

# Conflict between parent and offspring in plants: Predictions, processes and evolutionary consequences

R. Uma Shaanker and K. N. Ganeshiah\*

Department of Crop Physiology and \*Department of Plant Genetics and Breeding, University of Agricultural Sciences, Bangalore 560 065, India

In plants, as in animals, conflict occurs between parents and offspring over a range of issues such as allocation of maternal resources to seeds and number of seeds to be packed in a fruit. We have reviewed theoretical bases and empirical evidences for such conflict in plants and present the predictions, processes and evolutionary consequences of such conflict. We have shown that though 'plants can neither sing nor dance' they do indulge in sibling rivalry, fratricide and kin cooperation as intensely as animals do. For this, maternal parents and offspring have evolved strategies that are subtle, yet as effective as those in animals in upholding their respective interests. We argue that the evolution of a number of plant reproductive features can be profitably viewed as strategies and counter-strategies of the offspring and maternal parent towards ensuring their respective interests. For example, features such as polyembryony, endosperm, multi-carpellary ovaries which had thus far remained poorly explained, appear to have evolved as maternal counter-strategies against offspring-driven sibling rivalry. Thus, these 'highly anthropomorphic, sociobiological hypotheses' which were suggested to be 'best not applied to plants', have indeed been helpful in providing a new framework to view the evolution of plant reproductive strategies.

In humans, the relationship between a mother and her offspring is probably one of the most endearing ones. Across cultures, people have paid obeisance to this sublime relationship. However, in the early 1970s, this view was rudely shattered when Trivers<sup>1</sup> advanced the concept that, more as a rule than an exception, mothers and offspring can have conflicting interests. He argued that such conflict occurs even for the simplest of parental cares, such as suckling; a mother does not feed her offspring indiscriminately while the offspring persists in its demand for its mother's milk. The rationale behind such 'weaning' conflict is the differential fitness accrued to the mother by yielding parental resources, and to the offspring by demanding these resources.

Trivers<sup>1</sup> argued that the maternal parent will be selected to allocate a certain optimal amount of resources to each of her offspring, so as to maximize her inclusive

fitness. On the other hand, the offspring will be selected to demand much more than that defined by the mother's optimum to increase its own fitness. Hence there ensues a conflict between parent and offspring over the extent of resource allocation<sup>1,2</sup>.

Though Trivers' idea appeared heretical, it provoked widespread interest in the nature of the conflict between parent and offspring in animals. The most dramatic illustration of the conflict is seen in a bird nest where the fledglings demand food from the mother by 'intense begging calls'<sup>3,4</sup>. The mother is coerced to submit to the calls because these intense vocalizations, if persistent, would attract predators risking the entire brood. In a way it may be argued that the fledglings blackmail their mothers to part with parental resources.

The indiscriminate demand for maternal resources by an offspring may be manifested in the form of intense sibling rivalry<sup>1,2,5,6</sup>. In extreme situations, competition among siblings may take a violent form and dominant among the brood kills others to garner all the maternal resources for itself. Brood reduction in boobies and raptors wherein the older chick, invariably kills the later hatched fledglings is one such extreme form of sibling rivalry<sup>7-13</sup>.

That sibling rivalry and parent-offspring conflict might also occur in plants was proposed by Ganeshiah and Uma Shaanker<sup>14</sup> and Uma Shaanker *et al.*<sup>15</sup>. They argued that seeds developing in close physical and temporal proximity in a fruit, can be expected to interact as intensely among themselves as fledglings developing in the nest of a bird (Figure 1 *a, b*) and to conflict with the maternal parent over a range of issues. Three issues over which such conflicts can arise are (a) resource allocation to seed<sup>5,15</sup>, (b) brood size or seed number packed per fruit<sup>14,15</sup> and (c) seed dormancy or timing of seed germination<sup>15,16</sup>. These conflicts can be explained within the general framework of the theory of parent-offspring conflict proposed by Trivers<sup>1</sup>. Thus whether boobies or brassicas, raptors or rapeseed, it appears that sibling rivalry and parent-offspring conflict may be a common feature of animals and plants alike. In this paper we offer a brief overview of the work conducted at our laboratory on these issues and discuss the predictions, processes and the evolutionary consequences of the conflict between parent and offspring in plants.





Figure 1. *a*, Clutch of eggs in the nest of a bird and *b*) clutch of seeds in the pod of the tree, *Castanospermum australe*. Though apparently disparate systems, in both, offspring develop in close physical and temporal proximity with each other as well as with the mother leading to potential for sibling rivalry and parent-offspring conflict. Photo credits: Figure 1 *a*, S. Sridhar; Figure 1 *b*, K. N. Ganeshiah.

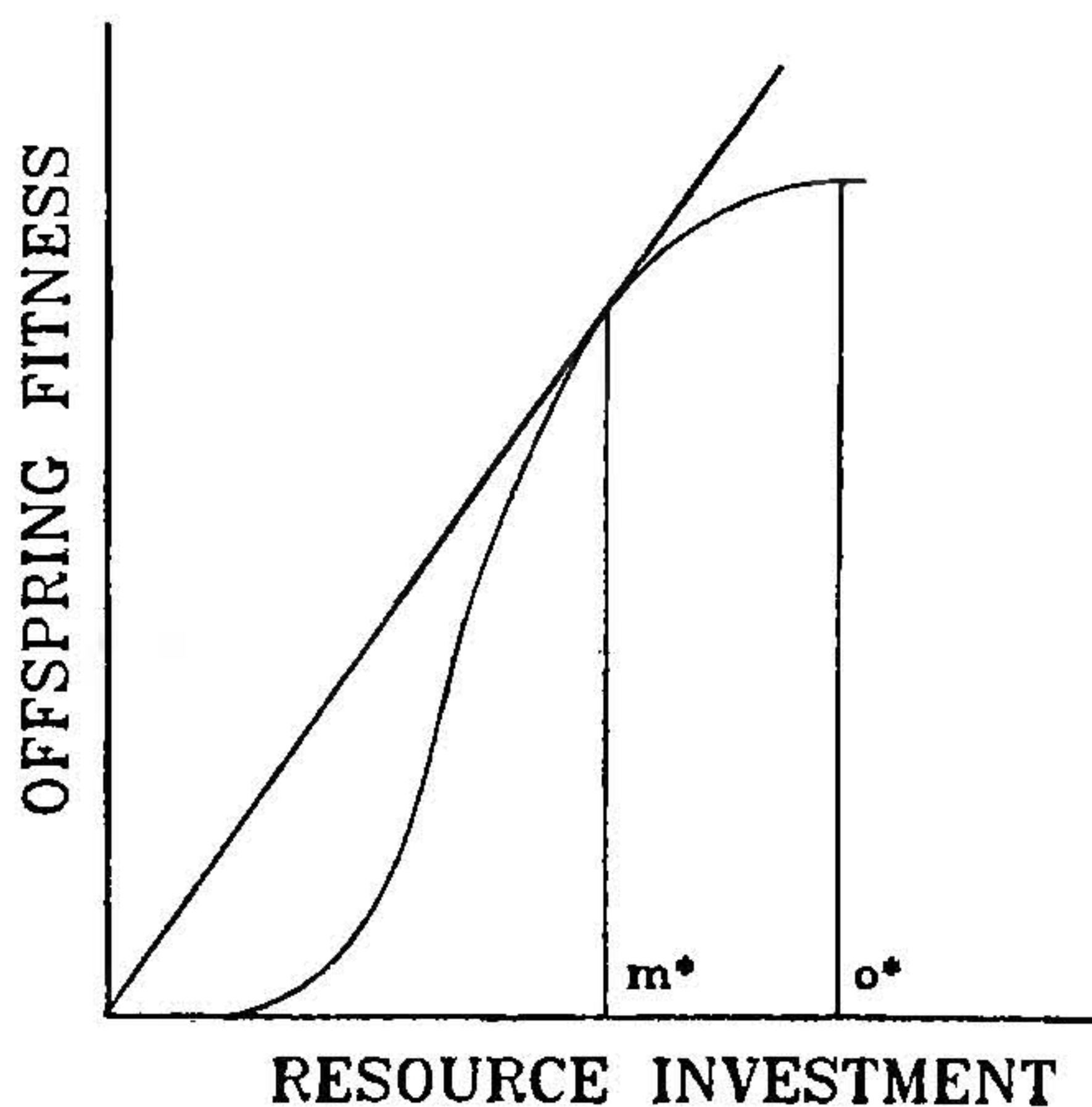


Figure 2. Relation between offspring fitness and resource investment in seed. The region between  $m^*$  and  $o^*$  represents the zone of conflict (from Uma Shaanker *et al.*<sup>15</sup>).

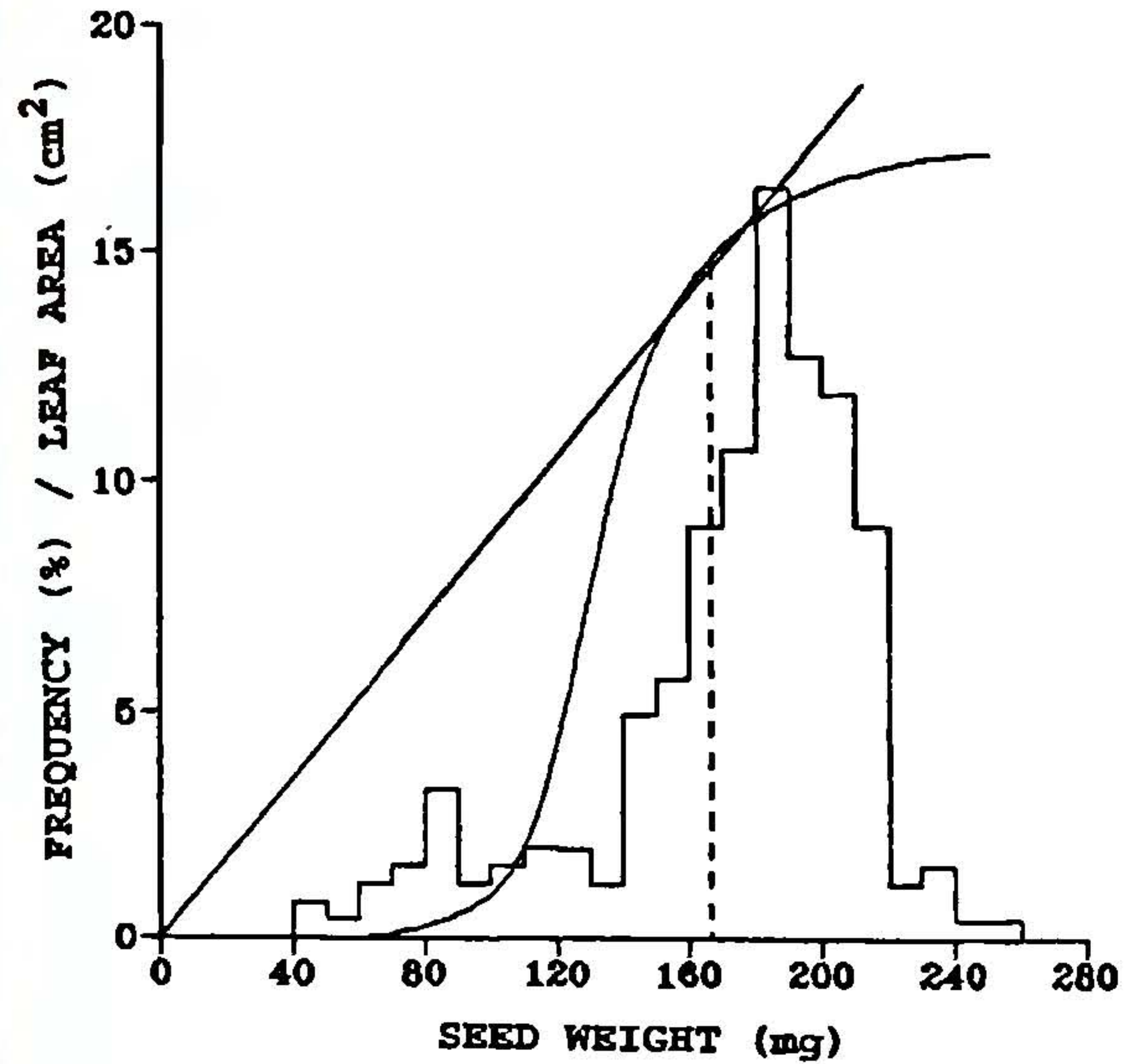


Figure 3. Relation between offspring fitness and seed weight in *Thespesia populnea* and frequency distribution of seed weights. Randomly collected seeds from trees of *Thespesia* were weighed and the frequency distribution plot was developed; offspring fitness was determined by recording the seedling leaf area after 20 days of germination. The optimum seed weight was obtained by drawing a tangent to the fitness curve.

### Parent-offspring conflict in plants Predictions and processes

#### 1. Conflict over resource allocation to seeds

Assuming that offspring fitness increases at a decreasing rate with resource investment, Smith and Fretwell<sup>17</sup> argued that the maternal parent would be selected to favour an optimal allocation of resources ( $m^*$ ) to each of her offspring, such that the marginal returns to her are maximized (Figure 2). However, as Trivers<sup>1</sup> argued, because the offspring by themselves do not invest any resources, they would be selected to demand the maximum amount of investment ( $o^*$ ) that they can possibly obtain from the maternal parent. This results in a conflict of interest between maternal parent and offspring over the extent of resource allocation to seeds.

Evidence in support of conflict over the extent of resource allocation to seeds has been obtained in *Thespesia populnea* (Malvaceae) at our laboratory (unpublished). In this species, the offspring fitness (as measured by seedling leaf area) increases nonlinearly with seed weight (Figure 3). The optimal level of resource at which the marginal returns to the mother is maximized is 165 mg. If the offspring conform to the maternal interest, then seed size in *T. populnea* should be normally distributed around this optimum. However,



the observed seed size distribution was highly skewed (Figure 3) suggesting that the maternal parent and the offspring may have conflicting interests over the extent of resource allocation to seeds.

The indiscriminate demand for maternal resources by an offspring may occur at the expense of the development of its siblings. In fact offspring could be expected to compete intensely among themselves for the maternal resource, leading under extreme conditions to the starvation and death of their siblings. However, the extent of sibling rivalry over resource allocation would be a function of the genetic relatedness among the offspring developing in a fruit<sup>15</sup>. Selection would not favour sibling rivalry among seeds that are genetically related because such rivalry reduces their inclusive fitness. In situations where the seeds are genetically less related, it would pay for a sibling to garner as much of the resource as it can, even at the expense of abortion of its siblings. But, sibling rivalry should theoretically be non-existent when siblings are completely related. Thus, a greater degree of concordance could be expected between maternal and offspring optima for seeds obtained from self-pollination (high genetic relatedness) than those obtained by cross-pollination (low genetic relatedness).

Evidence in support of this prediction is obtained from the fact that in several species, outbred seeds have a significantly higher seed weight than comparable inbred seeds whose weights more often correspond with the maternal interest<sup>18-21</sup>. In *Vigna unguiculata*, Radha<sup>22</sup> showed that the seed weight of F<sub>0</sub> seeds was significantly influenced by the sibling genetic environment. F<sub>0</sub> seeds developed by pollination with single pollen donors generally resulted in a single peak of seed weight distribution (probably corresponding to the maternal optimum); however when several pollen donors were mixed, the distribution of the weight of seeds sired by any of

the donors was characterized by two or more modes and the mean seed weight differed from that obtained under single donor pollination (Table 1). That is, the extent of resource allocation to a seed appeared to be influenced by competing sibling genotypes.

In *Phaseolus latheroides*, using mixtures of pollen grains derived from 5 and 20 pollen parents, Vasudeva<sup>23</sup> developed pods with decreasing extents of genetic relatedness among the developing siblings. While there was a significant increase in mean seed weight with the number of pollen donors used in the mixture, there was a concomitant increase in seed abortion. The increased rate of abortion was not due to either lack of fertilization of ovules or to lack of resources. Rather, increased seed abortion appeared to be a consequence of intense intra-fruit sibling rivalry for maternal resources with increase in the genetic heterogeneity among siblings.

#### *Manifestation of conflict – war of the hormonal kind?*

Conflict over the extent of resource allocation between mothers and offspring is readily apparent in animals. Admittedly, while such overt behaviours cannot be expected in plants, offspring and maternal parents might indulge in subtle but equally effective mechanisms to uphold their respective interests.

One such mechanism could be by signaling through hormones. Plant hormones are small molecular weight, highly diffusible compounds and are known to act at very low concentrations at sites away from where they are synthesized. Consequently, these could be effectively deployed by the offspring and the maternal parent to guard their respective interests. Thus while the offspring could deploy specific plant hormones to 'beg' or 'demand' resources from the mother, the latter could deploy her own hormones to 'quell' the indiscriminate signaling by the offspring for extra resources.

Ravishankar *et al.*<sup>24</sup> examined the hormonal basis of the conflict over resource allocation in plants. They predicted that in a developing seed, the offspring tissues (embryo, endosperm) should be selected to specifically synthesize such hormones that facilitate the uptake of resources, while the maternal tissues (seed coat, pericarp) should be selected to produce hormones that restrict resource uptake. Analysing both the genetic and physiological data on a number of plant systems, they provided evidence in support of these predictions. They showed that hormones such as gibberellic acid (GA) and indole acetic acid (IAA), that facilitate the active mobilization of photoassimilates from the maternal sporophyte into the developing seeds, are exclusively synthesized by the offspring tissue (embryo/endosperm). On the other hand, abscisic acid (ABA), which restricts the mobilization of resources into the seed, is exclu-

**Table 1.** Average seed weight (mg) of hybrids in single and mixed cross in *Vigna unguiculata*

Female parent	Cross	Male parents		
		TVX 118-09E	APC 1153	APC 773
Virginia	Single	89.76	113.44	96.52
	Mixed	96.96	91.96	96.64
APC 1078	Single	97.56	112.12	121.24
	Mixed	124.36	123.24	118.60
APC 1016	Single	109.48	137.56	129.68
	Mixed	126.04	128.04	114.20
APC 1034	Single	148.04	129.52	127.36
	Mixed	138.28	148.56	139.44

ANOVA, Female parents  $P < 0.01$ ; Male parents  $P < 0.01$   
*Vigna* (cowpea) genotypes were crossed with either pure (single donors) or a mixture of pollen donors, each with a distinct gene marker. The weight of each seed was recorded and the parentage identified at the seedling stage (from Radha<sup>22</sup>).

sively synthesized by the maternal tissues of the seed (seed coat, pericarp, etc.) and is deployed at a time coinciding with that of IAA or GA production in the seed (Figure 4). In other words, even as the offspring deploy hormones to draw resources from the mother, the latter deploys its own arsenal in the form of abscisic acid to

negate the indiscriminate demands made by the offspring. Thus, there might be a dynamic conflict between the mother and offspring over the extent of resource mobilization into the seeds, through the deployment of specific hormones.

## 2. Conflict over brood size

In plants, several components of offspring fitness such as dispersal efficiency<sup>14,15</sup>, escape from predation<sup>25</sup> and post-dispersal seedling survival<sup>26,27</sup> decrease with increase in the number of seeds packed per fruit (brood size). For instance, in species where the entire fruit is dispersed as a unit through wind, water or animals, the dispersal efficiency of the fruits decreases with the seediness of the fruits<sup>14,15,28-34</sup>. Furthermore, seeds in a large brood are more likely to be preyed upon than those in a small brood<sup>25</sup>. Ganeshaiyah and Uma Shaanker<sup>14</sup> and Uma Shaanker *et al.*<sup>15</sup> argued that under these conditions, selection would favour each sibling in a fruit to indulge in fratricide and kill others to become the lone survivor in order to enhance its own individual fitness. However such fratricidal behaviour among the offspring can directly conflict with the interest of the maternal parent. The maternal parent would be selected to optimize her brood size as a trade-off between the benefits (dispersal advantage, etc.) and the cost of packing seeds in fruits<sup>15</sup>. Since the offspring does not incur any packing cost, it will always be selected to favour a brood size smaller than that the mother is selected to favour.

Based on inclusive fitness models, Uma Shaanker *et al.*<sup>15</sup> analysed the conditions under which brood reduction will be favoured by the offspring or by the maternal parent. They showed that for a relatively low ratio of benefit (increased dispersal advantage due to brood reduction) to cost of killing sibs (loss of inclusive fitness due to brood reduction), the offspring would favour brood reduction while the maternal parent would not (Figure 5).

Thus, under conditions where offspring fitness is a decreasing function of the number of seeds packed in a fruit, Uma Shaanker *et al.*<sup>15</sup> predicted that selection would favour fratricide or sibling rivalry-driven seed abortion compared to situations where offspring fitness is unaffected by changes in brood size. Indeed in a study of over 200 species, Uma Shaanker *et al.*<sup>15</sup> found that seed abortion was significantly higher in species whose fruits were dispersed by wind, water or animals (where dispersal efficiency decreases with brood size) compared to those where the seeds were passively dispersed (where dispersal efficiency is independent of the size).

### *Manifestation of conflict – nature green but thorny and poisonous*

In recent years, certain unique mechanisms of intra-fruit sibling rivalry leading to seed abortion have been

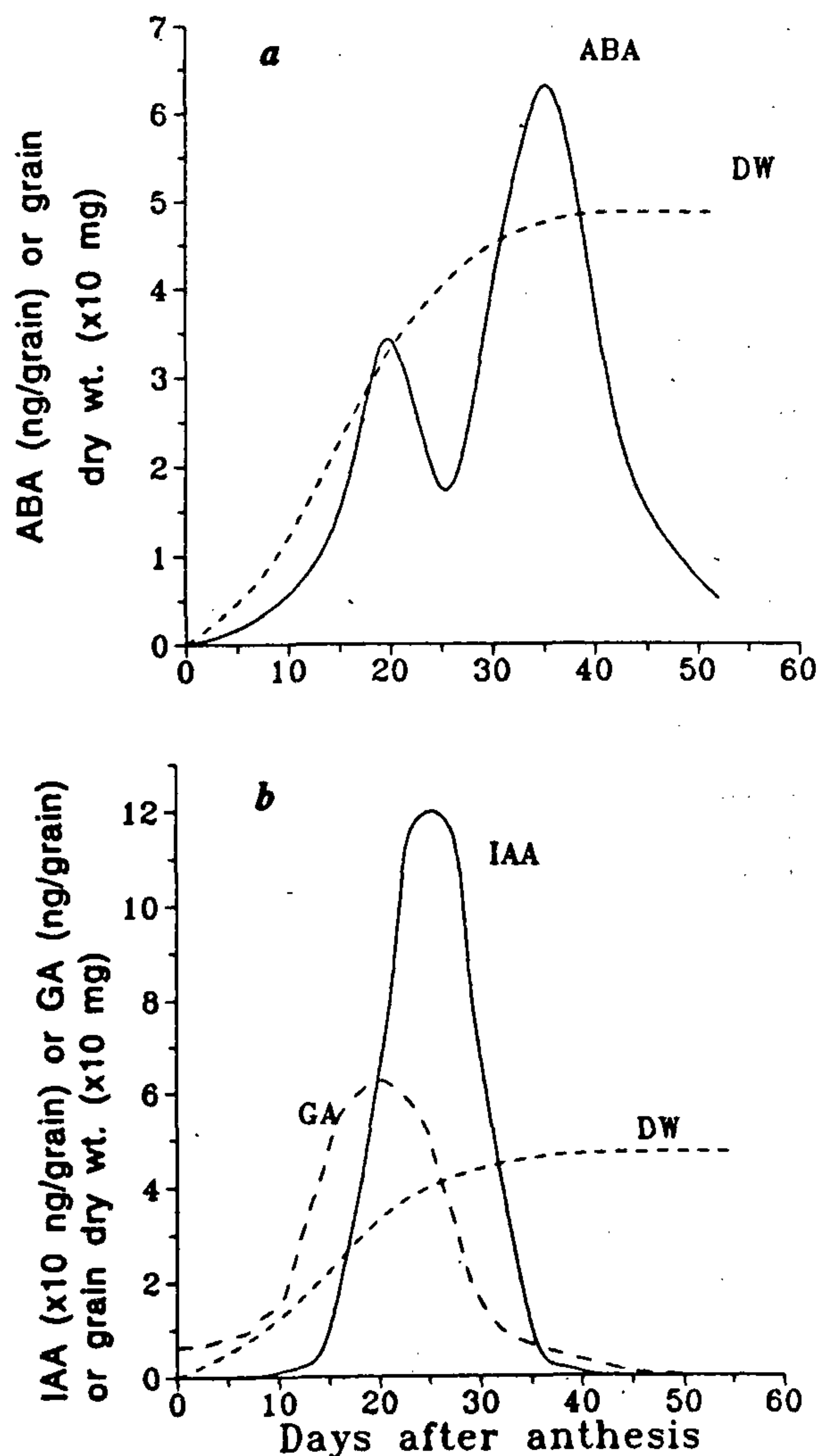


Figure 4. Deployment of hormonal strategies in the conflict over resource allocation between maternal parent and offspring during seed development. Temporal pattern of accumulation of (a) abscisic acid (ABA) and (b) auxins (IAA) and gibberellic acid (GA) and grain dry weight (DW). Notice the two peaks of accumulation of ABA; while the second peak is reported to impart desiccation tolerance to the embryo, the significance of the first peak is not known. It is proposed that the first peak may function as a maternal strategy to restrain the indiscriminate demands of the offspring for the maternal resources (from Ravishankar *et al.*<sup>24</sup>).



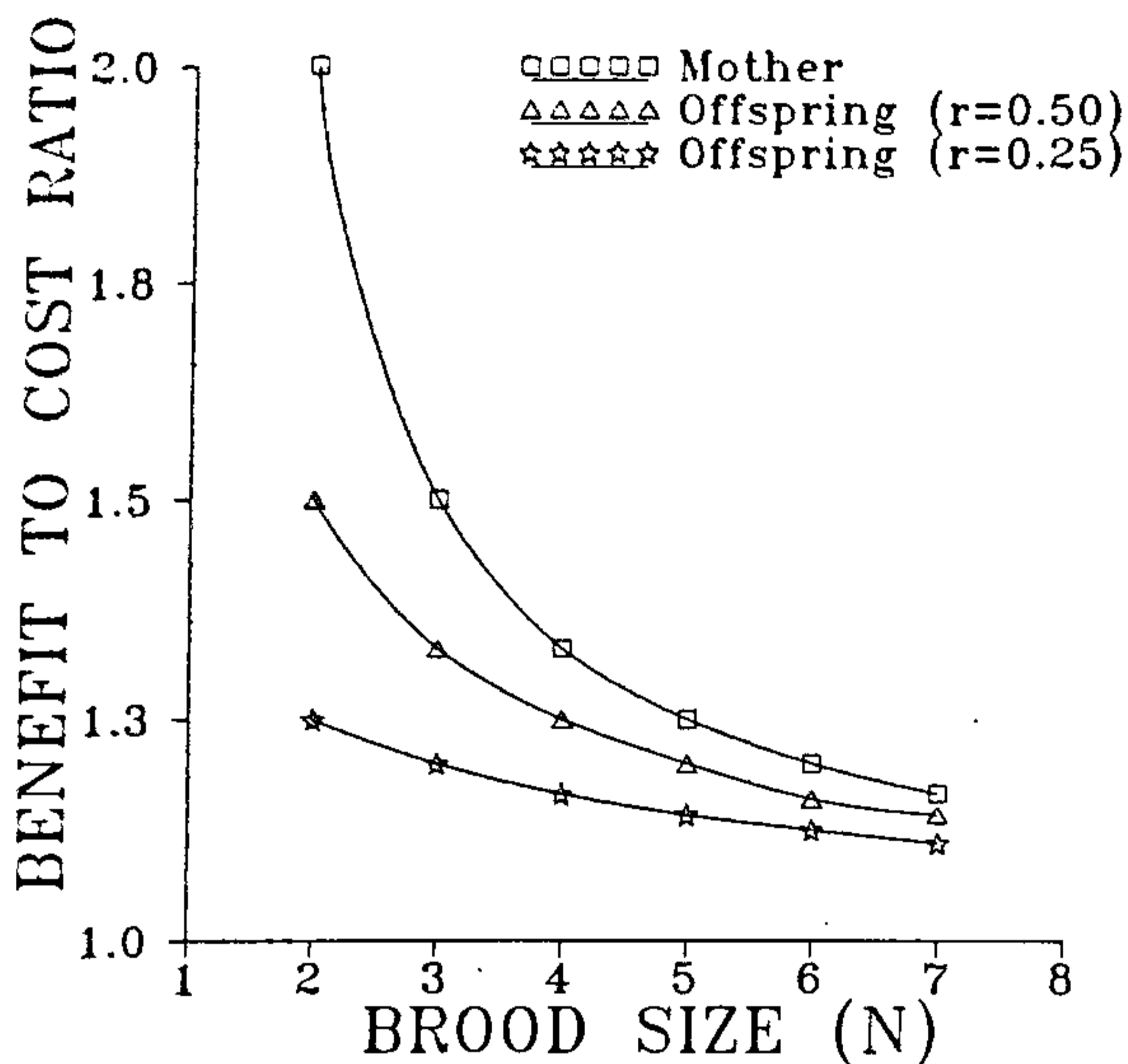


Figure 5. The relative ratio of benefit (B) to cost (C) required to favour brood reduction by mother and offspring. Note that for all values of brood size (ovule number per ovary), offspring favour brood reduction for relatively lower B/C ratios than the mother. Also note that the ratio required to favour brood reduction by the offspring decreases with decrease in the coefficient of relatedness among the siblings (modified from Uma Shaanker *et al.*<sup>15</sup>).

reported in plants<sup>14,36,38-41</sup>. These studies suggest that though plants may not match the adage 'nature red in tooth and claw', they might represent 'nature green but thorny and poisonous'.

#### Sibling rivalry in *Dalbergia sissoo*

In the wind-dispersed tree, *Dalbergia sissoo*, predominantly only one of the four or five ovules in an ovary develops to maturity<sup>14</sup>. Ganeshiah and Uma Shaanker<sup>14</sup> proposed that seed abortion in *Dalbergia* could be due to intra-fruit sibling rivalry to enhance the surviving seed's dispersal efficiency. The abortion of the rest of the 3 or 4 seeds occurs within a week after fertilization and is not attributable to either lack of pollination or resource limitation<sup>14,15,35-37</sup>. Abortion is mostly restricted to ovules at the base of the pod (distal to the stigmatic end). In the presence of the dominant stigmatic embryo, the uptake of labelled sucrose by the basal embryos is significantly inhibited. However, when their dominance was removed (by excising the dominant embryos), the uptake of labelled sucrose by the basal embryos equalled those of the dominant embryos. In fact, when the dominant stigmatic embryo is surgically excised, the ovules at the base develop normally. In other words, abortion of the basal embryos is probably a con-

sequence of their starvation by the dominant embryos developing at the stigmatic end.

Mohan Raju *et al.*<sup>36</sup> showed that dominance may be exerted by the production of a chemical by the stigmatic embryo. Extracts and diffusates of the dominant embryos significantly inhibited the uptake of labelled sucrose by subject (fertilized) embryos while those of control tissues such as fruit coat (maternal tissue) and unfertilized ovules did not. In other words, abortion of basal embryos appeared to be actively mediated by sibling rivalry (fratricide) and not due to any maternal intervention (infanticide). These results corroborate the prediction that seed abortion in fruits is favoured more by interests of the offspring than that of the mother. While the chemical nature of the diffusate causing the abortion is not clear, it is conjectured that it may be an indole compound, very likely the 'death hormone', 3-chloro-indole acetic acid<sup>36</sup>. A similar mechanism of seed abortion has been reported in the animal-dispersed species, *Syzygium cuminii*, where invariably only one out of 25 to 30 ovules develops to maturity<sup>38-41</sup>.

Based on these results, a general model explaining seed abortion in plants is proposed. According to this model, temporal differences in fertilization set in a dominance hierarchy among the ovules. The early fertilized, dominant embryos thus formed, gain a head start in the production of certain 'indole' compounds. These compounds not only further facilitate the build up of dominance due to a feedback flow of resources to the dominant ovules, but also starve the remaining later fertilized ovules of resources, thereby either directly or indirectly leading to their abortion<sup>41</sup>.

#### Sibling rivalry-driven brood reduction – function of genetic relatedness among sibs?

Based on inclusive fitness models, Uma Shaanker *et al.*<sup>15</sup> showed that the benefit-to-cost ratio required to favour brood reduction by offspring decreases with a decrease in genetic relatedness among the siblings (Figure 5). Consequently, the intensity of conflict between the mother and offspring increases with a decrease in the genetic relatedness among the siblings. For relatively small benefits due to brood reduction, an offspring would be more selected to favour killing its siblings when they are half sibs ( $r = 0.25$ ) than when they are full sibs ( $r = 0.50$ ) (Figure 5). Thus, they predicted that sibling rivalry-driven brood reduction should be more intense in outbred compared to inbred conditions.

Several lines of evidence support this prediction, albeit indirectly. In pigeon pea, intra-fruit seed abortion was positively correlated with the extent of outcrossing<sup>42</sup>. In *Epilobium*, congeneric species that were outbred had a higher degree of seed abortion than those that were inbred<sup>43,44</sup>. In *Phaseolus latheroides*, as men-

tioned earlier, Vasudeva<sup>23</sup> showed that the extent of seed abortion increased dramatically with an increase in the number of pollen donors used for pollination.

### Evolutionary consequences

If rivalry among siblings is in conflict with the interests of the mother, selection can be expected to favour counter-strategies in the maternal parent that either reduce sibling rivalry or make good the loss of fitness incurred to her as a result of rivalry. Here we examine briefly a few features of plant reproduction that might be argued to have evolved as maternal counter-strategies against the conflicting interests of the offspring.

#### *Evolution of polyembryony – maternal counter-strategy against offspring-driven brood reduction?*

Polyembryony, the differentiation and development of additional embryos from the tissues of the embryo sac, is a widespread phenomenon in angiosperms. An interesting feature, however, is that in over 78 per cent of species, the additional embryos emerge from the maternal tissues of the embryo sac (e.g. nucellus and integument) and in only about 22 per cent of species, they emerge from the cleavage of the sexual embryo or endosperm<sup>45</sup>. The evolutionary significance of this feature has largely remained unaddressed.

Ganeshiah *et al.*<sup>45</sup> and Uma Shaanker and Ganeshiah<sup>46</sup> suggested that polyembryony may be viewed as a possible maternal strategy of making good the fitness lost through offspring-driven brood reduction. Based on both genetic and inclusive fitness models, they showed that the maternal parent should favour the production of additional embryos for relatively small gains of producing them while the offspring do not (Figure 6). On the contrary, for relatively small benefits, the offspring favour brood reduction, while the mother does not (Figure 5). Thus, it is clear that in both situations, there is a conflict of interest between the maternal parent and the offspring over brood size. Ganeshiah *et al.*<sup>45</sup> argued that the evolution of polyembryony may hence represent a maternal strategy of making good the fitness lost due to offspring-induced brood reduction. Accordingly, they predicted that polyembryony should be more frequent in species that exhibit high rates of intra-fruit seed abortion than in those where seed abortion is less intense. In support of this prediction, they found that polyembryony was more frequent than expected in species where the entire fruit is dispersed as a unit through wind, water or animals (characterized by a high degree of seed abortion) than in species where the seeds are passively dispersed (characterized by lower rates of seed abortion).

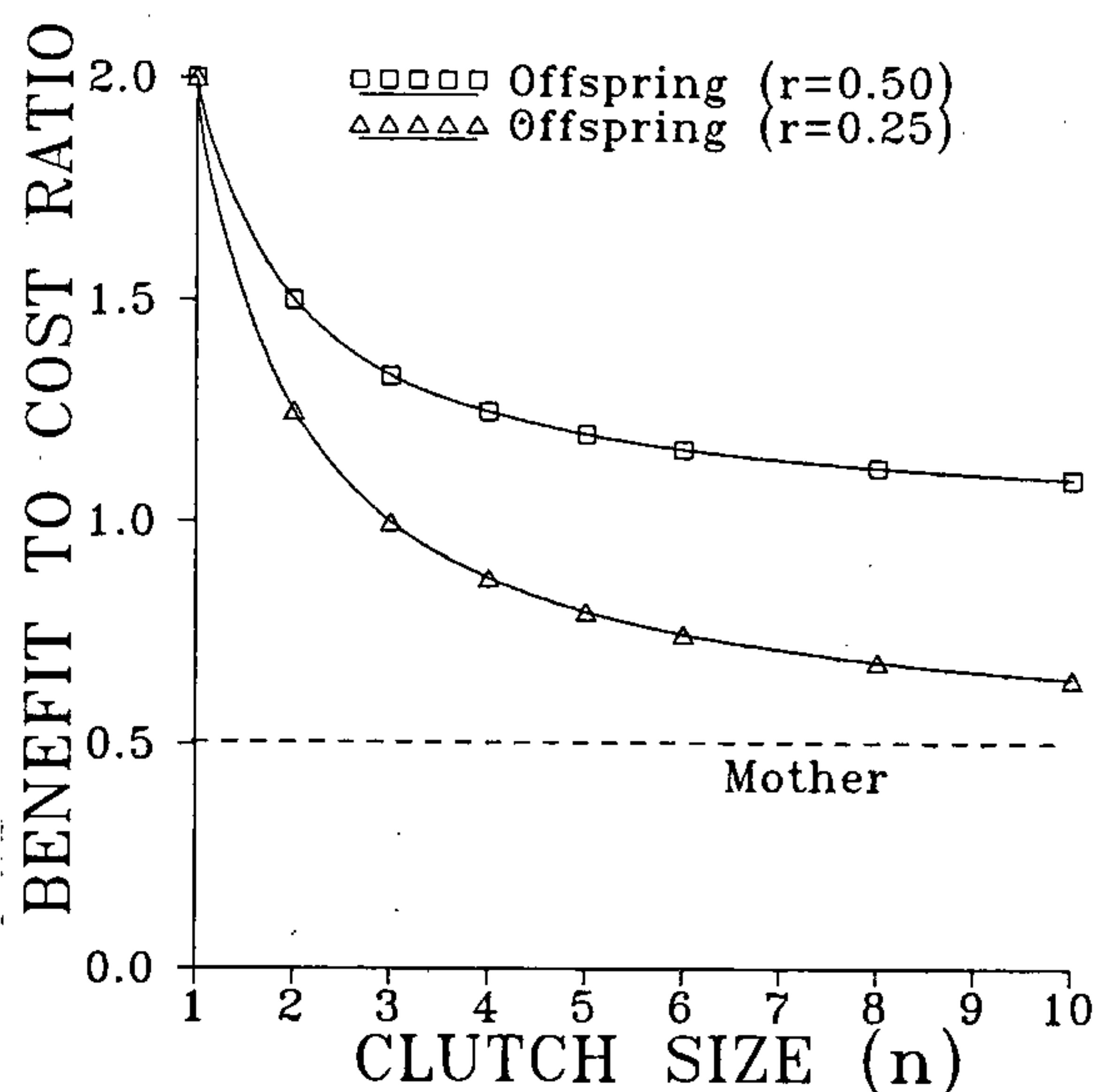


Figure 6. The relative ratio of benefit (B) to cost (C) required to favour polyembryony by the mother and offspring. Note that for all values of clutch size (ovule number per ovary), the mother favours the production of polyembryos for a lower B/C ratio than the offspring. Further, the ratio required to favour polyembryony by the offspring increases with increase in the genetic relatedness among the siblings (from Ganeshiah *et al.*<sup>45</sup>).

Furthermore, they also found a significant positive correlation between the number of polyembryos produced and the extent of seed abortion across species of *Citrus*.

#### *Evolution of endosperm – an enigma resolved?*

One of the most perplexing features of the angiosperm seed is the triploid storage tissue, the endosperm. With its two doses of maternal and one of paternal chromosomes, the evolution of endosperm has remained an enigma. Functionally, it draws resources from the maternal sporophyte and serves as a repository until the embryo is capable of using it. In most species, the endosperm degenerates as the seed matures; in others it is persistent and offers resources to the developing seedling. It has been argued that the endosperm, with its unique genetic composition might represent (a) paternal interest by increasing the genetic relatedness of the nourishing tissue to its own embryo such that there will be a greater allocation of resources to its own embryo<sup>47</sup> or (b) maternal interest by subduing the indiscriminate demand of resources by the offspring<sup>48</sup>. According to the latter argument, the endosperm as a nourishing tissue will be less biased in discriminating among the embryos than if embryos themselves were to function as nourishing tissue. In other words, it is argued that endosperm



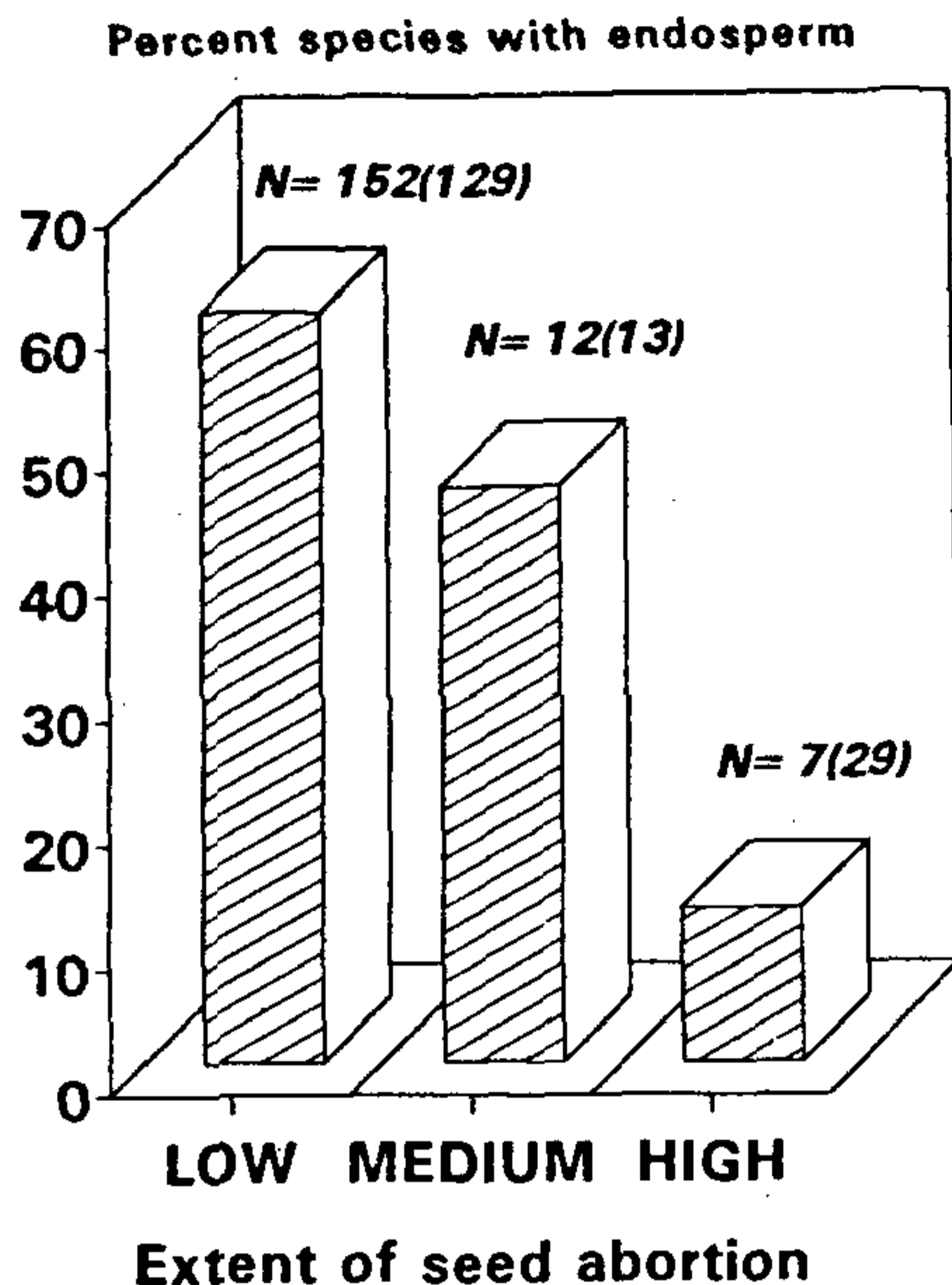


Figure 7. Relation between extent of seed abortion and presence of endosperm. Species ( $N = 335$ ) with varying extent of seed abortion were analysed for the presence or absence of well-developed endosperm (contingency chi-square analysis,  $\chi^2 = 42.53$ ,  $p < 0.005$ ,  $df = 2$ ). Species with high extent of seed abortion had endosperm less frequently than expected while those with less seed abortion had endosperm more often than expected. Values in the figure refer to species with endosperm; those in parentheses indicate the expected frequency (from Uma Shaanker *et al.*<sup>49</sup>).

might represent a maternal strategy to reduce intra-fruit sibling rivalry for maternal resources.

Accordingly, Uma Shaanker *et al.*<sup>49</sup> predicted that the endosperm should be more frequently found in multi-ovuled species (where there is a greater potential for sibling rivalry) than in uni-ovuled species. Furthermore, in species with well-developed endosperm, there should be less seed abortion (brood reduction) than in species with less well-developed endosperm. Analysing the association between the presence or absence of endosperm in 1131 species, they found that both these predictions were upheld. Well-developed endosperm was present more frequently than expected in multi-ovuled species than in uni-ovuled species. Furthermore, in species with a high degree of seed abortion, endosperm was less frequent than expected, compared to those in which seed abortion was less (Figure 7). Thus it appears that the evolution of the triploid endosperm might represent a maternal strategy of maintaining a more equitable allocation of resources among the siblings and thus reducing sibling-driven seed abortion or brood reduction.

#### Other features

A number of other flower and seed features might similarly be viewed to reflect a maternal counter-strategy in

subduing the conflicting interest of the offspring. The evolution of the hard seed coat or glumes, apart from their well recognized role of imparting protection to the embryos might also function to physiologically limit the indiscriminate mobilization of resources by the offspring<sup>15</sup>. The evolution of septa or locules between ovules might serve to insulate the siblings from intra-fruit sibling rivalry<sup>15</sup>. For example, in *Thespesia populnea*, where the ovary is pentacarpellary with three ovules in each carpel, seed abortion was found to be distributed across the carpels; mature fruits invariably had at least one seed in each carpel. Uma Shaanker *et al.*<sup>49</sup> showed that the development of endosperm and of locules might occur in a mutually exclusive manner. They found that well-developed endosperm occurs less frequently present than expected in species with locules than in those without locules.

#### Conclusions

When the concept of sibling rivalry and parent-offspring conflict was extended to plants, Wiens *et al.*<sup>50</sup> remarked that 'these highly anthropomorphic, sociobiological hypotheses are best not applied to plants'. However studies over the last decade have proven oth-

erwise<sup>51,52</sup>. Work in our laboratory and elsewhere have shown that as much as animals, plants too exhibit sibling rivalry and parent-offspring conflict over issues ranging from the maternal resource allocation to seeds to seed packing in fruits. Apart from providing a strong theoretical framework to explain the conditions under which the maternal parent and offspring have conflicting interests, our studies have provided empirical evidence in support of sibling rivalry and parent-offspring conflict and have unravelled the underlying proximate mechanisms through which the conflicting interests are manifested. Though the interactions may not be as apparent and dramatic as that in animals, plants have evolved equally effective, but subtle mechanisms to uphold the respective interests of the maternal parent and offspring. One of the major implications of our studies is that they have provided a new framework to view the evolution of a number of plant reproductive features, such as polyembryony, endosperm and locules, which hitherto had largely remained unaddressed.

1. Trivers, R. L., *Am. Zool.*, 1974, **14**, 249-264.
2. Lazarus, J. and Inglis, I. R., *Anim. Behav.*, 1987, **34**, 1791-1804.
3. Bengtsson, H. and Ryden, O., *Behav. Ecol. Sociobiol.*, 1983, **12**, 243-251.
4. Godfray, H. C. J., *Nature*, 1995, **376**, 133-138.
5. Mazer, S. J., *J. Biol. Linnaean Soc.*, 1987, **30**, 115-133.
6. O'Connor, R. J., *Anim. Behav.*, 1978, **26**, 79-96.
7. Gargett, V., *Ostrich*, 1978, **49**, 57-63.
8. Gargett, V., *Ostrich*, 1970, **41**, 256-257.
9. Harper, A. B., *Am. Nat.*, 1986, **128**, 99-114.
10. Procter, D. L. C., *Ibis*, 1975, **117**, 452-459.
11. Meyburg, B., *Ibis*, 1974, **116**, 224-228.
12. Ricklefs, R. E., *Condor*, 1965, **67**, 505-510.
13. Stinson, C. H., *Evolution*, 1979, **33**, 1219-1250.
14. Ganeshaiah, K. N. and Uma Shaanker, R., *Oecologia*, 1988, **77**, 135-139.
15. Uma Shaanker, R., Ganeshaiah, K. N. and Bawa, K. S., *Annu. Rev. Ecol. Syst.*, 1988, **19**, 177-205.
16. Ellner, S., *Evolution*, 1986, **123**, 173-185.
17. Smith, C. C. and Fretwell, S. D., *Am. Nat.*, 1974, **108**, 499-506.
18. Galen, C. and Weger, H. G., *Am. J. Bot.*, 1986, **73**, 346-352.
19. Nakamura, R. R., *Am. J. Bot.*, 1986, **73**, 1049-1057.
20. Sayers, E. R. and Murphy, R. P., *Crop Sci.*, 1966, **6**, 365-368.
21. Schoen, D. J., *Evolution*, 1983, **37**, 292-301.
22. Radha, M. R., M Sc (Agri.) thesis, University of Agricultural Sciences, Bangalore, 1990.
23. Vasudeva, R., Ph D thesis, University of Agricultural Sciences, Bangalore, 1995.
24. Ravishankar, K. V., Uma Shaanker, R. and Ganeshaiah, K. N., *J. Biosci.*, 1995, **20**, 89-103.
25. Mitchell, R., *Ecology*, 1977, **58**, 644-651.
26. Mohan Raju, B., Uma Shaanker, R. and Ganeshaiah, K. N., *Curr. Sci.*, 1995, **68**, 1114-1118.
27. Casper, B. B., *Am. Nat.*, 1990, **136**, 167-177.
28. Uma Shaanker, R. and Ganeshaiah, K. N., *Evol. Trends Plants*, 1988, **2**, 91-98.
29. Uma Shaanker, R. and Ganeshaiah, K. N., *Evol. Trends Plants*, 1989, **3**, 59-64.
30. Uma Shaanker, R., Ganeshaiah, K. N. and Radhamani, T. R., *Evol. Trends Plants*, 1990, **4**, 107-112.
31. Ganeshaiah, K. N. and Uma Shaanker, R., *Oikos*, 1991, **60**, 3-6.
32. Hegde, S. G., Uma Shaanker, R. and Ganeshaiah, K. N., *Oikos*, 1991, **60**, 20-26.
33. Hegde, S. G., Uma Shaanker, R. and Ganeshaiah, K. N., *Evol. Trends Plants*, 1991, **5**, 131-135.
34. Loksha, R., Hegde, S. G., Uma Shaanker, R. and Ganeshaiah, K. N., *Am. Nat.*, 1992, **140**, 520-525.
35. Mohan Raju, B., M Sc (Agri.) thesis, University of Agricultural Sciences, Bangalore, 1993.
36. Mohan Raju, B., Uma Shaanker, R. and Ganeshaiah, K. N., *Sexual Plant Reprod.*, 1996, **9**, 273-278.
37. Mohan Raju, B., Uma Shaanker, R. and Ganeshaiah, K. N., *Malaysian Forester*, 1996, **58**, 97-110.
38. Arathi, H. S., M Sc (Agri.) thesis, University of Agricultural Sciences, Bangalore, 1990.
39. Arathi, H. S., Ganeshaiah, K. N., Uma Shaanker, R. and Hegde, H. S., *Int. J. Plant Sci.*, 1996, **157**, 49-52.
40. Krishnamurthy, K. S., Ph D thesis, University of Agricultural Sciences, Bangalore, 1995.
41. Krishnamurthy, K. S., Uma Shaanker, R. and Ganeshaiah, K. N., *Curr. Sci.*, 1997 (submitted).
42. Cumaraswamy, A. and Bawa, K. S., *Plant Syst. Evol.*, 1989, **168**, 59-69.
43. Wiens, D., *Oecologia*, 1984, **64**, 47-53.
44. Wiens, D., Calvin, C. I., Wilson, C. A., Davern, C. I., Frank, D. and Seavey, S. R., *Oecologia*, 1987, **71**, 501-509.
45. Ganeshaiah, K. N., Uma Shaanker, R. and Joshi, N. V., *J. Genet.*, 1991, **70**, 103-127.
46. Uma Shaanker, R. and Ganeshaiah, K. N., *Trends Ecol. Evol.*, 1996, **11**, 26-27.
47. Queller, D. C., *J. Theor. Biol.*, 1983, **100**, 153-172.
48. Westoby, M. and Rice, B., *Evolution*, 1982, **36**, 713-724.
49. Uma Shaanker, R., Ravishankar, K. V., Hegde, S. G. and Ganeshaiah, K. N., *Plant Syst. Evol.*, 1996, **201**, 263-270.
50. Wiens, D. L., King, E. J., Nickrent, D. L., Calvin, C. L. and Vivrette, N. L., *Nature*, 1989, **342**, 626.
51. Bawa, K. S., Hegde, S. G., Ganeshaiah, K. N. and Uma Shaanker, R., *Nature*, 1989, **342**, 625-626.
52. Uma Shaanker, R. and Ganeshaiah, K. N., in *Towards a Holistic Ethology* (ed. Ramamurthy, R.), John Wiley, New Delhi, 1995, pp. 14-21.

ACKNOWLEDGEMENTS. The work reported here has been supported by grants from the Department of Science and Technology, Government of India, New Delhi.