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A COMPARATIVE STUDY OF INFLORESCENCE CHARACTERS AND POLLEN-OVULE RATIOS AMONG THE GENERA *PHILODENDRON* AND *ANTHURIUM* (ARACEAE)

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Floral characters in angiosperms may be involved in different relationships in order to ensure and maximize pollination. To assess these relationships, which may provide insight to understand floral evolution, we analyzed 14 floral characters in 23 species of *Philodendron* and 20 species of *Anthurium*, which are tropical long-living plants bearing spadiciform inflorescences. Contrary to what has been reported in the literature, no correlations were found between the pollen volume and either the style depth or the stigma depth. The trade-off between pollen size and number normally explained by limited resources was found only in *Philodendron*. Instead, pollen number was positively correlated with the inflorescence peduncle diameter. The higher range of variation of inflorescence peduncle diameters in *Anthurium* may explain the lack of correlation between pollen size and number. These results suggest that adaptive constraints driving pollen size and number could differ in the *Philodendron* and *Anthurium* genera from what is found for temperate angiosperms. Also, the stigma area and the pollen quantity were positively correlated with respect to the inflorescence flowering cycle and the flower morphology. Finally, the pollen-ovule ratio is not linked to the breeding system in the studied genera. Our data show that the aroid inflorescence, which behaves as a single flower, is the main pollination unit.

Keywords: pollination types, floral characters, pollen number, pollen size, stigma size, P/O, flowering cycle.

Introduction

Angiosperm flowers are regarded as complex and integrated systems in which floral traits are organized to ensure and maximize reproduction. Until now, studies involving relationships among floral characters (fig. 1) with regard to plant reproductive evolution were mostly performed on flowers of dicotyledons. However, little is known concerning monocotyledons, particularly those possessing spadiciform inflorescences, for example, Araceae, Cyclanthaceae, and Acoraceae. Understanding interactions among components of reproductive structures in such plant groups is essential to the global comprehension of the evolution of floral characters in relation to breeding systems and their level of selection/integration (flower or inflorescence).

Cruden (2000) has proposed a very useful model (fig. 1) showing the relationships among floral traits with regard to pollen transfer efficiency that will be used for comparison. However, many of these relationships remain to be verified in different plant groups and at different taxonomic levels: between stigma height or style length and pollen size, between pollen size and number of pollen grains, between number of pollen grains and stigma area, and between pollen-ovule ratio and breeding systems (fig. 1). In order to test these relationships, inflorescences of *Anthurium* and *Philodendron* were used as comparative models (fig. 2).

The existence of a positive correlation between pollen size and pistil length (not presented in fig. 1) has been found in different plant groups (Baker and Baker 1982; Plitmann and Levin 1983; Williams and Rouse 1990; Ramamoorthy et al. 1992; Kirk 1993; Ortega-Olivencia et al. 1997; Harder 1998; Lopez et al. 1999; Roulston et al. 2000; Torres 2000; Sarkissian and Harder 2001; Aguilar et al. 2002; Yang and Guo 2004). This correlation has been attributed to a relation between the storage capacity of pollen grains and the stigma-ovule distance (Baker and Baker 1982). Hence, the protein content of pollen grains represents up to 60% of its mass (Roulston et al. 2000), and it consists mainly of enzymes believed to have a functional role in pollen grain germination and pollen tube growth (Roulston et al. 2000). Therefore, larger pollen grains that have the potential to grow longer pollen tubes are associated with longer styles. In Nyctaginaceae species, pollen size–pistil length correlation is positive for species with starchy pollen but not for species with pollen with lipid (López et al. 2005). On the other hand, Cruden and Lyon (1985) found a positive correlation between pollen size and stigma depth and proposed the hypothesis that the pollen tube has to pass through the stigma to reach exogenous reserves present in the transmission tissue that allow tube growth in order to reach the ovule (Cresti et al. 1976; Knox 1984; Herrero and Hormaza 1996). On the basis of this information, pollen size should be linked to stigma depth and not style length (fig. 1).

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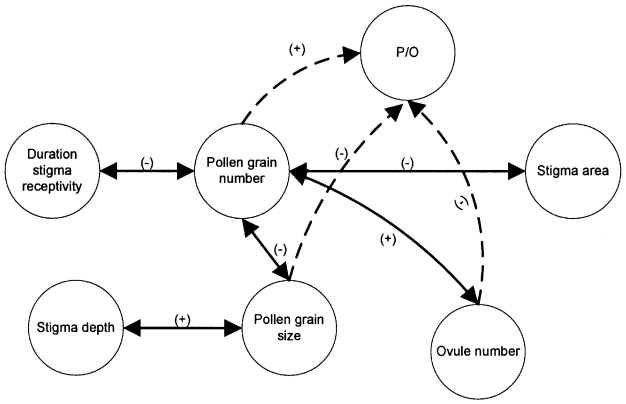

Fig. 1 Positive (plus sign) and negative (minus sign) correlations among floral traits in animal-pollinated plants proposed by Cruden (2000). Solid lines indicate relationships that were demonstrated empirically. Dashed lines indicate that the pollen-ovule ratio might be influenced by change in a given trait.

Another factor affecting pollen size is the number of pollen grains a flower can support. Studies suggest that plants evolved an optimal pollen size that balances the advantage of large pollen size for gametophytic competition against the fecundity disadvantage of fewer pollen grains produced (Aguilar et al. 2002; Yang and Guo 2004). A negative correlation between those two traits has been well documented at both inter- and intraspecific levels in many plant groups (Mione and Anderson 1992; Knudsen and Olesen 1993; Stanton and Young 1994; Vonhof and Harder 1995; Worley and Barrett 2000; Sarkissian and Harder 2001; Yang and Guo 2004) but not in others (Cruden and Miller-Ward 1981; Stanton and Preston 1986; Lopez et al. 1999; Aguilar et al. 2002). This relation has been interpreted as a simple trade-off between pollen size and number due to the limited resources available to the flower. Thus, for a given species, the competitive advantage of larger pollen grains may counterbalance the numerical advantage of small pollen (Sarkissian and Harder 2001).

Other than the relationships between pollen number and size and between pollen size and style or stigma depth, Cruden (1997, 2000) found a negative correlation between the number of pollen grains and the stigma area in both *Symphionema* and *Isopogon* (Proteaceae). It has been supposed that a larger stigmatic area has a greater chance of contacting the pollen-bearing area of the pollinator; this results in fewer pollen grains being required for pollination success.

Cruden (1977), after studying 80 different species, concluded that the pollen-ovule ratio (P/O) is related to the plant breeding system. The higher the degree of autogamy is, the lower the P/O will be. This relationship was based on the assumption that the P/O reflects the efficiency of pollination. "The more efficient the transfer of pollen is, the lower the pollen-ovule ratio should be" (Cruden 1977, p. 32). Many studies have more or less confirmed the relationship between the P/O and the breeding system (Schoen 1977; Lord 1980; Wyatt 1984; Campbell et al. 1986; Philbrick and Anderson 1987; Ritland and Ritland 1989; Plitmann and Levin 1990; Mione and Anderson 1992; Lopez et al. 1999; Jürgens et al. 2002; Wang et al. 2004) although some have not (Gallardo et al. 1994; Ramirez and Seres 1994; Wyatt et al. 2000; Chouteau et al. 2006). It has been mentioned that factors such as habitat, pollinators, pollination mechanism, and floral morphology could influence the variations of P/O among species.

To date, the P/Os of Neotropical aroids are known from only two studies (Ramirez and Seres 1994; Chouteau et al. 2006). The study of nine species from French Guiana aroids has shown that, in these species, the relationship between the P/O and the breeding system was opposite to that found by Cruden (1977) in other families. In Araceae, a link was hypothesized between the P/O and the type of pollination mechanism, habitat, and mode of growth. The more complex the pollination mechanism, the lower the P/O was, and terrestrial, holophyte, and geophyte species had higher P/Os than hemiepiphytic species (Chouteau et al. 2006).

On the basis of sex allocation theory (Charlesworth and Charlesworth 1981; Charnov 1982; Morgan 1992), there should be a trade-off in resource allocation between pollen and ovule. This relationship is due to the fact that plants have limited resources and should distribute the resources between reproductive male and female functions to maximize their fitness. Consequently, a negative relation is expected in cosexual (male and female functions on the same individual) species between the male and the female functions (Stearns 1992). However, few studies have reported negative correlations between male and female functions (Charlesworth and Charlesworth 1981; Charnov 1982; Morgan 1992; Stearns 1992; Mazer et al. 1999), and most of the recent studies reported positive correlations (Small 1988; Campbell 1992, 1997, 2000; Mazer 1992; O'Neil and Schmitt 1993; Gallardo et al. 1994; Agren and Schemske 1995; Ortega-Olivencia et al. 1997; Ashman 1999; Burd 1999; Lopez et al. 1999; Koelewijn and Hunscheid 2000; Yang and Guo 2004). Campbell (2000) explained that both positive and negative relationships between resource allocations into male and female functions are possible. According to Campbell, genetic variation in sex allocation (negative correlation) is often small compared with variation in traits related to resource acquisition and vigor (positive correlation), perhaps because

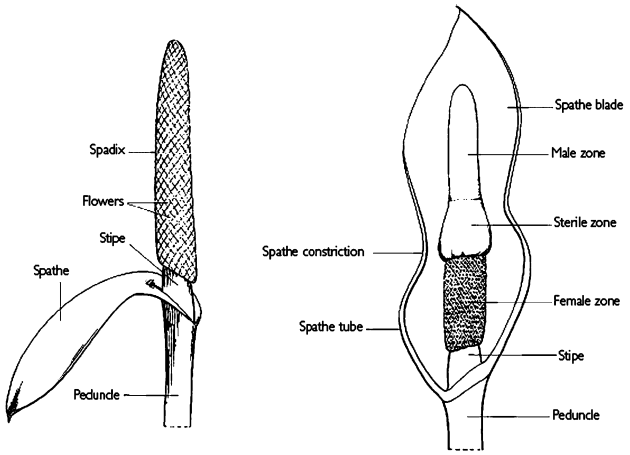

Fig. 2 *Left*, bisexual flowers inflorescence (*Anthurium*); *right*, unisexual flowers inflorescence (*Philodendron*) (from Mayo et al. 1997).

flowers can use different resource pools for male and female parts, as suggested by physiological studies (Ashman 1994).

In contrast to trees and shrubs, little is known about the reproductive biology of understory plant species. Even though the most conspicuous and dominant elements in the understory and canopy of tropical rainforests are the large herbaceous and broad-leaved monocots, the P/O has been poorly studied in these tropical plants displaying hemiepiphytic and epiphytic types of growth (Ramirez and Seres 1994; Chouteau et al. 2006). In this perspective, the Araceae family (105 genera, more than 3300 species), which possesses a great variability in reproductive mechanisms, constitutes very good material for studying the relationships presented in figure 1. Aroids have the particularity of possessing compact inflorescences, with bisexual flowers (*Anthurium*) and unisexual flowers (*Philodendron*) showing very different floral cycles. In this study, two genera with different inflorescence structures and pollination mechanisms, *Philodendron* and *Anthurium*, will be compared.

The genus *Philodendron* is the second largest of the Araceae, with about 400 species present in the Neotropics (Govaerts and Frodin 2002) but estimated to have up to 750 species (Croat, from Moscow Aroid Conference, 1992, cited in Govaerts and Frodin 2002). The *Philodendron* species sampled in our study are all hemiepiphytes. The protogynous inflorescences of the genus *Philodendron* are spadices, each bearing small flowers enclosed in a fleshy bract, the spathe (fig. 2). The pistillate flowers occupy the lower portion of the spadix, whereas the male flowers are located in the upper portion. In the median portion of the spadix, there is a zone consisting of sterile male flowers. The inflorescence is closed during its entire development except during anthesis. The inflorescences of *Philodendron* have a 24-h flowering cycle (Gibernau et al. 1999, 2000; Gibernau and Barabé 2002), beginning with the receptivity of the female flowers on the first night and finishing with the release of pollen on the second night (Gibernau et al. 1999, 2000). They are mainly pollinated by beetles of the genus *Cyclocephala* (Gibernau 2003) that are attracted to the inflorescence during the heating and odoriferous period of the spadix. In *Philodendron* species, the spathe plays an important role during pollination. During the first night, attracted beetles stay in the floral chamber formed by the basal portion of the spathe, where they mate and pollinate the female flowers (which are all receptive). During the following night, the beetles leave the spathe, and a resin is produced by the male portion of the spadix or the ventral (i.e., internal) side of the spathe, depending on the species. The resin, mixed with the pollen (all the pollen is released at the same time), sticks onto the bodies of the beetles that are leaving the inflorescence. This quite complex inflorescence morphology and cycle have the particularity of preventing self-pollination (sexual phases temporally separated, i.e., dichogamy) and of realizing pollination with only one visit: pollinators have to reach the inflorescences only once during the female phase to ensure the pollination cycle (Gibernau 2003).

The genus *Anthurium* is the largest of the Araceae, consisting of more than 700 species (Govaerts and Frodin 2002) but estimated to have as many as 1000 species (Croat cited in Govaerts and Frodin 2002). The inflorescences bear only bisexual flowers and do not have any distinct morphological zones (fig. 2). The bisexual flowers consist of four tepals and four stamens surrounding a pistil (Mayo et al. 1997). In the genus *Anthurium*, the flowering cycle can last more than 2 wk (Croat 1980; M. Chouteau and D. Barabé, unpublished data). During the first half of the flowering cycle, flowers are all in female phase, and stigmas are receptive. During the second half, the pollen is released progressively from the base of the inflorescence to the top. In *Anthurium*, the spathe is generally open and does not have a complex pollination function as in *Philodendron*. The pollination mechanism is also poorly known, but studies have pointed out that some species may be pollinated by euglossine bees, others by curculionid beetles, and one by hummingbirds (for a review, see Gibernau 2003). Moreover, in *Anthurium*, the inflorescence has no floral chamber, and thus pollinators come and go several times during the pollination cycle. The efficiency of pollination may be reduced by the fact that at least two visits are required, the first to bring pollen to a receptive inflorescence and the second to carry away pollen from the same inflorescence during the male phase (e.g., pollen released). Given that *Anthurium* and *Philodendron* have very different inflorescence structures and floral cycles, it may be possible to test whether some of the relationships presented in figure 1 remain the same in genera of the same family having different floral morphologies and pollination mechanisms.

The particular objectives of this study are as follows: (1) to ascertain whether pollen size is positively correlated with style or stigma depth; (2) to verify whether pollen number is negatively correlated with pollen size; (3) to analyze the relationships between investments in male function (e.g., stamen and pollen grain number, pollen volume) and female function (e.g., flower and ovule number, stigmatic size) at both the flower and the inflorescence levels; and (4) to analyze the link between the P/O and the breeding system and variations of floral characters in *Anthurium* and *Philodendron*.

Material and Methods

This study was conducted on 23 species of *Philodendron* (table 1) and 20 species of *Anthurium* (table 2) collected in the living collections of the Montreal Botanical Garden, the Montreal Biodôme, and in the field (French Guiana). Voucher specimens were deposited at the Marie-Victorin Herbarium (MT).

The *Philodendron* inflorescences were collected during the first day of the flowering cycle, when the spathe is open but before pollen is released. For each inflorescence, the total number of female flowers was counted directly, and the total number of stamens was estimated. To estimate the number of stamens per inflorescence, a 5-mm slice was cut in the middle of the male zone, and the number of stamens was counted on its entire surface. The total number of stamens was obtained by multiplying the number of stamens on the slice by the length of the male zone divided by 5. The male zone was considered to be a cylinder, and its height was measured with a digital caliper (0.01-mm resolution). *Anthurium* inflorescences were colected on the first day of pollen release, and the total number of flowers was determined by counting all the flowers for each inflorescence individually.

To estimate the number of stamens per male flower in *Philodendron* species, the male zone was cut off and dried for 7 d at the ambient air temperature. Once dried, the stamens of

Table 1

Floral Traits and Self-Pollination Capacity for 23 *Philodendron* Species

	Inflorescence peduncle diameter (cm) ($N \geq 3$)	Style length (mm) ($N \geq 30$)	Stigma height (mm) ($N \geq 30$)	Pollen grain volume (μm^3) ($N \geq 30$)	Pollen grain no./stamen ($N \geq 27$)	Stamen/flower ($N \geq 30$)	Ovule no./flower ($N \geq 30$)	Stigma area/flower (mm^2) ($N \geq 30$)	Stamen no./ inflorescence ($N \geq 3$)	Female flower no./ inflorescence ($N \geq 3$)	P/O of inflorescence ($N \geq 3$)	Self-pollination capacity
P. acutatum Schott	NA	NA	NA	NA	4286 ± 1476	4.76 ± 0.60	77.9 ± 16.8	2.63 ± 0.74	7987 ± 1254	737 ± 79	630 ± 275	No
P. bipinnatifidum Schott	3.40 ± 0.50	1.86 ± 0.15	0.79 ± 0.02	74,749 ± 10,777	9839 ± 1546	4.30 ± 0.48	16.6 ± 0.2	5.73 ± 0.50	7792 ± 465	411 ± 43	11,418 ± 3065	No
P. cannifolium (Dryander ex Sims) G. Don	1.60 ± 0.10	0.97 ± 0.04	0.38 ± 0.30	50,346 ± 5557	2353 ± 1413	2.10 ± 0.32	17.6 ± 3.9	0.99 ± 0.20	2603 ± 629	1070 ± 30	308 ± 4	No
P. distantlobum K. Krause	1.47 ± 0.06	1.27 ± 0.11	0.63 ± 0.04	79,915 ± 8304	1703 ± 787	4.70 ± 0.48	32.4 ± 3.8	1.55 ± 0.45	5135 ± 1040	888 ± 16	324 ± 201	No
P. erubescens C. Koch & Augustin	1.23 ± 0.03	1.40 ± 0.01	0.74 ± 0.02	63,218 ± 11,383	2713 ± 1335	2.60 ± 0.52	15.7 ± 0.9	1.04 ± 0.12	1989 ± 105	775 ± 129	469 ± 292	No
P. glaziovii Hook. f.	1.07 ± 0.06	0.80 ± 0.12	NA	54,649 ± 5446	4139 ± 2998	4.00 ± 0.66	26.4 ± 1.2	1.34 ± 0.15	1143 ± 40	695 ± 122	239 ± 150	No
P. gloriosum Andre	1.28 ± 0.05	1.00 ± 0.02	0.27 ± 0.04	NA	4389 ± 1951	6.40 ± 0.51	100.2 ± 7.1	1.75 ± 0.08	4203 ± 785	478 ± 106	454 ± 381	No
P. grandifolium Schott	NA	NA	NA	135,327 ± 33,322	1279 ± 824	NA	13.6 ± 0.1	2.04 ± 0.97	3664 ± 156	717 ± 61	474 ± 162	No
P. insigne Schott	1.16 ± 0.06	1.02 ± 0.04	NA	74,319 ± 7945	1289 ± 547	4.10 ± 0.32	15.4 ± 0.2	0.28 ± 0.01	2212 ± 44	1197 ± 102	152 ± 26	No
P. linnaei Kunth	1.05 ± 0.05	0.83 ± 0.09	0.35 ± 0.03	69,937 ± 5474	3086 ± 1116	3.80 ± 0.42	24.2 ± 0.2	0.99 ± 0.17	3632 ± 167	1424 ± 166	327 ± 37	No
P. melanochrysum Linden & Andre	1.69 ± 0.03	1.22 ± 0.37	0.75 ± 0.01	54,928 ± 5949	5313 ± 2665	5.90 ± 0.64	284.1 ± 31.1	1.63 ± 0.52	6457 ± 1781	761 ± 78	153 ± 74	No
P. megalophyllum Schott	1.00 ± 0.10	0.88 ± 0.02	0.21 ± 0.03	112,719 ± 9072	2416 ± 1362	3.60 ± 0.52	3.8 ± 0.3	0.98 ± 0.07	883 ± 495	621 ± 54	961 ± 577	No
P. melinonii Brongn. ex Regel	1.70 ± 0.21	3.10 ± 0.16	0.63 ± 0.01	46,917 ± 5636	6209 ± 2304	4.64 ± 0.12	52.8 ± 3.4	3.25 ± 0.86	4937 ± 1113	394 ± 56	1487 ± 529	No
P. microstictum Standley & L. O. Williams	1.06 ± 0.06	0.68 ± 0.08	0.11 ± 0.01	48,686 ± 8552	2516 ± 1172	4.10 ± 0.52	8.2 ± 0.1	0.90 ± 0.08	5126 ± 419	680 ± 58	2300. ± 657	No
P. sp. aff. *megalophyllum*	1.28 ± 0.02	1.03 ± 0.08	0.68 ± 0.06	92,449 ± 13,019	2610 ± 775	3.20 ± 0.42	3.8 ± 0.1	0.76 ± 0.08	1724 ± 791	564 ± 15	2157 ± 1,240	No
P. ornatum Schott	1.30	0.86 ± 0.01	0.30 ± 0.02	19,250 ± 1075	7354 ± 2000	4.90 ± 0.87	68.4 ± 0.2	0.91 ± 0.10	4033 ± 1749	708 ± 291	608 ± 48	No
P. pedatum Kunth	1.29 ± 0.03	1.10 ± 0.05	0.43 ± 0.02	83,061 ± 39,695	2893 ± 1276	6.00 ± 0.30	34.1 ± 2.0	1.28 ± 0.09	5789 ± 2140	1060 ± 76	484 ± 297	No
P. radiatum Schott[a]	2.13 ± 0.13	1.78 ± 0.09	NA	56,357 ± 3309	6386 ± 1810	4.20 ± 0.41	43.1 ± 6.0	2.30 ± 0.21	4377	647	1002	No
P. ruizii Schott	1.33 ± 0.15	1.67 ± 0.33	0.47 ± 0.01	107,823 ± 6946	2729 ± 1308	3.50 ± 0.71	23.1 ± 1.8	1.86 ± 0.17	5563 ± 719	1458 ± 80	448 ± 53	No
P. solimoesense A. C. Smith	2.83 ± 0.15	0.95 ± 0.09	0.72 ± 0.03	92,215 ± 6116	6169 ± 1992	5.00 ± 0.28	169.8 ± 24.7	10.44 ± 0.20	12,872 ± 2742	232 ± 34	2065 ± 989	No
P. squamiferum Poepp. & Endl.	0.86 ± 0.05	0.90 ± 0.11	0.32 ± 0.03	47,680 ± 26,117	3863 ± 1171	3.80 ± 0.42	25.8 ± 3.4	1.06 ± 0.54	4783 ± 1313	641 ± 36	1081 ± 86	No
P. talamancae Engl.[a]	NA	NA	NA	NA	4746 ± 300	NA	43.3 ± 6.3	4.81 ± 0.30	429	458	NA	No
P. tripartitum Schott	1.15 ± 0.05	NA	NA	65,929 ± 15,992	5406 ± 977	NA	15.2 ± 3.1	1.12 ± 0.32	3294 ± 303	782 ± 83	1579 ± 638	No

Note. NA = data not available.

[a] Smaller sampling, $n \leq 2$ inflorescences.

Table 2

Floral Traits and Self-Pollination Capacity for 20 *Anthurium* Species

	Inflorescence peduncle diameter (cm) ($N \geq 3$)	Pistil length (mm) ($N \geq 30$)	Stigma height (mm) ($N \geq 30$)	Pollen grain volume (μm^3) ($N \geq 30$)	Pollen grain no./flower ($N \geq 27$)	Ovule no./flower ($N \geq 30$)	Stigma area/flower (mm^2) ($N \geq 30$)	Flower no./inflorescence ($N \geq 3$)	P/O of inflorescence ($N \geq 3$)	Self-pollination capacity
A. acaule Schott	0.78 ± 0.10	0.61 ± 0.06	0.26 ± 0.03	1923 ± 274	22,966 ± 12,684	2 ± 0	0.27 ± 0.04	861 ± 230	11,482 ± 6387	Yes
A. barclayanum Engl.	0.88 ± 0.13	0.77 ± 0.03	0.18 ± 0.01	8768 ± 929	65,999 ± 4104	2 ± 0	0.13 ± 0.02	2235 ± 97	31,225 ± 2038	No
A. clavigerum Poepp.	1.26 ± 0.06	1.05 ± 0.05	0.46 ± 0.01	9452 ± 1163	61,565 ± 29,787	2 ± 0	0.80 ± 0.05	4522 ± 102	30,782 ± 18,173	No
A. crystalinum Linden & André	0.52 ± 0.10	0.73 ± 0.08	0.34 ± 0.01	3550 ± 505	35,465 ± 9767	4 ± 0	0.32 ± 0.05	733 ± 84	8866 ± 3016	Yes
A. truncicolum Engl. *(divaricatum)*	0.40 ± 0.09	0.83 ± 0.07	0.25 ± 0.02	1583 ± 179	11,349 ± 6855	2 ± 0	0.29 ± 0.05	1102 ± 469	5674 ± 1850	No
A. fendleri Schott	0.70 ± 0.10	0.56 ± 0.09	0.19 ± 0.10	2200 ± 338	43,415 ± 16,068	2 ± 0	0.20 ± 0.02	1903 ± 394	21,707 ± 10,005	Yes
A. harrisii (Grah.) G. Don	0.49 ± 0.09	0.94 ± 0.05	0.37 ± 0.01	3172 ± 794	35,488 ± 6683	2 ± 0	1.08 ± 0.17	369 ± 55	17,743 ± 2284	No
A. jenmanii Engl.	1.53 ± 0.15	1.01 ± 0.06	0.34 ± 0.01	4854 ± 1380	57,566 ± 8679	2 ± 0	0.76 ± 0.06	3134 ± 458	28,783 ± 2238	No
A. longistamineum Engl.	0.73 ± 0.25	0.85 ± 0.07	0.23 ± 0.02	2579 ± 334	27,499 ± 10,143	2 ± 0	0.57 ± 0.07	1742 ± 326	14,166 ± 5279	Yes
A. ornatum Schott	0.65 ± 0.06	NA	NA	NA	38,349 ± 4925	2 ± 0	NA	1409 ± 73	19,174 ± 2038	No
A. pedatoradiatum Schott	0.49 ± 0.10	1.36 ± 0.11	0.33 ± 0.02	3648 ± 605	36,932 ± 2701	2 ± 0	0.93 ± 0.05	454 ± 183	18,057 ± 459	No
A. polyrhizum (polyrhizon) K. Koch & Augustin *(rubrinervium)*	0.72 ± 0.08	0.97 ± 0.19	0.34 ± 0.01	3,695 ± 1,008	40,583 ± 26,292	2 ± 0	1.25 ± 0.23	1399 ± 201	20,282 ± 16,664	No
A. polyschistum R. E. Schult. & Idrobo	0.42 ± 0.03	1.02 ± 0.04	0.41 ± 0.01	2522 ± 453	41,799 ± 4029	2 ± 0	0.38 ± 0.08	445 ± 61	20,888 ± 675	No
A. radicans K. Koch & A. Haage	0.49 ± 0.02	1.65 ± 0.05	NA	4748 ± 871	18,616 ± 2455	2 ± 0	0.19 ± 0.04	104 ± 7	8460 ± 1540	No
A. salviniae Hemsl.	2.03 ± 0.25	1.71 ± 0.87	NA	2953 ± 823	59,632 ± 20,800	2 ± 0	0.19 ± 0.04	9087 ± 155	29,815 ± 5279	Yes
A. schlechtendalii ssp. *schlechtendalii* Kunth	0.73 ± 0.03	0.82 ± 0.04	0.25 ± 0.01	6858 ± 1233	36,882 ± 3269	2 ± 0	0.33 ± 0.05	2215 ± 54	18,441 ± 1001	Yes
A. spectabile Herincq	1.10 ± 0.18	3.30 ± 0.32	0.23 ± 0.02	5238 ± 938	56,182 ± 26,000	2 ± 0	1.68 ± 0.12	2761 ± 649	28,091 ± 16,557	Yes
A. fatoense K. Krause	0.96 ± 0.15	1.54 ± 0.08	0.29 ± 0.03	2163 ± 219	55,232 ± 22,959	2 ± 0	0.82 ± 0.07	693 ± 184	27,614 ± 13,174	No
A. trinerve Miq.	0.26 ± 0.04	0.81 ± 0.07	0.25 ± 0.03	4645 ± 823	24,749 ± 1980	4 ± 0	0.13 ± 0.04	43 ± 17	5916 ± 612	Yes
A. upalahense Croat & R. A. Baker	1.08 ± 0.13	1.16 ± 0.07	0.21 ± 0.02	3202 ± 438	31,016 ± 7798	2 ± 0	0.43 ± 0.06	2917 ± 378	15,507 ± 4373	Yes

Note. NA = data not available.

each male flower can be distinguished from nearby male flowers and can be directly counted. This method was validated by comparing our data to those obtained from developmental studies available for some species (Barabé and Lacroix 1999, 2000; Barabé et al. 2004).

The number of ovules per flower was estimated for each inflorescence by counting the number of locules of 10 flowers and the number of ovules per locule for 10 independent locules chosen randomly among the inflorescence flowers. The number of ovules per inflorescence was obtained by multiplying the mean number of ovules per flower by the mean number of flowers bearing ovules.

To estimate the number of pollen grains per stamen, three groups of five stamens were collected on inflorescences of *Philodendron*, and three groups of four stamens (i.e., one flower) were collected for *Anthurium*. Each group of stamens was digested in 300 μL of 95% sulphuric acid for 5 d at 24°C. The solutions were homogenized, and 1 μL was collected and carefully placed on a microscope slide. The number of pollen grains was counted for three independent replicates of 1 μL. The total number of pollen grains per stamen was obtained by multiplying the mean of the triplicate count by 300 and dividing the result by the number of stamens digested. The whole pollen count was made in triplicate for each inflorescence (3×5 or 4 stamens per inflorescence). Standard deviations were calculated by using the total number of the pollen grain counts for same species (generally $n = 9$). In order to estimate pollen grain number per inflorescence, the mean pollen grain number per stamen was multiplied by the mean number of stamens.

For each inflorescence studied, the stigma area (estimated as a circle) of 10 flowers was calculated using the diameter (0.01-mm resolution) of the stigmas measured at ×20 magnification under a dissecting microscope equipped with an ocular micrometer and using the formula $\pi D^2/4$, where D is the diameter measured. For obtaining the total stigmatic area of the inflorescences, the mean stigma area was multiplied by the mean number of flowers bearing stigma for each species.

The style lengths and stigma heights (fig. 3) were measured in 10 female flowers for each inflorescence using the same microscopic technique used for the stigma area. The size of pollen grains was estimated by measuring the diameter of the polar and equatorial axes of the grains from dehisced anthers. Measurements were made with an ocular micrometer at ×630. The volume of a single pollen grain was estimated by the formula $\pi PE^2/6$ (Harder 1998), where P is the polar axis and E is the equatorial axis diameter. Generally, 10 pollen grains per inflorescence were measured from three independent inflorescences ($n = 30$).

The inflorescence peduncle diameter was measured on all inflorescences collected (generally three) about 2–3 cm below the base of the spathe. This measure will be used in this study to evaluate the different species' capacity for resource acquisition (specific vigor).

A minimum of three inflorescences for each of the species listed in tables 1 and 2 were bagged at the bud stage. After anthesis, if at least one inflorescence had fructified, the species was considered to be able to self-pollinate, and if all the inflorescences faded without producing seeds, it was considered unable to self-pollinate. Correlation analyses were used to determine relationships between all variables for all the studied species; *t*-tests were used for variable comparisons between *Philodendron* and *Anthurium*.

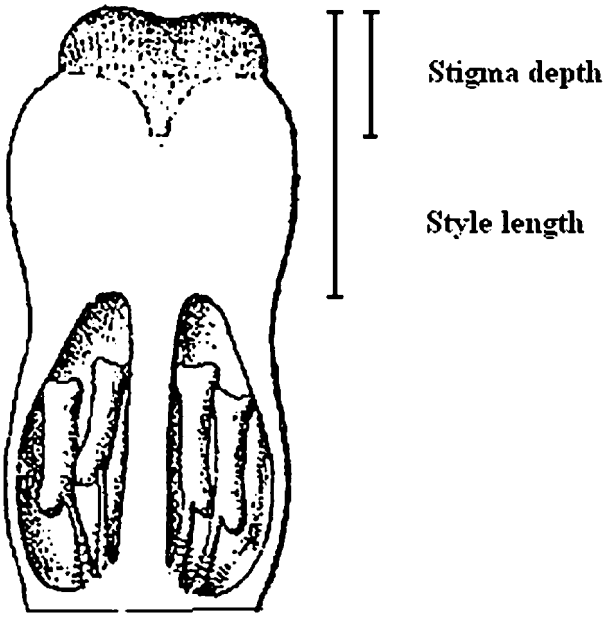

Fig. 3 Schematic representation of a longitudinal section of a *Philodendron* female flower showing the measures used in the analysis.

Results

Philodendron

The inflorescence peduncle diameter varied by only a fourfold range in the *Philodendron* species studied. The style length varied between 0.68 and 1.86 mm, except for *Philodendron melinonii* (3.10 mm), and stigma height ranged from 0.11 to 0.79 mm. The pollen volume was also variable among the *Philodendron* species studied, ranging from 19,250 to 135,327 μm^3. The number of pollen grains per stamen and the stamen number per flower were used to estimate the number of pollen grains per flower; this had a 10-fold range, varying from 47,230 for *Philodendron bipinnatifidum* to 4941 for *Philodendron cannifolium*. Also, the numbers of stamens per flower and per inflorescence were used to estimate the number of male flowers per inflorescence. The number of male flowers varied by a 10-fold range from 245 to 2574. The number of ovules per flower had a huge variation. The highest ovule count was found in *Philodendron melanochrysum* (284), while the lowest values were found in both *P. megalophyllum* and *P.* sp. aff. *megalophyllum*, with an average of 3.8 ovules per flower. The stigma area per flower also showed a great variation. It was above 5 mm^2 for the two species of subgenus *Meconostigma*, while for species of the subgenus *Philodendron*, the stigma area was below 5 mm^2 and as low as 0.28 mm^2. The number of female flowers ranged from 232 to 1458.

The calculation of the inflorescence P/O in *Philodendron* is the number of male flowers multiplied by the number of pollen grains per flower divided by the number of female flowers multiplied by the number of ovules per flower. In the

Philodendron species studied, the P/O ranged from 153 to 11,418. The highest P/O was found in *P. bipinnatifidum*, mostly because of the inflorescence's huge quantity of pollen, which characterizes the selected species of *Philodendron* subgenus *Meconostigma*. All species of *Philodendron* studied are considered to be self-incompatible because of the lack of fructification in bagged inflorescences (table 1).

At the level of the flower, the expected positive linear correlations between pollen volume and style length ($r = -0.043$, $P = 0.866$) or stigma height ($r = 0.174$, $P = 0.536$) were not found (fig. 7). At both flower and inflorescence levels, the pollen grain number was negatively correlated with pollen volume but only when the two species of subgenus *Meconostigma* (*P. bipinnatifidum* and *Philodendron solimoesense*, which have much higher quantities of pollen grains) were removed from the analysis (figs. 4, 7). Pollen number was positively correlated with ovule number in a logarithmic pattern at both the flower and the inflorescence levels when species of the subgenus *Meconostigma* were removed (fig. 5). Correlations were found between the inflorescence peduncle diameter and (1) the pollen grain number per flower ($r = 0.671$, $P = 0.002$; fig. 6), (2) the number of male flowers ($r = 0.700$, $P = 0.001$), and (3) the number of female flowers ($r = -0.484$, $P = 0.023$) but not with the ovule number per flower ($r = 0.294$, $P = 0.185$). The P/O values were positively correlated with the inflorescence peduncle diameter ($r = 0.743$, $P < 10^{-3}$).

In *Philodendron* species (fig. 7), a positive interspecific linear relation was found between the stigma area of an inflorescence and the pollen grain number per inflorescence (calculated as mean number of male flowers × mean pollen number per flower). A more accurate measure of investment in pollen is the pollen volume per flower (pollen number per flower × pollen grain volume) or per inflorescence (pollen volume per flower × number of male flowers). A strong positive linear relation was found between the stigmatic area of the inflorescence (stigma area per flower × number of female flowers), as well as the stigma area of one flower, and the pollen grain volume per inflorescence and per flower (table 3).

Anthurium

At the inflorescence level, the peduncle diameter varied from 0.26 to 2.03 mm. *Anthurium fendleri* had the smallest style length (0.56 mm), while the big *Anthurium spectabile* had the longest style (3.30 mm). *Anthurium spectabile* was an exception as most of the species had a style length less than 1.7 mm, with a mean of 1.16 mm. The stigma height had only a twofold range variation, varying from 0.23 to 0.46 mm. The pollen grain number per flower ranged from 65,999 (*Anthurium barclayanum*) to 8733 (*Anthurium divaricatum*). The pollen grain volume ranged from 1583 (*A. barclayanum*) to 9452 μm^3 (*Anthurium clavigerum*). The variable with the lowest variation was the ovule number per flower, which was two for most of the species studied and four in the small *Anthurium trinerve* and the medium-size *Anthurium crystallinum*. The most variable character was the flower stigmatic area. The smallest stigma were found in the small *Anthurium trinerve* (0.13 mm^2) while the biggest was found in *A. spectabile* (1.68 mm^2). The number of flowers per inflorescence had an enormous variation, with the smallest species (*A. trinerve*) having a mean flower number

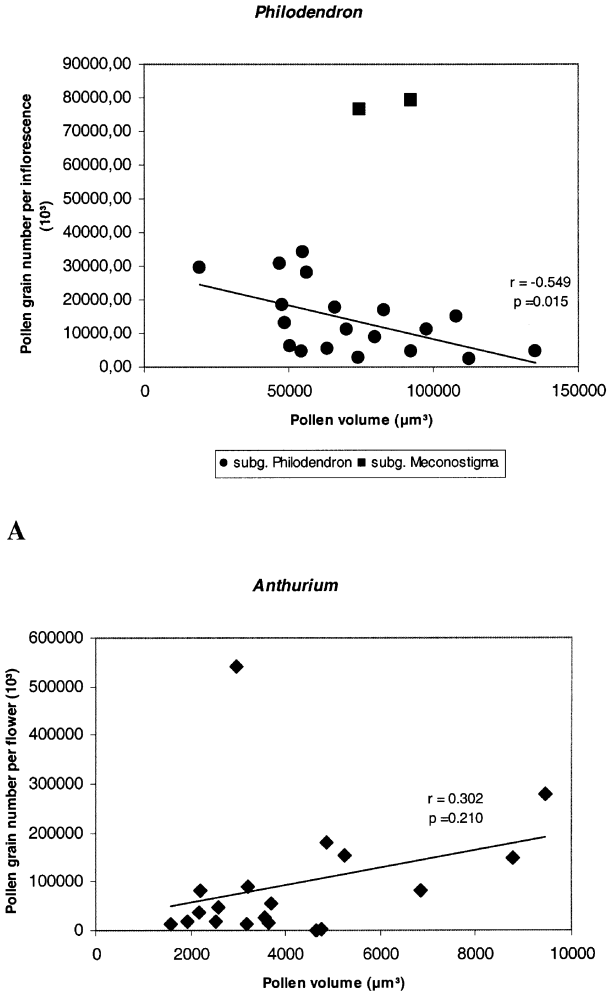

Fig. 4 Relationship between pollen volume and pollen grain number per flower for 21 species of *Philodendron* in two subgenera (*A*) and 19 species (*B*) of *Anthurium*. The two species of *Philodendron* subg. *Meconostigma* in *A* are plotted but were not included in the regression analysis.

of 43, while the gigantic *Anthurium salviniae* had a mean of 9087 flowers. The P/O ranged from 5674 (*Anthurium trunciculum*) to 31,225 (*A. barclayanum*) in the studied species. Because of the lack of variability in the number of ovules per flower (two or four), the variation of the P/O closely followed the variation of the number of pollen grains per flower. Among all *Anthurium* inflorescences bagged, nine species produced seeds and therefore were considered able to self-pollinate (table 2). No significant difference was found between the P/O of the group able to self-pollinate and that of the one that was unable to do so ($t_{18} = -1.05$, $P = 0.307$).

As in *Philodendron*, no relation was found at the flower level between pollen grain size and style length ($r = 0.082$, $P = 0.738$) or stigma height ($r = 0.135$, $P = 0.605$; fig. 7). Contrary to *Philodendron*, pollen size was positively related to pollen grain number at the flower level but not at the

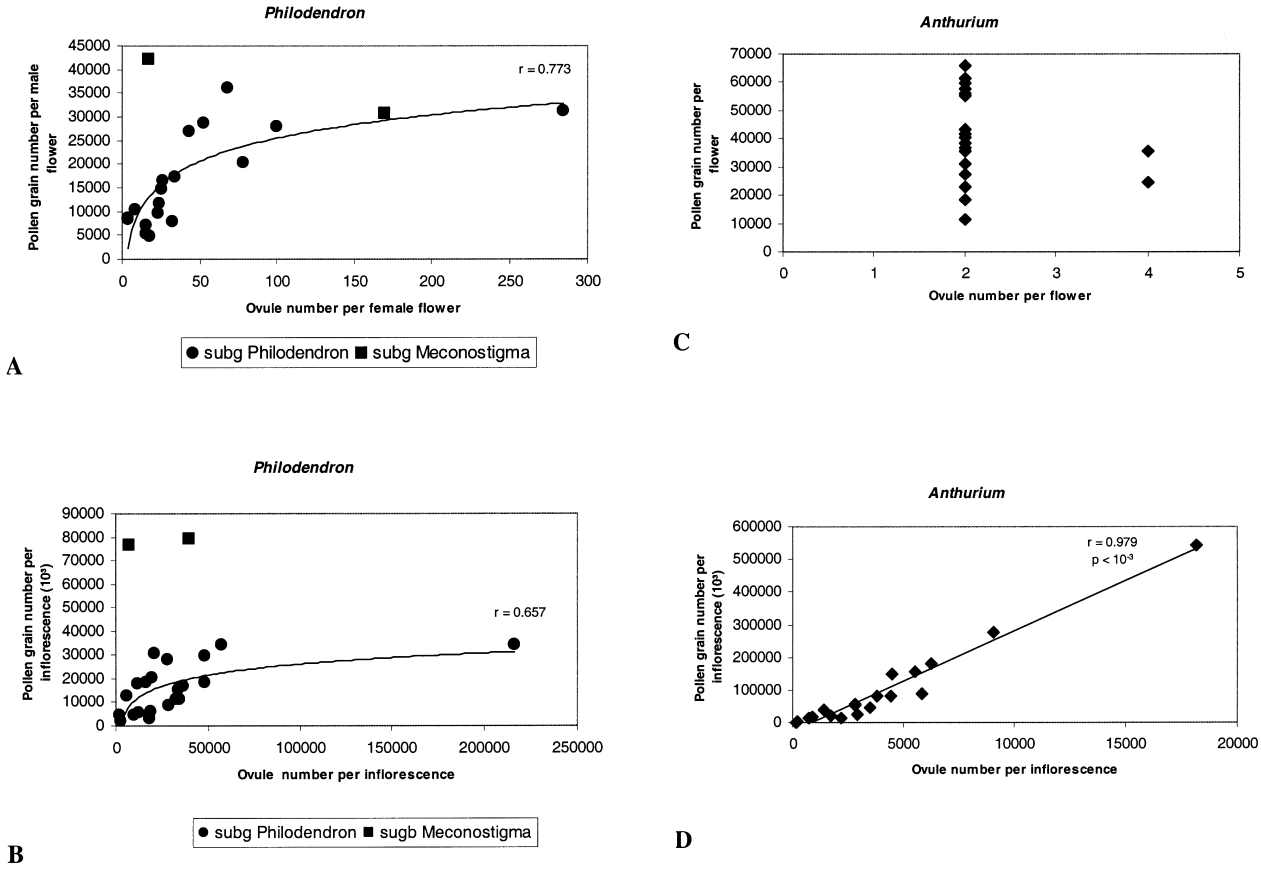

Fig. 5 Relationship between ovule number and pollen grain number at the flower and inflorescence level for the species of *Philodendron* (*A*, *B*) and *Anthurium* (*C*, *D*) studied. The two species of *Philodendron* subg. *Meconostigma* are plotted but were not included in the regression analysis.

inflorescence level (figs. 4, 7). In the genus *Anthurium*, no correlation was found between the pollen number and the ovule number at the flower level, while a strong correlation was found at the inflorescence level (figs. 5, 7). An interspecific positive correlation was found between the inflorescence peduncle diameter and both the flower number ($r = 0.906$, $P < 10^{-3}$) and the pollen grain number per flower ($r = 0.679$, $P = 0.001$; fig. 6). As in *Philodendron*, this result shows clearly that an interspecific increase in peduncle diameter is correlated with an augmentation of the number of flowers and of pollen grains per flower, resulting in inflorescences producing larger amounts of pollen. Note that we used the peduncle diameter as an estimate of the inflorescence size, suggesting that bigger inflorescences produce more pollen. Also, the stigmatic area and the pollen grain number among *Anthurium* species were positively correlated at the inflorescence level but not at the flower level (fig. 7). The pollen grain volumes per flower and per inflorescence were positively correlated with the total stigmatic area of the inflorescence, and no correlation was found with the stigmatic area per flower (see table 3). As in *Philodendron*, the P/O values were positively correlated with the inflorescence peduncle diameter ($r = 0.703$, $P = 0.001$) and the number of flowers per inflorescence ($r = 0.650$, $P = 0.002$). *Philodendron* P/Os were significantly smaller than *Anthurium* P/O ($t_{41} = 10.05$, $P \leq 0.0001$).

Discussion

Relationship between Style Length or Stigma Height and Pollen Size

Among species of *Philodendron* and *Anthurium* studied, there was no correlation between pollen size and style length or stigma height. These results are inconsistent with the positive correlation between style depth and pollen size found in other

Table 3

Correlation Coefficients between Pollen Volume per Flower and Inflorescence and Stigma Area of the Flower and Inflorescence for 20 Species of *Philodendron* and 19 Species of *Anthurium*

	Flower stigma area (r)	Inflorescence stigma area (r)
Philodendron:		
Pollen volume/flower	0.843^{**}	0.706^{**}
Pollen volume/inflorescence	0.949^{**}	0.725^{**}
Anthurium:		
Pollen volume/flower	0.146	0.516^{*}
Pollen volume/inflorescence	0.081	0.651^{**}

* $P \leq 0.05$.
** $P \leq 0.01$.

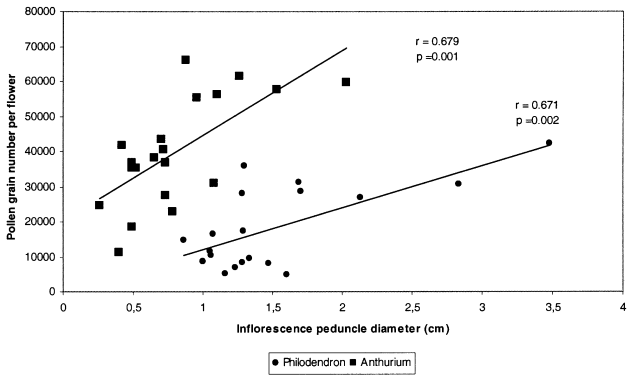

Fig. 6 Correlation analysis between inflorescence peduncle diameter and pollen grain number per flower for 19 species of the genus *Philodendron* and 20 of the genus *Anthurium*.

plant groups at both the inter- and intraspecific levels (Baker and Baker 1982; Plitmann and Levin 1983; Ramamoorthy et al. 1992; Kirk 1993; Harder 1998; Roulston et al. 2000; Torres 2000; Sarkissian and Harder 2001; Aguilar et al. 2002; Yang and Guo 2004). Larger pollen grains have a larger energy storage capacity (Baker and Baker 1982), and this energy is used for growing longer pollen tubes in longer styles. This correlation is believed to result from a nonrandom fertilization success of large pollen in pistils with a long style (Sarkissian and Harder 2001). Cruden and Lyon (1985) argued that pollen size is functionally linked to stigma depth and not style length. According to these authors, the pollen tube has to pass through the stigma with its own resources in order to reach exogenous resources in the transmission tissue. Thus, the positive correlation found between pollen size and style length in other studies (Cruden and Lyon 1985) would reflect a phyletic rather than a functional relationship in the context of our results.

The lack of correlation between these characters in *Philodendron* and *Anthurium* seems to indicate that the evolution of an optimal pollen size/style length is not the only mechanism implied in these character changes. Such a finding could result from the similar selective pressures tending to stabilize pollen size and style/stigma length in different species. Therefore, pollen has the prerequisite size to grow its pollen tube in order to reach the ovules, and the extra volume (i.e., that is not necessary for the pollen tube growth) could be explained by exogenous or endogenous factors. Exogenous factors could include the type (Taylor and Levin 1975) or size (Lee 1978; Muller 1979) of pollinator and the mode of pollen deposition on the pollinator (Harder 1998). Endogenous factors could include resistance to the humid condition of the rainforest, which limits pollen grain survival (Kerner von Marilaun 1897; Cruden 2000), or the pollen reserve type (López et al. 2005). Moreover, bigger pollen grains could be associated with faster pollen tube growth in relation to pollen competition (Ottaviano et al. 1983; Lord and Eckard 1984) or even with stronger and larger pollen tubes (Plitmann and Levin 1983).

Relationship between Pollen Size and Number of Pollen Grains

Most studies done at the interspecific level have demonstrated a negative correlation between pollen size and number (Mione and Anderson 1992; Knudsen and Olesen 1993; Vonhof and Harder 1995; Yang and Guo 2004; but see Cruden and Miller-Ward 1981). Such a trade-off between pollen size and number has been explained as a consequence of the subdivision of limited resources at the plant level (Vonhof and Harder 1995). Our data confirm this negative correlation at both the flower and the inflorescence levels in *Philodendron* subg. *Philodendron*, whereas for *Anthurium*, a positive relationship was found between pollen size and pollen number at the flower level, and no relation was found at the inflorescence level. According to Houle (1991), the genes that control the acquisition of resources can eliminate or reverse genetic correlation between competing entities (Young et al. 1994; Fenster and Carr 1997) such as pollen grain number and size. The strong positive correlation found between the pollen grain number per flower and the inflorescence peduncle diameter in both *Anthurium* and *Philodendron* confirms this hypothesis, and this could be particularly true for tropical long-living aroids. The *Anthurium* species studied vary greatly in size and growth speed (M. Chouteau, personal observation) and should therefore have different capacities for resource acquisition that may be well represented by the large variation of the inflorescence peduncle diameter.

Contrary to *Anthurium*, the negative correlation between pollen size and number in *Philodendron* is in accordance with other studies (Mione and Anderson 1992; Knudsen and Olesen 1993; Stanton and Young 1994; Vonhof and Harder 1995; Worley and Barrett 2000; Sarkissian and Harder 2001; Yang and Guo 2004). This relationship could be explained by the similar modes of growth and size (as indicated by the small range of variation of the peduncle diameter) and similar inflorescence structures among the *Philodendron* species (subgenus *Philodendron*) appearing in the analysis. With regard to this hypothesis, it would be interesting to test whether the quantitative relationships observed in the subgenus *Philodendron* also appear in the subgenus *Meconostigma*, which corresponds to the outlier points excluded from certain analyses (figs. 4, 5).

The results suggest that there is an interspecific variation in the capacity for resource acquisition measured by the peduncle diameter. Therefore, the amount of energy invested in inflorescences may differ among species. The results are in accordance with previous studies (Mione and Anderson 1992; Vonhof and Harder 1995; Yang and Guo 2004), indicating that there is a trade-off between size and number but only among closely related species with approximately the same capacity for resource acquisition. When studying species with large range of variation in capacity for resource acquisition (e.g., *Anthurium*), the difference in the amount of energy available for the reproductive structures may influence floral traits such as the pollen number, consequently masking the negative relationship between pollen size and number.

Flower Trait Evolution with Respect to Floral Cycle and Inflorescence Structure

The relation between the stigma area and pollen volume or number has been poorly documented with respect to pollination efficiency. Cruden (1997) demonstrated that the stigma area was negatively correlated with the number of pollen

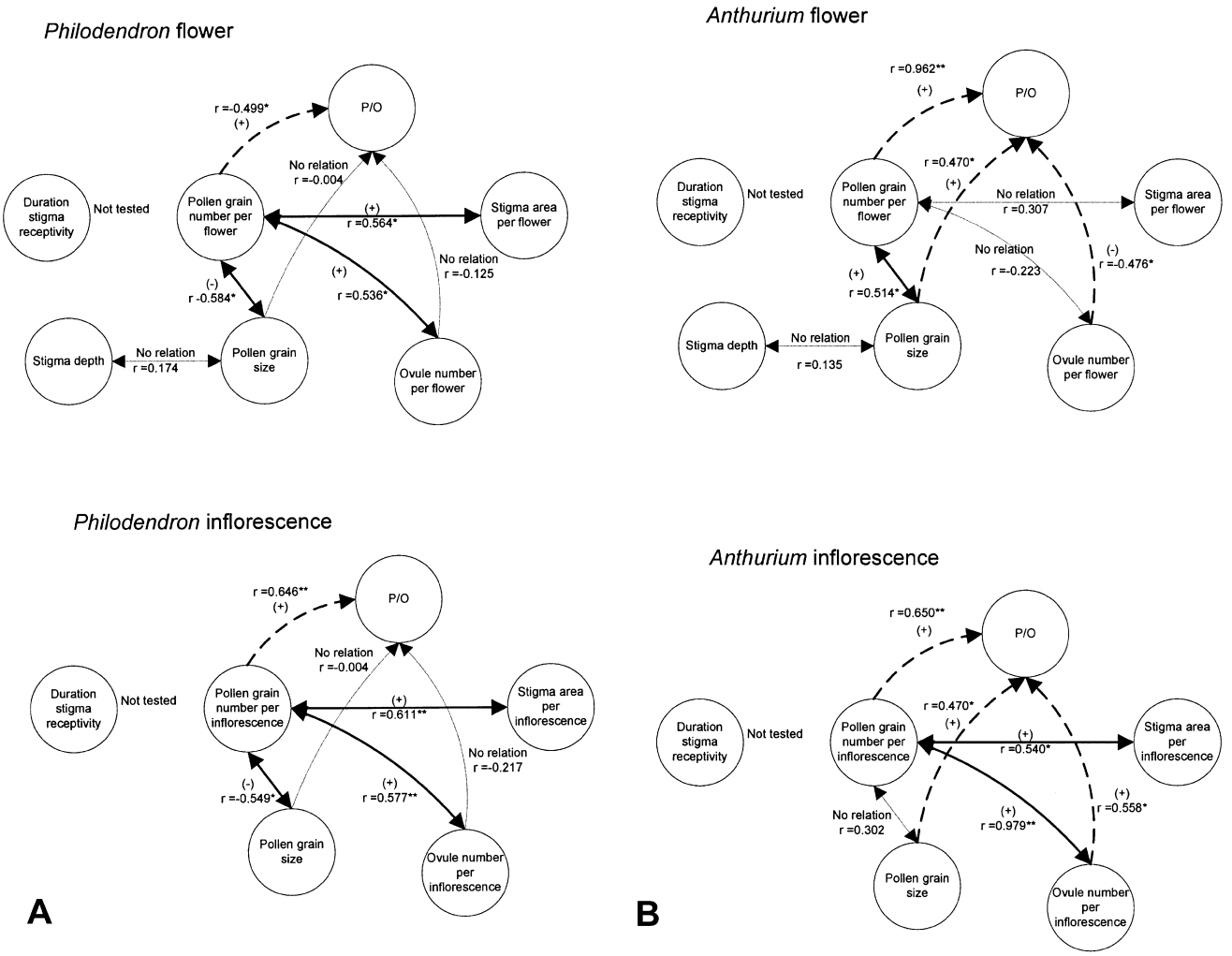

Fig. 7 Relationships among floral traits based on work by Cruden (2000) (see also fig. 1) in the genera *Philodendron* (*A*) and *Anthurium* (*B*) at both flower and inflorescence levels. Correlations are indicated for each relationship. Significance level: one asterisk = $P \leq 0.05$ and two asterisks = $P \leq 0.01$.

grains in two groups of plants (*Synphionema* and Isopogon). This relation has been explained as a trade-off between the investments in pollen and stigma area. A plant producing a low number of pollen grains would have a bigger stigma in order to increase the probability of pollen collection from pollinators with limited pollen loads. In contrast, plants producing a large number of pollen grains would have a smaller stigma because of the higher probability of collecting pollen (Cruden 1997).

In the *Philodendron* species studied, a strong positive relation was found between the pollen grain volume per flower (pollen number per flower × pollen grain volume) and per inflorescence (pollen volume per flower × number of male flowers) and the stigmatic area at both the flower and the inflorescence levels (stigma area per flower × number of female flower). Those relationships can be explained by the flowering cycle of this genus and its inflorescence morphology. As described in the "Introduction," *Philodendron* has a 24-h flowering cycle. Female and male flowers are synchronous over two successive nights during the female and male phases. Thus, the inflorescence of *Philodendron* behaves functionally as if it consisted of only one female and one male flower. Studies concerning the pollination and flowering cycles of *Philodendron* clearly show that the inflorescence is the main pollination unit (Gibernau et al. 1999, 2000; Gibernau and Barabé 2002). Our results also demonstrate how the flowers are well integrated into the complex functional unit represented by the inflorescence. The strong relationships at the inflorescence level between the plant's investment in pollen and the investment in the structure to collect it (the stigma area) are in accordance with the inflorescence being the pollination unit in *Philodendron*.

Anthurium species have a different flowering cycle. The cycles last for 2–3 wk, depending on the species. It begins with the simultaneous receptivity of the stigma of all the hermaphrodite flowers along the whole inflorescence. The receptivity lasts for about half of the flowering cycle. *Anthurium* flowers are dichogamic (sexual phases temporally separated). There

is a full day (24 h) when no sexual function is active between the end of stigma receptivity and the beginning of pollen release. After this interphase, the stamens begin to release pollen. In some species, female and male phases overlap briefly, allowing self-pollination to occur in the absence of visits by pollinators (Croat 1980). Contrary to *Philodendron*, whose pollen is released in an explosive way (all at the same time) along the inflorescence, *Anthurium* stamens open sequentially, beginning with the lower portion of the inflorescence and extending to the upper portion over a period of more than a week. The *Anthurium* cycle operates in such a way that each morning, a few flowers occupying a small portion of the inflorescence (a few rows) release their pollen. In summary, the flowering cycle of *Anthurium* can be explained simply as an inflorescence having all its stigmas receptive at the same time but only a small portion of stamens releasing their pollen at a given time.

The strong positive correlation between the stigmatic area of the whole inflorescence or the flower and the pollen grain volume of a single flower reflects this flowering cycle well. This result can be interpreted as being a way to increase pollination efficiency because the small proportion of *Anthurium* flowers releasing their pollen each day must have the potential to pollinate many flowers of a receptive inflorescence. This relationships is well represented by the fact that the bigger the stigmatic area on the inflorescence, the higher the number of pollen grains per flower will be. Inflorescences of *Philodendron* and *Anthurium* are integrated structures in which most floral traits are linked in order to optimize the inflorescence level and not individual flowers as the main pollination unit.

Pollen and Ovule Number

Recent studies about sex allocation theory have revealed an intraspecific intraflower positive genetic correlation between male (pollen) and female (ovule) functions (e.g., Campbell 1992, 1997; Mazer 1992; O'Neil and Schmitt 1993; Agren and Schemske 1995; Ashman 1999; Burd 1999; Koelewijn and Hunscheid 2000; Yang and Guo 2004). Few studies, however, have explored the relationship at the interspecific level (Small 1988; Gallardo et al. 1994; Ortega-Olivencia et al. 1997; Lopez et al.1999; Wyatt et al. 2000; Yang and Guo 2004). It appears that a strong positive correlation between investment in pollen grains and ovules could result from the genetic variation in resource acquisition (Campbell 2000; Koelewijn and Hunscheid 2000; Yang and Guo 2004).

Our data show an interspecific logarithmic correlation at the flower level between pollen and ovule number only in *Philodendron* subg. *Philodendron*. In the genus *Anthurium*, the lack of variability in ovule number (two or four) explains the lack of correlation in this genus at the flower level. For *Philodendron* subg. *Philodendron*, there is a positive correlation between the numbers of pollen grains and ovules at the flower and inflorescence levels. This indicates that the *Philodendron* inflorescence is well integrated as a functional unit. Even if the sampling was low (21 species of *Philodendron* subg. *Philodendron*), the logarithmic relationship between pollen and ovule number suggests that there is a maximum number of pollen grains produced. This maximum of pollen grains could be constrained by the fact that unisexual male flowers are densely compacted within the male zone, limiting their volume. Further, an increase in pollen number without a decrease in volume could induce an evolutionary change in the stamen morphology and consequently the inflorescence architecture, which is closely linked to the pollinators. In *Anthurium* inflorescences, a strong positive linear correlation was found between pollen and ovule numbers at the inflorescence level. This is due to the additive effect of flower number and the flowers being bisexual and thus all the same. We found a positive interspecific correlation between the numbers of pollen grains and ovules for two genera having compact inflorescences, suggesting that their inflorescence must be considered the effective pollination unit.

P/O and Breeding System

Our results clearly show that the breeding systems are different in *Philodendron* and *Anthurium*. Nearly half the species of *Anthurium* studied were able to self-pollinate, while species of *Philodendron* were strictly unable to self-pollinate. *Anthurium* species had a greater P/O than *Philodendron* species, suggesting that in the aroid family, P/O and breeding system do not correspond to what has been found in other groups of plants (Gallardo et al. 1994; Lopez et al. 1999; Wyatt et al. 2000; Jürgens et al. 2002; Wang et al. 2004). In aroids, the P/O decreases from self-compatible to self-incompatible species instead of increasing (Chouteau et al. 2006).

In addition, our results are consistent with the hypothesis that P/O is related to the pollination mechanism, as *Philodendron* has an extremely complex pollination mechanism while *Anthurium* appears to be less specialized. In *Philodendron*, the pollination mechanism has evolved into a very complex interaction combining a mechanical action of the spathe around the spadix during a short flowering cycle (24 h) with floral rewards (sterile flowers rich in protein) for the beetle pollinator, the secretion of resin to secure pollen on the pollinator, and the production of odors and heat (Gibernau et al. 1999, 2000; Seymour et al. 2003). In contrast, in *Anthurium*, the flowering cycle is much longer (up to 2 wk), the spathe is generally open and spreading (e.g., no complex pollination function), no floral chamber is present and thus pollinators come and go several times during the pollination cycle, and the main rewards are stigmatic exudates and pollen (Croat 1980; Schwerdtfeger et al. 2002; M. Chouteau and D. Barabé, personal observation).

Among *Anthurium* species studied, no significant difference in the P/O values was found between species able to self-pollinate and those unable to self-pollinate; this points to the fact that in this genus, the P/O is not an indicator of breeding system. In *Anthurium* and *Philodendron*, the P/O was positively correlated with the inflorescence peduncle diameters (our measure of capacity for resource acquisition), which is closely linked to pollen production. This indicates how plants invest the maximum amount of resources in the number of pollen grains independently of the breeding system.

In conclusion, our study provides new data and hypotheses concerning tropical herbaceous plants with two different

types of spadiciform inflorescences. Quantitative relationships between floral traits point to the fact that the inflorescence behaves like a single hermaphrodite flower, acting as the main pollination unit. This study shows that P/O in aroids may not be an indicator of breeding system, as it is in other plant families. Studying the variation in P/O with respect to exogenous factors such as pollinator type, habitats, and growth mode could provide new insights.

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Literature Cited

Agren J, DW Schemske 1995 Sex allocation in the monoecious herb *Begonia semiovata*. Evolution 49:121–130.

Aguilar R, G Bernardello, L Coletto 2002 Pollen-pistil relationships and pollen size-number trade-off in species of the tribe Lycieae (Solanaceae). J Plant Res 115:335–340.

Ashman T-L 1994 A dynamic perspective on the physiological cost of reproduction in plants. Am Nat 144:300–316.

——— 1999 Determinants of sex allocation in a gynodioecious wild strawberry: implications for the evolution of dioecy and sexual dimorphism. J Evol Biol 12:648–661.

Baker HG, I Baker 1982 Starchy and starchless pollen in the Onagraceae. Ann Mo Bot Gard 69:748–754.

Barabé D, C Lacroix 1999 Homeosis, morphogenetic gradient and the determination of floral identity in the inflorescences of *Philodendron solimoesense* (Araceae). Plant Syst Evol 219: 243–261.

——— 2000 Homeosis in the flower of the Araceae: the case of *Philodendron melinonii* (Araceae). Ann Bot 86:479–491.

Barabé D, C Lacroix, B Jeune 2004 The game of numbers in homeotic flowers of *Philodendron* (Araceae). Can J Bot 82: 1459–1467.

Burd M 1999 Flower number and floral components in ten angiosperm species: an examination of assumptions about trade-offs in reproductive evolution. Biol J Linn Soc 68:579–592.

Campbell CS, NC Famous, MG Zuck 1986 Pollination biology of *Primula laurentiana* (*Primulaceae*) in Maine. Rhodora 88: 253–260.

Campbell DR 1992 Variation in sex allocation and floral morphology in *Ipomopsis aggregate* (Polemoniaceae). Am J Bot 79: 516–521.

——— 1997 Genetic correlation between biomass allocation to male and female functions in a natural population of *Ipomopsis aggregate* (Polemoniaceae). Heredity 79:606–614.

——— 2000 Experimental tests of sex-allocation theory in plants. Trends Ecol Evol 15:227–232.

Charlesworth B, D Charlesworth 1981 Allocation to the male and female function in hermaphrodites. Biol J Linn Soc 15:57–74.

Charnov EL 1982 The theory of sex allocation. Princeton University Press, Princeton, NJ.

Chouteau M, D Barabé, M Gibernau 2006 Pollen ovule ratios in some Neotropical Araceae and their putative significance. Plant Syst Evol 257:147–157, doi:10.1007/s00606-005-0328–2.

Cresti MJL, E van Went, E Pacini, MTM Willenise 1976 Ultrastructure of transmitting tissue of *Lycopersicon peruvianum* style: development and histochemistry. Planta 132:305–312.

Croat TB 1980 Flowering behaviour of the Neotropical genus *Anthurium* (Araceae). Am J Bot 67:888–904.

Cruden RW 1977 Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. Evolution 31:32–46.

——— 1997 Implication of an evolutionary theory to applied pollination ecology. Acta Hortic 437:27–51.

——— 2000 Pollen grains: why so many? Plant Syst Evol 222: 143–165.

Cruden RW, DL Lyon 1985 Correlations among stigma depth, style length, and pollen grain size: do they reflect function or phylogeny? Bot Gaz 146:143–149.

Cruden RW, S Miller-Ward 1981 Pollen-ovule ratio, pollen size, and the ratio of stigmatic area to the pollen bearing area of the pollinator: an hypothesis. Evolution 35:964–974.

Fenster CB, DE Carr 1997 Genetics of sex allocation in mimulus (Scrophulariaceae). J Evol Biol 10:641–661.

Gallardo R, E Dominiguez, JM Muñoz 1994 Pollen-ovule ratio, pollen size, and breeding system in *Astragalus* (Fabaceae) subgenus *Epiglottis*: a pollen and seed allocation approach. Am J Bot 81: 1611–1619.

Gibernau M 2003 Pollinators and visitors of aroid inflorescences. Aroideana 26:66–83.

Gibernau M, D Barabé 2002 Pollination ecology of *Philodendron squamiferum* (Araceae). Can J Bot 80:316–320.

Gibernau M, D Barabé, P Cerdan, A Dejean 1999 Beetle pollination of *Philodendron solimoesense* (Araceae) in French Guiana. Int J Plant Sci 160:1135–1143.

Gibernau M, D Barabé, D Labat 2000 Flowering and pollination of *Philodendron melinonii* (Araceae) in French Guiana. Plant Biol 2: 331–334.

Govaerts R, DG Frodin 2002 World checklist and bibliography of Araceae (and Acoraceae). Royal Botanic Gardens, Kew.

Harder LD 1998 Pollen-size comparisons among animal-pollinated angiosperms with different pollination characteristics. Biol J Linn Soc 64:513–525.

Herrero M, JI Hormaza 1996 Pistil strategies controlling pollen tube growth. Sex Plant Reprod 9:343–347.

Houle D 1991 Genetic correlations of fitness correlates: what genetic correlations are made of and why it matters. Evolution 45: 630–648.

Jürgens A, T Witt, G Gottsberger 2002 Pollen grain numbers, ovule numbers and pollen-ovule ratios in Caryophylloideae: correlation with breeding system, pollination, life form, style number, and sexual system. Sex Plant Reprod 14:279–289.

Kerner von Marilaun A 1897 The natural history of plants. (Translated by FW Oliver.) Blackie, London.

Kirk WDJ 1993 Interspecific and number variation in pollen grains and seeds. Biol J Linn Soc 49:239–248.

Knox RB 1984 Pollen-pistil interactions. Pages 508–592 *in* A Pirson, MH Zimmermann, eds. Encyclopedia of plant physiology. Vol 17, 1st ed. Springer, Berlin.

Knudsen JT, JM Olesen 1993 Buzz-pollination and patterns in sexual traits in North European Pyrolaceae. Am J Bot 80: 900–913.

Koelewijn HP, MPH Hunscheid 2000 Intraspecific variation in sex allocation in hermaphroditic *Plantago coronopus* (L.). J Evol Biol 13:302–315.

Lee S 1978 A factor analysis of the functional significance of angiosperm pollen. Syst Bot 3:1–19.

López HA, AM Anton, L Galetto 2005 Pollen-pistil size correlation and pollen size-number trade-off in species of Argentinian

Nyctaginaceae with different pollen reserves. Plant Syst Evol 256: 69–73.

Lopez J, T Rodriguez-Riaño, A Ortega-Olivencia, JA Devesa, T Ruiz 1999 Pollination mechanisms and pollen-ovule ratios in some Genisteae (Fabaceae) from southwestern Europe. Plant Syst Evol 216:23–47.

Lord EM 1980 Intra-inflorescence variability in pollen-ovule ratios in the cleistogamous species *Lamium amplexicaule* (Labiateae). Am J Bot 67:529–593.

Lord EM, KJ Eckard 1984 Incompatibility between the dimorphic flowers of *Collomia grandiflora*, a cleistogamous species. Science 223:695–696.

Mayo SJ, J Bogner, PC Boyce 1997 The genera of Araceae. Royal Botanic Gardens, Kew.

Mazer SJ 1992 Environmental and genetic sources of variation in floral traits and phenotypic gender in wild radish: consequences for natural selection. Pages 281–325 *in* R Wyatt, ed. Ecology and evolution of plant reproduction. Chapman & Hall, New York.

Mazer SJ, VA Delesalle, PR Neal 1999 Responses of floral traits to selection on primary sexual investment in *Spergularia marina*: the battle between the sexes. Evolution 53:717–731.

Mione T, GJ Anderson 1992 Pollen-ovule ratios and breeding system evolution in *Solanum* section *Basarthrum* (Solanaceae). Am J Bot 79:279–287.

Morgan M 1992 The evolution of traits influencing male and female fertility in outcrossing plants. Am Nat 139:1022–1051.

Muller J 1979 Form and function in angiosperm pollen. Ann Mo Bot Gard 66:593–632.

O'Neil P, J Schmitt 1993 Genetic constraints on the independent evolution of male and female reproductive characters in the tristylous plant *Lythrum salicaria*. Evolution 47:1457–1471.

Ortega-Olivencia A, S Ramos, T Rodriguez, JA Devesa 1997 Floral biometry, floral rewards and pollen-ovule ratios in some *Vicia* from Extremadura, Spain. Edinb J Bot 54:39–53.

Ottaviano E, M Sari-Gorla, I Arenari 1983 Male gametophyte competitive ability in maize selection and implications with regard to the breeding system. Pages 367–374 *in* DL Mulcahy, E Ottaviano, eds. Pollen: biology and implication for plant breeding. Elsevier, Amsterdam.

Philbrick CT, GJ Anderson 1987 Implication of pollen/ovule ratios and pollen size for the reproductive biology of *Potamogeton* and autogamy in aquatic angiosperms. Syst Bot 12:98–105.

Plitmann U, DA Levin 1983 Pollen-pistil relationships in the Polemoniaceae. Evolution 37:957–967.

——— 1990 Breeding system in the Polemoniaceae. Plant Syst Evol 170:205–214.

Ramamoorthy JMS, MS Sreenivasan, CC Chinappa 1992 Relationships between pollen volume and pistil length and their possible influence on interspecific hybridation in the genus *Coffea* (Rubiaceae). J Coffee Res 22:103–113.

Ramirez N, A Seres 1994 Plant reproductive biology of herbaceous monocots in a Venezuelan tropical cloud forest. Plant Syst Evol 190: 129–142.

Ritland C, K Ritland 1989 Variation of sex allocation among height taxa of the *Mimulus guttatus* species complex (Scrophulariaceae). Am J Bot 76:1731–1739.

Roulston T, JH Cane, SL Buchmann 2000 What governs protein content of pollen: pollinator preferences, pollen-pistil interactions, or phylogeny? Ecol Monogr 70:617–643.

Sarkissian TS, LD Harder 2001 Direct and indirect responses to selection on pollen size in *Brassica rapa* L. J Evol Biol 14: 456–468.

Schoen DJ 1977 Morphological, phonological and pollen-distribution evidence of autogamy and xenogamy in *Gilia achilleifolia* (Polemoniaceae). Syst Bot 2:280–286.

Schwerdtfeger M, G Gerlach, R Kaiser 2002 Anthecology in the Neotropical genus *Anthurium* (Araceae): a preliminary report. Selbyana 23:258–267

Seymour RS, CR White, M Gibernau 2003 Heat reward for insect pollinators. Nature 426:243–244.

Small E 1988 Pollen-ovule patterns in tribe Trifolieae (Leguminosae). Plant Syst Evol 160:195–205.

Stanton ML, RE Preston 1986 Pollen allocation in wild radish: variation in pollen grain size and number. Pages 461–466 *in* DL Mulcahy, B Mulcahy, E Ottaviano, eds. Biotechnoloy and ecology of pollen. Springer, New York.

Stanton ML, HJ Young 1994 Selecting for floral character associations in wild radish, *Raphanus sativus* L. J Evol Biol 7: 271–285.

Stearns SC 1992 The evolution of life histories. Oxford University Press, Oxford.

Taylor TN, DA Levin 1975 Pollen morphology of Polemoniaceae in relation to systematics and pollination systems: scanning electron microscopy. Grana 15:91–112.

Torres C 2000 Pollen size evolution: correlation between pollen volume and pistil length in Asteraceae. Sex Plant Reprod 12: 365–370.

Vonhof MJ, LD Harder 1995 Size-number trade-offs and pollen production by papilionaceous legumes. Am J Bot 82:230–238.

Wang Y-Q, D-X Zhang, Z-Y Chen 2004 Pollen histochemistery and pollen : ovule ratio in Zingeberaceae. Ann Bot 94:583–591.

Williams EG, JL Rouse 1990 Relationships of pollen size, pistil length and pollen tube growth rates in *Rhododendron* and their influence on hybridation. Sex Plant Reprod 3:7–17.

Worley AC, SCH Barrett 2000 Evolution of floral display in *Eichhornia paniculata* (Pontederiaceae): direct and correlated responses to selection on flower size and number. Evolution 54: 1533–1545.

Wyatt R 1984 Evolution of self-pollination in granite outcrop species of *Arenaria* (Caryophyllaceae). III. Reproductive effort and pollen-ovule ratios. Syst Bot 9:432–440.

Wyatt R, SB Broyles, SR Lipow 2000 Pollen-ovule ratios in milkweeds (Asclepiadaceae): an exception that probes the rule. Syst Bot 25:171–180.

Yang CF, YH Guo 2004 Pollen size-number trade-off and pollen-pistil relationships in *Pedicularis* (Orobanchaceae). Plant Syst Evol 247:177–185.

Young HJ, ML Stanton, NC Ellstrand, JM Clegg 1994 Temporal and spatial variation in heritability and genetic correlations among floral traits in *Raphanus sativus*, wild radish. Heredity 73: 298–308.