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Main role of self-pollination rate on reproductive allocations in pseudogamous apomicts

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Abstract Most apomicts are hermaphroditic and pseudogamous (pollination is necessary to trigger parthenogenesis). In these plants, fitness depends on the number of progeny obtained by maternal reproduction. We determined the evolutionary stable strategy for male and female sex allocation. We show that the efficiency of pollination determines male and female resource allocations. Predictions are made of these allocations, of pollen/ovule ratio and of seed-set. We show that self-compatibility in apomicts is necessary for the maintenance of an apomictic population, and thus can account for the association between the loss of self-incompatibility and pseudogamous apomixis. In contrast to sexuals, male investment in pseudogamous apomicts increases with the rate of self-pollination.

Key words Pollination · Apomixis · Pollen/ovule ratio · Seed-set · Resource allocation

Introduction

In 1948, Bateman suggested explaining reproductive investment by selection, and more specifically that important investments in male function could be due to competition between males. To predict investments in male function, a trade-off relationship (the fitness-set) is assumed between the investments allocated to the male and female functions. Specifically, the more an individual invests in pollen production, the less it should invest in ovules, and vice versa. Given such a trade-off, one can determine the male-female resource allocation ratio that maximizes fitness. When this ratio characterizes the population at equilibrium, and when any variant is counter-selected, it is then considered as an evolutionary stable strategy (ESS) (Maynard Smith 1976). The existence and stability of modes of reproduction, such as dioecy, monoecy, androdioecy, andromonoecy, hermaphroditism, etc., were then studied from this view-point (Charnov et al. 1976; Charlesworth and Charlesworth 1978; Charnov 1979; Charlesworth 1984; Willson 1979; Spalik 1991). To-date this approach has not been addressed for pseudogamous and gametophytic apomixis.

Gametophytic apomixis is present in many genera of Poaceae, Rosaceae, and Asteraceae. In most gametophytic apomicts, parthenogenetic development of the embryo requires fertilization of the polar nuclei, i.e. pseudogamy (Nogler 1984; Kellog 1990). In the Poaceae, which are wind-pollinated plants, pseudogamy is the general rule but with three exceptions: *Calamagrostis* (Nygren 1946), *Cortaderia jubata* (Philipson 1978; Costas-Lippmann 1979) and *Lamprothyrsus* (Connor 1979). A particularity of pseudogamous apomicts is the presence of the male function, whereas the fitness of individuals is only expressed through the famale function. On one hand, one expects no reproductive allocation to male function. On the other hand, the presence of pollen suggests its participation in female fitness, possibly through an increase in its own seed-set. This hypothesis is consistent with the loss of self-incompatibility in pseudogamous apomicts (Voigt and Bashaw 1972; Pernès 1975; Stalker and Wright 1975; Ngendahayo et al. 1986; Quarin 1992).

In the present paper, we develop a model to predict the reproductive allocations in pseudogamous apomicts, depending on trade-off and self-incompatibility. Based on a calculation of female fitness including the pollination efficiency, the model explains the

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absence of self-incompatibility in these plants from a theoretical point of view. Predictions are made concerning the resource allocation ratio to male and female functions, the pollen-ovule ratio and the seed-set.

Model

The model implies the notion of reproductive space in which gametes can randomly meet. The reproductive space of pseudogamous apomicts is infinite as regards flower size. The model includes two assumptions: (1) pollen grains are distributed independently (the binomial distribution then allows computation of the probability of a pollen grain meeting an ovule), which should correspond more closely to wind-pollination than to animal-pollination, (2) a pollen grain can trigger the development of one seed at most, that is flowers are mono-ovulate, as is the case in the majority of obligate wind-pollinated plants (ovule distribution is uniform and independent of pollen distribution).

Some probabilistic effects of wind-pollination of seed-set were studied by Gregorius (1983), who employed a matrix of N cells, where cell area corresponds to the area of a stigma. In this matrix, Gregorius considered y stigmas and x randomly distributed pollen grains (Fig. 1), assuming that there could not be more than one stigma per cell ($y \leqslant N$). By contrast, the number of pollen grains per cell was not limited.

We use the model of Gregorius, emphasizing the analogy between his matrix and our reproductive space. The pollen pool of a plant is the total number of pollen grains distributed in the reproductive space of this plant. This pollen pool comprises $A_1 x$ self-pollen grains (where x is the pollen production of the plant, and A_1 is the part contributing to its own pollen pool) and $A_2 x^*$ allopollen grains (where x^* is the average pollen production of the other plants, and A_2 is the part contributing to the pollen pool of this plant). In the absence of any loss of pollen, $A_1 = A_2 = 1$. In contrast, when plant density is low $A2 \approx 0$, since pollen grains can fall between plants, outside of any pollen pool. Due to limit pollen dispersal, the probability of a pollen grain reaching its own stigmas is higher than that of it reaching the stigmas of another plant, that is $A1 >= A2$. Parameters A_1 and A_2 are characteristic of the population. We assume their value is identical for all individuals of the population.

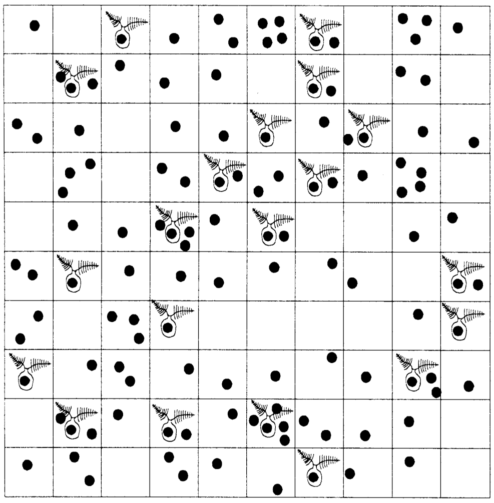

Fig. 1 The model: a reproductive space of N cells, in which we insert at random X grains of pollen and Y ovules (the number of ovules per cell is 0 or 1; that of pollen may by greater)

The pollen number randomly distributed in the reproductive space is $z = A_1 x + A_2 x^*$. We must also define p as the probability of a pollen grain deposited on the pistil to trigger parthenogenesis. When $p = 1$, a single pollen grain is sufficient to obtain a seed, whereas more than one pollen grain is necessary on average when $p < 1$. We consider the deposition of a pollen grain on the pistil, followed by the stimulation of parthenogenesis, as the result of a random event of probability p/N. Hence the probability that a seed does not develop because none of the z pollen grains triggered its developments is $(1 - p/N)^z$. Thus the expected number (Sn) of seeds produced by a plant, using the binomial distribution, is:

$$\mathrm{Sn} = y[1 - (1 - p/N)^z] \tag{1}$$

Reproductive resources available for male and female functions are m and f, respectively. The number of ovules y is by definition equal to Kf, where K is a constant representing the number of ovules produced by a plant that invests all reproductive resources in the female function, so that f = 1. The number of pollen grains x is equal to KTm, where T is the cost of an ovule expressed in terms of the number of pollen grains (note that if the cost is proportional to the mass, then T is directly related to the size of the pollen grain relative to the size of an ovule).

We add to this model of pollination the constraint $m^\gamma + f^\lambda = 1$, where m^γ and f^λ represent the relative investments in male function and female function, respectively. The positive parameters γ and λ determine the efficiency of investment in each sexual function: the lower γ (or λ), the lower that efficiency. The parameters also describe the shape of the trade-off between resources available for male and female functions, i.e. the fitness-set. The fitness-set is linear when both γ and λ are equal to 1, and is convex (sensu Charnov et al. 1976) when both are larger than 1 (which can be due to fixed investments that are common to male and female function or from a large temporal separation of sexual phases, that is dichogamy). The fitness-set is concave when both are smaller than 1 (see Olivieri et al. 1994 for the same parameters to represent variations of fitness-sets).

We obtain:

$$y = K[1 - (x/KT)^\gamma]^{1/\lambda}. \tag{2}$$

Substituting y by its equivalent in pollen in equation (1), we get:

$$\mathrm{Sn} = K[1 - (x/KT)^\gamma]^{1/\lambda}[1 - (1 - p/N)^z]. \tag{3}$$

When N tends to infinity, the expression $(1 - p/N)^z$ can be reduced, using Taylor's series, to $1 - zpN^{-1}$ (Bronstein and Semendiaev 1971), i.e. to $1 - p(A_1 x + A_2 x^*)/N$. By substituting in (3), we obtain:

$$\mathrm{Sn} = pK[1 - (x/KT)^\gamma]^{1/\lambda}[A_1 x \pm A_2 x^*]/N. \tag{4}$$

Results

The ESS for pollen production

The ESS is such that the number of seeds produced, Sn, is maximized. More specifically, the ESS for pollen production x^* is such that $\delta \mathrm{Sn}/\delta x = 0$, and $\delta^2 \mathrm{Sn}/\delta^2 x < 0$, for $x = x^*$ (Maynard Smith 1976).

$$\delta \mathrm{Sn}/\delta x = pK[1 - (x/KT)^\gamma]^{(1/\lambda)-1}[A_1[1 - (x/KT)^\gamma] + (A_1 x + A_2 x^*)(x/KT)^{\gamma-1}\gamma/\lambda KT]/N \tag{5}$$

Hence, x^* is such that

$$x^* = KT\left[\frac{A_1}{(1 + \gamma/\lambda)A_1 + \gamma A_2/\lambda}\right]^{\gamma^{-1}}. \tag{6}$$

Equation (6) shows more clearly (1) that the ESS is independent of p and N, and (2) that in the case of self-incompatibility ($A_1 = 0$) we have $x^* = 0$, i.e. the selection of male-steriles (i.e. female individuals) and then the extinction of the population. Consequently, pseudogamous apomicts have to be self-compatible for population survival.

When the population is self-compatible, A_1 is expected to be greater than or equal to A_2. We can then express A_2 as $A_2 = bA_1$, with $b \leqslant 1$. Equation (6) becomes:

$$x^* = \mathrm{KT}\left[\frac{1}{[1+\gamma(1+b)/\lambda]}\right]^{\gamma^{-1}}. \tag{7}$$

The ESS depends on b, γ, and λ, i.e. the rate of allopollination and the shape of the fitness-set. Male investment increases with the rate of self-pollination. When the fitness-set is symmetric, that is $\lambda = \gamma$, we obtain $x^* = \mathrm{KT}[1/(2+b)]^{\gamma^{-1}}$.

Resources available for sexual functions

When $A_1 > 0$, resources available for male and female function (i.e. m and f) are equal to

$$\left[\frac{1}{[1+\gamma(1+b)/\lambda]}\right]^{\gamma^{-1}}$$

and

$$\left[1-\frac{1}{[1+\gamma(1+b)/\lambda]}\right]^{\lambda^{-1}},$$

respectively. The rate of allopollination, which expresses the relative plant density of the population, can range from 0 (very scarce population) to 1 (very dense population with no discontinuities between inflorescences belonging to different plants). When $\gamma = \lambda$, i.e. when the fitness-set is symmetric, the ratio of resources available for male and female functions becomes close to $[1/(1+b)]^{1/\gamma}$. When the population is very scarce, the ratio tends to 1:1, the theoretical value predicted by Charnov et al. (1976) for xenogamous hermaphrodites. A similar convergence appears when the fitness-set becomes more convex, i.e. when γ increases. In addition, the ratio of contributions is equal to the self-pollination rate when the fitness-set is linear.

The pollen-ovule ratio (P/O)

The expected P/O is:

$$\mathrm{T}\left[\frac{1}{[1+\gamma(1+b)/\lambda]}\right]^{(\gamma^{-1}-\lambda^{-1})}.$$

In pseudogamous apomicts, P/O depends on the self-pollination rate and the fitness-set shape, except when the fitness-set is symmetric. In this case, P/O becomes equal to T, i.e. another theoretical value predicted by Charnov (1982) for xenogamous hermaphrodites.

Seed-set

When there is no resource limitation to fructification, seed-set is equal to $px^*A_1(1+b)/\mathrm{N}$. As $x^*A_1(1+b)$ represents the number of pollen in the reproductive space, seed-set is proportional to the pollen density in this space.

By substituting x^* by $\mathrm{KT}\left[\frac{1}{[1+\gamma(1+b)/\lambda]}\right]^{\gamma^{-1}}$ (see equation 7), we obtain:

$$\text{seed-set} = pA_1(1+b)\mathrm{KT}\left[\frac{1}{[1+\gamma(1+b)/\lambda]}\right]^{\gamma^{-1}}\Big/\mathrm{N}. \tag{8}$$

When the fitness-set is symmetric, equation (8) becomes:

$$\text{seed-set} = pA_1(1+b)\mathrm{KT}\left[\frac{1}{2+b}\right]^{\gamma^{-1}}\Big/\mathrm{N}. \tag{9}$$

The relationship with P/O is obvious (P/O = T), that is the seed-set varies like P/O, especially when the fitness-set is linear and the population is scarce, i.e. when seed-set is close to $pA_1\mathrm{KT}/\mathrm{N}$.

Discussion

This theoretical study explains why self-incompatibility is absent in pseudogamous opmicts and shows that the investments in male and female functions, the P/O, and the seed-set can all be analytically predicted.

The absence of self-incompatibility in pseudogamous apomicts

There are two advantages of self-compatibility in pseudogamous apomicts. First, as the pollen does not contribute to the genotype of the zygote, fertilization with self-pollen is not associated with inbreeding, and hence with inbreeding depression. In fact fecundity increases in the case of self-compatibility, since more seeds will be triggered to develop. This advantage corresponds to the one proposed by Gustafson (1946) which considers that self-incompatibility is a serious obstacle to the fertility of species spreading as clones over large area, and that self-compatibility improves the seed-set of these species. Second, self-incompatibility leads to counter-selection of pollen production, since there is no advantage in triggering the development of seeds of other genotypes without contributing to the genetic make-up of their offspring. As a result, there will be selection for male sterility (see eq. 7, case $A_1 = 0$). When male-sterile over-run the population, such population will not produce seeds any more and will disappear.

Data on self-compatibility in pseudogamous apomicts are rare, but all show the absence of self-incompatibility in these plants. This is the case in the Poaceae, especially in the genera *Bracharia* (Ngendahayo et al. 1986), *Eragrostis* (Voigt and Bashaw 1972; Stalker and Wright 1975), *Paspalum* (Quarin 1992) and *Panicum* (Pernès 1975). Each agamic species includes rare true sexuals and many apomicts differing in their ploidy level (this reproductive barrier greatly limits gene flow between the two types of plants). In all cases, sexuals are allogamous (high degree of self-incompatibility), whereas apomicts are self-compatible.

Loss of self-incompatibility and pseudogamous apomixis seem to be associated with a pleiotropic interaction of the gene responsible for pseudogamous apomixis. In *Panicum maximum*, hundreds of hybrids have been obtained between sexuals and apomicts (Savidan 1980; Noirot 1983). Progenies include sexuals and apomicts in the ratio 1 : 1 (Savidan 1980). Self-incompatibility exists in sexual hybrids but not in apomictic hybrids. Noirot (1993) explained this result through the repression of self-incompatibility by the gene for apomixis or by a linked gene. In the genus *Bracharia*, crosses between the sexual *B. ruziziensis* and the apomictic *B. brizantha* and *B. decumbens* have given apomictic or sexual hybrids in a 1 : 1 ratio (Ndikumana 1985). All sexual hybrids are self-incompatible, whereas all apomictic hybrids are self-compatible (Ngendahayo et al. 1986). In addition, the loss of distyly in *Erythroxylum undulatum* is linked to apomixis (Berry et al. 1991). This example involves a mode of self-incompatibility other than that produced by the genic systems, and the direct role of the apomixis gene is not known. However, its effects are similar in terms of self-pollination rate.

Relations between pollination efficiency and male and female resource allocations, pollen-ovule ratio, and seed-set

The efficiency of pollination determines reproductive allocations in pseudogamous and anemophilous apomicts. An ESS exists even with a linear fitness-set, whereas the fitness-set should be convex to maintain stability of the allogamous hermaphroditic population according to Charnov (1982). In addition, when the fitness-set is symmetric, the allocation ratio to the two sexual functions should tend to 1 : 1, as in allogamous hermaphrodites (Charnov 1979).

P/O increases with the degree of allogamy (Cruden 1977). According to Cruden, P/O should be optimized to maximize seed-set and should depend on pollination efficiency. Nevertheless, Charnov (1979) and Queller (1984) consider that optimization of the seed-set is equivalent to selecting only female fitness and cannot be applied to sexual hermaphrodites. By contrast, Cruden's interpretation can be perfectly applied to pseudogamous apomicts. Predictions in both cases can be very close. Note, for example, that P/O tends to T in obligate allogamy (Charnov 1979), as in pseudogamous apomixis.

Seed-set depends on the pollen germination rate and on the success of the triggering of parthenogenesis. It also depends on the efficiency of the anemophilous pollination, as our model shows. This efficiency is influenced by the investment in the male function, but also by the size of the reproductive space and the efficiency of the pollen transfer between plants, that is the efficiency of allo-pollination, two important characteristics of modes of reproduction.

The seed-set of allogamous plants, pseudogamous apomicts, and autogamous plants should be compared. In hermaphrodites, obligate allogamous plants have an averaged seed-set (0.206) clearly lower than that of autogamous plants (0.723) (Sutherland 1986). Data on seed-set in pseudogamous apomicts are rarer. Nevertheless, the seed-set of *Panicum maximum* was 4.5–45% in Puerto Rico (Warmke 1951) and 5.1–24.8% in Côte-d'Ivoire (Noirot 1996). These values are closer to the seed-set of allogamous plants than to that of autogamous plants. This agrees with our prediction that seed-set should depend on reproductive space, which suggest that the sizes of the reproductive spaces of allogamous plants and pseudogamous apomicts are similar when they are compared to that of autogamous plants.

Our model assumes that A_1 and A_2 characterize the population and that all individuals have the same values for these parameters. This can only be true on average. Nevertheless, we can interpret these parameters and consequently discuss them. A_1 depends especially on the reproductive structure of the plant (shape and size of the inflorescence), whereas A_2 also depends on the plant density of the population, that is on efficiency of allo-pollination. We would expect different ESS values not only between agamic species but also between populations within an agamic species. We would also expect changes in equilibrium within populations and variations in P/O and seed-set. More specifically, lower male investment is expected when the density increases, as a result of a lower self-pollination rate (see eq. 7). In fact, the expected effect of self-pollination rate on male investment is the inverse of what is expected in the case of sexuals (Charnov 1982). We would expect other patterns of selection of these parameters depending on the presence of male steriles in the population, a frequent occurrence as a result of the appearance of apomixis.

The efficiency of allo-pollination can be defined for all modes of reproduction, even in cleistogamous plants where it is nil. In allogamous plants, as in apomicts, the efficiency of allo-pollination depends on the flower density of the population, that is the flowering intensity of plants and the plant density of the population. This should prompt further studies of the influence of pollen on the control of reproduction by seeds, by comparison with vegetative reproduction by tillers or runners, assuming a relation between the flower density of the population and its plant density.

References

Bateman AJ (1948) Intra-sexual selection in *Drosophila.* Heredity 2: 349–368

Berry PE, Tobe H, Gomez JA (1991) Agamospermy and the loss of distyly in *Erythroxylum undulatum* (Erythroxylaceae) from northern Venezuela. Am J Bot 78: 595–600

Bronstein IN, Semendiaev KA (1971) Aide-mémoire de Mathématiques. Editions Eyrolles Paris

Charlesworth D (1984) Androdiecy and evolution of dioecy. Biol J Linn Soc 23: 333–348

Charlesworth B, Charlesworth D (1978) A model for the evolution of dioecy and gynodioecy. Am Nat 112: 975–997

Charnov EL (1979) Simultaneous hermaphroditism and sexual selection. Proc Natl Acad Sci USA 76: 2480–2484

Charnov EL (1982) Sex types in higher plants. In: Charnov EL (ed) The theory of sex allocation. Princeton University Press, New Jersey, pp 373–387

Charnov EL, Maynard Smith J, Bull JJ (1976) Why be an hermaphrodite? Nature 263: 125–126

Connor HE (1979) Breeding systems in grasses. A survey. NZ J Bot 17: 547–574

Costas-Lippmann M (1979) Embryogeny of *Cortaderia selloana* and *C. jubata* (Gramineae). Bot Gaz 140: 393–397

Cruden RW (1977) Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. Evolution 31: 32–46

Gregorius HR (1983) Efficiency of random pollination and optimal sex ratio. Math Biosci 66: 263–271

Gustafsson A (1946) Apomixis in higher plants. Acta Univ Lund 42: 1–67

Kellog EA (1990) Variation and species limit in agamospermous grasses. Syst Bot 15: 112–123

Maynard Smith J (1976) Evolution and the theory of games. Am Sci 64: 41–45

Ndikiduma J (1985) Etude de l'hybridation entre espèces apomictiques et sexuées dans le genre *Bracharia.* Transfert du caractère "reproduction apomictique" des espèces *Bracharia decumbens* Stapf et *Bracharia brizantha* (Hochst) Stapf à l'espèce sexuée *Bracharia ruziziensis* Germain et Evrard. Doctoral thesis, Université Catholique de Louvain, Belgium

Ngendahayo M, Coppens d'Eeckenbrugge G, Louant BP (1986) Self-incompatibility studies in *Brachiaria ruziziensis* Germain et Evrard, *Brachiaria decumbens* Stapf and *Brachiaria brizantha* (Hochst) Stapf and their interspecific hybrids. Proc Symp Rep Sex Archegoniates 9: 5p

Nogler GA (1984) Gametophytic apomixis. In: Johri BM (ed) Embryology of angiosperms. Springer-Verlag, Berlin, pp 475–518

Noirot M (1983) L'amélioration génétique des variétés apomictiques de *Panicum maximum* Jacq. Garcia de Orta Sér Agron 10: 161–168

Noirot M (1993) Allelic ratios and sterility in the agamic complex of the *Maximae* (*Panicoïdeae*): evolutionary role of the residual sexuality. J Evol Biol 6: 95–101

Noirot M, Ollitrault P (1996) Exsertion, flowering, and shedding in *Panicum maximum* (Poaceae). Am J Bot 83: 1323–1328

Nygren A (1946) The genesis of some Scandinavian species of *Calamagrostis.* Symp Bot Ups 17: 1–105

Olivieri I, Couvet D, Slatkin M (1994) Allocation of reproductive effort in perennial plants under pollen limitation. Am Nat 144: 373–394

Pernès J (1975) Organisation évolutive d'un groupe agamique: la section des Maximae du genre *Panicum* (Graminées). Mémoires Orstom no. 75, Editions de l'Orstom, Paris

Philipson MN (1978) Apomixis in *Cortaderia jubata* (Gramineae). NZ J Bot 16: 45–59

Quarin CL (1992) The nature of apomixis and its origin in Panicoid grasses. Apom Newslett 5: 8–15

Queller DC (1984) Pollen-ovule ratios and hermaphrodite sexual allocation strategies. Evolution 38: 1148–1151

Savidan Y (1980) Chromosomal and embryological analyses in sexual × apomictic hybrids of *Panicum maximum* Jacq. Theor Appl Genet 57: 153–156

Savidan Y, Pernès J (1982) Diploid-tetraploid-dihaploid cycles and the evolution of *Panicum maximum* Jacq. Evolution 36: 596–600

Smith GL (1963) Studies in *Potentilla* L. I. Embryological investigations into the mechanism of agamospermy in British *P. tabernaemontani* Aschers. New Phytol 62: 264–282

Spalik K (1991) On the evolution of andromonoecy and overproduction of flowers: a resource allocation model. Biol J Linn Soc 42: 325–336

Stalker HT, Wright LN (1975) Reproduction of *Eragrostis curvula* (Schrad.) Nees. J Ariz Acad Sci 10: 106–110

Sutherland S (1986) Patterns of fruit-set: what controls fruit-flowers ratios in plants? Evolution 40: 117–128

Voigt PW, Bashaw EC (1972) Apomixis and sexuality in *Eragrostis curvula.* Crop Sci 12: 843–847

Warmke HE (1951) Cytotaxonomic investigations of some varieties of *Panicum maximum* and of *P. purpurascens* in Puerto Rico. Agron J 43: 143–149

Willson MF (1979) Sexual selection in plants. Am Nat 113: 777–790