Reproductive effort or reproductive offer? – A revised approach to reproductive strategies of flowering plants

Krystyna M. Urbanska

Geobotanisches Institut ETH, Stiftung Rübel, Zürichbergstraße 38, CH-8044 Zürich, Switzerland

Abstract

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Reproductive strategies of flowering plants have until now been mostly considered in terms of resource allocation to reproduction called reproductive effort. The paper gives a brief review of this concept and of the problems related to the assessment of the reproductive effort. A revised approach to reproductive strategies based on performance of various reproductive units is proposed for plants reproducing by seed.

The essential strategic components of reproduction by seed are 1) reproductive offer RO, 2) reproductive efficiency EFF, and 3) germination percentage γ. Reproductive offer, defined as the amount of reproductive units occurring in female and male organs at early pre-mating stages, is determined by the number of ovules and primary pollen grains, respectively. Reproductive efficiency is defined as the ability to carry to term viable reproductive units; the evaluation time corresponds, respectively, to anthesis and seed dispersal. Female reproductive efficiency of sexually reproducing plants, and of pseudogamous taxa, too, is mainly influenced by male reproductive efficiency as well as further biological and ecological factors; on the other hand, male reproductive efficiency seems to be mostly controlled by genetic factors. In autonomously agamospermous species represented by pistillate plants only, female reproductive efficiency equals the global efficiency of a given individual/population.

Reproductive success, defined as the appearance of active individuals forming a new generation in demographic sense, is influenced both by reproductive efficiency and germination percentage; the two variables are accordingly included in the proposed formulae of evaluation.

Key words: strategy – reproductive effort – reproductive offer – reproductive efficiency – germination rate – reproductive success – male/female function.

The concept of reproductive effort and its assessment

The life history of an individual is characterized by a strategic allocation of resources, be it time, energy, or nutrients. The original concept of Cody (1966) is based on the assumption that different structures or functions are alternatives. One of these alternatives in the Angiosperms is supposedly represented by flowering vs. vegetative growth (Harper 1977).

The concept of reproductive effort based on resource allocation to reproduction was first introduced in studies on flowering plants by Ogden (1968), elaborated by Harper and Ogden (1970), and subsequently used by numerous authors (e.g. Quinn et al. 1972, Anderson and Loucks 1973, Hayashi and Kawano 1972, 1973, Kawano and Nagai 1975, Cartica and Quinn 1982, Campbell et al. 1983, Quinn and Hodgkinson 1984, Bell and Quinn 1986, Quinn 1987, Ohara and Utech 1988). According to Harper and Ogden (1970), reproductive effort may be estimated in three possible ways as 1/gross reproductive effort i.e. total energy as propagules relative to total energy as starting capital plus gross assimilation, 2/net reproductive effort i.e. total energy as propagules relative to total energy as starting capital plus net production and 3/net reproductive effort or crude reproductive efficiency i.e. total weight of propagules relative to total biomass weight at the propagule-bearing stage.

As justly pointed out by Harper (1977), detailed patterns of resource allocation in plants are exceedingly difficult to follow, and it is equally difficult to trace precisely the resource allocation between various plant parts. The choice of the most relevant resource or combination of resources, i.e. the currency of allocation (Bazzaz and Reekie 1985) represents, too, a complex problem, for the proportion of the total resource allocated to reproductive structures may differ significantly among resources (e.g. van Andel and Vera 1977, Abrahamson and Caswell 1982). Another difficulty concerns the distinction between reproductive and vegetative structures (see e.g. Bazzaz and Reekie 1985). Last, but not least, the single measurement of reproductive effort at the time when seeds or propagules are fully developed may provide incomplete information on total resource allocation to reproduction, especially in cases where the actual seed production stays is no relevant proportion to the intensity of the floral development (Urbanska 1980). In this context, the recent contribution of Hara et al. (1988) focusing on reproductive resource allocation at the flowering stage represents a step in the right direction; it is obvious, however, that a precise evaluation of resource allocation to reproduction in flowering plants is still far from being properly understood and some pertinent questions remain so far unanswered.

The currently accepted assessment of reproductive effort in flowering plants has another important deficiency: it combines reproductive allocation of resources with some aspects of reproductive performance of the seed/propagule-bearing parent (see also Willson 1983). Curiously enough, female function only is thus considered, although the general term "reproductive effort" does not convey any gender notion. However, the Angiosperms naturally produce both uni- and biparental progeny i.e. the gametes may be contributed by a single or two different individuals (Table 1). The seed production in flowering plants is obviously not always based on a sole reproductive effort of the female parent, but much more frequently depends on a separate reproductive effort of the pollen donor. This condition is clearly recognizable in e.g. sexually reproducing xenogamous plants where the most extreme cases are represented by dioecious trees with their considerable male reproductive effort; it occurs, too, in asexual taxa which are pseudogamous and self-incompatible (Table 1). In other words, some plants profit from the reproductive effort of other individuals, but the latter is not included in the evaluation of the reproductive effort. I am of the opinion that a clear distinction should be made between male and female function in studies on reproductive effort and reproductive biology in general. Such distinction may bring about some surprises, in particular when reproductive effort of male and female partners in self-incompatible species is assessed, although self-compatible plants, too, may devote a large portion of their resources to pollen which is already long shed at the seed maturity and therefore not evaluated as to its biomass

Table 1. Reproduction by seed: parental contribution to various seed components in relation to breeding system

Repro-duction	Breeding system	Origin of seed	Origin of embryo	Origin of endosperm	Gamete donors(s)
Sexual	xenogamy	BIP	BIP (♀+♂)	BIP (♀+♂)	two, ♀ and ♂
Sexual	autogamy	UNIP	UNIP (♀+♂)	UNIP (♀+♂)	single (♀+♂)
Asexual	autonomous agamospermy	UNIP	UNIP ♀	UNIP ♀	single ♀
Asexual	pseudogamy + self-incompatibility	BIP	UNIP ♀	BIP ♀+♂	two, ♀ and ♂
Asexual	pseudogamy + self-compatibility	UNIP	UNIP ♀	UNIP ♀+♂	single (♀+♂)

BIP   = biparental
UNIP = uniparental

weight or energetic value. Some indications in this respect emerge from studies on dioecious plants (.e.g. Freeman et al. 1976, Lloyd and Myall 1976, Barrett and Helenurm 1981, Gross and Soule 1981, Bullock 1984), but the large research field still remains largely unexplored. Some data presented are, unfortunately, rather vague; for instance, biomass allocation in the dioecious *Chamaedorea tepejilote* was studied separately in male and female individuals, but the authors mention only "male reproductive structures", no precise details being given (Oyama and Dirzo 1988). Here again, the fundamental problem of an exact definition is encountered.

Numerous scientists working on reproductive biology of flowering plants have recognized the need for a separate assessment of the partners interacting frequently in the process of reproduction by seed, but most data specifically referring to a given gender deal with various aspects of male function, and sexually reproducing plants only (e.g. Heslop-Harrison and Heslop-Harrison 1970, Knox and Heslop-Harrison 1970, Smart et al. 1979, Willemse and Reznickova 1980, Kenrick and Knox 1982, Russell and Cass 1983, Knox 1984a, b, Russell 1984, McConchie et al. 1985, Mogensen and Rusche 1985, Singh and Knox 1985, Stinson and Mascarenhas 1985). Recently, Knox (1987) reviewed pollen differentiation and male function; the reader is referred to this interesting paper for more information. As far as female function is concerned, there is an abundance of data on e.g. seed production (see. e.g. Salisbury 1942 or Shaanker et al. 1988); however, more recent data are mostly given as means of evaluation of reproductive effort (e.g. Meagher and Antonovics 1982, Quinn and Hodgkinson 1984). The details available are, regrettably, scattered in the literature, and some quantitative characters have been largely ignored to date. Two of the rare studies where e.g. number of ovules and pollen grains are given is the outstanding contribution of Cruden (1977) and the elegant study of Kawano and Nagai (1975).

While the estimations of the resource allocation to reproduction based on biomass weight or energy at the seed/propagule maturity undoubtedly have an interesting comparative value and significantly contribute to a better comprehension of the plant budget as a whole, they are not helpful in the assessment of biological aspects of plant life history (see Kawano and Nagai 1975). They are unsatisfactory, too, when demographic problems requiring numerical data gathered at various life phases are studied.

Strategy understood as a "general plant of action" (the Oxford Dictionary), may be considered in terms of the currency invested on the one hand, but on the other hand may be viewed as movements of troops. While the "allocation of currency" is directly related to the *capital* disposable, the "movements of troops" give more insight into the *strategic units* involved. I tend to think that the same principle applies to reproductive strategies of the Angiosperms and propose therefore an approach based on performance of various reproductive units.

The concept presented in this paper links up three components which play the key rôle in reproductive strategies of plants reproducing by seed viz. 1/reproductive offer, 2/reproductive efficiency, and 3/germination percentage (Fig. 1). The present paper deals with theoretical considerations, definitions and evaluation formulae. Field and laboratory data on male and female function in some sexual species, various agamospermous plants, and reproduction by specialized vegetative propagules will be dealt with in subsequent publications, now in preparation.

Before I proceed any farther, it is convenient to define reproduction in flowering plants, for there seems to be some confusion in this respect (see e.g. Harper 1977, Grime 1979, Silvertown 1987). We proposed elsewhere (Urbanska 1985) that reproduction be considered as temporal and spatial propagation of parental genes which results in the formation of *physiologically independent* offspring representing a new generation in the demographic sense. This definition is accepted as the departure point in the present paper. It shall be used in the subsequent publications, too, since the physiological autonomy represents a basic notion in the concept of an individual, considered as an active organism not depending on mother, siblings, or neighbour ramets in its life functions.

Reproductive offer

Reproductive offer is defined here as *the amount of reproductive units occurring in female and/or male organs at early pre-mating stages*. As far as female function is concerned, the potential number of descendants is related to the number of ovules, whereas male reproductive performance is undoubtedly influenced by the number of primary pollen grains. These units are accordingly used in the respective formulae of evaluation.

Female reproductive offer $\female RO$ is determined by number of ovules and number of flowers. It may be calculated for an individual as follows:

(a) $$\female RO_I = \sum_{i=1}^{n_I} ov_i \approx \overline{ov} \cdot \bar{n}_I = \overline{ov}_I \quad \text{where}$$

n_I = number of flowers in an individual
$\bar{n}_I$ = average number of flowers per individual
ov_i = number of ovules within the ith flower of the individual
$\overline{ov}$ = average number of ovules per flower
$\overline{ov}_I$ = average number of ovules per individual

For a population, female reproductive offer $\female RO_P$ can be calculated according to the formula

(b) $$\female RO_P = \sum_{j=1}^{P} \female RO_{Ij} \approx p \cdot \overline{ov} \cdot \bar{n}_I \quad \text{where}$$

P = number of individuals within a given population.
$\female RO_{Ij}$ = female reproductive offer of the jth population member

As far as the number of ovules per flower is concerned, it is well known that some flowering plants have uniovulate ovaries, whereas the others may produce numerous to very numerous ovules (see e.g. Kress 1981). According to some authors, evolution of the pollinating system from insect pollination to anemophily is accompanied by reduction in the number of ovules per ovary (Whitehead 1969, Stebbins 1970, Faegri and Van der Pijl 1971). In this respect, the largely insect-pollinated Asteraceae with uniovulate ovaries represent a particularly interesting group.

While the number of ovules per ovary is constant in some plants, the others show variation in this character. For instance, most species of the duckweed family (Lemnaceae) have uniovulate ovaries, but *Lemna gibba* may produce up to seven ovules in a single ovary (Landolt, personal communication). In some closely related taxa of *Cardamine* inhabiting the same limited area, number of ovules per ovary varies within and among individuals (Urbanska unpubl.). The data on plants with variable number of ovules per ovary are very fragmentary and, to the best knowledge of the author, no factors possibly influencing this variation have been studied to date. It should be very interesting to find out whether the variation in the ovule number per ovary is related only to e.g. phenotypic plasticity or remains under some genetic control.

The second variable determining the female reproductive offer is the number of flowers produced. This character may be strongly influenced by environmental factors; for instance, flower buds in high arctic plants are cold hardy, but freezing temperatures kill expanded flowers and prevent maturation of seeds (see e.g. Bell and Bliss 1980). Annual variation in the number of flowers per shoot may be frequently observed in plants inhabiting extreme ecosystems (e.g. *Eschscholzia mexicana,* Urbanska unpubl.; *Cassiope tetragona,* Nams and Freeman 1987). A particularly interesting example of this variation represents *Biscutella levigata* (Gasser 1986); the number of spontaneously aborted flower buds per shoot varies from one to all with any intermediary number in between (Gasser, personal communication). In some plants, on the other hand, the number of flowers per shoot seems to be genetically fixed. For instance, *Taraxacum alpinum* occurring in high-altitude sites shows a pronounced variation in the length of the flowering shoot, but a single capitulum per ramet is the rule; the alpine dandelion represents but a single example of the well-known plants with this kind of the ramet architecture. Another factor influencing the number of flowers produced may be the number of flowering shoots per ramet; this aspect, too, should be carefully considered.

The Asteraceae are an intriguing object for studies on reproductive offer because not only the number of capitula per shoot but also the number of florets per capitulum may be variable in some species. This variation seems to be influenced by various factors. For instance, the excellent study of Tschander (in preparation) revealed that the number of florets per capitulum in *Cirsium spinosissimum* is apparently correlated with the position of a given capitulum within the collective inflorescence formed in the terminal part of the shoot: centrally situated, more numerous capitula consist of fewer florets than the less numerous heads occurring at the perimeter of the large inflorescence. An inverse tendency occurs in *Antennaria pulcherrima* where numerous capitula of female plants are grouped in a loose raceme. Further data on this aspect of variation should be desirable.

Male reproductive offer ♂RO can be calculated for an individual with the equation:

(c) $$\text{♂RO}_I = \sum_{i=1}^{n_I} pg_i \approx \overline{pg} \cdot \bar{n}_I = \overline{pg}_I \qquad \text{where}$$

n_I = number of flowers in an individual
$\bar{n}_I$ = average number of flowers per individual

pg_i = number of primary pollen grains within the ith flower of the individual
$\overline{pg}$ = average number of primary pollen grains
$\overline{pg}_I$ = average number of primary pollen grains per individual

For a population, male reproductive offer $\male RO_P$ can be calculated as follows:

(d) $$\male RO_P = \sum_{I=1}^{P} \male RO_{Ij} \approx p \cdot \overline{pg} \cdot \bar{n}_I \quad \text{where}$$

P   = number of individuals within a given population.
$\male RO_{Ij}$ = male reproductive offer of the jth population member

Data on the number of young pollen grains in the Angiosperms are virtually non-existent since most authors focused on the course of microsporogenesis and/or pollen fertility tests at later developmental stages. It is regrettable because there may be large discrepancies between the number of young and mature pollen grains both per anther as well as per flower. The number of pollen grains notwithstanding their exact development phase is but rarely given in relation to anthers or flowers anyway (e.g. Kawano and Nagai 1975, Smart et al. 1979, Knox 1987). Virtually nothing is known about a possible variation in number of pollen grains within or among individuals of a given population (for some information on grasses, see Campbell et al. 1983). In this respect, too, detailed reports are awaited with much interest.

Reproductive efficiency

The term "reproductive efficiency" has been used previously in the literature without gender specification. On account of a rather arbitrary use, its precise meaning seems a little obscure. For instance, Harper and Ogden (1970) considered a "crude reproductive efficiency" as a synonyme for net reproductive effort; this terminology was followed by some later authors (e.g. Kawano and Nagai 1975). Evans (1971) used a term "mobilization efficiency" also approaching the concept of net reproductive effort. Chester and Shaver (1982) described reproductive efficiency as a "viable seed reproductive effort relative to total reproductive effort". Last but not least, Ruiz Zapata and Arroyo (1978) considered a "reproductive efficacy" as a natural fruit set divided by fruit set in controlled crosses.

I propose to consider reproductive efficiency as *the ability to carry to term* viable reproductive units. The terminating point is defined in male function by the onset of pollen dispersal, whereas female reproductive efficiency should be measured at the seed dispersal. I am fully aware of the fact that the two phenological stages are quite different, but they do have one important feature in common viz. the separation of reproductive units from the plant/plant part which produced them. Bar a few exceptions, pollen and seeds become thus directly exposed to environmental hazards. Before anthesis/seed dispersal, ecological factors influence the reproductive units only indirectly; once dispersed, however, pollen and seeds follow their separate destinies, and the fate of each single unit may be quite different. This essential biological distinction represents, in my opinion, a suitable criterion of evaluation timing.

As in the case of the reproductive offer, reproductive efficiency EFF in sexual plants, and in pseudogamous taxa, too, has two component components viz. female and male efficiency (Table 1, Fig. 1). On the other hand, reproductive efficiency in autonomously agamospermous taxa which are represented by pistillate plants only (e.g. *Antennaria*

porsildii, A. stolonifera), or in taxa reproducing by specialized vegetative propagules is related exclusively to female function. Autonomously agamospermous plants which do produce some pollen (e.g. *Hieracium alpinum, Taraxacum alpinum*) represent a more complex situation because the pollen does not contribute to the seed development. This problem will be discussed in a forthcoming paper, now in preparation.

Female reproductive efficiency ♀EFF i.e. the ability to carry viable seed to term may be expressed by the number of fertile seeds at dispersal relative to the female reproductive offer ♀RO. For an individual, it can be thus calculated by the formula:

$$(e) \qquad ♀EFF_I = \frac{\sum\limits_{i=1}^{n_I} s_i}{♀RO_I} \approx \frac{\bar{n}_I \cdot \bar{s}}{♀RO_I} = \frac{\bar{s}_I}{\overline{ov}_I} \qquad where$$

n_I = number of flowers in an individual
$\bar{n}_I$ = average number of flowers per individual
s_i = number of seeds within the ith flower of an individual
$\bar{s}$ = average number of seeds per flower
$\bar{s}_I$ = average number of seeds per individual
$\overline{ov}_I$ = average number of ovules per individual

For a population, female reproductive efficiency ♀EFF$_P$ may be considered as an average individual efficiency, thus

$$(f) \qquad ♀EFF_P = \frac{\sum\limits_{I=1}^{P} ♀EFF_{Ij}}{P} \qquad where$$

P = number of individuals forming a given population
♀EFF$_{Ij}$ = female reproductive efficiency of the jth population member

Male reproductive efficiency ♀EFF, i.e. the ability to carry viable pollen to term, may be expressed by the number of viable pollen grains at anthesis relative to the male reproductive offer ♂RO; it can thus be calculated for an individual as

$$(g) \qquad ♂EFF_I = \frac{\sum\limits_{i=1}^{n_I} vp_i}{♂RO_I} \approx \frac{\bar{n}_I \cdot \overline{vp}}{♂RO_I} = \frac{\overline{vp}_I}{\overline{pg}_I} \qquad where$$

n_I = number of flowers in an individual
$\bar{n}_I$ = average number of flowers per individual
vp_i = number of viable pollen grains within the ith flower of the individual
$\overline{vp}$ = average number of viable pollen grains per flower
$\overline{vp}_I$ = average number of viable pollen grains per individual
$\overline{pg}_I$ = average number of primary pollen grains per individual

For a population, male efficiency ♂EFF$_P$ may be regarded as an average individual efficiency, thus

$$(h) \qquad ♂EFF_P = \frac{\sum\limits_{i=1}^{P} ♂EFF_{Ij}}{P} \qquad where$$

P = number of individuals forming a given population
♂EFF$_{Ij}$ = male reproductive efficiency of the jth population member

Reproductive efficiency is related to reproductive offer because the reproductive offer determines the maximum number of male germ units or seeds produced by a given individual/population. The efficiency index may equal 1 but mostly is lower than 1; in some intriguing cases the exceedingly low ratio of e.g. seed number to ovule number might even be considered as a waste of the reproductive offer (see e.g. Wiens 1984).

What are the conditions which results in a low reproductive efficiency? Generally speaking, any circumstances which reduce the number of viable seeds or pollen grains will produce this effect; however, the biological/ecological component to female reproductive efficiency may ultimately prevail over genetic factors, whereas male reproductive efficiency seems to be mostly controlled by sterility genes. A low seed acount may result from a low female reproductive offer, but much more frequently is influenced by low reproductive efficiency of the pollen donor, pollinator limitation, female choice, meteorological conditions during the seed ripening period, herbivore/pathogen damage to seeds, fitness of the mother plant, etc. On the other hand, a low pollen and thus sperm count seems to be most frequently influenced by genetic factors; developmental disturbances resulting from e.g. unfavourable weather conditions during the pollen ripening period or damage to anthers prior to the anthesis are important indeed in some cases, but not likely to be predictable hazards of a general consequence.

Similarly to the reproductive offer, reproductive efficiency may be influenced by the number of flowers or their position within inflorescences, but not much is known about this aspect of variation. It might be expected that the more flowers an individual/population has produced, the more viable male germ units or seeds will be developed, but some data clearly demonstrate that, for example, the seed production may sometimes follow rather curious patterns. For instance, an inverse relationship between fruit set per flower and the number of flowers was found in *Asclepias tuberosa* (Wyatt 1980). In *Cirsium spinosissimum* smaller capitula produce more fertile seeds than the larger heads within the same collective inflorescence (Tschander, in preparation). In *Cardamine insueta* flowers occur in profusion but fertile seeds are exceptionally rare (Urbanska 1977, 1980, 1981). With a very few exceptions (e.g. Campbell et al. 1983), no detailed data are available on the number of viable pollen grains relative to the flower position within inflorescence; it should be very interesting to explore this field. Last but not least, a minimum amount of pollen which still ensures the seed development should be further investigated (see Cruden 1977); this aspect would be particularly interesting in pseudogamous plants which are known to have a frequently disturbed microsporogenesis (see e.g. Gustafsson 1946/47, Smith 1963, Nogler 1972). Striking differences in pollen development and its viability occurring among individuals of *Cardamine insueta* (Urbanska 1977, 1978, Urbanska unpubl.) suggest that also this facet of variation should be taken into consideration in studies on reproductive efficiency. Individual differences in male function may be also influenced by differences in fertile stamen number (see e.g. Sterk 1969 a, b).

Seed germination and reproductive success

Reproductive strategies serve the purpose of a successful reproduction resulting in the appearance of active individuals. The seed production alone does not yet represent the reproductive success; since the metabolic activity of seeds is reduced to the indispensable minimum, seed in considered as a cryptobiotic phase in life history of flowering plants (e.g. Amen 1966, Urbanska and Schütz 1986). The appearance of new individuals is
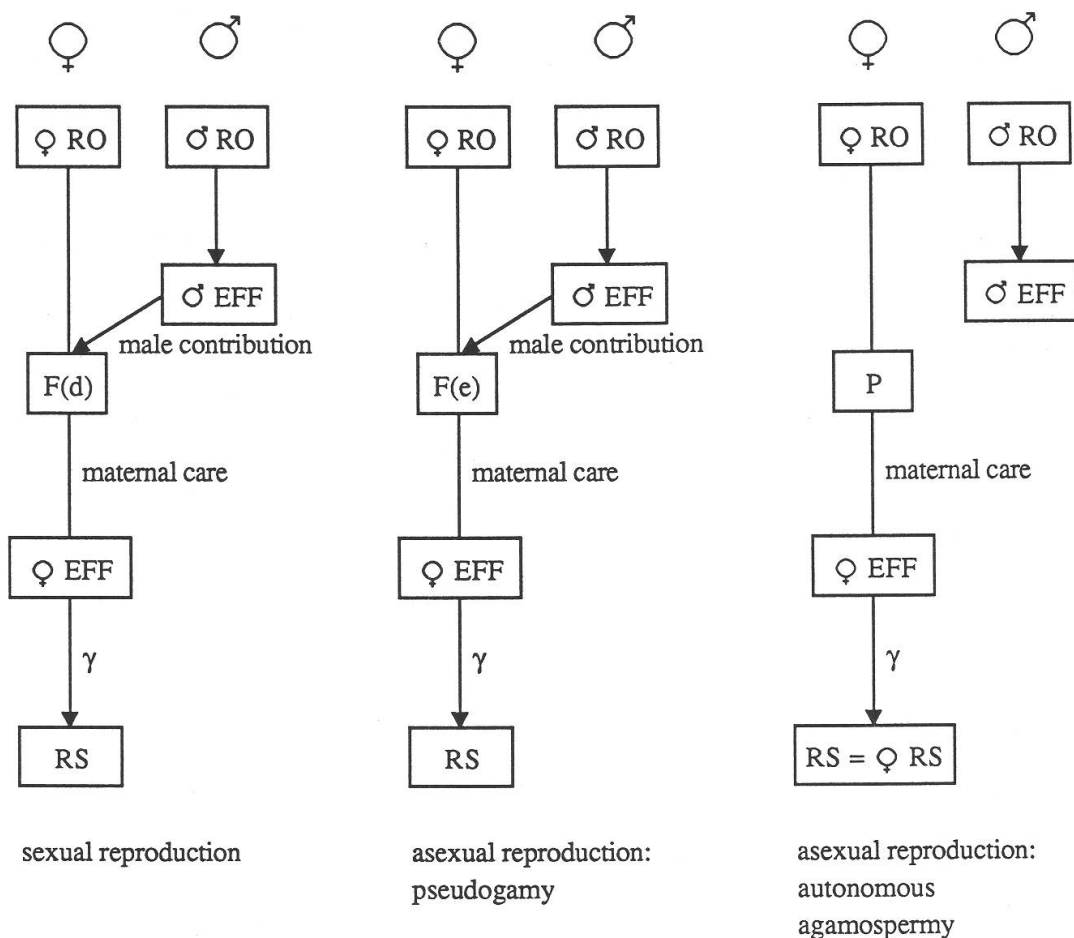
♀   ♂   ♀   ♂   ♀   ♂

♀ RO	♂ RO
♀ RO	♂ RO
♀ RO	♂ RO

♂ EFF   ♂ EFF   ♂ EFF

F(d)   *male contribution*   F(e)   *male contribution*   P

maternal care   *maternal care*   *maternal care*

♀ EFF   ♀ EFF   ♀ EFF

γ   γ   γ

| RS | | RS | | RS = ♀ RS |

sexual reproduction   asexual reproduction: asexual reproduction:
                             pseudogamy   autonomous
                                                            agamospermy

Fig. 1. Reproduction by seed in the Angiosperms: male and female function. RO = reproductive offer. EFF = reproductive efficiency. F(d) = double fertilization. F(e) = fertilization of the endosperm nucleus. P = parthenogenesis. g = germination (%). RS = reproductive success.

heralded by the onset of germination; for this reason germination should be regarded as the third strategic component to reproduction by seed. It is true that seedling dynamics may be quite variable and high mortality rates at this stage are not unusual in some species (e.g. Sarukhan and Harper 1973, Harper 1977, Symonides 1979, Silvertown 1987), but then the mortality risk may be distributed over all life stages and an assessment of reproductive success would accordingly border on metaphysics. The reproductive process can be considered accomplished by germination; the concept of reproductive success is therefore applicable to this phase of plant life history.

Reproductive success in seminiferous plants is determined by reproductive efficiency and germination of the seeds produced. The percentage of germinable seeds produced by a given mother plant indicates female reproductive success; male reproductive success is reflected in the percentage of germinable seeds "fathered" i.e. developed with the sperm contribution from a given male donor. In sexually reproducing plants the seeds are truly fathered in the process of the double fertilization; on the other hand, pseudogamous plants do require the sperm contribution for a successful seed development, but there is no ferilization of the egg cell so that the "fathering" is restricted to the endosperm (Fig. 1). From the genetic point of view, the distinction is obvious but the fathering, true and restricted alike, is essential as far as the biological process of seed development is

concerned. The term has therefore been accepted in the present paper as a synonyme for male contribution. Autonomously agamospermous plants do not require any fathering for the seed development (Fig. 1).

Germinating behaviour of flowering plants represents a very complex phenomenon. It will not be discussed in the present paper; for ample information, the reader is referred e.g. to some recent publications of our research group dealing with diversity and variability in germinating behaviour of alpine plants (Urbanska and Schütz 1986, Schütz 1988, Urbanska et al. 1988, Schütz 1989).

Reproductive success of sexual or pseudogamous Angiosperms can be considered as reproductive success of female and male partners; however, evaluation of reproductive success in self-incompatible plants is related to two different individuals, whereas male and female function in a single individual is to be assessed in self-compatible plants. In autonomously agamospermous or vegetatively reproducing plants reproductive success is related to the single female parent only.

Female reproductive success $♀RS$ can be calculated for an individual by the formula

(i) $$♀RS_I = ♀EFF_I \cdot \gamma_{MI} \approx \frac{\bar{s}_I}{\overline{ov}_I} \cdot \gamma_{MI} \quad \text{where}$$

$♀EFF_I$ = female reproductive efficiency of an individual
γ_{MI} = germination percentage of the seeds produced by a given mother individual

For a population, female reproductive success $♀RS_P$ can be expressed as follows:

(j) $$♀RS_P = ♀EFF_P \cdot \gamma_{MP} \quad \text{where}$$

$♀EFF_P$ = female reproductive efficiency of a given population
γ_{MP} = germination percentage of the seeds produced within this population

Male reproductive success $♂RS$ can be calculated for an individual according to the formula

(k) $$♂RS_I = \frac{♂EFF_I \cdot s_{FI} \cdot \gamma_{FI}}{\sum\limits_{i=1}^{n_I} vp_i} \approx \frac{\bar{s}_{FI} \cdot \gamma_{FI}}{\overline{pg}_I} \quad \text{where}$$

$♂EFF_I$ = male reproductive efficiency of an individual
s_{FI} = number of seeds fathered by a given individual
$\bar{s}_{FI}$ = average number of seeds fathered by a given individual
γ_{FI} = germination percentage of the seeds fathered by a given individual

For a population, male reproductive success can be expressed as follows:

(l) $$♂RS_P = \frac{♂EFF_P \cdot s_{FP} \cdot \gamma_{FP}}{\sum\limits_{j=1}^{P} \left(\sum\limits_{i=1}^{n} vp_{ij} \right)} \approx \frac{s_{FP} \cdot \gamma_{FP}}{p \cdot \overline{pg}_I} \quad \text{where}$$

$♂EFF_P$ = male reproductive efficiency of a given population
s_{FP} = number of seeds fathered by members of a given population
γ_{FP} = germination percentage of these seeds
vp_{ij} = number of viable pollen grains in the ith flower of the jth population member

I deliberately include reproductive efficiency and germination percentage as the parameters in the evaluation of reproductive success because the formulae proposed permit theoretical prognoses concerning a potential input from a given generation of ovules/primary pollen grains. As far as female success is concerned, the fraction of female reproductive offer which may give rise to new individuals via seed is indicated; the evaluation of male reproductive success gives the fraction of male reproductive offer expected to contribute to new individuals via male germ units. Formulae based only on the number of seeds produced and their germination percentage would give incomplete information on reproductive strategies because important pre-mating stages would have been ignored.

Concluding remarks

The purpose of the present paper was certainly not to review in detail all the data available on reproduction by seed in flowering plants. Rather, I wished to link up the most essential strategic elements of this reproduction, and to point out the importance of various strategic units involved.

Since the concept presented is based on different reproductive stages, different methods will have to be used in assessment of female and male function. Some useful approaches are long known. For instance, the routine squashes stained with aceto-carmine proved well-suited to the counting of ovules in fresh and fixed material of *Cardamine;* they were helpful, too, in determination of the pollen grain number, and it was even possible to distinguish the components of male germ unit (Urbanska unpubl.). Other interesting methods are described e.g. by Kawano and Nagai (1975), Smart et al. (1979) as well as Kenrick and Knox (1982). The latter authors worked out a spectacular method to determine the number of ovules by means of incident fluorescence microscopy; it is well worth trying in further studies, for not only fresh or fixed material but also rehydrated herbarium samples may be studied in this way. While the studies on reproductive offer, reproductive efficiency, and germination are rather easy to carry out and do not require sophisticated laboratory equipment, the assessment of male reproductive success may be a different matter entirely. The autogamous and, in particular, cleistogamous taxa should not be too difficult, but xenogamous and pseudogamous plants may represent quite a challenge. As far as the self-incompatible sexual taxa are concerned, paternity analyses based on identification of polymorphic loci seem promising (see e.g. Hamrick and Schnabel 1985, Meagher and Thompson 1986, Hamrick 1987); this methodical approach does not apply, however, to pseudogamous plants which produce maternal progeny. Further studies in this field truly offer exciting perspectives, and experimental populations may be the best suited to this purpose.

The concept presented and the general notion of reproductive effort are by no means mutually exclusive but complement one another. While the measurements of reproductive effort indicate a global resource allocation to reproduction, data on e.g. reproductive offer demonstrate how was invested some part of this allocation and what its distribution patterns were. In fact, *both* approaches may be indispensable indeed to a complete assessment of life-history strategies in plants.

Data on reproductive offer/efficiency/germination percentage are important for a better understanding of why the flowering plants do things the way they do. Species with a specialized reproductive behaviour (e.g. amphicarpic or agamospermous) would be prime objects for future studies. It should be pointed out, however, that the concept of reproductive strategies outlined in the present paper may not only be interesting for basic

research, but represents an impotant basis for applications. This importance is rather well demonstrated by the current research of our group (e.g. Schütz 1988, 1989, Urbanska et al. 1988). So far data on germination of about 120 alpine taxa were gathered; studies on reproductive offer and reproductive efficiency are in progress. Our long-term objective is to run a functional database, helpful in selection of the material which would be optimally suited to the revegetation of erosion-endangered sites above the timberline. In this respect, the concept presented may bring some new insights to the old problem of biological erosion control in extreme ecosystems.

Zusammenfassung

Fortpflanzungsstrategien der Blütenpflanzen wurden bisher meistens als Resourcenverteilung zugunsten der Fortpflanzung betrachtet. Dies wurde Fortpflanzungsaufwand (reproductive effort) genannt. Die vorliegende Arbeit gibt eine kurze Übersicht dieses Konzepts sowie der Probleme, die mit der Auswertung des Fortpflanzungsaufwandes verbunden sind. Es wird ein revidierter Ansatz zu Erfassung von Fortpflanzungsstrategien für sich durch Samen fortpflanzende Angiospermen vorgeschlagen. Dieser wird gestützt auf das Verhalten von verschiedenen Fortpflanzungseinheiten.

Die wesentlichen strategischen Komponenten der Fortpflanzung durch Samen sind 1) das Fortpflanzungsangebot RO (reproductive offer), 2) die reproduktive Effizienz EFF und 3) der Keimungsprozentsatz γ. Das Fortpflanzungsangebot, definiert als Menge von Fortpflanzungseinheiten, die in weiblichen und männlichen Organen während früher Fortpflanzungsphasen vorhanden sind, wird durch die Anzahl von Samenanlagen bzw. primären Pollenkörnern bestimmt. Die reproduktive Effizienz wird als Fähigkeit definiert, lebensfähige Fortpflanzungseinheiten auszutragen; der Auswertungszeitpunkt entspricht der Anthesis bzw. Samenverbreitung. Die weibliche reproduktive Effizienz von sexuellen oder pseudogamen Pflanzen ist meistens durch die männliche reproduktive Effizienz sowie weitere biologisch-ökologische Faktoren beeinflußt; die männliche reproduktive Effizienz dagegen scheint meistens durch genetische Faktoren kontrolliert zu sein. Die weibliche reproduktive Effizienz von jenen autonom agamospermen Arten, die nur durch weibliche Pflanzen vertreten sind, gleicht der globalen Effizienz von Individuen/Populationen.

Der reproduktive Erfolg, definiert als das Erscheinen von aktiven Individuen, die eine neue Generation im demographischen Sinne bilden, ist sowohl durch die reproduktive Effizienz als auch durch den Keimungsprozentsatz bestimmt. Diese beiden Variablen sind deshalb in der vorgeschlagenen Formel zur Berechnung des reproduktiven Erfolges inbegriffen.

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