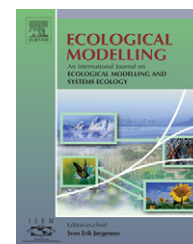


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Optimal biomass allocation in heterogeneous environments in a clonal plant—Spatial division of labor

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ARTICLE INFO

Article history:

Received 12 November 2006

Received in revised form

20 November 2007

Accepted 27 November 2007

Published on line 20 February 2008

Keywords:

Biomass allocation

Clonal plant

Division of labor

Heterogeneous environment

Optimization model

ABSTRACT

When interconnected ramets of clonal plants are growing in heterogeneous environments, ramets may specialize to uptake locally abundant resources rather than scarce resources. This biomass allocation pattern may result in more efficient sharing of resources through physiological integration and an overall benefit to the plants (spatial division of labor; DoL).

For specialization, allocating the largest biomass to organs growing under a resource rich condition while allocating least biomass to organs under a resource poor condition could be profitable, but empirical studies showed those allocation patterns are hardly to be observed. To evaluate the degree of specialization of DoL, we constructed a simple plant growth model in sets of two ramets, physiologically interconnected or independent, growing in different environments. The model is designed to determine an optimal biomass allocation and an optimal water transport within a ramet. The model also maximizes total biomass acquisition for connected ramets.

In our model, the degree of specialization of ramets is determined by the interplay among the costs of water transport, the contrast in resource availability and the efficiency of resource capturing per unit biomass. If two ramets growing independently then each ramet allocates biomass to the organ that captures the locally scarce resource and two ramets achieve a lower biomass in a patch with a higher contrast in resource availabilities. The interconnected two ramets showed DoL if the benefit through the DoL is larger than the costs of water transportation. Interconnected ramets showed DoL if the benefit of DoL is greater than the costs of water transport. When interconnected ramets show DoL, each ramet allocates biomass to the organ that captures the locally abundant resource and the pair achieves higher total biomass in patches with a higher contrast in resource availabilities. The degree of specialization increases as the contrast in resource availabilities increases, and full specialization occurs when the contrast is high. We also find that the efficiencies in resource capturing per unit biomass of each organ are important. When an organ of a ramet reaches a larger size, the efficiencies in resource capturing per unit biomass decreases. A small organ growing under low resource conditions may capture more resources per unit biomass than a large organ growing under high resource conditions; as a result the modeled plant also allocates biomass to the organ growing under low resource conditions.

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0304-3800/\$ – see front matter © 2008 Published by Elsevier B.V.

doi:10.1016/j.ecolmodel.2007.11.016

1. Introduction

Environmental heterogeneity is a non-uniform distribution of environmental factors, such as water, light, nutrients, or plant density. Light and water are primary resources for plant growth and their availability may be highly variable over short distances. In the field, generally, high light availability tends to correlate with low water availability, whereas low light availability tends to correlate with high water availability (Young and Smith, 1979, 1980; Schulze and Hall, 1982; Schlesinger et al., 1990). 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 can be unfavorable in another respect.

Clonal plants can spread horizontally by vegetative growth. Individual ramets are modules capable of independent existence but often remaining physiologically connected. Thus, 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 (Stuefer and Hutchings, 1994; Alpert, 1995; Hutchings and Wijesinghe, 1997; Shipley and Meziane, 2002).

In heterogeneous 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 allocation patterns in heterogeneous environments because in a clonal plant ramets may stay interconnected and grow under different environmental conditions while non-clonal plants grow in a single environment. Basically, a non-clonal plant tends to allocate more biomass to an organ that has 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; Werger, 1983; Iwasa and Roughgarden, 1984). Such a pattern of investment is called compensatory investment (Iwasa and Roughgarden, 1984).

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 (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 low resource conditions (Marshall, 1990; Hutchings and de Kroon, 1994). Thus, clonal plants can perform well under conditions of patchy heterogeneity (Alpert and Mooney, 1986; Wijesinghe and Handel, 1994; Alpert, 1995; Hutchings, 1999; Wijesinghe and Whigham, 2001).

In some recent experiments, clonal plants showed another response. In some clonal plants, ramets in environments with

inversely correlating availability of two or more resources show functional specialization to capture locally abundant resources and exchange resources among ramets through physiological integration (Stuefer et al., 1996; Alpert and Stuefer, 1997). 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. Since resources are captured where they are most abundant and then are transported to where they can be used best through physiological integration, clonal plants could produce greater biomass. Stuefer et al. (1996) referred to this allocation pattern as spatial division of labor (DoL), a term that has analogy in economic theory. 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).

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., 1996). Intuitively, however, it seems more profitable if the plants locally allocate large biomass to those organs that capture the locally abundant resources. Those allocation patterns are rarely observed thus there should be some reasons that individual ramets still allocate some biomass to all organs (i.e., increasing potential independency).

A garden experiment is one approach to investigate the degree of specialization in DoL but measuring resource capturing efficiency and costs for resource transportation under various parameter settings can be difficult. Thus, 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 or at high water transport between 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 but stable environments. Since the specialization of ramets depends on environments, we

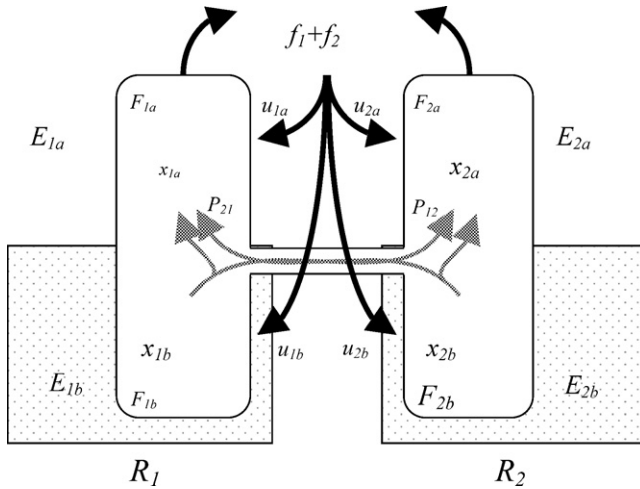


Fig. 1 – Schematic representation of the biomass and allocation pattern in the modeled plant system. Each ramet (R_1 and R_2) consists of aboveground and belowground organs. x_{1a} and x_{2a} represent the biomass of the aboveground organs, and x_{1b} , and x_{2b} the biomass of the belowground organs. The resource availability at organ i is represented by E_i and organ i captures resources with an efficiency of F_i . Water can be transported between ramet 1 and ramet 2; p_{12} is the ratio of acquired water transported from ramet 1 to ramet 2, and p_{21} is this ratio from ramet 2 to ramet 1. 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 .

study environmentally induced division of labor (plastic DoL) as defined in Stuefer (1998).

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 Eq. (1) (Iwasa and Roughgarden, 1984).

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

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. This equation implies organs with large biomass can uptake large amount of resources but 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.

From Eq. (1), we develop an equation system that describes the photosynthetic rate for a plant system with two interconnected ramets. Eqs. (2)–(1) and (2)–(2) give the rate for ramets 1 and 2, respectively.

$$f_1 = \left(\frac{1}{E_{1a}x_{1a}^{F_{1a}}} + \frac{1}{E_{1b}(1-p_{12})x_{1b}^{F_{1b}} + E_{2b}(1-D)p_{21}x_{2b}^{F_{2b}}} \right)^{-1} \quad (2)-(1)$$

$$f_2 = \left(\frac{1}{E_{2a}x_{2a}^{F_{2a}}} + \frac{1}{E_{2b}(1-p_{21})x_{2b}^{F_{2b}} + E_{1b}(1-D)p_{12}x_{1b}^{F_{1b}}} \right)^{-1} \quad (2)-(2)$$

x_i is the size of organ i , E_i is the resource availability for organ i , and F_i is the index of resource capturing efficiency by organ i ($i = 1a, 1b, 2a, 2b$). Aboveground biomass is represented by x_{1a} and x_{2a} , while x_{1b} and x_{2b} stand for belowground biomass of ramet 1 and 2, respectively. We do not assume environmental changing (e.g. dilution due to resources uptake), thus, resource availability and resource capturing efficiency are constant throughout a simulation. Through physiological integration, water moves from one ramet to the other, p_{12} is the ratio of acquired water transported from ramet 1 to ramet 2, and p_{21} is this ratio from ramet 2 to ramet 1. Due to hydraulic resistance between two ramets, water transport efficiency decreases at certain percentage. We define this is the cost of water transport as the ratio D ; water can reach the other ramet with the ratio of $1-D$.

Eq. (3) gives the total photosynthetic production of the two ramets. To find the optimal growth pattern, we use dynamical programming with numerical computer simulations (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 for the plant system.

$$f(x_{1a}, x_{1b}, x_{2a}, x_{2b}) = f_1 + f_2 \quad (3)$$

At time step t , the modeled plant system allocates new biomass (carbohydrates) to organ i at a relative ratio $u_i(t)$. Thus, the changing in biomass of each organ is given in Eq. (4).

$$\begin{aligned} \frac{dx_{1a}}{dt} &= u_{1a}(t)f(x_{1a}, x_{1b}, x_{2a}, x_{2b}) \\ \frac{dx_{1b}}{dt} &= u_{1b}(t)f(x_{1a}, x_{1b}, x_{2a}, x_{2b}) \\ \frac{dx_{2a}}{dt} &= u_{2a}(t)f(x_{1a}, x_{1b}, x_{2a}, x_{2b}) \\ \frac{dx_{2b}}{dt} &= u_{2b}(t)f(x_{1a}, x_{1b}, x_{2a}, x_{2b}) \end{aligned} \quad (4)$$

Each $u_i(t)$ varies between 0 and 1 and the sum of all $u_i(t)$ is 1 (Eq. (5)).

$$u_{1a}(t) + u_{1b}(t) + u_{2a}(t) + u_{2b}(t) = 1 \quad (5)$$

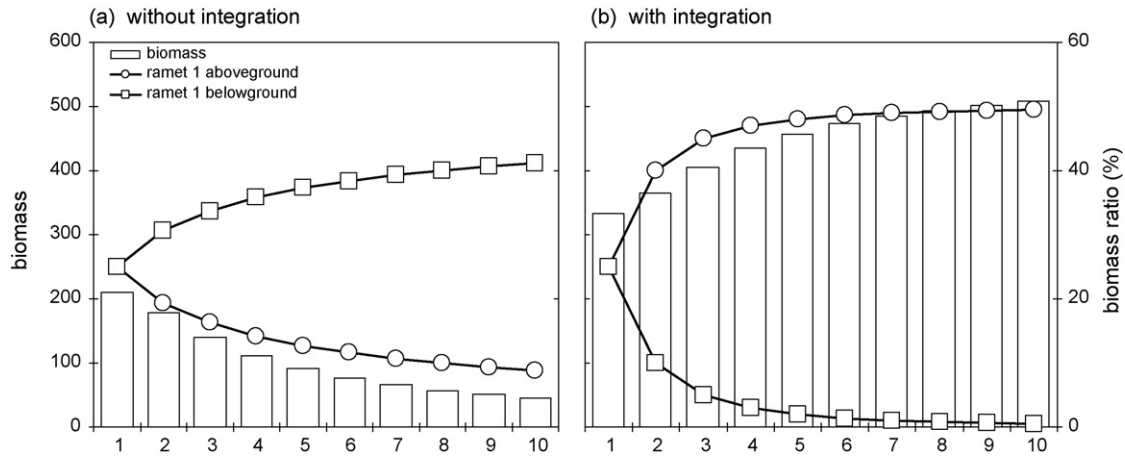


Fig. 2 – The total biomass of two ramets and the ratio of the biomass of each organ to the total biomass of ramet 1 (a) without integration, and (b) with integration, as a function of contrast in resource availability. Open squares show the ratio of the belowground biomass to the total biomass of ramet 1 and the open circles show the ratio of the aboveground biomass to the total biomass of ramet 1. Settings are $D = 0$, $F_i = 0.5$.

For simplicity, we ignore the cost of biomass allocation (no cost for carbohydrate transport). 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. 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.

3. Results

3.1. Contrasting resource availability

First we evaluate the effect of increasing contrast in resource availability at a negative spatial association between resources 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 ($C = E_{1a}/E_{2b} = E_{1b}/E_{2a}$). The sum of the aboveground and belowground resource availabilities for each ramet is constant and set at 13. When the contrast of environment increases, the amount of one resource increases while the other resource decreases. Although the amount of the resource availabilities is constant, the growth of a ramet without physiological integration is limited by a decrease in resources. On the other hand, if two physiological integrated ramets growing under heterogeneous environment, the increasing the contrast of resource availabilities means that the total amount of resource available, that two ramets can use, increases. We evaluate this for contrasts in resource availability (C) from 1 to 10 ignoring the cost of water transport ($D = 0$).

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 ramets without physiological integration allocates more biomass to the organs that grow under poor-quality conditions and the total biomass of the two ramets decreases (Fig. 2a).

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 the contrast in resource availability increases, the modeled plant allocates more biomass to the organ that grows under better conditions and the total biomass of the two ramets increases (Fig. 2b). When the contrast in resource availabilities, the modeled plant which is not physiologically integrated allocate about 80% of their total biomass to the organ that grows under poor conditions. If modeled plant is 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.

3.2. Cost of water transport

We also evaluate the cost of water transport, D at moderate resource availability and a negative spatial association between resources. Resource availability levels for each organ, E_{1a} , E_{1b} , E_{2a} and E_{2b} are set at 9, 4, 4 and 9, respectively.

If the cost of water transport is high, the modeled plant does not show DoL (i.e., the modeled plant allocates more biomass to the organs that grow under poor-quality conditions, Fig. 3). With decreasing costs of water transport (less than 60%) the plant starts exchanging water between two ramets. 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 for 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

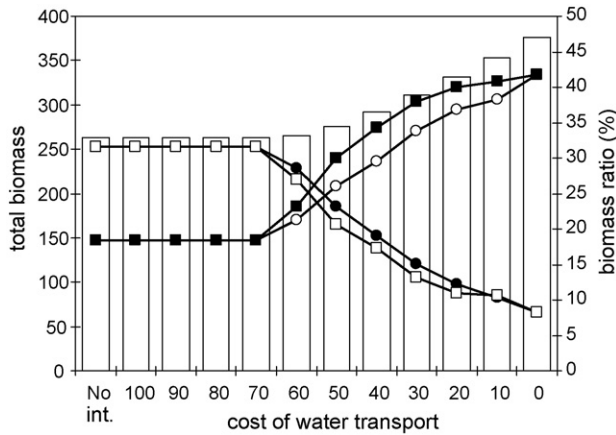


Fig. 3 – The total biomass of two ramets and the ratio of the biomass of each organ to the total biomass of the plant system at symmetric resource distribution, as a function of the cost of water transport (x-axis, No int. at the x-axis represents the results when there is no physiological integration of the ramets). The open and closed circles show the ratio of the aboveground biomass to the total biomass and the ratio of the belowground biomass to the total biomass of ramet 1 respectively, and the open and closed square show the ratio of the aboveground biomass to the total biomass and the ratio of the belowground biomass to the total biomass of ramet 2, respectively. Settings are $E_{1a} = E_{2b} = 9$, $E_{1b} = E_{2a} = 4$, $F_i = 0.5$.

grow under better conditions (Fig. 3). If there is no cost of water transport, the biomass allocation to the two ramets is equal, and the allocation to aboveground and belowground organs is inversely symmetric in the two ramets, but with costs, the allocation pattern becomes asymmetric (Fig. 3). Due to hydraulic resistance, water uptake per unit biomass in ramet 2 is less than ramet 1 when water moves from ramet 2 to ramet 1, thus, the plant increases its biomass allocation to the belowground organ of the ramet 2 (closed square in Fig. 3). As a result, belowground biomass of ramet 2 is larger than aboveground biomass of ramet 1, although environmental quality is equal ($E_{1b} = E_{2a} = 9$). As a result the plant transports enough

water to ramet 1 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 contrasts in resource availabilities and the total biomass of the two-ramet plant system i.e., the allocation balance between aboveground and belowground biomass in ramet 1 at different transport costs. The DoL can be observed when the ratios of above ground biomass of ramet 1 to total biomass of two-ramet systems are less than 25% in Fig. 4a. 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 local water capturing and consumption. 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 of water transport is lower and/or contrast of resource availability is higher, 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 even when the transport is costly. Thus, the plant allocates more biomass to the belowground organ of ramet 2 (not shown) and the aboveground organ in ramet 1 (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 than plants without cooperative growth when transport costs are lower than 30% ($D < 0.3$, Fig. 4b).

3.3. Asymmetric conditions of ramets

To evaluate asymmetric resource availability, we set the resource availability levels for each organ E_{1a} , E_{1b} , E_{2a} and E_{2b} at 8, 7, 5 and 6, respectively. Thus, we keep a negatively covarying distribution of resources, but the aboveground and belowground conditions for ramet 1 are better than those for ramet 2.

If the cost of water transport is high, the modeled plant system does not show DoL. The ramets do not exchange water and each ramet specializes in capturing the resource that

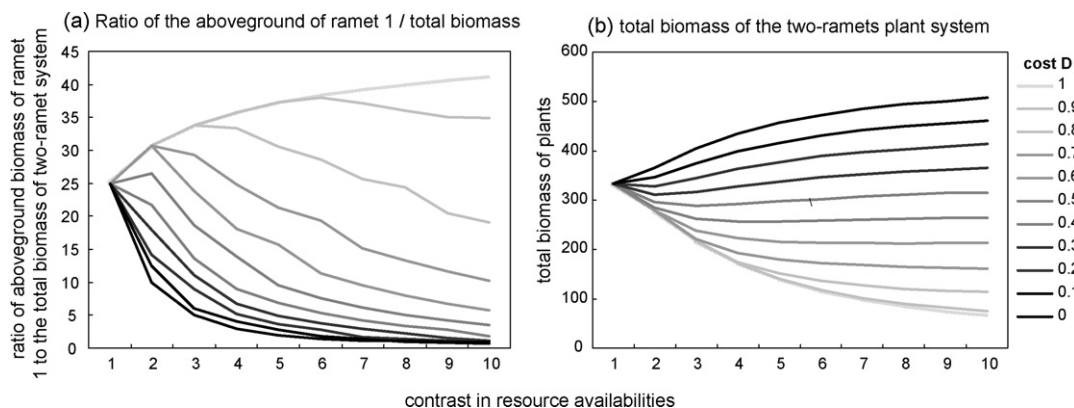


Fig. 4 – (a) Ratio of the aboveground biomass of ramet 1 to the total biomass of two-ramet systems and (b) total biomass of the two-ramets plant system, as a function of contrast in resource availability at the different costs of water transport. The darker the line is, the less the transport costs.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

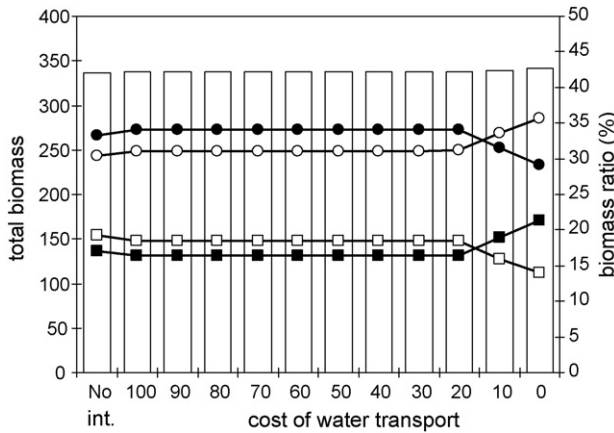


Fig. 5 – The total biomass of two ramets and the ratio of the biomass of each organ to the total biomass of the plant system as asymmetric resource distribution, as a function of the cost of water transport (x-axis, No int. at the x-axis represents the result when there is no physiological integration of the ramets). The open and closed circles show the ratio of the aboveground biomass to the total biomass and the ratio of the belowground biomass to the total biomass of ramet 1, respectively, and the open and closed square show the ratio of the aboveground biomass to the total biomass and the ratio of the belowground biomass to the total biomass of ramet 2, respectively. Settings are $E_{1a} = 8$, $E_{1b} = 7$, $E_{2a} = 5$ and $E_{2b} = 6$, and $F_i = 0.5$.

is locally in short supply. Since the modeled plant can allocate carbohydrates without translocation costs, the plant with physiological integration allocates slightly more biomass to both parts of ramet 1 than a plant without physiological integration (“No int.” and “100” in Fig. 5, also see Fig. 3). This is because both aboveground and belowground environmental qualities of ramet 1 are slightly better than those of ramet 2, thus, allocating slightly more biomass to ramet 1 is beneficial to capture resources at better environmental patches. 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 but each ramet specializes in capturing the locally abundant resource (Fig. 5). Because the contrast in resource availability is not strong, the plant systems benefits from DoL only at low levels of transport costs ($D < 0.1$ Fig. 5).

3.4. Resource capturing efficiency

To evaluate the effect of varying the resource capturing efficiency, we change the efficiency index F_i in Eq. (2). The cost of transport is 0 and the resource availability levels for each organ E_{1a} , E_{1b} , E_{2a} and E_{2b} 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 per unit biomass decreases as the biomass increases (Fig. 7). As a result, the organs that grow under lower quality conditions can have

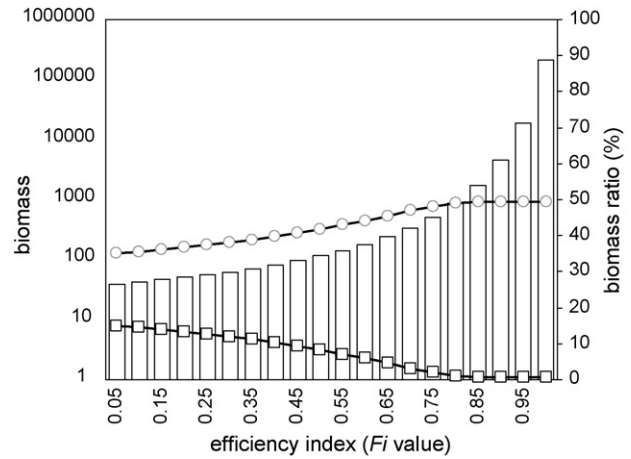


Fig. 6 – Total biomass of the two-ramets plant system (left y-axis) and the ratio of the biomass of the aboveground and belowground organs of ramet 1 to the total biomass (right y-axis) as a function of the efficiency index (x-axis). Closed squares show the ratios for the belowground organ and closed circles the ratios for the aboveground organ of ramet 1. Settings are $E_{1a} = E_{2b} = 9$, $E_{1b} = E_{2a} = 4$, $D = 0$, and $F_{1a} = F_{1b} = F_{2a} = F_{2b}$.

high resource capturing efficiencies per unit biomass 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.

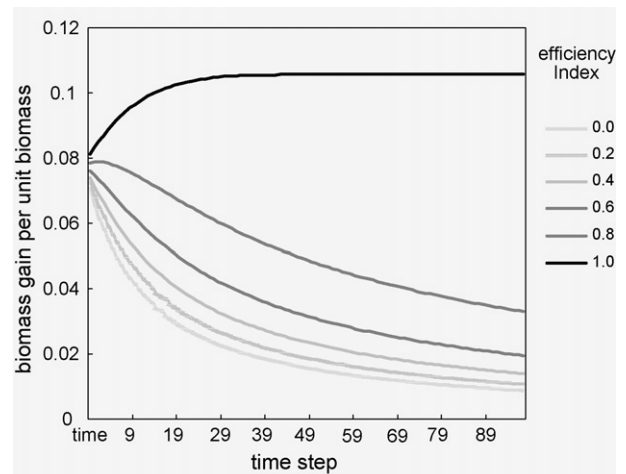


Fig. 7 – Efficiency of biomass gain per unit biomass at time step t under various F_i values. As plant size increases, biomass gain per unit biomass decreases if efficiency index is lower than 1. Settings are $E_{1a} = E_{2b} = 9$, $E_{1b} = E_{2a} = 4$, $D = 0$, and $F_{1a} = F_{1b} = F_{2a} = F_{2b}$.

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 an independent plant, and each 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; Iwasa and Roughgarden, 1984; Hutchings and de Kroon, 1994; Shipley and Meziane, 2002). If two interconnected ramets can exchange resources, then both ramets allocate biomass so as to maximize photosynthetic gains of the whole plant system. In clonal plants, biomass allocation pattern of organs, in other words the degree of specialization of the ramets, is determined by the interplay among the cost of transport, the contrast in resource availability and the efficiency of resource capturing. 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 (Fig. 2b) because of the phenomenon called spatial division of labor (Stuefer et al., 1996).

Many studies have shown that clonal plants transport water from ramets in wet patches to ramets in dry patches (Alpert, 1990; Stuefer, 1995; de Kroon et al., 1996). But usually, the transport does not work perfectly due to hydraulic resistance in the vessel (Stuefer and Hutchings, 1994; Stuefer, 1995; Stuefer et al., 1996, 1998), 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 modelling study by Stuefer et al. (1998). They pointed out that the optimal allocation patterns were very sensitive to the conductivity of the internode, since that will control the water exchange process. Conductivity of internodes in the model of Stuefer et al. (1998) is analogous to cost of water transport in our model. We show that if the cost is high, the modeled plant needs to allocate more biomass to the belowground organ of ramet 2 in the wet patch to assimilate more water to translocate (e.g. at cost 60% in Fig. 3). If the cost for DoL is larger than biomass gain from DoL, then the plant does not operate DoL (i.e. over 70% cost in Fig. 3). Although the costs of water transport is high, if the contrast in resource availability is high enough that the plant can capture more resources at the other ramet than locally then the plant system can benefit from DoL (Fig. 4a and b). This is because the interconnected ramets can achieve a larger biomass in contrasting environments rather than homogeneous environments.

The costs for translocation may have two aspects; costs for connecting tissues (e.g., building and maintaining rhizome, stolon, stems) and costs for transporting (e.g., hydraulic resistance, active transport). In this study, however, we ignored the costs of connecting tissues and carbohydrate translocation to simplify the model structure. This results in asymmetric allocation patterns in less contrast and symmetric environ-

ment (Fig. 3) and slight changes between integrated and not-integrated plants in asymmetric environmental settings (Fig. 5). If there are costs for carbohydrate translocation and connecting tissues, however, these results may not happen or to a lesser degree.

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 might 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 (Stuefer et al., 1998). Magyar et al. (2007) used a spatial explicit model and showed that the plant with module plasticity showed DoL under heterogeneous habitats when resource availability in patches did not change. If patch environments are not persistent or if a connection between ramets is served then DoL may become not beneficial, since each ramet specializes in locally abundant resources, once the connection is served or environment changed then each ramet immediately faces shortage of locally scarce resources (Stuefer, 1998; Magyar et al., 2007). In our study, we focused on the biomass allocation under stable environmental conditions. Although we have not investigated it, if the connection between two ramets are served in our model then each ramet will change allocation pattern to invest all biomass to the organ that takes up locally scarce resources until it establishes optimal balance (if possible) among organs as shown in Iwasa and Roughgarden (1984). In real plants, however, ramets may die due to lacking resources to maintain minimum requirements; especially the ramet specialized for capturing light faces to severe shortage of water. Our model can be easily expanded to simulate the degrees and risks of specialization in ramets under unstable conditions and connection lost.

In this study, we show the importance of resource capturing efficiency per unit biomass. When a real plant reaches a large size, then many costs associated with support, maintenance and aging increase, and thus, the efficiencies of resource capturing and transport to each organ decrease (Iwasa and Roughgarden, 1984). 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 a value smaller than 1, thus, the efficiency of each organ decreases as the biomass of each organ increases (Fig. 7). If the environmental heterogeneity is not highly contrasting, then differences in resource availability among patches are small. Under this setting, a small organ growing under a poor-quality condition may capture more resources per unit biomass than a bigger organ growing under a better-quality condition, because the decrease in efficiency of resource capturing per unit biomass in the bigger organ growing under the better-quality condition can be strong. Thus, in such a situation the modeled plant also allocates biomass to the organ growing under the poor-

quality condition. All available experiments and model studies of DoL assumed a high contrast in environmental heterogeneity (Alpert and Mooney, 1986; Stuefer et al., 1994; Alpert and Stuefer, 1997; Hutchings and Wijesinghe, 1997; Stuefer et al., 1998). In a clonal plant system in the field, the patch quality can be highly variable over short distances especially light and nutrients in soil but the contrast in environments, where two resources are negatively distributed, of adjacent ramets could unlikely be to be strong. Consequently, ramets should not show extreme specialization, and thus, DoL may be rather difficult to observe in the nature. Our results suggest, however, that even at a lower environmental contrast clonal plants can change their allocation balance drastically and show DoL. As we showed in Fig. 5, even in less contrasting environments, plants changed their biomass allocation to specialize in capturing locally abundant resources, although the benefit of DoL is small in terms of biomass. Ikegami (2004) studied the DoL with a two connected ramet groups of *Schoenoplectus americanus* placed into contrasting environments and found the ratio of aboveground to total biomass showed clear differences among treatments while total biomass and number of ramets showed much weaker differences. These results could confirm the findings in our model.

Acknowledgements

This study was financially supported by a grant to MJAW from the Andrew W. Mellon Foundation through the Smithsonian Institution and by the Faculty of Biology at Utrecht University. We thank Dr. Feike Schieving and Dr. Heinjo During in Utrecht University for their critical comments and suggestions in this study. We also thank two anonymous reviewers for their comments that have improved this manuscript.

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