Evolution of polyembryony: Consequences to the fitness of mother and offspring

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Abstract. Polyembryony, referring here to situations where a nucellar embryo is formed along with the zygotic embryo, has different consequences for the fitness of the maternal parent and offspring. We have developed genetic and inclusive fitness models to derive the conditions that permit the evolution of polyembryony under maternal and offspring control. We have also derived expressions for the optimal allocation (evolutionarily stable strategy, ESS) of resources between zygotic and nucellar embryos.

It is seen that (i) Polyembryony can evolve more easily under maternal control than under that of either the offspring or the 'selfish' endosperm. Under maternal regulation, evolution of polyembryony can occur for any clutch size. Under offspring control polyembryony is more likely to evolve for high clutch sizes, and is unlikely for low clutch sizes (<3). This conflict between mother and offspring decreases with increase in clutch size and favours the evolution of polyembryony at high clutch sizes. (ii) Polyembryony can evolve for values of "x" (the power of the function relating fitness to seed resource) greater than 0·5758; the possibility of its occurrence increases with "x", indicating that a more efficient conversion of resource into fitness favours polyembryony. (iii) Under both maternal parent and offspring control, the evolution of polyembryony becomes increasingly unlikely as the level of inbreeding increases. (iv) The proportion of resources allocated to the nucellar embryo at ESS is always higher than that which maximizes the rate of spread of the allele against a non-polyembryonic allele.

Finally we argue that polyembryony is a maternal counter strategy to compensate for the loss in her fitness due to brood reduction caused by sibling rivalry. We support this assertion by two empirical evidences: (a) the extent of polyembryony is positively correlated with brood reduction in *Citrus*, and (b) species exhibiting polyembryony are more often those that frequently exhibit brood reduction.

Keywords. Polyembryony; brood reduction in plants; parent–offspring conflict; inclusive fitness and genetic models, evolution.

1. Polyembryony and its prevalence in plants

The emergence of multiple seedlings from a single seed was first observed by Leeuwenhoek as early as 1719 (Maheshwari 1950; Bhojwani and Bhatnagar 1974; Tisserat *et al.* 1979). This condition, referred to as polyembryony (PE), is widely prevalent among angiosperms (Tisserat *et al.* 1979).

The additional embryos in PE result from the differentiation and development of various maternal and zygotic tissues associated with the embryo sac; the maternal tissues include nucellus, integument, antipodals and synergids, while the embryonic tissues include the suspensor and zygote *per se*. The triploid tissue, endosperm, comprising one paternal and two maternal genomes also contributes to the formation of PE (Maheshwari 1950; Bhojwani and Bhatnagar 1974). The process of

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the development of embryo from tissues other than the zygote or endosperm is generally referred to as adventitious embryony (AE) (Maheshwari 1950; Tisserat *et al.* 1979).

About 244 species from 140 genera belonging to 59 angiosperm families are reported to exhibit either AE or PE (Tisserat *et al.* 1979; Adarsh Kumar *et al.* 1991, and references therein). Surprisingly, despite its wide occurrence, the evolution of PE is poorly understood (Lovett Doust and Lovett Doust 1988).

Several workers have discussed the evolution of apomixis and AE in the context of their similarity to asexual propagation (Stebbins 1941; Gustaffson 1946; Khoklov 1976; Kaur *et al.* 1978). Because of the lack of a clear distinction between PE, apomixis and AE, the former is also assumed to be akin to asexual reproduction. However, we distinguish PE from the other two processes on the basis of its requirement of sexual reproduction and the genetic composition of the resulting offspring and argue that equating PE with asexual reproduction is erroneous.

In PE, generally both sexual and asexual embryos develop in the same seed (Maheshwari 1950; Tisserat *et al.* 1979; Lakshmanan and Ambegaokar 1984). For instance, Rangaswamy (1959), Lakshmanan and Ambegaokar (1984), Pieringer and Edwards (1965), Rangan *et al.* (1969), Iglesias *et al.* (1974) in Rutaceae, Sachar and Chopra (1957) in Anacardiaceae, Van der Pijl (1934) in Myrtaceae, Tiagi (1970) in Cactaceae, Sachar (1955) in Papavaraceae and several others (Tisserat *et al.* 1979; Lakshmanan and Ambegaokar 1984) have reported the simultaneous formation and development of zygotic and asexual embryos. Occasionally the zygotic embryo does not survive and multiple embryos arise from adventitious tissues such as the nucellus and integument (Roy 1953, 1961; Narayanswami and Roy 1960). Even in these situations, where the zygotic embryo does not survive, the initiation and development of an asexual embryo is shown to be dependent on the initial development of the sexual embryo (Sachar and Chopra 1957; Copeland 1966) or on the process of fertilization of ovules (Tisserat *et al.* 1979) or on pollination (Strasburger 1878; Toxopeus 1930; Desai 1962). A pertinent example is provided by *Spiranthes cernua*, where the development of an already differentiated nucellar embryo depends upon the fertilization of the ovules (Swamy 1948). Thus asexual embryos in PE apparently cannot develop independently of the process of sexual reproduction and in most cases require the development of the sexual embryo. Thus, to the extent that PE involves costs associated with features of sexual reproduction such as the production of floral sex organs, pollination, fertilization and development (of the zygotic embryo), it is not equivalent to asexual propagation. In other words, PE is not associated with the same advantages as asexual reproduction. Hence the arguments developed for the evolution of asexual reproduction are inadequate to explain the evolution of PE.

2. Aim of the paper

We assume that producing both asexual and sexual embryos in the same seed, combines the advantages associated with both sexual and asexual reproduction. Our interest in this paper is to develop genetic and inclusive fitness models to arrive at the conditions that favour the evolution of PE. We derive these conditions separately from the points of view of maternal and offspring fitness and discuss the results in the context of possible conflicts between the two over the evolution of PE.

Using these arguments, we suggest that nucellar PE has evolved as a counter strategy by the maternal parent to mitigate the consequences of brood reduction driven by sibling rivalry. Finally, we provide supportive evidence for some of the predictions of our model in the form of associations between PE and other reproductive features of plants.

3. Inclusive fitness and genetic models

Table 1a, based on data from 233 species, presents the frequencies of different tissues of the embryo sac giving rise to an asexual embryo. Seventy eight percent of the species have additional embryos emerging from the maternal tissues (table 1b). In a majority of cases the additional embryos arise from the diploid nucellar and integument tissues (table 1a); only 19% of the species have additional embryos resulting from the division of the zygotic embryo (table 1a & b). In other words, additional embryos in PE generally contribute to the fitness of the maternal parent rather than to the fitness of the offspring. The formation of additional embryos thus seems more in the interest of the mother than the offspring. For this reason, our models in this paper are constructed by considering the differential fitness contributed through the additional embryo to the mother and the offspring separately.

Further, the models are constructed to study the evolution of additional embryos from the maternal tissues, especially from nucellus, as this represents the major type of PE (tables 1a & b).

Table 1a. Species showing various types of polyembryony*.

Tissues of embryo sac giving rise to additional embryos	Number of species
Nucellar	122
Suspensor	22
Synergids	34
Embryo	21
Integument	21
Endosperm	7
Antipodals	6

*Data collected from Maheshwari (1950), Tisserat *et al.* (1979) and Lakshmanan and Ambegaokar (1984).

Table 1b. Frequency of maternal, endosperm and embryo structures giving rise to additional embryos.

Tissues	Number of species	Percent
Maternal	183	78
Endosperm	7	3
Embryo	43	19

Maternal structures include nucellar, synergids, antipodals and integument.

4. Assumptions

We wish to obtain conditions under which an allele that leads to the production of nucellar embryos can invade a purely sexually reproducing population (i.e., one which does not produce nucellar embryos). The fixation of this allele is subject to the condition that the sexual embryo survives and has some positive fitness value because, as stated previously (see § 1), we consider the formation of a zygotic embryo as a prerequisite for PE.

We develop both inclusive fitness and genetic models for the parent and the offspring separately.

The models assume the following:

1. Offspring fitness increases nonlinearly (figure 1) with resources invested in a seed (R). A number of studies demonstrate an increasing convex relationship between seed size and seedling characteristics (McGinley *et al.* 1987 and Lloyd 1989 and references therein). This relation is given by (Lloyd 1989).

$$\text{fitness} = (R - c)^x,$$

where, R = resource invested in seed, c = minimum resource threshold for positive fitness to be attained, and x = constant or power describing the shape of the curve. Since many fitness parameters such as seedling leaf area, vigour, plant height etc. follow an increasing convex relationship with seed size (McGinley *et al.* 1987; Lloyd 1989), the power of the fitness function, x, is less than 1. The value of x is therefore restricted to $0 < x < 1$.

2. In the absence of PE, there exists an optimal allocation of resources (R^*) to seeds given by $c/(1 - x)$; this is a consequence of the assumed fitness function (Lloyd 1989).

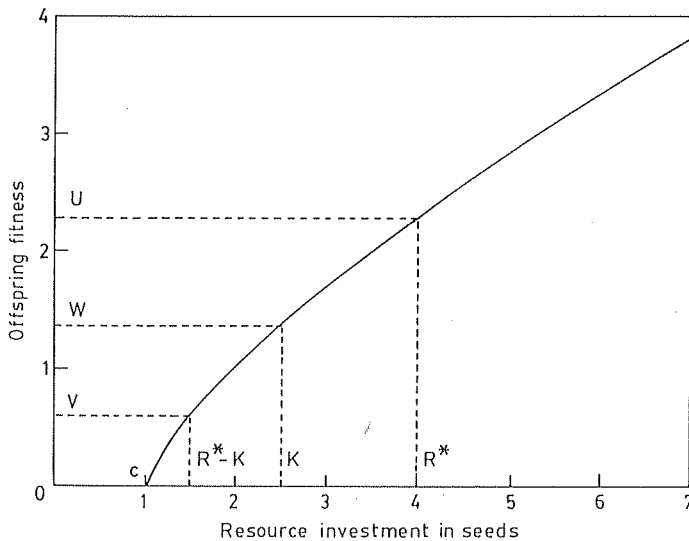If the total resource available to the maternal parent is T and if it invests an

Figure 1. The fitness of the offspring as a function of resource investment in seeds. Also shown in the figure are the optimal investment (R^*), resources allocated to the nucellar embryo (K) and resources allocated to the accompanying zygotic embryos (R^*-K), with their fitness values U, W and V respectively.

amount R in each seed, a total of T/R seeds will be produced, each with a fitness $(R-c)^x$. The net fitness of the maternal parent is thus $(T/R) \cdot (R-c)^x$. Differentiating this quantity with respect to R and equating the derivative to zero, we obtain R^*, the investment in a seed which maximizes the fitness of the maternal parent equal to $c/(1-x)$ as given above.

3. The maternal parent does not alter this optimal resource (R^*) allocated to the seed in which an additional embryo is formed. In fact, in the event of an additional (nucellar) embryo being formed in the seed, the already optimized resource (see assumption 2) is reallocated between the zygote (sexual offspring) and the additional nucellar embryo. Further, the optimal allocation by the mother to the entire fruit would remain valid even after the formation of the additional embryo considering certain important parameters of survival such as the dispersal efficiency of the fruit. Hence, the nucellar embryo obtains certain resources K, from R^*. The value of K, however, can range between the limits of c and (R^*-c). Since the minimum resource needed to obtain a positive fitness is c, we need $K > c$. The resource available for the zygotic embryo when the additional embryo is formed is $R^* - K$, and, by a similar argument, needs to be greater than c. Hence, $K < (R^* - c)$ and $c < K < (R^* - c)$, i.e. $c < K < cx/(1-x)$. Since we have assumed that both the zygote and the nucellar embryo have non-zero fitness, each of them gets at least "c" units of resource. Therefore the total resources (R^*) should be greater than $2c$. Thus we get, $c/(1-x) > 2c$ or $x > 0.5$. Thus from assumption 1 above, it follows that $0.5 < x < 1$.

4. The power (x) of the fitness function does not differ between the sexual and nucellar embryos, meaning that the fitness functions of the two genotypes, that of the sexual and asexual embryos, are identical. This may not always be true, since the sexual embryos generally enjoy heterozygous advantage (hybrid vigour). However, in a highly cross pollinated species, the nucellar embryos can be expected to be as heterozygous as the sexual embryo and hence would have the same hybrid vigour.

5. Inclusive fitness model

Let n be the number of offspring (seeds) produced by the mother in her clutch, each with a zygotic embryo.

The inclusive fitness of the mother is given by

$$M_f = n \cdot (R-c)^x \cdot r_{zm},\tag{1}$$

where

r_{zm} = genetic relatedness between the offspring and the mother.

Similarly, the inclusive fitness of any offspring in that clutch is given by,

$$O_f = (R-c)^x + (n-1)(R-c)^x \cdot r_{zz},\tag{2}$$

where r_{zz} = the genetic relatedness among offspring.

Now, consider a mutant that produces an additional embryo from the maternal tissue in each seed, drawing K amount of resources from the zygotic embryo. Since the additional embryo is genetically identical to the mother ($r_{zm} = 1$), the inclusive fitness of the mother is given by,

$$M'_f = n \cdot (R - K - c)^x \cdot r_{zm} + n\,(K-c)^x.\tag{3}$$

On the other hand, since the relatedness of the offspring to the nucellar embryo is equal to that with the mother (r_{zm}), the inclusive fitness of a randomly chosen zygotic offspring from the clutch is given by,

$$O'_f = (R - K - c)^x + (n - 1)(R - K - c)^x \cdot r_{zz} + n (K - c)^x \cdot r_{zm}. \tag{4}$$

5.1 *Conditions favouring polyembryony*

5.1a *Maternal parent:* Maternal parent would favour PE if $M'_f > M_f$. From (3) and (1), after rearranging the terms, we get

$$(K - c)^x / [(R - c)^x - (R - K - c)^x] > r_{zm}. \tag{5}$$

Note that the numerator of the LHS represents the benefit (B) or fitness accrued through each nucellar embryo and the denominator the cost (C) in terms of the loss in fitness of the zygotic embryo due to the reallocation of resources to an additional nucellar embryo (figure 1). Thus (5) shows that benefit to cost ratio (B/C) of producing a nucellar embryo should be greater than r_{zm} for maternal parent to favour polyembryony.

(i) *Maximization of B/C and limits on x and K —.* Without loss of generality, we can take c to be equal to unity. Consequently, the optimal investment, R^*, is seen to be equal to $1/(1 - x)$ (see assumption 2). The B/C expression can then be written as

$$(K - 1)^x / \{ [x/(1 - x)]^x - [(x/(1 - x)) - K]^x \}. \tag{6}$$

Further, expressing K as a fraction f of the optimal resource, $1/(1 - x)$, we get

$$B/C = [f - (1 - x)]^x / [x^x - (x - f)^x]. \tag{7}$$

Since $1 < K < [x/(1 - x)]$ (from assumption 3), we get, $(1 - x) < f < x$; these limits of f for the evolution of PE are shown in figure 2. Further it can be seen that as f increases from $1 - x$ to x, B/C first increases, and then decreases to $(2x - 1)^x / x^x$ (shown in figure 3 for $x = 0.6$).

By differentiating the expression for B/C, (7), with respect to f, we get $\hat{f}$, the value of f at which B/C is maximized as

$$\hat{f} = x - [(2x - 1)/x^x]^{[1/(1 - x)]}. \tag{8}$$

As x increases from 0.5 to 1, $\hat{f}$ increases from 0.5 to $1 - \exp(-1)$ ($\simeq 0.63$) and the B/C increases nonlinearly from 0 to 1 (figure 2). Thus B/C can NEVER exceed 1.

For polyembryony to be favoured, B/C has to be greater than r_{zm}, (5). Obviously there are some values of r_{zm} (above the B/C line; figure 2), for which even the maternal parent does not favour nucellar embryony. Since even in a randomly mating outbreeding population, $r_{zm} = 0.5$, the maternal parent favours polyembryony only for $B/C > 0.5$. Substituting values of $\hat{f}$ in (7), it is seen that B/C is greater than 0.5 only for values of $x > 0.5758$. This further limits the condition under which the maternal parent can favour PE (figure 2). Substituting this value of x in $R^* = 1/(1 - x)$, we find that PE can evolve only if $R^* > 2.358$ times c. That is, in situations where the optimum seed size (R^*) is less than $2c$, PE cannot evolve because at such low R^* levels, reallocation of resources would result in resource levels of nucellar (K) and zygotic ($R - K$) embryos being less than required for their survival (i.e., c). However though $R^* > 2c$ is necessary for PE to evolve, this is not a
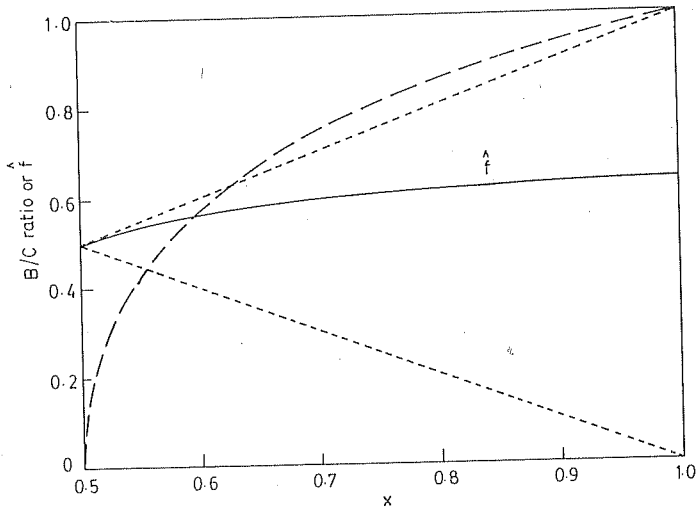
Figure 2. Optimal fractional investment $\hat{f}$ (solid line) which maximizes the benefit to cost (*B/C*) ratio, and the ratio so obtained (dashed line) as a function of *x*, the exponent of the fitness function. The two dotted lines indicate the minimum and maximum permitted values of *f*, the fractional investment in the nucellar embryo.

sufficient condition by itself; the necessary condition for PE to evolve as seen above is for R^* to be greater than 2·358 times c.

(ii) *Effect of inbreeding* – For a population with inbreeding coefficient I, the expression for r_{zm} is given by (Hamilton 1972)
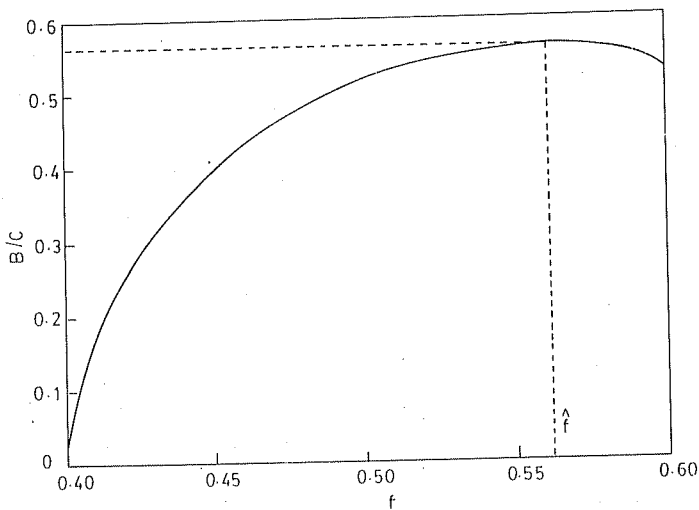
$$r_{zm} = (1 + I)/2.$$

Figure 3. The benefit to cost ratio as a function of f, the fractional investment in the nucellar embryo for $x = 0.60$. The optimal investment $\hat{f}$ is also shown in the figure.
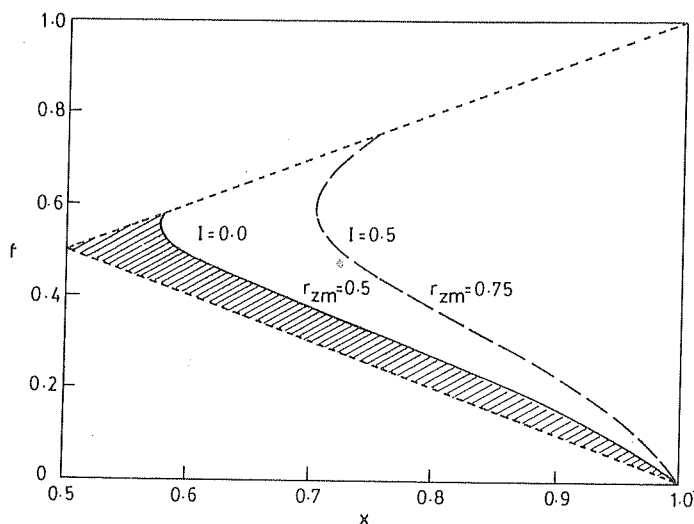
Figure 4. Regions in the $f-x$ space where polyembryony can evolve under maternal regulation. The region between the two dotted lines indicate the valid combinations of x and f. Polyembryony can evolve in the regions above and to the right of the continuous curve in a fully outbred population. For an inbreeding coefficient of 0·50, the region is above and to the right of the dashed curve. The hatched region·indicates the region where polyembryony cannot evolve.

Since r_{zm} increases with I, at higher levels of inbreeding, the B/C required for the evolution of polyembryony under maternal control would also be higher. In other words, higher levels of inbreeding make the evolution of PE more constrained. Figure 4 depicts the region in the $x-f$ space where PE can evolve for different values of I. It·is seen from the figure that, for example, for $I = 0·5$, the available region in the $x-f$ space where PE can evolve is much smaller compared to when $I = 0$.

5.1b *Offspring control*: The zygotic offspring favours polyembryony if $O'_f > O_f$, i.e., if

$$\frac{B}{C} = \frac{(K-c)^x}{(R-c)^x - (R-K-c)^x} > \frac{1+(n-1)r_{zz}}{|n \cdot r_{zm}} = \frac{r_{zz}}{r_{zm}} + \frac{1-r_{zz}}{|n \cdot r_{zm}} .$$

(9)

The left hand side of the inequality (9) is identical to that of (5), representing B/C for the mother producing a nucellar embryo.

(i) *Effect of r_{zz} and n in an outbred population* – Equation (9) shows that the condition under which the maternal parent favours polyembryony depends only on r_{zm}, while that under which offspring favours it depends additionally on r_{zz} and n. In an outbred population, $r_{zm} = 0·5$, while r_{zz} can take values· between 0·25 and 0·5 (see appendix A, also Hamilton 1972). Figure 5 shows the B/C ratio required for the offspring to favour polyembryony as a function of n, for $r_{zz} = 0·5$ and 0·25.

Clearly, the value of B/C required for the offspring to favour polyembryony
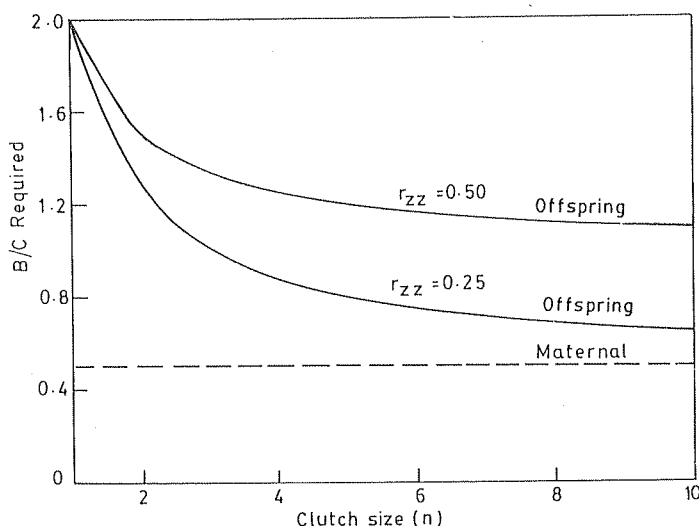
Figure 5. The benefit to cost ratio required for polyembryony to evolve under offspring regulation (solid lines) as a function of clutch size, for two different values of r_{zz}, the coefficient of relatedness between siblings. For comparison, the required ratio corresponding to maternal regulation is also shown in the figure (dashed line).

decreases with n and reaches a minimum of r_{zz}/r_{zm} as n tends to infinity. At low values of n, there are wide differences between B/C values required by the maternal parent and that by the offspring to favour nucellar embryony. At high values of n, these differences narrow down (figure 5), and in fact polyembryony can evolve in species with clutch size > 3, for sufficiently low values of r_{zz}.

(ii) *Effect of inbreeding* – The coefficient of relatedness among offspring is a function of the inbreeding coefficient, I, and the number of pollen donors, H, and is given by (see appendix A)

$$r_{zz} = (1 + 3I)/4 + (1 - I)/4H.   \tag{10}$$

Substituting for r_{zz} and r_{zm} in (9) and rearranging the terms we get as the condition to be satisfied,

$$\frac{B}{C} > \frac{3}{2} - \frac{1}{I+1} + \frac{1-I}{2(I+1)}\left[\frac{1}{H} + \frac{3}{N} - \frac{1}{NH}\right].   \tag{11}$$

Thus polyembryony, when under offspring control, is favoured by high values of H and n. On the other hand, a high level of inbreeding makes evolution of polyembryony difficult. As shown in figure 6a, even under ideal conditions ($n \to \infty$, $H \to \infty$),

$$B/C > 3/2 - 1/(1+I),$$

is the required condition; a higher value of B/C is needed for polyembryony to evolve as the degree of inbreeding increases.

Similarly, for a given value of B/C, higher levels of inbreeding make it more difficult for polyembryony to evolve; figure 6b shows that the region in $H - n$ space
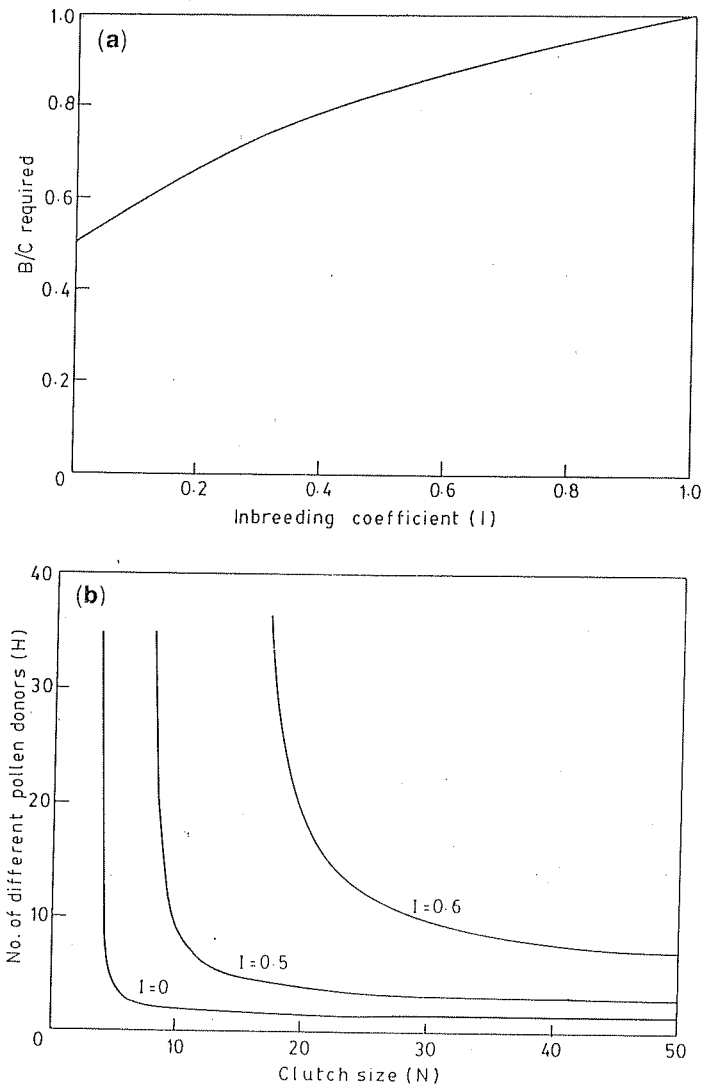
Figure 6. (a) The benefit to cost ratio required for polyembryony to evolve under offspring regulation, as a function of I, the coefficient of inbreeding. Both the clutch size and number of pollen donors are assumed to be infinite. (b) Regions favourable to the evolution of polyembryony under offspring regulation, in the parameter space of n, the clutch size and H, the number of pollen donors. Polyembryony can evolve in the regions above and to the right of the curves. The three curves correspond to three different values of the coefficient of inbreeding.

where polyembryony can evolve shrinks as the level of inbreeding increases.

From (10) it can be seen that for species with $H = 1$, r_{zz} would be equal to $(1 + I)/2$, which is equivalent to r_{zm} (Hamilton 1972). Under these conditions $r_{zz}/r_{zm} = 1$. Hence even in species with an infinite number of ovules and with a single pollen parent, polyembryony cannot evolve since the B/C required is more than 1 [see (9)]. However as H increases, r_{zz} decreases making it possible for PE to evolve.

Thus it can *be predicted that PE could evolve in species with high clutch size and with high multiple mating (where fertilization of ovules is effected by pollen from varied pollen donors). Conversely, it is less likely that PE evolves in self-pollinated species.*

5.2 *Parent offspring conflict over polyembryony*

From (11), it is clear that in species with very large clutch size and pollen donors, the benefit to cost ratio required for zygotes to favour PE is given by $B/C > (3/2) - 1/(1 + I)$.

Substituting values of x in B/C expression and of I in the RHS that meet this inequality, it is possible to estimate the maximum level of I that permits the evolution of PE under offspring control as a function of x, the power of the fitness function. This has been plotted in figure 7 along with a similar threshold of I that permits the evolution of PE under maternal parent regulation.

The maximum value of the inbreeding coefficient I for which the maternal parent favours PE is more than the corresponding value of I for offspring. Thus the evolution of PE under offspring control is more restricted than under maternal control. The region between the two curves corresponds to the combinations of x and I where polyembryony is favoured by the maternal parent, but not by the offspring: this represents the area of conflict between the parent and the offspring over polyembryony. The degree of the conflict first increases and then decreases with the power of the fitness function, x (figure 7), suggesting that *polyembryony is more likely to evolve at low and high values of x and is less likely at intermediate values of x.*

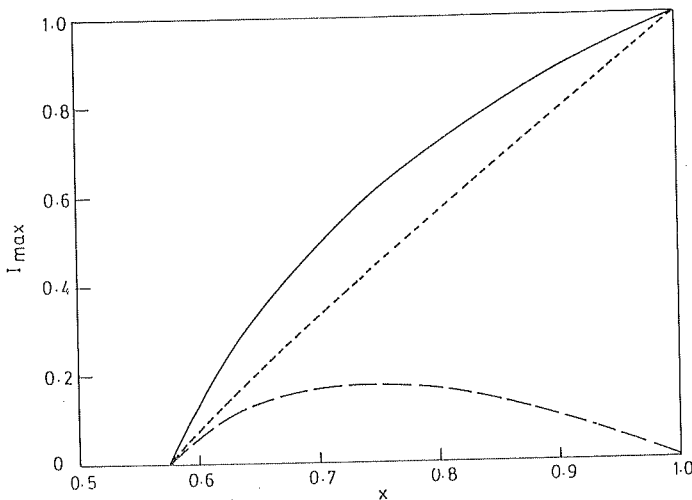Further, as shown earlier (§ 5.1b(i)), the maternal parent seems to favour nucellar

Figure 7. I_{max}, the maximum value of the inbreeding coefficient for which evolution of polyembryony is possible, as a function of x, the exponent of the fitness function. The continuous curve corresponds to maternal regulation, and the dotted line, to offspring regulation. The dashed curve indicates the difference between the two values of I_{max} corresponding to these two situations. As in figure 6a, n and H are assumed to be infinite.

embryony for relatively low values of B/C compared to the offspring (figure 5). Even at high clutch size, for low B/C values, the maternal parent favours nucellar embryony but the offspring does not (figure 5). In other words, there is a conflict of interest between the parent and offspring for the production of nucellar embryo (and hence for PE); the degree of conflict however reduces with increase in the clutch size and *hence polyembryony can be predicted to be more frequent in species with higher clutch size.*

6. Genetic models

Our interest is to obtain the conditions under which, in one-locus, 2-allele models, the allele causing the formation of the additional (nucellar) embryo can successfully invade a population which is otherwise purely sexually reproducing.

6.1 *Conditions permitting the spread of the allele*

Let the purely sexually reproducing genotype be denoted by NN. Let the fitness of these individuals be U. The allele for polyembryony, P, leads to a reallocation of K amount of resources from the sexual zygote to the differentiation and development of the nucellar embryo. Let the fitness values of the nucellar and the sexual embryos developing in the same seed be W and V respectively.

We consider three different scenarios pertaining to the induction of an additional nucellar embryo.

6.1a *Maternal parent regulation*: The allele P induces the nucellar tissue to differentiate into embryos if it is present in the maternal tissue, irrespective of the genetic constitution of the zygote and the endosperm. This is akin to the maternal parent regulating the formation of nucellar embryo and hence the scenario is similar to that of the inclusive fitness model where the maternal parent favours the formation of additional embryos. Under this model, the condition under which the allele P, whether dominant or recessive, is able to successfully invade a population where N has gone to fixation is given by (see appendix B1)

$$W > (U - V)/2. \tag{12}$$

On the other hand, the condition under which the allele N, whether dominant or recessive, invades a population where P has gone to fixation is given by (appendix B1)

$$W < (U - V)/2. \tag{13}$$

Thus, regardless of whether polyembryony is controlled by dominant or recessive alleles, for $W > (U - V)/2$, i.e. when the fitness of the nucellar embryo is greater than half the difference between the fitnesses of the zygotic embryos without and with polyembryony, the polyembryonic allele goes to fixation, otherwise the non-polyembryonic allele goes to fixation.

6.1b *Endosperm regulation*: In this situation, the allele P induces an additional nucellar embryo only if it is present in the endosperm. Since the zygote also shares

all the alleles of the endosperm, such a regulation is indistinguishable from that of zygotic regulation of nucellar embryony in its consequences. We however call this "endosperm regulation" because this tissue is supposed to play a mediatory role between the maternal parent and the zygote over the development of, and resource allocation to, the embryos (Westoby and Rice 1982; Queller 1983, 1989; Uma Shaanker *et al.* 1988; Haig and Westoby 1989).

Such an allele spreads if (see appendix B2)

$$W > 2(U - V), \text{ when it is dominant,} \tag{14}$$

and

$$W > U - V, \text{ when it is recessive,} \tag{15}$$

6.1c *Selfish endosperm regulation*: This is similar to the model in §6.1b except that the allele acts selfishly; the allele P in the endosperm favours the formation of a nucellar embryo only if the same allele is also present in the maternal tissue. The consequences are akin to that of interaction between maternal parent and offspring genomes. Whether recessive or dominant, the allele spreads if (see appendix B3),

$$W > U - V, \tag{15}$$

Assuming the fitness of the sexual embryo, U, to be equal to unity, and expressing the other two fitnesses relative to the fitness of the sexual embryo, we have plotted W, the fitness of the nucellar embryo required for the spread of the allele P, as a function of V, the fitness of the zygotic embryo developing with nucellar embryo (figure 8). Clearly, the fitness of the nucellar embryo required for the maternal parent to favour it is always less than that for the endosperm or selfish
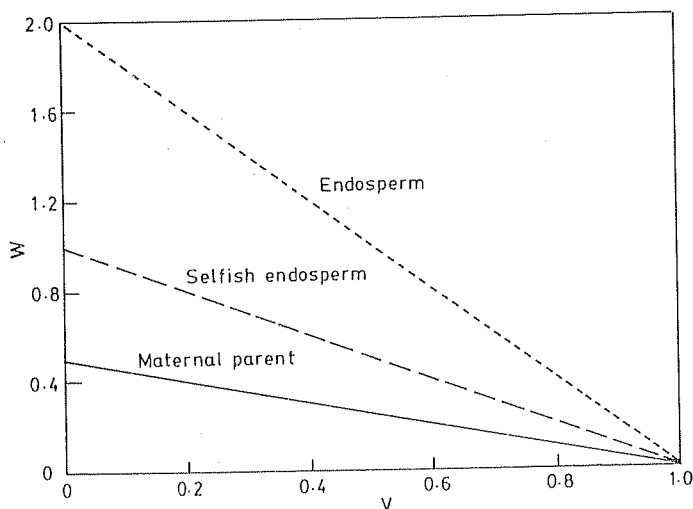

Figure 8. Regions in the parameter space of W, the fitness of the nucellar embryo and V, the fitness of the corresponding zygotic embryo, which permit the spread of the polyembryonic allele. The fitness of the nonpolyembryonic allele is assumed to be unity. Polyembryony can evolve (i) under maternal regulation, in the region above the continuous line, (ii) under selfish endosperm regulation, above the dashed line and (iii) under endosperm regulation, in the region above the dotted line.

endosperm. In other words, the maternal parent is likely to favour PE more frequently than the endosperm or the zygote and indeed it is unlikely that polyembryony will evolve under the regulation of the offspring or the selfish endosperm (also see below).

6.2 *Limits of x and K permitting the spread of the allele*

6.2a *A comparison between genetic and inclusive fitness models*: Following the assumptions listed earlier (see §4) and expressing the fitness of embryos as in the inclusive fitness model (§5·1a,(6)), we write

$$U = [x/(1-x)]^x, \tag{16}$$

$$V = \{ [x/(1-x)] - K \}^x \tag{17}$$

and

$$W = (K-1)^x. \tag{18}$$

Substituting these in (12) to (15) and rearranging, we get the conditions that permit the invasion and spread of P in a population of N, as shown in table 2.

It can be seen that the expression for B/C for the formation of the nucellar embryo is identical to that obtained under the inclusive fitness model. Hence the region in the $x - K$ space permitting the evolution of polyembryony under the genetic model is the same as that obtained under the inclusive fitness model. Further, the conditions permitting the spread of P through maternal regulation (model a) is a special case of the inclusive fitness model, (5), where $r_{zm} = 0·5$. It is clear that nucellar embryony is favoured for $B/C > 0·5$ when it is under maternal regulation and $> 1·0$ when it is under selfish endosperm regulation (table 2). Thus the maternal parent favours nucellar embryony for lower values of B/C than even the selfish endosperm. However, the maximum value the LHS (B/C) can take is less than 1 (figure 2). Hence only the alleles that regulate nucellar embryony through maternal parent can invade the sexually reproducing population while those regulating it through even a selfish endosperm (or zygote) cannot. Thus both the inclusive fitness models and the genetic models *predict that PE can evolve only if it is under the genetic regulation of the maternal parent and not if under offspring or endosperm regulation.*

Table 2. Conditions for the spread of the polyembryonic allele. A polyembryonic allele will successfully invade a nonpolyembryonic population if its B/C ratio is greater than the value given in the table for an appropriate situation (i.e., combination of regulation control and whether dominant or recessive).

Regulation by	Condition ($B/C >$)*	
	Dominant	Recessive
1. Maternal parent	0·5	0·5
2. Offspring	2·0	1·0
3. Selfish endosperm	1·0	1·0

$$* \quad B/C = \frac{(K-1)^x}{[x/(1-x)]^x - \{ [x/(1-x)] - K \}^x}$$

6.3 *Altered resource allocation to embryos under evolutionarily stable strategy*

In § 5.1 we showed that B/C can be maximized by investing $K = \hat{f} \cdot R^*$ amount of resources into the nucellar embryo. An allele which corresponds to such an allocation goes to fixation when it invades a non-polyembryonic allele. On the other hand, this allele itself can be successfully replaced by another allele which corresponds to an investment which maximizes the fitness (in contrast to maximizing B/C).

Under the condition where maternal parent favours polyembryony (i.e., where $W > (U - V)/2$), it can be shown that the allele with an investment of

$$K^* = \{ [x/(1-x)] + 2^{[1/(x-1)]} \} / \{ 1 + 2^{[1/(x-1)]} \}$$

in the nucellar embryo is uninvadable by any other allele (i.e. an allele with any alternative amount of investment). In other words K^* represents an evolutionarily stable strategy (ESS).

Further if f^* denotes the fraction of R^* invested in the nucellar embryo, (i.e. $K^* = f^* \cdot R^*$), we get

$$f^* = \{ x + 2^{[1/(x-1)]} (1-x) \} / \{ 1 + 2^{[1/(x-1)]} \}.$$

As seen from figure 9, the evolutionarily stable allele always invests more resources into the nucellar embryo than the B/C maximizer. However, in a dynamically competing population of three alleles, where a population of the non-polyembryonic allele is invaded by both B/C maximizer and fitness maximizer, it is always the frequency of B/C maximizer that increases rapidly (as seen from the deterministic simulations which we have carried out). Nevertheless, once the frequency of the non-polyembryonic allele reduces and when the B/C maximizer and the fitness maximizer are the main competing alleles, the latter always wins. In
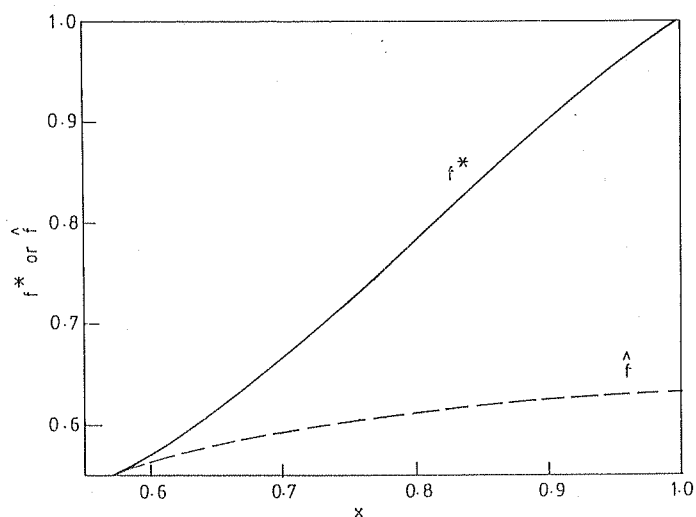

Figure 9. The evolutionarily stable investment in the nucellar embryo, f^*, as a function of x, the exponent of the fitness function (solid line). For comparison, $\hat{f}$, the fractional investment in the nucellar embryo that maximizes the B/C ratio is also given (dashed line).

the absence of a *B/C* maximizer, the spread of the fitness maximizer against the non-polyembryonic allele is relatively slow.

7. Polyembryony as a maternal counter strategy against brood reduction

Our models show that the maternal parent is more likely to favour PE than even a selfish offspring; hence there is a conflict between the maternal parent and the offspring over the production of additional embryos.

   This conclusion that for low *B/C*, the mother favours production of additional embryos is in conformity with the conditions under which the maternal parent and offspring favour brood reduction (O'Connor 1978; Uma Shaanker *et al.* 1988). It is shown that for relatively small benefits, the offspring favour brood reduction while the mother does not. Similarly, for low benefits, mother favours polyembryony while the offspring do not. Thus in both these situations, there is an active conflict between the mother and the offspring over the number of offspring. While brood reduction decreases maternal fitness, polyembryony increases it through additional embryos. We hence suggest that polyembryony can serve as a counter-strategy by the mother against brood reduction driven by sibling rivalry. Brood reduction at early stages of offspring development saves the maternal parent considerable amounts of resources. By investing such saved resources in the nucellar embryos along with the surviving sexual embryo, the maternal parent can make good her fitness loss due to brood reduction. Some of the hitherto unrealized associations between PE and reproductive features support this view.

   Most species of *Citrus* exhibit polyembryony (Frost 1926; Tisserat *et al.* 1979; Uma Devi 1983). They produce a very large number of ovules, of which invariably only a few develop to maturity. Hence, the number of seeds set in a fruit provides an inverse index of the extent of brood reduction. If polyembryony is a maternal counter strategy to overcome the loss in her fitness due to brood reduction, then one can predict that the average number of polyembryos per seed should be negatively related to the seed number per fruit (i.e., a smaller number of seeds implies a higher level of brood reduction; which should be countered by a higher extent of polyembryony, obtained by producing more nucellar embryos). Analysing the data from 27 cultivars of 8 species of *Citrus* (Uma Devi 1983), we found that the number of polyembryos per seed was indeed negatively correlated with the number of seeds per fruit (figure 10; $N = 27$, $r = -0.45$, $P < 0.025$; one-tailed test). While the statistical significance is somewhat sensitive to the presence of outliers, the data is suggestive of the correlation predicted by us.

   Uma Shaanker *et al.* (1988) have argued and demonstrated that brood reduction driven by sibling rivalry is intense in species where the indehiscent fruits are dispersed as a single unit through wind, water or animals compared to those where seeds are the unit of dispersal. Hence our assertion that polyembryony is a maternal counter strategy demands that it be more prevalent in species where entire fruits or parts thereof are dispersed through wind, water or animals. This is borne out in the data provided in tables 3a & b. Species with PE have fruits as units of dispersal and are dispersed by animals significantly more frequently than expected on the basis of their respective distributions in angiosperms (tables 3a & b). Of the 170 species that exhibit PE, 74% had fruits as the unit of dispersal and 26% seeds (table 3a). Among the different modes of dispersal, 28·8% and 45·3% of the species that exhibited PE
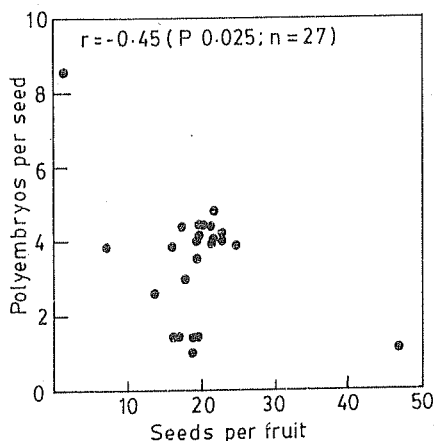
Figure 10. Relationship between the number of polyembryos per seed and number of seeds per fruit in *Citrus* (data from Uma Devi 1983).

were dispersed through wind and animals respectively, while only 25·9% showed explosive or passive dispersal of seeds (table 3b).

Thus our assertion that polyembryony is a maternal counter strategy to make

Table 3a. Association between polyembryony and the unit of dispersal*.

Unit of dispersal:	Seed	Fruit
Observed frequency:	44	126
	(25·9)	(74·1)
Expected frequency:	96	74
	(56·5)	(43·5)

$N = 170$ species; $X^2 = 64·7$; $P < 0·001$
*Expected frequencies obtained from Uma Shaanker *et al.* (1990). Values in parentheses refer to percentages. [Data from Venkatesh and Sharma (1974), Adarsh Kumar *et al.* (1977a,b), Dabral (1977), Tisserat *et al.* (1979), Adarsh Kumar and Gupta (1987), Uma Singh and Adarsh Kumar (1990), Adarsh Kumar *et al.* (1991).].

Table 3b. Association between polyembryony and the various dispersal modes*.

Dispersal mode:	Wind	Animal	Explosive	Total
Observed frequency:	49	77	44	170
	(28·8)	(45·3)	(25·9)	
Expected frequency:	59	30	81	
	(34·7)	(17·6)	(47·6)	

$N = 170$ species; $X^2 = 92·2$, $P < 0·001$
*Expected frequencies were obtained from Uma Shaanker *et al.* 1990. Values in parentheses refer to percentages.
(Data from Venkatesh and Sharma (1974), Adarsh Kumar *et al.* (1977a,b), Dabral (1977), Tisserat *et al.* (1979), Adarsh Kumar and Gupta (1987), Uma Singh and Adarsh Kumar (1990), Adarsh Kumar *et al.* (1991).

good her loss in fitness due to brood reduction is supported by the evidence presented above.

Appendix A. Coefficient of relatedness between zygotes when the pollen can arrive from any of H different plants, and when the coefficient of inbreeding is I.

Consider a randomly picked allele in an individual.

(i) The probability that it is inherited from the mother $= \frac{1}{2}$, and the probability that the same allele was passed on from the mother into the other offspring $= \frac{1}{2}$. On the other hand, the probability that the second offspring has the other allele $= \frac{1}{2}$; and the probability that the two alleles are identical by descent $= I$. Thus, the probability of the alleles being identical by descent through the maternal parent

$$= \frac{1}{2}(\frac{1}{2} \cdot 1 + \frac{1}{2} \cdot I) = (1 + I)/4. \tag{A1}$$

(ii) The probability that the allele is from the father $= \frac{1}{2}$.

(a) The probability that the two zygotes derive pollen from the same plant $= 1/H$. The probability that the same allele is passed on to the other offspring $= \frac{1}{2}$. The probability that the other allele is passed on is $\frac{1}{2}$, and the probability that the two are identical by descent $= I$.

(b) However, the two zygotes may be derived from pollen from different plants, an event which occurs with probability $(H-1)/H$. These two alleles may nevertheless be identical by descent, and the probability of this is I.

Thus, the probability of identity by descent through the paternal parent

$$= \frac{1}{2}\left[\frac{1}{H}\left[\frac{1}{2} + \frac{I}{2} \right] + \frac{H-1}{H} \cdot I \right]. \tag{A2}$$

The coefficient of relatedness, obtained by summing (A1) and (A2) equals $\frac{1+I}{4} + \frac{1+I}{4H} + \frac{I}{2} - \frac{I}{2H}$, which simplifies to $\frac{1+3I}{4} + \frac{1-I}{4H}$

Appendix B. Population genetic models for the evolution of polyembryony

We consider an infinite, panmictic random mating population with non-overlapping generations. Let P and N denote alleles which code for polyembryony and for non-polyembryony respectively. Let n, y and z denote the frequencies of NN, NP and PP genotypes. Let U be the fitness of the zygotic embryos produced by a nonpolyembryonic phenotype. The polyembryonic phenotype is assumed to produce zygotic embryos with fitness V and nucellar embryos with fitness W.

We consider a pure population of one allele, subjected to invasion by the other. The success or otherwise of the invasion is investigated in most cases by linearized stability analysis.

B.1 *Maternal regulation*

B.1a *Nonpolyembryonic population (N) invaded by a dominant polyembryonic allele (P)*

Let y, $z(\simeq 0)$ be the frequencies of NP and PP respectively.

The frequency of P is then $(y/2) + z$.

Table B1 illustrates the contribution, in terms of fitness, to the next generation from the various matings, involving the P allele, whose frequencies are nonzero to first order.

Table B1. Contributions to the next generation when N is invaded by dominant P (maternal regulation).

Maternal genotype	Pollen	Mating frequency	Whether poly-embryony	Contribution to		
				NN	NP	PP
NN	P	$(y/2) + z$	No	—	U	—
NP	N	y	Yes	$V/2$	$W + (V/2)$	—
PP	N	z	Yes	—	V	W

The frequency of $NN \cdot N$ matings will be equal to $1 - 2z - 3y/2$ and these will produce NN genotypes with fitness U. For the next generation, we thus obtain, using the above table,

$$\text{genotype } NN = U \cdot (1 - 2z - 3y/2) + V/2 \cdot y,$$

$$\text{genotype } NP = U \cdot (y/2 + z) + (W + V/2) \cdot y + V \cdot z,$$

$$\text{genotype } PP = W \cdot z.$$

To obtain say the frequency of PP in the next generation, we divide $W \cdot z$ by the sum of contributions from the three genotypes as shown above. The sum is seen to be equal to $U +$ terms involving y and z. When $W \cdot z$ is divided by ($U +$ terms with y and z), by retaining terms only upto the first order, we get $W \cdot z/U$ as the frequency of PP in the next generation. More generally, if y' and z' denote the frequencies of NP and PP in the next generation, it can be shown that

$$\begin{bmatrix} y' \\ z' \end{bmatrix} = \begin{bmatrix} (U + V + 2W)/2U & (U + V)/U \\ 0 & W/U \end{bmatrix} \begin{bmatrix} y \\ z \end{bmatrix}.$$

The dominant eigenvalue of the matrix is $(U + V + 2W)/2U$, which should be greater than unity if the allele P is to successfully invade the population of N. The condition for the spread of P is thus $(U + V + 2W)/2U > 1$ or $W > (U - V)/2$.

B.1b *Nonpolyembryonic population (N) invaded by a recessive P allele*

Table B2 gives the contributions to the next generation from matings involving the P allele, to first order.

Table B2: Contributions to the next generation when N is invaded by recessive P (maternal regulation)

Maternal genotype	Pollen	Mating frequency	Whether poly-embryony	Contribution to		
				NN	NP	PP
NN	P	$(y/2)+z$	No	—	U	—
NP	N	y	No	$U/2$	$U/2$	—
PP	N	z	Yes	—	V	W

We obtain

$$\begin{bmatrix} y' \\ z' \end{bmatrix} = \begin{bmatrix} 1 & 1+(V/U) \\ 0 & W/U \end{bmatrix} \begin{bmatrix} y \\ z \end{bmatrix}.$$

The dominant eigenvalue is unity, indicating neutral stability. However, the frequency of the P allele in the next generation $=(y'/2)+z'$

$$= [y+z+(V\cdot z/U)]\cdot(1/2)+(W\cdot z/U)$$

$$= (y/2)+z\cdot[(1/2)+(V/2U)+(W/U)]$$

$$= \frac{y}{2} + z + z\cdot[(V/2U)+(W/U)-(1/2)].$$

This is greater than the frequency in the previous generation if the quantity in the brackets is greater than zero, i.e.

$$(V/2U)+(W/U)>(1/2) \text{ or } W>(U-V)/2,$$

which is the condition for a successful invasion by P, and is the same as obtained for the dominant allele.

B.1c *Polyembryonic (P) population invaded by a dominant nonpolyembryonic allele (N)*

Let $y\ (\simeq 0)$ be the frequency of the NP genotype. Since N is nonpolyembryonic, NN homozygotes would be generated only by $NN\cdot N$ and $NP\cdot N$ matings, and the frequencies of these are zero to first order, so N would exist only in NP heterozygotes.

Table B3 indicates contributions to the next generation from matings involving N.

Table B3. Contributtions to the next generation when P is invaded by dominant N (maternal regulation).

Maternal genotype	Pollen	Mating frequency	Whether poly-embryony	Contribution to		
				NN	NP	PP
PP	N	$y/2$	Yes	—	V	W
NP	P	y	No	—	$U/2$	$U/2$

The frequency of NP in the next generation, y' is obtained as

$$y' = [1/(V+W)][(V/2)+(U/2)] \, y,$$

Hence, $y' > y$ if $(U+V)/[2(V+W)] > 1,$

i.e. if $(U-V)/2 > W,$

which is the condition for a successful·invasion by N.

B.1d *Polyembryonic (P) population invaded by a recessive nonpolyembryonic (N) allele*

Linearized stability analysis to first order, carried out in a same manner as before, indicates neutral stability, since, to first order, N exists only in NP heterozygotes. To second order, nonzero mating frequencies are possible for $NP \cdot N$ and $NN \cdot P$ matings. Only the latter exhibits nonpolyembryony, and produces embryos of genotype NP and fitness U. Had it exhibited polyembryony, it would have produced NP embryos with fitness V, and NN embryos with fitness W. The difference in the frequency of N alleles produced under these two scenarios is

$$(U/2) - [W+(V/2)].$$

For a successful invasion, this has to be positive, i.e.

$$(U/2) - [W+(V/2)] > 0 \text{ or } (U-V)/2 > W.$$

This condition is the same as the one obtained for a successful invasion by a dominant N allele.

In summary, polyembryony under maternal control will go to fixation if $W > (U-V)/2$, whereas nonpolyembryony will go to fixation otherwise. There can be no stable polymorphism.

B.2 *Endosperm regulation*

Under this scenario, whether a nucellar embryo is produced or not depends on the genotype of the zygote, and not on the genotype of the maternal parent

B.2a *Nonpolyembryonic population (N) invaded by a dominant P allele*

Table B4 depicts the genotype contributions to the next generation involving the P allele, using the same notation as used earlier.

Table B4. Contributions to the next generation when N is invaded by dominant P (endosperm regulation).

Maternal genotype	Pollen	Mating frequency	Whether poly-embryony	Contribution to		
				NN	NP	PP
NN	P	$(y/2)+z$	Yes	W	V	—
NP	N	y	Yes (in half the cases)	$U/2$	$V/2 + W/2$	—
PP	N	z	Yes	—	V	W

For the next generation, we get

$$\begin{bmatrix} [V+(W/2)]/U & 2V/U \\ 0 & W/U \end{bmatrix}\begin{bmatrix} y \\ z \end{bmatrix}.$$

The dominant eigenvalue is $(V+W/2)/U$. For this to be greater than unity, we need $W > 2(U-V)$. A less stringent condition is obtained for a recessive allele (details not shown). It is seen that a recessive allele can invade the population if $W > U - V$.

To recapitulate, U represents the fitness of the zygote (embryo) produced by a nonpolyembryonic phenotype. By the assumptions of the model, this is an optimal allocation of resources PER SEED. Now, V and W stand for the fitnesses of the zygotic and nucellar embryos from the same seed produced in a polyembryonic phenotype. By the definition of optimality, the sum of these two fitnesses cannot exceed the fitness of a nonpolyembryonic zygote, i.e. $V + W < U$. Hence the above condition can never be satisfied, and the polyembryony promoting allele cannot evolve under endosperm regulation.

B.2b　*Polyembryonic population (P) invaded by a dominant nonpolyembryonic (N) allele*

Table B5 illustrates the contributions to the next generation under this scenario.

Table B5. Contributions to the next generation when P is invaded by dominant N (endosperm regulation).

Maternal genotype	Pollen	Mating frequency	Whether poly-embryony	Contribution to		
				NN	*NP*	*PP*
PP	*N*	$y/2$	No	—	U	—
NP	*P*	y	Yes (in half the cases)	—	$U/2 + W/2$	$V/2$

$$y' = [1/(V+W)][U+(W/2)]y.$$

The allele will spread in a population if

$$[U+(W/2)]/(V+W) > 1, \text{ i.e., } U+(W/2) > V+W.$$

Since $U > V + W$, this condition is always satisfied, and a nonpolyembryonic allele can always invade the population.

In summary, evolution of dominant polyembryony under endosperm regulation is unlikely.

B.3　*Selfish endosperm regulation*

In this scenario, too, polyembryony is under endosperm control. However, a nucellar embryo is formed only if the endosperm and the maternal parent both have the P allele.

B.3a　*Nonpolyembryonic population (N) invaded by a dominant P allele.*

Table B6 indicates the contributions to the next generation.

Table B6. Contributions to the next generation when N is invaded by dominant P (selfish endosperm regulation).

Maternal genotype	Pollen	Mating frequency	Whether poly-embryony	Contribution to		
				NN	NP	PP
NN	P	$(y/2)+z$	No	—	U	—
NP	N	y	Yes (in half the cases)	$U/2$	$V/2+W/2$	—
PP	N	z	Yes	—	V	W

This leads to

$$\begin{bmatrix} y' \\ z' \end{bmatrix} = \begin{bmatrix} (U+V+W)/2U & (U+V)/U \\ 0 & W/U \end{bmatrix} \begin{bmatrix} y \\ z \end{bmatrix}.$$

The dominant eigenvalue is $(U+V+W)/2U$, and the condition for invasion is $U+V+W > 2U$ or $V+W > U$ which is not possible under the present model (as explained in B2a).

A similar result is obtained (details not shown) when the invading allele is recessive.

B.3b *Polyembryonic population (P) invaded by a dominant N allele*

Table B7 indicates the contributions to the next generation for the N allele. To first order, only NP will be non-zero.

Table B7. Contributions to the next generation when P is invaded by dominant N (selfish endosperm regulation).

Maternal genotype	Pollen	Mating frequency	Whether poly-embryony	Contribution to		
				NN	NP	PP
PP	N	$y/2$	No	—	U	—
NP	N	y	Yes (in half the cases)	—	$U/2+W/2$	$V/2$

Frequency of NP genotype in the next generation is

$$y' = [1/(V+W)] [U+(W/2)] y,$$

For the allele to invade,

$$U+(W/2) > V+W,$$

which is always satisfied, and the N allele would always be able to invade the polyembryonic population.

In summary, polyembryony cannot evolve even under the selfish endosperm regulation model.

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