Pl. Syst. Evol. (2006)
DOI 10.1007/s00606-005-0328-2

**Plant Systematics
and Evolution**
Printed in Austria

Pollen-ovule ratios in some Neotropical Araceae and their putative significance

M. Chouteau[1], **D. Barabé**[1,]*, and **M. Gibernau**[2]

[1]Institut de Recherche en Biologie Végétale, Université de Montréal, Jardin Botanique de Montréal, Montréal, (Québec) Canada
[2]Laboratoire d'Evolution & Diversité Biologique (UMR 5174), Université Paul Sabatier, Toulouse, France

Received August 27, 2004; accepted March 2, 2005

Abstract. The correlation between pollen-ovule (P/O) ratio and breeding system has generally been analysed with respect either to pollination efficiency, or in terms of sex allocation theory. Pollen/ovule ratios were measured in nine species of Araceae belonging to two genera with bisexual flowers (*Anaphyllopsis*, *Monstera*) and three genera with unisexual flowers (*Dieffenbachia*, *Philodendron*, *Montrichardia*). The family Araceae with its unique inflorescence morphology allows the analysis of variations of the P/O ratio with respect to two basal morpho-functional pollination units: the flower or the inflorescence. We found a relationship between the value of the P/O ratio and the breeding system that is partially different from Cruden's results (1977). Some facultative xenogamous species have a higher P/O than the obligatory xenogamous species. A link was found between the P/O and the type of inflorescence, the floral cycle, and the mode of growth.

Key words: Inflorescence, pollination, pollen-ovule ratios, French Guiana, *Anaphyllopsis*, *Dieffenbachia*, *Monstera*, *Montrichardia*, *Philodendron*.

Introduction

The ratio of pollen grains to number of ovules (P/O) in a flower is a useful tool to study plant breeding systems (autogamy vs. xenogamy) in relation to habitat or successional stage (Cruden 1977, Ramirez and Seres 1994). Xenogamy occurs by the transfer of pollen between flowers of different individuals, and autogamy by pollen transfer among flowers of a single individual (Endress 1994, p. 199). In the evolution of plants, the shift from xenogamy to autogamy may have induced alterations in floral morphology (Ornduff 1969), particularly a reduction of the energetic cost of flowering (Cruden 1977). It was also reported that the existence of certain factors (habitat, pollinator, flower size…) influences differences in P/O ratios between species (Gallardo et al. 1994, Ramirez and Seres 1994, Jürgens et al. 2002).

Cruden (1977), after studying 80 different species, concluded that the P/O ratio was related to the breeding system of the plant.

The higher the degree of autogamy, the lower the P/O will be. This relationship was based on the assumption that the P/O ratio reflects the efficiency of pollination. "The more efficient the transfer of pollen is, the lower the P/O ratio should be" (Cruden 1977, 2000). A number of studies have now more or less confirmed the validity of the P/O ratio as an indicator of the breeding system (McDade 1985, Gallardo et al. 1994, Lopez et al. 1999, Cruden 2000, Wyatt et al. 2000, Jürgens et al. 2002).

Some studies have investigated the correlation between the P/O ratio and the morphology of the flower in Acanthaceae (McDade 1985), Asclepiadoideae-Apocynaceae (Wyatt et al. 2000), and *Zingiberaceae* (Wang et al. 2004), and between the P/O ratio and the floral reward for the pollinator such as nectar production, and the mechanism of pollen delivery in Fabaceae (Lopez et al. 1999). Other studies dealing with the correlation between the P/O ratio and pollen grain morphology were used to analyze variations in sex allocation between taxa of Fabaceae (Gallardo et al. 1994). Later, Jürgens et al. (2002) completed Cruden's data (1977) by correlating the P/O ratio of Caryophylloideae with the breeding system, type of pollination (diurnal, nocturnal), life form, style number, and sexual system in the context of the taxonomy of the species.

P/O ratio studies deal mainly with dicotyledonous taxa, and monocotyledonous species are poorly documented, particularly for families with spadiciform inflorescences (e.g. Araceae, Cyclanthaceae). Also, the analysis of P/O ratios was done mainly on temperate plants. Little is known about flowering plants growing in equatorial ecosystems. In that context, aroids of French Guiana are interesting for this type of study because they are plants found mainly in undisturbed habitats, they are long living, and they present a diversity of habits and types of flowers.

To date, the P/O ratio is only known for two Neotropical aroid species, namely *Xanthosoma undipes* and *Dieffenbachia sp.* (Ramirez and Seres 1994). In aroids, we find epiphytic, hemiepiphytic, geophytic as well as aquatic plants, and species pollinated by bees, beetles and flies (Gibernau 2003). This great diversity in habit, pollination ecology and floral characters allows to compare the P/O ratio between genera characterized by different morphologies and flowering cycles.

The Araceae family consists of about 105 genera and 3,300 species (Mayo et al. 1997). There are two main types of inflorescences: (1) those with only bisexual flowers represented in the genus *Anthurium*, and (2) those with unisexual flowers represented in the genus *Philodendron*. Inflorescences with bisexual flowers do not have any distinct morphological zones. The bisexual flowers generally consist of a whorl of stamens surrounding a pistil, with (e.g. *Anthurium*) or without (e.g. *Monstera*) a perianth (Mayo et al. 1997). On inflorescences of the *Philodendron* type, the female flowers are located in the lower portion and the male flowers in the upper portion. An intermediate zone of sterile male flowers is also present in certain genera (e.g. *Caladium*, *Philodendron*).

Given that inflorescences with bisexual flowers and unisexual flowers do not correspond to the same pollination mechanisms and functional morphology, one may expect to find a different P/O ratio in both types of inflorescence. To test this hypothesis we will compare the P/O ratio of genera with unisexual flowers (*Dieffenbachia*, *Montrichardia*, *Philodendron*) to genera with bisexual flowers (*Anaphyllopsis*, *Monstera*).

The inflorescences of *Montrichardia* and *Philodendron* have a 24-hour flowering cycle, beginning with the receptivity of the female flowers (first night) and ending with the release of pollen in the second night (Gibernau and Barabé 2000, 2002; Gibernau et al. 1999, 2000, 2003). These inflorescences are mainly pollinated by beetles of the genus *Cyclocephala* (Gibernau 2003) that are attracted to the inflorescence during the heating period of the spadix. Depending on the species, the spathe may play an important role in pollination mechanisms. For example, in the genus *Philodendron*, 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. During the following night, the beetles leave the spathe, and a resin is produced by the male portion of the spadix or the ventral side of the spathe, depending on the species. The resin, mixed with the pollen, will stick to the body of beetles that are leaving the inflorescence. *Dieffenbachia* has a flowering cycle similar to *Philodendron* (Beath 1999) but a cycle of 3 days has been reported in one species (Young 1986).

In the genus *Anaphyllopsis*, the flowering cycle can last a month (Chouteau et al. unpublished data) and the pollen is released progressively. In species with bisexual flowers, the spathe is generally open (e.g. *Anthurium*, *Spathiphyllum*), but can also have a very complex shape (e.g. spirally twisted apically, in *Anaphyllopsis*). However, the function of these complex structures in pollination is unknown. In the genus *Monstera*, contrary to *Anaphyllopsis*, the flowering cycle only lasts around one week and the release of pollen occurs simultaneously along the surface of the spadix (Chouteau et al. unpublished data). Species of *Monstera* are supposed to be pollinated by bees (Ramirez and Gomez 1978), whereas pollinators of *Anaphyllopsis* are still unknown.

In Araceae with unisexual flowers (e.g. *Montrichardia*, *Philodendron*) it makes sense to consider the P/O ratio at the inflorescence level, because it is the reproductive unit involved in pollination mechanisms (Gibernau et al. 1999, 2003). However, is there a difference between the flower level and the inflorescence level? In inflorescences with bisexual flowers it is obvious that the P/O ratio is the same at the flower level and the inflorescence level. However, is it also the case in inflorescences with unisexual flowers? If the inflorescence is the functional unit, we should find the same magnitude of P/O at the inflorescence level in closely related species presenting the same breeding system, independently of the P/O ratio at the flower level. To test this hypothesis we will compare four xenogamous species of *Philodendron* pollinated by *Cyclocephala*.

In the general framework of the floral biology of the Araceae family, the main goals of this study on Neotropical species are : 1) to analyze the variation of the P/O ratio in relation to the basal morpho-functional pollination unit considered (flower or inflorescence); 2) to test if the P/O ratios in some genera of Araceae follow the general rule deduced by Cruden (1977, 2000); 3) to ascertain whether there is any relationship between the P/O ratio and the pollination system.

Materials and methods

This study was conducted during the months of May to August 2003 in French Guiana (5°00′N, 53°00′W). The species of Araceae studied (Table 1) were sampled during their flowering period.

For species with unisexual flowers, inflorescences were collected during the first day of the flowering cycle, when the spathe is open but before the release of pollen. For each inflorescence, the

Table 1. Species studied, and Voucher specimen number

Species	Voucher (deposited at MT)
Anaphyllopsis americana (Engl.) A. Hay	*Barabé et al. 258*
Dieffenbachia seguine (Jacq.) Schott	*Chouteau & Lavallée 3*
Monstera adansonii Schott	*Chouteau & Lavallée 5*
Montrichardia arborescens (L.) Schott	*Barabé et al. 263*
Montrichardia linifera (Arruda) Schott	*Chouteau & Lavallée 4*
Philodendron acutatum Schott	No specimen
Philodendron melinonii Brongn. ex Regel	*Barabé et al. 261*
Philodendron pedatum (Hook.) Kunth	*Barabé et al. 260*
Philodendron solimoesense A. C. Sm.	*Barabé 42*

Table 2. Number of stamens per flower. Mean ± standard deviation

Species	Average number of stamens per flower	Flower sample	Source
Anaphyllopsis americana	4 ± 0	n = 40	This study
Dieffenbachia seguine	4 ± 0.37	n = 30	This study
Monstera adansonii	4 ± 0	n = 50	This study
Montrichardia arborescens	5.4 ± 0.53	n = 40	This study
Montrichardia linifera	5.4 ± 0.42	n = 30	This study
Philodendron solimoesense	5 ± 0	n = 5	Barabé and Lacroix 1999
Philodendron pedatum	6 ± 0.30	n = 20	Barabé et al. 2002
Philodendron melinonii	4.64 ± 0.12	n = 50	Barabé and Lacroix 2000
Philodendron acutatum	4.76 ± 0.60	n = 30	This study

total number of female flowers was directly counted, and the total number of stamens was estimated. To estimate the number of stamens, 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 with the total length of the male zone and dividing by 5. The male zone was considered to be a cylinder and its height was measured with a digital calliper (±0.01 mm). The total number of male flowers was determined by dividing the total number of stamens on the inflorescence by the number of stamens per flower (Table 2).

For species with bisexual flowers, *Anaphyllopsis* inflorescences were collected on the first day of pollen release. In the case of *Monstera*, which has a short flowering cycle of approximately 7 days, the inflorescences were collected when the spathe had just opened. The total number of flowers was determined by counting all the flowers individually.

For both types of inflorescences, the number of ovules per flower was estimated by counting the number of locules of ten flowers and the number of ovules per locule for ten locules (Table 3). The diameter of 10 female flowers was measured with a digital calliper for each inflorescence collected (±0.01 mm).

To estimate the number of pollen grains per stamen, 3 groups of 5 stamens were collected on inflorescences with unisexual flowers and 3 groups of 4 stamens on inflorescences with bisexual flowers. Each stamen was digested in 300 µl of 95% sulphuric acid, for 5 days at 24 °C. The solution was then homogenized, and 1 µl was collected and placed carefully 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 used (5 for unisexual flowers and 4 for

Table 3. Number of locules per flower and number of ovules per locule. Mean ± standard deviation

Species	Locules / flower	Ovules / locule
Anaphyllopsis americana	1 ± 0	1 ± 0
Monstera adansonii	2 ± 0	2 ± 0
Dieffenbachia seguine	2.2 ± 0.2	1 ± 0
Montrichardia arborescens	1 ± 0	1 ± 0
Montrichardia linifera	1 ± 0	1 ± 0
Philodendron solimoesense	33.2 ± 4.2	5.1 ± 0.1
Philodendron pedatum	8.7 ± 0.4	3.9 ± 0.2
Philodendron melinonii	5.1 ± 0.2	10.4 ± 0.2
Philodendron acutatum	10.1 ± 1.1	7.7 ± 1.3

bisexual flowers). The whole pollen count was done in triplicate for each inflorescence (3 X 5 or 4 stamens per inflorescence). Standard deviations were calculated by using the total number of the pollen count (generally n = 30) of the same species.

Differences in floral sex ratio among taxa were analysed using a Kruskal-Wallis one way nonparametric analysis of variance (Systat 1998). When there are only two groups of values, the Mann-Whitney test, the nonparametric analog of the two-sample t test, is used (Systat 1998). In both cases, the significance of the statistics is tested by a Chi-square approximation (Systat 1998). The same statistical analyses were performed to test differences between taxa for the number of pollen grains per stamen and flower, and for the P/O ratios per flower and inflorescence. Mean comparisons among taxa (genera and species of *Philodendron*), were performed using a two-sample Kolmogorov-Smirnov test among pairs of groups (Systat 1998).

Results

Flower characters. The average number of stamens per male flower varies between 4 and 6 (Table 2). The lowest value (i.e. 4) is found in the two bisexual taxa (*Anaphyllopsis* and *Monstera*) and in *Dieffenbachia seguine*. The average number of stamens per flower is not consistent within the genus *Philodendron* (four species sampled) and ranges from 4.6 to 6 between species. The genus *Montrichardia* (two species sampled) appears to have a fixed average number of stamens per flower of 5.4 (Table 2).

The number of locules per female flower and the number of ovules per locule are highly variable among species (Table 3). The sampled species can be divided in two groups: the genus *Philodendron* with both high and variable numbers of locules and ovules and the other taxa (*Dieffenbachia*, *Montrichardia*, *Anaphyllopsis* and *Monstera*), which have constant and low numbers of locules and ovules (Table 3). In the latter taxa, the number of locules is one (in *Montrichardia* and *Anaphyllopsis*) or two (*Dieffenbachia* and *Monstera*). The same holds for the number of ovules per locule which is one, with the exception of *Monstera*, with two (Table 3). In contrast, in the genus *Philodendron* (four species studied), the number of locules varies on average from 5 to 33 with a corresponding variable number of ovules per locules ranging from 4 to 10.4 (Table 3).

By definition, the two species with bisexual flowers have a floral ratio of 1. Among species with unisexual flowers, only *Philodendron pedatum* has a comparable floral ratio (Table 4). For the other genera with unisexual flowers, the number of male flowers was 2.2 to 11.3 times higher than that of the female flowers (Table 4).

Number of pollen grains. When looking at variations between inflorescence types, two distinct groups can be recognized. The inflorescences with unisexual flowers have a pollen grain number per male flower that ranged from 9,789 to 29,845. In bisexual flowers this number ranges from 57,204 to 106,324 (Table 4). The numbers of pollen grains per stamen and flower are significantly greater for inflorescences with bisexual flowers than for species with unisexual flowers ($\chi^2_1 = 45$, $p < 10^{-4}$; $\chi^2_1 = 44$, $p < 10^{-4}$ respectively). Among the two bisexual species, the number of pollen grains is significantly higher in *Anaphyllopsis* than in *Monstera* at both the stamen and the flower levels ($\chi^2_1 = 11.6$, $p = 7 \times 10^{-4}$ in both cases). The number of pollen grains is significantly different between the three unisexual genera (Table 4) at both the stamen and the flower level ($\chi^2_2 = 17.6$, $p = 2 \times 10^{-4}$; $\chi^2_2 = 22.3$, $p < 10^{-4}$ respectively). Mean comparisons indicate that the three unisexual genera are different ($P = 0.02$). *Dieffenbachia* produces significantly fewer pollen grains than *Montrichardia*, whose pollen production is in average lower than *Philodendron*. Significant differences in the number of pollen grains also exist among the four *Philodendron* species (Table 4) at both the stamen and the flower levels ($\chi^2_3 = 20.7$, $p = 10^{-4}$; $\chi^2_3 = 16.5$, $p = 9 \times 10^{-4}$ respectively). Mean comparisons indicate that three groups can be distinguished ($P = 0.03$): *Philodendron pedatum* produces significantly less pollen than both *P. solimoesense* and *P. melinonii*, while *P. acutatum* occupies an intermediate ranking.

Table 4. Male-female flowers ratios, number of pollen grains per stamen and female flower, growing habits and breeding systems characteristics. Mean ± standard deviation. N, number of inflorescences studied

Species	N	Type of flowers	Male flowers / female flowers	Pollen/ stamen	Pollen / flower	Growing habits	Breeding systems
Anaphyllopsis americana	10	Bisexual	1.0 ± 0.0	26,581 ± 8,681.2	106,324.2 ± 34,724.8	geophyte/swamp	unknown
Dieffenbachia seguine	10	Unisexual	7.3 ± 1.0	2,175.3 ± 306.6	9,788.7 ± 1,379.7	geophyte/ underwood	unknown
Monstera adansonii	10	Bisexual	1.0 ± 0.0	14,300.9 ± 2,072.3	57,203.7 ± 8,289.4	hemiepiphyte	unknown
Montrichardia arborescens	10	Unisexual	6.1 ± 1.4	3,601.1 ± 984.5	19,445.8 ± 5,316.3	geophyte/swamp	facultative autogamous (Gibernau et al 2003)
Montrichardia linifera	4	Unisexual	5.4 ± 0.7	3,194.7 ± 1,535.6	17,251.4 ± 8,292.5	geophyte/swamp	unknown
Philodendron solimoesense	10	Unisexual	11.3 ± 3.2	5,969.1 ± 1,611.8	29,845.3 ± 8,058.8	hemiepiphyte/ terrestrial (secondary)	xenogamous (Gibernau et al. 1999)
Philodendron pedatum	10	Unisexual	0.9 ± 0.3	3,012.8 ± 1,319.6	18,076.7 ± 7,917.5	hemiepiphyte	xenogamous (Chouteau et al. unpublished data)
Philodendron melinonii	10	Unisexual	2.7 ± 0.6	6,209 ± 1,991.2	28,809.9 ± 9,239.4	hemiepiphyte	xenogamous (Gibernau et al. 2000)
Philodendron acutatum	12	Unisexual	2.2 ± 0.2	4,159.1 ± 1,293.1	19,797.5 ± 6,155.1	hemiepiphyte	xenogamous (Chouteau et al. unpublished data)

Table 5. Flower and inflorescence pollen-ovule ratios and pollinators of selected species. Mean ± standard deviation

Species	P/O flower	P/O inflorescence	Pollinator
Anaphyllopsis americana	106,324.2 ± 34,724.7	106,324.2 ± 34,724.7	Unknown
Dieffenbachia seguine	4,574.3 ± 779.7	33,276.9 ± 6,453.7	Beetle (Young 1986)
Monstera adansonii	14,300.9 ± 2,072.3	14,300.9 ± 2,072.3	Bee supposedly (Ramirez and Gomez 1978)
Montrichardia arborescens	19,445.8 ± 5,316.2	119,020 ± 42,929	Beetle (Gibernau et al. 2003)
Montrichardia linifera	17,251.3 ± 8,292.4	92,355.6 ± 45,682.1	Beetle (Mayo et al. 1997)
Philodendron solimoesense	179.6 ± 55.5	2,065.2 ± 989.5	Beetle (Gibernau et al. 1999)
Philodendron pedatum	524.0 ± 210.8	484.9 ± 297.5	Beetle (Gibernau et al. 2000)
Philodendron melinonii	541.6 ± 154.6	1,487.0 ± 529.4	Beetle (Gibernau et al. 2000)
Philodendron acutatum	258.2 ± 121.5	588.3 ± 283.6	Beetle (Gibernau et al. 2000)

P/O ratio at the flower and inflorescence levels. At the flower level, the pollen-ovule ratio ranges from 180 to 19,446 for unisexual flowers, and from 14,301 to 106,324 for bisexual flowers. At the inflorescence level, the P/O ratio ranges from 484 to 119,020 for inflorescences with unisexual flowers, and from 14,300 to 106,324 for those with bisexual flowers.

The distinction between unisexual flower species and bisexual flower species is not so clear. The P/O ratios at both the flower and the inflorescence levels show differences among the five genera ($\chi^2_4 = 73.5$, $p < 10^{-4}$; $\chi^2_4 = 72.9$, $p < 10^{-4}$ respectively). Each genus is significantly different ($P = 0.001$) from all the others at both the flower and the inflorescence levels. The only exception is that the P/O ratio, at the inflorescence level, is the same in *Montrichardia* and *Anaphyllopsis*.

At the flower level (Table 5), *Philodendron* species have P/O values lower than 1,000. This is followed by *Dieffenbachia* with around 5,000, *Monstera* and *Montrichardia* 15–20,000, and finally *Anaphyllopsis* about 100,000. At the inflorescence level (Table 5), the species of the genus *Philodendron* are characterized by P/O values around 1,000, *Monstera* around 14,000, *Dieffenbachia* around 33,000, and *Montrichardia* and *Anaphyllopsis* around 100,000. Note that the ranks of *Monstera* and *Dieffenbachia* are exchanged between the flower and the inflorescence levels.

Independently of the functional unit considered (flower or inflorescence), the P/O ratio of all species of *Philodendron* is lower than that of any other genus. Significant differences in P/O values exist among *Philodendron* species at both the flower and the inflorescence levels ($\chi^2_3 = 26{,}1$ $p < 10^{-4}$; $\chi^2_3 = 28.2$, $p < 10^{-4}$ respectively). At the flower level, three groups can be distinguished ($P = 0.04$). *P. solimoesense* has the lowest P/O values, *P. acutatum* is intermediate and *P. pedatum, P. melinonii* have equally the highest P/O values of the genus. At the inflorescence level, two groups are distinct ($p < 10^{-4}$), *P. pedatum* and *P. acutatum* have low P/O values, while *P. solimoesense* and *P. melinonii* have higher P/O values.

The greatest P/O ratio after *Montrichardia arborescens* was found in *Anaphyllopsis* (Table 5), which had the smallest inflorescence (mean inflorescence height = 3.57 cm) of the species sampled.

In the case of species with unisexual flowers, the P/O ratio of the inflorescence is greater than that of the P/O of the flower, with the exception of *P. pedatum* where both P/O ratios are similar. The difference between the value of P/O ratios for the inflorescence and the flower, in a given species, is due mainly to the ratio between male and female flowers in the inflorescence (Table 4). The greater the difference between the number of male and female flowers is, the greater the difference between the flower P/O ratio and inflorescence P/O ratio will be. For example, in *Philodendron solimoesense*, the inflorescence would need 11.35 times fewer male flowers to have an inflorescence P/O ratio equal to that of the P/O ratios of flowers.

Discussion

The values of the P/O ratios of the flower and inflorescences are different between all genera analysed in this study. However, within a genus, for example in *Philodendron*, the P/O of the flower and the inflorescence belong to the same order of magnitude. The difference between P/O ratios for the inflorescence and the flower, in a given species, is due mainly to the ratio between male and female flowers in the inflorescence (Table 4). On the other hand, in the case of *Montrichardia*, there is a great difference between the flower and inflorescence levels due to the small number of ovules per flower. This suggests that the difference between genera in the P/O values is a flower characteristic in inflorescences with unisexual or bisexual flowers. However, within a given genus, the variation of P/O ratio is due to flower characters (e.g. number of locules) as well as inflorescence characters, for example the number of male and female flowers, which are involved in pollination mechanisms.

Our results indicate that in the Araceae family there is a difference in the P/O ratio between the unisexual and bisexual species. In species that are mostly xenogamous (e.g. *Philodendron*) or facultatively xenogamous (e.g. *Montrichardia*), the floral sex ratio is male-biased. Here the male reproductive effort is maximized as should be the case in (self-incompatible) xenogamous species (Ganeshaiah and Uma Shanker 1991). Cruden (1977, 2000) found that the average P/O decreased from xenogamous to autogamous species. However, in their study of the P/O ratio of 29 herbaceous tropical monocots, Ramirez and Seres (1994) did not find any correlation between breeding system and P/O.

The higher P/O ratios according to Cruden's data, are found in xenogamous species ($n = 25$; mean $P/O = 5{,}859 \pm 936.5$). Facultatively xenogamous species have a lower average P/O ratio of 796 ± 88 (Cruden 1977, 2000). In species of Araceae analyzed in this study, the lowest P/O ratio ($< 2{,}500$) was found in species of *Philodendron* that are obligate xenogamous (Gibernau et al. 1999). Based on Cruden's (1977, 2000) classification, they should be theoretically facultatively xenogamous species, except maybe for *Philodendron solimoesense*, whose high P/O ratio could be considered xenogamous. All the other studied genera (*Anaphyllopsis*, *Dieffenbachia*, *Monstera*, and Montrichardia) have higher P/O ratios ($\log P/O > 4$) and should be classified as xenogamous taxa. However, *Montrichardia* (Gibernau et al. 2003) and *Dieffenbachia* (Young 1986) are facultatively xenogamous. This is not in accordance with general trends observed by Cruden (1977, 2000). Our results concerning the P/O ratio of the inflorescence of *Dieffenbachia seguine* are in accordance with those found in *Dieffenbachia* sp. (25,001, $\log(P/O) = 4.4$) by Ramirez and Seres (1994).

The lowest P/O ratios in *Philodendron* may be due to very efficient pollinating mechanisms. 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 odours and heat (Gibernau et al. 1999, 2003; Seymour et al. 2003). The pollination system is quite efficient even if beetles are involved. Once attracted, the beetles remain in the inflorescence floral chamber up to pollen release. Thus, the limiting factor is the attraction of the beetles to the inflorescences.

Montrichardia has developed a way of achieving pollination similar to *Philodendron,* but with less specialisation and a much higher P/O ratio. The main differences are the lack of sterile flowers (reward for pollinators) and its ability to produce seeds by self-pollination or apomixis (Gibernau et al. 2003). But its pollination appears to be globally less efficient. The proportion of inflorescences of *M. arborescens* visited by the pollinators is 57.5% (n = 141), 53% of them sheltering 1.95 ± 1.34 beetles (Gibernau et al. 2003). On the other hand, *Philodendron solimoesense* (xenogamous species), also pollinated by the same *Cyclocephala* species, had 100% of its inflorescences visited by pollinators (n = 68), and they were visited by 21 ± 12 beetles each (Gibernau et al. 1999).

The flowering mechanism of *Dieffenbachia* is less complicated than that of *Philodendron solimoesense* because of the lack of resin secretion but more complex than in *Montrichardia* due to the presence of staminodia (for beetle reward). *Dieffenbachia* has a P/O ratio intermediate between the two former genera. Also, Young (1986) found that between 69% and 96.7% of the inflorescences were visited, depending on the year, by an average of 3.1 to 8.7 beetles each. *Dieffenbachia* is also self-compatible. In two other populations of *Dieffenbachia*, efficient beetle pollination has also been reported (Beath 1999). Therefore, the importance and success of scarab beetle attraction, which is not the same in these three species (*Philodendron solimoesense*, *Dieffenbachia seguine* and *Montrichardia arborescens*), seem to be linked with the P/O ratio values. However, it is important to note that the data compared originated from different geographical locations and different years.

The bisexual species *Monstera adansonii* has an intermediate P/O ratio with a flowering cycle lasting approximately 6 days (Chouteau et al., unpublished data). Even if the flowering cycle is long, pollination remains efficient. First, as previously mentioned, species with an inflorescence reward tend to have a lower P/O ratio, and in *Monstera,* sterile flowers located at the base of the inflorescence produce nectar (Ramirez and Gomez 1978). Contrary to the previous species, in *Monstera*, the inflorescence has no floral chamber and thus pollinators come and go several times during the pollination cycle. The efficiency of the pollinators is reduced by the fact that at least two visits are required to bring pollen to a receptive inflorescence and take pollen from the same inflorescence when it is released. But pollination is achieved by trigonid bees (Ramirez and Gomez 1978) which are numerous and quite efficient pollinators. Ramirez and Seres (1994), while studying 29 tropical monocots, found that the P/O ratio is higher in beetle-pollinated species compared to species pollinated by bees. In the aroids used in our study, the type of pollinator does not seem to be correlated with P/O ratios. Instead, we found that genera such as *Philodendron*, *Dieffenbachia* and *Montrichardia* that are beetle-pollinated tend to have less than 30,000 pollen grains per flower while *Monstera* that is supposedly bee-pollinated has a higher number of pollen grains per flower (57,204). This result may indicate that more pollen is used as a resource by bees than by beetles.

Finally, a higher P/O was found in *Anaphyllopsis*, which has the longest flowering cycle (3–4 weeks) with very low visiting rates (Chouteau et al., unpublished data). Thus, such high P/O ratio could reflect an inefficient pollination system.

According to Ramirez and Seres (1994), xenogamy is frequently associated with the arboreal habit, and autogamy is most frequent among tropical herbaceous species. In our study, the variation in P/O ratio seems to be correlated with the habit of the species. The lowest P/O ratio was found in the unisexual hemiepiphyte *Philodendron* species. The highest P/O ratios were found in *Montrichardia*, *Dieffenbachia* and *Anaphyllopsis*. *Dieffenbachia seguine* is a rhizomatous species growing in the understorey of forests. *Montrichardia* is a rhizomatous genus growing abundantly in swampy areas and river banks. *Anaphyllopsis* is a geophyte found in wet understorey habitats. *Monstera adansonii* is a hemiepiphyte with bisexual flowers. It grows primarily as a climbing vine and may become epiphytic if the lower portion of its stem dies. It has an intermediate P/O ratio, appearing between the species of *Philodendron* (hemiepiphyte with unisexual flowers) and *Anaphyllopsis* (terrestrial with bisexual flowers). The intermediate value of P/O in *Monstera* may be linked to the hemiepiphytic life form, and not the presence of bisexual flowers, because *Anaphyllopsis*, which is a geophyte, has a higher P/O ratio than *Monstera*.

Conclusion

In conclusion, the inflorescence P/O ratio in aroids appears to be linked to the breeding system, but with trends that tend to be opposite to Cruden's data (1977, 2000). The average P/O ratio increases from xenogamous to facultatively xenogamous systems instead of decreasing. Our results show that more than the breeding system, it is the pollination efficiency through several characters (pollinator frequencies, production of resin and/or rewards, floral chamber) that heavily affects P/O ratios in Araceae. Another general trait correlated to P/O ratios in the studied Araceae is the species habit, but further studies are needed to determine if this is linked to pollination efficiency.

We would like to thank Prof. Christian Lacroix, and two anonymous reviewers for their valuable comments on the manuscript. This research was partly supported by grants from the Ministère de l'Éducation du Québec (M. C.), and Natural Sciences and Engineering Research Council of Canada (D.B.). We are grateful to the staff of the Laboratoire Environnemental de Petit Saut (EDF-CNEH), Kourou, French Guiana, for the logistical help, and to Karine Lavallée for her help during the field work.

References

Beath D. N. (1999) Dynastine scarab beetle pollination in *Dieffenbachia longispatha* (Araceae) on Barro Colorado Island (Panama) compared with La Selva biological station (Costa Rica). Aroideana 22: 63–71.

Cruden R. W. (1977) Pollen-ovule ratios: A conservative indicator of breeding systems in flowering plants. Evolution 31: 32–46.

Cruden R. W. (2000) Pollen grains: why so many? Pl. Syst. Evol. 222: 143–165.

Endress P. K. (1994) Diversity and evolutionary biology of tropical flowers. Cambridge University Press, Cambridge.

Gallardo R., Dominguez E., Munoz J. M. (1994) Pollen-ovule ratio, pollen size, and breeding system in *Astragalus* (Fabaceae) subgenus *Epiglottis*: A pollen and seed allocation approach. Amer. J. Bot. 81: 1611–1619.

Ganeshaiah K. N., Uma Shaanker R. (1991) Floral sex ratios in monoecious species. Why are trees more male-biased than herbs? Curr. Sci. 60: 319–321.

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

Gibernau M., Barabé D. (2000) Thermogenesis in three *Philodendron* species (Araceae) of French Guiana. Canad. J. Bot. 78: 685–689.

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

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

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

Gibernau M., Barabé D., Labat D., Cerdan P., Dejean A. (2003) Reproductive biology of *Montrichardia arborescens* (Araceae) in French Guiana. J. Trop. Ecol. 19: 1–5.

Jürgens A., Witt T., Gottsberger G. (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.

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

Mayo S. J., Bogner J., Boyce P. C. (1997) The genera of Araceae. Royal Botanic Gardens, Kew.

McDade L. A. (1985) Breeding systems of central American *Aphelandra* (Acanthaceae). Amer. J. Bot. 72: 1515–1521.

Ornduff R. (1969) Reproductive biology in relation to systematics. Taxon 18: 121–133.

Ramirez W. B., Gomez L. P. D. (1978) Production of nectar and gums by flowers of *Monstera deliciosa* (Araceae) and of some species of *Clusia* (Guttiferae) collected by New World *Trigona* bees. Brenesia 14–15: 407–412.

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

Seymour R. S., White C. R., Gibernau M. (2003) Heat reward for insect pollinators. Nature 426: 243–244.

Systat (1998) Systat for Windows Statistics, Version 8.0 edition. Evanston, IL.

Wang Y.-Q., Zhang D.-X., Chen Z.-Y. (2004) Pollen histochemistry and pollen: ovules ratios in Zingiberaceae. Ann. Bot. 94: 583–591.

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

Young H. J. (1986) Beetle pollination of *Dieffenbachia longispatha* (Araceae). Amer. J. Bot. 73: 931–944.

Addresses of the authors: Mathieu Chouteau, Denis Barabé (*e-mail: denis.barabe@umontreal.ca), Institut de Recherche en Biologie Végétale, Université de Montréal, Jardin Botanique de Montréal, 4101 Rue Sherbrooke Est, Montréal (Québec), Canada H1X 2B2. Marc Gibernau, Laboratoire d'Evolution Biologique (UMR 5174), Université Paul Sabatier, 118 route de Narbonne, 31062 Toulouse Cedex 4, France.