the daughter ramets with carbohydrates, water and minerals (Marshall, 1996; Slade and Hutchings, 1987; Stuefer *et al.*, 1996). Individuals originating from seeds are smaller at birth than clonal ramets and they receive no support, other than resource supplied to the seed, from mother plants. Seeds are more vagile than clonal ramets because they can be dispersed over a larger area. The balance between sexual and vegetative propagation is an important evolutionary and ecological feature of the life history strategies among clonal plants.

In a Chapter 4 we described how *Scirpus olneyi* produced more flowering shoots and seeds in patches with higher shoot densities both in a field study and a garden experiment. Others have also reported that seed production is positively correlated with plant density in clonal plants (Abrahamson, 1975; Abrahamson, 1980; Giroux and Bedard, 1995) and no clonal plants.

Under field conditions, where resources are mostly likely patchily distributed, the result of our study would be expected because patches with more resources would be exploited by *S. olneyi* by the production of ramets that would occupy the space. At the same time, resources would be sufficient for the genet to invest in seed production. In our garden experiment, however, the increase in seed production at higher shoot densities was not expected. In addition, it is well known that differences in density affect the sexual reproduction much stronger than nutrient availability for annual plants (Kawano *et al.*, 1990; Kawano *et al.*, 1989; Kawano and Nagai, 1986; Nagai and Kawano, 1986). The amount of resources (*i.e.*, nutrients) in the tubs that were used in the experiment was similar in the high and low density treatments. Thus, on average, the resources per ramet were less in the tubs with high shoot densities compared to the resources available to ramets in the tubs with low shoot densities. Moreover, competition for light would also have been higher in the tubs with high shoot densities. Even though competitive stresses are greater at high densities (Winn and Pitelka, 1981) we would expect that the resources per ramet would have been less in the high density treatment and available resources would have limited seed production. Results from other studies would also suggest that plants growing in relatively poor environmental conditions (*i.e.*, our high density treatment) would increase their allocation to clonal propagation (Callaghan, 1988; Raven *et al.*, 1981). Abrahamson (1980) theorized that even with uniformly distributed resources, vegetative propagation would be advantageous at low plant density as it facilitates local spread and occupation while seed propagation is advantageous at high plant density as it enables dispersal to new and perhaps more favorable sites. On the other hand, some research has shown the opposite results. At high shoot density, since competition between ramets is severe, clonally growing ramets have more chance of establishment than seedlings. Thus in dense patches clonal propagation is to be expected (Williams *et al.*, 1977) or seed production can decrease (Law *et al.*, 1979).

To investigate possible explanations to explain the results of the field and garden experiments, we developed a spatially explicit simulation model to evaluate competition between clonal plants that have different reproductive strategies in response to variation in ramet density. In clonal plants, mother plants produce ramets only in neighboring patches, so that ramet performance may be expected to be highly regulated by local density (LD) rather than the whole population density (Global density; GD). Seed dispersal tends to take place in the whole habitat of a population, and thus seed performance may be highly regulated by GD rather than LD. In the simulation, for this reason, we used a lattice model which allows us to explore spatially explicit interactions at a small scale (Pacala and Silander, 1990). We used two plant strategies in the modeling effort. We refer to one as the Density Dependent Seed Strategy (DDSS) in which plants produce seeds at higher shoot density. The other is referred to as the Density Dependent Ramet Strategy (DDRS) in which plants produce ramets at higher shoot density. The objective of the simulation effort was to determine strategy is better adapted under various density conditions.

2) Model

We use a two-dimensional regular square lattice model with 100X100 cells. To avoid boundary effects, we assume a periodic boundary condition that allows us to connect all cells in the model across all boundaries. Each lattice cell has two states, occupied or unoccupied and only one plant can occupy a cell at a time. Each cell is surrounded by 8 cells and plant interactions take place among neighboring cells. We use two densities in the model; global density (GD) is defined as the ratio of the number individual plants in the lattice to the total of lattice cells (total number of individuals/10000), and local density (LD) is defined as the ratio of the number of occupied cells to all cells within the neighboring field (3X3 cells) for each plant number of occupied (cells/3X3). In the model, plants can propagate vegetatively by producing new ramets and sexually by producing seeds. In each time step in the model, each plant propagates sexually or asexually depending on its life history strategy and LD. Individuals can not produce both seeds and asexual ramets at one time step. Individuals are assigned as having either the DDSS or DDRS strategy. DDSS plants produce seeds at higher densities and ramets at lower densities. DDRS plants produce ramets at higher densities and seeds at lower densities. Individuals are able to switch between DDSS and DDRS depending on threshold values of LD. If LD exceeds the threshold value, DDSS individuals switches from vegetative to sexual propagation and DDRS plants switches from sexual to vegetative propagation. For convenience, we use as threshold values the number of occupied cells around each plant. Thus the threshold value varies from 0 to 8. In the model, individual plants are not able to identify the reproduction strategy of a neighboring plant and it is only sensitive to the number of occupied neighboring cells. Each strategy has a fixed genotype, thus offspring ramets has the same characteristics as its mother plant. New clonal individuals can only occupy adjacent vacant cells. Mother plants can only propagate ramets into the 8 adjacent cells, thus if a vacant cell is surrounded by occupied

cells, an individual can be established in it by vegetative propagation from one of surrounding cells. For each occupied cell, the model checks the propagation mode of the occupying plant and if the plant is in the vegetative propagation mode, then the model determines if the plant propagates a new individual into the vacant cell or not, depending on its Ramet Production Probability (RPP), the probability that the plant produces a new individual into a neighboring cell. If more than one ramet invades a vacant cell, the model randomly chooses which one is successful.

Seeds are assumed to be produced and dispersed in sufficient numbers to potentially reach every cell in the lattice independent of the number of flowering individuals in the lattice. Seeds are dispersed to vacant cells if the cells does not have any occupied neighboring cells, or if no individual produces an asexual ramet into the cell. Seedlings are established in a vacant cell depending on a Seed Establishment Probability (SEP), defines as the probability of seed establishment in every cell in the lattice. For convenience SEP is fixed and independent of the total number of seeds produce in each time step. If a seedling successfully establishes in a cell then the model determines which life history strategy it is assigned depending on the seed proportion of the two strategies at each time step. During each time step in the model, each individual in the lattice ran the risk of death based on a fixed death rate. At the end of each time step, each plant is examined to determine if it survives or not. If a plant dies, the cell that it occupied becomes vacant for the next time step in the model. Death rates are independent of whether an individual was produced by sexual or vegetative propagation.

We run three types of simulations: 1) all plants has a single strategy and the density threshold values are varied, 2) Individuals are either DDRS or DDSS strategies competes using nine density threshold values, and 3) DDSS individuals competes with different density threshold values. To evaluate the performance of the two strategies at different threshold values, we run single strategy simulations using 4 different death rates. At the start of each simulation we randomly assign plants to initially occupy 5% of all cells in the lattice. Every plant in a simulation has the same strategy with the same threshold value.

At 5 and 10 simulation time steps, we randomly take 40 blocks of 36 cells within a 6X6 square patch in the lattice to evaluate the relationships between density and seed production. We count the total number of all individuals and the number of seedlings and calculate the ratio of seedlings to all individuals. We do not use samples with less than 5 individuals for the evaluation, because ratios of seedlings to all individuals tend to be highly variable in lower density patches. At 100 simulation time steps, we measure LD, GD, the ratio of individuals that produce ramets to all individuals, and the number of individuals from vegetative propagation, and from sexual propagation.

To evaluate the results of competition between two strategies with different density threshold values and competition within DDSS with different threshold values, we examine simulations under 4 different death rates and 4 different SEP. At the start of each simulation, we randomly assigned DDSS and DDRS plants or two DDSS plants with two different threshold values to initially occupy 5% of all in the lattice. In the simulations, one of the two strategies excludes the other most of the time. In some instances, however, both strategies co-existed. We do not know if the two strategies actually can coexist in this system or that the results happen because the simulation times are not long enough.

In some simulations, we obtain contradictory results when the initial conditions are similar, in particular when death rates are high (Harada, 1999). In spatial models, due to demographic stochasticity, one strategy can exclude another by chance, even though the two strategies have rather similar competitive capabilities. Thus, when two strategies co-exist after 100,000 time steps, we decided that the winner is the one that has the largest number of individuals at the end of the simulation. To evaluate this protocol, we run the same set of simulations 10 times, and decided that the final winner is that strategy which won most often.

3) Results

Single strategy simulation with DDSS and DDRS

In both strategies, the mean LD and GD increase when as death rate decreases (Fig. 1). When the death rate is 1, and the switching threshold for DDSS is higher than 5, or that the switching threshold for the DDRS is 0, no plants survives (Fig. 1). For DDSS, both the LD and the GD increase gradually as threshold values increase (Fig. 1a,c). This was because DDSS plants tend to propagate vegetatively at higher threshold values (Fig. 2a), and vegetative propagation has a greater chance of establishing new individuals than sexual propagation. As a result, in the case of the DDSS strategy, most individuals originate from vegetative propagation at higher threshold values (Fig. 3a,c). At a death rate of 0.7 or 1, LD and GD decreases with higher threshold values (Fig. 1a,c). On the other hand, for DDRS, LD and GD suddenly decrease as density threshold values increase (Fig. 1b,d), but the decrease starts at lower density threshold values as the death rate decrease. This pattern is the result of DDRS plants tending to propagate sexually at higher threshold values and sexual propagation tends to lower LD because seeds are dispersed equally over the lattice and have less chance to establish in any one cell. Thus when DDRS plants grow at higher threshold values, they do not reach the local density that would result in as witch in the mode of propagation. Subsequently, plants continue to propagate sexually and consequently most individuals originate from sexual propagation (Fig. 2b,3b and d). The relationship between density and the proportion of seedlings is positive for DDSS and negative for DDRS (Fig. 4, RPR=0.2, SEP=0.08, death rate=0.4, the threshold value of the DDRS and DDSS=4).

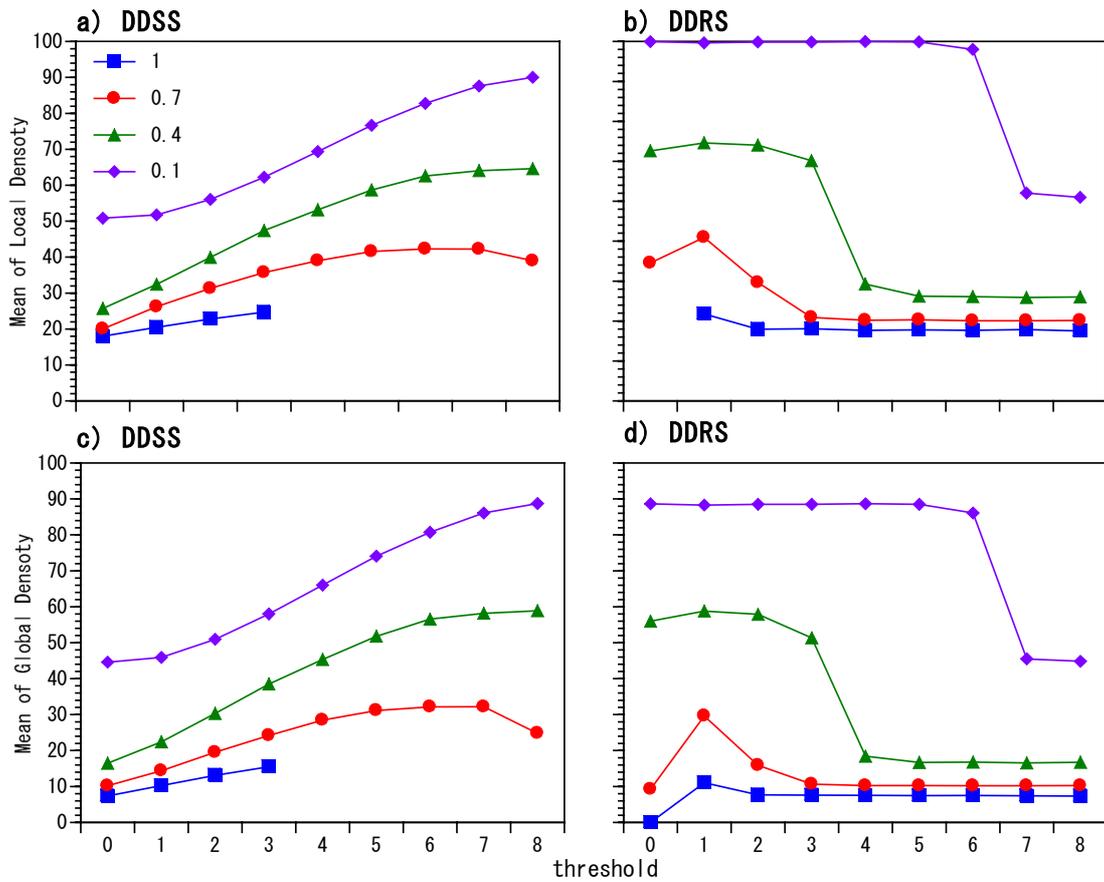


Figure 1. Mean Local Density of DDSS (a), DDRS (b), and Global Density of DDSS (c) and DDRS (d) at 4 death rates. Y-axes: density (%), and X-axes: threshold values at which the strategy changes its mode of reproduction. RPR=0.2, SEP=0.08, ■: death rate=1, ●: death rate=0.7 ▲: death rate=0.4 ◆: death rate=0.1

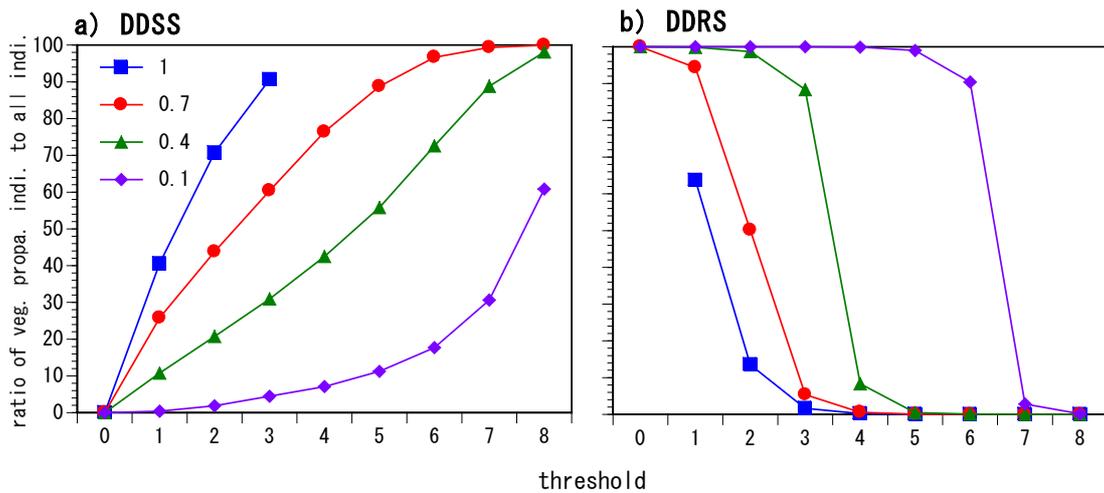


Figure 2. Ratio of vegetatively propagating individuals to the number of all individuals of DDSS (a) and DDRS (b) at 4 death rates. Y-axes: ratios of vegetatively propagating individuals to the number of all individuals, and X-axes: thresholds values at which the strategy changes its mode of reproduction. RPR=0.2, SEP=0.08, ■: death rate=1, ●: death rate=0.7 ▲: death rate=0.4 ◆: death rate=0.1

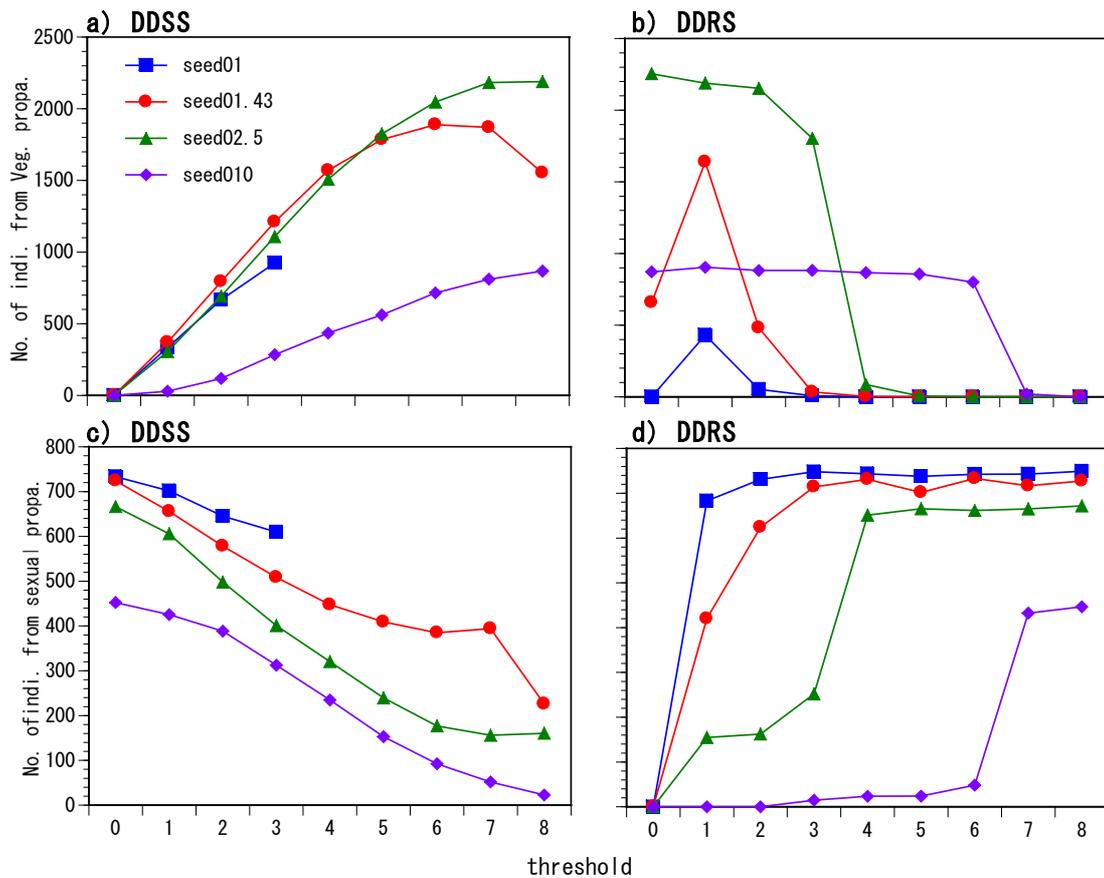


Figure 3. Mean number of individual that originated from vegetative propagation of the DDSS (a) and DDRS (b), mean number of individuals that originated from sexual propagation of the DDSS (c) and DDRS (d) at 100 time steps in each simulation at 4 death ratios. Y-axes: number of individual, and X-axes: thresholds values at which the strategy changes its mode of reproduction. RPR=0.2, SEP=0.08, ■: death rate=1, ●: death rate=0.7 ▲: death rate=0.4 ◆: death rate=0.1

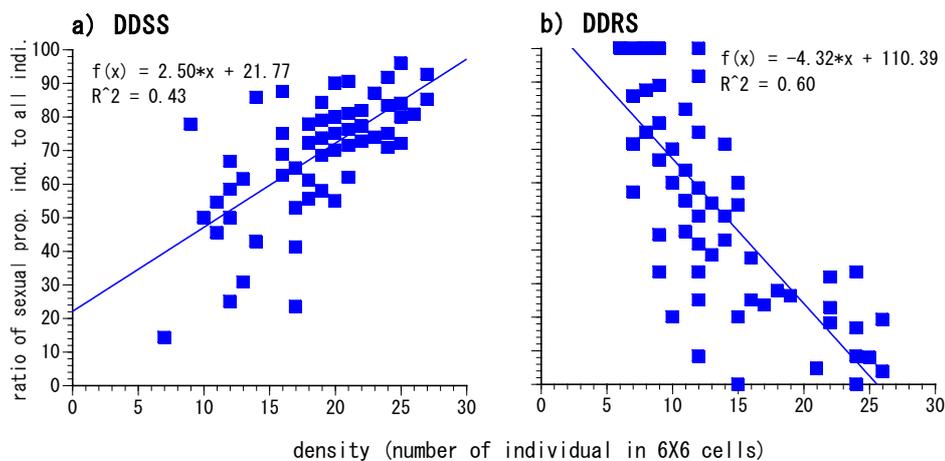


Figure 4. The rate of the number of seeding individuals to all individuals against density in 6X6 cells from the DDSS (a) and DDRS (b). Y-axes: the ratio of the number of seeding individuals to all individuals, and X-axes: individual number. RPR=0.2, SEP=0.08, death rate=0.4, the threshold value for the DDRS and DDSS=4.

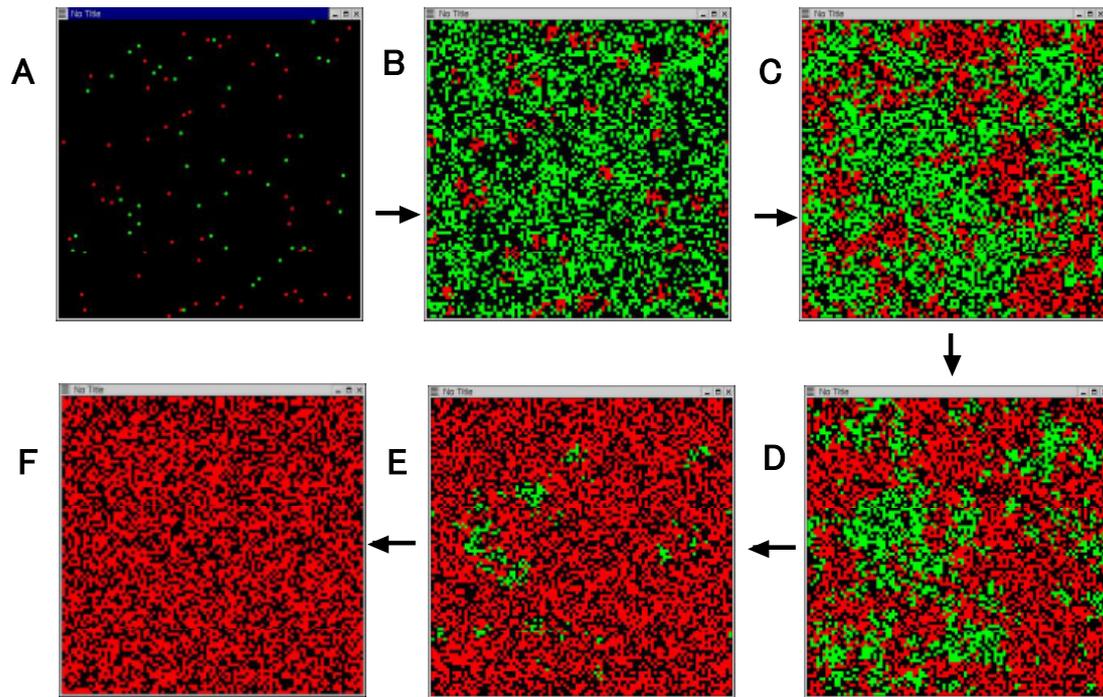


Figure 5. A simulation procedure. A cell occupied by the DDSS is shown as a darker dot, a cell occupied by the DDRS is shown as a whiter dot, and an unoccupied cell is shown as a black dot in the simulation. A is an initial condition with 1% of the cells occupied. B is after 5 time steps. At B, DDRS produces seeds and DDSS produces ramets so that the DDRS occupies most cells. C is after 10 time steps. Since most cells are occupied, DDSS begins to produce seeds and DDRS produce ramets. At both D and E, most, but not all and these tendencies become stronger as density increase. However, local plant death may reduce local density below the density value of the switch in reproductive mode, and in that case the DDSS that produces ramets has a higher chance of occupying the vacant cell. It becomes the dominant strategy at F. RPR=0.2, SEP=0.08, death rate=0.1, threshold values for both strategies=4.

Competition between DDSS and DDRS strategies

A simulated competition process between the DDSS and DDRS is shown in Fig. 5 where the initial condition is that 1% of the cells is occupied by plants at the beginning. The outcome of the competition between the DDRS and DDSS change along with variation in the death rate. Generally, DDRS plants exclude DDSS individuals when the death rate is either very high or very low (Fig. 6). When the death rate is 1, DDSS plants that have density threshold values higher than 5 and DDRS individuals with a threshold value of 0 are not able to survive. When DDSS or DDRS plants have these values just listed, the other strategy automatically wins, or no plants survive. Under the highest death rate scenario, both DDRS and DDSS recruit from seeds (Fig. 3). When the death rate decreases, DDSS plants that have higher threshold values tend to exclude DDRS plants: At the death rate of 0.7, DDSS plants with density threshold values between 1 to 4 always win. At a death rate of 0.4, DDSS plants with a threshold values between 6 to 7 win, and at a death rate of 0.1, DDSS plants with a density threshold of 8 always win (Fig. 6).

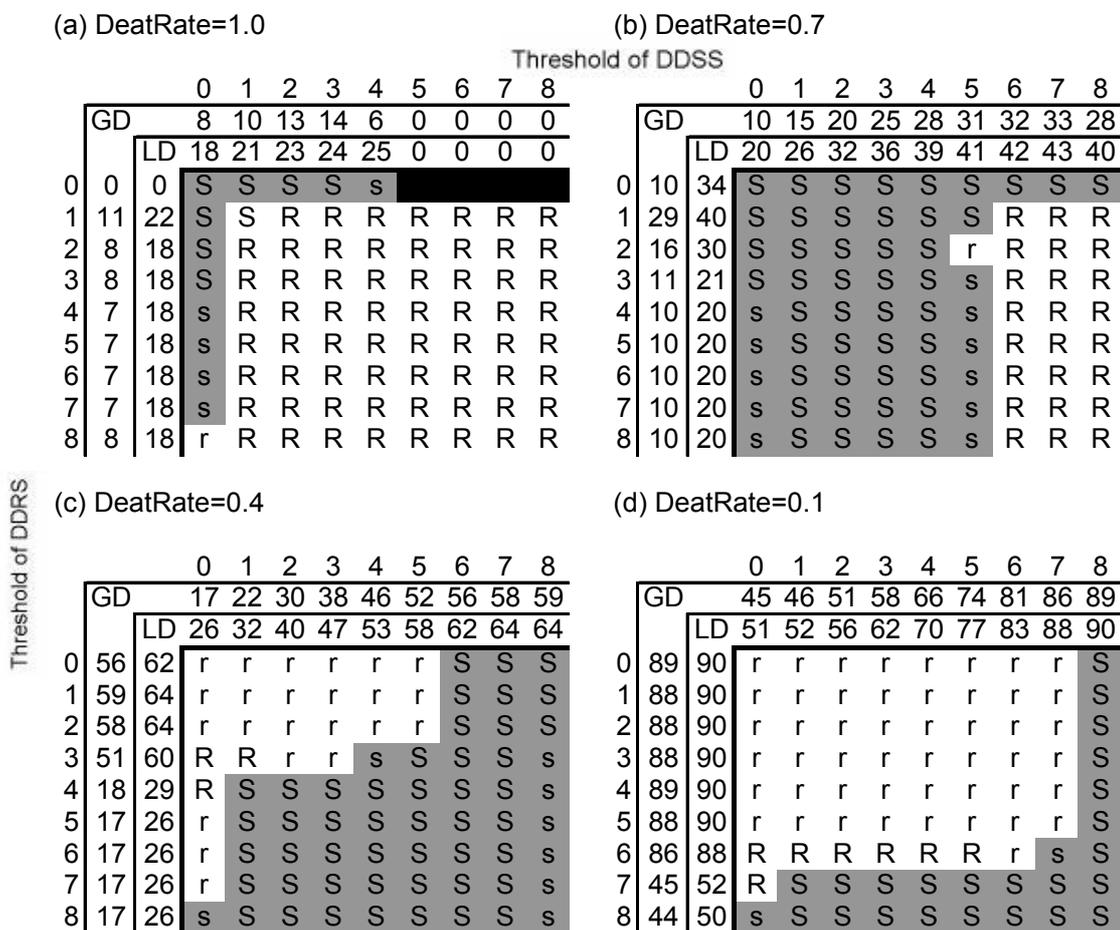


Figure 6. Results of competition between the DDSS and DDRS under 4 death rates. Death rate is (a) 1.0, (b) 0.7, (c) 0.4 and (d) 0.1. R means that the DDRS won that combination, and S means that the DDSS won. A capital means that one strategy excluded the other strategy, and lower-case letter means that the two strategies existed at the end of the simulation, or both strategies won in different simulations. First column: threshold values at which the strategy change its mode of propagation; second and third columns are GD and LD which are from the results of the Single strategy simulation for the DDRS. Rows are threshold values, GD and LD for the DDSS respectively. RPR=0.2, SEP=0.08.

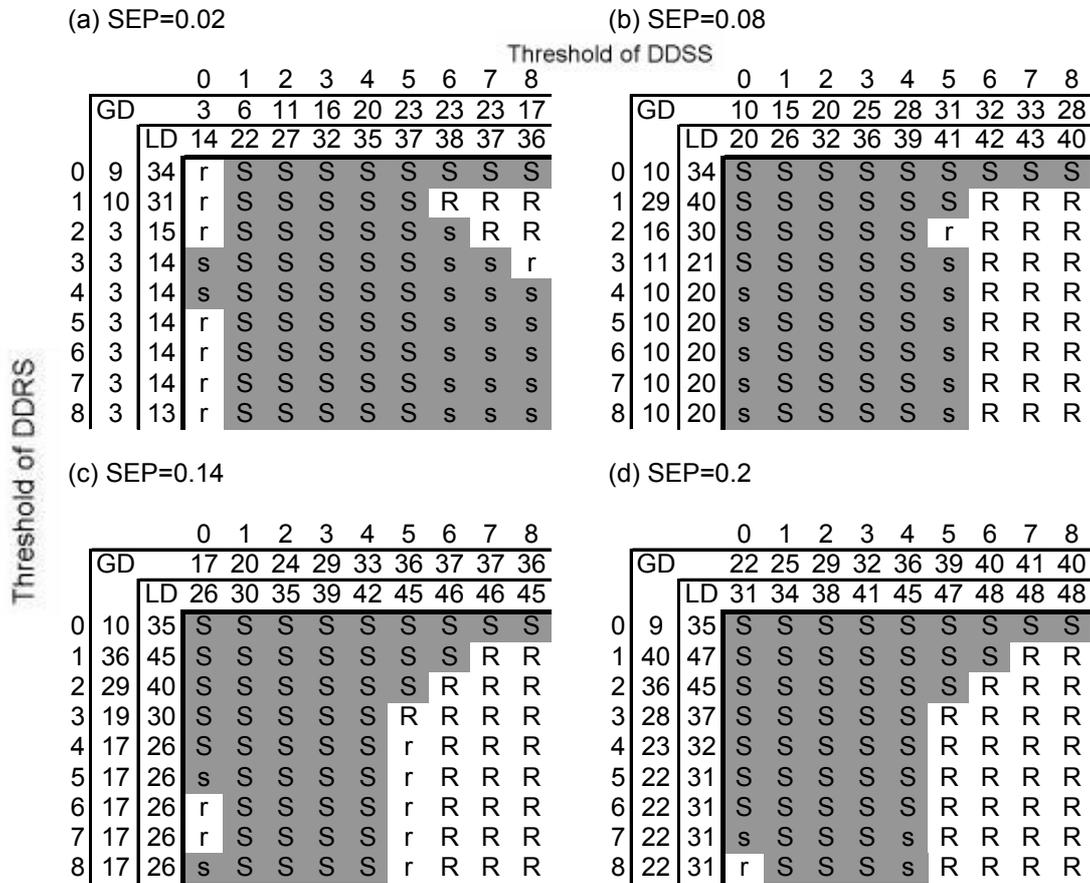


Figure 7. Results of competition between the DDSS and DDRS under 4 Seed Establishment Probability (SEP). SEP is (a) 0.02, (b) 0.08, (c) 0.14 and (d) 0.2. R means that the DDRS won that combination, and S means that the DDSS won. A capital means that one strategy excluded the other strategy, and lower-case letter means that the two strategies existed at the end of the simulation, or both strategies won in different simulations. First column: threshold values at which the strategy change its mode of propagation; second and third columns are GD and LD which are from the results of the Single strategy simulation for the DDRS. Rows are threshold values, GD and LD for the DDSS respectively. RPR=0.2, death rate=0.7

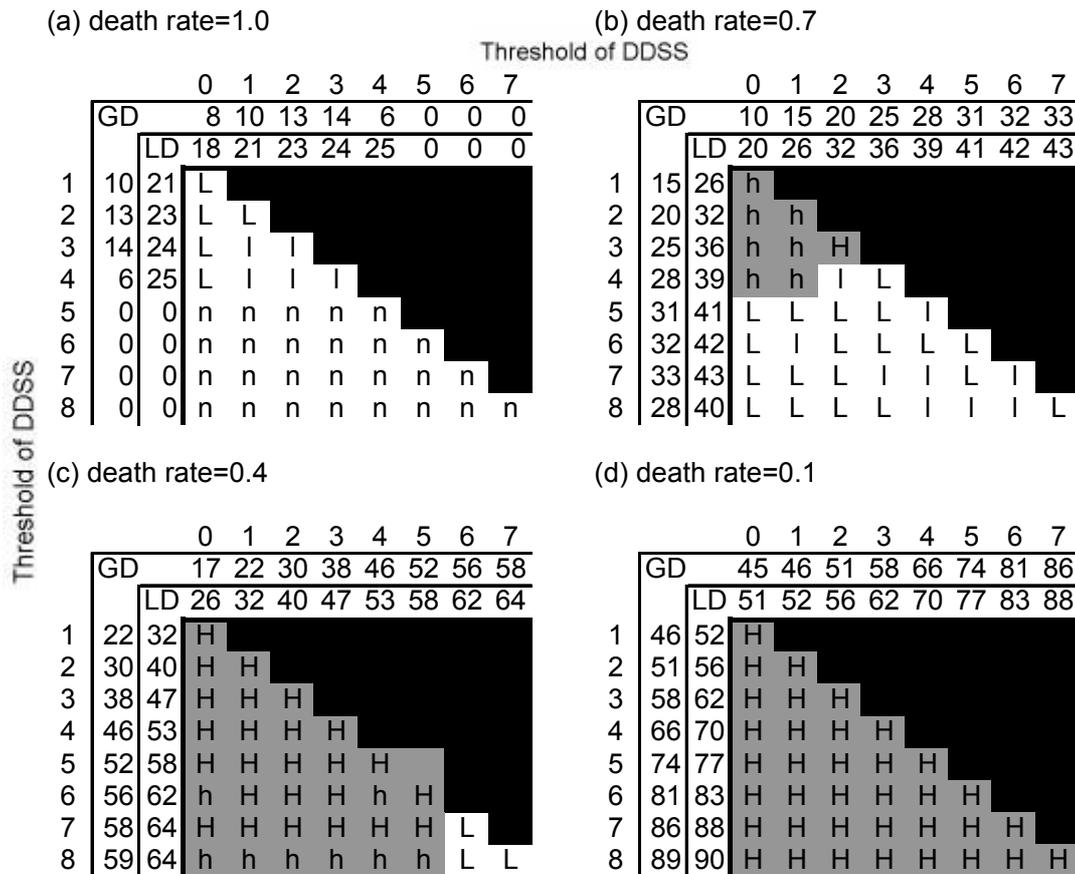


Figure 8. Results of competition between the DDSS with different thresholds. H means that the strategy with the higher threshold value won and L means that the strategy with the lower threshold value won. A capital means that one strategy excluded the other strategy, and lower-case letter means that the two strategies existed at the end of the simulation, or both strategies won in different simulations. First column: threshold values at which the strategy change its mode of propagation; second and third columns are GD and LD which are from the results of the Single strategy simulation for the DDSS. Rows are threshold values, GD and LD for the DDSS respectively.

Variations in SEP does not significantly affect the results; if SEP increases then DDRS plants that have higher threshold values tend to outcompete DDSS (Fig. 7). In the simulated competition between individuals with two DDSS individuals with different density threshold values, plants with lower threshold values win over plants with higher thresholds at higher death rates (Fig. 8), and plants with higher threshold values always win at lower death rates (Fig. 8). Thus at lower death rates, the DDSS with higher threshold values always win from the DDRS and DDSS that have lower threshold values.

4) Discussion

When the death rate is high, the DDSS plants with lower or the DDRS plants with higher threshold values tend to win (Fig. 5) and they recruit mainly from seed. Under a high

death rate, many plants die at every time step in the simulation and the GD or LD are low so that some vacant cells are not occupied by neighboring plants. Since vegetative propagules can not invade these isolated vacant cells while individuals can establish from seed, the simulations demonstrate that sexual reproduction potentially contributes a larger number of offspring compared to the maximum of 8 individuals that can be produced vegetatively. There is thus a higher chance that the cell would be occupied by a sexually propagated individual than by vegetative propagation. Thus allocation strategies that propagate exclusively or almost completely seeds would be at a selective advantage. This situation occurred for the DDSS plants with a threshold value of 0. In comparison, LD never reach the threshold values for the DDRS plants with relatively high threshold values, thus those DDRS plants only produced seeds. Several studies suggested that disturbance and high mortality favors sexual propagation because seeds disperse better than vegetative propagules and newly established individuals do not have to compete with vegetative propagules or adults (Antons, 1988; Douglas, 1981; Loehle, 1987; Sakai, 1995). In a model study, Winkler and Fischer (1999) studied optimal resources allocation under disturbance conditions, and found that plants tend to allocate more resources to vegetative propagation under stable conditions and to sexual propagation under highly disturbed conditions. This outcome is of selective advantage because seed can spread widely and occupy disturbed areas, while vegetative propagation can enter only from the edge of the disturbed areas.

When the death rate is low, the DDSS plants with higher threshold values are the most successful in these simulations. Due to lower death rates both the GD and the LD is high and DDSS plants tend to propagate sexually. When there are vacant cells, LD decreases and the DDSS plants produce new ramets which are able to colonize adjacent cells. This result indicates that DDSS plants with higher threshold values have an equal or higher chance to become established by vegetative propagation than DDRS plants at higher densities. DDRS plants with lower threshold values tend to propagate vegetatively and with higher threshold values tend to propagate sexually. In addition, DDSS plants with high threshold values also produce seeds when there are no or few adjacent vacant cells and those seeds can, although perhaps rarely, establish new individuals (Fig. 3c, 3d). Generally, it is believed that clonal plants rarely recruit by seeds (Abrahamson, 1980; Cook, 1985; Crawley, 1990; Harper, 1977) especially in established populations (Barrett and Silander, 1992; Giroux and Bedard, 1995; Jonsson, 1996; Molau, 1992). Sakai (1995) showed, in plants with fixed reproductive strategies, that only when establishment from seed is higher than establishment from ramets, plants would profit to allocate most resources to seed production, and according to Takada and Nakajima (1996) the same applies when death rates in the older life stages are high.

Over short time periods, it is possible that a genotype which propagates clonally could overwhelm genotypes which propagate both sexually and vegetatively because the production of ramets is less costly energetically and plants can allocate more resources to ramet production and the ramets have a higher chance of establishment, compared to individuals with a mixed strategies (Nishitani *et al.*, 1995; Nishitani *et al.*, 1999). These conditions are, however, rather unrealistic under fields conditions, since the establishment from ramets tend to be higher than the establishment from seeds and survival rates at older stages are higher than at younger stages. Moreover, species that only propagate clonally are not common in nature (Barrett, 1993; Grace, 1993).

Harada (1999) developed a spatial model to evaluate the evolutionarily stable strategy (ESS, Maynard Smith 1982), of a vegetatively and sexually propagating plant. Harada showed that plants with an ESS strategy invested more resources into vegetative propagation than the optimal allocation pattern which maximizes the population sizes at equilibrium (Harada, 1999). This result suggests that the optimal strategy of clonal plants is to allocate resources to both vegetative and sexual propagation in the spatially explicit structure. Harada also explains this result from the fact that ramets can enter only neighboring cells, while seed can reach vacant cells at the outside of dense patches.

Williams (1975) suggested that seed dispersal with a genetically variable offspring is adaptive as a means of escaping the competitive effect of clonal crowding in order to colonize new environments. This means propagating sexually at higher density is an adaptive trait. This hypothesis is confirmed by several studies (Abrahamson, 1975; Abrahamson, 1980; Giroux and Bedard, 1995).

Generally, if local ramet density increases, then competition among ramet increases (Winn and Pitelka, 1981) and resource availability per ramet decreases. Loehle (1987) and Newell & Tramer (1978) expected that sexual propagation should be favored at low density where potential success of sexual propagation is higher. In a field study on two forms of *Elymus lanceolatus*, Humphery and Pyke (1998) confirmed that both forms decreased the number of flowering tillers at higher densities. One explanation of decreased flowering and seed production at higher density may be that nutrients get limiting under such conditions.

Loehle (1987) therefore suggested that Abrahamson's (1975) finding in *Rubus* that high density and the high flowering ratio may be due to good qualities of the patches (or Abrahamson's measure of density may not have been appropriate). In our previous study (Chapter 4), we found that the sexual propagation of *Scirpus olneyi* became higher in dense treatments despite lower resource availability per ramet. Also in our model, the quality of each cell is uniform and does not change, DDSS plants win against DDRS plants. Thus independent of resource availability the production of ramets at lower densities and the production of seeds at higher densities seems to be evolutionarily the most efficient strategy.

5) Acknowledgment

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Chapter 6:

Spatial Division of labor of Scirpus olneyi A. Gray

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Summary

Two interconnected ramets, in which each ramet grows in different environments where resource availability is inversely distributed can show spatial division of labor (DoL). For example, ramets under light and dry conditions allocate biomass to the leaves while ramets under shaded and wet conditions allocate to the roots. The plants in such a system possibly achieve a higher biomass than connected ramets growing both under equal conditions. DoL is rather new finding and some important factors, such as water consumption, leaf size or specific leaf area have not been well studied. To evaluate the spatial DoL and functional specialization of each ramet, we evaluate DoL for a wetland species, *Scirpus olneyi* that is common to brackish wetlands in eastern North America in this study. We construct light and salt conditions for water stress environments, and shaded and fresh water conditions for light stress environments. These conditions were created in different halves of containers in which a connected clonal fragment was planted.

In light and salt halves, in containers with heterogeneous conditions, plants allocate proportionally more biomass to aboveground parts than plants in containers with homogeneous conditions. In shaded and fresh water halves, in containers with conditions plants allocate proportionally more biomass to belowground than plants in containers with homogeneous conditions. Plants in containers with heterogeneous conditions reached higher biomass values than the plants in containers with homogeneous conditions. These results meant the plants in containers with heterogeneous conditions showed spatial DoL. In the light and salt halves in containers with heterogeneous conditions, shoot height was higher and shoot SGA was larger than plants in the light and salty halves in containers with homogeneous conditions. These results suggested that plants in light and salty halves in containers with heterogeneous conditions specialize in light capturing instead of water capturing. The ramet groups in the light and salty halves in containers with heterogeneous conditions allocate proportionally less biomass to their belowground parts and draw water from their shady and freshwater counter halves.

Thus ramets in containers with heterogeneous conditions morphologically specialized to capture locally abundant resources and transport water. And spatial DoL allows the plants to achieve a larger biomass for the whole plant system.

Keywords: allocation, clonal plant, environmental heterogeneity, physiological integration, *Scirpus olneyi*

1) Introduction

Resource sharing among ramets is a common and important feature in clonal plants. Since clonal plants can spread horizontally by vegetative growth, they have the potential to grow across a heterogeneous environment. In clonally growing plants, resource sharing allows buffering against external differences in resource supply and compensatory growth in organs of the clone where ramets are growing at low resource conditions (Hutchings and de Kroon, 1994; Marshall, 1990). Thus, clonal plants can perform well in patchy environments (Alpert, 1995; Alpert and Mooney, 1986; Hutchings, 1999; Wijesinghe and Handel, 1994).

In patchy, heterogeneous environments, resource availabilities may be negatively correlated (Schlesinger *et al.*, 1990; Schulze and Hall, 1982; Young and Smith, 1979; Young and Smith, 1980). In such environments some clonally growing plants show functional specialization to capture locally abundant resources and exchange resources among ramets through physiological integration (Alpert and Stuefer, 1997; Stuefer *et al.*, 1996). Accordingly, in patches with high light but low water availability, ramets invest strongly in leaves, instead of in roots, to capture and assimilate the highly available light resources, while in patches with low light but high water availability ramets strongly invest in roots, instead of in leaves, to exploit the highly available water resources, and through physiological integration, the ramets exchange these resources. Thus, resources are captured where they are most abundant and then transported to places where those resources are in short supply. Physiological integration allows this functional specialization of ramets, and as a consequence, the integrated 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 (hereafter referred to as DoL) in analogy to such a term in Economy.

DoL is a rather new finding, and has not been thoroughly studied. Stuefer *et al.* (1996) focused on the biomass of the ramets and allocation to the aboveground and belowground parts of ramets, but did not investigate water consumption, leaf size or specific leaf area. A larger aboveground biomass does not necessarily mean that plants allocate more biomass to the light-capturing organs. To evaluate that, measurements of leaf area or specific leaf area are important. To evaluate whether plants in a shaded and wet environment specialize in water capturing, water consumption data are important. In this study, we evaluate DoL for a wetland species that is common to brackish wetlands in eastern North America.

Scirpus olneyi demonstrates highly variable patterns of growth in a wide range of brackish wetlands. Thus one genet sometimes seems to be growing in different habitat patches. In the Chesapeake Bay salt marshes, some patches become bare due to disturbances with spring tides, winter storms or animal feeding. Such bare patches have a high light availability, but at the same time, tend to have a higher salinity than the surrounding patches because of evaporation (Bertness *et al.*, 1992). On the other hand, if the light availability is low, salinity will also be low, especially if the habitat is shaded by tree crowns. Since a genet of *S. olneyi* can grow across such different environmental patches and keep its physiological integration intact, this species may benefit from such growth conditions, and possibly shows spatial DoL. To evaluate this, we conducted a garden experiment focusing on light availability and salinity.

2) The Experiment

Test species

Scirpus olneyi A. Gray, a common wetland species in brackish wetlands in eastern North America (McCormick 1982; Drake 1984), was used in this study. In the field (D. Whigham, personal observation), *S. olneyi* demonstrates highly variable patterns of growth and genets appear to place ramets in more than one habitat simultaneously. The presence of individual ramets of a genet in more than one habitat suggest that the species would exhibit DoL. An individual ramets consists of a shoot, roots and a tuber that will produce one or more rhizomes that vary in length (Chapter 2 and 3). The aboveground shoot is either vegetative or reproductive. Shoots are erect, sharply triangular, needle-like, and green with rudimentary leaves.

Methods

In 1999, we collected plant material from brackish tidal marshes at the Smithsonian Environmental Research Center, Edgewater, Maryland, USA. The plants were propagated clonally in the greenhouse at the Uithof Botanical Gardens at Utrecht University, the Netherlands. Because the plants were collected over a wide area, we believe that they were all of different genotypes.

In 2000, we chose healthy clonal fragments, each consisting of a two groups shoots that were connected by a long rhizomes. The oldest group of ramets is hereafter referred to as the Primary Ramet Group (PRG). The newest ramet group is hereafter referred to as the Following Ramet Group (FRG) (Fig. 1). Each pair of ramets groups was subjected to different light (2 levels) and salinity (2 levels) conditions. Each ramet pair was planted in two connected containers (Fig. 1) and the ramets remained connected. Slots were cut in each container to accommodate the rhizome that connected the ramet groups.

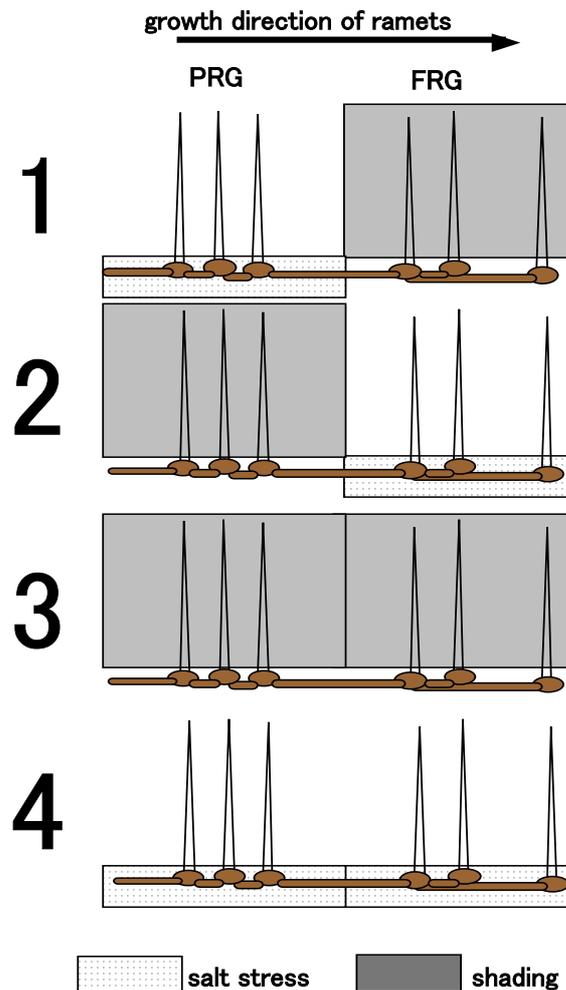


Figure 1. Schematic representation of the four experimental treatments. 1) and 2) are environmentally heterogeneous treatments with a combination of shade & freshwater and ambient light & 1% salt conditions. 3) and 4) are homogeneous treatments with shade & freshwater conditions in (3) and ambient light & 1% salt in (4).

Plastic putty was used to seal the container halves around the rhizome to prevent the movement of water between container halves.

Shading was imposed by placing shade cages, covered with black cloth, over ramets. The cages transmitted 20% of ambient photosynthetic flux density (PPFD). Unshaded plants were exposed to ambient PPFD in the greenhouse (90% of full sunlight). Salinity treatments were 1% salt and freshwater. Low light availability was always coupled to freshwater and high light availability was always coupled to 1% salt (Fig. 1). In the experiment, we accounted for ramet age. In treatment 1, PRG ramets were placed in ambient light and 1% salt while the FRG ramets grew in shade with freshwater (Fig. 1). Treatment 2 was the reverse of treatment 1 (Fig. 1). We used two control treatments in which both groups of ramets were placed in homogeneous conditions (Fig. 1). The planting medium was a 3:1 mixture of peat and sand at 3:1 that received an N-based fertilizer (25 kg-N/ha of OSMOCOTE) at the beginning of the experiment. Water levels were maintained at a constant level by regularly adding tap water.

Experiment

The paired clonal fragments were planted at the beginning of summer and salinity was gradually increased to 1% over a two week period. Shading treatments were added at the end of the two week period. The amount of water added to each container half was measured each time. We harvested the experiment after 4 months of growth. For each treatment, we first we severed the shoots from rhizomes keeping the material from each treatment combination separate. We then removed the belowground biomass from each container and washed the roots and rhizomes free of sediment. We randomly chose 5 shoots from each container half and measured the length, the width of the broadest side of the triangular shoots at about 10 cm above the soil surface, and the hypotenuse of the “triangle” at that point. We used the shoot data to calculate the Green Area (GA) per shoot, defined as the total surface area of the triangular pyramidal shoot. After 72 hours of drying at 68°C, we measured total shoot weight, rhizome weight and calculated the SGA, as GA divided by shoot weight.

Data analysis

One-way ANOVA was used to compare the mean number of ramets, the mean biomass of ramets, the ratio of aboveground to total biomass, [mean water consumption and mean water consumption per unit biomass in the FRG and PRG among treatments. We also used one-way ANOVA to compare mean shoot height and SGA among the four treatments in heterogeneous and the homogeneous environments. Bonferroni-Dunn post-hoc tests were used to compare the differences among treatments. The T-test was used to compare differences between the FRG and PRG per treatment.

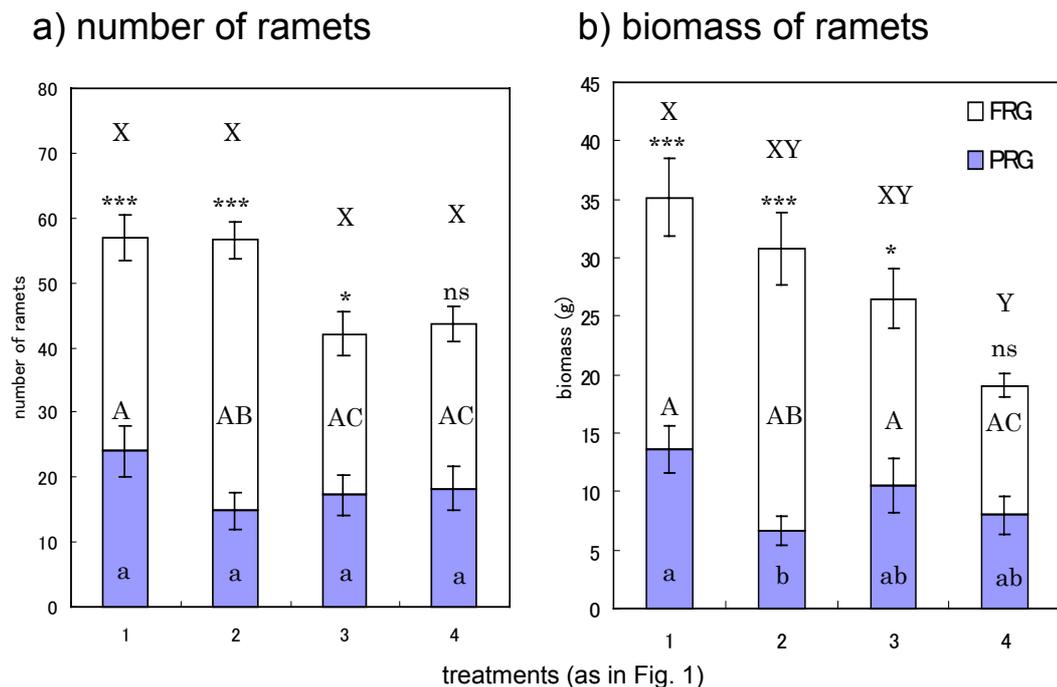


Figure 2. Biomass and number of ramets produced by *Scirpus olneyi* in the four treatments. Treatments as in Fig. 1. Shaded and open bars give mean values of the number of ramets (a) and biomass (b) for the Primary Ramet Group (PRG) and the Offspring Ramet Group (FRG) respectively. Letters inside bars represent differences among the PRG and among the FRG with capitals for the differences among the FRG and lower case for the PRG. Capitals above the bars indicate differences among the PRG and FRG in total number of ramets (a) and biomass (b). Error bars are standard errors of the mean. Different letters indicate statistically significant differences among treatments ($p < 0.0083$) with the Dunn Bonferroni multiple test. Asterisks indicate statistical significance between the PRG and FRG within each treatment as tested by the t test. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns not significant.

3) Results

Biomass Allocation

The total number of ramets did not differ significantly among treatments even though heterogeneous treatments had more shoots (Fig. 2a). Total biomass was also higher in the heterogeneous treatments (Fig. 2b), but the difference was only statistically different between treatments 1 and 4 ($p < 0.083$, Fig. 2b). The FRG ramets had more shoots and greater biomass in treatments 1-3, ($p < 0.05$, Fig. 2a, 2b, also see 3a, 3b).

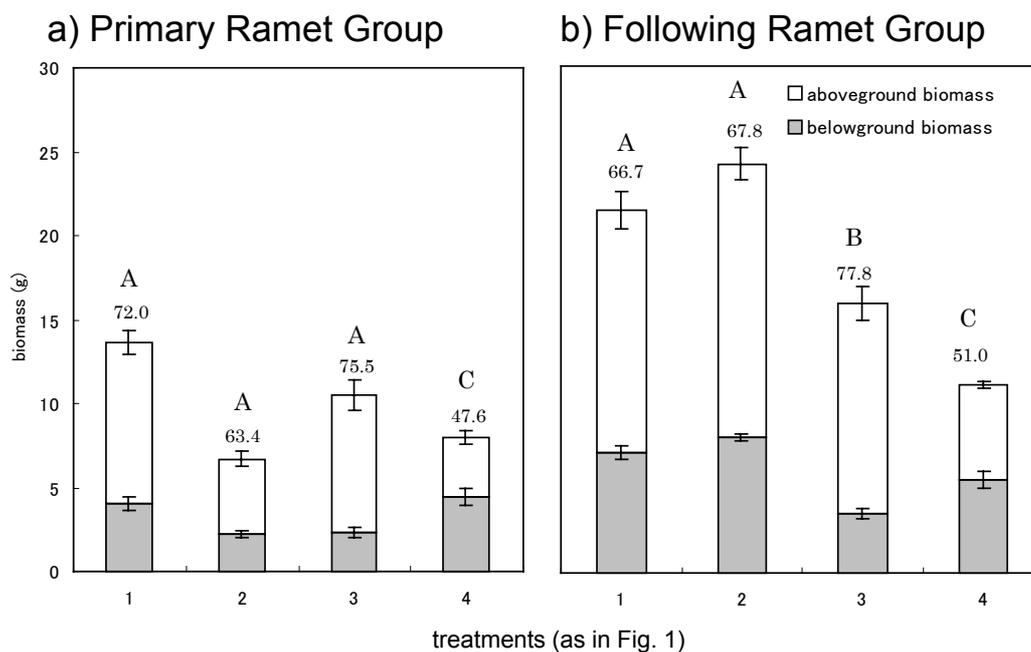


Figure 3. Biomass allocation within ramet groups in the four treatments. Treatments as in Fig. 1. Open and shaded bars give mean values for aboveground and belowground values of the Primary Ramet Group (a) and the Following Ramet Group (b) respectively. Numbers above bars give the ratio of aboveground biomass to total biomass and letters indicate statistical differences among treatments. Error bars are standard errors of the mean biomass. Different letters indicate statistically significant differences among treatments with the Dunn Bonferroni multiple test ($p < 0.0083$).

Aboveground Biomass Ratio

Ramets in treatment 4 had the lowest ratio of aboveground to total biomass for both PRG and FRG ($p < 0.0083$, Fig. 3a), while ramet groups in treatment 3 had the highest ratio (75.5%, statistically significant in treatments 1 and 2 in the FRG at $p < 0.0083$, (Fig. 3b) but not in the PRG (Fig. 3a)). Generally, plants in the homogeneous environments allocated more biomass to the belowground parts, while plants in the homogeneous environments allocated more biomass to the aboveground parts. Ramets in heterogeneous environments had intermediate values for all variables.

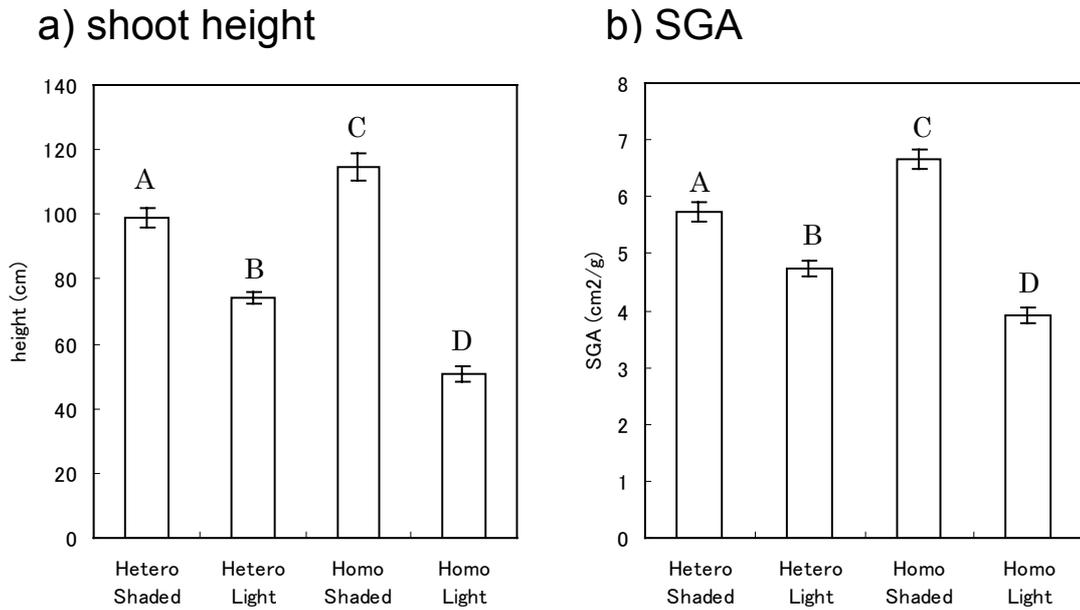


Figure 4. a) Shoot Height and b) Specific Green Area (SGA) with \pm standard errors in the four treatments. Treatments as in Fig. 1. Hetero Shaded is the shaded-freshwater portion of treatment 1. Hetero Light is the ambient light and 1% salt portion of treatment 2. Homo Shaded is treatment 3 and Homo Light is treatment 4. Different letters indicate statistical significance among treatments with the Dunn Bonferroni multiple test ($p < 0.0083$).

Shoot Shape

Shoot height and SGA showed clear differences among treatments (Fig. 4). Shoots in the homogeneous shaded and freshwater treatments were tallest and had the largest SGA ($p < 0.0083$). Shoots in the homogeneous light and saltwater treatments were shortest and had the smallest SGA ($p < 0.0083$, Fig. 4a, 4b). Shoots in the two heterogeneous treatments had intermediate values. Plants in shaded and freshwater conditions, even in the heterogeneous treatments 1 and 2, had taller shoots with larger SGA values than plants in homogeneous environments ($p < 0.0083$, Fig. 4a, 4b).

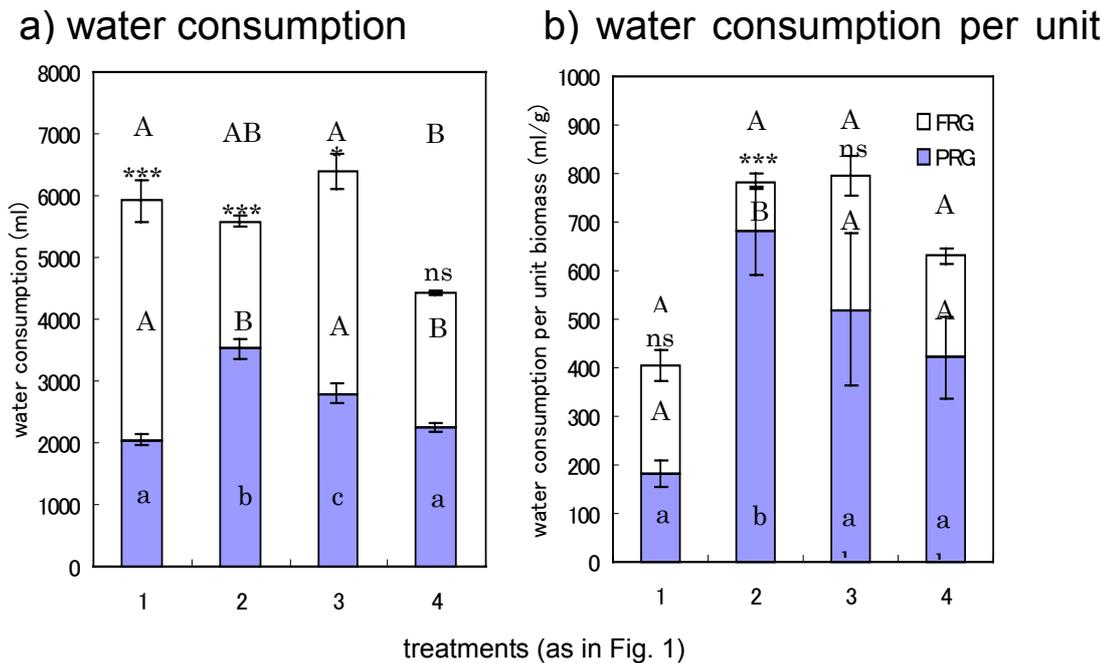


Figure 5. Water consumption of ramets (a) and water consumption per unit biomass (b) with standard errors of the Primary Ramet Group (PRG) and the Following Ramet Group (FRG) in the four treatments. Treatments as in Fig. 1. Letters inside bars indicate differences among the PRG and among the FRG, and letters outside bars represent differences among the sum of the PRG and FRG in water consumption (a) and water consumption per unit biomass (b). Different letters indicate statistical significance among treatments with the Dunn Bonferroni multiple test ($p < 0.0083$). Asterisks indicate statistical significance between the PRG and FRG with the t test. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns not significant.

Water Consumption

Among PRG, ramets growing in the shaded and freshwater conditions in treatment 2 consumed most water ($p < 0.0083$, Fig. 5a), and ramets in the light and 1% salt portions of treatments 1 and 4 consumed least water ($p < 0.0083$, Fig. 5a). Among the FRG, ramets in the shaded and freshwater halves of treatments 1 and 3 consumed more water than plants in ambient light and 1% salt halves of treatments 2 and 4 ($p < 0.0083$, Fig. 5a). Water consumption per unit biomass by ramets plants in ambient light and 1% salt halves of treatments 1 and 2 was less than plants in treatment 4 (statistically significant in FRG, tendency in PRG).

4) Discussion

Plants in shaded and freshwater conditions, both in the homogeneous and heterogeneous treatments, allocated proportionally more biomass to aboveground shoots than plants in ambient light and 1% salt (Fig. 4). This response occurred because ramets compensated for resources that were locally limiting (*i.e.*, light) and allocated more biomass to the organ that has to capture the most limiting resource (Aung, 1974; Chapin, 1980; Iwasa and Roughgarden, 1984). *Scirpus olneyi* also showed functional specialization in shoots as shoot height and SGA were greatest in plants in shaded freshwater conditions and

lowest in plants grown in light and 1% salt (Fig. 3). These results confirm that DoL results in plants specialization to improve light capturing capacity in shaded and freshwater conditions. Ramets in the conditions of treatments 1 and 2 had proportionally more biomass aboveground than the ramet groups in treatment 2. Compared with plants in homogeneous treatments, plants under heterogeneous treatments had increased shoot height and SGA in ambient light and 1 % salt conditions and decreased shoot height and SGA in shaded and freshwater conditions (Fig. 3). These results suggest that plants grown in ambient light and 1 % salt in heterogeneous environments specialize in light capture instead of water consumption. Since the plants under heterogeneous treatments reached higher biomass than the plants under homogeneous conditions we can conclude that *Scirpus olneyi* shows spatial DoL in the sense of Stuefer *et al.* (1996).

If DoL is operative, we expect that ramets growing in ambient light and 1 % salt halves of the heterogeneous environments (*i.e.*, treatments 1 and 2), would obtain water from the shaded and freshwater halves, resulting in proportionally less biomass allocation to belowground parts in the ambient light and 1% salt halves of treatments 1 and 2 compared to treatment 4. Figure 4 shows that the expected outcome was observed. We also found that water consumption per unit biomass in ambient light and 1% salt halves of treatments 1 and 2 was less than water consumption in treatment 4. These results also support the conclusion that in treatments 1 and 2, *Scirpus olneyi* benefited by DoL.

Stuefer *et al.* (1996) studied spatial DoL in *Trifolium repens* and showed clear differences in allocation pattern and biomass. In their study, plants grown under patchy conditions produced 67% more biomass and 72% more ramets than plants under homogeneous conditions. In our study, plants under heterogeneous conditions had, on average, 44% more biomass and 32% more offspring ramets than plants under homogeneous conditions. The lower values for % biomass and number of ramets produced indicated that the contrast in environmental conditions in our experiment was less than those in Stuefer *et al.*'s experiment (Stuefer *et al.*, 1996).

In Chapter 7, we studied the spatial division of labor with a mathematical model and found that the interplay between the cost of water transportation, the contrast in resource availability and the efficiency of resource capturing, determine the degree of specialization of the ramets in clonal plants. They also found that the allocation pattern between above and belowground reacts more sensitive than total biomass and that even if plants did not show an increase in biomass, the allocation pattern could change drastically. Our experimental results showed that the ratio of aboveground to total biomass was clearly different among treatments while biomass totals and number of ramets showed much weaker differences. These results confirm the finding in Chapter 7.

5) Acknowledgment

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Chapter 7:

Spatial division of labor -a model study-

IKEGAMI Makihiko and Marinus J.A. WERGER

Summary

Interconnected two ramets, in which each ramet grows in different environments where resource availability distributed inversely corresponding can show spatial division of labor (DoL): ramets under light and dry condition allocates biomass to the leaves while ramets under shaded and wet allocates to the roots and possibly achieve higher biomass than ramets in single conditions. It seems more profitable if the ramets fully specialized in capturing the locally abundant resource, but full specialization is hardly to be observed. To evaluate the degree of specialization in ramets, a mathematical model was constructed. The model is based on biomass growth and simulates water and carbohydrates flow through physiological integration. Plants allocate photosynthesized carbohydrates to organs to optimize photosynthesis in the next time steps. We simulated two-ramet systems under various contrasts in resource availability.

In our model, the interplay between the cost of water transport, the contrast in resource availability and the efficiency of resource capturing, determine the degree of specialization of the ramets. If the cost is larger than benefit through the DoL, modeled plants do not show DoL. The single plant allocates biomass to the organ that captures the resource locally in short. A single plant achieves a lower biomass in a patch with a higher contrast in the aboveground and belowground growth conditions. Because the plant system can achieve a larger biomass in contrasting environments, the plant system can benefit from DoL under the high costs of water transport, if the contrast in resource availability is high. The degree of specialization increases as the contrast in resource availability increases, and full specialization occurs when the contrast is high. We also found the efficiencies in resource capturing of each organ is important. When a plant reaches a larger size, then many costs, associated with support, maintenance and aging, increase and thus the efficiencies in resource capturing and transport to each organ decrease. If the contrast in resource availability is not high, the organ in the poor-quality condition can capture more resources per unit biomass than a bigger organ in the better-quality condition, because the decrease in efficiency in the organ in the better-quality condition is strong at larger biomass. Thus, in such a situation the plant system also allocates biomass to the organ in the poor-quality condition.

Keywords: allocation, clonal plant, environmental heterogeneity, mathematical model physiological integration

1) Introduction

Environmental heterogeneity is a non-uniform distribution of environmental factors, such as water, light, nutrients, or plant density. Since clonal plants can spread horizontally by vegetative growth, they have the potential to grow across a heterogeneous environment. It is for this reason that small-scale environmental heterogeneity has been getting more and more attention in studies of clonal plants (Alpert, 1995; Hutchings and Wijesinghe, 1997; Shipley and Meziane, 2002; Stuefer and Hutchings, 1994). Light and water are primary resources for plant growth and their availability may be highly variable over short distances. In the field, generally, higher light availability tends to correlate with lower water availability, whereas lower light availability tends to correlate with higher water availability (Schlesinger *et al.*, 1990; Schulze and Hall, 1982; Young and Smith, 1979; Young and Smith, 1980). Since plants need both resources for growth, the environmental conditions of some patches can be favorable for growth in one respect but at the same time unfavorable in another respect.

In different environments, a plant can change its biomass allocation pattern in response to the actual environmental conditions. Clonal plants and non-clonal plants show different biomass allocations in heterogeneous environments because in a clonal plant some interconnected ramets may grow under different environmental conditions while non-clonal plants grow in a single environmental patch. Basically, a non-clonal plant tends to allocate more biomass to that organ that meets the severest shortage of resources because that limiting resource controls the rate of photosynthesis (Aung, 1974; Chapin, 1980; Hutchings and de Kroon, 1994). For instance, plants will allocate proportionally more biomass to the belowground organs in patches with high light and low water availability, and allocate proportionally more to the aboveground organs in patches of low light and high water availability (Brouwer, 1983; Iwasa and Roughgarden, 1984; Werger, 1983). Such a pattern of investment is considered compensatory investment.

On the other hand, in clonal plants, ramets in patches with high light and low water availability can maintain a proportionally large investment in leaves, if they are able to import water from connected ramets in a patch with low light and high water availability; under such conditions carbohydrates may be transported the other way around (Alpert and Mooney, 1986). Thus clonal plants are able to share resources and compensate for local shortage of resources by drawing from other ramets (de Kroon and Knops, 1990; Dong, 1996; Stuefer *et al.*, 1996). Resource sharing allows buffering against external differences in resource supply and compensatory growth in organs of the clone where ramets are growing in low resource conditions (Hutchings and de Kroon, 1994; Marshall, 1990). Thus, clonal plants can perform well under conditions of patchy heterogeneity (Alpert, 1995; Alpert and Mooney, 1986; Hutchings, 1999; Wijesinghe and Handel, 1994; Wijesinghe and Whigham, 2001).

In some recent experiments, clonal plants showed another response. In some clonal plants, ramets in environments with negatively correlating availability of two or more resources show functional specialization to capture locally abundant resources and exchange resources among ramets through physiological integration (Alpert and Stuefer, 1997; Stuefer *et al.*, 1996). Accordingly in patches of high light but low water availability, ramets invest strongly in leaves, instead of in roots, to capture and assimilate the highly available light resources, while in patches of low light but high water availability ramets strongly invest in roots to exploit the highly available water resources. These studies demonstrate that through physiological integration, ramets are able to

exchange resources. Thus, resources are captured where they are most abundant and then are transported to where they can be used best. Physiological integration allows ramets to specialize in capturing the locally abundant resources, and as a consequence the integrated clone performs significantly better in spatially heterogeneous than in homogeneous environments (Alpert and Stuefer, 1997; Hutchings and Wijesinghe, 1997). Stuefer *et al.* (1994) referred to this allocation pattern as spatial Division of Labor (DoL), a term that has analogy in economic theory.

Yet, there are several questions that have not been answered. One of them is the degree of specialization. Garden experiments showed that each ramet specializes for 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.*, 1994). Intuitively, however, it seems more profitable if the plants locally allocate all biomass to those organs that capture the locally abundant resource.

To evaluate the degree of specialization in plants growing according to a DoL program under various environmental conditions, a theoretical model can be a helpful tool. Stuefer *et al.* (1998) studied the optimal root-shoot allocation pattern and water transport in clonal plants with a mechanistic model and found that clonal plants showed full specialization only at very strong contrast in the resource availabilities of the two interconnected ramets. Their model is designed to determine an optimal root-shoot allocation pattern of ramets under a given set of conditions. But the model gives an instantaneous evaluation and does not include the dynamic process of plant growth (Stuefer *et al.*, 1998). Since the DoL concerns the dynamic process of biomass allocation among ramets and organs, it is important to evaluate biomass allocation throughout the period of growth. In our study, to evaluate the degree of specialization of ramets growing under environmental heterogeneity, we constructed a simple plant growth model. The model is designed to determine optimal shoot and root investments, 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.

2) Model

The modeled plant consists of two ramets, connected by a rhizome (or stolon). Each ramet consists of two parts, aboveground and belowground organs (Fig.1). The aboveground organs capture light and the belowground organs capture water. The process of photosynthesis needs light and water, and the output is carbohydrates. The rate of photosynthesis can be described by several equations, but we use the equation from Iwasa and Roughgarden (1984) in this study. If the two ramets are not physiologically integrated, the photosynthetic rate of each individual ramet can be described by equation 1 (Iwasa and Roughgarden, 1984).

$$f(x,y) = \left(\frac{1}{L \times x^b} + \frac{1}{W \times y^c} \right)^{-1} \quad (1)$$

In that equation, x is the biomass of the aboveground organ and y is the biomass of the belowground organ; L is light availability, W is water availability, and b and c are the efficiencies of capturing the resources by each organ. For a maximal photosynthetic rate,

the plant needs both water and light at a certain ratio, thus the plant should allocate biomass to the two organs in a balanced way. Iwasa and Roughgarden (1984) showed that a modeled plant first allocates all biomass to one organ to repair any functional imbalance of the plant and subsequently biomass is allocated at a steady ratio to keep the balance to maximize its photosynthetic gain.

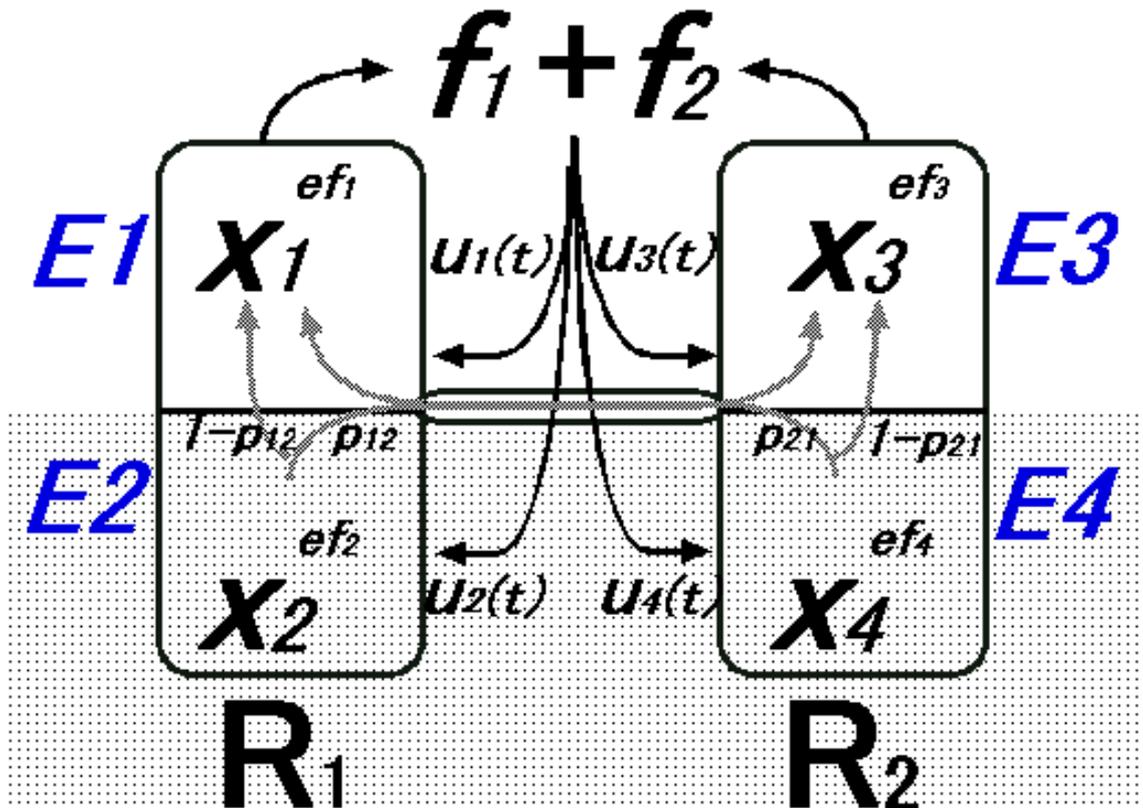


Figure 1. Schematic representation of the biomass and allocation pattern in the modeled plant system. Each ramet (R_1 and R_2) consists of aboveground and belowground organs. x_1 and x_3 represent the biomass of the aboveground organs, and x_2 , and x_4 the biomass of the belowground organs. The resource availability at organ i is represented by E_i and organ i captures resources with an efficiency of ef_i . Water can be transported between ramet 1 and ramet 2 at a p_{12} ratio, or p_{21} ratio depending on the direction of transport. The photosynthetic rates are represented by f_1 and f_2 in ramet 1 and ramet 2, respectively, and the modeled plant system allocates carbohydrates to each organ at ratios $u_i(t)$ at time step t .

From eq.1, we develop an equation that describes the photosynthetic rate for a plant system with two interconnected ramets.

$$f_1 = \left(\frac{1}{E_1 \times x_1^{ef_1}} + \frac{1}{E_2 \times (1 - p_{12}) \times x_2^{ef_2} + E_4 \times D \times p_{21} \times x_4^{ef_4}} \right)^{-1} \quad (2-1)$$

$$f_2 = \left(\frac{1}{E_3 \times x_3^{ef_3}} + \frac{1}{E_4 \times (1 - p_{21}) \times x_4^{ef_4} + E_2 \times D \times p_{12} \times x_2^{ef_2}} \right)^{-1} \quad (2-2)$$

Eq.2-1 and 2-2 give the rate for ramets 1 and 2 respectively. x_i is the size of organ i , E_i is the resource availability for organ i , and ef_i is the index of resource capturing efficiency by organ i ($i=1,2,3,4$). Aboveground biomass is represented by x_1 and x_3 and x_2 and x_4 are belowground biomass of ramet 1 and ramet 2 respectively. Through physiological integration, water moves from one ramet to the other, and p_{12} is the ratio of water transport from ramet 1 to ramet 2, and p_{21} is that ratio from ramet 2 to ramet 1. Due to water loss between two ramets, we define the cost of water transport as the ratio D , thus water can reach the other ramet with the ratio $1-D$.

$$f(x_1, x_2, x_3, x_4) = f_1 + f_2 \quad (3)$$

Eq. 3 gives the total photosynthetic production of the two ramets. To find the optimal growth path, we use dynamical programming with numerical computer simulation (Bellman, 1957). In the simulation, the optimal water allocation ratio in the modeled plant system is determined per time step for a maximization of eq.3, the gain of carbohydrates. At time step t , the modeled plant system allocates new biomass (carbohydrates) to organ i at a ratio $u_i(t)$. The allocations to each organ are given in eq. 4.

$$\frac{dx_i}{dt} = u_i(t) f(x_1, x_2, x_3, x_4) \quad (4)$$

$$u_1(t) + u_2(t) + u_3(t) + u_4(t) = 1 \quad (5)$$

Each $u_i(t)$ varies between 0 to 1 and the sum of all $u_i(t)$ is 1 (eq.5). The modeled plant system allocates biomass at time step t to maximize photosynthetic gains during the next time step $t+1$. At the beginning, every organ starts with biomass 1 ($x_i(1)=1$) and once biomass is allocated it can not be reallocated. For simplicity, we ignore the cost of biomass allocation. Throughout all simulations, ramet 1 is always in a patch with a high light and low water availability while ramet 2 is in a patch with a low light and high water availability.

3) The simulations

Contrasting resource availability

First we evaluate the effect of increasing contrast in resource availability at an inversely corresponding resource distribution with and without physiological integration. We define the contrast in resource availability (C) as the ratio of resource availability to each organ in a ramet ($C = E_1 / E_2 = E_4 / E_3$). The sum of the aboveground and belowground resource availabilities for each ramet is constant and set at 13. We evaluate this for contrasts in resource availability (C) from 1 to 10 and we ignore the cost of water transport.

If the two ramets are not physiologically integrated, then each ramet specializes in capturing the resource that is locally in short supply (Fig. 2a). Ramet 1, in the patch with high light and low water availability, allocates more biomass to its belowground organ and ramet 2, in the patch with low light and high water availability, allocates more biomass to its aboveground organ. As the contrast in resource availability increases, the modeled plant system allocates more biomass to the organs that grow under poor quality conditions and the total biomass of the two ramets decreases (Fig. 2a).

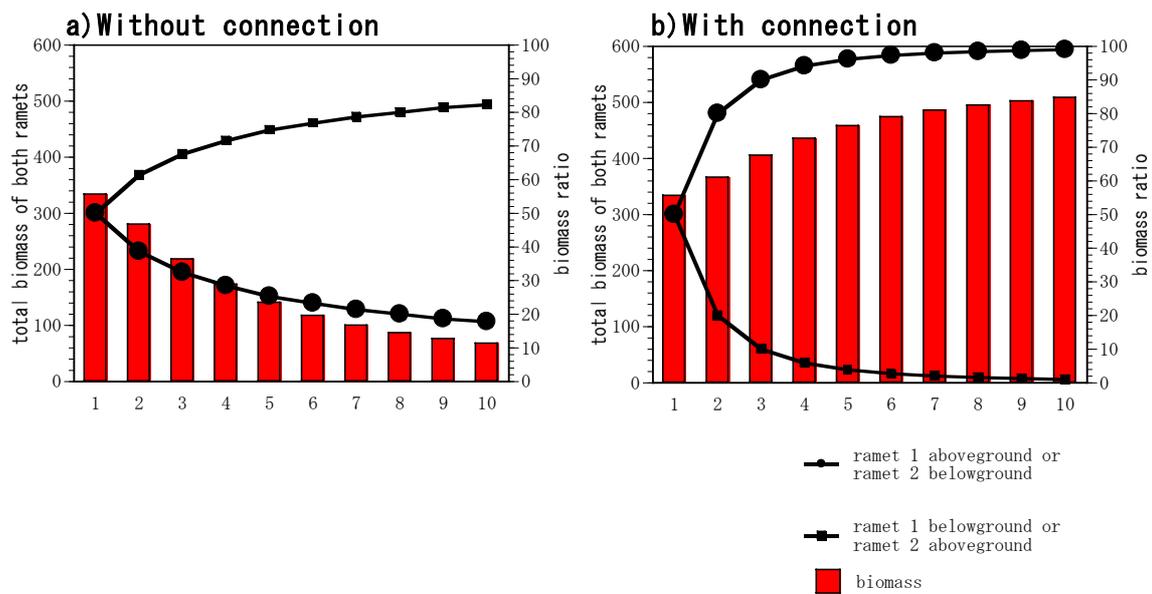


Figure 2. The total biomass of two ramets and the ratio of the biomass of each organ to the total biomass of ramet 1 a) without physiological integration, b) with physiological integration, as a function of contrast in resource availability. The left y-axis scales the total biomass of two ramets, and the right y-axis scales the ratio of the biomass of each organ to the total biomass. Closed squares show the ratio of the belowground biomass to the total biomass of ramet 1 and the closed circles show the ratio of the aboveground biomass to the total biomass of ramet 1. Settings are $D=0$, $ef_i=0.5$.

If the two ramets are physiologically integrated, then each ramet specializes in capturing the locally abundant resource. Ramet 1 allocates more biomass to its aboveground organ, and ramet 2 allocates more biomass to its belowground organ (Fig. 2b). As contrast in resource availability increases, the plant allocates more biomass to the organ that grows under better quality conditions and the total biomass of the two ramets increases (Fig. 2b). At the strongest contrast in resource availabilities ramets which are not physiologically integrated allocate about 80% of their total biomass to the organ that grows under poor conditions. If the plants are physiologically integrated, the ramets allocate almost 100% of their total biomass to the organ that grows under better conditions (Fig. 2b). This result suggests that ramets should highly specialize at strongly contrasting resource availabilities.

The cost of water transport

We also evaluate the cost of water transport, D at moderate resource availability and inversely correspondent distribution of resources. Resource availability levels for each organ, E_1, E_2, E_3 and E_4 are set at 9, 4, 4 and 9, respectively.

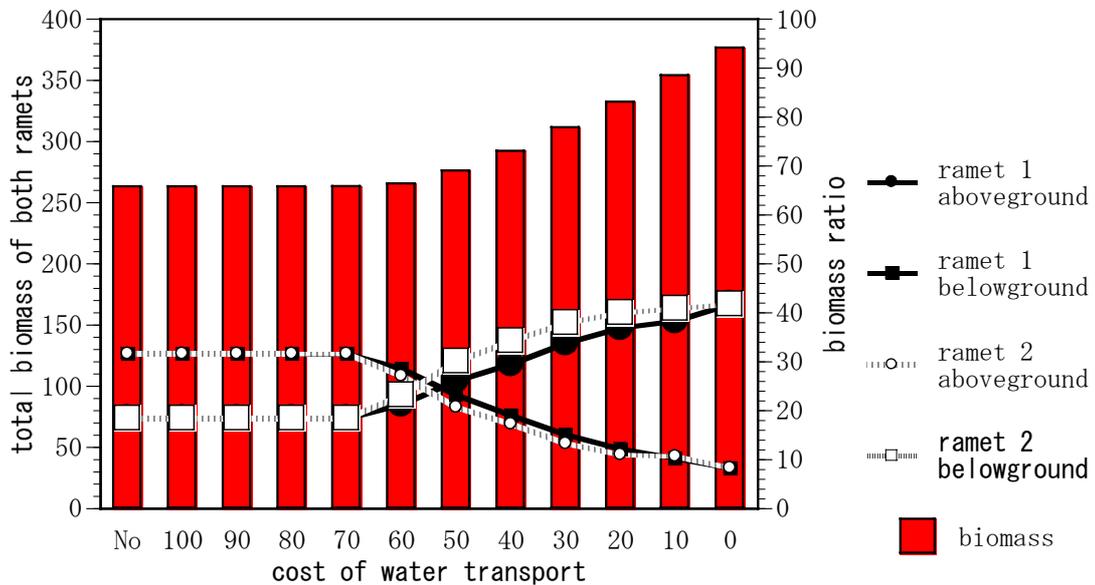


Figure 3. The total biomass of two ramets and the ratio of the biomass of each organ to the total biomass of the plant system at symmetric resource distribution, as a function of the cost of water transport (x-axis, No at the x-axis represents the results when there is no physiological integration of the ramets). The left y-axis scales the total biomass of the two ramets and the right y-axis scales the ratio of the biomass of each organ to the total biomass. The closed and open squares show the ratio of the belowground biomass to the total biomass of ramet 1 and ramet 2, respectively, and the closed and open circles show the ratio of the aboveground biomass to the total biomass of ramet 1 and ramet 2, respectively. Settings are $E_1 = E_4 = 9, E_2 = E_3 = 4, ef_i = 0.5$.

If the cost of water transport is high, plants do not show DoL (*i.e.*, the modeled plant allocates more biomass to the organs that grow under poor quality conditions (Fig. 3)). When the plant does not show DoL, the total biomass of the two ramets and the allocation ratio to each organ show the same values as the two ramets without physiological integration (Fig. 3). As the cost of water transport decreases, the plant shows an increasingly stronger DoL, achieves a larger total biomass and allocates more biomass to the organs that grow under better quality conditions (Fig. 3). If there are no costs of water

transport, the biomass allocation to the two ramets is equal, and the allocation to aboveground and belowground organs is inversely symmetric, but with costs, the allocation pattern becomes asymmetric (Fig. 3). With increasing cost of water transport, one of the ramets receives less water thus the plant increases its allocation of biomass to the belowground organ of the ramet under wet conditions to compensate for the water shortage. As a result the plant transports enough water to the ramet under dry conditions. On the other hand, the plant does not have to increase its allocation to the aboveground organs of the ramets because there is no translocation cost of carbohydrates. As a consequence, the plant shows an asymmetric allocation pattern.

Fig. 4 shows the relationship between contrasting resource availability and the total biomass of the two-ramet plant system e.g. the allocation balance between aboveground and belowground biomass in ramet 1 at different transport costs. If the cost of water transport is high and/or the contrast in resource availability is low, the plant does not show DoL. Under low contrast and high cost of transport, water capturing and transport from one ramet to the other costs more than water capturing in the other ramet. Under those conditions, water transport is not beneficial. As a result, each ramet specializes to alleviate the local shortage of resources and grows independently. If the cost in water transport is lower and/or contrast of resource availability is high, then the plant shows DoL. At high contrast, the water availability in one ramet is limiting, thus the plant profits by transporting water from the other ramet to the first ramet even when the transport is costly. Thus the plant allocates more biomass to the belowground organ of the second ramet (not shown) and the aboveground organ in the first ramet (Fig. 4a) to capture the locally most abundant resources. As a result of this cooperative growth pattern, the plant performs better and attains a larger biomass (Fig. 4b).

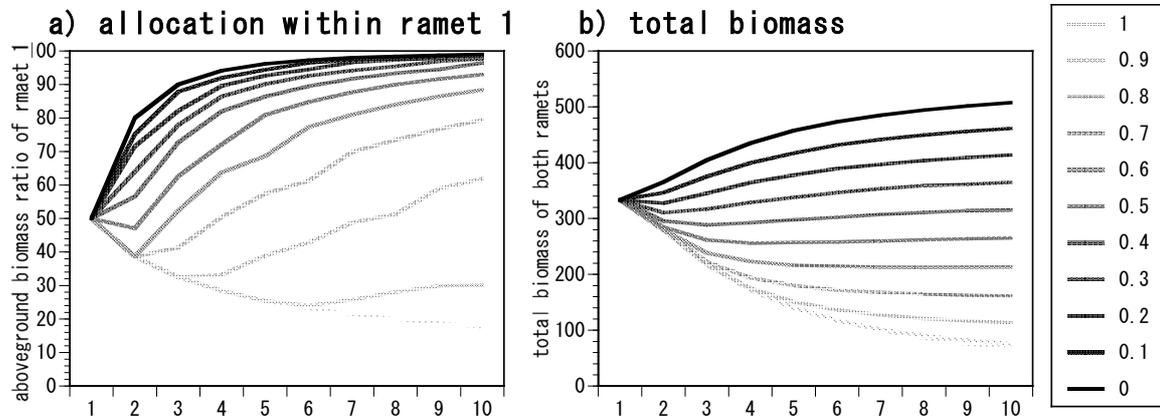


Figure 4. a) Ratio of the aboveground biomass to the total biomass of ramet 1 and b) total biomass of the two-ramets plant system, as a function of contrast in resource availability at the different costs of water transport. The darker the line is, the less the transport costs. Setting is $ef_i = 0.5$.

Asymmetric conditions

To evaluate asymmetric resource availability, we set the resource availability levels for each organ E_1 , E_2 , E_3 and E_4 at 8, 7, 5 and 6, respectively. Thus, we keep a negatively co-varying distribution of resources, but the aboveground and belowground conditions for ramet 1 are better than those for ramet 2.

If the costs of water transport are high, the modeled plant system does not show DoL. The ramets do not exchange water and each ramet specializes in capturing the resources that are locally in short supply. Since our plants can allocate carbohydrates without translocation costs, the plant with physiological integration allocates slightly more biomass to ramet 2 than a plant without physiological integration (see “No” on the x-axis in Fig. 5). If the cost of water transport is low, the modeled plant shows DoL. The total biomass is slightly higher than that of a no-DoL plant and each ramet specializes in capturing the locally abundant resource (Fig. 5). Because the contrast in resource availability is not strong, the plant systems do not strongly benefit from DoL.

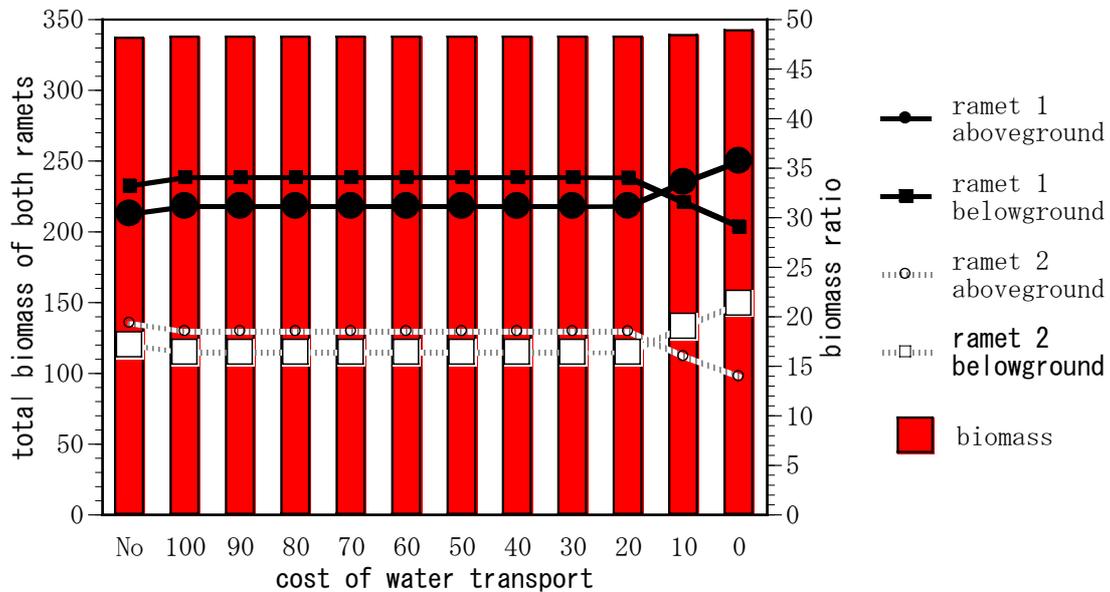


Figure 5. The total biomass of two ramets and the ratio of the biomass of each organ to the total biomass of the plant system at asymmetric resource distribution, as a function of the cost of water transport (x-axis, No at the x-axis represents the result when there is no physiological integration of the ramets). The left y-axis scales the total biomass of the two ramets and the right y-axis scales the ratio the biomass of each organ to the total biomass. The closed and open squares show the ratio of the belowground biomass to the total biomass of ramet 1 and ramet 2, respectively, and the closed and open circles show the ratio of the aboveground biomass to the total biomass of ramet 1 and ramet 2, respectively. Settings are $E_1=8$ $E_2=7$, $E_3=5$ and $E_4=6$, $ef_i=0.5$.

The resource capturing efficiency

To evaluate the effect of varying the resource capturing efficiency, we change the efficiency index ef_i in eq. 2. The cost of transport is 0 and the resource availability levels for each organ E_1, E_2, E_3 and E_4 are set at 9, 4, 4 and 9, respectively.

As the efficiency index increases, the plant tends to show a stronger specialization of the ramets. When efficiency approaches 1, the plant allocates all biomass to the organs that grow under better conditions (Fig. 6), and the total biomass of the two-ramet system increases exponentially. If the efficiency index is less than 1, the resource capturing efficiency decreases as the biomass increases. As a result, the organs that grow under lower quality conditions can have high resource capturing efficiencies when those organs have small biomass values. It means that those organs may need less biomass to capture a fixed amount of resources than other larger organs that grow under better conditions. Thus the plant also allocates biomass to organs that grow under lower quality conditions. As the efficiency index approaches 1, the decrease in efficiency with size is weaker, and as a consequence the plant tends to allocate more biomass to organs that grow under better quality conditions. Ultimately, this leads to the full specialization of ramets for capturing locally abundant resources.

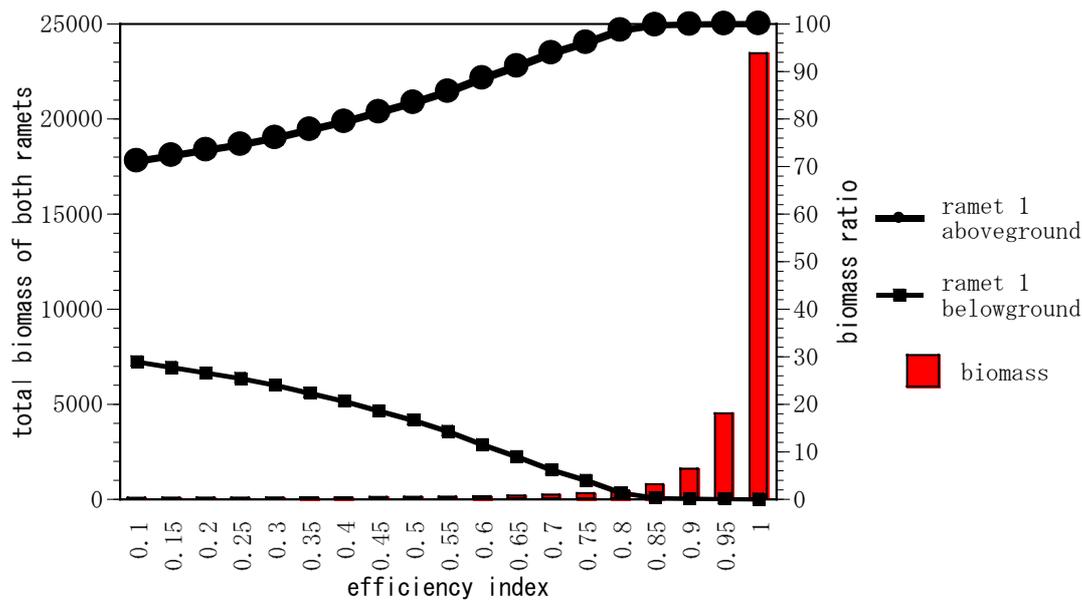


Figure 6. Total biomass of the two-ramets plant system (left y-axis) and the ratio of the biomass of the aboveground and belowground organs to the total biomass of ramet 1 (right y-axis) as a function of the efficiency index (x-axis). Closed squares show the ratios for the belowground organ and closed circles the ratios for the aboveground organ of ramet 1. Settings are $E_1 = E_4 = 9$, $E_2 = E_3 = 4$, $D = 0$.

4) Discussion

Generally if two ramets cannot exchange resources due to lack of physiological integration, or due to high costs of water transport, each ramet works as a single plant, and the single plant allocates biomass so as to maximize its own photosynthetic gains. A single plant achieves a lower biomass in a patch with a higher contrast in the aboveground and belowground growth conditions (Fig. 2a). This is because the resource that is locally short is the limiting factor for plant growth and the plant allocates more biomass to the organ that has to capture the most limiting resource (Aung, 1974; Chapin, 1980; Hutchings and de Kroon, 1994; Iwasa and Roughgarden, 1984; Shipley and Meziane, 2002). If two interconnected ramets can exchange resources, then the whole plant system allocates biomass so as to maximize photosynthetic gains of the whole plant system. If two interconnected ramets grow across a patchy environment where resources are distributed reciprocally, the ramets together achieve a larger biomass and show a different biomass allocation pattern because of the Division of Labor (Fig. 2b). In clonal plants, the interplay between the cost of water transport, the contrast in resource availability and the efficiency of resource capturing, determine the pattern in allocation to organs, in other words, the degree of specialization of the ramets.

Many studies have shown that clonal plants transport water from ramets in wet patches to ramets in dry patches (Alpert, 1990; de Kroon *et al.*, 1996; Stuefer, 1995). But usually, the transport does not work perfectly due to water loss and hydraulic resistance in the vessel (Stuefer, 1995; Stuefer *et al.*, 1996; Stuefer *et al.*, 1998; Stuefer and Hutchings, 1994), which depends on the vessel diameter and the distance between two ramets (Lewis, 1992; Lewis and Boose, 1995). Our modeled plants do not show DoL if the cost of water transport is high. This result agrees with the model study by Stuefer *et al.* (1998). They pointed out that the optimal allocation patterns are very sensitive to the conductivity of the internode, since that will control the water exchange process. We show that if the cost is high, the modeled plant needs to allocate more biomass to the belowground organ of the ramet in the wet patch. If the biomass of belowground organs is larger than the biomass the plant system can gain through DoL, then it is more beneficial not to operate through DoL. But if the contrast in resource availability and the costs of water transport are high, the plant system can benefit from DoL. This is because the plant system can achieve a larger biomass in contrasting environments.

In our model, the degree of specialization increases as the contrast in resource availability increases (Fig 2b), and full specialization occurs when the contrast is high. We also found full specialization when the efficiency index is close to 1 (Fig. 6). A complete morphological specialization of the interconnected ramets to capture resources may occasionally be observed in some clonal plants, but it has not been a common characteristic of clonal plants under experimental or field conditions (Jonsdottir and Callaghan, 1989; Stuefer *et al.*, 1998). Stuefer *et al.* (1998) suggested that clonal plants may be unlikely to show full specialization, because of the risk of severing the connection which would put the fully specialized ramets in a disadvantageous situation.

In this study, we show the importance of resource capturing efficiency. When a plant reaches a larger size, then many costs, associated with support, maintenance and aging, increase and thus the efficiencies of resource capturing and transport to each organ decrease. As a result, plant biomass growth generally follows a logistic curve. In this model, we use a hyperbolic function in the equation, for reasons of simplification. And we set the efficiency index of resource capturing at smaller than 1, thus the efficiency of

each organ decreases as the biomass of each organ increases. If the environmental heterogeneity is not highly contrasting, the organ in the poor-quality condition can capture more resources per unit biomass than a bigger organ in the better-quality condition, because the decrease in efficiency in the organ in the better-quality condition is strong at larger biomass. Thus, in such a situation the plant system also allocates biomass to the organ in the poor-quality condition. All available experiments and model studies of DoL assumed a high contrast in environmental heterogeneity (Alpert and Mooney, 1986; Alpert and Stuefer, 1997; Hutchings and Wijesinghe, 1997; Stuefer *et al.*, 1994; Stuefer *et al.*, 1998). In a clonal plant system in the field, the patch quality can be highly variable on short distance but the contrast in environments of adjacent ramets is unlikely to be strong. Consequently, ramets should not show extreme specialization and thus Division of Labor may be rather difficult to observe in the nature. Our results suggest, however, that even at a lower contrast clonal plants can change their allocation balance drastically and show DoL.

5) Acknowledgment

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Chapter 8:

General Discussion and summary
- Functional specialization of ramets in a
clonal network -

IKEGAMI Makihiko

Functional specialization of ramets in Clonal plants has received little attention (Alpert and Stuefer, 1997; Charpentier and Stuefer, 1999; Stuefer, 1998). Yet, differential specialization of ramets for different functions may be highly beneficial in clonal plants. Due to specialization, each ramet can work efficiently for specific tasks, *e.g.* to exploit resources that are locally abundant (Alpert and Stuefer, 1997; Eriksson and Jerling, 1990), or to escape from patches of poor quality with long spacer ramets or to exploit patches of high quality with short spacer ramets (de Kroon and Knops, 1990; Harper, 1985; Hutchings and De Kroon, 1994; Hutchings and Slade, 1988; Schmid and Bazzaz, 1992), or function as a storage organ (Charpentier and Stuefer, 1999).

Non-clonal plants can not move from where they germinate and grow. Thus regardless of the local conditions, individual plants adjust themselves to their environment or die. In clonal plants, on the other hand, each ramet has the capability to perform all of the developmental and functional processes of growth itself, but each ramet, as part of the whole interconnected network of ramets, can also function as a unit within the network and individuals within the network can specialize for specific tasks. In a clonal network, the genet does not have to produce seeds in an environment of poor quality because ramets can escape the local habitat through vegetative propagation, and potentially can reach better quality patches and start producing seeds there. Even if one resource is short supply in one patch but abundant in another, inter-connected ramets can capture resources by placement of ramets in the resource patch and transporting it to ramets in the poor resource patch. Through physiological integration, all ramets in a network can support each other, and thus one ramet can specialize on a specific task, and other ramets on other tasks.

In this thesis, I hypothesized that *Scirpus olneyi* produces functionally specialized ramets and performs better under heterogeneous conditions. I especially focused on specialization in vegetative spread, sexual or asexual propagation and resource capturing. *S. olneyi* occurs in a range of salt marsh habitats and shows a high plasticity in architecture. Since *S. olneyi* produces two morphologically different types of ramets, Long Rhizome Ramets (LRRs) and Short Rhizome Ramets (SRRs), the species is able to develop different combinations of LRRs and SRRs under different conditions.

These facts suggest that this species is able to modify its growth pattern in different environments, and different ramets are capable of specializing in different tasks. I studied *S. olneyi* 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 – functional specialization in vegetative spread

We hypothesized that two types of ramets, LRRs and SRRs, are specialized for different tasks for spreading in space and time. The garden experiments showed that plants tended to produce more SRRs and branch frequently in the high quality patches, while plants produced LRRs and branch less in the low quality patches. These results suggested that the task of SRRs was to consolidate occupancy and exploit favorable habitats while the task of LRRs was to explore new and possibly high-quality habitats (de Kroon and Hutchings, 1995; de Kroon and Knops, 1990; Dong and De Kroon, 1994; Hutchings and De Kroon, 1994). This result confirms the notion that individual ramets are functionally specialized to perform different tasks.

Unlike the garden experiments, plants in the field observation did not show clear patterns of ramet production (Chapter 3). Based on the garden experiment, we expected that plants would branch more frequently in environments where resources were potentially greater. The *Scirpus* High Marsh community seems to occur in an environment of better quality because here plants produced the largest number of sexual shoots. The ramets in this community, however, branched less frequently than in other communities. On the other hand, in the *Spartina* Community, where plants were growing in full sun and where shoot densities were low, *S. olneyi* produced almost no seeds. These two communities occur in very short distance from one another and may have similar environments except that they differ in density and associated species. Does density or species assemblage affect the propagation strategy of this species? This led us to study the density effects on sexual and vegetative propagation (Chapter 4).

Another theme of Chapter 3 is to evaluate differences in seasonal patterns among functionally specialized ramets. We hypothesized that SRRs would mainly appeared early in the growing season. If the function of SRRs is to occupy and consolidate favorable habitats, it is important to occupy favorable patches before other ramets do. We hypothesized that LRRs would be produced throughout the growing season. If the function of LRRs is to explore and find new and possible better habitats, it is important to spread ramets until better habitats are reached. Both hypotheses were confirmed in the field observations. These results implies that the plants may benefit from the production of a large number of SRRs early in the growing season by using resources stored over winter; subsequently plants produce LRRs with the photosynthetic gains from the SRRs. The observed pattern in the field and some other studies on tree species (Kikuzawa, 1983; Kikuzawa, 1984) may support this hypothesis, yet, further study is necessary to confirm and validate this hypothesis. In clonal plants, the translocation of water and resources has been examined (de Kroon *et al.*, 1996; de Kroon *et al.*, 1998; Jonsdottir and Callaghan, 1990) but these studies are not based on seasonal changes nor focus on the specialization of ramets. Seasonal change and phenology of specialized ramets is important to understand the life history of clonal plants.

2. Ramet specialization at different plant densities - functional specialization in sexual or asexual propagation

It is well known that seedlings of clonal plants are very rare. As we saw in Chapter 2, due to high salinity and possibly due to competition from adults in the dense vegetation, seeds of *Scirpus olneyi* are rare in this salt marsh (Ikegami personal observation). In order to persist, this species is highly dependent on vegetative propagation. Yet, this species produces a large number of seeds that form a seed bank in the *Scirpus* High Marsh community (Ikegami personal observation). Why does this species produce seeds in the *Scirpus* High Marsh community and why does this species not specialize in vegetative propagation? If a genet specializes in vegetative propagation, that genet is locally more competitive than a genet with both sexual and vegetative propagation.

To evaluate the observed pattern of seed production in Chapters 2 and 3 in detail, we conducted field observations and a garden experiment (Chapter 4). Both garden and field observations showed that plants produce more seeds at higher density. In the garden, individual ramets had less nutrient availability per ramet at higher density, but plants produced more seeds at high density. This result indicates that plant density can affect on the propagation strategy of *S. olneyi* more strongly than nutrient availability.

S. olneyi produced proportionally more LRRs at lower ramet density and more SRRs at higher ramet density. As we saw in Chapters 2 and 3, SRRs are suitable for occupation and exploitation of a locality while LRRs are suitable for exploration and finding new localities. In the patches with a high shoot density, plants may have less chance to encounter an open locality, since most localities are already occupied. Under this condition the production of SRRs that can occupy the same locality where the mother ramets grew before would be suitable. On the other hand, at the patches with a low shoot density, LRRs would be suitable to spread rapidly and occupy possibly favorable empty patches. As ramet density increases, *S. olneyi* shifts its propagation strategy from exploration with LRRs to exploitation with SRRs and spreading by seeds. Thus plants effectively use two functionally specialized ramets for vegetative spread, and sexual ramets. We conclude that ramet density of *S. olneyi* regulate the clonal propagation strategy of this species.

Some studies suggested that seed production is positively correlated with plant density (Abrahamson, 1975; Abrahamson, 1980; Giroux and Bedard, 1995) while other studies suggested that in dense patches clonal propagation is to be expected (Eriksson, 1989; Loehle, 1987). To explain the results of our field and garden experiments in Chapter 4 and evaluate contradicting hypotheses, we developed a simulation model to evaluate the outcome of competition among clonal plants that have different patterns of reproduction (Chapter 5). We assume two strategies: One strategy is the Density Dependent Seed Strategy (DDSS) in which plants produce seeds as density increases, and the other is the Density Dependent Ramet Strategy (DDRS) in which plants produce ramets as density increases.

The results of the simulation show that when the death rate is high, both DDSS and DDRS can win when they produce mainly seeds. Under a high death rate, many plants die at every time step thus seed production results in a higher chance of establishing a new individual. As a result, the strategy that mainly propagates through seeds wins. When the death rate is low, plants with the DDSS strategy produce seeds at highest density have the best strategy. Due to a low death rate density is high and then DDSS plants tend to

propagate sexually, and when there are vacant adjacent cells both DDRS and DDSS plants may produce new ramets which may establish a new individual in the cell. This means that DDSS plants have an equal or higher chance to get established than DDRS plants.

Thus independent of resource availability the production of ramets at lower densities and the production of seeds at higher densities seem to be a proper strategy. In the *Scirpus* High marsh community, plants have huge amount of old rhizomes (Chapter 2), this result implies that plants may have no use for resource at high density except for seed propagation because ramet establishment is strictly limited while seed possibly reach far and wider range.

In this thesis, we did not discuss how plants detect density. Some plants detect density from changes in the R:FR ratio. Once plants detect a high density, they change their shoot height, their architecture of their branching leaf morphology and so on to avoid or win the competition (Smith, 1990). Evans and Cain (1995) suggested that the growth direction of *Hydrocotyle bonariensis* can be affected by either changes in resource depletion zones around nearby grass roots or changes in the R:FR ratio (Evans and Cain, 1995; Smith *et al.*, 1990). For *Scirpus olneyi*, as shown in Chapters 2, 3 and 4 the resource depletion hypothesis is not relevant. And to hold the R:FR ratio hypothesis is also rather difficult. In the *Scirpus* Shaded Marsh community, the whole community is completely shaded by overhanging tree crowns (Chapter 2 and 3). In this community, however, plants have a different architecture from the *Scirpus* High Marsh community, where shoot density is extremely high. The location of light capturing offers another possibility. In the *Scirpus* High Marsh community, *S. olneyi* reaches the canopy of the community, so the top part of the shoot can capture the full light, and the middle of the shoot captures lower quality light. On the other hand, plants in the *Scirpus* Shaded Marsh community only receive light filtered by tree leaves. Thus if this triggers the plants we can do experiments to create such situations: one treatment is fully covered by green transparent sheet, and the other treatment is subjected to a light gradient with the lower part of shoots in gradually more decreasing light conditions (see the experiment by Leeftang, 1999 and Leeftang *et al.*, 1998). Density effects on clonal architecture have not been studied, but since clonal architecture can strongly affect ramet density (*i.e.* phalanx strategy or guerilla strategy), it is quite important to evaluate the relation between density and architectures.

3. Ramet specialization in environments where resources are inversely distributed - functional specialization in resource capturing

In clonal plants, the interplay between the cost of water transport, the contrast in resource availability and the efficiency of resource capturing among ramets determine the pattern in allocation to organs, in other words, the degree of specialization of the ramets. To evaluate the degree of specialization and the Division of Labor (DoL) in *Scirpus olneyi*, I constructed a mathematical model and conducted a garden experiment.

In the Chapter 6, we conducted a garden experiment focusing on light availability and salinity. In the experiment, plants in the heterogeneous treatments showed the DoL in the sense of Stuefer *et al.* (1996). In the experiment, we manipulated light and salinity to provide varying levels of resources to connected ramets of individual genets. These conditions were created in different halves of containers in which a connected clonal fragment was planted. The plants in our experiment showed functional specialization of

shoots. In the containers with heterogeneous conditions, plants increased their shoot height and shoot Specific Green Area in the light and salty halves to capture the locally abundant resource, light. We also found that the water consumption per unit biomass in the light and salty halves with heterogeneous conditions was less than that in light and salty halves with homogeneous conditions. This result leads to the conclusion that the plants transported water from the shaded and freshwater halves. These results suggest that ramets in the light and salty halves with heterogeneous conditions specialize in light capturing instead of water capturing and vice versa in the shaded and freshwater halves, and plants achieved a larger biomass than plants in homogeneous conditions.

In the Chapter 7, we describe a mathematical model to evaluate the degree of specialization between two ramets. Under conditions of spatial DoL specialization of ramets in capturing only the locally abundant resources seems to be most efficient, but this “full” specialization does not happen in the field. With the model, I demonstrate the importance of the costs of the efficiency of resource capturing. When a plant reaches a larger size, the efficiencies of resource capturing and transport to each organ decrease since the costs for support, maintenance and aging increase. If the environmental heterogeneity is not highly contrasting, the organ in the poor-quality condition can capture more resources per unit biomass than a bigger organ in the better-quality condition, because the decrease in efficiency in the organ in the better-quality condition is strong at larger biomass. Thus, in such a situation the plant system also allocates biomass to the organ in the poor-quality condition, and does not show full specialization.

In their model, we focus on the costs of transportation and costs associated with the size of organs. Yet, there is another possible cost at full specialization under DoL (Stuefer *et al.*, 1998). If ramets fully specialize, each ramet relies vitally on resource import from the connected clone parts (Alpert and Mooney, 1986), and once the connection is severed, this can be lethal for the plant (Stuefer *et al.*, 1998). To avoid this risk, each ramet should keep an amount of essential organs to survive.

When the contrast in resource availability is high or a decrease in efficiency does not occur, full specialization occurs in our model. In the field, however, contrast in resource availability is not likely to be strong over short distances. Thus I suggest each ramet can have benefit to capture the resource even locally in shortage because of decrease in efficiency of resource capturing, thus plants do not show full specialization.

Physiological integration is the most important feature for DoL, but how long do plants maintain physiological integration? To evaluate the duration of physiological integration we did a garden experiments. We used plants that had been used in the DoL experiment in Chapter 6. The plants were grown over winter and then harvested. The results showed that plants did not show any evidence of DoL. It is difficult to evaluate the preliminary results of this experiment, but in *Scirpus olneyi*, it may be that plants maintain physiological integration, but do not have a “strong connection” between ramets for a longer period. For DoL to be beneficial, plants need low costs of water transport (Chapter 7), but when aging, the efficiency of the xylem in the rhizomes decreases (Lewis, 1992; Lewis and Boose, 1995). Therefore, we assume that plants do not receive a large benefit from DoL with old rhizome connections.

Plasticity of ramets

Scirpus olneyi clearly showed functional specialization of ramets for different tasks under different conditions. For functional specialization of ramets, phenotypic plasticity and physiological integration are the most important factors. Environmental conditions around a plant can vary spatially and temporally. Thus it is necessary that individual plants adapt themselves to their environments to perform well. As a result plants tend to show different growth forms in different environments. This change in their phenotypic features is called phenotypic plasticity. Plasticity is defined as the different response of a genotype to different environmental conditions (Bradshaw, 1965). For non-clonal plants, plasticity is based on one individual while for clonal plants, plasticity can be based not only on ramets in a specific environment, but also on inter-connected ramets that are possibly growing in other environments.

Yet, some functionally specialization of ramets is not necessary plasticity. For some specialization plasticity of ramets is not required. There are two different types of functional specialization of ramets: one is plastic specialization and the other is non-plastic specialization (Charpentier and Stuefer, 1999; Stuefer, 1998). In some clonal plants, ramets persist more than one growing season without aboveground parts, and those ramets can capture water and nutrients from the soil, and transport that to current year ramets with shoots. Or old ramets can function as uptake organs for water and nutrients and storage organs for carbohydrates (Jonsdottir and Callaghan, 1990; Jonsdottir *et al.*, 1996). These old ramets are specialized but this is not based on plasticity. It is developmentally programmed specialization. Such ramets are pre-fixed to specialize in specific tasks at the certain stages in their development, and that is independent of environmental variation. This specialization is called non-plastic or inherent specialization of ramets (Alpert and Stuefer, 1997; Charpentier and Stuefer, 1999; Stuefer, 1998).

In this thesis, I mainly focus on the plastic specialization of ramets, and evaluate the task of each ramet type under various environmental conditions. But *Scirpus olneyi* also shows non-plastic specialization of ramets. In the *Scirpus* High Marsh community, plants keep many old ramets without shoots. These ramets have dormant buds. If the connections to the current year ramets are severed, these buds start producing new ramets (Ikegami personal observation). Thus these ramets function as a “ramet bank” which is useful in case of disturbances. In *Carex bigelowii*, current year ramets have aboveground parts and few roots, and photosynthesize. On the other hand, older ramets have no aboveground parts but keep their roots and capture water and nutrients to transport to the young ramets. Older ramets also have dormant buds and store resources (Jonsdottir and Callaghan, 1990; Jonsdottir *et al.*, 1996). Thus the older ramets of *S. olneyi* most likely also show non-plastic specialization, and this can be beneficial in the *Scirpus* High Marsh community.

Physical connection and physiological integration

Physiological integration is the essential feature for functional specialization of ramets. Specialization in some tasks means, abandonment or reduction of other tasks. Ramet specialization always needs inter-connected counter ramets which will carry out the tasks that are abandoned by the former. Thus, the duration and degree of physiological

integration will determine the duration and degree of specialization of ramets, as I saw in chapter 6.

Some clonal plants maintain physiological integration between ramets briefly, e.g. *Trientalis europaea* (Dong *et al.*, 1997), while other species keep it for longer periods. In some cases, ramets possess physical connections, but do not or hardly have physiological integration. A model study suggested that the proportion of favorable to unfavorable patches strongly influenced the strategy of integration (Oborny *et al.*, 2000). Some clonal plants under forest trees spread vegetatively. Sometimes, the mother ramets disintegrate after one season. These plants are often called pseudo-annuals (Verburg and Grava, 1998; Verburg and During 1998). Their ramets show ramet specialization (Verburg and Grava, 1998), sexual or vegetative ramets, but will not show spatial DoL due to totally lack or diminished physiological integration among ramets.

In the field, *Scirpus olneyi* maintains its older ramets longer in the Scirpus High Marsh community than in the Scirpus Shaded Marsh community. In low quality patches, plants have to escape from that patch to find a better one. When exploring for new patches and escape from poor quality patches, plant turnover can be rapid and once a ramet reaches a better patch, it is better to invest most biomass into that ramet. This implies that plants will not maintain the older ramets over a longer period, thus, the duration of physiological integration can be short. In the patches of higher quality physiological integration is maintained for a longer period of time. To evaluate the duration and degree of physiological integration, *S. olneyi* would be suitable to study the effects of environmental quality on the degree and duration of physiological integration.

Conclusion

In newly created bare patches plants possibly establish new individuals from seeds, or if the conditions allow invasion by vegetative growth, *S. olneyi* can invade new patches vegetatively. If the quality of the patch is sufficient, *S. olneyi* will produce short spacer ramets to consolidate the patch, while if the patch quality is low, it keeps producing long spacer ramets to escape from that patch. If the patch quality is good and *S. olneyi* keeps producing short spacer ramets to exploit the local habitat, the ramet density increases. Individuals then begin to produce ramets which branch less and produce seeds. Under heterogeneous conditions, if interconnected ramets growing in an environment where resource availability is inversely distributed, this species shows DoL and potentially achieves a larger biomass.

All these results show that *S. olneyi* realizes various functional specialization of ramets in different environments and situations. Yet, I have not shown whether the functional specialization of ramets in this species actually gives it more benefits. This species occurs in various communities and seems to be strongly competitive but that does not mean that this species performs best in each habitat because of specialization. To demonstrate this, I need to evaluate the costs and benefits of specialization with field or gardens experiments, and validate the results with conceptual models. For further research on functional specialization of ramets this species may have great potential.

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Samenvatting:

Deze dissertatie gaat over de specialisatie in een bepaalde functie, die ramets plaatselijk kunnen aannemen en de samenwerking tussen dergelijke onderling verbonden ramets, als ze in een heterogeen milieu groeien. Omdat clonale planten zich door vegetatieve groei kunnen uitbreiden, is een genet in staat om over heterogeniteiten in het milieu heen te groeien. In overeenstemming hiermee kunnen ramets in vorm van elkaar verschillen en kan elke ramet zich functioneel in een bepaalde taak specialiseren. Een dergelijke functionele specialisatie van de ramets op verschillende groeiplekken stelt de plant in staat om efficiënt verschillende standplaatsen te bezetten en de hulpbronnen daar te benutten. Daarom is het belangrijk om de specialisatie van ramets te bestuderen als men de strategie ('life history strategy') van clonale planten wil begrijpen. In deze dissertatie heb ik de volgende aspecten van de functionele specialisatie van de ramets van de clonale plant *Scirpus olneyi* bestudeerd:

1. Specialisatie van ramets in verschillende plantengemeenschappen en verschillende seizoenen
2. Specialisatie van ramets bij verschillende plantdichtheden
3. Specialisatie van ramets in een heterogeen milieu waarin de hulpbronnen op verschillende plekken in omgekeerde verhouding beschikbaar zijn.

1. Specialisatie van ramets in verschillende plantengemeenschappen en verschillende seizoenen - functionele specialisatie en vegetatieve uitbreiding

De functionele specialisatie en vegetatieve uitbreiding wordt in de hoofdstukken 2 en 3 besproken. In hoofdstuk 2 beschrijf ik de soort waaraan ik onderzoek heb gedaan, het milieu waarin de plant groeit, en de architectuur van de clonen in de verschillende plantengemeenschappen. Ik laat in hoofdstuk 2 zien, dat *Scirpus olneyi* twee typen ramets heeft, namelijk ramets met een lang rhizoom (LRR) en ramets met een kort rhizoom (SRR). In hoofdstuk 3 formuleer ik de hypothese, dat de twee typen ramets op een verschillende manier gespecialiseerd zijn wat betreft ruimtelijke uitbreiding (de architectuur van de ramets) en temporele ontwikkeling (fenologie). Ik veronderstel dat het de functie van de SRRs is om gunstige plekjes te bezetten en bezet te houden. Dat zou dan met zich meebrengen, dat SRRs vooral vroeg in het groeiseizoen geproduceerd worden, zodat ze de gunstige plekjes kunnen bezetten voordat andere ramets dat doen. De veronderstelde functie van de LRRs is echter om de omgeving te exploreren en nieuwe, mogelijk betere plekjes te vinden. Zulke LRRs zouden dan gedurende het hele groeiseizoen geproduceerd worden om voortdurend ramets uit te sturen op zoek naar betere plekjes.

Experimenten in de proeftuin lieten zien, dat de planten ertoe neigden om meer SRRs te maken en vaker te vertakken als ze op hele goede plekjes groeiden, terwijl planten op slechte plekjes LRRs maakten en veel minder vertakten. Deze resultaten suggereren, dat het de taak van de SRRs inderdaad is om de bezetting van een plekje te consolideren en de rijkelijk aanwezige hulpbronnen te exploiteren, terwijl het de taak van de LRRs is om nieuwe en mogelijk gunstige plekjes te zoeken.

Mijn hypothesen over de patronen in de fenologie van de planten werden in veldwaarnemingen bevestigd. De resultaten suggereerden, dat het voor de planten van voordeel kan zijn als ze hun voorraden, die ze over de winter hebben opgeslagen, gebruiken en vroeg in het seizoen een groot aantal SRRs aanmaken; daarna

produceren die planten dan LRRs waarvoor ze de fotosyntheseproducten gebruiken, die de SRRs leveren. Deze resultaten bevestigen mijn idee, dat de twee typen ramets functioneel verschillend gespecialiseerd zijn om verschillende taken op verschillende plaatsen en op verschillende tijdstippen uit te voeren.

2. Specialisatie van ramets bij verschillende plantdichtheden - functionele specialisatie op geslachtelijke of ongeslachtelijke voortplanting

In de hoofdstukken 4 en 5 bespreek ik het effect dat de dichtheid waarmee de planten op een plek groeien heeft op de voortplantingsstrategie van clonale planten en of er van een functionele specialisatie op geslachtelijke of ongeslachtelijke voortplanting sprake is. In hoofdstuk 3 heb ik vermeld, dat de zaadproductie van *Scirpus olneyi* in de verschillende plantengemeenschappen verschilde, en dat de planten meer zaden produceerden als de plantdichtheid in de plantengemeenschap toenam. Ik veronderstel, dat als de hulpbronnen in een bepaald milieu onregelmatig verdeeld zijn, dat de planten de gunstige plekken met veel voedingsstoffen dan zullen exploiteren en er ter plekke in hoge dichtheid groeien en dat dit ter plaatse ook tot een hoge zaadproductie leidt. Maar als de planten uit de plekken met een geringe hoeveelheid voedingsstoffen weggroeien, dan is daar ter plaatse de plantdichtheid laag en de zaadproductie wordt laag. Het is moeilijk om deze hypothesen middels veldwaarnemingen te evalueren. Daarom heb ik een aantal speciale veldstudies en een tuin-experiment gedaan (hoofdstuk 4), aangevuld met een theoretisch onderzoek (hoofdstuk 5).

De veld- en tuinwaarnemingen (hoofdstuk 4) lieten allebei zien dat planten in hogere dichtheden meer zaden produceren. In het tuin-experiment hadden de individuele ramets in de bakken met een hoge plantdichtheid per ramet minder voedingsstoffen beschikbaar, maar met toenemende plantdichtheid produceerde de planten toch meer zaden per ramet. Dit resultaat wijst erop dat de plantdichtheid meer effect op de voortplantingsstrategie van *Scirpus olneyi* heeft dan de beschikbare hoeveelheid voedingsstoffen.

Scirpus olneyi maakte verhoudingsgewijs meer LRRs bij een lage rametdichtheid en meer SRRs bij een hoge rametdichtheid. Zoals we in hoofdstuk 3 hebben gezien zijn SRRs geschikt voor bezetting en exploitatie van een plek en LRRs voor exploratie en het vinden van nieuwe plekken. Planten zullen in een begroeiing met hoge rametdichtheid minder kans hebben om een open plekje tegen te komen, omdat alle plekken immers al bezet zijn. Onder deze omstandigheden is het beter om SRRs aan te maken, die dan hetzelfde plekje als waar de moeder ramet eerst groeide kunnen bezetten. Maar op plekken met een lage rametdichtheid zijn LRRs heel geschikt; ze kunnen zich snel verspreiden en zich op open, mogelijk gunstige plekken vestigen. Naarmate de rametdichtheid toeneemt verandert *Scirpus olneyi* zijn voortplantingsstrategie van exploratie middels LRRs naar exploitatie middels SRRs en het verspreiden van zaden. De plant maakt dus effectief gebruik van twee typen functioneel gespecialiseerde ramets voor vegetatieve uitbreiding en geslachtelijke verspreiding.

In hoofdstuk 5 ontwikkel ik een simulatiemodel om te onderzoeken wat het resultaat is als clonale planten met verschillende patronen van reproductie met elkaar concurreren. In dat hoofdstuk onderzoek ik twee strategieën: 1. planten die bij hogere dichtheden zaden produceren (DDSS), en 2. planten die bij hogere dichtheden ramets produceren (DDRS). Ik heb een rastermodel ontwikkeld om het resultaat van concurrentie tussen deze twee strategieën bij verschillende dichtheden te onderzoeken.

De simulaties lieten zien, dat als de mortaliteit hoog is, zowel de DDSS als de DDRS kunnen winnen als ze voornamelijk zaden produceren. Als de mortaliteit hoog is sterven er per tijdsstap veel planten af en als er dan veel zaden zijn, kunnen zich daaruit veel planten vestigen. De strategie die voornamelijk zaden produceert wint dus. Maar als de mortaliteit laag is winnen planten met de DDSS strategie, want zij produceren zaden bij hoge plantdichtheden. Als gevolg van de geringe mortaliteit is de plantdichtheid hoog en als er dan lege buurcellen zijn kunnen zich daar zowel DDRS als DDSS planten uit ramets vestigen. Als er geen lege buurcellen zijn hebben DDSS een licht voordeel, omdat ze zaden maken, en die hebben een kleine kans om zich in een lege cel te vestigen, terwijl DDRS planten, die ramets aanmaken, geen kans hebben zich te vestigen. Dit betekent dat DDSS planten en even grote of grotere kans hebben als DDRS planten om zich te vestigen. Het tuin-experiment en de modelresultaten geven aan dat, onafhankelijk van de beschikbare hoeveelheid hulpbronnen, het aanmaken van ramets bij lage plantdichtheden en zaadproductie bij hoge plantdichtheden goede strategieën zijn.

3. Specialisatie van ramets in een heterogeen milieu waarin de hulpbronnen op verschillende plekken in omgekeerde verhouding beschikbaar zijn - functionele specialisatie voor het bemachtigen van hulpbronnen

In de hoofdstukken 6 en 7 komt de functionele specialisatie van verschillende ramets ten behoeve van het bemachtigen van hulpbronnen aan de orde (taakverdeling). Om de mate van specialisatie te beoordelen heb ik een tuin-experiment uitgevoerd en een wiskundig model ontwikkeld.

In het tuin-experiment (hoofdstuk 6) richtte ik me op de beschikbare hoeveelheid licht en het zoutgehalte van het bodemwater om de mate van specialisatie in *Scirpus olneyi* te beoordelen, als de planten in een heterogeen milieu groeien waarin de beschikbaarheden van de hulpbronnen (in dit geval licht en water) in de deelmilieus negatief met elkaar gecorreleerd zijn. In het experiment manipuleerde ik de hoeveelheid licht en het zoutgehalte zodanig dat onderling verbonden ramets verschillende hoeveelheden ervan kregen aangeboden. Dat kon ik doen door onderling verbonden rametparen in bakken te laten groeien, waarvan de twee helften van elkaar gescheiden waren en het verbindende rhizoom van de ene helft naar de andere liep. In sommige bakken maakte ik de milieu-omstandigheden in beide helften gelijk; in andere zorgde ik ervoor dat er in beide helften verschillende milieu-omstandigheden heersten. In de bakken met twee verschillende helften werden de planten in de helft met veel licht en een hoog zoutgehalte hoger en was hun "specifieke groenoppervlak" (SGA) groter dan in de bakken met twee dezelfde helften. Deze hogere planten specialiseerden zich dus in het bemachtigen van de hulpbron die rijkelijk beschikbaar was, namelijk licht. In deze lichte en zoute helften van de heterogene bakken was de waterconsumptie per eenheid biomassa minder dan in de lichte en zoute helften van homogene bakken. De planten in de heterogene bakken bereikten een grotere biomassa dan planten in homogene bakken. Deze resultaten laten zien, dat de ramets in de lichte en zoute helften van de heterogene bakken zich specialiseren in het onderscheppen van licht in plaats van het bemachtigen van water. Het omgekeerde geldt voor de ramets in de bakhelften met schaduw en zoetwater.

In de hoofdstukken 2 en 3 heb ik al laten zien, dat onderling verbonden ramets van *Scirpus olneyi* over de grenzen van plekjes waarin de milieu-omstandigheden contrasteren en de beschikbaarheid van hulpbronnen negatief met elkaar gecorreleerd

zijn heengroeien. Nu concludeer ik daarom, dat *Scirpus olneyi* onder veldomstandigheden voordeel kan hebben van taakverdeling (Division of Labor). In hoofdstuk 7 ontwikkel ik het theoretische model om de mate van specialisatie en taakverdeling onder verschillende milieu-omstandigheden te beoordelen. Het model berekent, voor combinaties van twee onderling verbonden ramets die elk in verschillende milieu's groeien, de optimale investeringen in bovengrondse (spruit) en ondergrondse (wortel) plantendelen, en de patronen van watertransport, die nodig zijn om aan het eind van het groeiseizoen een maximale biomassa te hebben opgebouwd. Ik laat met dat model zien hoe belangrijk het is om de kosten, die een efficiënte manier om hulpbronnen te bemachtigen met zich meebrengen, goed te onderzoeken. Als een plant groter wordt kan de efficiëntie waarmee de hulpbronnen worden bemachtigd en naar de verschillende organen worden getransporteerd afnemen, waarschijnlijk omdat de kosten voor stevigheid, onderhoud en veroudering toenemen. Als het contrast in de beschikbaarheid van hulpbronnen niet groot is, dan kan het orgaan dat onder slechte omstandigheden groeit meer hulpbronnen per eenheid biomassa verwerven dan een groter orgaan dat onder de betere omstandigheden groeit. Dat komt, omdat de efficiëntie van het orgaan in het gunstige milieu minder is naarmate het orgaan groter is. In een dergelijke situatie alloceert het clonale plantensysteem dus biomassa naar het orgaan in het ongunstige milieu. Dit verklaart waarom ramets geen volledige specialisatie met betrekking tot het bemachtigen van hulpbronnen vertonen.

Conclusie

Als er nieuwe lege plekken ontstaan vestigen er zich waarschijnlijk nieuwe planten van *Scirpus olneyi* uit zaad. Maar als de omstandigheden invasie door uitlopers mogelijk maken kan *Scirpus olneyi* er zich ook zo vestigen. Als de kwaliteit van de groeiplek goed is zal *Scirpus olneyi* er ramets met korte rhizomen vormen en zijn bezetting van die plek consolideren. Maar als de kwaliteit van de groeiplek slecht is blijft *Scirpus olneyi* ramets met lange rhizomen produceren, zodat hij van die plek weg kan groeien. Als de groeiplek goed is en *Scirpus olneyi* ramets met korte rhizomen blijft aanmaken om die plek te exploiteren, dan neemt de rametdichtheid toe. De plant begint dan ramets te produceren die minder vertakken, en hij begint zaad te vormen. Onder heterogene groei-omstandigheden waarbij onderling verbonden ramets in een milieu met inverse beschikbaarheid van hulpbronnen groeien, vertoont *Scirpus olneyi* taakverdeling (Division of Labor). Deze planten bereiken daardoor een grotere biomassa. Al deze resultaten laten zien dat *Scirpus olneyi* diverse functionele specialisaties van zijn ramets op verschillende milieu-plekken en onder verschillende omstandigheden weet te realiseren.

Acknowledgement

-Ik ben blij-

I chose my career in Ecology when I was an undergraduate student, but at that time I did not imagine that I would study in foreign countries for my Ph.D. research. I even boasted “if I can learn Ecology in Japan, why do I have to go to a foreign country!!” Now, where I am? I am in my office and have finished writing my Ph.D. thesis, at Utrecht University, the Netherlands. And for my Ph.D. I was studying in the Smithsonian Environmental Research Center (SERC), USA. Life is full of unexpected things. For me it was very interesting to live in two different continents at both sides of the Atlantic Ocean. Sometimes, however, living in foreign countries is tougher than one can imagine. You have to use the foreign language, deal with people whose customs you do not understand (I like Dutch culture but still I do not understand why Dutch people do not rinse the dishes after washing them). And, you do not have your old friends or families around you. It is tough.

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“Dank je wel, ik heb gezegd.”

IKEGAMI Makihiko

12 December 2003, Utrecht, Netherlands

Curriculum vita

I was born in Okayama, Japan, on 11th November 1972. I went to three different primary schools, including a few years to a school in Singapore. I attended junior high and high schools in Kanagawa, Japan. I did my undergraduate course in the Faculty of Agriculture in Kyoto University and belonged to the Applied Botany Group for my undergraduate research projects: I studied the relationships between parasitic nematodes, their vector insects and their host plants. I received a Bachelor of Agriculture in March 1997 with my bachelor thesis, “Transmission behavior of the Pine Wood Nematode *Bursaphelenchus xylophilus* (Nematoda: Aphelenchoidiae) To 4 Pine species Through Feeding Wounds of *Monochamus alternatus*”. From April 1997, I started my master study in Plant Ecology at the graduate school of Science in Kyoto University. I studied several topics on plant ecology, both in field work and theoretical studies. The title of my master thesis was “Theoretical Study of Masting –how plants synchronize seed production-“. I developed a few lattice models to analyze how forest trees synchronized their seed production, and these modeling techniques were applied in this thesis. From April 1999, I started to work on my Ph.D. thesis on clonal plants, as a Ph.D. fellow in the Smithsonian Environmental Research Center, USA and AIO at the Faculty of Biology, Utrecht University, the Netherlands, funded by a grant to prof. dr. M.J.A. Werger from the Andrew W. Mellon Foundation through the Smithsonian Institution and by the Faculty of Biology, Utrecht University.