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 ramet 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.
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 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.
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.
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 4. a) Shoot Height and b) Specific Green Area (SGA) with ± 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 ($p<0.0083$).
Water Consumption

Among PRG, ramets growing in the shaded and freshwater conditions in treatment 2 consumed most water \( (p<0.0083, \text{Fig. 5a}) \), and ramets in the light and 1% salt portions of treatments 1 and 4 consumed least water \( (p<0.0083, \text{Fig. 5a}) \). 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 \( (p<0.0083, \text{Fig. 5a}) \). 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 \( (i.e., \text{light}) \) and allocated more biomass to the organ that has to capture the most limiting resource \( (\text{Aung, 1974; Chapin, 1980; Iwasa and Roughgarden, 1984}) \). Scirpus olneyi also showed functional specialization in shoots as shoot height and SGA were greatest in plants in shaded freshwater conditions and

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.
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.
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6) References


