A hierarchical perspective in allocation to reproduction from whole plant to fruit and seed level

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Abstract

Allocation to reproduction is often examined at the whole plant level from an allometric perspective; however, investment in reproduction is a hierarchical process which represents the integration of adjustments at different hierarchical levels. This essay review presents some key issues in reproductive allocation by examining problems of allocation at different hierarchical levels within plant. At the whole plant level, the application of 'Rensch's rule' to plants is discussed as a mechanism that might explain size differences in relation to gender in dioecious species. At branch level, the existence of vegetative branches may be explained by hypotheses on branch specialization and costs of reproduction. However, vegetative branches might also constitute an 'assurance' for reproduction in variable environments. At a lower hierarchical level, fruit abortion is a process widely observed in plants that impose limits to our capacity to estimate and develop general laws about reproductive allocation in plants. The question of whether fruit abortion can be used by the parent to produce a more homogeneous progeny that limits asymmetric competition among sibs is discussed. Finally, it seems that in some cases the allocation within seeds is in accordance with some predictions of kin selection theory. Most of these topics contain open questions that deserve further research.

Key words: branch autonomy, dioecious plants, fruit and seed abortion, reproductive investment, sibling rivalry

Introduction

Many plants invest in competing activities, for example growth, storage, maintenance costs and defences against predators in ways that will maximize the value of various life-history traits. Among these allocation to reproduction is particularly important because it is closely related to fitness and may represent a measure of success in terms of allocation of limiting resources to other activities (Obeso 2002). In this sense, the study of reproductive allocation should allow us to understand various aspects of life-history evolution in plants.

During recent times the theory of allometry has been developed as an important framework for explaining patterns of plant allocation to reproduction. The model by Niklas & Enquist (2003) provides the basis for understanding the scaling of reproductive biomass across and within species. Allometric rules dictate how metabolic production and biomass are partitioned between different plant parts at the level of the individual and they provide a general theory of allometric scaling. The scaling of biomass allocation to reproduction roughly follows the 3/4-power law, which is connected to an even more general theory of

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allocation, derived from the 3/4-power scaling of the metabolic rate in relation to plant size. It seems that this general law applies well from the whole plant level to the community level (Enquist 2002). However, there are still many situations in which allocation to reproduction is scarcely understood and this general law is difficult to apply. This is, for instance, the case of dioecious plant species in which the scaling of allocation to reproduction may differ between genders (Obeso 2002).

Allocation to reproduction is often studied at the whole plant level from an allometric perspective; however, investment in reproduction is a hierarchical process. If reproductive allocation (RA) is determined by the scaling of allocation at the whole plant level, the RA at lower hierarchical levels could be controlled by a top-down process. On the contrary, RA may be examined using a bottom-up approach. RA at plant level represents the integration of adjustments of investments at different levels: allocation to different seed tissues (embryo, endosperm, seed coats), number and mass of seeds per fruit, number of fruits per branch and the proportion of fruiting branches. Therefore, to obtain a complete picture of the whole process we should understand the patterns of reproductive allocation at each hierarchical level.

This contribution addresses some problems in allocation to reproduction in plants based on the following two leading ideas: First, the consideration of the hierarchical structure of plant modules and how allocation to reproduction is determined at each hierarchical level. Second, the application of the 'Principle of Similarity' by examining in plants some questions that have been addressed for a long time in animals (Barton-Wright 1932).

Specifically, the following issues will be addressed at different hierarchical levels:

(1) At the whole plant level, I will consider the particular case of dioecious plants in which reproductive allocation not only depends on plant size but also on the gender of the plant.

(2) At the branch level, reproductive investment is not evenly distributed between branches. In fact we can distinguish between reproductive and vegetative branches. Therefore, the question emerges why are there vegetative branches?

(3) At fruit level, the observation that plants produce more flowers than fruits is an old problem in evolutionary ecology that remains unsolved. A considerable fraction of reproductive investment is lost through fruit abortion and this represents a problem in understanding the patterns of reproductive allocation.

(4) Other questions are: How are resources allocated within fruit? Are resources homogeneously or heterogeneously distributed between the seeds within the same brood? Is there sibling rivalry? How are resources allocated within the seed? A seed is a combination of tissues from different origins and might develop different functions. Why allocate different amounts of resources to these tissues?

Allocation at the whole plant level: the case of dioecious species

In a review considering about 100 dimorphic species, female plants were found to invest proportionately more in reproduction than males regardless of their size (Obeso 2002). RA was consistently higher for females in most species. Females invested up to ten times more in reproduction than males. Only three references reported no significant differences between sexes and males did not allocate more than females in any species. If females of dioecious species use proportionally more resources on reproduction they should have less resources available for competing activities such as maintenance and growth compared to males. As a result, females should be smaller. If we scale RA in dioecious species, females invest more than males but the scaling might be the same (Fig. 1).

The same review showed also that the sex that outperformed the other was significantly dependent on the growth form (Obeso 2002). Males of woody species were larger than females, but females of herbaceous species were frequently larger than males. These results are difficult to explain because in concordance with the model, woody females were consistently smaller than males supporting the hypothesis of the costs of reproduction. In contrast, in herbaceous perennials females
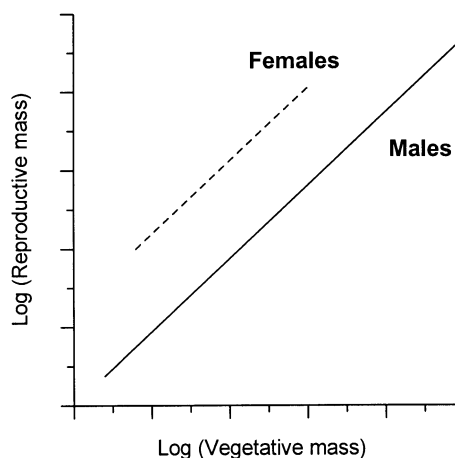

Fig. 1. Model for reproductive allocation in dioecious species resulting from the 'cost of reproduction' hypothesis. Females invest more than males in reproduction, start reproducing at higher size than males and grow less than males.

were generally larger contradicting the expectations of the cost of reproduction hypothesis.

We can apply the principle of similarity by plotting for each species the mean mass of the female against the mean mass of male. Within related groups of animals, males tend to be larger than females in larger species whereas females tend to be the larger sex in smaller species. This has been widely accepted in studies of sexual size dimorphism in animals and is known as 'Rensch's rule' (Rensch 1960; Abouheif & Fairbairn 1997; Fairbairn 1997; Colwell 2000).

If we take into account the fact that in general terms herbaceous plants tend to be smaller than woody ones, Rensch's rule might provide an explanation for the above patterns found for dioecious plants. Figure 2 shows the results of a literature review including the mass of both sexes in the case of herbaceous species and the diameter at breast height (DBH) for woody species. In both cases the slope of the relationship between the mean mass of the sexes did not significantly differ from 1, whereas the rule predicts a slope lower than 1. This negative result might be explained by the fact that 50% of the species in Fig. 2 either showed no significant differences between sexes (eight species out of 23) or differences in size did not fit the expectations of larger females for herbs and larger males for woody plants (four species out of 23). Size differences between sexes have been reported for plant height in most of the species but information about plant mass in dioecious species is still scarce.

Although the prospect of applying the Rensch's rule to plants needs further development it seems clear that sexual dimorphism in life history traits in dioecious species is not fully explained by the hypothesis of costs of reproduction. In fact, in the case of large animals Rensch's rule is usually explained in the context of sexual selection. In woody species, the advantage of males exhibiting larger size may include higher reproductive success, as larger males produce more pollen and therefore increase their sired progeny (Willson 1994; Emms et al. 1997). On the other hand, in herbs and small animals, the advantage for females of larger size lies in higher fecundity and, at the same time, smaller size in males might permit earlier maturation and achieve the related demographic advantages of precocious reproduction (Stearns 1992). If this is true, the evolution of sexual dimorphism in life history traits may be related to different selection pressures in woody and herbaceous plants (Obeso 1993a). However, these questions remain open and it remains a challenge to determine the relative importance of sexual selection, cost of reproduction and physiological differentiation hypotheses to explain life-history evolution in dioecious plants.

Allocation to reproduction at branch level: Why vegetative branches?

As a null hypothesis for RA at the branch level, the RA should be evenly distributed among branches within a
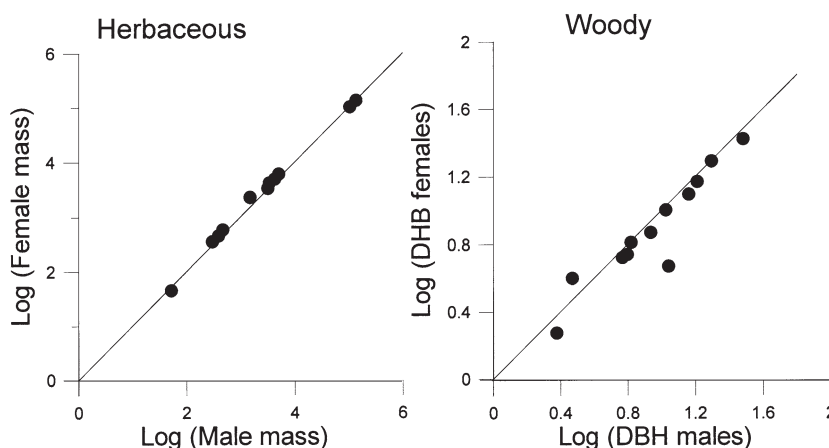

Fig. 2. Female mass (mg, log-transformed) versus male mass in different herbaceous species and diameter at breast height (DBH, cm, log-transformed) of females against DBH of males in woody dioecious. The slopes of the regression did not significantly differ from 1, whereas Rensch's rule predicts a slope lower than 1 (b = 0.99 ± 0.02, t_{10} = 0.381, P = 0.711 for herbaceous species; b = 0.93 ± 0.11, t_{11} = 0.629, P = 0.542 for woody species). Herbaceous species: *Aralia nudicaulis* (Barret 1981); *Borderea pyrenaica* (García & Antor 1995); *Buchloe dactyloides* (Quinn 1991); *Carex picta* (Delph et al. 1993); *Fragaria chiloensis* (Hancock & Bringkurst 1980); *Silene alba* (Armstrong & Irving 1989); *Silene latifolia* (Delph & Meagher 1995); *Sipanura grandifolia* (Nicotra 1999); *Spinacia oleracea* (Onyekwelu & Harper 1979); *Urtica dioica* (Mutikainen et al. 1994) and *Vallisneria americana* (Lovett-Doust & Laporte 1991). Woody species: *Acer rufinerve* (Matsui 1995); *Aporusia microstachya, A. symplocoides, Baccaurea parviflora* (Thomas & LaFrankie 1993); *Ilex aquifolium* (Obeso 1997); *Jacaratia dolichaula* (Bullock & Bawa 1981); *Juniperus virginiana* (Vasiliauskas & Aarssen 1992); *Nyssa sylvatica* (Cipollini & Stiles 1991); *Populus grandidentata, P. tremuloides* (Sakai & Sharik 1988); *Rhamnus alpinus* (Bañuelos & Obeso 2004); and *Triplaris americana* (Opler & Bawa 1978).

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tree. However, this is not the case. First, RA varies considerably between branches; second and more importantly, non-reproductive branches may constitute an important fraction of tree branches, e.g. in *Alnus hirsuta* (Hasegawa & Takeda 2001) and *Baccharis halimifolia* (Krischik & Denno 1990). Even when most branches are reproductive, there is a small reserve of vegetative branches (*Ilex aquifolium,* Obeso 1997; *Rhamnus alpinus,* Bañuelos & Obeso 2004).

The existence of vegetative branches might be explained by the need for maintenance after reproduction (Obeso 2002). The costs of reproduction are often paid by reducing the frequency of reproduction, so branches might become vegetative after a bout of reproduction. On the other hand, the paradigm of branch autonomy states that branches within a tree are either autonomous or semiautonomous (Sprugel et al. 1991). Autonomy entails that there is no translocation of resources between branches and that branches may specialize in one particular activity such as reproduction, maintenance or space exploration (Hasegawa & Takeda 2001), a phenomenon known as 'branch specialization hypothesis'.

Another possibility is that branches are autonomous for some resources such as water, but integrated for other resources such as photosynthate. I propose here the application of the 'assurance hypothesis' or 'carbohydrate reserve hypothesis': Vegetative branches might constitute a reserve of carbohydrates, and reproductive branches, which work as strong sinks, may draw carbohydrates from them.

There are several lines of evidence that support this latter hypothesis. Firstly, the fate of buds may be experimentally changed which means that their fate is plastic rather than fixed and specialized. For instance, in a pruning experiment with *Cercis canadensis*, some buds that would normally develop into reproductive shoots became vegetative shoots after stems were pruned (Owens & Ewers 1997). Secondly, vegetative branches might support greater leaf mass than reproductive branches. One might suppose that reproductive branches bearing stronger sinks than vegetative ones should bear a greater mass of leaves. However, the opposite trend was found in some cases (Obeso 1997; Bañuelos & Obeso 2004), which can be explained if we consider that reproductive branches may import resources from vegetative ones. In fact, the translocation of photosynthates to reproductive branches has been demonstrated in several case studies (i.e. Obeso 1998). Finally, the efficiency of photosynthesis may be higher in vegetative branches than in branches maturing fruits, despite reproductive branches being stronger sinks. Under low light conditions, the efficiency of Photosystem II measured on holly leaves was significantly greater in leaves on non-fruit-
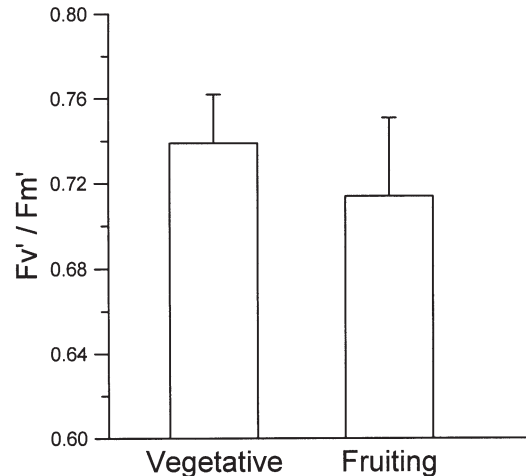

Fig. 3. Mean (+ SD) effective quantum yield of photochemical energy conversion, or energy capture efficiency of the Photosystem II open centres, assessed by fluorescence (Fv′ / Fm′) in leaves from vegetative and fruiting branches of *Ilex aquifolium* ($F_{1, 28}$ = 5.28, P = 0.029; data from Obeso et al. 1998).

ing female branches than in leaves on fruiting branches (Fig. 3), despite the latter being stronger sinks, such as green fruits (Obeso et al. 1998; Obeso & Retuerto 2002).

Some new studies are now needed to explore in different ecological conditions the relative importance of the three hypotheses: maintenance after costs of reproduction, 'branch specialization hypothesis' and 'assurance hypothesis'.

Allocation of resources at the fruit level

Why fruit and seed abortion?

Most studies on the allometry of reproductive allocation have estimated reproductive output in terms of seed production (e.g. Shipley & Dion 1992; Obeso 2002; Niklas & Enquist 2003), although this static perspective neglects not only the investment in male function but also fruit abortion. If we consider that overproduction of flowers and subsequent abortion is a widespread phenomenon (Sutherland 1986; Lee 1988), an important fraction of the resources invested in reproduction are lost during this process. Hence, to understand the patterns of allocation to reproduction at both branch and fruit level, we need to understand why parents create more offspring that can be reared to independence. There are several hypotheses that may be applied to both fruit and seed abortion trying to explain why plants produce more flowers than fruits ('fruit abortion') and more zygotes within fruit than seeds ('brood reduction'). These hypotheses are the following: (1) the resource availability (Stephenson
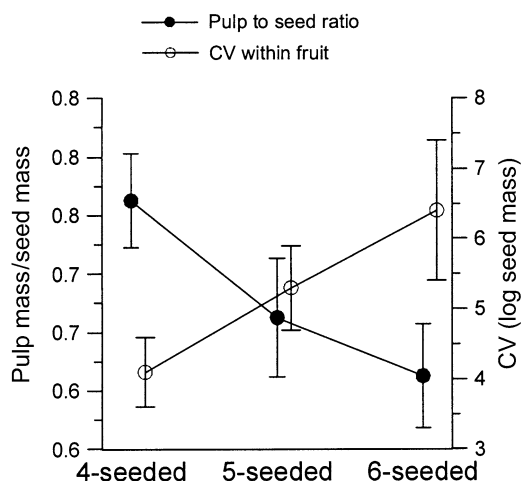
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Fig. 4. Mean (± SD) seed packaging costs (ratio of pulp to seed mass) and coefficient of variation for log-transformed seed masses within fruits in *Tamus communis* with different brood size. $F_{2, 392} = 4.16$, $P = 0.016$ for pulp to seed mass, and $F_{2, 392} = 3.21$, $P = 0.042$ for log-transformed CV of log-transformed seed mass.

1981) or resource-tracking hypothesis (Lloyd 1980); (2) the insurance or ovary reserve hypothesis (Ehrlén 1991); (3) the selective abortion or progeny choice hypothesis (Stephenson 1981); (4) the sib facilitation or attraction hypothesis (Willson & Price 1977; Schemske 1980); (5) the male function hypothesis (Sutherland 1986; Bertin 1988); and (6) the sibling rivalry hypothesis (Lee 1988; Uma Shaanker et al. 1988, 1996). Most of these hypotheses are not mutually exclusive and may work at the same time.

We can also examine seed abortion from the perspective of seed packaging costs and seed size variability. Seed packaging costs are investments in fruit tissue that provide protection, dispersal and/or nutrition to the seeds and thus may contribute to seed mass variation (McGinley et al. 1990; Mehlman 1993). In the particular case of fleshy fruits, the proportion of total fruit resources allocated to package (i.e. fleshy pulp) usually decreases in fruits with larger brood size. As a general trend, brood reduction increases packaging costs per seed (Snow & Snow 1988; Mehlman 1993). The question is then why brood reduction occurs if it could contribute to fitness reduction by both a reduction in offspring number and an increase in parental costs per seed. Aborted fruits do not represent a random sample of developing fruits. When compared to aborted fruits, successful fruits not only show higher brood size (Lee 1988; Obeso 1993b) but also lower packaging costs. Thus, from the parental point of view, fruits with larger broods are more profitable than fruits with smaller broods. It seems reasonable to think that while fruit abortion favours parental inter-
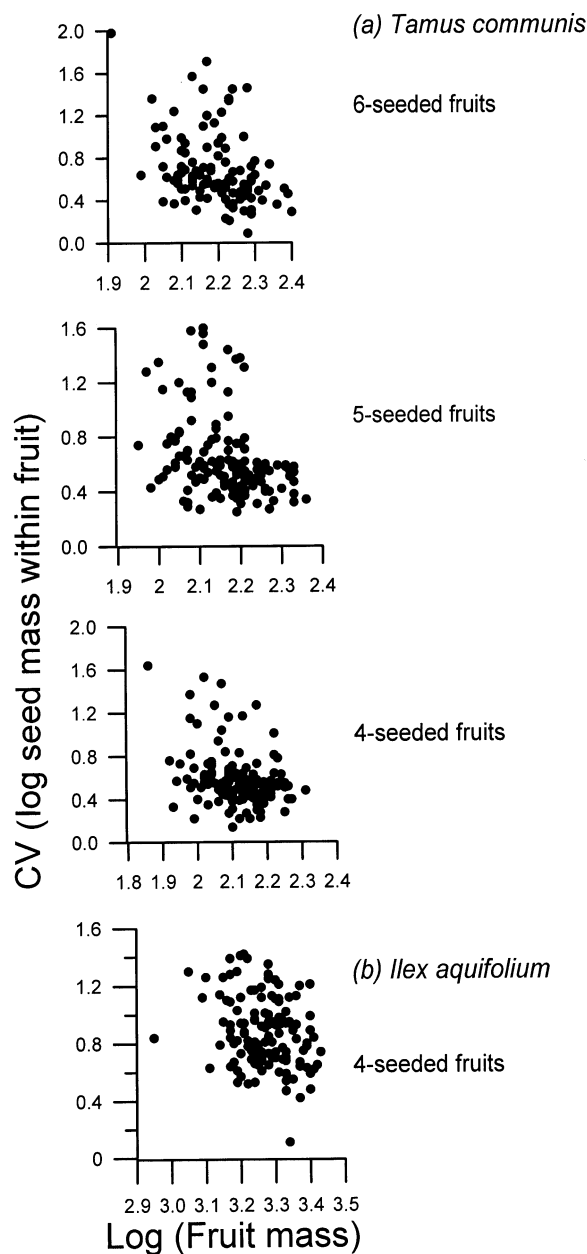

Fig. 5. Coefficient of variation (CV) for log-transformed seed masses within fruit against fruit dry mass (mg, log-transformed). (a) *Tamus communis* fruits with different brood size: 6-seeded fruits ($r^2 = 0.13$, $b = -1.32 \pm 0.33$, $F_{1, 112} = 16.6$, $P < 0.001$), 5-seeded fruits ($r^2 = 0.12$, $b = -1.20 \pm 0.27$, $F_{1, 141} = 19.2$, $P < 0.001$), and 4-seeded fruits ($r^2 = 0.11$, $b = -1.04 \pm 0.26$, $F_{1, 134} = 16.0$, $P < 0.001$). (b) Four-seeded fruits of *Ilex aquifolium* ($r^2 = 0.06$, $b = -0.74 \pm 0.25$, $F_{1, 130} = 8.85$, $P = 0.004$).

est, seed abortion (brood reduction) might be against parental interest.

To consider some possible benefits of brood reduction I have examined the particular case of the fleshy fruits in *Tamus communis* and determined the masses of pulp and seeds in 600 fruits from 30 plants from three northern Spanish localities. *Tamus communis*

flowers contain six ovules and brood size reduction entails a significant increase in seed packaging costs (Fig. 4). We can use the coefficient of variation of seed masses within a fruit as a measure of whether resources are evenly distributed between offspring (low CV) or heterogeneously distributed between the offspring (high CV). The larger the brood size the larger the CV (Fig. 4). Thus brood reduction implies not only an increase in packaging costs but also a reduction in CV, which means more homogeneous progeny within fruit. The advantages of homogeneous progeny might be related to a reduction of asymmetric competition between sibs, which might lead to an increase in inclusive fitness. Brood reduction might occur preferably in fruits exhibiting larger CV where smaller sibs are much smaller than larger sibs, which increases probability of abortion. When brood size is fixed, the larger CVs belong to smaller fruits, and brood reduction should take place preferably on these small fruits through abortion of the smallest seed (Fig. 5a).

In *Tamus communis* it seems that brood reduction may favour parental interests by producing homogeneous progeny, which can reduce sibling competition or at least asymmetric competition between sibs. Brood reduction in fruits showing seed size asymmetry gives the maternal plant the opportunity to drive the conflict (competition between developing seeds) in its own interests (Zhang & Jiang 2000; Bañuelos & Obeso 2003). However, there are still a number of open questions, since it remains a challenge to determine whether brood reduction is a consequence of sibling rivalry (siblicide) rather than a maternal decision.

Allocation to seeds within fruit and sibling competition

It has been demonstrated in several studies that seed abortion is a non-random process (Obeso 1993b); the question is how the seeds to abort are selected. Abortions may be a consequence of parental decisions (i.e. progeny choice) in which the parent plant favours offspring of high genetic quality. However, they may be also the result of competition between sibs, which is known as sibling rivalry (Uma Shaanker et al. 1988).

On the basis of kin selection theory, we can assume that because parents are equally related to all their offspring the available resources should be equally distributed among offspring; however, sometimes parents may favour some seeds rather than others (Forbes et al. 2002). Contrarily, offspring are selected to be more selfish in obtaining resources from the parents because they are less closely related to their sibs than to themselves. As a result sibs compete for parental resources, which under certain levels of resource limitation, may lead to differences in the amount of resources obtained by each sib and, in extreme situations, to siblicide or brood reduction (Mock & Parker 1997).

In the case of plants, developing fruits provide a perfect arena for the expression of parent-offspring conflict and sibling rivalry. Resources move towards the strongest sinks, so healthy embryos that attract more resources from the maternal sporophyte disadvantage faltering embryos. The models of sibling rivalry predict that competition between developing embryos should decrease when resources are not limited (Parker et al. 1989; Bañuelos & Obeso 2003). Then, the variance in the distribution of resources between sibs should decrease with resource increase. In this sense, it is expected that the larger the fruit the lower the CV for seed masses within a fruit. This prediction was tested in two fleshy-fruited species, *Tamus communis* and *Ilex aquifolium*, and in both cases resources were more evenly distributed (lower CV) in large fruits than in small ones (Fig. 5a, b). These results may be explained by a hierarchical distribution of resources between developing seeds (Obeso 2004), as has been shown for certain bird species (Parker et al. 1989) but might also be explained by structural limitations within fruits. For instance, smaller fruits may constrain the development of seeds in determinate positions due to vascular architecture which could often cause some seeds to be better provisioned than others.

Allocation to different tissues within seed

Finally, we can examine the allocation of resources between different seed tissues in the light of kin selection theory. An offspring sporophyte developing within a fruit includes different tissues showing different degrees of relatedness with the maternal sporophyte. Following kin selection theory, to improve the inclusive fitness the tissues should be provisioned by the maternal sporophyte according to their coefficient of relatedness (Westoby & Rice 1982).

The different tissues that are provisioned within a seed are the embryo, the endosperm and the endocarp. While the genotype of the maternal sporophyte is present in all these tissues the paternal genotype is only present in embryo and endosperm. According to the coefficient of relatedness, it is predicted that the variance in the distribution of shares should be higher in endosperm than in maternally derived tissues (the endocarp). All sibs within a fruit share the same maternal genotype in their endocarp or stone, so strong competition for resources among them is not expected. However, the endosperms differ in genotype (these differences are particularly important in cases of multiple paternity), and therefore intense competition between them is predicted. As a result of this competition the shares should be heterogeneously distributed between the sibs.
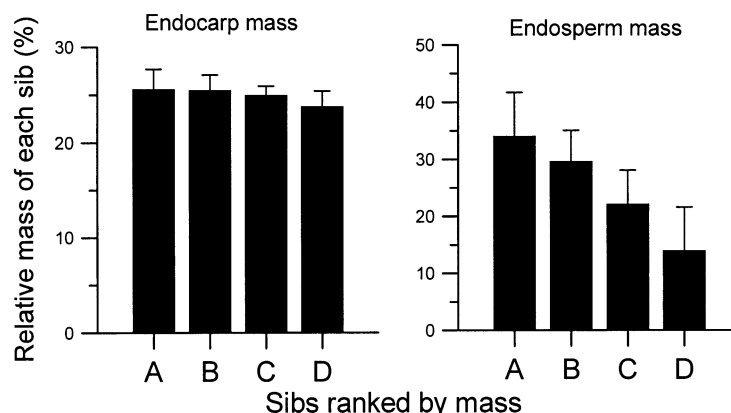
Fig. 6. Distribution of resources between sibs within four-seeded *Ilex aquifolium* fruits. Mean (+ SD) percent of total endocarp mass per fruit obtained by each individual endosperm according to their rank in the size hierarchy within the fruit. The same is represented for the endosperm. A is the largest and D the smallest sib (data from Obeso 2004).

I have examined this question in the case of *Ilex aquifolium* fruits in which the allocation in dry mass to stones and endosperm was determined (Obeso 2004). Four-seeded fruits were selected and the four sibs within a fruit were ranked by their mass and the proportion of total resources allocated to seeds was estimated. The resources were equitably distributed between the stones but unevenly distributed between the endosperms (Fig. 6). It seems clear here that the maternal resources were equitably distributed between maternally-derived tissues, the stones of the seeds, but unequally distributed in the case of the endosperms. This result may be attributed to sibling rivalry or competition between endosperms containing different genotypes. However, we cannot discard other interpretations such as morphogenetic and physical constraints during fruit development (Obeso 2004). More focus is needed on allocation to reproductive structures to examine the hypothesis presented here.

Concluding remarks

A number of key issues in reproductive allocation have been presented by examining different hierarchical levels within the plant: (1) Could we apply to dioecious plants Rensch's rule that explains size variation in relation to sex in animals? (2) At the branch level, may vegetative branches constitute an 'assurance' for reproduction in variable environments? (3) At the fruit level, can fruit abortion be explained as a mechanism to produce homogeneous progeny and to reduce asymmetric competition between sibs? (4) Finally, at the seed level, it seems that in some cases allocation to different seeds tissues might be in accordance with the predictions of the kin selection theory. Could we explain allocation within seed using the theoretical

framework of the kin selection theory? All these questions are not fully solved and deserve further attention, i.e. studies should be purposely designed to test the hypotheses presented.

To understand the patterns of allocation in plants we should use at the same time a 'top-down' approach, considering that investments at lower hierarchical levels are determined by scaling at whole plant level, and a 'bottom-up' approach combining the information of the lower levels to reconstitute the allocation at plant level.

For this purpose we can use two different tools. Firstly the application of the same principles at different levels of biological organization may reveal the existence of common underlying mechanistic bases. Secondly, the application of the principle of similarity by examining in plants some theories applied to animals (Rensch's rule and socio-biology of plants, i.e. sibling competition). Shifting our view of allocation to reproduction in plants toward the inclusion of sociobiological models might be a positive step to understand plant life-history evolution.

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