

A theoretical framework for resource translocation during sexual reproduction in modular organisms

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Abstract An individual of modular organisms, such as plants and fungi, consists of more than one module that is sometimes physically and physiologically connected with each other. We examined effects of translocation costs, resource–fitness relationships and original resource conditions for modules on the optimal resource translocation strategy for reproductive success in modular organisms with simple models. We considered two types of translocation cost: amount-dependent and ratio-dependent costs. Three optimal resource translocation strategies were recognized: all resource translocation (ART), partial resource translocation (PRT), and no resource translocation (NRT). These strategies depended on the translocation cost, shape of resource–fitness curve, and original resource condition for each module. Generally, a large translocation cost and a concave resource–fitness relationship promoted NRT or PRT. Meanwhile, a small translocation cost and convex resource–fitness relationship facilitated ART. The type of translocation cost did not strongly affect the optimal resource translocation patterns, although ART was never an optimal strategy when the cost was ratio-dependent. Resource translocation patterns found in modular plants were discussed in the light of our model results.

Keywords Mathematical model · Module · Resource-fitness relationship · Resource translocation · Translocation cost

Introduction

Individuals of modular organisms (e.g. higher plants, fungi, and corals) consist of the assembly of similar structures such as shoots, hyphae and polyps (Harper et al. 1986;

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Tuomi and Vuorisalo 1989). In an organism with physically and physiologically connected modules, each module has the potential to interact with others, for example through physiological integration among modules, so that the whole organism may attain a higher energy gain or fitness than behave independently (Caraco and Kelly 1991; Stuefer et al. 1994; Alpert 1999; Chesson and Peterson 2002; Herben 2004) or it may spread the risk of mortality among modules under some conditions (Eriksson and Jerling 1990).

Higher plants are among the well-studied examples of modular integration. Shoots are the smallest modular units of the above-ground plant parts, and branches which are composed of neighboring shoots and ramets (clonal offspring) can also be regarded as modular units (Tuomi and Vuorisalo 1989; Eriksson and Jerling 1990; Sprugel et al. 1991; Caraco and Kelly 1991; Alpert 1999). Modules belonging to an individual are often subjected to different environmental conditions (Eriksson and Jerling 1990; Caraco and Kelly 1991; Sprugel et al. 1991; Hutchings and Wijesinghe 1997; Alpert 1999; Oborny et al. 2001; de Kroon et al. 2005). For example, branches of a tree are exposed to different light environments such that those on the crown are in sunny conditions and those at lower positions are shaded. Trees synthesize carbohydrates independently in each shoot, and the distribution of carbohydrates is not always uniform among branches, each of which is composed of neighboring shoots sharing a similar condition (Watson and Casper 1984; Sprugel et al. 1991). Sprugel et al. (1991) found a pattern that behavior of each branch was dependent upon the carbohydrate economy of the branch and independent of other branches. However, such branch autonomy is not always the absolute rule governing the branch growth (Sprugel 2002). For individual or population growth of clonal plants, module (ramet) autonomy and integration can be adaptive under certain habitat conditions (Alpert 1999; Oborny et al. 2001; Kun and Oborny 2003).

Reproductive characteristics such as the flower and fruit numbers and sex expression of flowers often vary among modular units (e.g. shoots, branches or ramets) of an individual plant (Sakai 1978; Hibbs and Fisher 1979; Bertin 1982; Sprugel et al. 1991; Ito and Kikuzawa 2000; Ushimaru and Matsui 2001). Branches have been supposed to act as autonomous modules during sexual reproduction in many trees (Sprugel et al. 1991; Hasegawa et al. 2003). On the other hand, whole-tree regulation (or physiological integration among branches) may occur, for example, during fruiting in *Aesculus californica* (Newell 1991) and in sex expression of *Alunus hirsuta* (Hasegawa and Takeda 2005). These reports imply that there exists a spectrum with regard to module regulation during sexual reproduction in plant species: complete module autonomy at one end and whole-individual regulation at the other.

The relationship between the resource amount and its resultant fitness in each module is a critical factor determining the presence or absence of whole-individual regulation (Caraco and Kelly 1991). In fact, the sizes of ramets have been often used as the index of resource status (Eriksson and Jerling 1990). Resource translocation pattern between ramets should be strongly affected by the resource–fitness (resource–performance) curve in clonal plants (Eriksson and Jerling 1990; Caraco and Kelly 1991; Alpert 1999). Resource translocation can be optimal if one module (module A) attains considerably high fitness by translocating a resource from another (module B) with a small amount of fitness loss in module B, when the relationship between resource amount and fitness is not linear (Eriksson and Jerling 1990; Caraco and Kelly 1991).

Whole-individual regulation means resource translocation between modules. In general, translocation of resources between modules necessarily involves a cost (Penning De Vries 1975; Bloom et al. 1985; Caraco and Kelly 1991). How costs affect resource translocation has rarely been examined (but see Herben 2004). In this paper, we theoretically studied the

optimal strategy of resource translocation between modules within an individual organism (i.e. whole-individual regulation) during reproduction in relation to the translocation cost and resource–fitness relationships. Previous theory has considered partial resource translocation unidirectionally from resource-rich to resource-poor modules (e.g. Eriksson and Jerling 1990; Kaitaniemi and Honkanen 1996). However, the opposite direction of resource translocation or translocation between modules with similar resource conditions may occur in plants, especially during reproduction (Alpert 1999; Alpert et al. 2002). In theory, all resource of a module could be translocated to other modules so as to maximize the fitness for reproduction. In this article, we include them in our analysis to understand broader patterns of resource translocation in modular organisms. Our extended model revealed a variety of patterns of translocation strategies, some of which have not been shown by the existing models. We discuss factors affecting these translocation patterns in relation to the cost and resource–fitness relationships.

The model

We assume that an individual organism consists of two modules (i.e. Module 1 and Module 2) for simplicity. Here we consider only the resource for reproduction, not for asexual growth. Some plant species invest in reproduction their resources that are surplus to requirements for vegetative growth (Crawley 1985; Suzuki 2000, 2001; Ida and Kudo 2008). The reproductive resource conditions R_1 for Module 1 and R_2 for Module 2 without resource translocation between modules can be different, depending on several factors such as light condition in plants (Eriksson and Jerling 1990; Caraco and Kelly 1991; Sprugel et al. 1991; Alpert 1999). We refer these R_1 and R_2 values without resource translocation as the original resource conditions. Although resource conditions of modules could be altered dynamically depending on the balance between resource acquisition and respiration, the initiation of reproductive organs generally occurs at a certain period of time or season in many modular organisms such as plants and fungi. We therefore define the original resource conditions as the resource status just before the initiation of reproductive organs and assume that the amount of resource translocation is determined according to the original resource conditions.

We assume that the resource is unidirectionally translocated from Module 1 (source module) to Module 2 (sink module). Thus, $0 \leq x \leq R_1$ holds, provided that the amount of translocated resource is x . The amount of x relative to R_1 could be considered as the sink strength of Module 2 (Clifford 1992; Honkanen et al. 1999), and evolved under selection maximizing the whole fitness of the individual (Tuomi and Vuorisalo 1989). Because we deal with both cases where $R_1 < R_2$ and $R_1 > R_2$, the unidirectional translocation does not lose the generality that a resource can be translocated from a larger module to a smaller one, and vice versa. Unidirectionally acropetal translocation of sugars and nutrients is often found in plants (Caraco and Kelly 1991 and references therein).

Translocation cost

We consider two types of translocation cost. First, the translocation cost increases linearly with the amount of translocated resource x (amount-dependent cost). In this case, the resource conditions for Modules 1 and 2 after translocation are respectively represented as

$$r_1(x) = R_1 - x \quad (1)$$

$$r_2(x) = R_2 + (1 - k)x, \quad (2)$$

where R_1 and R_2 are the original resource conditions of Modules 1 and 2, respectively, and $r_1(0) = R_1$ and $r_2(0) = R_2$. Because of resource translocation, the actual resource conditions (r_1 and r_2) available to the modules can be different from the original conditions (R_1 and R_2). We assumed that a proportion k ($0 \leq k \leq 1$) of the conveyed resource was consumed as the cost for resource translocation.

Second, the translocation cost increases linearly with the ratio of the current resource amount in Module 2 to that in Module 1 at the moment when an infinitesimal resource dx is translocated from Module 1 to Module 2 (ratio-dependent cost). The resource conditions for Modules 1 and 2 after resource x has been translocated are respectively expressed as

$$r_1(x) = R_1 - x \quad (3)$$

$$r_2(x) = R_2 + x - k \int_0^x \frac{r_2(x')}{r_1(x')} dx'. \quad (4)$$

Applying Eq. 3 to Eq. 4, we can solve Eq. 4 with regard to $r_2(x)$:

$$r_2(x) = \left(R_2 R_1^k - \frac{R_1^{k-1}}{k-1} \right) (R_1 - x)^k + \frac{R_1 - x}{k-1}. \quad (5)$$

Resource translocation occurs within a short time, independent of reproduction or growth, in the case of ratio-dependent cost as well.

Translocation of sugars in phloem usually involves metabolic costs (Bloom et al. 1985; Caraco and Kelly 1991). We adopt the translocation cost at $k = 0.1$ in the following calculation, based on the estimation that 10% of the amount of carbon translocated is lost during phloem loading of sucrose (Bloom et al. 1985).

Resource–fitness relationships

In general, fitness increases with the amount of resource. How fitness responses to an increase in resource is variable, depending on organisms. In this study, five cases of the resource–fitness relationships were considered according to the previous study (Caraco and Kelly 1991). For mathematical simplicity, a minimal function was applied in each case.

Case 1: Fitness per module (f) linearly increases with the amount of resource (R):

$$f(R) = R. \quad (6)$$

Case 2: The fitness–resource relationship is described by a convex (accelerating) function:

$$f(R) = R^2. \quad (7)$$

Case 3: The relationship is a concave (decelerating) function:

$$f(R) = \sqrt{R}. \quad (8)$$

Case 4: The relationship is convex when resource is small ($R < 1$) and concave when resource is large ($R > 1$), i.e. a sigmoid curve:

$$f(R) = \frac{4R^2}{R^2 + 3}. \quad (9)$$

Case 5: The relationship is concave when resource is small ($R < 1$) and convex when resource is large ($R > 1$):

$$f(R) = \sqrt{\frac{3R}{4 - R}}. \quad (10)$$

Note that these functions have the following common characteristics: (1) fitness attains to 1 when the resource amount is 1 (i.e. $f(1) = 1$) and (2) the inflection point is located at $R = 1$ if any (i.e. $f''(1) = 0$ in Cases 4 and 5). For the sake of Case 5 (Eq. 10) to be valid, we calculated the optimal amount of resource translocation with the assumption that the combined amount of the resources in Modules 1 and 2 is at most 4 (i.e. $0 < R_1 + R_2 \leq 4$).

Whole fitness of an individual organism

The whole fitness of an individual organism (W) is given as

$$W = f(r_1(x)) + f(r_2(x)). \quad (11)$$

We examined the optimal amount of resource translocation (x) to maximize the whole fitness (W) for five cases of the resource–fitness relationships (Eqs. 6–10) with two types of translocation cost (amount-dependent vs. ratio-dependent).

Results

Our model analysis showed that there were seven strategies for optimal resource translocation: (a) no resource translocation (NRT), fitness monotonically decreases with resource translocation ($x^* = 0$, Fig. 1a); (b) all resource translocation (ART), fitness monotonically increases with resource translocation ($x^* = R_1$, Fig. 1b); (c) all resource translocation with risk (ART with risk), all resource translocation is theoretically optimal but there is a trough (i.e. minimum) in fitness between no resource translocation and all resource translocation, so that the fitness is a decreasing function at $x = 0$ (Fig. 1c); (d) all resource translocation with local risk (ART with local risk), all resource translocation is theoretically optimal but there is a trough in fitness between partial resource translocation ($x_{\text{sub-opt}}$) and all resource translocation, so that the fitness is an increasing function at $x = 0$ (Fig. 1d); (e) partial resource translocation (PRT, $x^* = x_{\text{opt}}$, Fig. 1e); (f) partial resource translocation with risk (PRT with risk), partial resource translocation ($x^* = x_{\text{opt}}$) is theoretically optimal but there is a trough in fitness between $x = 0$ and $x = x_{\text{opt}}$ (Fig. 1f); (g) partial resource translocation with local risk, partial resource translocation ($x^* = x_{\text{opt}}$) is theoretically optimal but there is a trough in fitness between $x = x_{\text{sub-opt}}$ and $x = x_{\text{opt}}$ ($x_{\text{sub-opt}} < x_{\text{opt}}$, figure not shown because this strategy was rarely found). Note that, in strategies (c), (d), (f) and (g), the organism has a risk to reduce its fitness if resource translocation is accidentally interrupted before the translocation is completed.

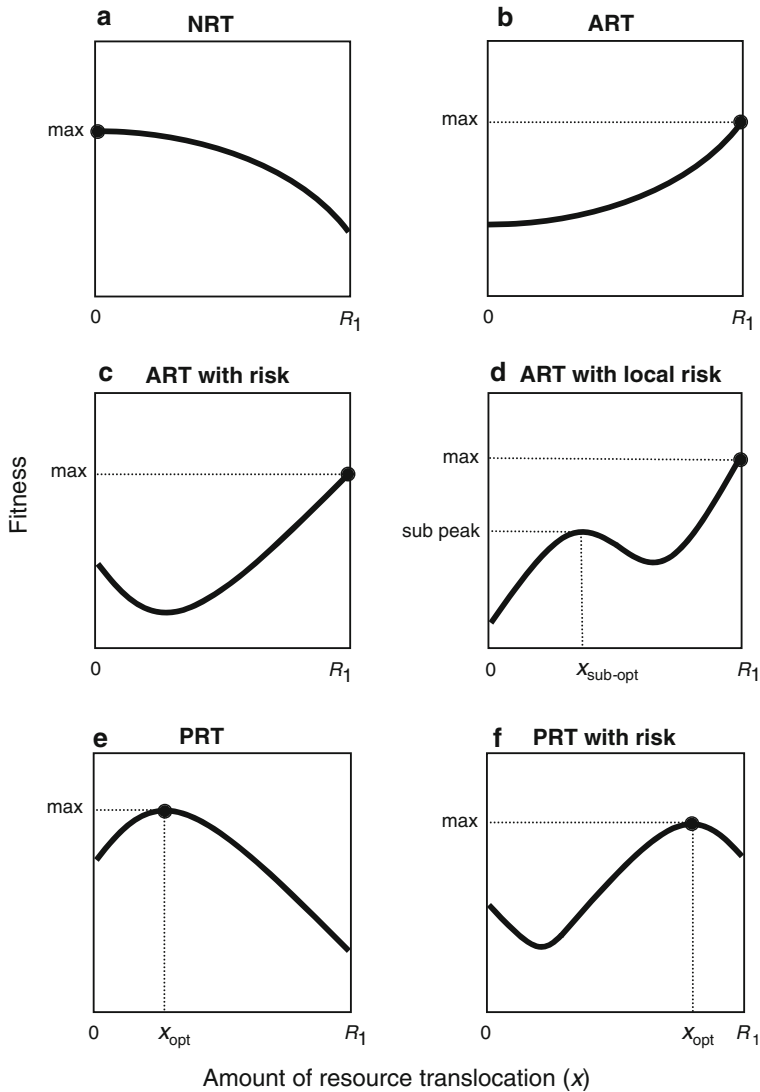


Fig. 1 Relationships between the amount of resource translocation and fitness for six optimal resource translocation strategies: **a** NRT, no resource translocation; **b** ART, all resource translocation; **c** ART with risk, all resource translocation with risk; **d** ART with local risk, all translocation with local risk; **e** PRT, partial resource translocation; **f** PRT with risk, partial resource translocation with risk. Closed circles show the maximum fitness

Optimal resource translocation with amount-dependent cost

Case 1: When the resource–fitness relationship is expressed as a linear correlation (Eq. 6), the whole-individual fitness with resource translocation x is written as

$$W = (R_1 - x) + \{(R_2 + (1 - k)x\} = R_1 + R_2 - kx.$$

This equation indicates that the whole fitness linearly decreases with x . Thus, NRT ($x = 0$) is always optimal when there is a translocation cost.

Case 2: From Eqs. 1, 2, 7 and 11, an organism with the convex resource–fitness relationship has the whole-individual fitness:

$$\begin{aligned} W &= (R_1 - x)^2 + \{R_2 + (1 - k)x\}^2 \\ &= \{1 + (1 - k)^2\}x^2 - 2\{R_1 - (1 - k)R_2\}x + R_1^2 + R_2^2. \end{aligned} \quad (12)$$

Assuming that the amount of resource translocation (x^*) should be optimal so as to maximize W in Eq. 12, the optimal translocation strategies are

$$\begin{aligned} (\text{ART}) \ x^* &= R_1 \text{ when } \frac{R_1}{(1 - k)} < R_2, \\ (\text{ART with risk}) \ x^* &= R_1 \text{ when } \frac{k(2 - k)}{2(1 - k)}R_1 < R_2 < \frac{R_1}{(1 - k)}, \\ (\text{NRT}) \ x^* &= 0 \text{ when } R_2 < \frac{k(2 - k)}{2(1 - k)}R_1. \end{aligned}$$

NRT was not optimal when $k = 0$. With a translocation cost, the optimal strategy for resource translocation depended on the original resource conditions of Modules 1 and 2 (R_1 and R_2) and the translocation cost k (Fig. 2). ART had a lower limit (line $R_2 = R_1/(1 - k)$) and NRT had an upper limit (line $R_2 = k(2 - k)R_1/\{2(1 - k)\}$) in the R_1 – R_2 space (see Fig. 2). An accelerating fitness curve leads to ‘specialization’ of resources, as it will be more rewarding to have one resource-rich module rather than two intermediate-sized modules. This arises because the fitness gain in the sink module is greater than the fitness loss in the source module when the source is smaller in resource than the sink. NRT is optimal as long as the source is larger than the sink, whereas ART is optimal if the source is smaller. Thus, PRT is never beneficial in this case. The optimal translocation patterns hardly changed (ART was optimal in a wider area) as long as the translocation cost was low ($k \leq 0.1$). When the cost was high (e.g. $k = 0.5$), NRT was optimal in a wider area.

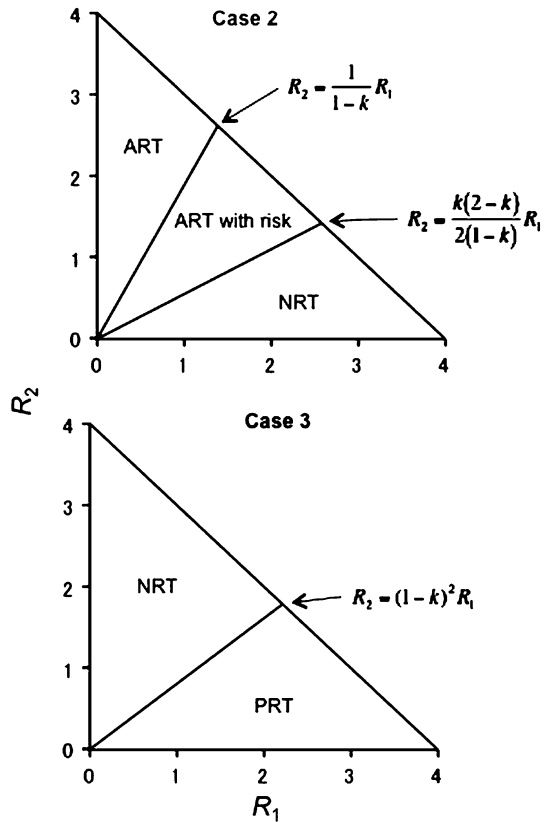
Case 3: The optimal resource translocation strategy of an organism with the concave resource–fitness relationship is given by

$$\begin{aligned} (\text{NRT}) \ x^* &= 0 \text{ when } (1 - k)^2 R_1 < R_2 \\ (\text{PRT}) \ x^* &= x_{\text{opt}} = \frac{(1 - k)^2 R_1 - R_2}{(1 - k)(2 - k)} \text{ when } (1 - k)^2 R_1 > R_2. \end{aligned}$$

PRT could be adaptive when $R_1 > R_2$ depending on the cost k , while NRT was always optimal when $R_1 < R_2$ (Fig. 2). A decelerating fitness curve leads to ‘equalization’ of resources, because a small amount of resource translocation is likely to result in a greater fitness gain in a smaller module and a smaller fitness loss in a larger module (i.e. net positive gain as the whole fitness). As a result, it will be more beneficial to have two intermediate modules rather than one large module when the source is larger than the sink.

Case 4: The optimal resource translocation pattern was complicated, compared with the previous cases (Fig. 3a–c). The resource–fitness curve (sigmoid) can be considered as the combination of a convex curve for $x < 1$ (Case 2) and a concave curve for $x > 1$ (Case 3). Thus, Case 4 is special cases of accelerating and decelerating resource–fitness functions.

Fig. 2 Optimal resource translocation strategies expressed in the R_1 – R_2 space. Case 2, a convex resource–fitness relationship. Case 3, a concave resource–fitness relationship. See Fig. 1 for key to abbreviations



If resource level is overall small (lower-left region) then the resulting translocation pattern of the sigmoid curve is similar to that of an accelerating curve. If resource level is overall large (upper-right region), the resulting translocation pattern is similar to that of a decelerating curve. The region in which NRT was optimal increased as the cost for translocation became higher.

Case 5: The optimal resource translocation pattern in this case is a reversed pattern of Case 4 (Fig. 3d–f), because the resource–fitness curve is convex for $x < 1$ and concave for $x > 1$. The patterns in the lower-left and upper-right regions are similar to those of decelerating and accelerating curves, respectively.

Effect of ratio-dependent cost on optimal resource translocation

In Case 1, NRT was always optimal, since

$$\frac{dW}{dx} = \frac{dR_1(x)}{dx} + \frac{dR_2(x)}{dx} = -k \frac{R_2(x)}{R_1(x)} < 0,$$

where $R_1(x)$ and $R_2(x)$ were given by Eqs. 3 and 4. The optimal resource translocation patterns for the ratio-dependent cost were, in general, similar to those obtained for the amount-dependent cost in Cases 2–5 (Fig. 4). Note, however, that the ART was never optimal, because the translocation cost became extremely high when the resource amount of Module 1, $R_1(x)$, approached zero (Eq. 4).

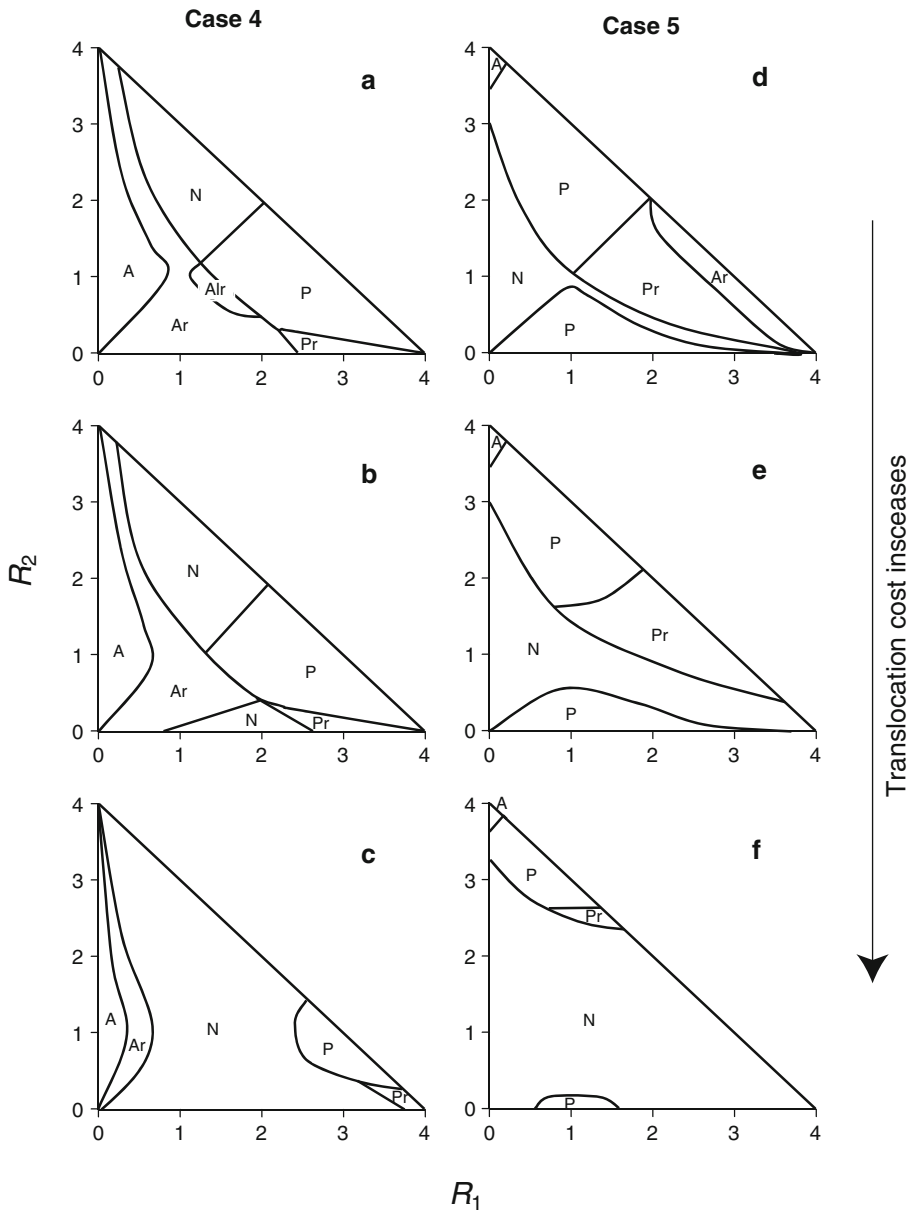


Fig. 3 Optimal resource translocation strategies with a sigmoid resource–fitness relationship (Case 4) expressed in the R_1 – R_2 space: **a** $k = 0.01$ **b** $k = 0.1$ **c** $k = 0.5$, and an inverse-S shape (Case 5): **d** $k = 0.01$ **e** $k = 0.1$ **f** $k = 0.5$. *A* ART; *Ar* ART with risk; *Alr* ART with local risk; *N* NRT; *P* PRT; *Pr* PRT with risk

Discussion

We found three optimal resource translocation strategies: all resource translocation (ART), partial resource translocation (PRT), and no resource translocation (NRT). These strategies

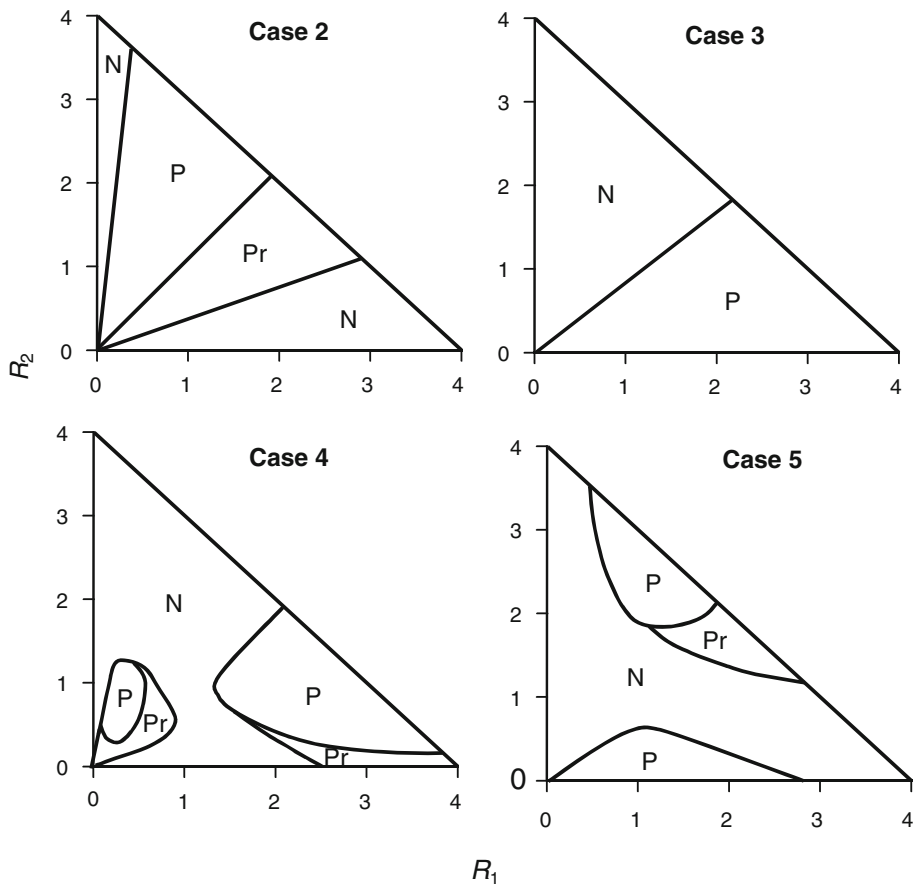


Fig. 4 Optimal resource translocation strategies for the ratio-dependent cost. In all cases, $k = 0.1$. *P* PRT; *Pr* PRT with risk; *N* NRT

were dependent upon the translocation cost, shape of resource–fitness curve, and original resource conditions for modules.

Translocation cost

It is considered that resource translocation inevitably accompanies with energy expenditure for synthesis of transport compounds such as sucrose and phloem loading of sucrose (Penning De Vries 1975; Geiger 1979; Bloom et al. 1985; Caraco and Kelly 1991; Martin et al. 1993), although no direct measurement of translocation cost has been conducted. A low cost (ca. 10%) may be the case for phloem loading (Bloom et al. 1985). The model showed that the optimal resource translocation patterns were strongly affected by the translocation cost. NRT became more adaptive as the cost was higher. As long as the cost was low, our model showed that the optimal strategy was specialization of resources when the resource–fitness relationship was a convex (accelerating) function, and equalization of resources when the relationship was a concave (decelerating) function (Fig. 2). A strategy of equalization conforms to previous theory as resource sharing during vegetative growth

(Eriksson and Jerling 1990; Caraco and Kelly 1991). Since the existing theory has dealt with resource sharing among modules, our model with extended assumptions theoretically showed a possibility of a strategy of specialization in which resource can be translocated from resource-poor to resource-rich modules.

The type of translocation cost (amount-dependent or ratio-dependent) hardly affected the optimal resource translocation patterns in all cases, except that ART was never an optimal strategy for the ratio dependent cost. This means that it does not matter whether the translocation cost is amount-dependent or ratio-dependent. Instead, it might be more important that the translocation cost increases with the distance of transportation. In practice, the majority of photosynthate allocated to flowers and fruits comes from the nearest shoot in many tree species (Sprugel et al. 1991; Hasegawa et al. 2003; but see Matthew et al. 2004).

Resource–fitness relationships

Concave and convex curves in resource–fitness relationships are generally expressed by

$$f(R) = R^\alpha \quad (13)$$

($\alpha < 1$: concave, $\alpha = 1$: linear, $\alpha > 1$: convex), although we analyzed minimal functions for simplicity. Qualitative patterns described in Fig. 2 held with the generalized curve (Eq. 13). When $\alpha < 1$, the slope of the boundary between NRT and PRT decreased with increasing α . The slope approached $1 - k$ at $\alpha \rightarrow 0$ and 0 at $\alpha \rightarrow 1$. When $\alpha > 1$, the slopes of ART–ART with risk (Ar)' and Ar–NRT boundary lines decreased with increasing α . These boundary lines both approached the y-axis at $\alpha \rightarrow 1$. The slopes of ART–Ar and Ar–NRT boundary lines approached 1 and k at $\alpha \rightarrow \infty$, respectively.

A concave curve in which fitness increases deceleratingly with the resource amount (Case 3) has been often accepted as a first-order approximation for resource–fitness relationships of flowering plants (Alpert 1999). Our model without a translocation cost revealed that PRT was optimal when the source module had a larger resource than the sink module as a result of equalization as shown by Caraco and Kelly (1991), whereas NRT was optimal when the resource conditions of the source and sink modules were reversed (Fig. 2). With a translocation cost ($k > 0$), NRT can be optimal even when the resource in the source module was larger than in the sink module. A sigmoid curve with an accelerating phase when the resource is small and then a decelerating phase when the resource becomes larger (Case 4) may be applied as a second-order approximation for resource–fitness relationships. In flowering plants, a sigmoid curve would be the case when an increase in flower number results in an increased efficiency of pollinator attraction which will be then saturated. For example, the relationship between the numbers of flowers and pollinator visits is often modeled by a sigmoid curve (Ohashi and Yahara 2001).

If fitness increases acceleratingly with the amount of resource (convex relationship, Case 2), the translocation strategies were shown to be different from those with a concave relationship. Our model including both partial and all resource translocation revealed for the first time that all resource should be translocated when the resource amount of the source module is smaller than the sink module as a result of specialization (Fig. 2). This suggests that organisms displaying both reproductive and non-reproductive modules within an individual, which is often the case with plants in the field (Kawamura and Takeda 2006), could be due to resource translocation (Alpert et al. 2002).

Organisms that experience sex change in their life are thought to have a convex resource–fitness relationship as a first-order approximation (Policansky 1981; Charnov 1982; Kinoshita and Harada 1990), although a convex relationship (Case 2) has been considered unlikely for growth stage in natural plants (Bloom et al. 1985; Alpert 1999; but see Eriksson and Jerling 1990). Case 5 may be a second-order approximation for resource–fitness relationships of sex changing organisms. The relationship that female fitness is lower than male fitness when the resource is small is reversed when the resource exceeds a critical level (Charnov 1982). This critical level of resource is represented by the inflection point at (1, 1) in Case 5.

In sex changing *Acer* trees, sex expression of several branches within a large tree does not often synchronize with each other (Sakai 1978; Hibbs and Fisher 1979; Matsui 1995; Ushimaru and Matsui 2001). Large trees generally have large crowns and therefore their original resource conditions are likely to vary among branches due to different light conditions, resulting in mixed sex expression within an individual tree such that some branches have male flowers and others female ones. This implies that no resource translocation occurred between branches in the *Acer* species (Ushimaru and Matsui 2001). Female reproduction in general needs more resource than male reproduction and female inflorescences are often distributed among lower branches than male ones in *Acer* species (Sakai 1978; Matsui 1995). Lower branches may have a larger amount of resource for reproduction than upper ones, because upper sunny branches allocate most resources to vegetative growth whereas lower shaded branches allocate most resources to reproduction (Suzuki 2000) and often behave as source modules due to apical dominance. Our model with a convex relationship (Case 2) suggests branch autonomous sex expression (i.e. NRT) when the source module has a larger amount of resource than the sink module and the translocation cost is considerable (Fig. 2).

Original resource conditions

Even when a translocation cost and a resource–fitness curve were given for an organism, the optimal resource translocation strategy differed depending on the original resource condition for each module. This result supports previous field, experimental and theoretical findings (e.g. Caraco and Kelly 1991; Kelly 1994; Kelly et al. 2001; Alpert et al. 2002; Sprugel 2002; Herben 2004; Hay and Kelly 2008), although previous studies showed that the optimal resource translocation of an individual is often considered to be a fixed strategy depending on the given resource–fitness curves in clonal species or populations (Eriksson and Jerling 1990; Alpert 1999; Oborny et al. 2001; Kun and Oborny 2003). Clonal plants and trees may plastically change their translocation strategies in response to the resource distribution of their modules (Alpert et al. 2002; Sprugel 2002). Resource translocation strategies including PRT and ramet fragmentation (i.e. NRT by severed physical connection) are suggested to be physiologically controlled depending on intra-individual resource conditions in clonal plants (Lötscher and Hay 1997; Alpert et al. 2002; Hay and Kelly 2008). This implies that plastic response of resource translocation to within-individual resource distribution is adaptive in heterogeneous environments (Hay and Kelly 2008).

Future extension

In our model, we assumed a two-module system and unidirectional translocation for mathematical simplicity. However, poly-module system and bidirectional translocation are

often found in real plant species. In such plant species, sink–source relationships among modules could be changed under stressed conditions (Sprugel et al. 1991). Alpert et al. (2002) suggested that hormones can modify direction of resource translocation between ramets in clonal plants. An extension of our model could treat these factors.

We assumed that resource translocation was independent of reproduction or growth for the sake of simplicity in this article. Plants may translocate resources along with growth or reproduction, in which there may be time-dependent changes in resource state of modules. In this situation, the modules would respond more dynamically to the changing status to maximize the individual fitness. It is an important question whether a plant is capable of monitoring and responding to the current resource status of the modules, and if it can, whether it can do it instantaneously without any time delay.

Although detailed information on the translocation cost, resource–fitness relationship, original resource conditions, and hormonal control of translocation is still an important uncertainty and should be a priority for future experimental and field research, our model results reinforced the possibility of resource translocation between modules in plant species.

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