

War of hormones over resource allocation to seeds: Strategies and counter–strategies of offspring and maternal parent

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Abstract. It is suggested that maternal parent and offspring have conflicting interests over the extent of resource allocation to developing seeds. While maternal parent would be selected to allocate her resources optimally among her offspring, the latter would be selected to demand more. In animals, offspring are known to demand additional resources either visibly (through intense vocal calls) or subtly through the production of hormones. In plants though parent offspring conflict over resource allocation has been invoked, the mechanism through which the parent and offspring interact in regulating resource allocation into developing seeds is not yet clear.

In this paper, we propose that the strategies and counter–strategies of the offspring and mother during the development of seeds might be manifested through the production of appropriate growth hormones. Accordingly, we predict (i) hormones that mobilize resources into seeds (*e.g.* auxins and gibberellic acid) shall be synthesized exclusively by the offspring tissue and (ii) hormones that inhibit resource flow in to seeds (*e.g.* abscisic acid) be produced exclusively by the maternal tissue. We show that these predictions are supported by existing literature on the temporal dynamics and source of production of growth hormones during seed development. Finally, we suggest that such analysis viewing the production of different hormones during early seed development, as strategies and counter–strategies of mother and offspring tissue, helps offer a meaningful interpretation of the otherwise complex dynamics of hormone fluxes.

Keywords. Parent–offspring conflict; seed development; offspring strategy; plant hormones; auxins; gibberellic acid; abscisic acid.

1. Introduction

Trivers (1974) observed that parents and offspring have conflicting interests over the allocation of maternal resources to the offspring. He proposed that while the mother is selected to allocate her resources optimally among her offspring, the latter are selected to demand more than that. The resultant conflict, termed parent–offspring conflict (POC), is argued to be the underlying basis of several behavioural interactions between parent and offspring. In fact, these behavioural features represent the most visible manifestations of the strategies adopted by the participants in furthering their own interests. In raptors, for example, the developing sibs resort to fratricide where the elder fledglings kill the younger often through violent means (Gargett 1970, 1978; Meyburg 1974). In certain other birds, the

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dominant among the fledglings in a brood produce highly vocal "begging" calls to attract the attention of the mother.

All such behaviours may help the dominant sib of the brood in eliminating the competition for resources from others such that it garners most from the mother. While such behaviours constitute the most visible manifestations of POC, Haig (1993) has suggested that parents and offspring might also indulge in more subtle ways of furthering their own interests. He suggested that in mammals, the maternal regulation over, and offspring's demand for maternal resources could occur through the production of distinct hormones by them; the hormones produced by the participants would facilitate or inhibit the flow of resources to the offspring in accordance with their respective interests.

2. POC in plants

The theory of POC has been recently extended to plants as well (Westoby and Rice 1982; Queller 1983, Ellner 1986; Mazer 1987; Doust and Doust 1988; Ganeshaiyah and Uma Shaanker 1988; Uma Shaanker and Ganeshaiyah 1988; Uma Shaanker *et al* 1988; Bawa *et al* 1989). Fruits, in which several seeds develop simultaneously, deriving resources from the common maternal pool, are suggested to constitute potentially an interesting arena where conflict between parent and offspring is manifested over the maternal resources (Uma Shaanker *et al* 1988). Accordingly, it has been shown that intense sibling rivalry and POC occurs in multiovulated fruits over resource allocation, and in certain situations over seed number per fruit (Uma Shaanker *et al* 1988; Ganeshaiyah and Uma Shaanker 1988, 1992; Uma Shaanker and Ganeshaiyah 1988, 1989; Casper 1990). However, unlike in animals, in plants, the participants may not be able to indulge in highly visible and vocal interactions. In fact, probably for the same reason, the existence of such conflicts in plants is not easily noticed and hence has been frequently questioned (Wiens *et al* 1989; see also Ganeshaiyah and Uma Shaanker 1993).

The most plausible mechanism by which the participants in plants can interact is through the production of hormones. Because of their diverse formative effects and role as signal transducers in plants, hormones can be employed as potential weapons by the participants to facilitate and/or inhibit the flow of resources, and even to inactivate spatially isolated target tissues. Utilizing these features of hormones, offspring can "beg" resource from the mother, and "kill" the neighbouring seeds, while the mother can "quench" the demand for additional resources by the greedy offspring.

In this paper, we propose that the pattern of production of different hormones during seed development is probably shaped by the evolutionary conflict between the parent and offspring to meet their own interests. Based on this, we derive certain predictions and show that they are, in fact, supported by the existing literature on plant hormones. In the process, we show that the development of seeds is characterized by the production of two distinct kinds of hormones that are synthesized in two disparate tissues of the fruit and have opposite functions in mobilizing resources. Finally, such analysis offers a new framework in which the otherwise complex dynamics of hormone fluxes during seed development can be meaningfully interpreted.

3. Offspring strategy

POC theory argues that offspring are generally selected to demand more than what the mother is selected to offer them. In plants such selection can be expected to favour the evolution of mechanisms that enhance the resource-drawing ability of the developing ovules to facilitate them drawing resources from the surrounding maternal tissue. Since sink strength or resource drawing ability of a tissue is generally dependent on the production of certain hormones in it (Seth and Wareing 1967; Patrick 1976; Ho 1988), it is likely that offspring evolve with them the machinery to produce these hormones. More importantly, it follows that maternal tissue would not be selected to produce such hormones that induce greater sink strength in the offspring tissue.

In fact, maternal parent has been shown to be a passive participant in resource mobilization to the offspring tissue; the phloem vessels emanating from the maternal tissue never grow into the developing seed (Felker and Shannon 1980; Patrick and McDonald 1980; Thorne 1985) and for this reason, the extent to which resources flow in to the offspring depends completely on the latter's ability to actively draw them across the passive barriers—the maternal tissue. In other words, the survival and development of offspring is contingent upon the evolution of strategies that convert the developing seeds into strong sinks. Therefore, we predict that *hormones that impart resource-drawing ability to the developing seeds should be produced by the offspring rather than by the maternal tissue*. (See the end of this section for a discussion on whether this prediction could emerge independent of POC theory).

3.1 Seed weight and hormones that induce resource drawing ability

Hormones such as auxins, gibberellins and cytokinins have been identified to be the most important growth promoters and have been shown to actively mobilize resources to the sites to which they are applied (Kriedmann 1968; Mullins 1970; Prasad *et al* 1977; Gilford *et al* 1976; Patrick and Wareing 1981; Gifford and Evans 1981; Sturgis and Rubery 1982; Morris and Arthur 1984; Hayes and Patrick 1985; Pereto and Beltram 1987). In a number of systems, it is shown that their application to the tissues has enhanced the translocation of resources by (i) increased differentiation of sieve tubes connecting the sinks to sources (Aloni 1987), (ii) enhancing the metabolic (Cook and Evans 1978) and enzyme activities (Morris 1982) of the sink tissues and (iii) increasing the size and rate of division of cells in the sink tissue (Leonard *et al* 1983; Kinet *et al* 1986). Due to their ability to mobilize resources during the development of fruits these hormones can also be expected to help the development of seeds and accumulation of resources in them. There are a number of studies suggesting such positive influence of hormones on formation and development of seeds.

In *Pisum sativum*, the developing seeds of gibberellic acid mutants have reduced levels of gibberellic acid compared to those of the wild type (Swain *et al* 1993). These seeds of the mutants are shown to undergo a high rate of abortion (50%) compared to the wild type and if matured, weigh significantly less ($\bar{x} = 179 \pm 6$ mg) than those of the wild type ($\bar{x} = 202 \pm 5$ mg, $p < 0.001$). In other words, the enhanced levels of gibberellic acid in the seeds of the wild type appear to facilitate mobilization of resources in to them leading to their successful development.

In barley, isogenic lines with relatively high concentration of cytokinin in the developing seeds exhibit increased rate of mitosis in the endosperm tissue and increased weight of seeds compared to those with low concentration of cytokinin (Michael and Seiler Kelbitsch 1972). In a similar study involving isogenic lines of barley, Mounler *et al* (1980) found that grain weight was positively correlated with their indole acetic acid (IAA) levels.

Thus the growth promoters that are known to mobilize resources also seem to aid in the development of offspring and in the garnering of resources. However, the source of these hormones is as much crucial to the test of our prediction as is their function. Our argument that the hormones that mobilize resources into the seeds are synthesized in the interest of the offspring demands that they originate from offspring than from the maternal tissue.

3.2 *Are resource-mobilizing hormones synthesized in the offspring tissue?*

There are strong evidences to suggest that resource mobilizing hormones of the developing seeds are synthesized in the offspring tissue. In *P. sativum*, Swain *et al* (1993) developed F_o seeds (Lh/lhⁱ) on gibberellic acid (GA) mutant mothers (lhⁱ/lhⁱ) by pollinating them with wild type (Lh/Lh) pollen grains. These F_o seeds had gibberellic acid levels and seed weights comparable to those of the wild parent and significantly more than the selfed seeds of the mutant mother. In other words, though the mutant mother was deficient in GA, the presence of a single copy of the wild type allele (Lh) in the hybrid embryo could restore the normal seed development. These results strongly suggest that the resource-mobilizing hormone in *P. sativum* is derived from the offspring tissue and not translocated from the maternal tissue (Brenner 1987).

A characteristic feature of seed growth is the enhanced levels of auxins and gibberellic acid in the fertilized ovules (Crane 1964). Such enhanced levels of auxins and gibberellins are shown to help in differentiation of the sieve tube and mobilization of assimilates to the developing seeds (Crane 1964; Patrick 1976; Aloni 1987). In several systems, it is unequivocally demonstrated that such increase in the auxin and gibberellic acid levels during the post fertilization period is due to their active synthesis by the embryo and not because of their translocation from the maternal tissue (Crane 1964; Euwens and Schwabe 1975; Pharis and King 1985; Barendse *et al* 1970).

There are also indirect evidences to suggest that increased levels of these hormones in the ovules, immediately following fertilization, are mediated through the offspring rather than the maternal genetic system. For instance, post-fertilization increase of hormones in the ovule in some species is known to be facilitated by the enzymatic machinery contributed by the pollen tube that fertilizes them (Lund 1956). Pollen grains of a variety of species are very rich sources of such hormones (Stanley and Linskens 1974; Bandhyopadhyay *et al* 1976) and are frequently shown to supplement the hormone pool of the ovules they fertilize. For instance, orchid pollen are known to be a rich source of indole acetic acid (Stanley and Linskens 1974) and at least two different fractions of gibberellic acid are found in pine pollen grains (Kamienska and Pharis 1975). Studies have shown that in these and in other species, ovules receive such hormones from the pollen grains at the time of fertilization (Crane 1964). Therefore the hormonal content of the pollen grains can be viewed as gifts

from the paternal parent that aid their offspring in acquiring resources from the mother plant. Thus, the genetic and other evidences presented above are consistent with our prediction that the production of resource mobilizing hormones of the seeds occurs in the offspring tissue *per se*.

3.3 *Are these predictions about the offspring producing resource mobilizing hormones exclusive to POC theory ?*

The prediction of this section that resource mobilizing hormones shall be synthesized exclusively in the offspring tissue might also emerge from the optimum resource allocation theory (Smith and Fretwell 1974) if one assumes that the offspring also evolve strategies that ensure their survival and development independent of their conflict with the mother. However, resource supply to the offspring by the mother can be facilitated in two ways: (i) mother invests certain optimal amount of resources into the offspring independent of the offspring's ability to draw resources or (ii) mother offers resources to offspring in proportion to that demanded by the latter. In the second strategy, obviously the mother may not be able to restrict the flow of resources into the offspring to the optimum level and hence might run the risk of being exploited by the offspring for additional resources. It is not immediately clear which of these two strategies will be selected. If mother adopts the first strategy than the source of the resource mobilizing hormone could well be the maternal tissue *per se*. On the other hand if it adopts the second strategy, than the source of resource mobilizing hormone would be clearly the offspring. For this reason, it is difficult to delineate whether the prediction and observations made in this section represents purely parent offspring conflict or demand dependent allocation of resources by the mother. However, since these predictions and those following in the next section conform well with POC, we propose that the synthesis of resource mobilizing hormone in the offspring might likely represent sibling rivalry than mere strategies of the offspring to survive.

4. Maternal strategy

POC theory implies that the mother would be selected to resist any extra demands by the offspring for resources than she is selected to give. Accordingly, selection can be expected to favour strategies or mechanisms in her that antagonize or quench the offspring-driven demand for extra resources. In plants, as argued above, offspring are likely to exert their demand for maternal resources through the production of resource mobilizing hormone especially during early stages of seed development. Therefore, *selection can be expected to favour the maternal tissue to produce, during these early phases of seed development, hormones that antagonize or quench the resource demand by the offspring.* This prediction implies that (i) the hormones that inhibit the resource mobilization into the seed are produced at the stage corresponding to that of the synthesis of resource mobilizing hormone by the offspring and (ii) they are synthesized exclusively by the maternal tissue.

4.1 *Hormones that inhibit resource mobilization*

Among several hormones known, abscisic acid (ABA) seems to be the most probable candidate that might aid the maternal tissue in subduing the offspring-driven resource

mobilization to developing ovules. It has been demonstrated that ABA inhibits the mobilization of assimilates in several systems (Mullins 1970; Porter 1981; Vreugdenhill 1983; Estruch *et al* 1989; Kasim 1991) and is antagonistic to the effects of growth promoters (Alvin *et al* 1976; Chrispeels and Varner 1966). For instance, enriching winter wheat plants with ABA greatly reduced the translocation of ^{14}C -sucrose into the developing ears resulting in reduced grain dry weight (Borkovec and Prochazaka 1990). In barley, application of ABA to developing grains during the first week of anthesis significantly reduced the movement of assimilates to the grains as compared to the control grains (Tietz *et al* 1981). Porter (1981) demonstrated that the transport of sucrose and asparagine into reproductive sinks of lupins could be reduced by increasing the levels of ABA in those tissues. In fact, Porter (1981) and Ober *et al* (1991) clearly showed that ABA reduces the resource-mobilizing ability of the sinks in lupins and in maize respectively. In several systems, ABA has been shown to inhibit the effects of growth-promoting hormones (Thomas *et al* 1965). For example, ABA application reduced the gibberellic acid induced sucrose uptake in excised veins of *Pisum sativum* (Estruch *et al* 1989) and fusicoicin induced glucose uptake in beet root protoplasts (Getz *et al* 1987).

ABA has also been shown to inhibit cell division in endosperm tissue. In maize, the number of cells in kernels *in vitro* decreased with ABA concentration ($r = -0.92$, $P < 0.001$; Myers *et al* 1990) and the endosperm cultured continuously in $90\ \mu\text{M}$ of ABA had significantly less dry weight than that in control (Myers *et al* 1990).

From a survey of 55 studies, we compiled the effect of ABA on three parameters *viz.*, seed weight, ^{14}C -assimilate uptake and cell division. Among the trials/experiments that reported significant effect, 46 showed inhibitory, while 22 reported a promotory effect suggesting an overwhelmingly inhibitory effect of ABA on resource mobilization (table 1). The 22 studies that reported otherwise might be confounded by the fact that the eventual effects might be dependent not as much on the absolute as on the relative concentrations of ABA and growth promoters (Davis and Addicott 1972; Sujt and Bangerth 1981; Marschner *et al* 1984). Unfortunately, in most of these studies, such ratios were not available. In one study however, it was in fact shown that growth of potato tubers in culture was negatively correlated

Table 1. Effect of abscisic acid on seed weight, uptake of ^{14}C -assimilates and cell division*.

Feature	Effects	
	Enhanced	Inhibited
Seed weight	10	28
^{14}C -assimilate uptake	9	9
Cell division	3	9
Total	22	46

*These results are collated from experiments reported in 55 studies. The effects include those derived from manipulative treatments as well as those from correlative studies.

with the ratio of ABA to IAA in the medium ($r = -0.43$, $P < 0.01$; Marschner *et al* 1984).

4.2 Temporal pattern of ABA production in developing seeds

Several studies report that the accumulation of ABA in developing seeds generally shows two distinct peaks—the first during the early stages of resource accumulation in the seed and the second during the seed maturation period (figure 1a and table 2, and references therein). The functional significance of the second peak is well studied and has been implicated in (i) the synthesis of late embryogenesis proteins that protect the embryos against desiccation damage at later stages (Dure *et al* 1989) and (ii) the inhibition of precocious germination of seeds on the mother plant (Ackerson 1984; Quatrano 1987). It has been suggested that the second peak of ABA is predominantly embryonic in origin (Karssen *et al* 1983). On the other hand, the functional significance of the first peak, coinciding with the seed-filling stage, is less understood, and confusing (Davison *et al* 1976; Hsu 1979; Vernieri *et al* 1989).

Several studies suggest that the early peak of ABA accumulation coincides substantially with the peak synthesis of resource mobilizing hormones in the developing seeds (King 1976; Mengel *et al* 1985; Hein *et al* 1984; figure 1). Such temporal correspondence of ABA accumulation with that of resource mobilizing hormones can be expected to subdue the sink strength of developing seeds. In other words, the pattern of accumulation of ABA during early stages of seed development appear to support our argument that it could represent a maternal counter-strategy of quenching the greedy demand of the selfish offspring.

However, if it is an evolutionary counter strategy of the mother, then, as predicted earlier, the production of ABA should be exclusively under maternal regulation. We offer below evidence in support of this.

4.3 Is ABA produced by the maternal tissue?

The developing seeds of wild type (Aba/Aba) *Arabidopsis thaliana*, exhibit an early peak of ABA accumulation 10 days after fertilization coinciding with the seed-filling period while that of ABA deficient mutants (aba/aba) do not. Karssen *et al* (1983) found that F_0 seeds (Aba/aba) developing on a wild type mother exhibit this peak while those F_0 seeds (Aba/aba) developing on a mutant (aba/aba) mother do not. Clearly, embryos by themselves do not seem to produce ABA though they are genetically capable (Aba allele). Rather ABA of the first peak appears to be synthesized only in the maternal tissue but is then translocated to the embryo. Another possibility is that the ABA is produced in the endosperm by the selective expression of maternal allele with the corresponding allele from the paternal parent being imprinted. Evidence suggesting the maternal origin of the early peak of ABA in developing seeds is also available from the studies on the viviparous (vp) mutants of maize (Ober and Setter 1992). Homozygous viviparous plants (vp/vp), do not produce ABA. But homozygous recessive seeds (vp/vp) developing on a heterozygous parent (+/vp) obtained by selfing the latter, showed ABA levels comparable to that of +/+ and +/vp seeds, also developing on the heterozygous parent. Clearly, since (vp/vp) seeds are by themselves incapable of synthesizing the hormone, ABA in

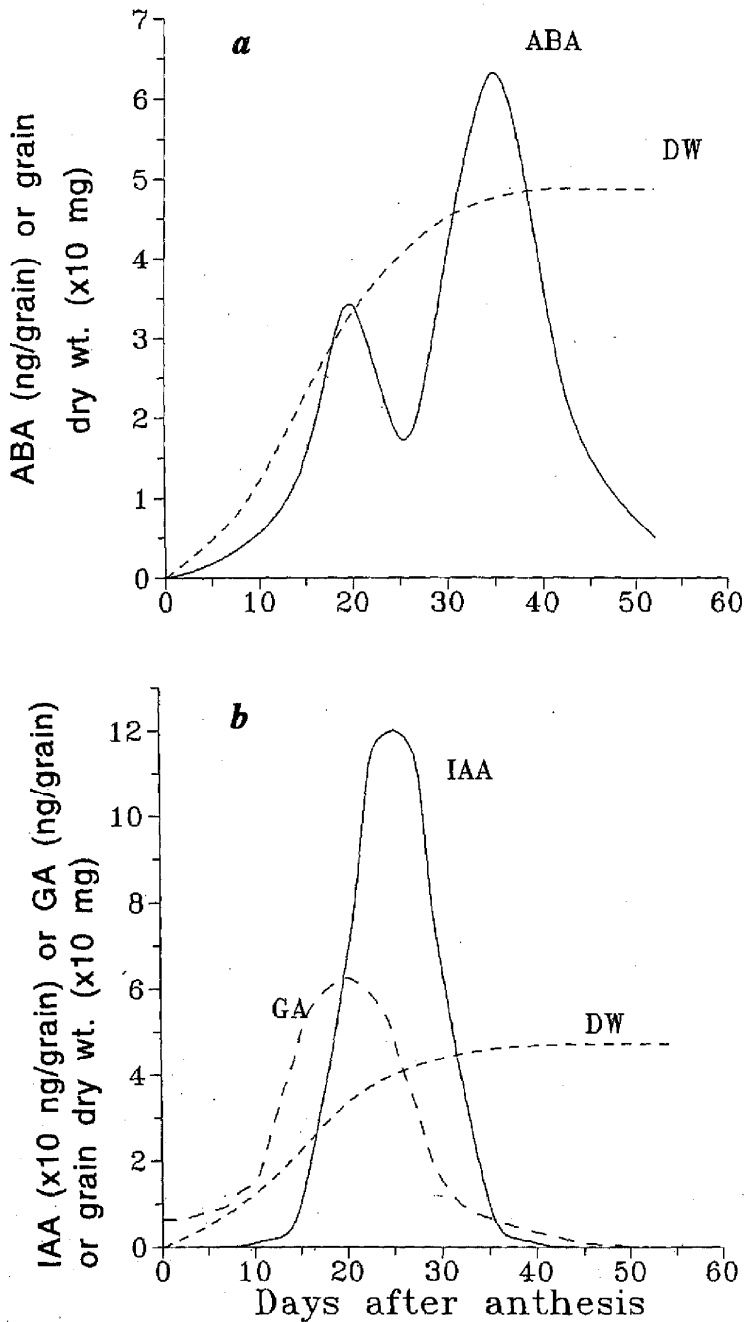


Figure 1. Temporal patterns of accumulation of (a) abscisic acid (ABA) and (b) auxins (IAA), gibberellic acid (GA) and grain dry weight (DW) during seed development in wheat. Data adapted from Wheeler (1972) for auxin and gibberellic acid and from King (1976) for abscisic acid and grain dry weight.

Table 2. Species in which early peak of abscisic acid accumulation in seed has been demonstrated.

Species	Tissues	Temporal pattern of accumulation of ABA during seed development (days after anthesis)		References
		First/early peak	Second/late peak	
<i>Prunus cerasus</i>	Seed	14	45	Davison <i>et al</i> 1976
<i>Triticum aestivum</i>	Grain	19	38	King 1976
<i>Triticum aestivum</i>				
(a)	Grain (ng/gdw)	7	–	McWha 1975
(b)	Grain (ng/grain)	14	–	McWha 1975
<i>Glycine max</i>				
(a)	Seed (ng/g)	11	–	Quebedeaux <i>et al</i> 1974
(b)	Seed (ng/grain)	21	–	Quebedeaux <i>et al</i> 1976
<i>Phaseolus vulgaris</i>				
(a) var. T. H. Ponds	Embryo	22	30	Hsu 1979
(b) var. P1226895	Embryo	20	26	Hsu 1979
<i>Hordeum vulgare</i>	Grain	?	?	Naumann and Dorffling 1982
<i>Arabidopsis thaliana</i>	Siliqua	10	16	Karszen <i>et al</i> 1983
<i>Zea mays</i>	Endosperm	6	–	Jones and Brenner 1987
<i>Pisum sativum</i>	Embryo	30	50	Wang <i>et al</i> 1987
<i>Secchium edule</i>	Fertilized ovule	2	–	Vernieri <i>et al</i> 1989
<i>Oryza sativa</i>	Endosperm	13	21	Qin <i>et al</i> 1990

–, Data not available; ?, Dates not mentioned.

these seeds should have originated from the heterozygous maternal tissue. Further evidence in support of the maternal source of ABA in seeds is provided from radiotracer experiments. Substantial translocation of radiolabelled ABA from leaves to seeds, particularly after a period of water stress, has been demonstrated by several workers (Goldbach and Goldbach 1977; Hoad 1978; Dewdney and McWha 1979; Brenner *et al* 1982; Smith *et al* 1987; Ober and Setter 1990). Thus, in contrast to the resource mobilizing hormones, ABA, the hormone that inhibits resource-mobilization into offspring tissue, appears to be synthesized exclusively in the maternal tissue and translocated to the embryo. This, in other words, supports our prediction that maternal tissues are selected to produce hormones that quench the offspring driven resource drawing ability.

5. Conclusions and implications

We have attempted to view the otherwise complex dynamics of hormone production during the development of seeds, from an evolutionary perspective of the strategies of mother and offspring tissues in pursuing their respective interests. An important prediction emerging from our analysis and supported by the literature is that there is a striking asymmetry in the origin of the two distinct groups of hormones with opposite functions in the promotion and inhibition of resource flow to the developing

seeds. While resource mobilizing hormones of the seed such as auxins and gibberellic acid are exclusively synthesized in the embryonic tissue, ABA, the hormone pool of the seed that inhibits the mobilization of resources in to it, is contributed by maternal tissue.

It may be important to realize that in this war of hormones between the mother and the offspring over the regulation of resource allocation to the seed, the absolute levels of the respective hormones may not matter as much as their relative proportions in the seed. Most certainly, during seed development, these ratios may be far from being static. The relative concentrations of the hormones synthesized by the offspring and that transported by the maternal tissue may be sensitive to a wide variety of factors such as genetic relatedness between the offspring and mother, breeding systems, as well as environmental features.

We propose that viewing hormone production in the developing seeds as strategies and counter-strategies of offspring and mother may help in a meaningful interpretation of the otherwise complex fluxes and interactions of hormones. This is evident from the fact that the early peak of ABA in developing seeds which hitherto had no known function can be implicated in regulating seed resource allocation. Such an understanding might also offer a physiological basis to manipulate the development of seeds. It might also help in understanding the physiological basis of certain features such as xenia, metaxenia and heterosis of seeds.

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