Sex Plant Reprod (2002) 14:279–289
DOI 10.1007/s00497-001-0124-2

ORIGINAL ARTICLE

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Pollen grain numbers, ovule numbers and pollen-ovule ratios in Caryophylloideae: correlation with breeding system, pollination, life form, style number, and sexual system

Received: 7 September 2001 / Accepted: 5 November 2001 / Published online: 15 December 2001

Abstract Pollen-ovule ratios (P/O) were measured for 79 species of Caryophylloideae (*Agrostemma*, *Dianthus*, *Saponaria*, *Silene*, and *Vaccaria*). We analyzed if these features are best correlated with (1) the breeding system (outcrossing or selfing), (2) diurnal or nocturnal pollination, (3) life form (annual versus perennial), (4) style number, (5) the sexual system (hermaphroditism, gynodioecism, dioecism), or (6) the taxonomy of species. According to the classification of Cruden [(1977) Evolution 31:32–46] most species in the subfamily Caryophylloideae are facultative autogamous or facultative xenogamous. Autogamous or cleistogamous species showed significantly lower P/Os than outcrossing species. We found no differences between night- and day-flowering species; thus from our data diurnal and nocturnal flower visitors may be considered as equally efficient in transferring pollen. However, other factors are also important for the interpretation of P/Os. Pollen grain numbers and ovule numbers were found to correlate with style number, life form, and breeding system. The low P/Os of some dioecious, and therefore obligate outcrossing, species are discussed in relation to morphological traits that improve pollen deposition by pollinators on the stigma, and in relation to different flower numbers of male and female plants.

Keywords Caryophyllaceae · Pollen-ovule ratio · Breeding system · Sexual system

Introduction

The subfamily Caryophylloideae comprises mainly herbs with actinomorphic, usually protandrous flowers. The genus *Silene* exhibits an especially great variety of ecological and morphological characters and a great diversity of reproductive systems (Walters 1964; Desfeux et al. 1996). Bees, bumblebees, butterflies, moths, hawkmoths, syrphid flies and mosquitos have all been recorded as pollinators in the Caryophylloideae (Brantjes and Leemans 1976; Meusel and Mühlberg 1979; Jürgens et al. 1996). The high proportion of night-flowering species is remarkable, especially in the genus *Dianthus* and the genus *Silene* (Friedrich 1979). Besides outcrossing, selfing regularly occurs (autogamy or geitonogamy) in many annual species of Caryophylloideae and self-compatibility is suspected for nearly all members of the subfamily (Kugler 1970) and has been confirmed for many species (Table 1). An evolutionary shift from predominantly outcrossing to predominantly selfing is often correlated with alterations in flower morphology, and/or changes of flower anthesis (Wyatt 1983). Compared to outcrossing species, many cleistogamous species have a relatively small flower size. However, some pseudocleistogamous species such as *Silene noctiflora* show clear adaptations to pollination by insects, but flowers are already self-pollinated upon opening (Jürgens et al. 1996).

Among the traits measurable in living and dried specimens, the pollen-ovule ratio (P/O) provides the best insight into the breeding system of a species (Plitmann and Levin 1990). Pollen-ovule ratios reflect the pollination efficiency, i.e., the likelihood of a pollen grain reaching the stigma (Cruden 1977, 2000). There is a substantial decrease in P/O from xenogamy to facultative xenogamy to autogamy. However, other traits and interactions may also affect the evolution of pollen number and ovule number, and thus also the P/O. There is evidence that P/Os are also affected by the sexual system, the pollen vectors, pollination mechanisms, and ecological factors (Small 1986; Cruden 2000). The objective of this study was to analyze differences in pollen grain numbers,

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ovule numbers and P/Os in Caryophylloideae in relation to: (1) the breeding system (outcrossing versus selfing), (2) pollination (diurnal versus nocturnal pollination), (3) the life form of the species (annual versus perennial), (4) the taxonomy (*Dianthus* L., *Saponaria* L., *Vaccaria* Medik., *Agrostemma* L., and the *Silenean* complex including *Lychnis, Viscaria* and *Melandrium*, (5) the style number, or (6) the sexual system (hermaphroditism, gynodioecism, dioecism). We also present data from a number of gynodioecious species to test the hypothesis that P/Os of gynodioecious species are higher or equivalent to those of hermaphrodite species (Webb 1984; Lawrence 1985; Cruden 2000).

Materials and methods

Plants were grown from seed in the Botanical Garden of the University of Ulm, Germany (1994–1997). A total of 79 species were investigated: 7 *Dianthus*, 5 *Saponaria*, 1 *Vaccaria*, 2 *Agrostemma*, and 64 from the *Silenean* complex (according to Oxelman and Lidén 1995) including *Lychnis, Viscaria* and *Melandrium*. The generic delimitation and classification of the genus *Silene* is, apparently, problematic. DNA sequencing studies by Oxelman and Lidén (1995) and Desfeux et al. (1996) support the assumption that *Silene* L., *Lychnis* L. and *Viscaria* Röhl. are unnatural assemblages (Greuter 1995). Therefore, we have tried to integrate the results of Greuter 1995), Oxelman and Lidén (1995), and Desfeux et al. (1996) into the taxonomical subdivision of the "*Silenean* complex” in Table 1 and subdivided the "*Silenean* complex” into the groups *Eudianthe*, *Viscaria*, *Lychnis*, and *Silene*. Classification of species as highly selfing, and day- or night-flowering (Table 1) was based on our own observations or those reported in the literature. For the purposes of the present study, we classified the flower visitors into eight categories: RHO = Rhopalocera, DSP = day-active Sphingidae, NSP = night-active Sphingidae, LEP = Lepidoptera without Rhopalocera and Sphingidae: i.e., mostly Noctuidae and Geometridae but also Microlepidoptera, HY = Hymenoptera (mostly Apidae), CUL = Culicidae (mosquitos), DI = Diptera without Culicidae: i.e., mostly Syrphidae, CO = Coleoptera. If no information was available, the following criteria were used to classify the pollination system of the species. The criteria for night-flowering species were: synchronized anthesis or repeated flower opening at night or in the evening, corolla colored white to cream, scent emission beginning in the evening or becoming more intense in the evening. The criteria for day-flowering species were: flowers open during the day (or day and night), corolla red or pink colored, no obvious change of scent intensity between day and night. The classification of the species life form and the sexual system was based on information found in the literature and our own observations of cultivated plants in the Botanical Garden of the University of Ulm. Species with a life form ranging from annual to biennial (a–b) were classified as annual, species described as biennial to perennial (b–p) were classified as perennial (Table 1). If the description of the sexual system was not clear, the apparently dominant type of the plants used in this investigation, normally hermaphrodite (H), gynodioecious (Gd), or dioecious (D), was used in the statistical analysis.

For the determination of pollen grain number and ovule number, mature buds just before flower opening were used. Buds were collected and preserved in 70% ethyl alcohol. To determine the pollen grain number, anthers were opened under a dissecting microscope and all pollen grains were transferred to plastic tubes containing 5 ml of 0.9% NaCl solution. Pollen grains were counted with a cell counter and analyzer system CASY (Schärfe System, Reutlingen, Germany). Ovaries were prepared, placed in a drop of water on a microscope slide, and ovules were counted at 40× magnification under a dissecting microscope. The P/O of hermaphrodite species was calculated according to Cruden (1977). The number of pollen grains per anther multiplied by 10 gave us pollen per flower. For dioecious species, the mean pollen grain number of at least ten male flowers was divided by the mean ovule number of ten female flowers. For gynomonoecious and gynodioecious species only hermaphrodite flowers were considered for the calculation of P/Os. Differences in pollen grain number per flower, ovule number per flower and P/Os among pollination syndromes, breeding systems, taxonomic groups, and sexual systems were analyzed by Mann-Whitney *U*-test (MWU).

Results and discussion

Pollen grain numbers, ovule numbers, and P/Os for each of the species investigated are detailed in Table 2. Means and standard deviations for the different pollination syndromes, breeding systems, life forms, taxonomic groups, number of styles, and reproductive systems are given in Table 3. MWU results are reported in Table 4.

Mean pollen grain numbers ranged from 1,995±272 in the selfing *Saponaria orientalis* to 80,263±4,865 in the day-flowering *Silene atropurpurea* (Table 2). Ovule numbers ranged from 14±2 in the day-flowering *Sap. ocymoides* to 540±63 in the night-flowering *S. latifolia*. The mean P/Os in the Caryophylloideae investigated range from 36±6 in the cleistogamous species *S. apetala* to 1,155 in the night-flowering *S. roemeri*. According to the classification of Cruden (1977), most of these species are either facultative autogamous or facultative xenogamous. In an investigation of *S. vulgaris*, Dulberger and Horovitz (1984) stated that the P/O ratio, calculated for hermaphrodite flowers alone without taking male-sterile components of populations into account, is well below values given by Cruden (1977) for xenogamous species. Our data show that all investigated Caryophylloideae have relatively low P/O ratios for xenogamous plants. Nevertheless, the results for most species are consistent with the data on floral characters and observation of flower visitors and P/Os are a good indicator of the breeding system if compared within the Caryophylloideae.

Breeding system (outcrossing versus selfing)

Self-compatibility is a general trait in Caryophyllaceae (see Bocquet 1968; Kugler 1970; Erhardt and Jäggi 1995). Because of the close position of mature anthers and stigmas, a breakdown of dichogamy in Caryophylloideae leads easily to selfing. In species with a long and narrow flower tube adapted to pollination by butterflies, moths, or long-tongued bees, the switch from outcrossing to selfing is especially easy. An evolutionary trend from butterfly pollination to selfing has been found in Polemoniaceae (Grant and Grant 1965) and is also proposed for *Dianthus* species (Erhardt and Jäggi 1995).

Selfing based on pollen transfer between flowers (geitonogamy) needs vectors and hence results in higher P/Os as compared to those of autogamous species. Pollen grain numbers and P/Os are significantly higher in

Table 1 Life form, sexual system, breeding system, and flower visitors according to the literature for each species investigated. Taxonomic grouping of *Silene* species is according to Desfeux and Lejeune (1996), Oxelman and Lidén (1995) and Oxelman et al. (1997). Species not considered by these authors are marked with an *asterisk* and were grouped according to the section designations in Walters (1964). *LF* Life form, *a* annual, *b* biennial, *p* perennial, *CA* category used for the statistical analysis, *S* high selfing ability observed (autogamy to cleistogamy), *d* diurnal, *n* nocturnal, *H* hermaphrodite, *Gm* gynomonoecious, *Gd* gynodioecious, *D* dioecious, *T* trioecious, *Am* andromonoecious, *Psy* psychophilous, *Sph* sphingophilous, *RHO* Rhopalocera, *DSP* day-active Sphingidae, *NSP* night-active Sphingidae, *LEP* Lepidoptera except Rhopalocera and Sphingidae, *HY* Hymenoptera (mainly Apidae), *CUL* Culicidae, *DI* Diptera except Culicidae (mainly Syrphidae), *CO* Coleoptera, *nr* nectar robbing. Index numbers refer to the reference numbers below

Group/taxon/species	LF	Sexual system	CA	Selfing ability / pollination syndrome / flower visitors	CA
(I) *Dianthus* L.					
D. arenarius L.	p	Gm-d[29]	Gd	Sph[1,4]	n
D. armeria L.	a	H[29], Gm-d[1,10]	H	S[1,10,30] / Psy[1] / RHO single observation[1], CO[29]	S (d)
D. carthusianorum L.	p	H-Gm[10,29], Gm-d[1]	H	Psy[1,4,10] / RHO[1,21,29], DSP[1,22,29], NSP[22], LEP[1,19,22], HY[1], DI[1], CO[1]	d
D. deltoides L.	p	H[29], Gm-d[10], Gd[1]	H	Psy[1,4,10] / RHO[1,16], HY[16], DI[1], LEP[22]	d
D. monspessulanus L.	p	Gm-d[1,10,29]	Gd	DSP[1]	n
D. superbus L.	p	Gm-d[1,29], Gd[10]	Gd	Sph[1,10] / DSP[1], NSP[17], LEP[17,21]	n
D. sylvestris Wulfen	p	Gd[10,29], Gm-d[1,14]	Gd	S[14] / Psy[1] / RHO[1,10,14,21], DSP[1,10,14,29], NSP[14,22], LEP[14], DI[14,29]	d
(II) *Saponaria* L.					
Sap. cypria Boiss.	p	H[29]	H	–	d
Sap. ocymoides L.	p	H[29], Gm-d[1,10], Am-d[1,10], T[1]	H	Psy[1,4] / RHO[1,10], DSP[29], HY[1,10,29], DI[1,10]	d
Sap. officinalis L.	p	H[10,25,29], Gm-d[1]	H	S[25] / Sph[1,4,10] / NSP[1,10,19,22,29], LEP[1,10,19,25,29], DSP[1,22], DI[1,25,29], HY[1], nr[25]	n
Sap. orientalis L.	a	H[29]	H	S[30]	S
Sap. sicula Rafin	p	H[29]	H	–	d
(III) *Vaccaria* MEDIK.					
V. hispanica (Miller) Rauschert	a	H[29], Gm-d[1,10]	H	S[1] / Psy[1,10] / RHO[1], HY[29]	d
(IV) *Agrostemma* L.					
A. githago L.	a	H[1,10,29], Gm-d[1]	H	S[1,10,30] / Psy[1] / RHO[1,29], LEP[1], DI[1]	S (d)
A. gracile Boiss.	a	H[10,29]	H	RHO[29], HY[29]	d
(V) "*Silene* complex"					
(Va) *Eudianthe* group					
S. coeli-rosa (L.) Godron	a	H[29], Gd[24]	H	HY[29], DI[29]	d
S. laeta (Aiton) Godron	a	H[29]	H	S[30]	S (d)
(Vb) *Viscaria* group					
S. alpestris Jacq.*	p	H[10,29]	H	–	d
S. armeria L.	a-b	Gd[1,10,24,29]	Gd	Psy[1,10] / RHO[1,29], DSP[1,10,22], LEP[1]	d[10]
S. atropurpurea (Griseb.) Greut and Burd.*	p	Gd[29]	Gd	–	d
S. asterias Griseb.	p	Gm-d[29]	Gd	RHO[29]	d
S. rupestris L.	p	H[29], Gm-d-Am-d[1,10]	H	RHO[1,10,21], HY[1,10], LEP[1,10], DI[1,10]	d[4]
S. suecica (Lodd.) Greut. and Burd.*	p	Gm-d[1,6,29]	Gd	S[1] / RHO single observation[1], HY[2], LEP[29], DI[2]	d
S. viscaria (L.) Jessen	p	H[29], Gm-d[1,10], Am-d[1]	H	Psy[1,10] / RHO[1,10,15], HY[1,10,13,15], nr[29], LEP[1,15], NSP[15], DSP[13,15], CO[1,10], DI[1,15]	d
(Vc) *Lychnis* group					
S. chalcedonica (L.) E.H.L. Krause	p	H[29]	H	RHO[21,29]	d
S. coronaria (L.) Clairv.	p	H[29], Gd[24], Gm-d[1,29]	H	S[1,30] / Psy[1] / RHO[1,21,29], DSP[22]	S (d)
S. flos-cuculi (L.) Greut. and Burd.	p	H[29], Gm-d[1,10], Am-d[1,10]	H	Mel-Psy[1,2,10] / RHO[1,2,4,10,21,29], HY[1,2,10,29], DSP[1, 22], LEP[1,10,19,22,29], DI[1,2,10]	d
S. flos-jovis (L.) Greut. and Burd.	p	H[1,29]	H	Psy[1] / RHO[1,29], HY[29], DI[1]	d
(Vd) *Silene* group					
S. acaulis (L.) Jacq.	p	D[1,6,10,29], Gm-d[20], T[1,2,6,10]	D	RHO[1,2], HY[1,2,20], LEP[1,2], DI[1,2], CO[1,2]	d
S. andryalifolia Pomel*	p	Gd[29]	Gd	–	n
S. apetala Willd.*	a	H[24,29]	H	S[1,30]	S
S. bupleuroides L. ssp. *staticifolia* (Sibth. and Sm.) Chowdhuri	p	H[10,29]	H	(LEP or NSP)[1,10], DI[29]	n[1]

Table 1 (continued)

Group/taxon/species	LF	Sexual system	CA	Selfing ability / pollination syndrome / flower visitors	CA
(Vd) *Silene* group					
S. chlorantha (Willd.) Ehrh.*	p	H[10,29]	H	LEP[29]	n[10]
S. colorata Poiret	a	H-Gm[29]	H	HY[29], LEP[29]	d
S. conica L.	a	H[1,10,24], H-Gm[29]	H	S[1,10,24,30]	S (d)
S. conoidea L.*	a	H[24,29]	H	S[24,30]	S (d)
S. cretica L.	a	H[10,29]	H	S[10,30]	S (d)
S. dichotoma Ehrh. ssp. *racemosa* (Otth) Graebner	a	Gd[1,10,29]	Gd	LEP[29], HY[29]	n[10]
S. dioica (L.) Clairv.	p	D[1,3,6,10,12,25,29], Am[1]	D	Psy[1,7] / RHO[1,2,3,4,7,12,21], HY[1,3,12,23,25,29], LEP[1,19,23,25,29], NSP[19,22,25], DI[1,2,3,12,23,25,29], CO[2,3]	d[1,10]
S. disticha Willd.*	a	H[29]	H	S[30] / HY single observation[29]	S (d)
S. echinata Otth*	a	H-Gm[29]	H	Psy[4] / DI[29]	d
S. flavescens Waldst. and Kit.*	p	H-Gm[29]	H	–	n
S. friwaldszkyana Hampe*	p	H[29]	H	LEP[29]	n[10]
S. fruticosa L.	p	H[29]	H	–	n
S. gallica L.	a	H[1,10], H-Gm[29]	H	S[1,30] / Psy[4] / HY[1,29]	S (d)
S. hayekiana Hand.-Mazz. and Janchen	p	Gd[29]	Gd	–	n
S. inaperta L.*	a	H[24,29]	H	S[1,30]	S
S. italica (L.) Pers.	p	Gm-d[24], Gd[29]	Gd	LEP[29]	n
S. latifolia Poir. ssp. *alba* (Miller) ssp. *alba* (Miller) Greut. and Burd.Greut. and Burd.	p	D[1,3,6,10,25,29], Am[1]	D	Sph[4] / LEP[1,3,8,19,25,27,29], NSP[1,3,22,25,27], DSP[27,29], RHO[27], HY[3,27], nr[25], DI[3,27], CO[3]	n[1,3,4,25]
S. linicola C.C. Gmelin	a	H[1,10,29]	H	S[1,10,30] / no flower visitors[1,10]	S (n)
S. littorea Brot.	a	Gm-Gd[29]	Gd	–	d
S. micropetala Lag.*	a	H-Gm[29]	H	S[30]	S (n)
(Vd) *Silene* group					
S. multicaulis Guss. ssp. *sporadum* (Halácsy) Greut. and Burd.*	p	H[29]	H	DI[29]	n
S. muscipula L.	a	H[29]	H	–	d
S. nicaeensis All.	a	H[29]	H	–	n
S. noctiflora L.	a	H[1], H-Gm[26,29], Gm-d[1,3,25]	H	S[1,3,24,25,26,30] / Sph[4] / LEP[3,26,29], HY[3,25,26], NSP[3], DI[3], CO[3]	S (n[1,4,26])
S. nocturna L.	a	H[24,29]	H	S[6, 30]	S (n)
S. nutans L.	p	Gm-d[1,10,24,25,29], Am-d[1]	Gd	Pha[1,10], Sph[4] / LEP[1,19,25,29], RHO[1,21], NSP[22,25], HY[1,25,29], DI[25]	n[1,4,10,25]
S. otites (L.) Wibel	b–p	D[1, 6,10,29], Ad[1]	D	LEP[1,9], HY[1], CUL[9]	n[9,10]
S. paradoxa L.*	p	H[29]	H	–	n
S. parnassica Boiss. and Spruner	p	H[29]	H	–	n
S. pendula L.	a	Gd[24,29]	Gd	HY[29], LEP[29]	d
S. portensis L.*	a	H[29]	H	–	n
S. pseudoatocion Desf.	a	Gm-d[29]	Gd	HY[29], LEP[29]	d
S. roemeri Friv.	p	H-Gd[29], Gd-Am[6]	Gd	DI[10]	n
S. saxifraga L.	p	Gm[24], Gm-d[10,29], Gm-Am-T[1]	Gd	Pha[1,4] / LEP[29]	n[10]
S. schafta S.G. Gmel. ex Hohen	p	Gd[29]	Gd	Psy[28]	d[10,28]
S. secundiflora Otth*	a	H[29]	H	S[30]	S (d)
S. sericea All.*	a	Gd[29]	Gd	–	n
S. spergulifolia (Willd.) Bieb.*	p	H[29]	H	–	n
S. subconica Friv.*	a	Gd[29]	Gd	–	n
S. succulenta Forskål ssp. *corsica* (DC.) Nyman*	p	H[29]	H	LEP[29]	n
S. thessalonica Boiss. and Heldr.*	p	H-Gm[29]	H	S[30]	S (n)
S. vallesia L.	p	Gd[10,29]	Gd	–	n[1,10]
S. viridiflora L.*	p	H[10], Gm-d[29]	Gd	Sph[4]	n[1,4]
S. viscosa (L.) Pers.	a–b	H[10,29]	H	DSP[29]	n
S. vulgaris (Moench) Garcke ssp. *vulgaris* (Moench) Garcke	p	Gm-d[1,5,11,18,25], Am-d-T[1], Gd[29]	Gd	S[11] / Pha-Mel[1] / LEP[1,5,11,18,19,25,29], NSP[5,18,22,25,] HY[1,5,11,18,25,29], RHO[1,5,21], DI[1,5,25], CO[5,11]	n[5,11]
S. waldsteinii Griseb.	p	H-Gm[29]	H	S[30]	S (n)
S. zawadzkii Herbich	p	H[29]	H	HY[29]	n

[1] Knuth 1898–1899; [2] Willis and Burkill 1903; [3] Schulz 1905; [4] Vogel 1954; [5] Marsden-Jones and Turill 1957; [6] Walters 1964; [7] Vogel 1975; [8] Brantjes 1976; [9] Brantjes and Leemans 1976; [10] Meusel and Mühlberg 1979; [11] Dulberger and Horovitz 1984; [12] Kay et al. 1984; [13] Dreisig 1985; [14] Erhardt 1988; [15] Jennersten 1988a; [16] Jennersten 1988b; [17] Erhardt 1991; [18] Pettersson 1991; [19] Esche 1992; [20] Shykoff 1992; [21] Ebert and Rennwald 1993; [22] Ebert et al. 1994; [23] Westerbergh and Saura 1994; [24] Desfeux et al. 1996; [25] Jürgens et al. 1996; [26] Folke and Delph 1997; [27] Altizer et al. 1998; [28] Vogel 1998; [29] A. Jürgens and T. Witt, unpublished observations (mainly from Botanical Garden, Ulm); [30] T. Witt, unpublished data from doctoral thesis

Table 2 Pollen grain number per flower, number of ovules per flower (*f* female, *h* hermaphrodite), pollen-ovule ratio (*P/O*), and style number per flower (*SN*); *Fl* hermaphrodite flowers; for female flowers *n*=10; – = no female flowers

Taxon	Fl nh	SN	P/O *x* ±SD	Pollen grain number *x* ±SD	Ovule number/h *x* ±SD	Ovule number/f *x* ±SD
(I) *Dianthus*						
D. arenarius	13	2	310±99	23,451±5,139	81±16	80±19
D. armeria	10	2	145±28	13,522±2,723	93±5	–
D. carthusianorum	10	2	419±135	30,060±7,254	75±14	–
D. deltoides	10	2	280±49	27,215±3,854	98±10	–
D. monspessulanus	10	2	148±18	27,808±5,043	187±15	210±21
D. superbus	10	2	228±42	31,323±6,764	138±15	152±8
D. sylvestris	10	2	453±100	35,620±5,411	81±14	87±10
(II) *Saponaria*						
Sap. cypria[a]	5	2	282±19	10,825±710	38±2	–
Sap. ocymoides	10	2	370±63	5,010±1,124	14±2	–
Sap. officinalis	10	2	206±34	13,521±1,888	66±6	–
Sap. orientalis	13	2	90±17	1,995±272	23±2	–
Sap. sicula[a]	5	2	249±48	11,055±2,050	45±4	–
(III) *Vaccaria*						
V. hispanica	10	2	368±182	6,560±2,878	19±2	–
(IV) *Agrostemma*						
A. githago	10	5	461±74	13,863±2,824	30±6	–
A. gracile	10	5	910±99	36,078±3,646	40±7	–
(V) *"Silene"*						
(Va) *Eudianthe group*						
S. coeli–rosa	10	5	188±48	37,815±8,422	204±20	–
S. laeta[a]	5	5	129±27	7,310±1,658	61±27	–
(Vb) *Viscaria group*						
S. alpestris	10	3	176±29	10,505±995	61±6	–
S. armeria	10	3	179±28	19,201±2,942	111±11	85±2
S. asterias[a]	5	3	188±29	21,285±2,760	114±9	No data
S. atropurpurea	10	5	225±17	80,263±4,865	358±14	369±31
S. rupestris	10	3	258±79	11,068±1,848	46±14	–
S. suecica	10	5	270±36	34,068±5,864	126±9	121±7
S. viscaria	10	5	205±45	64,452±15,347	315±34	–
(Vc) *Lychnis group*						
S. chalcedonica	14	5	201±46	22,146±5,566	110±12	–
S. coronaria	10	5	199±35	50,523±9,004	254±6	–
S. flos–cuculi	10	5	192±23	40,193±7,410	209±27	155±27
S. flos–jovis	10	5	459±46	42,418±2,565	93±9	–
(Vd) *Silene* group						
S. acaulis	10	3	1062	13,827±2,533	–	13±2
S. andryalifolia[a]	5	3	531±207	26,208±2,487	55±18	No data
S. apetala[a]	5	3	36±6	2,364±337	65±4	–
S. bupleuroides	10	3	195±30	31,375±6,052	161±20	–
S. chlorantha	10	3	101±25	16,120±2,335	165±24	–
S. colorata	12	3	129±25	8,758±2,278	69±18	68±7
S. conica	10	3	142±89	14,785±9,175	103±9	–
S. conoidea[a]	16	3	85±14	9,647±1,654	114±11	–
(Vd) *Silene* group						
S. cretica	10	3	51±22	10,538±5,100	200±26	–
S. dichotoma	10	3	292±58	18,548±2,095	65±8	64±21
S. dioica	10	5	150	42,111±18,177	–	280±46
S. disticha[a]	15	3	165±14	5,923±1,437	91±12	–
S. echinata[a]	10	3	226±23	16,335±1,765	73±5	–
S. flavescens	10	3	216±50	22,078±3,366	105±19	–
S. friwaldszkyana[a]	5	3	237±13	27,870±1,377	118±4	–
S. fruticosa[a]	5	3	403±48	36,680±5,048	92±19	–
S. gallica	16	3	85±45	5,820±3,382	64±13	58±5
S. hayekiana[a]	5	3	360±52	31,655±3,259	88±6	–
S. inaperta	9	3	75±13	7,508±1,080	101±6	–
S. italica	20	3	229±37	22,068±3,624	97±9	132±17

Table 2 (continued)

Taxon	Fl nh	SN	P/O x ±SD	Pollen grain number x ±SD	Ovule number/h x ±SD	Ovule number/f x ±SD
(Vd) *Silene* group						
S. latifolia	10	5	55	29,288±8,248	–	540±63
S. linicola	10	3	143±39	4,558±1,240	33±3	–
S. littorea[a]	12	3	170±41	16,250±3,548	96±12	–
S. micropetala[a]	5	3	39±3	3,765±459	96±5	No data
S. multicaulis[a]	6	3	254±52	24,096±4,665	95±6	–
S. muscipula[a]	5	3	535±29	44,095±1,616	83±4	–
S. niceensis[a]	13	3	83±19	8,358±1,742	101±11	–
S. noctiflora	53	3	188±49	24,760±11,227	130±34	101±22
S. nocturna	11	3	51±17	3,823±1,008	76±9	–
S. nutans	10	3	200±86	27,615±13,520	135±9	132±19
S. otites	10	3	719	26,655±1,675	–	37±3
S. paradoxa[a]	5	3	290±42	39,690±5,634	137±5	–
S. parnassica[a]	5	3	189±15	34,660±2,332	184±7	–
S. pendula	11	3	414±87	19,915±3,107	50±8	54±7
S. portensis[a]	5	3	199±38	14,875±1,668	76±9	–
S. pseudoatocion	12	3	479±148	9,577±2,565	21±4	16±2
S. roemeri[a]	5	3	1155±389	29,660±3,953	27±6	No data
S. saxifraga	14	3	229±54	22,933±3,611	97±7	91±9
S. schafta	10	3	255±51	22,285±6,319	86±13	89±6
S. secundiflora[a]	15	3	215±41	7,203±1,118	34±4	–
S. sericea	10	3	103±35	10,703±5,943	101±29	155±20
S. spergulifolia	10	3	347±30	23,799±2,969	69±6	–
S. subconica	10	3	257±53	22,443±2,457	90±16	73±17
S. succulenta	10	3	134±43	11,183±2,157	88±23	–
S. thessalonica[a]	5	3	115±10	20,000±3,685	174±26	–
S. vallesia	5	3	389±32	30,105±3,004	77±4	79±6
S. viridiflora[a]	6	3	91±9	16,325±2,651	180±22	No data
S. viscosa	10	3	205±45	45,630±5,046	350±21	–
S. vulgaris	10	3	236±65	21,953±5,775	94±9	88±19
S. waldsteinii[a]	5	3	164±9	32,850±3,504	201±11	No data
S. zawadzkii[a]	5	3	341±67	26,070±2,073	80±21	–

[a] Unpublished data from the doctoral thesis of T. Witt

outcrossing species than in selfing species. Mean pollen grain numbers and P/Os of selfing species were lower than in nocturnal and diurnal species. However, we found no significant differences in ovule numbers between these groups (Table 3). There are some cases in which P/Os and the breeding systems are in conflict: unexpectedly low P/Os were found for the dioecious, and therefore obligate outcrossing, species *S. dioica* (150) and *S. latifolia* (55). These low P/Os may be due to very efficient pollinating mechanisms ensuring that sufficient numbers of pollen grains are deposited on the stigmas. Compared with other Caryophylloideae, both species have extremely large stigma areas and, due to the relatively long calyx length of these species, the pollen load is deposited mainly on the head and the proboscis of the pollinators (A. Jürgens, unpublished observation). According to Cruden (2000), stigma area relative to the pollen-bearing area directly influences the likelihood of a pollen grain reaching the stigma, and species with large stigma areas relative to pollen-bearing areas often show quite low P/Os (Mehrhoff 1983; Osborn et al. 1991; Cruden 2000). There is, however, an alternative explanation for the low P/Os in *S. dioica* and *S. latifolia*. Higher flower numbers of male compared to female plants have been reported for both species (Gross and Soule 1981; Kay et al. 1984; Meagher 1992; Gehring and Linhart 1993). Therefore, it could be argued that if the ratio of male to female flowers is included in the calculation of P/Os, the resulting values would be higher and thus more typical for outcrossing *Silene* species.

Life form (perennial versus annual)

There is a relationship between breeding system, life form and sexual system. All 19 selfing species investigated are hermaphrodite and 14 are annuals. We found significant differences in average pollen grain numbers, ovule numbers, and P/Os between different life forms (Table 3). Pollen grain number of perennials was found to be almost twice that of annuals. The ovule number and the P/O were also clearly higher in perennials compared to annual species. Autogamy is common in annual Caryophylloideae whereas perennial species are mostly xenogamous. Correlations between life form and breeding system are well known (Raven 1979; Plitmann and Levin 1990). Therefore, as stated by Small (1986) for the genus *Medicago*, causal interpretations of differences in P/Os might be confounded with degree of outbreeding and longevity also in Caryophylloideae.

Table 3 Means and standard deviations of pollen grain number, ovule number and P/Os of hermaphrodite flowers in different taxonomic groups and groups with different pollination syndromes, breeding systems, life forms, number of styles, and sexual systems in Caryophylloideae

	Species number	Pollen grain number	Ovule number	P/O
Pollination syndrome				
Diurnal	29	26,036±17,763	104±88	327±214
Nocturnal	31	25,157±8,429	126±98	279±213
Breeding system				
Outcrossing	60	25,281±13,729	114±93	301±212
Selfing	19	12,677±12,202	102±64	131±97
Life form				
Annual	33	14,661±11,528	89±63	206±183
Perennial	46	28,086±13,617	128±98	301±213
Taxonomic groups				
Dianthus	7	27,000±7,039	108±41	283±122
Saponaria	5	8,481±4,786	37±20	239±103
Vaccaria	1	6,560	19	368
Agrostemma	2	24,970±15,708	35±7	685±317
"Silene complex"				
Eudianthe group	2	22,563±21,570	132±101	159±42
Viscaria group	7	34,406±27,462	161±123	214±38
Lychnis group	4	38,819±11,969	166±77	263±130
Silene group	51	20,522±11,276	113±87	251±226
Style number				
2	13	18,305±11,323	74±50	273±110
3	53	19,549±10,655	99±56	254±221
5	13	38,594±19,497	202±148	280±222
Sexual system				
Hermaphrodite (all)	51	20,421±14,743	106±72	221±154
Hermaphrodite (selfing)	19	12,677±12,202	102±64	131±97
Hermaphrodite (outcrossing)	32	25,019±14,337	109±76	274±157
Gynodioecious	24	25,886±13,393	106±67	308±214
Dioecious	4	28,268±12,087	218±246	497±478
Total	79	22,478±14,349	112±87	261±205

Diurnal versus nocturnal pollination

Although some diurnal, bee-pollinated, species such as *S. atropurpurea*, *S. dioica*, *S. flos-cuculi*, and *S. viscaria* (Tables 1 and 2) have relatively high pollen grain numbers per flower, we found no significant differences in pollen grain numbers and P/Os between diurnal and nocturnal species. Therefore, from our data, diurnal and nocturnal flower visitors may be considered as equally efficient in transferring pollen. There are many reports of flower visitors on Caryophylloideae but only a few investigations give quantitative data of flower visitors in relation to the pollination efficiency of a pollinator group or a single species. In most cases, it is not clear how important single pollinator groups are for the reproduction of the plant species. Main flower visitors of day-flowering Caryophylloideae are day-active Lepidoptera, Hymenoptera, and Diptera (Table 1). Nocturnal species are mainly visited by Noctuidae, Sphingidae, and Geometridae (Table 1). There has been much discussion on the importance of butterflies as pollinators (Courtney et al. 1982; Jennersten 1984). Jennersten (1984) showed that North European butterflies are comparatively unimportant as pollinators, although findings of pollen from *Dianthus deltoides* and *Silene viscaria* on the skipper *Thymelicus lineola* and *Ochlodes venata* indicate that they are important flower visitors of these plants (Jennersten 1984). In a later study Jennersten (1988a) suggested that bumblebees are probably the most important pollinators of *S. viscaria*. In night-flowering species, the importance of various moth species for reproduction seems to be very different (Pettersson 1991; Esche 1992). However, many factors have to be included for an estimation of the pollinator efficiency and both groups of diurnal and nocturnal flower visitors are very diverse. Besides nectar-drinking, Diptera and Hymenoptera feed on pollen or collect pollen as larval food, whereas Lepidoptera only use nectar as a food resource. The use of pollen as a food resource may have an influence on the pollen production of a plant species. This might explain the higher number of pollen grains in the bee-pollinated species *S. atropurpurea*, *S. dioica*, *S. flos-cuculi*, and *S. viscaria* as an adaptation to the use of pollen as a food resource by bees.

Table 4 Results of the Mann-Whitney U (MWU)-test testing for differences of pollen grain number, ovule number, and P/Os of hermaphrodite flowers in different taxonomic groups and groups with different pollination syndromes, breeding systems, number of styles, and sexual systems. *H* Hermaphrodite, *Gd* gynodioecious, *D* dioecious, *oc* outcrossing

	Pollen grain number	Ovule number	P/O
Pollination syndrome			
Diurnal – nocturnal	U=404, *P*=0.501	U=335, *P*=0.091	U=381, *P*=0.311
Diurnal – selfing	U=120, *P*<0.001	U=255, *P*=0.666	U=56, *P*<0.001
Nocturnal – selfing	U=94, *P*<0.01	U=250, *P*=0.374	U=105, *P*<0.001
Breeding system			
Outcrossing – selfing	U=214, *P*<0.001	U=546, *P*=0.783	U=161, *P*<0.001
Life form			
Annual – Perennial	U=289, *P*<0.001	U=548, *P*<0.05	U=423, *P*<0.01
Taxonomic groups			
Dianthus – Silene	U=107, *P*=0.088	U=164, *P*=0.729	U=123, *P*=0.185
Dianthus – Saponaria	U=0, *P*<0.01	U=0, *P*<0.01	U=14, *P*=0.570
Dianthus – Lychnis	U=6, *P*=0.131	U=5, *P*=0.089	U=13, *P*=0.850
Dianthus – Viscaria	U=22, *P*=0.749	U=20, *P*=0.565	U=16, *P*=0.277
Silene – Lychnis	U=29, *P*<0.05	U=47, *P*=0.075	U=82, *P*=0.517
Silene – Viscaria	U=136, *P*=0.310	U=133, *P*=0.277	U=161, *P*=0.676
Silene – Saponaria	U=47, *P*<0.05	U=26, *P*<0.01	U=105, *P*=0.518
Saponaria – Lychnis	U=0, *P*<0.05	U=0, *P*<0.05	U=8, *P*=0.624
Lychnis – Viscaria	U=9, *P*=0.345	U=14, *P*=1.0	U=12, *P*=0.705
Style number			
2–3	U=330, *P*=0.815	U=240, *P*=0.092	U=249, *P*=0.124
2–5	U=26, *P*<0.01	U=34, *P*<0.01	U=68, *P*=0.397
3–5	U=130, *P*<0.001	U=197, *P*<0.05	U=308, *P*=0.556
Sexual system			
H (all) – Gd	U=453, *P*=0.071	U=573, *P*=0.658	U=401, *P*<0.05
H (oc) – Gd	U=380, *P*=0.947	U=356, *P*=0.643	U=348, *P*=0.551
D – H	U=62, *P*=0.195	U=98, *P*=0.897	U=80, *P*=0.476
D – Gd	U=39, *P*=0.555	U=47, *P*=0.948	U=47, *P*=0.948

Sexual system and breeding system

Traditionally, P/Os are used only with hermaphrodite species (Cruden 1977). The only P/Os reported for gynodioecious species are in animal pollinated Apiaceae and they are higher than those of related hermaphrodite species (Webb 1984). As stated by Cruden (2000), variation in pollen grain number in species with other than hermaphrodite sexual systems may reflect the percentage of male flowers per plant and/or male plants. Likewise, in gynodioecious and dioecious species, ovule number may vary as a function of the number of female flowers per plant and/or female plants. The higher P/Os of gynodioecious species may reflect selection to maintain the pollen pool available to vectors above some critical level (Cruden 2000). This is also true when comparing the closely related species *S. atropurpurea* and *S. viscaria*. The gynodioecious species *S. atropurpurea* has a higher pollen grain number, ovule number and P/O than *S. viscaria*. Moreover, we found significantly higher pollen grain numbers and P/Os of gynodioecious species relative to hermaphrodite species. However, many hermaphrodite species are annuals with high selfing abilities (e.g. *S. apetala*, *S. linicola*, *S. nocturna*). Including only outcrossing species into the MWU test, gynodioecious species still have higher pollen grain numbers and P/Os but the differences are not significant. Desfeux et al. (1996) stated that within the genus *Silene*, hermaphroditism is unlikely to be the ancestral sexual system, but it seems to have been derived at least twice from a gynodioecious ancestral state. Further, they point out that it is highly probable that cleistogamy has arisen several times. Our personal observations show that even in normally outcrossing *Silene* species hermaphroditism is often correlated with a mechanism of reproductive assurance. If pollinator frequency is low, selfing often occurs in older protandrous flowers due to movements of anthers still bearing pollen and the mature styles which come into contact with them. In highly selfing species, reproductive assurance is probably optimized by the breakdown of dichogamy leading to high selfing rates. Everything points in the same direction: within the genus *Silene*, hermaphroditism, selfing and even cleistogamy have developed several times independently to ensure reproductive success. Particularly in geographically or ecologically marginal environments, selection may favor individuals that can complete reproduction early. Under these conditions, the reduction of flower size and self-fertilization may have arisen as a by-product of selection for rapid maturation (Runions and Geber 2000). Alternatively, the evolution of self-pollination may be due to greater reproductive assurance of self-pollinating plants in habitats where pollinators may be scarce (Baker 1955).

As stated earlier, the question of whether the sex ratio of flowers per population should be included in the calculation of the P/Os of gynodioecious and dioecious species remains open. In fact, it is not the pollen grain number and ovule number per flower, but the total number of pollen grains and ovules in a population that are important for increasing the probability that a sufficient number of pollen grains are deposited on stigmas of female (male sterile) and hermaphrodite flowers. Assuming that flower numbers of hermaphrodite and female plants are equal in gynodioecious species, and that female plants make up 30% of the population, the inclusion of female plants in the calculation of P/Os would reduce P/O values to the level of selfing species. For dioecious species, the calculation of P/Os on the basis of flower-sex ratios can be even more complicated because: (1) sex ratios of male and female plants can be biased (Gehring and Linhart 1993) and (2) flower production of male and female plants can differ. In *S. latifolia*, populations are often female-biased and male plants have many more flowers than female plants (Mulcahy 1967; Gross and Soule 1981; Meagher 1992; Gehring and Linhart 1993). In the study of Gross and Soule (1981), male flower production ranged from 3 to 4.2 times that of similar-sized females. As proposed by Gehring (1993) for *S. latifolia*, high male flower numbers probably evolved after the evolution of dioecy in response to sexual selection for a large male inflorescence (Eckhart 1991) or to selection for increased pollen output (Charlesworth et al. 1987; Stanton et al. 1987).

Style number

We found significant differences in the number of pollen grains and ovules when comparing species with two or three styles with species having five styles. In species with five styles the number of pollen grains and ovules is twice as high as in species with two to three styles. However, differences in P/Os were not significant. As stated by Cruden and Miller-Ward (1981), species with relatively large stigma areas compared to the pollen-bearing area of the pollinator often have lower P/O ratios. This holds true for *S. dioica* and *S. latifolia*, both five-styled species with a large stigma area pollinated by long-tongued bees and moths. However, in other five-styled species of the *Lychnis* and *Viscaria* group, stigma areas are smaller (A. Jürgens, unpublished observation) and P/Os are much higher.

Taxonomy of species

We found significant differences between some taxonomic groups in pollen grain numbers and ovule numbers but not in P/Os (Tables 3, 4). However, because of the small sample number in some taxa (*Vaccaria* and *Agrostemma*) and the consequent lack of statistical power, it was not possible to properly judge the difference between all taxa. Moreover, differences can be explained mostly by the combination of features typical for each taxonomic group and it seems that the taxonomy is only indirectly correlated with pollen grain number, ovule number, and P/O. High pollen grain numbers were found in species of the *Viscaria* and *Lychnis* groups. Most species of these groups are diurnal perennials and many are five-styled.

Other factors that might affect pollen grain number, ovule number and P/O

In the Caryophylloideae, other factors operating on each species may interact evolutionarily on pollen grain numbers and ovule numbers and these factors should be taken into account when analyzing P/Os in this subfamily. As stated by Wyatt et al. (2000), it seems reasonable to suppose that ecological processes, such as seed predation, seed dispersal, or seedling establishment, determine the life-history tradeoffs in parameters such as seed size and seed or ovule number (Wilbur 1976). Among the various moths reported as visitors, noctuid moths of the genus *Hadena* act as pollinators and also feed as larvae on various caryophyllaceous plants (Brantjes 1976; Pettersson 1991). It is possible that the parasitism of some Caryophylloideae by *Hadena* moths may have an influence on the production of ovules. A reduction of ovules per flower would force caterpillars to move more often to new flowers, thus increasing the risk of being captured by predators. An increase of ovule numbers per flower on the other hand, would reduce the number of flowers that are damaged by caterpillars thus ensuring a higher fruit set. In *S. latifolia*, the larval host of *Hadena bicruris*, ovule numbers are high compared to other species. However, this might be not an adaptation of the plant species to *H. bicruris* moths, but rather a host preference for high ovule numbers, which has the secondary effect of increasing the survival rate of caterpillars.

A factor that might influence the pollen grain number per flower is the anther-smut infection of Caryophyllaceae caused by *Ustilago violaceae* (Pers.) Fuckel (Alexander 1990; Shykoff and Bucheli 1995; Shykoff et al. 1997; Altizer et al. 1998). It is possible that the infection of *Silene* species by *U. violaceae* might cause pollen limitation in infected populations. In this way, the anther smut infection might have been one of the selective forces acting on the evolution of the pollen grain numbers of Caryophyllaceae. However, further investigations are needed to clarify if factors such as infection by *U. violaceae* or parasitism by *Hadena* moths might also have an evolutionary influence on the production of pollen grains and ovules in Caryophylloideae.

Acknowledgements We wish to thank Hans Malchus for help in the field and laboratory. We thank the members of the Botanical Garden of Ulm for cultivating plants.

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