Frequency distribution of seed number per fruit in plants: A consequence of the self-organizing process?

K. N. Ganeshaiah and R. Uma Shaanker*

Departments of Plant Genetics and Breeding and *Crop Physiology, University of Agricultural Sciences, GKVK Campus, Bangalore 560 065, India

Plants exhibit wide variation in the frequency distribution of seed number per fruit. These distributions have been explained on the basis of proximate factors such as limitation of pollen and resource, lethal alleles, and developmental abnormalities. However, such explanations are inadequate and are not parsimonious in explaining the wide range of distributions of seed number per fruit. In this paper we propose an alternative model, based on the process of self-organization, involving simple rules of resource flow into ovules. We show that the wide range of observed frequency distributions of seed number per fruit can be generated as a function of resource-drawing ability of ovules, which interact stochastically during their development.

PLANTS exhibit species-specific patterns of frequency distribution of seed number per fruit ranging from highly positively skewed (where the majority of fruits have few seeds) to normal to negatively skewed (where the majority of fruits have many seeds)[1-7]. These patterns have been shown to be a consequence of specific rates of seed abortion, and are argued to be adaptive[1]. For instance, species with fruits as the units of dispersal through wind, water or animals show a high rate of seed abortion (hence positively skewed distribution) in order to increase dispersal efficiency of fruit. On the other hand, those in which seeds themselves are the units of dispersal show a low rate of seed abortion (hence negatively skewed distribution)[1,2,7].

The species-specific rates of seed abortion have been explained on the basis of several factors such as resource[8] and pollen limitation[9-12], predators[13,14], developmental abnormalities and lethal alleles[15,16]. These explanations, however, are either true for only specific instances or have been proved inadequate[1,17]. For instance, seed abortion is often species-specific, and nonrandom with respect to the position of the aborted ovule in the ovary[1,6,17,18]. Manipulation of pollen or resource level were shown to be ineffective in altering the species-specific rates of abortion and the position of the ovule aborted[1]. Further, the above factors also cannot explain the association between dispersal mode and seed abortion[1].

In other words, these proximate factors cannot parsimoniously explain the wide range of seed abortion and hence the distribution patterns of seeds per fruit. In this paper we propose the process of self-organization as an alternative model that involves simple intrinsic rules regulating the flow of resource into ovules. We simulate the process of fruit development as a self-

organizing mechanism involving stochastic interactions among the developing ovules in drawing resource from the maternal parent, and demonstrate that such a process can generate the entire range of seed-distribution patterns in plants. We show that data from field and those from manipulative experiments support the major conclusions of the simulation, suggesting that fruit development follows a self-organizing process.

Self-organization

Self-organization has been used to explain several physical and chemical systems, such as the laminar flow of water and cyclic reactions[19]. The process basically involves certain elements and rules intrinsic to the system. The elements of the system interact stochastically on the basis of local rules, and the consequences of this interaction are fed back into the system. Though the system is symmetric to begin with, such an 'autocatalytic' process eventually breaks the initial symmetry and generates order in it[19-21].

The process has also been extended to explain a few biological phenomena, such as formation of skin patterns in animals[22,23] and construction of termite mounds[24]. Recently, several examples of apparently complex and collective behaviour in social insects have been shown to be the consequence of a self-organizing process involving stochastic interaction among independent behaviours of individual members of the colony[25,26]. For instance, it was shown that the spatial distribution of honey, pollen and brood in a honeycomb[27,28], finding the shortest path to food source in trail-forming ants[29], temporal and spatial fidelity of foraging ants[30], synchronous periodicity of foragers in some species[31], and forager recruitment in proportion to the nutritional requirement of the colony[32] can all be explained by recourse to the process of self-organization.

Rationale of the approach

One important feature of the self-organization process is breakdown of symmetry in the system due to an 'autocatalytic' feedback mechanism[19,33]. We extend this feature to the generation of varying levels of asymmetry in the development of the otherwise identical ovules in a fruit. We do this by assuming that the sink drawing ability[34] (SDA) of an ovule is nonlinearly related to the resource accumulated in it. This 'autocatalytic' process of accumulation of resource in the ovules generates differences in the total resource accumulated among the seeds; the extent of difference among the seeds is a function of the degree of nonlinear relation between the resource level and the SDA of the ovule. In other words, starting from n identical ovules in an ovary, the process of self-organization, as modelled here, is

capable of generating fruits with different numbers (1 to n) of surviving seeds. Accordingly, the emerging pattern in the frequency distribution of seed number per fruit would range from a positively skewed distribution (high SDA) to a negatively skewed one (low SDA).

The model, assumptions and conditions

A. Initial state of the ovules

1. We consider an ovary with n identical ovules, each with R units of resource. R represents the amount of resource already provided to the haploid ovule before it is fertilized. Though plants exhibit wide variation in their pre-fertilization ovule weight, it generally constitutes a very small fraction (less than a tenth) of the final seed weight R_f. For the simulation we considered values of R from 1/25th to 1/6th of R_f.
2. We assume that the ovules are equidistant from the resource supply point and that there is no bias among them in either their sequence of fertilization or in getting resource from the parent.

B. Patterns of resource flow into ovules

The maternal parent is assumed to be non-discriminative and passive in providing resource to the developing ovules; it offers a certain known amount of resource r at each instance (hereafter referred to as 'bout'). The amount r expressed as a fraction of R_f would be very low. Hence, in the simulation, we considered values of r from 1/1000th to 1/25th of R_f. However, at each instance, only r or a fraction of it flows to only one among the n ovules according to the conditions defined below.

Accumulation of the r unit of resource at each bout results in a linear increase in seed weight. However, in reality, the accumulation of resource in an ovule follows a hyperbolic or sigmoidal curve[35,36]. Hence we carried out the simulation in the following two, alternative ways:

(i) The incremental resource flowed to ovules at each bout is r

(ii) The incremental resource flowed into the ith ovule at time t is

$$d\,Y(i,t) = \left[\frac{R_f - Y(i, t-1)}{R_f}\right] r \qquad 1$$

The ovule that gets resource is chosen based on the probability defined in equation 2 (see below). The fraction of r not flowed $[r - d\,Y(i,t)]$ into the ovules is left behind with the maternal parent. Clearly, owing to this condition, the pattern of accumulation of resource in the ovule would be an asymptote. The results of the

simulation following both conditions were similar except for the rapidity with which asymmetry was built up among the ovules. Indeed, at very high values of r, which are not representative of the real situation, condition (i) resulted in asymmetry building up too rapidly to be realistic. We therefore consider here only the results of the simulation following condition (ii), because this condition results in a realistic pattern of growth of seeds, such as that observed in the natural situation[35,36].

At each bout only one ovule gets resource, and the probability, $P(i)$, that the ith ovule gets resource at any bout is given by the following equation adapted from the Polya urn equation[19,25].

$$P(i) = \frac{[Y(i) + R]^x}{\sum_{i=1}^{n} [Y(i) + R]^x}, \qquad 2$$

where $Y(i)$ is the resource level of the ith ovule, and x is an index of the resource-mobilizing ability (or SDA) of the ovules. Note that (i) the power x is constant for all the ovules throughout the process of fruit development and (ii) to begin with, since $Y(i) = 0$, all ovules have equal probability of getting resource. However, once an ovule gets r unit of resource, the probability of its getting resource in the next bout increases by the proportion defined by equation 1. In other words, it 'autocatalytically' alters the probability of ovules getting resource. Hence we computed the probability that an ith ovule gets resource for each bout; the ovule that gets it was stochastically (randomly) chosen on the basis of its probability of getting resource.

Clearly, at $x = 0$, any amount of accumulation of resource in an ovule does not increase its probability of getting further resource; with increase in x, asymmetry among the ovules increases. *Note that this asymmetry is built up not because of basic differences among the ovules, rather it is built up because of the process of self-organization.*

C. Termination of development of seed and fruit

1. A seed was considered completely developed if $Y(i,t) > 0.95 R_f$. This is because, if the resource flowed into the ovule is greater than 95 per cent of the maximum weight, the shoulder of the asymptote is reached and further flow of resource into the seed will be very slow. In other words, the seed has almost attained maturity at this stage. Though this is an arbitrary condition, lowering it to $0.80 R_f$ did not affect the results of the simulation.

2. The fruit was considered to be completely developed if one of the following two conditions were met:
Condition (i). All the ovules are completely mature ($Y(i) > 0.95 R_f$)
Condition (ii). Generally, in a fruit containing mature

seeds, if there are other seeds weighing less than half the mature seed, they seldom develop further because resource flow ceases thereafter. Hence we considered a fruit to have developed when one of the ovules (ith ovule) matured (i.e. $Y(i) > 0.95 R_f$) and had garnered most of the total resource $Y_t \left[Y_t = \sum_{i=1}^{n} Y(i,t) \right]$ flowed into the fruit. We tested this by introducing an arbitrary condition: if $Y(i,t) > (0.5 + 0.5/n) Y_t$. The ith ovule was considered dominant over the other, $n - 1$ ovules; this is because all the other ovules sharing the rest of the resource ($Y_t - Y(i,t)$) flowed into the fruit are less likely to mature by the time the dominant ovule attains maturity.

Accordingly, if a mature ovule in a two-seeded fruit has garnered more than 75 per cent of the total resource flowed (Y_t), the other ovule, with less than 25 per cent of the resource, has very little probability of survival because of the dominance of the mature ovule.

Simulation

A program incorporating the above assumptions and conditions was run, with sufficient number of iterations to allow the seeds to 'form' in a fruit; though the number of iterations required varied with chosen values of r and R, generally 1000 iterations were found to be more than adequate in all our simulations. At each iteration, developing seeds were checked for the two conditions defined in the previous section (C1 and C2) in that order. Iteration was stopped when a fruit had formed according to these conditions. The process was simulated 500 times each for various values of x and R with $n = 5$ and $n = 10$; R_f was considered as 1 and R and r as fractions of it; the mean, variance, coefficient of variation (CV) and frequency distribution of seeds per fruit were generated for these values of x and R. Five hundred simulations were found adequate as there was no change in the pattern of results obtained by further increasing the number of simulations. Though, during a simulation, we specified that a seed was mature only if it had reached resource level greater than $0.95 R_f$, while counting the developed seeds at the end of each simulation, we relaxed this condition. We counted all those seeds with $Y(i) > 0.75 R_f$ (as an arbitrary level) as developed. This is because, since iteration is stopped when the dominant ovule has garnered $> 0.95 R_f$, we presume that by the time it accumulates the maximum resource (R_f), the other ovule(s) with $0.75 R_f$ would also develop to maturity ($0.95 R_f$). This might be true because the rate of accumulation of resource into developing seeds with $> 0.95 R_f$ is slow compared to that in seeds with $> 0.75 R_f$. Setting this new arbitrary condition while counting developed seeds did not change the results substantially.

For a given value of r the results of the model were

highly sensitive to x and less so to R. Varying the ovule number n did not change the results, especially with respect to the patterns observed. We therefore discuss the observed patterns with respect to only n = 5.

Build-up of asymmetry

With increase in x, ovules exhibited increased asymmetry in their development; at x = 0 all the ovules of a fruit developed to maturity, while at high levels of x a few ovules dominated and garnered most of the resource. At extremely high x values invariably only one of the ovules developed to maturity. Consequently, the mean seed number per fruit decreased with x (Figure 1,a); in other words, percentage of brood reduction increased
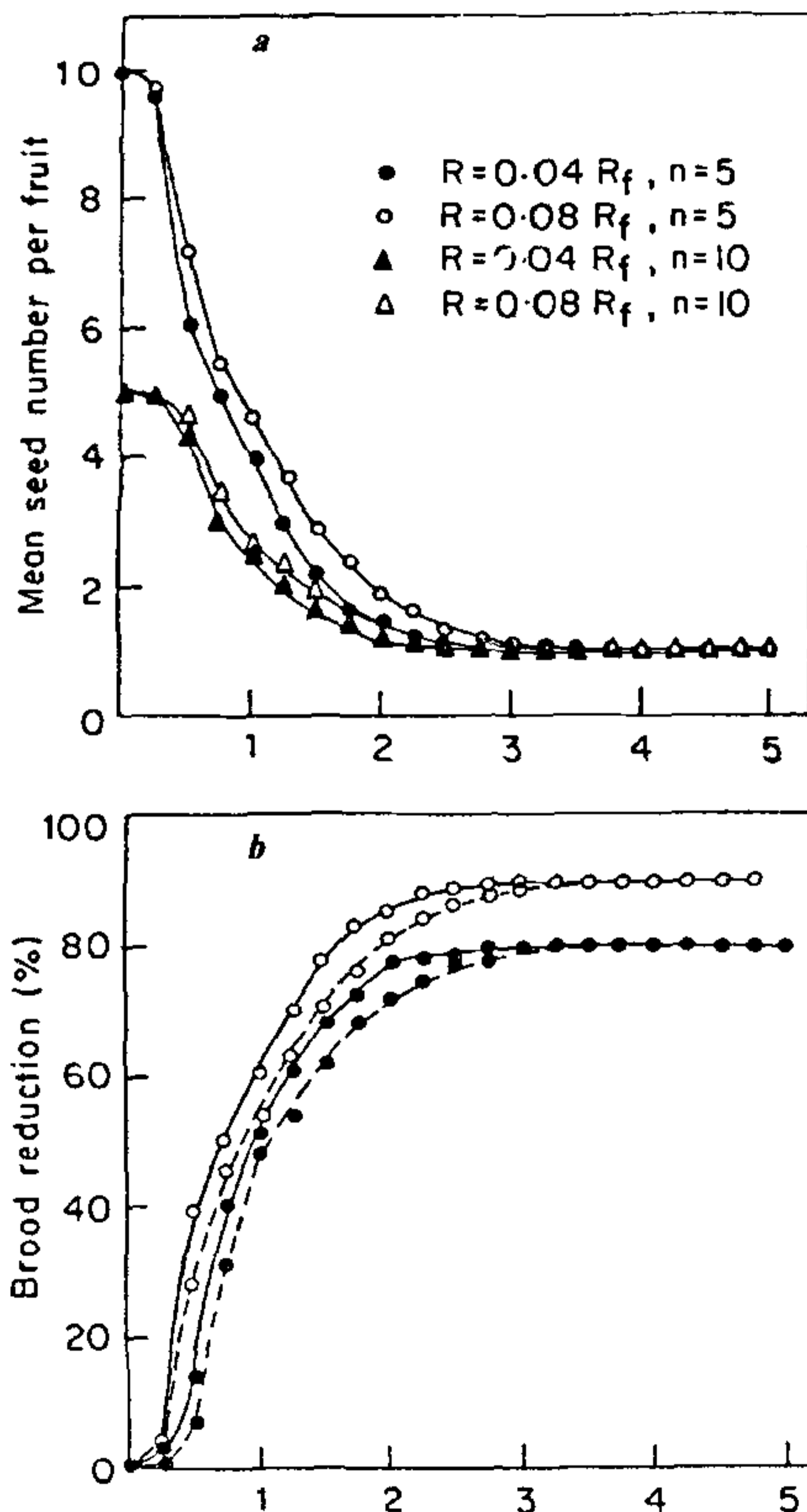
with x (Figure 1,b). This negative relation between x and mean seed number per fruit did not change with either R or n though higher values of these parameters retarded the rate (here iterations or time) at which asymmetry was built.

Thus it appears that the wide range of mean seed number per fruit observed in plants can be explained by applying the rules of self-organization to resource flow into ovules during fruit development. The results of the simulation imply that species with high resource-drawing ability of ovules (as indicated by x) would produce fruits with few seeds while those with low resource-drawing ability of ovules produce fruits with many seeds. We tested this prediction in Derris indica, which exhibits regular abortion of ovules (n = 2).

Experimental verification. The parameter x as used in the model indicates the resource-drawing ability per unit weight of ovules. Generally this is estimated as the amount of labelled sucrose taken up by unit weight of the tissue in a given unit of time (specific activity)[34].

Resource-drawing ability of ovules immediately after fertilization was estimated for nine trees of Derris indica that consistently differed in the percentage of the ovules aborted. We harvested ovules 12 hours after fertilization, weighed them and incubated them in 10 μl (25 μCi) of [^{14}C] sucrose (BARC, Bombay) for 18 hours in a cavity slide. The ovules were then washed thoroughly to remove external [^{14}C] sucrose and macerated in Bray's solution. Uptake was determined using an ECIL LSS-20A liquid scintillation counter[37].

We found a positive association between the percentage of ovules aborted in a tree and the specific activity of its ovules (Figure 2; Spearman rank correlation 0.654, P < 0.05, one-tailed test). Thus, as predicted, the extent of asymmetry built up among the ovules and hence the reduction in number of seeds per fruit appear to be positively related to SDA (x).

Distribution of seed number per fruit

With increase in x, the frequency distribution of seeds per fruit changed from highly negatively skewed to normal to highly positively skewed (Figure 3). Thus the process of self-organization resulted in an intriguing pattern of relation between the coefficient of skewness of the distribution and the mean seed number per fruit, independent of the R values.

This is particularly interesting because there is no a priori reason to expect that the nature of the frequency distribution should change with increase in the value of the mean; a given mean value can be generated with different distribution patterns. Thus the close association between mean seed number per fruit and skewness

Figure 1. a, Relationship between mean seed number per fruit and x, the index of the sink drawing ability, for different values of R and n. (b) Per cent brood reduction as a function of x.
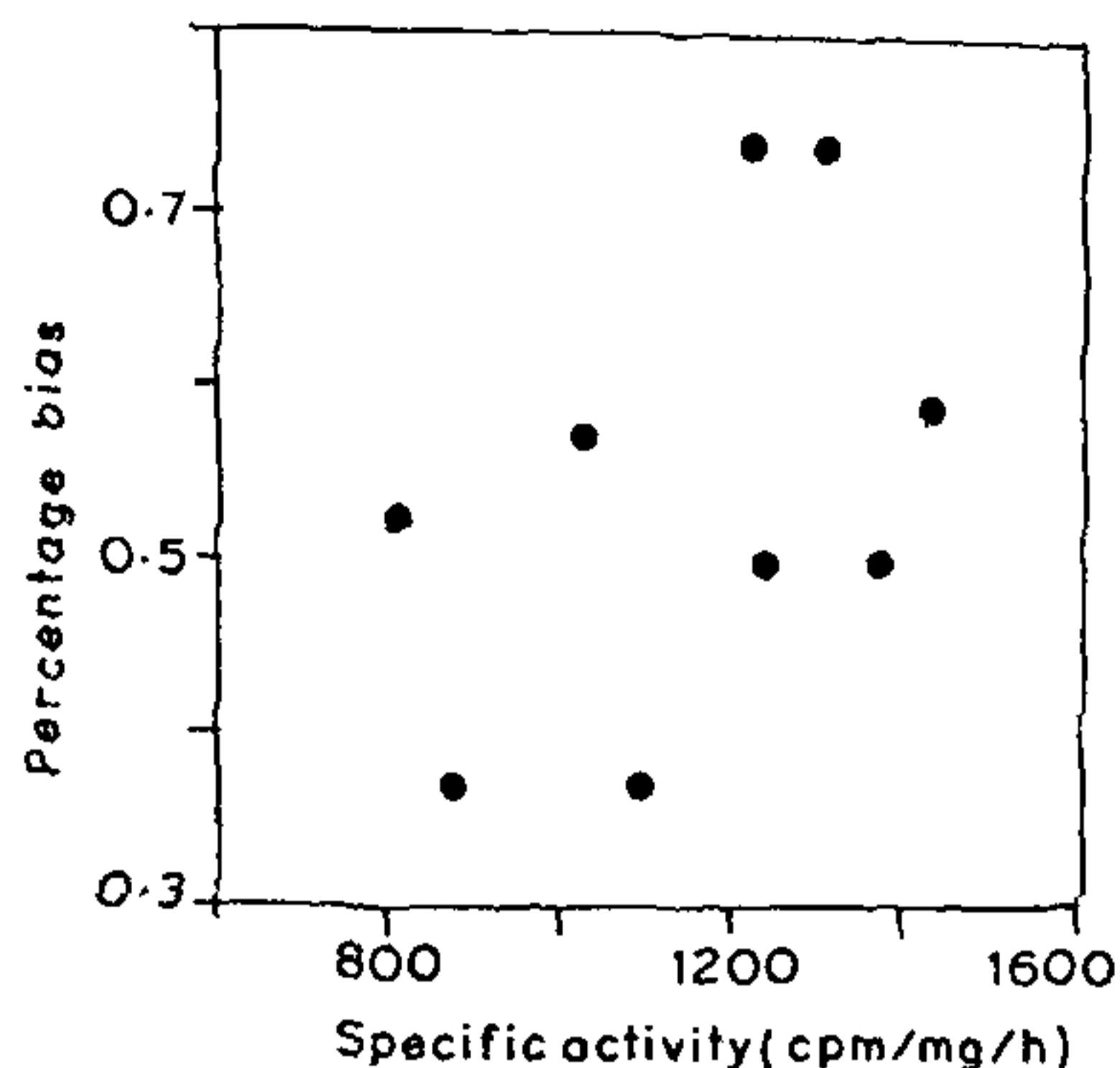
Figure 2. Relationship between percentage of fruits with asymmetrical development of ovules and sink capacity in nine trees of *Derris indica*. Asymmetry was measured as the frequency of fruits with one of the ovules showing visible dominance[37] 48 hours after flowering, and expressed as percentage bias. Ovule sink capacity is indicated by specific activity of ovules expressed as cpm mg^{-1} per h of incubation in [^{14}C]sucrose; sink capacity values are means for 20 fruits from each tree. The data points are from two experiments. Rank correlation (0.654, $P<0.05$) was computed after normalizing the data from the two experiments.

coefficient appears to be a specific feature emerging from the process of self-organization.

If self-organization is indeed the process underlying the formation of seeds in plants, the pattern of relation between skewness coefficient and mean seed number per fruit across species should correspond to that obtained through the simulation. Figure 3 also shows the observed frequencies for three species of plants with ovule number $n \simeq 5$ and mean seed number per fruit corresponding to those generated by the x values represented in the figure. It can be seen that the shift in the pattern of frequency distribution of the observed mean seed number per fruit closely corresponds to that resulting from the simulation. We also computed skewness coefficient and mean seed number per fruit for 18 species with $n \simeq 5$. The relation (Figure 4) strikingly

coincides with that predicted through the self-organization model.

Coefficient of variation

The simulation also generated a distinct parabolic relation between the coefficient of variation (CV) and the mean seed number per fruit. With increase in mean, CV initially increased sharply, attained a maximum between 40 and 50%, and then gradually decreased (Figure 5); altering the ovule number or R did not change this relation. For mean values of seed number per fruit between 1 and 5, the CV can range from zero (when the frequency distribution is of a single peak) to > 62% (when the frequency distribution is bimodal). But the maximum CV attained in the simulations was always between 40 and 50%. This indicates that the observed relation between CV and mean is a specific outcome of the process of self-organization.

In Figure 5 we have also plotted the observed CV against respective mean seed number per fruit for 18 species with $n \simeq 5$. Interestingly, the observed values corresponded closely with the curve obtained through simulation. The maximum CV for the observed values also lies between 40 and 50%, though some points were below the simulation curve for mean greater than 3 and above the curve for mean between 2 and 3.

Discussion

We have shown that self-organization appears to be a process that is not only capable of generating the wide range of seed numbers in fruits of different species but also the species-specific rates of seed abortion. The model implies that species with low SDA show low abortion and those with high SDA high abortion.

What does x represent?

As can be seen from equation 2 (Polya urn equation), the model is more sensitive to change in x than to
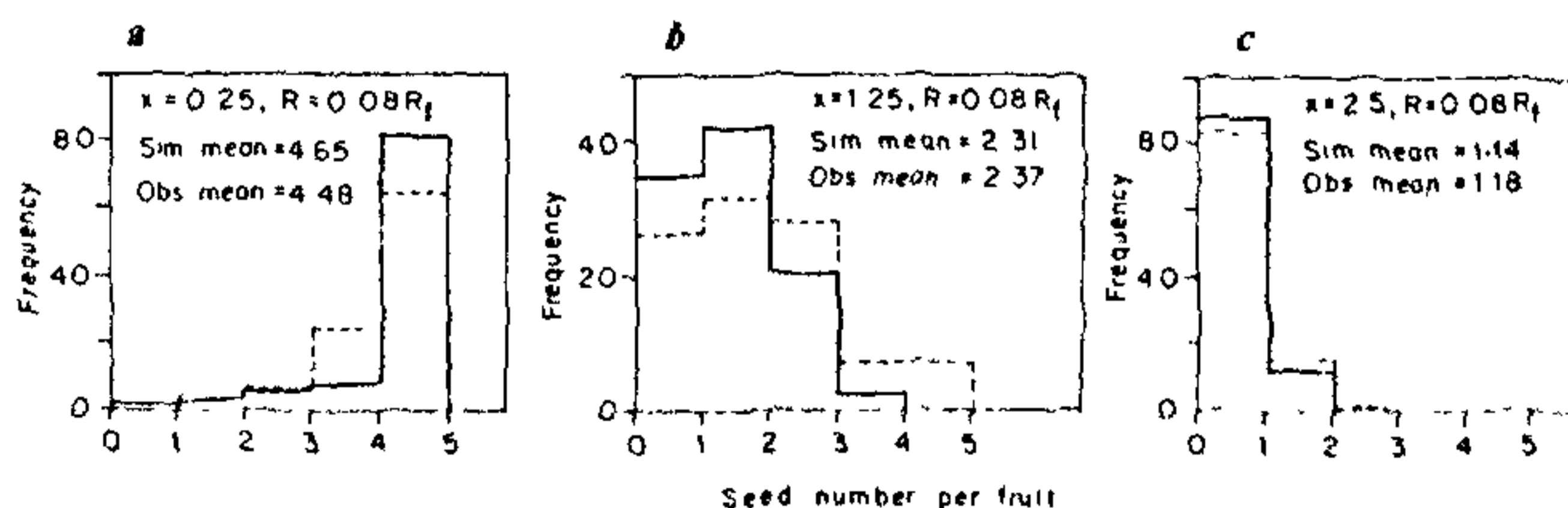

Figure 3. Shift in frequency distribution of seed number per fruit with increase in x (solid line) (a) $x = 0.25$, (b) $x = 1.25$ (c) $x = 2.50$ The frequency distributions for three species (a, *Desmodium* sp; b, *Diospyros montana*, c, *Dodonea viscosa*) are also shown (dashed histogram) with those obtained from the simulation at corresponding x
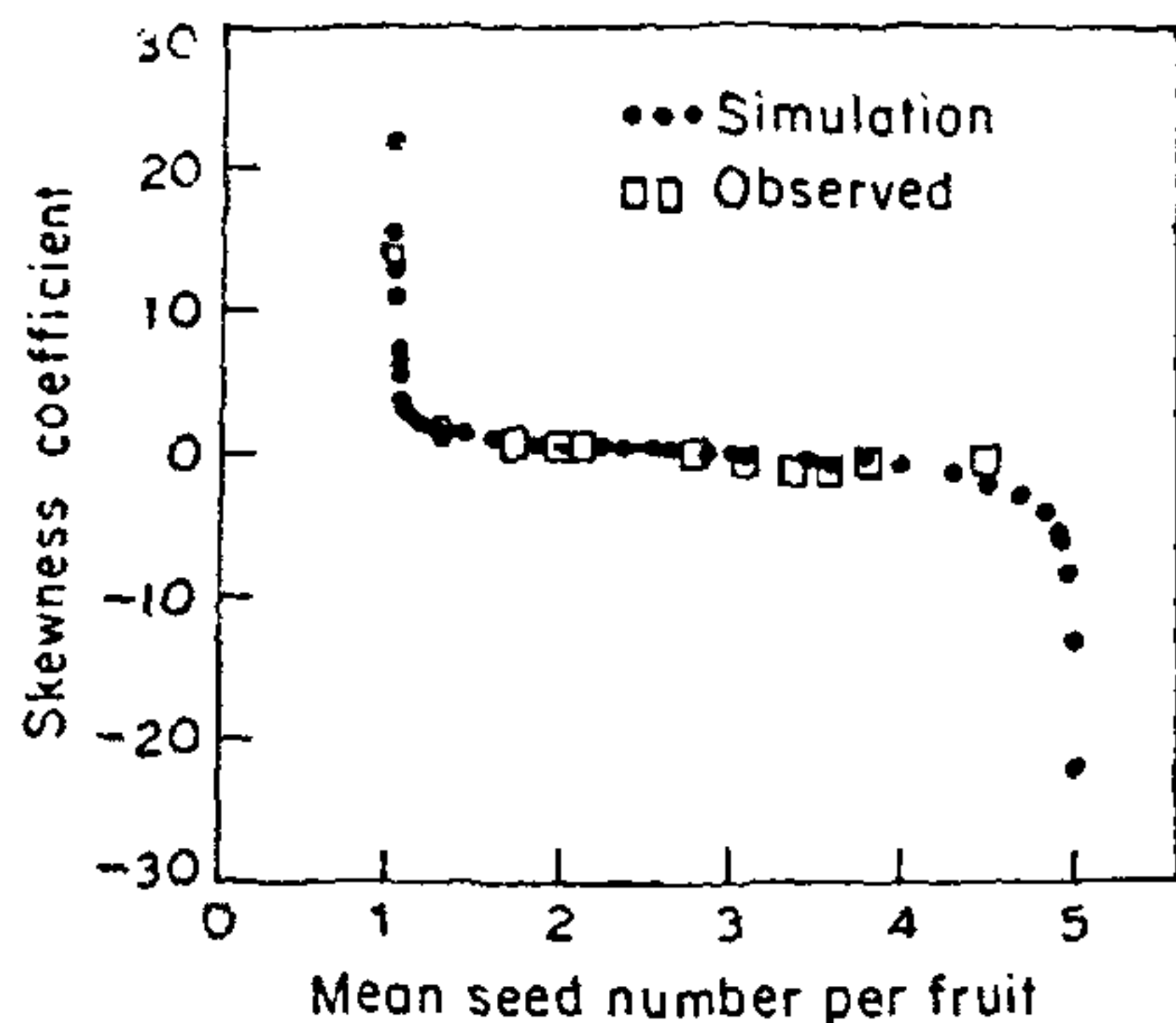
Figure 4. Relation between skewness coefficient and mean seed number per fruit obtained from simulation (circles) with different values of R, and for data from 18 species (open squares). The species are *Butea monosperma*, *Cajanus cajan*, *Crotalaria* sp. 1, *Crotalaria* sp. 2, *Cyppadessa baccifera*, *Dalbergia sissoo*, *Diospyros montana*, *Diospyros* sp., *Dodonea viscosa*, *Ipomea muricata*, *Ipomea pericarpa*, *Lablab niger*, *Milletia ovalifolia*, *Milletia* sp., *Mimosa pudica*, *Mimosa* sp., *Peltophorum ferrugineum*, *Tipauna tippo*.
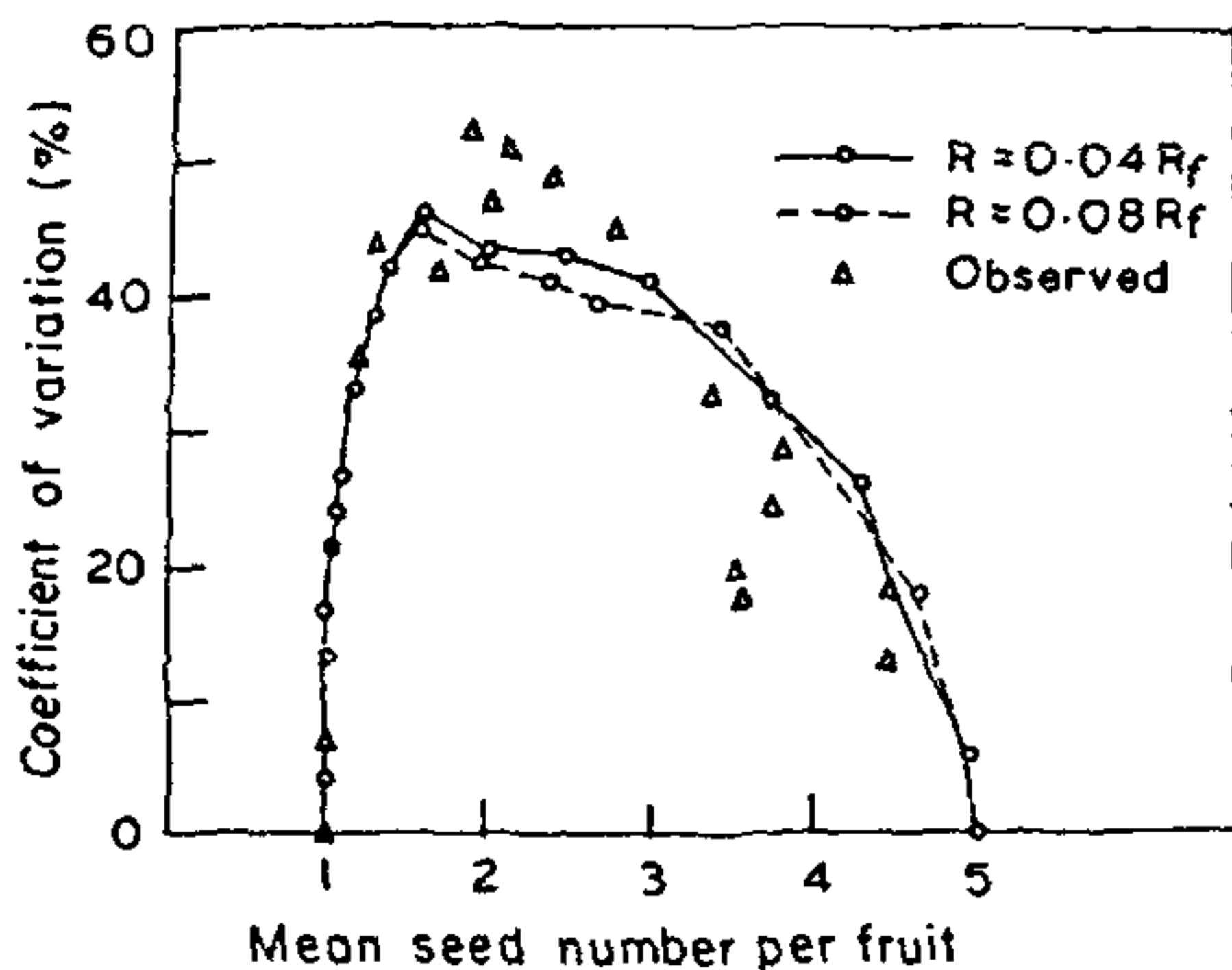

Figure 5. Relation between coefficient of variation and mean seed number per fruit obtained from simulation for different values of R (solid and broken lines), and from data (open triangles) for the 18 species listed in Figure 4.

change in R. The parameter x, as modelled here, indicates the sink capacity, i.e. the resource-drawing ability per unit weight of ovule. The simulations indicate that variation in x affects seed number. Hence selective forces that shape seed number can also be expected to influence sink capacity of the ovules. Thus, in species where production of fruits with a small number of seeds is advantageous (such as wind-, water-

and animal-dispersed fruits), selection favours increased sink capacity of ovules.

We have assumed that, to begin with, the ovules within a fruit are identical in their sink capacity. However, this might not be generally true, as ovules can be expected to differ in R and x depending on the extent of heterozygosity. Under such conditions, asymmetry among the ovules builds up faster, depending on the differences in x values (results not shown).

Our results indicate that the model of development of ovules through a self-organizing process generates several specific features that are strikingly similar to those prevailing in the fruits of plants. However, it is possible that the same features could also be generated through other, alternative models. To this extent, the close correspondence between the simulated and the naturally observed patterns (Figures 2 to 5) is suggestive but not conclusive proof of involvement of the process of self-organization in the formation of fruits.

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