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## INVESTING IN ADAPTATIONS TO RARE EVENTS- A REPRODUCTIVE STRATEGY

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**Summary.** The occurrence of apparently unused organs and mechanisms related to reproduction has been described in various plants. A hypothesis is presented, suggesting that such structures will be retained if involved, even very rarely, in reproductive events with important evolutionary consequences. Two such cases are demonstrated: In the heterocarpous *Calendula arvensis*, cross-pollination, which is very rare, can occur only in the most peripheral among the ray florets. These florets, whether self-or cross-pollinated, always form the largest achenes with the most elaborate adaptations for dispersal and the largest embryos. Flowers of *Medicago polymorpha* were shown to be self-pollinated previous to anthesis and their unused «explosive» tripping mechanism seems superfluous. However, at least in one region where this species is naturalized, a high percentage of outbreeding was observed. Selection for increased outbreeding during colonization and habitat-dependent regulation of the breeding system are proposed as possible explanations.

It is suggested that investing in adaptations to rare reproductive events with far-reaching consequences may be a rather widespread reproductive strategy.

**Resumen.** Se ha descrito en varias plantas la existencia de órganos y mecanismos aparentemente inútiles relacionados con la reproducción. Se presenta una hipótesis por la que se sugiere que cuando se presentan, aunque sea muy rara vez, estas estructuras se mantienen en situación en que la reproducción tiene consecuencias evolutivas importantes. Se muestran dos de estos casos. En *Calendula arvensis*, que presenta heterocarpia, la polinización cruzada, que es muy rara, puede tener lugar sólo en las flores liguladas más externas. Estas flores, sea por autogamia o por alogamia, forman siempre los aquenios más largos que son los que presentan una mejor adaptación para la dispersión y los embriones más grandes. En *Medicago polymorpha*, las flores se autopolinizan antes de la anthesis, por lo que parece superfluo su excepcional mecanismo de apertura explosivo. Sin embargo, al menos en una región en que esta especie se encuentra naturalizada, se ha observado un alto porcentaje de alogamia. Se propone para explicarlo la influencia de la selección para aumentar la alogamia durante la colonización y la regulación del sistema de reproducción por factores ambientales. Se sugiere que la utilización de sistemas reproductores especiales con consecuencias de largo alcance puede ser una estrategia reproductora bastante extendida.

## INTRODUCTION

While engaged many years ago in the study of the annual species of the genus *Medicago*, I became fascinated by the fact, that while the majority of the species have an elaborate pollination mechanism (explosive tripping mechanism), they are self-compatible and do not seem to be visited at all by any pollinating agents (HEYN, 1963). At that time I was content to interpret this phenomenon as the result of the common assumption that anatomy and morphology are more conservative than the use of organs and are the expression of the evolutionary history of the genus.

However, up to date evolutionary thinking, including the relation of cost of investment/fitness concept, has brought me back in recent years to ask more questions about the existence of «unused organs» and «superfluous production», especially connected with reproduction.

The hypothesis I am going to present here is that organs and mechanisms, which seem to be unused and superfluous, may be found by meticulous research to be involved in such very rare events which have far-reaching consequences.

Living in the country of the bible, I tend to call this hypothesis after Ecclesiastes (11,1) «Cast thy bread upon the waters for thou shalt find it after many days».

In this lecture I shall try to illustrate the principle in two species which were studied at our laboratory during recent years.

## CALENDULA

While working on various aspects of the genus *Calendula* (HEYN & al., 1974, JOEL, 1978, HEYN & JOEL, 1983), we observed self-compatibility in all annual *Calendula* species and the amount of fruit formed was identical under conditions of open pollination and in an insectproof nethouse. In an additional study of *C. arvensis* L. with the aim of learning about pollen allocation (HEYN & SNIR, 1986), it was found that on the average only about 30% of the pollen grains, produced in each flowering head, have a definite allocation: deposited on the stigmas (6%) or permanently lost, either by being not viable (5%) or by remaining in the floret tube after wilting (19%). The residue (70%) of the pollen produced is, in fact, «cast upon the waters». This, together with the high P/o ratio per head (considered not as an absolute

measure of the breeding system but as an approximation, cf. PRESTON, 1986) seems to point towards the occurrence of, at least, some outbreeding.

In HEYN & SNIR (1986) the outbreeding potential of *C. arvensis* was assessed by monitoring the phenology of florets and capitula. In flowering heads of this species (as in the genus as a whole) the ray florets are female and the disc florets function exclusively as male. The plants have to be considered, therefore, as monoicous and according to the sequence of flowering of florets from the periphery inwards, the heads are protogynous. However as shown in the phenological scheme in that study, protogyny is obliterated by the simultaneous flowering of all female florets with one third of the male florets. Some additional factors contribute to causing geitonogamous pollination in each flowering head. (1) The stigmatic style-branches of the ray florets are radially orientated, as found also in some other Asteraceae (ROBINSON, 1984), so that they easily touch the pollen presented on the unfunctional style of the male florets. (2). At the end of the first day of flowering the heads close (as subsequently every evening) and the stigmatic surfaces cannot avoid to get in touch with the pollen of the disc florets. (3) It was observed that the flies (*Usia* sp. and *Empis* sp.), which are the main pollinators of *C. arvensis* in the region observed, collect nectar while walking radially towards the center of the capitulum and back again to the periphery. Consequently their visits, except when alighting on the head, mainly result in geitonogamous pollination.

As can be seen, the possibility that any florets in a capitulum will be outcrossed is rather small: it may happen if ever, only in the most peripheral ray florets following immediately the opening of the capitulum (during the short period between the arrival of pollinators and before the style-branches touch the pollen presented by the disc florets).

We have had, however, previous indications that some outbreeding in *C. arvensis* may occur. First, populations are usually extremely heterogeneous and side by side plants with a great variation in capitulum size and colour can be observed (HEYN & al., 1974). Second, in some populations we find pollen grains with typical «hybrid» characters, micropollen and pollen with more than the normal three apertures (JOEL, 1978).

The third, perhaps most conspicuous indication of outbreeding, can be found in the fruit variation and the occurrence of pure forms together with intermediates (cf. HEYN & al. 1974). The proven fact that intraspecific and interspecific artificial hybridization is very easily achieved experimentally (HEYN & JOEL, 1983) may be an additional indication that some outbreeding in the capitula of *C. arvensis* might occur.

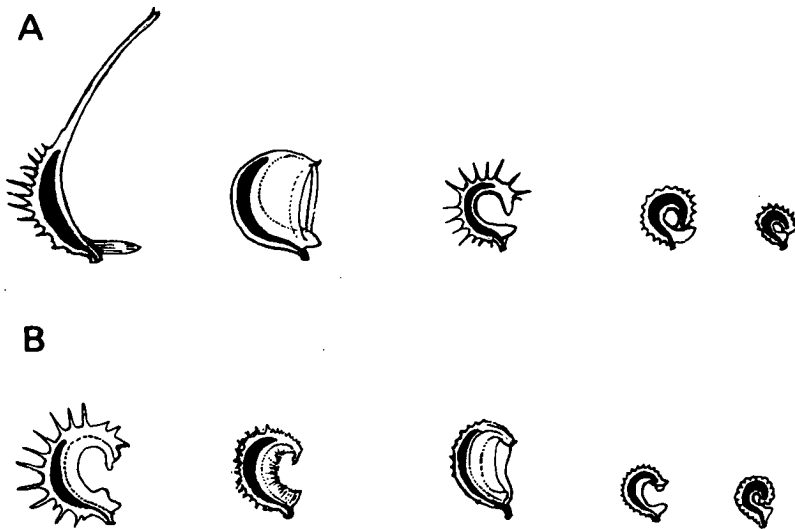


Fig. 1. Achenes from two heads, A and B, of *Calendula arvensis*; achenes are arranged in order of anthesis of the florets, embryos are shaded.

We should keep in mind that the most striking character of the genus *Calendula* in general, and of *C. arvensis* in particular, is the heterocarpy prevailing in the flowering heads. A single head may comprise achenes of five or more different shapes (Fig. 1). There is, however, a constant pattern in the shape of the achenes: according to the sequence of flowering they decrease in size, in the means for dispersal away from the mother plant (exozoochoric or anemochoric) and in embryo size. The last (innermost) achenes are always very small, without any devices for dispersal by wind or animals and with a very small embryo (Fig. 1).

#### MEDICAGO

The pollination mechanism of legumes with papilionate flowers -tripping mechanism- can be defined in general terms as a mechanism which «occurs as the staminal column is released under pressure of the pollinating vector as it alights on the wing petals...» (KALIN ARROYO, 1981). It is assumed that tripping is usually enhancing cross-pollination and that the thick cuticle, typical for the papilionaceous legumes, covering the stigma (each secreting

papilla separately or the stigma as a whole) is ruptured as a direct or indirect result of tripping (a sample of records: JOST, 1907, MOENCH, 1911, BRINK & COOPER, 1938, J. & Y. HESLOP-HARRISON, 1983).

Various tripping mechanisms, usually considered to be of four main types, have been repeatedly described since the nineteenth century. In this context it should be only pointed out that tripping mechanisms are as a rule reversible: during anthesis each visit by a pollinator causes presentation of pollen (like in *Trifolium*, *Lotus*, *Lupinus*, *Vicia*, etc.). The only irreversible tripping mechanism is the «explosive tripping mechanism» in which the staminal column and stigma, compressed inside the keel, erupt suddenly, thereby scattering the pollen. Such mechanism has been described in several unrelated genera including *Medicago*.

In recent years KREITNER & SORENSEN (1984, 1985) and ALON (1986) studied the connection between pollination and stigma development in *Medicago*, the former in *M. sativa* and the annual *M. scutellata*, the latter in some species of several legume genera, including *M. sativa* and the annual *M. polymorpha*. Though their results in *M. sativa* somewhat differ (perhaps due to using different cultivars), their conclusions concerning pollination and breeding system in the two annual species fairly agree. Their studies of stigma development by light and electron microscopy, showed that pollination occurs in the flowers of the annual species prior to anthesis. At that time the cuticle covering the surface of the stigma is already disrupted and the stigma is covered by the pollen embedded in the copious stigmatic secretion. Self-pollination occurs without any activation of the tripping mechanism.

ALON (1986) further showed that in *M. polymorpha* fertility is equal under conditions of open pollination, and in an insect-proof nethouse, whether flowers are artificially tripped or not. She found pollen tubes reaching as far as the ovules 2-3 days prior to anthesis.

All results mentioned above point towards self-pollination (and resulting self-fertilization) to be the rule in *M. polymorpha* and possibly in the majority of the annual species of *Medicago*. However, JAIN (1976) recorded a high outcrossing rate in several Californian populations of *M. polymorpha* (average 8.2%).

## DISCUSSION

The data concerning reproduction of *C. arvensis* and *M. polymorpha* are presented in this paper, not in order to serve as an additional illustration

of the evolutionary advantage of combined inbreeding and outbreeding (cf. JAIN, 1979, and references there) or of «alternative modes» in reproduction (PLITMANN, 1986). Our aim is to show here, that the compensation for the investment in excessive pollen (in *C. arvensis*) and in the «unused» tripping mechanism (in *M. polymorpha*) is «paid for» by the special and far-reaching consequences of outcrossing (in addition to the normal evolutionary importance of outbreeding in mainly inbreeding species).

In *C. arvensis* with predominantly geitonogamous pollination in the flowering heads, it was shown that any achenes formed by outcrossing will be in the most peripheral florets. These always form the largest achenes with the most elaborate adaptations for dispersal and the largest embryos. So we can assume that some of the achenes which have the means for reaching new habitats, will be heterozygous, and have advantage under new conditions. Furthermore their comparatively easy establishment is warranted by the large embryo. Such dispersal units seem ideal for colonizing new habitats; the distribution pattern of the synanthropic species *C. arvensis* can bear witness to the large colonizing capacity of the species.

It should be added that the extent of outbreeding can be regulated by environmental factors: climatic factors influence the phenology of the flowering head (slower rhythm of anther development enhances outcrossing) as well as pollinator density.

The high outcrossing rates found by JAIN (1976) in Californian populations of *M. polymorpha* seem incompatible with the data obtained by ALON (1986) for flower development and pollination (equal to those of KREITNER & SORENSEN, 1984, 1985, in *M. scutellata*), causing obligatory self-pollination.

We should, however, keep in mind, that Jain's studies were made in *M. polymorpha* in California, where it grows as a naturalized species, whereas ALON (1986) investigated plants from their natural habitats. It will not be farfetched to assume that selection has played a major role in the invasion and successful establishment of *M. polymorpha* in California. Especially because, no doubt, habitat conditions (climatic, edaphic, etc.) in California differ in many characteristics from those in the natural habitats of *M. polymorpha*.

Retaining the tripping mechanism makes outcrossing possible if, for some reason, self-pollination and self-fertilization are postponed till anthesis, when foreign pollen can «enter the competition». This could be not only the result of selection, but also may be caused by environmental changes. Cases of changes in the breeding system through changes in the flower phenology as

the result of added soil moisture have been recorded recently by LORD & Y. HESLOP-HARRISON (1984) in *Vicia* and by ALON (1986) in *Spartium*.

If such environment-regulated changes in the breeding system are not an exception, it is much easier to understand the investment in the apparently unused tripping mechanism: It is used if the environment triggers off the change from obligatory to facultative selfing. This will happen in new habitats and as a result will have great impact on the colonizing capacity of the species.

It is assumed that in many species, with apparently unused structures, we shall be able to find similar cases of rare use with far-reaching consequences and that this may be a reoccurring reproductive strategy.

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