Seasonal cleistogamy: a conditional strategy to provide reproductive assurance

PETER REDBO-TORSTENSSON and HENRIK BERG

Department of Ecological Botany, University of Uppsala, Villavägen 14, S-752 36 Uppsala, Sweden

SUMMARY

Three populations of the cleistogamous species *Oxalis acetosella* and one population of the cleistogamous species *Viola hirta* (during 2 years), were investigated to determine whether the fertilization success of chasmogamous flowers influences the number of per ramet produced chasmogamous seeds, cleistogamous flowers, cleistogamous seeds and the total number of released seed per ramet. In both species chasmogamous (CH) flowers are produced before the cleistogamous (CL) ones.

Fertilization success influenced number of produced CH seeds per ramet. In both species, ramets with one or more unfertilized CH flowers produced significantly fewer CH seeds. The number of produced CL flowers per ramet varied due to site membership (*O. acetosella*) and ramet size, but also due to the fertilization success of CH flowers. In both species, ramets with some CH flowers left unfertilized, responded with an increased production of CL flowers and seeds. In none of the species did the fertilization success of CH flowers influence the total seed output per ramet. Consequently, the increased production of CL flowers compensated for any loss in fruit- and seed-set owing to unsuccessful fertilization of CH flowers.

Key-words: Oxalis acetosella, Viola hirta, fruit-set, chasmogamous flowers, seed-set.

INTRODUCTION

Possession of two or more distinct types of structures that perform the same general function is a common phenomenon in plants. The two types may occur simultaneously on one individual and constitute a multiple strategy, or occur separated in time and compose a conditional strategy. In the latter case, the occurrence of each respective type is triggered by some specific environmental cue or the plant's own status, representing a plastic response (Lloyd 1984).

One example of a strategy that is either multiple or conditional is the production of both open and potentially outcrossed chasmogamous (CH) flowers, and closed, selfed cleistogamous (CL) flowers. This strategy has been recorded in 56 angiosperm families (Lord 1981).

The evolution of cleistogamy is a complex phenomenon and there are many hypotheses for the genetic and ecological advantages and disadvantages of the respective flower types (e.g. see Mitchell-Odds & Waller 1985 for references). To explain

the occurrence of cleistogamy, however, it is necessary to consider why cleistogamous plants maintain two types of flowers and what factors influence the relative allocation of resources to the two reproductive modes (Schoen 1984).

Concerning the regulation of flower-type it is possible to discern at least two different types of cleistogamous species: those in which the allocation to CH and CL flowers is mediated largely by plant growth and plant size, and those where photoperiod and temperature determine the floral form produced (Lord 1981). In addition, depending on species, the CL flowers are developed before, after, or simultaneously with the open ones (Lord 1981). Although the production of the two flower types may be separated in time, Schoen & Lloyd (1984) regard cleistogamy as a multiple strategy provided that both flowers are produced during the same flowering season. Yet, if the two flowering modes are separated in time their proportions may be adjusted in relation to current environmental conditions or plant status and, consequently, cleistogamy may be viewed as a conditional strategy (*sensu* Lloyd 1984).

For 'normally' open flowers, Lloyd (1992) showed that the primary advantage of self-fertilization is in providing reproductive assurance when cross-fertilization is inadequate, and by delayed selfing the plant may optimize the advantage of both self- and cross-fertilization. In several seasonally regulated cleistogamous species, the outcrossed CH flowers are produced before the selfed CL ones. A division of fertilization strategy, like this, into two distinct and phenologically separated reproductive structures, implies the possibility of regulating the allocation of resources to delayed selfing in relation to cross-fertilization success. Thus, production of CL flowers may buffer the yearly seed output under circumstances with low pollinator activity.

In this paper we present the result from a field study on the fruit and seed set in two seasonally regulated cleistogamous species. We examine whether the fertilization success of CH flowers influences (i) the per ramet production of CH seeds, CL flowers and CL seeds; and (ii) the total number of released seeds per ramet. The data was collected from three different populations of *Oxalis acetosella* L. in 1993 and from one population of *Viola hirta* L. during 1993 and 1994.

MATERIALS AND METHODS

Oxalis acetosella is a low-growing perennial herb with a slender creeping rhizome rooting adventitiously and bearing prominent swollen, fleshy petiole bases which act as storage organs. *O. acetosella* is a circumpolar species. In Europe it is found from Scandinavia to the mountains of central Spain, Italy and Greece. *O. acetosella* is found in many types of plant communities but is most common in moist forest. All flowers are produced singly on peduncles arising from the petiole bases. CH flowers are 5-merous and actinomorphic. Petals are white with purple veins serving as nectar guides (Packham 1978). They are slightly protandrous with the 10 anthers releasing their pollen as the stigmas are exerted. Insect visitors include flies, thrips, beetles, bees and bumblebees (Packham 1978; Jasieniuk & Lechowicz 1987; Redbo-Torstensson, personal observation).

Viola hirta is a low-growing perennial rosette hemicryptophyte with a short thick rhizome. The species is mainly restricted to Europe and W Asia and occurs as an adventive in some outlying localities in Fennoscandia (Hultén & Fries 1986). The species grows in grazed and ungrazed limestone grassland, in the edge of woods and in clayey ditchbanks. Similar to *O. acetosella*, the flowers are produced singly on peduncles

arising from the petiole bases. Chasmogamous flowers are 5-merous and zygomorphic with blue-violet petals. The insect-pollinated CH flowers are mostly visited by bees and bumblebees (Clapham *et al.* 1987; Redbo-Torstensson, personal observation). The CH flowers are apparently never selfed in nature though self-fertile (Clapham *et al.* 1987).

In both species CL flowers are greatly reduced in size and remain closed throughout their development. Anthers contain fewer pollen grains compared with CH flowers. Pollen grains germinate within the anther and pollen tubes grow through the anther wall into the stigma (Packham 1978; Lord 1981).

The study on fruit and seed set in *O. acetosella* was carried out in 1993 at three different sites.

Site 1. A mixed forest 20 km east of Uppsala (59°50′03″N, 17°50′03″E). Besides Norway spruce (*Picea abies* (L.) Karst) it also contains *Quercus robur* L. and *Corylus avellana* L. The field layer is comparatively rich. In the spring it is dominated by *O. acetosella* and *Anemone nemorosa* L.

Site 2. A coniferous forest (*P. abies* and *Pinus sylvestris* L.) next to site 1 (59°50′06″N, 17°50′03″E). At this site *O. acetosella* occurs in small patches in the field layer which is dominated by the grass *Deschampsia flexuosa* (L.) Trin.

Site 3. A deeply shaded coniferous forest (*P. abies* and *P. sylvestris*) on Grimskär, a small island (2 km^2) (61°13′50″N, 17°14′30″E), in the archipelago of Söderhamn, 200 km north of Uppsala. The field layer in the area is very sparse and *O. acetosella* grows in small patches in the moss-layer both on the ground and on boulders. At site 3 the growing season is approximately 3–4 weeks shorter than at the two sites near Uppsala.

The study on *V. hirta* was carried out in 1993 and 1994 on a grazed meadow in the vicinity of *O. acetosella*'s site 1 and 2 (59°50′09″N, 17°50′10″E). In the area *V. hirta* grows on dry hillocks together with, e.g. *Chrysanthemum leucanthemum* L., *Filipendula vulgaris Moench, Viola riviniana* Rchb. and *Heliathemum nummularium* (L.) Mill.

In May 1993, ten 40 × 40 cm plots were established at each of the three sites of *O. acetosella*. Each plot was marked with two 400 × 20 mm plastic tubes securely driven into the ground, leaving only *c.* 15 mm above-ground, on to which a wooden frame could be fitted during observation. We randomly selected 10 ramets with CH flower buds in each plot early in May. Tagging was made by slipping small pieces of straw over each of the selected ramets.

In 1993 and 1994 *c.* 80% of the rosettes of *V. hirta* with CH flower buds were tagged with small numbered flags and their locations were mapped. Only rosettes growing just beneath or within thorny shrubs were excluded. For convenience, in the following text the term ramet is used instead of rosette.

All flowers produced by the tagged ramets between May and September in both years were subsequently marked (by slipping small pieces of straw over the peduncles) and their fates registered. All mature capsules were collected and the contents of the capsules were inspected. During the first 2 months we visited the sites at weekly intervals, but later in the season we returned only fortnightly. In May we also counted the number of leaves per ramet. Unfortunately, a small number of the marked *O. acetosella* ramets were lost at each site.

We analysed the relationship between CH seed, CL flower, CL seed production per ramet, and the total seed output per ramet and fertilization success of CH flowers with

Table 1. The number of chasmogamous and cleistogamous flowers, and the number of these flowers that developed to a fruit and to a dehisced capsule of *Oxalis acetosella* at three different sites in central Sweden. Mean number of chasmogamous and cleistogamous flowers per ramet (± SD) and seeds per capsule (± SD) are also presented

	Chasmogamous			Cleistogamous		
	site 1	site 2	site 3	site 1	site 2	site 3
No. of ramets	90	97	99	90	97	99
No. of flowers	142	134	147	256	220	71
No. of fruits	98	101	135	248	213	66
No. of dehisced capsules	70	48	126	123	154	57
Fruit:flower ratio	0·69	0·75	0·92	0·97	0·97	0·93
Dehisced capsule:fruit ratio	0·71	0·48	0·93	0·50	0·72	0·86
No. of seeds per capsule	6·9 (2·5)	6·6 (2·2)	7·5 (2·1)	6·5 (2·4)	6·2 (2·3)	7·3 (2·0)
No. of flowers per ramet	1·6 (0·7)	1·4 (0·5)	1·5 (0·6)	2·8 (1·7)	2·4 (1·4)	0·7 (0·7)

analyses of deviance using generalized linear models (McCullagh & Nelder 1989). The response variables that were counts were considered to have a Poisson distribution. The order of inclusion of the explanatory variables in the analyses followed the principle of first including (and thus removing the effect of) variables of least interest in the analyses. In the analysis we first included ramet size by using leaf number per ramet as a measure of ramet size, after which site membership (*O. acetosella*) or year (*V. hirta*) and fertilization success and their interactions were included. The ramets were divided into only two classes according to fertilization success; with or without unfertilized CH flowers. The contribution of any term in the model is measured by the change in deviance.

The analyses of deviance were performed with GENSTAT5, release 3.1 (Lawes Agriculture Trust 1993). All other statistics were calculated using SYSTAT (Wilkinson 1992).

RESULTS

The production of CH and CL flowers in *O. acetosella* and *V. hirta* is phenologically separated. In both species the CH flowers were produced in the spring early in May. The flowering period of the CH flowers was completed within 3 weeks. In both species the dispersal of the CH seeds occurred in the second week of June.

We observed the first CL flowers in both species in the middle of May. The first CL seeds were dispersed during the last week of June. In both species most CL-flowers were produced in June but in contrast to the CH ones the production of CL flowers continued throughout the growing season from May to late September. A few ramets of *V. hirta*, for instance, produced their first CL flowers in August.

Fruit- and seed-set

Mean number of CH and CL flowers per ramet in the respective species are presented in Tables 1 and 2. In *O. acetosella* the number of CL flowers per ramet varied considerably between sites. In contrast, the number of CH flowers per ramet was almost

Table 2. The number of chasmogamous and cleistogamous flowers, and the number of these flowers that developed to a fruit and to a dehisced capsule during 1993 and 1994 in a population of *Viola hirta* in central Sweden. Mean number of chasmogamous and cleistogamous flowers per ramet (± SD) and seeds per capsule (± SD) are also presented

	Chasmogamous		Cleistogamous	
	1993	1994	1993	1994
No. of ramets	95	98	95	98
No. of flowers	189	200	81	82
No. of fruits	124	87	73	65
No. of dehisced capsules	91	60	68	58
Fruit:flower ratio	0·66	0·44	0·90	0·79
Dehisced capsule:fruit ratio	0·73	0·69	0·93	0·89
No. of seeds per capsule	12·8 (6·9)	10·9 (7·8)	14·8 (6·8)	14·8 (5·5)
No. of flowers per ramet	2·0 (0·9)	2·1 (1·1)	0·8 (1·1)	0·8 (1·0)

the same in the three sites. We observed no differences between years in the number of CH or CL flowers produced per ramet in *V. hirta*.

In *O. acetosella* the fruit-set of CH flowers differed among the three sites (Likelihood ratio $\chi^2=26\cdot4$, d.f.$=2$; $P<0\cdot001$), while the fruit-set of CL flowers was independent of site (Table 1). At sites 1 and 2 the open pollinated flowers had a significantly lower fruit-set compared with the self-pollinated CL flowers (site 1, Likelihood ratio $\chi^2=61\cdot6$, d.f.$=1$, $P<0\cdot001$; site 2, Likelihood ratio $\chi^2=36\cdot2$; d.f.$=1$, $P<0\cdot001$), but not at site 3.

In *V. hirta* the fruit-set of CH flowers differed between year (Likelihood ratio $\chi^2=19\cdot3$, d.f.$=1$, $P<0\cdot001$), while the fruit-set of CL flowers was independent of year (Table 2). In both years CH flowers had a significantly lower fruit-set compared with CL flowers (1993, Likelihood ratio $\chi^2=19\cdot6$, d.f.$=1$, $P<0\cdot001$; 1994, Likelihood ratio $\chi^2=33\cdot3$, d.f.$=1$, $P<0\cdot001$).

In both species a considerable number of both CH and CL fruits respectively were lost before they dehisced (Tables 1 and 2). In *O. acetosella*, we found remains of bitten off capsules or flowering stalks which probably suggest that mice and/or voles preyed upon the capsules. At sites 1 and 2 the proportion of fruits consumed was dependent on flower type (site 1, Likelihood ratio $\chi^2=19\cdot3$, d.f.$=1$, $P<0\cdot001$; site 2, Likelihood ratio $\chi^2=19\cdot8$, d.f.$=1$, $P<0\cdot001$). At site 3, a lower proportion of the capsules were preyed upon compared with the other sites, independent of flower type.

In a minority of cases, we observed predation by slugs on *V. hirta* fruits, but usually only the flowering stalk was to be found. In both years the proportion of fruits lost was dependent on flower type (1993, Likelihood ratio $\chi^2=13\cdot1$, d.f.$=1$, $P<0\cdot001$; 1994, Likelihood ratio $\chi^2=9\cdot40$, d.f.$=1$, $P=0\cdot002$)

Relationship between fertilization success of CH flowers and production of CL flowers and seeds

Fertilization success influenced number of produced CH seeds per ramet. In both species, ramets with one or more unfertilized CH flowers produced significantly fewer CH seeds (Tables 3 and 4).

In *O. acetosella* about one quarter (28%) of the ramets had one or two unfertilized CH flowers. One difference found between these ramets and ramets with all CH flowers

Table 3. Analysis of deviance for number of produced chasmogamous seeds, cleistogamous seeds, cleistogamous flowers, cleistogamous seeds, and released seeds per ramet in *Oxalis acetosella*, growing at three sites in central Sweden and predictions (and standard errors) derived from the analyses. The explanatory variables (source of variation) and their interactions are given in the order of their inclusion in the analyses. Mean deviance ratios are tested for significace by referring them to a *F* distribution. The predictions are derived from the 'final model'

Source of variation	d.f.	CH seeds per ramet		CL flowers per ramet		CL seeds per ramet		Total seeds per ramet	
		Mean dev. ratio	P	Mean dev. ratio	P	Mean dev. ratio	P	Mean dev. ratio	P
Ramet size	1	15·54	<0·001	6·00	<0·05	11·29	<0·005	22·48	<0·001
Site	2	21·90	<0·001	104·62	<0·001	36·76	<0·001	4·43	<0·05
Fertilization success	1	45·22	<0·001	40·14	<0·001	24·18	<0·001	0·26	NS
S × F	2	0·33	NS	1·00	NS	1·51	NS	6·62	<0·005
Residual	272								

Ramets class	Site 1				Site 2				Site 3			
	CH seeds per ramet	CL flowers per ramet	CL seeds per ramet	N	CH seeds per ramet	CL flowers per ramet	CL seeds per ramet	N	CH seeds per ramet	CL flowers per ramet	CL seeds per ramet	N
All CH flowers fertilized	3·9 (0·56)	2·2 (0·21)	9·5 (1·00)	50	8·0 (0·92)	2·0 (0·18)	6·5 (0·94)	65	9·2 (0·75)	0·6 (0·08)	3·5 (0·50)	87
Some CH flowers unfertilized	1·5 (0·54)	3·8 (0·31)	16·5 (2·06)	40	2·9 (0·60)	3·6 (0·37)	13·4 (1·50)	25	2·4 (0·92)	0·7 (0·22)	3·7 (0·94)	12

Table 4. Analysis of deviance for number of produced chasmogamous seeds, cleistogamous flowers, cleistogamous seeds, and released seeds per ramet in *Viola hirta*, growing on a grazed meadow in central Sweden, and predictions (and standard errors) derived from the analyses. The explanatory variables (source of variation) and their interactions are given in the order of their inclusion in the analyses. Mean deviance ratios are tested for significance by referring them to a F distribution. The predictions are derived from the 'final model'

Source of variation	d.f.	CH seeds per ramet		CL flowers per ramet		CL seeds per ramet		Total seeds per ramet	
		Mean dev. ratio	P	Mean dev. ratio	P	Mean dev. ratio	P	Mean dev. ratio	P
Ramet size	1	9·24	<0·01	25·61	<0·001	33·78	<0·001	30·52	<0·001
Year	1	12·55	<0·005	0·11	NS	0·11	NS	6·76	<0·05
Fertilization success	1	16·00	<0·001	12·00	<0·005	15·77	<0·001	0·02	NS
Y × F	1	3·69	NS	0·05	NS	0·001	NS	0·76	NS
Residual	187								

Ramet class	1993				1994			
	CH seeds per ramet	CL flowers per ramet	CL seeds per ramet	N	CH seeds per ramet	CL flowersper ramet	CL seeds per ramet	N
All CH flowers fertilized	15·2 (2·21)	0·5 (0·12)	5·3 (1·36)	43	13·0 (2·66)	0·4 (0·14)	4·3 (1·57)	28
Some CH flowers unfertilized	9·5 (1·62)	1·0 (0·15)	12·6 (1·93)	52	4·0 (0·88)	1·0 (0·13)	10·4 (1·48)	70

fertilized, although significant only at site 1, was that the proportion of ramets producing no CL flowers at all was higher for the latter group of ramets (site 1, 14% vs. 0%, Fisher's exact test (two-tailed) $P=0.039$; site 2, 8% vs. 0%; site 3, 50% vs. 8%). The same pattern was found in *V. hirta*, although significant only in 1993. In 1993 72% and in 1994 63% of the ramets with all CH flowers fertilized produced no CL flowers at all compared with 38% and 43% of the ramets with some unfertilized CH flowers (1993, Likelihood ratio $\chi^2=11.0$, d.f.$=1$, $P<0.001$); 1994, Likelihood ratio $\chi^2=3.18$, d.f.$=1$, $P=0.075$).

The analysis of deviance with number of CL flowers or CL seeds per ramet as response variable (ramet size taken into consideration), showed a significant difference in the number of CL flowers and CL seeds per ramet in relation to fertilization success of CH flowers (Tables 3 and 4). In both species ramets with unfertilized CH flowers produced more CL flowers and seeds compared with ramets in which all CH flowers were fertilized. In *O. acetosella* the predictions derived from the analyses of deviance indicated that the increase in CL flower and seed production due to fertilization success was more obvious at sites 1 and 2 compared with site 3 (Table 3). Inclusion of the number of CH fruits lost as explanatory variable in the models did not affect the results for any of the two species.

In none of the species did the fertilization success of CH flowers influence the total seed output per ramet, but in *O. acetosella* a significant interaction between site and fertilization success was detected (Table 3). The predictions from the analyses of deviance showed that in contrast to sites 1 and 2, unsuccessful fertilization of CH flowers at site 3 brings about decreased reproductive result in terms of number of seeds per ramet.

DISCUSSION

Cleistogamous flowers are structurally modified to ensure self-pollination (Lord 1981), and are expected to have a greater certainty of fertilization compared with CH flowers. Our results show an obvious difference in fruit set between the two flower types in *O. acetosella* and *V. hirta*. The fruit-set of CH flowers was lower and varied to a larger extent between sites (*O. acetosella*) and between years (*V. hirta*) compared with CL flowers. The latter flower type showed a next to complete fruit-set. A higher fertilization rate for CL ovules compared with CH ovules, as observed in other cleistogamous species (Schoen 1984), will favour the selection and maintenance of cleistogamy (Schoen & Lloyd 1984). With regard to the substantial fruit predation, however, we consider it necessary to study the reproductive success for the respective flower types over several growing seasons before concluding whether CL flowers in *O. acetosella* and *V. hirta* generally provides a 'safer' way of seed production compared with CH flowers.

Allocation to CL flower production varied due to site (*O. acetosella*) and ramet size, but also due to fertilization success of open CH flowers. In both species, a reduced fruit set of cross-pollinated CH flowers, resulted in an increased production of self-pollinated CL flowers and seeds. In fact, the results showed that this increased production of CL flowers compensated for any loss in fruit- and seed-set owing to unsuccessful fertilization of CH flowers.

The mechanism behind this plastic response is most probably mediated by the resource pool. Resources otherwise allocated to CH seed maturation are allocated to production of CL flowers. This assumption is supported by the fact that loss of mature

CH capsules, with resources already invested in the seeds, did not affect the number of produced CL flowers. Consequently, a division of cross- and self-fertilization into two distinct and phenologically separated flowers, makes it possible to regulate the allocation of resources to delayed selfing in relation to cross-fertilization success. Such environmentally induced selfing provide maximum outcrossing and back-up self-pollination (Schoen &Lloyd 1984) and represent an example of an adaptive plastic response.

In *O. acetosella* the plastic response to fertilization success of CH flowers buffered the yearly seed output in only two of the three sites studied. At site 3, unsuccessful fertilization resulted only in a small increase in number of produced CL flowers and consequently the total seed-set was not buffered. We can imagine two reasons for the different response at site 3. First, the plastic response (increase in CL flower and seed production) may have been limited by unfavourable habitat conditions. In the densely shaded site 3, the production of CL flowers was comparatively low and Jasieniuk & Lechowicz (1987) observed a similar decrease in the production of CL flowers under unfavourable conditions in the closely related *Oxalis montana*. Secondly, the differences may be due to a differentiation between populations in plastic response; for instance, in the allocation of resources between production of CL flowers and clonal growth. In order to exclude either or both of these hypotheses, further studies under controlled conditions are needed.

One of many advantages of cleistogamy suggested is to ensure seed production under adverse environmental conditions for cross-fertilization (Darwin 1877), especially in species where the separation of anthers and stigma for some reason prevents autogamy (Schoen & Lloyd 1984). There is, for instance, general agreement that flowers of early flowering insect-pollinated species in cool temperate climates, like *O. acetosella* and *V. hirta*, may suffer pollen limitation due to reduced pollinator activity during harsh weather (Schemske *et al.* 1978) or competition for pollinators due to extensive overlap in flower time of most species (Helenurm & Barrett 1987). Hence, Richards (1986) and Masudo & Yahara (1992) consider the development of cleistogamous flowers later in the season in seasonally regulated cleistogamous species, as a 'fail-safe' device. By showing that the CL flowers do not merely act as a 'fail-safe' device, but may even act as a buffer for any loss in seed-set as a result of limited pollinator activity, the results from the present study corroborate this view.

ACKNOWLEDGEMENTS

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