

POLLEN-OVULE RATIOS AND BREEDING SYSTEM EVOLUTION IN SOLANUM SECTION BASARTHURUM (SOLANACEAE)¹

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Pollen-ovule ratio, pollen grains per flower, pollen grain volume, pollen biomass, ovules per ovary, seeds per fruit, seed volume, seed biomass, and corolla size were studied to reveal patterns of variation within a monophyletic group. *Solanum* sect. *Basarthrum* includes 22 neotropical species of two clades, one having small, few-seeded red fruits, and the other having larger, many-seeded green fruits. The former includes self-incompatible species and a dioecious species, while the latter includes self-incompatible species, self-compatible (and autogamous) species, and a domesticate (the “pepino”). Although the pollen quantity and ovule quantity of the self-incompatible species are significantly higher in the green-fruited subgroup than in the red-fruited subgroup, the pollen-ovule ratios of the self-incompatible species are not significantly different between the two subgroups, suggesting parallel evolution of the pollen-ovule ratio. Furthermore, the pollen-ovule ratio tracks the breeding system: self-incompatible species have significantly higher pollen-ovule ratios than self-compatible species, resulting both from fewer pollen grains and more ovules of the latter. The pollen-ovule ratio of the dioecious species is among the highest of all, resulting only from fewer ovules. The pepino is self-compatible but has a pollen-ovule ratio like its wild self-incompatible progenitors and shows wide variation in seed production and pollen quality, but not in pollen quantity. Among all species, pollen size and quantity are inversely proportional, as are seed size and quantity.

Although pollen-ovule ratios (P/Os) are widely used in breeding system studies, there is no clear consensus on why P/Os are higher for outcrossers than for selfers (Queller, 1984; Preston, 1986). Central to this issue is the question of what factors influence the evolution of P/Os. Cruden (1977, p. 32) wrote that “P/O’s reflect the likelihood of sufficient pollen grains reaching each stigma to result in maximum seed set. The more efficient the transfer of pollen, the lower the P/O should be.” Alternatively, based on the theory of local mate competition, Charnov (1982, p. 263) argued that what drives the allocation ratio is “the opportunities for an individual to gain reproductive success, through male or female function Pollen does not exist so as to ensure seed set, but as an *equivalent (to seeds) means towards fitness gain.*” Cruden’s and Charnov’s ideas are not incongruent. The two theories can be bridged by reasoning that for a unit increase in male fitness, a species with a relatively inefficient pollination system (i.e., pollen grains have a relatively low probability of reaching stigmata) requires a greater increase in pollen quantity than does a species with a more precise pollination system.

Seed maturation, although traditionally treated as a female cost, perhaps should not always be treated as such. Clearly seed maturation in dioecious species is a cost borne by females alone. However, the cost of seed maturation in monocious and perfect-flowered species is a

different issue. Our contention, like that of Queller (1984), is that for such species, the cost of seed borne by the female is $100 - (\frac{1}{2} \text{ the } \% \text{ self-set seed})$.

For this study we chose a monophyletic group (Anderson, unpublished morphological and cpDNA data). This allowed us to attribute differences in traits to the breeding system or other ecological and evolutionary factors rather than to different phylogenetic origins. *Solanum* section *Basarthrum* includes 22 suffrutescent, mostly perennial species native to Central or South America (Correll, 1962; Anderson, 1975, 1977, 1979b; Anderson, Cooper-Driver, and Steinharter, 1987; Anderson and Bernardello, 1990). This group is most closely related to the tuber-bearing species (including cultivated potatoes) and to the tomato (*Lycopersicon*) (Correll, 1962; Spooner, Anderson, and Jansen, 1990). Morphological data (Anderson, unpublished data) indicate that sect. *Basarthrum* includes two monophyletic, sister subgroups of similar size (Table 1). Subgroup A includes one dioecious (*S. appendiculatum*) and eight self-incompatible (SI) species with small (≈ 1 cm), mostly red, few-seeded fruits ($\bar{X} = 27$ seeds) that are presumably bird dispersed. Subgroup B includes a self-compatible (SC) (and autogamous) domesticate (*S. muricatum* “pepino” or “pepino dulce”) and both SI and SC wild species with larger (approximately 3 to 5 cm long in nondomesticates), green, many-seeded ($\bar{X} = 187$ seeds) fruits that are presumably dispersed by gravity and/or small mammals. The SC state is interpreted as derived (Anderson, unpublished data). Two species, *S. sanctae-marthae* and *S. taeniotrichum*, intermediate between groups A and B, are of uncertain placement and are treated as a distinct group (Table 1).

Two of the SC species (*S. canense* and *S. suaveolens*) are autogamous annuals of disturbed habitats (Anderson, 1977). The evolution of self-compatibility and relatively high ovule and seed production in these two species may be associated with their derived life cycle and habitat.

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TABLE 1. Reproductive characters^a

	Compatibility	\bar{X} Pollen grains/fl. \pm SE ($\times 1,000$)	\bar{X} Ovules/ovary \pm SE	\bar{X} Pollen-ovule ratio \pm SE	\bar{X} Corolla radius \pm SE	\bar{X} Pollen grain volume μm^3	\bar{X} Seed volume mm^3	\bar{X} Seeds/fruit \pm SE	Fruit color
Red fruited, few-seeded subgroup (A)									
<i>appendiculatum</i>	D	137 \pm 21 (8 ^b)	13 \pm 2 (8 ^c)	10,655 (8 ^b ,8 ^c)	6.4 \pm 0.1 (8 ^b ,8 ^c)	7,197 ^d (^b)	4.21 (^c)	8.0 \pm 0.2 (121 ^c)	Red
<i>brevifolium</i>	SI	191 \pm 49 (13)	38 \pm 2 (13)	3,672 \pm 428 (13)	9.2 \pm 0.4 (8)	5,806 ^d	2.70	21 \pm 2.6 (23)	Red
<i>chimborazense</i>	SI	90 \pm 8 (10)	42 \pm 2 (10)	2,153 \pm 162 (10)	5.3 \pm 0.2 (6)	8,031 \pm 0.3 ^c (50)	2.78	12 (1)	Red
<i>carchiense</i>	SI	284 \pm 38 (5)	85 \pm 11 (5)	3,366 \pm 246 (5)	14.3 \pm 0.9 (5)	3,904 \pm 0.2 ^c (50)	3.05	41 \pm 7.0 (6)	Red
<i>skutchii</i>	?	278 \pm 24 (3)	125 \pm 15 (3)	2,268 \pm 89 (3)	6.6 \pm 0.3 (7)	5,266 \pm 0.2 ^c (50)	1.11	—	Red
<i>sodiroi</i>	SI	253 \pm 31 (8)	109 \pm 9 (8)	2,449 \pm 371 (8)	9.4 \pm 0.5 (8)	3,214 \pm 0.2 ^c (50)	3.71	56 \pm 6.0 (10)	Red
<i>subvelutinum</i>	?	102 (1)	33 (1)	3,081 (1)	3.6 \pm 0.1 (3)	6,505 \pm 0.2 ^c (50)	—	—	Green
<i>tacanense</i>	?	171 \pm 24 (2)	49 \pm 7 (2)	3,483 \pm 18 (2)	4.0 \pm 0.3 (5)	5,939 \pm 0.2 ^c (50)	6.78	—	Red
<i>tetrapetalum</i>	SI	328 \pm 20 (8)	79 \pm 4 (8)	4,193 \pm 313 (8)	11.9 \pm 0.3 (8)	3,574 ^d	2.78	26 (1)	Red
Intermediate subgroup									
<i>sanctae-marthae</i>	SI	983 \pm 153 (2)	41 \pm 2 (2)	23,839 \pm 2,557 (2)	9.5 \pm 0.8 (3)	3,089 ^d	6.53	25.0 (6)	Green
<i>taeniotrichum</i>	SI	538 \pm 89 (3)	39 \pm 8 (3)	14,056 \pm 900 (3)	10.8 \pm 0.8 (4)	1,780 \pm 0.1 ^c (50)	2.32	26 \pm 1.2 (53)	Red
Green fruited, many-seeded subgroup (B)									
<i>muricatum</i>	X	467 \pm 23 (44)	277 \pm 13 (46)	1,809 \pm 109 (43)	11.6 \pm 0.3 (64)	2,220 ^d	2.63	85 \pm 9.2 (77)	Variable
<i>basendopogon</i>	SI	327 \pm 21 (15)	173 \pm 14 (15)	1,960 \pm 85 (15)	7.0 \pm 0.2 (6)	3,518 ^d	1.29	196 \pm 15.9 (17)	Green
<i>caripense</i>	SI	591 \pm 49 (16)	178 \pm 19 (16)	3,560 \pm 245 (16)	9.0 \pm 0.4 (7)	2,586 ^d	1.08	104 \pm 7.2 (18)	Green
<i>cochoae</i>	SI	332 \pm 20 (10)	146 \pm 7 (10)	2,315 \pm 164 (10)	6.9 \pm 0.7 (10)	2,795 \pm 0.2 ^c (50)	1.78	135 \pm 6.9 (28)	Green
<i>filiforme</i>	?	709 \pm 45 (7)	364 \pm 28 (7)	1,990 \pm 125 (7)	10.2 \pm 0.3 (7)	2,304 \pm 0.2 ^c (50)	1.64	138 (1)	Green
<i>fraxinifolium</i>	SI	452 \pm 22 (13)	212 \pm 24 (13)	2,384 \pm 246 (13)	8.9 \pm 0.4 (7)	2,559 ^d	1.07	209 \pm 9.5 (34)	Green
<i>heiseri</i>	SI	958 \pm 69 (5)	153 \pm 9 (5)	6,203 \pm 208 (5)	8.0 \pm 0.5 (5)	1,382 ^d	2.35	83 \pm 7.8 (12)	Green
<i>tabanoense</i>	SI	588 \pm 69 (7)	237 \pm 19 (7)	2,622 \pm 418 (7)	9.3 \pm 0.4 (6)	3,095 ^d	2.37	306 \pm 37.8 (4)	Green
<i>trachycarpum</i>	SC	185 \pm 19 (9)	249 \pm 14 (9)	766 \pm 91 (9)	7.6 \pm 0.6 (10)	3,614 ^d	0.56	209 \pm 15.8 (26)	Green
<i>canense</i>	SC	321 \pm 27 (10)	277 \pm 19 (10)	1,158 \pm 60 (10)	7.0 \pm 0.4 (5)	2,461 ^d	0.78	321 \pm 8.4 (99)	Green
<i>suaveolens</i>	SC	204 \pm 22 (10)	297 \pm 32 (10)	748 \pm 108 (10)	5.7 \pm 0.2 (3)	2,604 ^d	0.56	274 \pm 11.1 (27)	Green

^a SI, self-incompatible; SC, self-compatible; ?, compatibility unknown; D, dioecious; X, cultigen; Fl, flower.

^b Staminate plants.

^c Pistillate plants.

^d From Anderson and Gensel (1976).

^e Standard error (SE) presented for sphere diameter not volume.

The third SC species, *S. trachycarpum*, is also autogamous and is distinct phylogenetically from *S. canense* and *S. suaveolens* (Anderson and Jansen, unpublished data). Self-compatibility in this perennial species may be associated with low population density in the xeric habitats it occupies (Anderson, 1975).

Our objectives were to reveal and interpret patterns of variation: 1) among species; 2) between compatibility-groups; and 3) between clades (subgroups), for the reproductive characters: P/O, pollen grains/flower, pollen grain

volume, pollen biomass, ovules/ovary, seeds/fruit, seed volume, seed biomass, and corolla radius. The biomass of seeds and pollen grains was considered to be a more accurate indication of energy investment than could be obtained with either size or quantity alone. These objectives are of particular interest because we utilized a monophyletic group, and because the genus *Solanum* offers only pollen as a reward to floral visitors (Anderson and Symon, 1985).

The cultigen in sect. *Basarthrum*, the pepino, has been

TABLE 2. Correlations among all species (except *S. appendiculatum* and *S. muricatum*) on parameter means^a

	PGV	PB	O	S	SV	SB	P/O	CR
P	**	***	ns	ns	ns	ns	**	ns*
PGV	-0.657	0.774	0.180	-0.098	0.184	0.255	0.622	0.385
PB		ns	*	ns	ns	ns	ns	*
		-0.235	-0.546	-0.357	0.313	-0.291	-0.202	-0.463
			ns	ns	ns*	ns	***	ns
O			-0.060	-0.190	0.455	0.280	0.699	0.341
			***	**	ns*	*	*	ns
S				0.817	-0.644	0.444	-0.447	0.012
					**	**	ns*	ns*
SV					-0.639	0.643	-0.465	-0.430
						ns	**	ns
SB						-0.073	0.584	0.019
							ns	ns
P/O							-0.166	-0.057
								ns
								0.267

^a P, pollen grains/flower; PGV, pollen grain volume; PB, pollen biomass; O, ovules/ovary; S, seeds/fruit; SV, seed volume; SB, seed biomass; P/O, pollen-ovule ratio; CR, corolla radius. *** $P < 0.001$, only these are significant with the sequential Bonferroni technique at $\alpha = 0.05$; ** $P > 0.001$ and $P < 0.01$; * $P > 0.01$ and $P < 0.05$; ns* > 0.05 and $P < 0.095$; ns, not significant $P > 0.095$; all sample sizes $N = 17-20$.

a popular fruit in the Andes since pre-Colombian times (Anderson, 1979b; Heiser, 1985; National Research Council, 1989). It is almost exclusively propagated vegetatively today, as it probably has been for much of its existence. When a species under artificial selection (the pepino is known only from cultivation) is a member of a well-studied, fairly small monophyletic group, it affords the unique opportunity for comparisons of variability of important life history traits. Thus, we compared the cultigen *S. muricatum* with its closely related wild species to determine how a change in selection (from natural to artificial) may be associated with variability of its reproductive characters.

MATERIALS AND METHODS

The specimens studied (Appendix) included living and alcohol-preserved material obtained from plants grown from seed field-collected by GJA, supplemented where needed by herbarium specimens. Buds studied were near anthesis, so pollen was mature but anthers had not dehisced. Pollen quantity was estimated using Anderson and Symon's (1989) modification of Lloyd's (1965) technique. Ovules were counted with a dissecting microscope; those from one locule were doubled to obtain the total for an ovary. The mean P/O for each species was generated from individual ratios of separate buds. For dioecious *S. appendiculatum* the ratio was derived from the mean pollen quantity and the mean ovule quantity.

Pollen grain volume was calculated from the pollen grain sizes presented in Anderson and Gensel (1976) and from size determinations made utilizing the same technique for species not included in their study. When more than one accession of a species was used for pollen grain size determinations, the mean diameters of different accessions were used to calculate a grand mean, and this value was used for conversion to pollen grain volume. Seed volumes were taken from an unpublished study by G. J. Anderson and M. Fergusson, with the exception of *S. filiforme*, which we measured.

Pollen viability was estimated with percent stainability of 300–350 grains/flower using aniline blue in lactophenol

(Hauser and Morrison, 1964). Corolla radii were measured as the length from the androecium to the tip of the corolla lobe.

The data were analyzed using SAS (1985). Most variables were continuous; exceptions (nominal variables) were: 1) compatibility-group (levels were self-incompatible and self-compatible); 2) subgroup (levels were subgroup A and subgroup B); and 3) species (levels were the species listed in Table 1). All ANOVAs were nested, with species nested within the appropriate level of either compatibility-group or subgroup, depending on the test; F and partial F values were determined with GLM type III SS and GLM type I SS, respectively. The statistics were calculated, and statistical comparisons made, without the data from the dioecious species *S. appendiculatum* and the cultigen *S. muricatum*.

To investigate association of characters, correlations between all pairs of continuous variables were calculated by using the mean of each variable for each species. *Solanum muricatum* and *S. appendiculatum* were not included in correlation analyses. Correlations were calculated with both SI and SC species (Table 2) and independently for only SI species. The two correlations that became nonsignificant with the removal of the SC species are discussed separately. The sequential Bonferroni technique for adjusting for simultaneous tests (e.g., Rice, 1989) was also performed (Table 2).

RESULTS

Data for all variables for all species are summarized in Table 1. Mean (\pm SE) pollen grains/flower (= pollen quantity), ovules/ovary (= ovule quantity), and P/O are presented for each species in Figs. 1, 2, and 3, respectively. Mean pollen quantity ranges among species from 90,000 to 983,000 grains per flower (Fig. 1; Table 1), a near 11-fold range. Although the pollen quantity values of the SC species are relatively low, several SI species, largely in subgroup A, have similar or lower means (Fig. 1). When only the species of the green-fruited subgroup (B) are considered, however, pollen quantity is significantly lower for SC vs. SI groups of species (df 1, 92; $F = 152.2$; $P <$

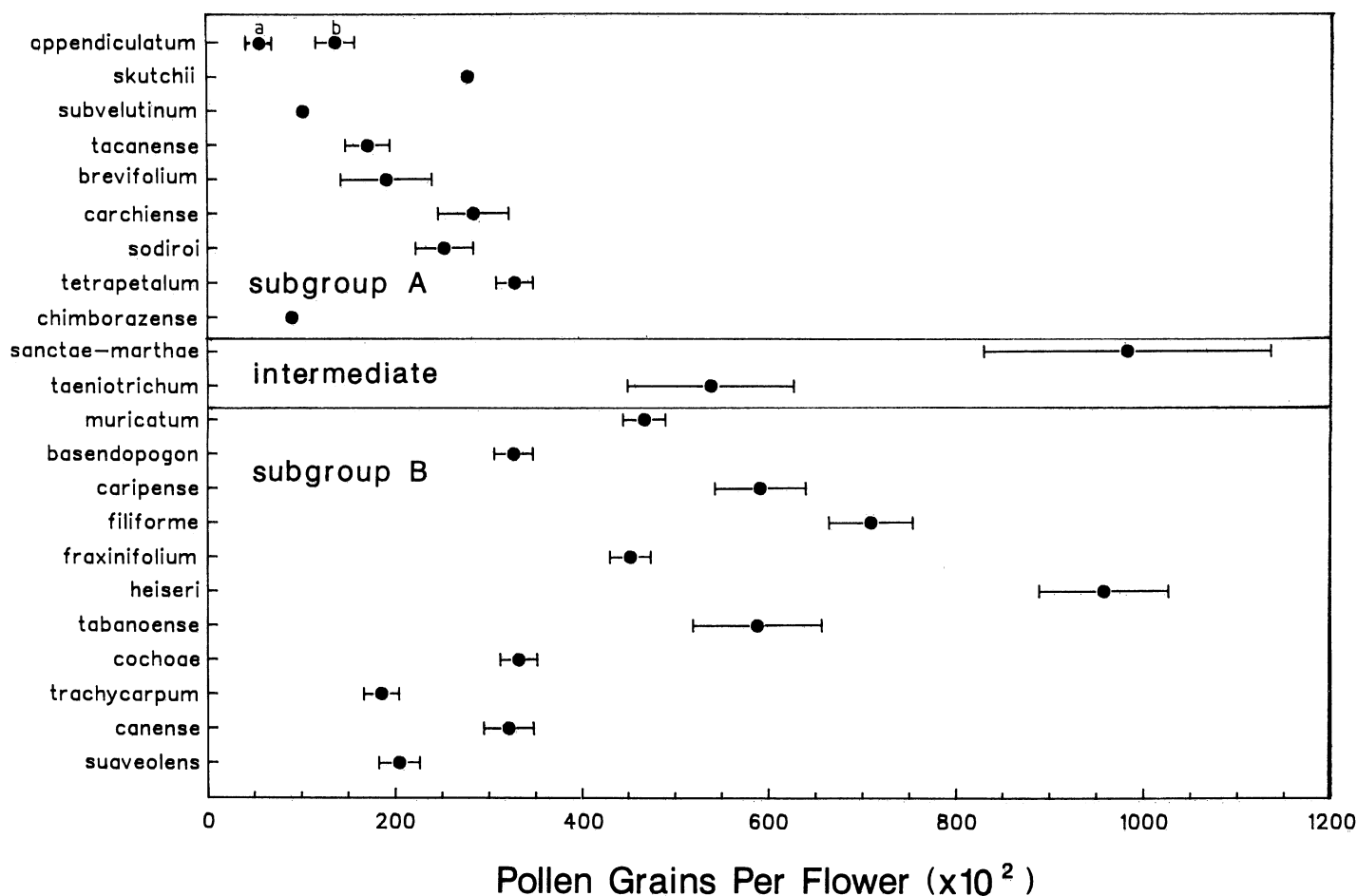


Fig. 1. Mean pollen grains per flower ± 1 SE. The bottom three species are self-compatible; all other species are self-incompatible or unknown. Presented for the dioecious *S. appendiculatum* are both the mean pollen grains per flower of pistillate flowers (a, nongerminable, inaperturate pollen) and staminate flowers (b, germinable, tricolporate pollen). See text for details about subgroup A, subgroup B, and the intermediate group.

0.0001). Pollen quantity is significantly greater in subgroup B than in subgroup A with or without the inclusion of the SC species (df 1, 145; $F = 107$; $P < 0.0001$; df 1, 119; $F = 167$; $P < 0.0001$; respectively).

Ovule quantity ranges from 33 to 364 among the perfect-flowered species (Fig. 2), also an 11-fold range. The three SC species have higher ovule quantities than all other species (except *S. filiforme*, for which compatibility is presently unknown). Ovule quantity is significantly higher for SC vs. SI groups of species (all species, df 1, 139; $F = 193.6$; $P < 0.0001$; only subgroup B, df 1, 86; $F = 35.9$; $P < 0.001$). The dioecious species *S. appendiculatum* has the lowest mean ovule quantity (13) of all species, and the pepino is among the species with the highest ovule quantities (Fig. 2). Ovule quantities of the species of subgroup B are all greater than those of subgroup A (Fig. 2).

P/Os are lowest for the SC species (Fig. 3; Table 1), ranging from 748 to 1,158 with a mean of 891. P/Os are significantly higher in the SI group of species than in the SC group of species (df 1, 145; $F = 526.8$; $P < 0.0001$). The P/O ratios for the 18 SI species range from 1,960 to 23,839, with a mean of 5,340. Thus, in sect. *Basarthurium* there is a nearly 32-fold range in P/Os; this is nearly three times the range present in either pollen or ovule quantity.

P/Os are significantly higher in subgroup A than in subgroup B (df 1, 145; $F = 18.8$; $P < 0.0001$). When SC species are not considered, however, P/Os of the two subgroups of species are not significantly different (df 1, 119; $F = 0.22$; $P < 0.637$).

The correlations significant at $P < 0.001$ (all positive) were pollen quantity with pollen biomass, ovule quantity with seed quantity, and pollen biomass with P/O (Table 2). Only these were significant with the sequential Bonferroni technique, which is conservative with this number of simultaneous tests. With this technique, if the variable pollen biomass is dropped (it is highly correlated with pollen quantity and therefore redundant) from the correlation analysis the negative correlation between pollen quantity and pollen grain volume becomes significant. This results from the reduction of the number of simultaneous tests (36 to 28 when one variable is not considered), which increases the "table-wide" significance level relative to that of a larger correlation matrix (see Rice, 1989).

Pollen grain volume is significantly negatively correlated with pollen quantity (Table 2). There is a significant positive correlation between pollen quantity and corolla radius only when one apparent outlier (*S. carchiense*) is dropped ($P = 0.02$, $r = 0.53$, $N = 19$). There are intra-

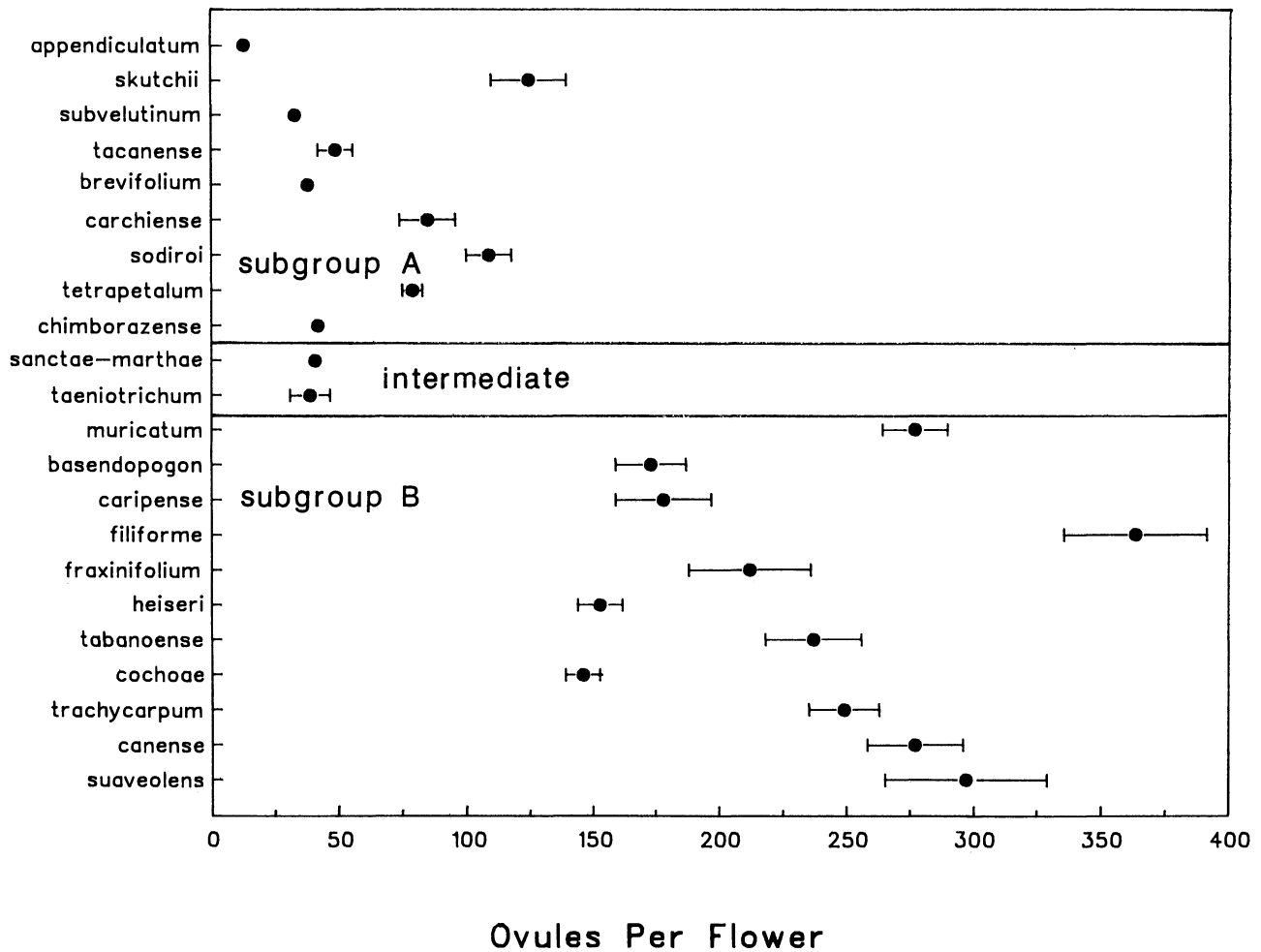


Fig. 2. Mean ovules per flower ± 1 SE. Order of species as in Fig. 1.

specific, positive correlations between pollen grains/flower and ovules/ovary in six species (*S. basendopogon*, *S. canense*, *S. caripense*, *S. fraxinifolium*, *S. heiseri*, and *S. taeniotrichum*). This correlation is not evident in other species, but for many, the sample sizes available (Table 1) were too small to address this issue.

Seed volume is significantly negatively correlated with both ovule and seed quantity, and significantly positively correlated with P/O (Table 2). The correlation between seed quantity and seed volume becomes nonsignificant when the SC species are dropped ($P = 0.0576$). Ovule quantity and P/O are significantly negatively correlated. When the SC species are dropped, however, this correlation also becomes nonsignificant ($r = -0.371$, $P = 0.142$, $N = 17$).

DISCUSSION

Several studies (cited in Cruden, 1977) show that xenogamous species produce more pollen grains, without systematic variation of ovule quantity, than related SC and/or autogamous species (i.e., the lower P/Os of the SC and/or autogamous species resulted from lower pollen quantity). Preston (1986) as well reported that the mean number of ovules per flower in 66 species of the Cruciferae

did not differ significantly between autogamous and allogamous groups of species, and Philbrick and Anderson (1987) found ovule quantity to be relatively constant in *Potamogeton*. In contrast, the SC species of sect. *Basarthurum* (all autogamous) have arrived at low P/Os apparently as a result of both lower pollen quantities (57% less on average) and higher ovule quantities (26% more on average), relative to the other members of subgroup B. Similarly, Schoen (1982) found significantly higher ovule production in populations of a hermaphroditic species having naturally high rates of selfing, relative to populations with lower rates of selfing.

For SI species, both pollen quantity and ovule quantity are significantly higher in subgroup B than in subgroup A. In spite of this, the mean P/Os of SI species of these subgroups are not significantly different. This suggests that the pollen and ovule quantities have evolved within some constraint of (subgroup) phylogeny, and that in the two subgroups the SI species have arrived at similar P/O values in parallel. This difference among subgroups in pollen and ovule quantities and similarity of P/O values suggests that it is not only absolute number, but also the ratio between pollen and ovule quantity that is biologically meaningful. This could be a consequence of a similar pollinator fauna and/or effective pollination rate.

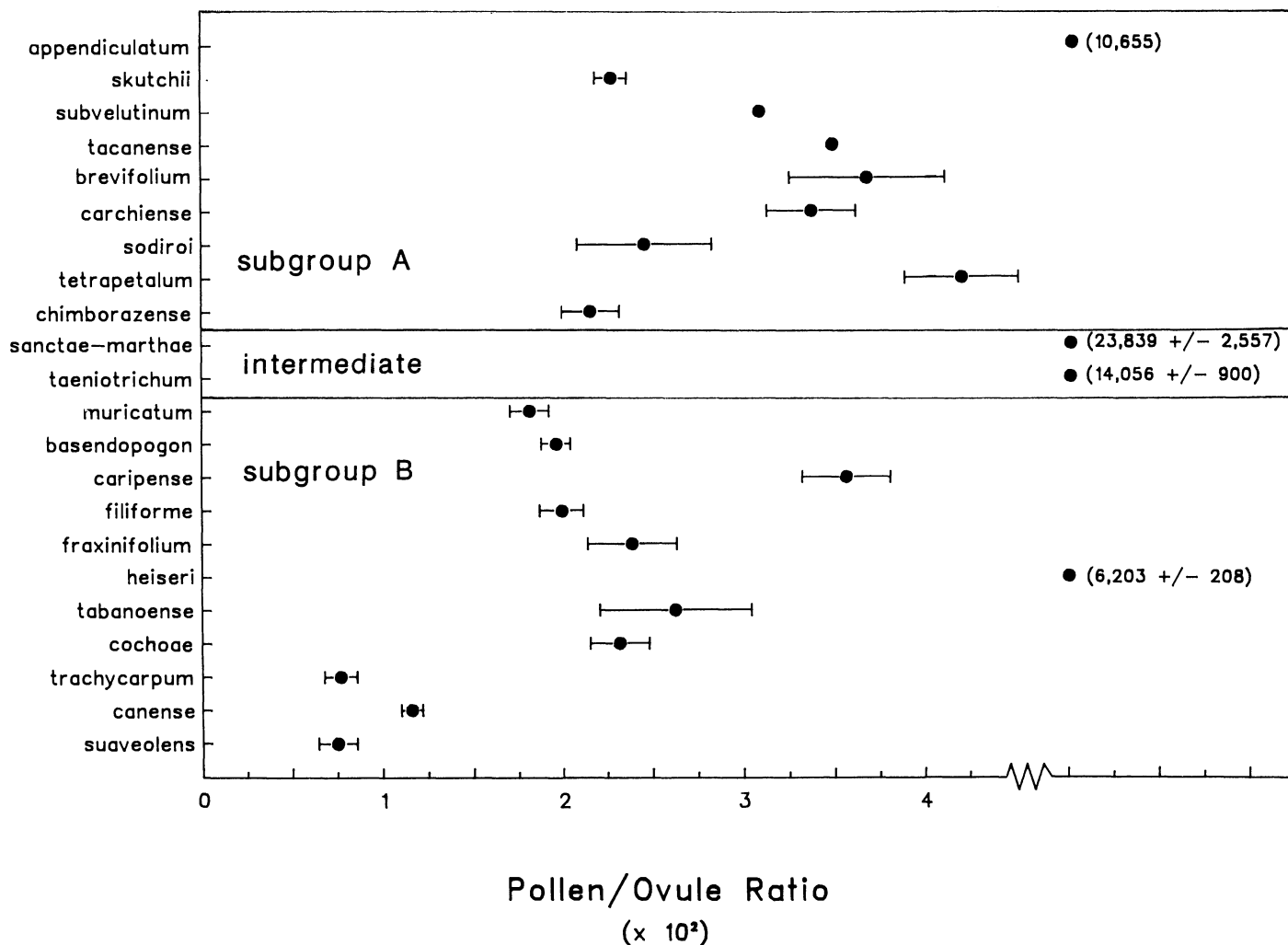


Fig. 3. Mean pollen-ovule ratios ± 1 SE. Order of species as in Fig. 1.

The seed to ovule ratio expresses the proportion of ovules developing into seeds. For annuals ($N = 2$) and perennials ($N = 17$) our estimated (from Table 1) mean seed-ovule ratios of 100% and 65%, respectively, parallel similar differences reported by Wiens (1984) and Small (1988). When the species we studied are grouped by breeding system (giving groups very similar to the annual/perennial categories) the outcome is similar. Mean seed/ovule ratios are 97% for SC species ($N = 3$) and 64% for SI species ($N = 16$).

The highly significant correlation between pollen quantity and pollen biomass, and lack of a significant correlation between pollen grain volume and pollen biomass, indicates that in sect. *Basarthurm* pollen quantity alone serves adequately as an indicator of allocation to pollen. The significant correlation between pollen biomass and P/O follows from this relationship. Pollen quantity is significantly correlated both with pollen grain volume (negatively) and corolla radius (positively, when one apparent outlier is dropped). Although likely not biologically meaningful, from these two correlations it then follows that pollen grain volume must be negatively correlated with corolla radius, which in fact is the case. The positive

correlation between pollen quantity and corolla radius may indicate that corolla size evolved in relation to male function, or simply that bigger flowers produce more pollen.

The negative correlation between seed (and ovule) quantity and seed volume implies a trade-off between seed quantity and size, as discussed by Primack (1987). However, our data do not allow exclusion of the possibility that selection for increase in seed quantity could be accompanied by seed size reduction due to ovary (or ripening ovary) size constraints, and not to energetics. We also found a significant negative correlation between pollen quantity and pollen grain volume. Such a trade-off was not found among populations of the annual *Arenaria uniflora*, which form a continuum from obligate selfers to obligate outcrossers (Wyatt, 1984).

As described earlier, the two subgroups are characterized by distinctive fruit types: small, red, few-seeded fruits (subgroup A) and larger, green, many-seeded fruits (subgroup B). All three of the SC species of sect. *Basarthurm* are in the many-seeded, large-fruited subgroup. In general, typical features of selfers (Ornduff, 1969; Wyatt, 1988), such as close proximity of anthers and stigmata, annual-

ness, and residence in disturbed or extreme habitats, characterize these species. Important and particularly relevant among these features is the large number of seeds/fruit. This feature is best attributed to the common phylogeny of subgroup B whereas the other features associated with self-compatibility among these species are unique to the compatibility-group. Given that large fruits are representative of all of subgroup B, we suggest that the larger fruits with their many seeds may have predisposed the members of subgroup B vs. members of subgroup A to the evolution of self-compatibility and autogamy.

Based on sex allocation theory, Charnov (1982) predicted that if the proportion of resources allocated to male vs. female functions remains constant among species (as may be the case within a given compatibility-group and breeding system), then P/O should be inversely proportional to pollen grain volume. A plot of the log of these two parameters would then have a slope of -1 if seed size does not vary systematically with pollen size. Charnov offered general support for this hypothesis using Cruden and Miller-Ward's (1981) data. Our data for subgroup B, but not for subgroup A, support this prediction. For subgroup B, P/O was inversely proportional to pollen grain volume when the data were not log transformed, with or without the SC species ($r = -0.684$, $P = 0.029$, $N = 10$; $r = -0.801$, $P = 0.031$, $N = 7$, respectively). With log transformation this correlation was significant only when SC species were dropped. For subgroup A ($N = 8$) this correlation was not significant, either with or without log transformation ($r = -0.292$, $P = 0.484$; $r = -0.351$, $P = 0.394$, respectively). For sect. *Basarthurum* as a whole we did not find a significant correlation between P/O and pollen grain volume either with (Table 2) or without the SC species ($r = -0.274$, $P = 0.29$, $N = 17$), or with log transformation (with SI and SC species $r = -0.172$, $P = 0.47$, $N = 20$; only SI species $r = -0.354$, $P = 0.16$, $N = 17$). Nowhere have we found a systematic relation of seed size and pollen size. One explanation for the incongruence of our subgroup A data with Charnov's prediction is that the proportion of resources allocated to male vs. female function may differ among species, even if they share the same breeding and compatibility system. One cause of differences in male:female allocation may be differences among species in the efficiency of pollination systems (defined in Introduction). Species with inefficient pollination systems should invest more energy in male function per unit gain in fitness. Similarly, differences in the efficiency of fruit/seed dispersers could result in differences among species in the fitness return on energy invested. However, the relative uniformity of the floral and fruit morphology and what is known of the pollination and dispersal of the species of subgroup A would not argue for such interspecific differences, so the incongruence of our subgroup A data with Charnov's prediction remains unexplained.

Charnov (1982) also predicted that species with higher P/Os will have proportionally larger seeds when pollen size is fixed. Our correlation between P/O and seed volume is positive and significant even without holding pollen size constant. But we also found significant correlations indicating that lower ovule numbers are associated with higher P/Os, and species with the lowest ovule (and seed) quantities have the largest seeds. Given any two of

the above three correlations the third must follow. Thus, the positive correlation between P/O and seed volume may be an artifact. However, in support of Charnov's prediction, the partial correlation of P/O with ovule quantity was not significantly different from 0 (seed volume controlled, partial $F = 0.1$; $P = 0.75$), but the partial correlation of P/O with seed volume was significant (ovule quantity controlled, partial $F = 21.3$; $P = 0.0002$).

The domesticated *S. muricatum*, the pepino, which is propagated almost entirely vegetatively, has been under the influence of artificial selection for at least 100–300 generations. Thus, one might predict relatively high amounts of variability in reproductive characteristics due to mutations not being lost to natural selection and drift. Pepinos are sometimes seedless as a direct or indirect result of artificial selection (Anderson, 1979b). Accordingly, the coefficient of variability (CV, an assessment of variability independent of the unit of measurement) of seeds/fruit was relatively high for *S. muricatum*. The highest variability in the cultigen was most obvious for percent pollen stainability (an approximation of percent pollen viability) where the CV was 136%, as compared to a mean of 49% among all wild species (range 2% to 101%). In contrast to this variation in pollen quality, the pollen quantity of the cultigen is relatively uniform, and is similar to that of its possible progenitors (*S. basendopogon*, *S. caripense*, *S. tabanoense*, *S. cochoae*, all wild; Anderson, 1979b, unpublished data). Such a pollen quantity is remarkably high for a species that is at least autogamous and possibly apomictic or parthenocarpic (Anderson, 1979b). Thus, one could conclude that over the short time (a few thousand years) *S. muricatum* has been subject to artificial selection, pollen viability has been more labile than pollen quantity. Pollen quality in some instances and viability in others is low in other fruit-producing domesticates (Purseglove, 1968).

The single dioecious species, *S. appendiculatum*, has a mean pollen grains/staminate flower to mean ovules/pistillate flower ratio of 10,655. We consider this to be a reasonable estimate of the overall P/O ratio because in natural populations the ratio of female to male plants is nearly 1:1 and the number of flowers/inflorescence is equal on plants of both sexes (Anderson, 1979a). However, the number of inflorescences per plant (long, branched climbing vines) of each sex in natural populations remains to be studied. In Fig. 1 we also present the mean pollen grain quantity of pistillate flowers because, although the pollen grains of pistillate flowers never germinate (Levine and Anderson, 1986), they are a component of the "breeding system" sensu lato in that they serve as reward to pollinators and have the potential to cause stigma clogging. In agreement with Webb's (1984) report for the Umbelliferae, dioecious *S. appendiculatum* has a higher P/O than most of the perfect-flowered species we studied. Webb (1984) presumed that the high P/Os were due to high pollen quantities and male-biased sex ratios. In *S. appendiculatum*, however, the pollen quantity (staminate flowers only) is the third lowest of all the species studied. The high P/O thus results primarily from the low ovule quantity of this species (20% of the average ovule quantity of the species of the red-fruited subgroup).

If species that provide pollen instead of nectar as a reward to pollinators (see Vogel, 1978) must produce extra

pollen to compensate for the quantity consumed by pollinators, one might expect (at least within the same breeding system and compatibility-group) pollen-providing species to have higher P/Os than nectar-providing species. Thus, we compared the mean P/O of these pollen-rewarding obligate outcrossing *Solanum* species with Cruden's (1977) mean for 25 presumably nectar rewarding, obligate outcrossing species. Our mean P/O of 5,340 is similar to, and not higher than, Cruden's mean of 5,859 for presumably nectariferous species. This may indicate that the quantity of pollen consumed by *Solanum* pollinators is not a factor. More likely, it shows that comparisons of P/Os for this purpose should be made, as we have done in this study, among species in monophyletic groups. A more meaningful comparison would involve sister groups with the same compatibility and breeding system, but with different pollinator rewards.

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APPENDIX. *Species studied. Collection numbers of specimens without an herbarium acronym are those of G. J. Anderson*

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- S. appendiculatum* Humb. & Bonpl. ex Dunal Mexico: 654; 656; 672; 704; 708; 1,401.
S. basendopogon Bitter Peru: 43; 44; S. D. Correll, E. E. Smith, R. Ferreyra P284, US; R. Ferreyra 6,068, US; R. Ferreyra 7,195, USM^a; J. Gomez 51, USM^a; G. Vilcapoma 160, USM.^a
S. brevifolium Humb. & Bonpl. ex Dunal Ecuador: 836; 873; 885; C. B. Heiser 6,855 (GJA 21).
S. canense Rydb. Costa Rica: 507; 509; Panama: D'Arcy 5,188 (GJA 46), MO.
S. carchiense Correll Ecuador: 813.
S. caripense Humb. & Bonpl. ex Dunal Costa Rica: 493; Ecuador: 220; 239; C. B. Heiser 6,548 (GJA 13).
S. chimborazense Bitter & Sodiro Ecuador: 858.
S. cochoae G. J. Anderson & Bernardello Peru: C. Ochoa 13,249 (GJA 934).
S. filiforme Ruiz Lopez & Pavón Peru: C. Ochoa 15,307 (GJA 1452).
S. fraxinifolium Dunal in DC Costa Rica: 498; 500; 505; 1,476.
S. heiseri G. J. Anderson Colombia: C. B. Heiser 6,800.
S. muricatum Aiton Chile: 1,461; 1,462; 1,463; Colombia: 734; 751; C. B. Heiser 6,318; Ecuador: 348; 349; 619; 642; 844; 686; New Zealand: 1,453; Peru: 33, 35, 910.
S. sanctae-marthae Bitter Colombia: 84.
S. skutchii Correll Mexico: C. Conzatti 631, GH; C. L. Lundell and A. A. Lundell 7185, NY.
S. sodiroi Bitter Colombia: 724; 738; M. Nee 32,565 (GJA 1479).
S. suaveolens Knuth & Boché Peru: 40; G. Klug 4,139, US; Venezuela: 625.
S. subvelutinum Rydb. Mexico: H. S. Gentry 6,235, NY.
S. tabanoense Correll Colombia: 769; Ecuador: 242; C. B. Heiser 6,544 (GJA 29).
S. tacanense Lundell Mexico: E. Matuda 5,464, F.
S. taeniotrichum Correll Costa Rica: 1,437.
S. tetrapetalum Rusby Ecuador: 796; 827.
S. trachycarpum Bitter & Sodiro Ecuador: C. B. Heiser 7,087 (GJA 26).

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