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Relation entre les caractères floraux, le mode de croissance, l'habitat et la pollinisation chez les Araceae

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Relation entre les caractères floraux, le mode de croissance, l'habitat et la pollinisation chez les Araceae

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Résumé

Les fleurs des Angiospermes sont considérées comme étant des systèmes complexes et intégrés où les caractères floraux auraient co-évolué afin de maximiser le transfert du pollen jusqu'à l'ovule. On soupçonne que d'autres facteurs externes au système reproductif tels le type de pollinisateurs, l'habitat et le mode de vie, ont un effet sur l'architecture florale. La famille des *Araceae* représente un modèle original pour étudier l'architecture florale compte tenu de l'inflorescence spadiciforme pouvant être composée de fleurs unisexuées ou bisexuées, ainsi que de la grande diversité des habitats, des modes de croissance et des types de pollinisateurs dans cette famille.

Mon projet de maîtrise consiste à déterminer comment un changement dans un trait floral va engendrer des changements dans les autres caractères floraux. Également, les contraintes induites par différents facteurs externes à l'inflorescence sont analysées afin de comprendre leurs effets sur l'architecture florale. Les différentes relations quantitatives entres les caractères floraux, au niveau de la fleur et de l'inflorescence, ont été analysées pour les deux types d'inflorescences. Mes résultats démontrent que l'inflorescence des *Araceae* est l'unité de pollinisation principale et se comporte de façon similaire à une fleur hermaphrodite. Le ratio pollen-ovule, normalement utilisé pour déterminer le système de reproduction, se comporte inversement à ce qui a été trouvé chez d'autre groupes de plantes en raison de l'écologie de la pollinisation particulière à la famille. Aussi, la durée et la rigueur de la saison de croissance peuvent influencer la disponibilité des ressources pour l'inflorescence, et les différents types de pollinisateurs (coléoptère, diptère et hyménoptère) sont liés à certains traits floraux comme le volume et la quantité de pollen afin d'optimiser la pollinisation pour la plante. Finalement, mes résultats ont permis de mieux comprendre la spécialisation de l'architecture florale en fonction du type de pollinisateurs, ce qui permettrait d'identifier les syndromes de pollinisation pour une espèce spécifique.

Mots clés

Pollinisation, caractères floraux, ratio pollen-ovule, cycle floral, forme de vie, conditions climatiques, *Philodendron*, *Anthurium*, *Araceae*.

Abstract

Angiosperm flowers are regarded as a complex and integrated system where floral traits coevolved to ensure and maximize pollen transfer to the ovule. Other external factors to the reproductive system such as pollinator type, habitat and life form are believed to have an effect on floral architecture. The Araceae family represents an original model for studying floral architecture due to their spadiciforme inflorescence which can have unisexual or bisexual flowers as well as the great range of habitats, growth modes, and pollinator types found in the family.

My Master's project consisted in investigating how changes in a given floral trait are correlated to changes in other floral traits. In addition, the constraints induced by different external factors on the inflorescence were studied in order to understand their effect on floral architecture. The different quantitative relationship among floral traits, both at the inflorescence and flower levels, were analysed for the two types of inflorescence. My data show that the aroid inflorescence is the main pollination unit which behaves similarly to a hermaphrodite flower. Furthermore, the pollen-ovule ratio, which is normally used as a measure of the breeding system, behaves oppositively to what has been previously found in other plant groups, which might result from the particular pollination ecology of the family. The duration and harshness of the growing season may influence the availability of resources for the inflorescence, and the different type of pollinator (beetle, fly and bee) which are linked to some floral traits such as pollen volume and quantity in order to optimise pollination. Finally, my results give new insight and understanding of specialised floral structure in relation to the pollinator type and could aid in identifying pollination syndrome for specific species.

Keywords

Pollination, floral characters, pollen-ovule ratio, flowering cycle, life forms, climatic conditions, *Philodendron*, *Anthurium*, Araceae.

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cm:	centimètre
D:	diamètre
E:	equatorial axis diamater
P/O:	ratio pollen-ovule
mm:	millimètre
MT:	herbier Marie-Victorin
P:	polar axis diameter
pers. obs.:	personal observation
s.d.:	standard deviation
sect.:	section
sp.:	species
subg.:	subgenus
µl:	microlitre
UM	herbier du Missouri Botanical Garden
µm:	micromètre
°C:	degrés celcius

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Chapitre 1

Introduction générale

Les fleurs des angiospermes sont considérées comme ayant une architecture complexe et intégrée où les caractères floraux ont coévolué (i.e. évolué conjointement) pour maximiser le transfert du pollen jusqu'à l'ovule (Cruden 2000). Le système de reproduction de la plante (cléistogamie, autogamie, xénogamie, etc.) est étroitement lié à l'architecture de la fleur et peut être déterminé par le ratio du nombre de grains de pollen par ovule (Cruden 1977, 2000). D'autres facteurs externes à la fleur peuvent influencer l'architecture florale, tels que le type de pollinisateur, le mode de vie et l'habitat. Contrairement aux relations entre les différents caractères floraux et le système de reproduction, qui ont déjà fait l'objet de recherches, les relations entre les caractères floraux et les facteurs externes à la fleur/inflorescence ont rarement été étudiés chez les angiospermes (Raven 1979; Plitmann & Levin 1990; Ramirez & Seres 1994; Jürgens et al 2002; Chouteau et al. 2006).

À l'opposé des vastes connaissances que l'on a sur les arbres et arbustes tempérés, on sait connaît peu de choses sur la biologie de la reproduction des plantes tropicales (Cruden 2000). Chez les angiospermes, les études concernant les relations entre les caractères floraux et la reproduction ont été majoritairement réalisées sur des fleurs bisexuées organisées en inflorescences typiques (grappe, thyrse, corymbe, etc.; Cruden 2000). Peu de choses sont connues sur les inflorescences spadiciformes que possèdent par exemple, les *Araceae*, *Cyclanthaceae*, *Piperaceae* et *Acoraceae*. Établir des relations quantitatives entre les différentes composantes des structures reproductives dans de tels groupes de plantes, est essentiel à la compréhension globale de l'architecture de la fleur et de l'inflorescence.

Dans cette perspective, la famille des *Araceae* (105 genres, plus de 3 300 espèces), qui possède une grande diversité de mécanismes de reproduction, de types de pollinisateurs, d'habitats, et de modes de vie et de croissance (Mayo 1997, Gibernau 2003), constitue un modèle intéressant et approprié pour ce type d'étude.

Je propose ici d'étudier ces relations à 2 niveaux différents dans une famille de plantes:

-Une étude à l'échelle du genre sera réalisée au moyen d'une comparaison entre les genres *Philodendron* et *Anthurium*. Cette section permettra de comparer deux genres ayant des morphologies et des biologies florales différentes afin de comprendre comment une variation dans un caractère floral influence les autres caractères floraux.

-Une étude à l'échelle de la famille permettra d'identifier des facteurs externes à l'inflorescence (pollinisateur, habitat, forme de vie) reliés quantitativement à sa morphologie.

1.1 Relations entre les différents caractères floraux et la pollinisation

L'existence d'une corrélation positive entre la taille du pollen et la longueur du pistil a été documentée dans plusieurs familles de plantes (Baker & Baker 1982; Plitmann & Levin 1983; William & 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 & Harder 2001; Aguilar et al. 2002; Yang & Guo 2004). Cette corrélation a été attribuée à une relation entre la capacité d'accumulation de réserves énergétiques du pollen et la distance entre le stigmate (i.e. extrémité du style) et l'ovule (Baker & Baker 1982). La quantité de protéines contenue dans un grain de pollen est supposée atteindre plus de 60 % de sa masse et la majorité d'entre elles aurait un rôle fonctionnel pour les processus de germination du grain et la croissance du tube pollinique (Roulston et al. 2000). De fait, les grains de pollen ayant le potentiel de générer de plus grands tubes polliniques seraient associés à des styles plus profonds et auraient un avantage compétitif face aux grains de pollen ayant un plus court tube pollinique.

À l'opposé, Cruden et Lyon (1985) ont démontré une corrélation positive entre la taille du pollen et la profondeur du stigmate (fig. 2.1) et non du style. Ils ont alors proposé l'hypothèse que le grain de pollen doit pouvoir générer un tube pollinique

ayant la capacité de traverser le stigmate pour parvenir à atteindre les ressources exogènes présentes dans le tissu de transmission du style qui lui fourniront l'énergie nécessaire pour parvenir à l'ovule (Cresti et al. 1976; Knox et al. 1984; Herrero & Hormaza 1996).

Un autre facteur influençant la taille du pollen est la quantité de grains de pollen que la fleur peut contenir. Une corrélation négative entre ces deux traits floraux a été bien documentée aux niveaux inter-spécifique et intra-spécifique chez un bon nombre de groupes de plantes (Mione & Anderson 1992; Knudsen & Olesen 1993; Stanton & Young 1994; Vonhof & Harder 1995; Worley & Barrett 2000; Sarkissian & Harder 2001; Yang & Guo 2004) tandis que chez d'autres groupes aucune relation n'a pu être démontrée (Cruden & Miller-Ward 1981; Stanton & Preston 1986; Lopez et al. 1999; Aguilar et al. 2002). Cette relation négative a été interprétée comme étant un simple compromis entre la taille et le nombre de grains de pollen du fait que les ressources disponibles pour la fleur sont limitées (fig. 2.1).

Selon Cruden (1997, 2000), le nombre de grains de pollen serait aussi lié à la surface stigmatique (fig. 2.1). Une corrélation négative entre ces deux caractères a été trouvée chez *Symphionema* et *Isopogon* (*Proteaceae*) et on a supposé qu'une surface stigmatique plus grande a plus de chance d'être en contact avec la surface du pollinisateur couverte de pollen. Il en résultera donc que la fleur produirait moins de grains de pollen pour parvenir à la pollinisation.

Finalement, selon la théorie de l'allocation des ressources à la reproduction (Chalesworth & Charlesworth 1981; Charnov 1982; Morgan 1992), il devrait y avoir chez les angiospermes un compromis pour l'allocation des ressources entre les sexes (le pollen et les ovules ; fig. 2.1). Cette relation est due au fait que les plantes ont des ressources limitées et doivent les attribuer aux fonctions mâle ou femelle pour obtenir une valeur adaptative ''fitness'' optimale. En conséquence, une relation négative devrait être mesurable entre les fonctions mâle et femelle (Stearns 1992). Par contre, peu d'études ont mis en évidence une telle relation (Chalesworth & Charlesworth 1981; Charnov 1982; Morgan 1992; Mazer et al. 1999) et la majorité des études récentes ont plutôt mis en évidence une corrélation positive (Small 1988; Campbell 1992, 1997, 2000; Mazer 1992; O'Neil & Schmitt 1993; Gallardo et al. 1994; Agren

& Schemske 1995; Ortega-Olivencia et al. 1997; Ashman 1999; Burd 1999; Koelewijn & Hunscheid 2000; Yang & Guo 2004). Campbell (2000) explique que chacune des relations positives et négatives dans l'allocation des ressources entre les fonctions mâle et femelle est possible. Selon cet auteur, la variation génétique dans l'allocation des sexes (corrélation négative) est souvent moindre comparée aux variations occasionnées par les différences d'acquisition des ressources et la vigueur de la plante (corrélation positive). Aussi, comme cela est suggéré par une étude physiologique (Ashman 1994), la fleur pourrait utiliser différentes réserves d'énergie pour les fonctions mâle et femelle.

1.2 Relation entre le ratio pollen-ovule et le système de reproduction

À l'échelle de la fleur, le ratio pollen-ovule (P/O) est considéré comme une mesure permettant d'évaluer le système de reproduction des plantes par rapport à l'habitat ou au niveau de succession (Cruden 1977). Ceci est dû au fait qu'au cours de l'évolution des plantes le passage de la xénogamie (plante non autoféconde) à l'autogamie (plante autoféconde) a induit des changements dans la morphologie de la fleur (Ornduff 1969) de façon à réduire le coût énergétique de la reproduction et ainsi faciliter l'auto-pollinisation (Cruden 1977). Des études antérieures ont montré qu'une fleur xénogame tend à produire plus de grains de pollen qu'un taxon taxonomiquement proche à fleur autogame (Arroyo 1973), tandis que le nombre d'ovules par ovaire ne change pas (Cruden 1977).

Après avoir étudié 80 espèces appartenant à 30 familles, Cruden (1977) a conclu que le ratio du nombre de grains de pollen par ovule (P/O) était lié au système de reproduction de la plante (tab. 1.1). Plus le degré d'autogamie est élevé, plus le P/O est bas. Cette relation a été établie en supposant que le ratio P/O reflète l'efficacité de pollinisation : "*The more efficient the transfer of pollen is, the lower the P/O ratio should be*" (Cruden 1977, 2000). Plusieurs études jusqu'à présent ont confirmé la validité du ratio pollen-ovule comme indicateur du système de reproduction (Schoen 1977; Lord 1980; Wyatt 1984; Campbell et al. 1986; Philbrick & Anderson 1987; Ritland & Ritland 1989; Plitmann & Levin 1990; Mione & Anderson 1992; Lopez et

al. 1999; Jürgens et al. 2002; Wang et al. 2004; Wang et al. 2005), mais d'autres l'ont infirmé (Gallardo et al. 1994; Ramirez & Seres 1994; Wyatt et al. 2000; Chouteau et al. 2006). Cela serait dû à l'existence de certains facteurs (habitat, pollinisateur, morphologie des fleurs, etc.) qui influenceraient différemment les ratios pollen-ovule, les traits floraux et les systèmes de reproduction.

Tableau 1.1 Système de reproduction et ratio pollen-ovule associé (Cruden 1977, 2000)

Système de reproduction	P/O Moy. ± E.T.	Log P/O Moy. ± E.T.
Cléistogamie	4,7 ± 0,7	0,65 ± 0,07
Autogamie obligatoire	27,7 ± 3,1	1,43 ± 0,05
Autogamie facultative	168,5 ± 22,1	2,15 ± 0,06
Xenogamie facultative	796,6 ± 87,7	2,81 ± 0,05
Xenogamie	5859 ± 936,5	3,65 ± 0,06

Des études ont aussi été réalisées sur les relations entre le P/O et la morphologie de la fleur chez les *Acanthaceae* (McDade 1985), les *Asclepiadaceae* (Wyatt et al. 2000), de même qu'entre le P/O et les récompenses florales pour le pollinisateur comme la production de nectar et les mécanismes de relâchement du pollen chez les *Fabaceae* (Lopez et al. 1999). Une autre étude sur la corrélation entre le P/O et la morphologie du grain de pollen ont été menée pour permettre d'analyser les variations dans l'allocation des ressources entre les taxa de *Fabaceae* (Gallardo et al. 1994). Jürgens et al. (2002) ont complété les données de Cruden (1977) en corrélant le P/O chez les *Caryophylloideae* avec le système de reproduction, le type de pollinisation (diurne, nocturne), la forme de vie de la plante, le nombre de styles et le système sexuel dans un contexte taxonomique.

Jusqu'à maintenant, le P/O des Aracées (et autres plantes à inflorescence spadiciformes) n'a fait l'objet que de deux études (Ramirez & Seres 1994; Chouteau et al. 2006). Ramirez & Seres (1994) n'ont étudié que deux espèces d'Aracées, alors que Chouteau et al. (2006) ont travaillé sur neuf espèces néotropicales de Guyane Française. Ces derniers ont montré que chez les neuf Aracées étudiées, la relation entre le système de reproduction et le P/O est contraire à celle trouvée par Cruden

(1977) dans différentes familles. Chez les *Araceae*, le lien entre le P/O et le type de mécanisme de pollinisation, l'habitat et le type de croissance a fait l'objet de l'hypothèse suivante. Plus les mécanismes de pollinisation sont complexes (chambre florale, thermogenèse, odeur, fleurs stériles servant de récompense pour le pollinisateur, nectar, résine…), plus le P/O sera bas; de plus les aracées terrestres, géophytes et holophytes avaient des P/O plus élevés que les aracées hémiépiphytes (Chouteau et al. 2006).

1.3 Relation entre les caractères floraux et les facteurs externes à la fleur/inflorescence

Jusqu'à présent, peu de travaux ont documenté le rôle des facteurs externes (pollinisateur, forme de vie, mode de croissance) à la fleur/inflorescence pouvant être lié à sa structure (Plitmann & Levin 1990; Ramirez & Seres 1994; Cruden 2000; Jürgens et al. 2002; Chouteau et al. 2006). Certains auteurs ont mis en évidence une relation entre le type de pollinisateur et le P/O (Plitmann & Levin 1990; Ramirez & Seres 1994) qui est explicable par les différences d'efficacité des pollinisateurs, tandis que d'autres n'ont rien établi de tangible a ce sujet (Jurgen et al. 2002; Chouteau et al. 2006). Aussi, le type de pollinisateur pourrait influencer la taille et le nombre de grains de pollen (Lee 1978; Muller 1979; Cruden 2000; Chouteau et al. 2006) car la plante doit s'adapter à son pollinisateur pour maximiser son succès reproducteur tout en minimisant ses coûts (Cruden 2000). Finalement, des liens entre l'architecture florale et la forme de vie de la plante ont été documentés chez les *Caryophylloideae* (Jurgen et al. 2002). Selon les résultats obtenus par ces auteurs, les espèces vivaces investiraient plus de ressources dans la production (nombre) de grains de pollen et d'ovules que les espèces annuelles.

Bien que les travaux sur ce sujet soient peu nombreux et que les résultats soient difficilement interprétables, il semblerait qu'il existe des liens complexes entre l'architecture florale et les facteurs externes à la structure reproductrice.

1.4 La famille des Aracées

La famille des Aracées est d'une diversité étonnante tout en ayant une caractéristique générale uniforme : la structure de l'inflorescence. Elle comprend près de 105 genres et plus de 3 300 espèces qui se divisent en deux groupes majeurs : les Proto-Aracées et les Aracées vraies (Mayo et al. 1997). Le groupe majeur des Proto-Aracées est composé des sous-familles *Gymnostachydoideae* (1 genre) et *Orontioideae* (3 genres); tandis que le groupe majeur des Aracées vraies est composé des sous-familles *Pothoideae* (4 genres), *Monsteroideae* (12 genres), *Lasioideae* (10 genres), *Calloideae* (1 genre) et *Aroideae* (74 genres).

Les Aracées sont réparties sur tous les continents entre les latitudes 50° Nord et 35° Sud. On les retrouve donc autant dans les zones tempérées que tropicales et subtropicales. Il s'agit de plantes épiphytes, hémi-épiphytes, terrestres, géophytes ou aquatiques (Mayo et al. 1997). La pollinisation est assurée par des vecteurs aussi divers que le vent, les coléoptères, les hyménoptères et les diptères (Gibernau 2003). Chez les Aracées, on peut distinguer deux types d'inflorescence (fig. 2.2) : à fleurs unisexuées, représentées par le genre *Philodendron,* et à fleurs bisexuées, représentées par le genre *Anthurium*.

Chez les inflorescences à fleurs unisexuées, les fleurs femelles sont localisées à la base de l'inflorescence, tandis que les mâles se situent dans la portion supérieure. On trouve parfois dans certains genres (e.g. *Philodendron*) une zone intermédiaire, comprenant des fleurs males stériles (Barabé & Lacroix 1999, 2000) et, d'autres fois, un appendice terminal sans fleurs (e.g. *Arisaema*), présentant diverses formes et ayant pour fonction de produire des odeurs et/ou de la chaleur (Vogel & Martens 2000).

Dans les genres à fleurs unisexuées, on trouve des mécanismes de pollinisation élaborés caractérisés par la présence de caractères spécifiques : production de résine pour coller le pollen sur les scarabées (i.e. *Philodendron*; Gibernau & Barabé 2000, 2002; Gibernau et al. 1999, 2000), production de chaleur,présence de fleurs stériles servant à nourrir les pollinisateurs (i.e. *Philodendron;* Gibernau & Barabé 2000, 2002; Gibernau et al. 1999, 2000), production d'odeurs variées (obsv. perso.) et, forme et mouvement de la spathe qui permet à l'inflorescence de diriger les insectes

pollinisateurs dans la chambre florale (i.e. *Philodendron*, *Syngonium;* Gibernau & Barabé 2000, 2002; Gibernau et al. 1999, 2003; données non publiées concernant *Syngonium*). L'apparition d'une spathe ayant la capacité d'étrangler le spadice permet à l'inflorescence en phase femelle de garder les insectes pollinisateurs dans une chambre florale jusqu'à la libération du pollen. Une seule phase d'attraction des pollinisateurs (durant la phase femelle) est alors nécessaire pour assurer la pollinisation. Chez les espèces sans chambre florale, le pollinisateur ne peut rester ou être capturé par l'inflorescence et, de ce fait, doit faire des allers-retours. Pour ces plantes, une première période d'attraction est nécessaire durant la phase femelle pour attirer le vecteur de pollinisation et féconder les ovules, et une seconde durant la phase mâle pour assurer la collecte du pollen et sa dispersion (Gibernau 2003). En conséquence, la relation avec le pollinisateur est passée au cours de l'évolution d'une interaction à deux phases à une interaction à une phase (Meeuse 1978).

Chez les inflorescences à fleurs bisexuées, on ne retrouve pas de zone distincte. Chaque fleur est hermaphrodite, constituée d'étamines entourant un pistil, avec (e.g *Anthurium*) ou sans (e.g. *Monstera*) périanthe (Mayo et al. 1997). Chez ces espèces, le cycle de pollinisation est souvent beaucoup plus long. Par exemple, *Anthurium* a un cycle floral d'environ 3 semaines (Croat 1980; Chouteau et al. données non publiées) et le pollen est relâché séquentiellement, tandis que chez *Philodendron* (fleurs unisexuées) le cycle floral ne dure que 2 jours et tout le pollen est relâché simultanément (Gibernau & Barabé 2000, 2002; Gibernau et al. 1999, 2000). La forme de la spathe peut être simple ou complexe, comme chez *Anaphyllopsis,* mais la chambre florale est absente chez ces espèces, ce qui contraint la pollinisation à un système à deux phases (Gibernau 2003).

Cette grande diversité au niveau de la biologie florale permet de faire des études comparées à partir d'une morphologie commune.

Jusqu'à présent, les études sur les Aracées ont surtout été faites sur le développement (Barabé & Forget 1988; Barabé & Bertrand 1996; Barabé & Lacroix 1999, 2000; Barabé et al. 2002, 2004), la thermogenèse (voir ci-dessous) et le cycle reproducteur (voir ci-dessous).

Les *Araceae* sont l'une des rares familles avec les *Annonaceae*, *Cycadaceae*, *Cyclanthaceae*, *Magnoliaceae*, *Nymphaeaceae*, *Palmae* et *Zamiaceae* (Prance & Arias 1975; Tang 1987; Gottsberger 1990; Azuma et al. 1999; Dieringer et al. 1999) où l'on observe la thermogenèse de l'inflorescence. Cette production de chaleur est associée, chez les Aracées, à la pollinisation : arrivée du pollinisateur (coléoptère ou diptère) avec émission d'odeur. Elle a été souvent observée, mais plus rarement quantifiée. Les études ayant quantifié le cycle thermogénique ont été réalisées sur *Anubias*, *Arum*, *Cercestis*, *Alocasia*, *Colocasia*, *Dieffenbachia*, *Dracunculus*; *Helicodiceros*, *Homalomena*, *Montrichardia*, *Philodendron* et *Symplocarpus* (Knutson 1974; Seymour et al. 1983; Young 1986; Yafuso 1993; Bermadinger et al. 1995; Gibernau et al. 1999; Seymour & Schultze-Motel 1999; Barabé & Gibernau 2000; Gibernau et al. 2000, 2003; Gibernau & Barabé 2000; Albre et al. 2003; Seymour et al. 2003; Ivancic et al. 2004, 2005).

Des 105 genres et 3 300 espèces d'aracées, seuls 49 genres et 125 espèces ont été documentés concernant leurs pollinisateurs et leurs cycles reproducteurs (Gibernau 2003). Parmi les genres tropicaux les mieux étudiés, on trouve *Philodendron* (Gibernau et al. 1999, 2000; Gibernau & Barabé 2002), *Dieffenbachia* (Young 1986; Beath 1999) et *Montrichardia* (Gibernau et al. 2003) qui sont pollinisés par des scarabaeideae du genre *Cyclocephala*. De même, les genres tempérés tels *Arum, Arisaema et Symplocarpus,* pollinisés par des diptères, ont aussi été bien étudiés (Uemera et al. 1993; Vogel & Martens 2000; Albre et al. 2003). Les pollinisateurs recensés chez les Aracées sont majoritairement des insectes pouvant être classés dans 3 groupes : les hyménoptères, les coléoptères et les diptères (Gibernau 2003).

1.5 Objectifs

Le premier objectif de cette étude est de déterminer les relations quantitatives entre les caractères floraux afin d'élaborer un modèle permettant d'examiner comment un changement dans un caractère peut influencer un changement dans un autre caractère. Cette section de l'étude sera réalisée sur deux genres, *Philodendron* et *Anthurium*, représentatifs des deux grands types floraux des Aracées (fleurs uni- ou bi-sexuées).

Les objectifs plus détaillé sont : 1) Vérifier si la taille du pollen est corrélé positivement à la profondeur du style et/ou du stigmate; 2) Établir si le nombre de grains de pollen est corrélé négativement à la taille du pollen; 3) Analyser les relations entre l'investissement des ressources dans les fonctions mâle et femelle aux niveaux de la fleur et de l'inflorescence; 4) Analyser les liens entre le ratio pollen-ovule, le système de reproduction et les variations dans le traits floraux.

Le deuxième objectif est de comprendre comment la morphologie florale est influencée par 1) la capacité d'autopollinisation; 2) le type de croissance; 3) l'habitat et 4) le type de pollinisateurs. Cette section de l'étude sera menée sur l'ensemble de la famille des Aracées par une étude comparative de 54 espèces réparties en 32 genres.

Chapitre 2

A comparative study of inflorescence characters and pollen-ovule ratios among the genera *Philodendron* and *Anthurium* (Araceae)

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Abstract

Floral characters in Angiosperms may be involved in different relationships in order to ensure and maximise pollination. To assess these relationships, which may provide insights in understanding floral evolution, we analysed 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 correlation was found between pollen volume and either style or stigma depth. The trade-off between pollen size and number normally explained by limited resources was only found in *Philodendron*. Instead, pollen number was positively correlated with 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 *Philodendron* and *Anthurium* from what is found in temperate Angiosperms. Stigma area and pollen quantity were positively correlated to inflorescence flowering cycle and 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 is the main pollination unit and behaves as a single flower.

Keywords

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

2.1 Introduction

Angiosperm flowers are regarded as complex and integrated systems in which floral traits are organized to ensure and maximize male gametes (via pollen) transfer to the ovule. Until now, studies involving relationships among floral characters (fig. 2.1) 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).

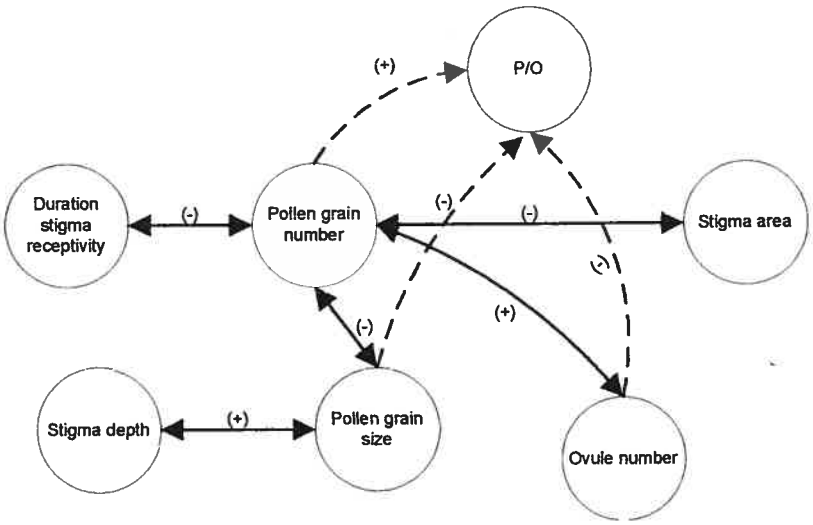


Figure 2.1. Positive (+) and negative (-) correlations among floral traits in animal-pollinated plants proposed by Cruden (2000). Solid lines indicate relationships that were demonstrated empirically. Dashed lines indicate that the pollen-ovule ratio (P/O) might be influenced by change in a given trait.

Cruden (2000) proposed a model (fig. 2.1) showing the relationships among floral traits in 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; between pollen-ovule ratio and breeding systems (Fig. 2.1). In order to test these relationships, inflorescences of *Anthurium* and *Philodendron* were used as comparative models (Fig. 2.2).

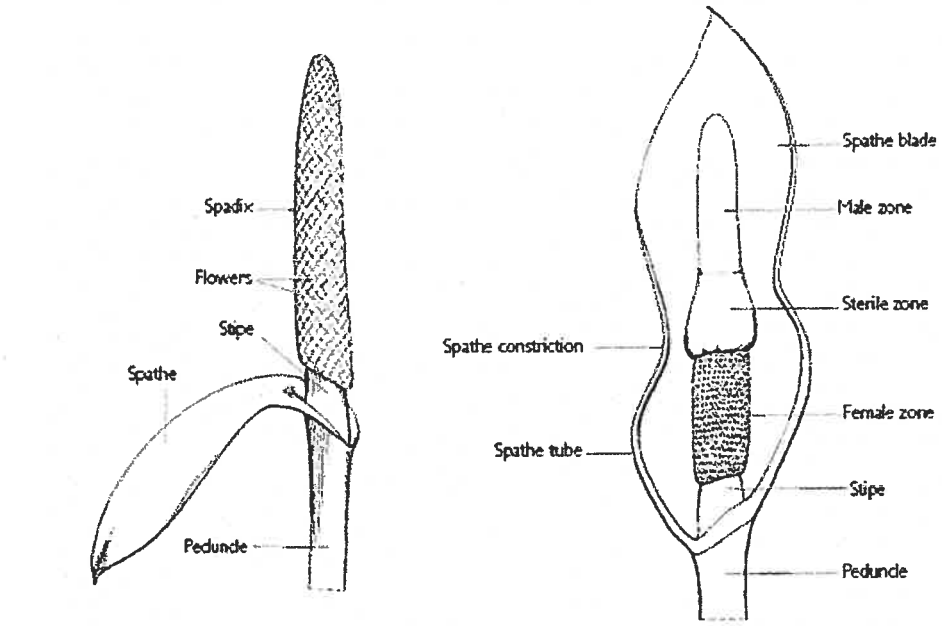


Figure 2.2. Types of inflorescence: left, bisexual flowers inflorescence (*Anthurium*); right, unisexual flowers inflorescence (*Philodendron*) (From Mayo et al. 1997).

The existence of a positive correlation between pollen size and pistil length (not presented in fig. 2.1) 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 is supposed to represent up to 60% of its mass (Roulston et al. 2000) and it is constituted mainly by 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 lipid-containing pollen (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, which allows tube growth in order to reach the ovule (Cresti et al. 1976; Knox et al. 1984; Herrero and Hormaza 1996). Based on this information, pollen size should be linked to stigma depth and not to style length (fig. 2.1).

Another factor affecting pollen size is the number of pollen grains a flower can support. Studies suggest that plants evolved an optimal pollen size, which balances the advantage of large pollen size for gametophytic competition against the fecundity disadvantage of fewer pollen grains produced (Aguilar et al. 2002; Yuang and Guo 2004). A negative correlation between those two traits has been well-documented at both inter- and intra-specific 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 20001; 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 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 *Synphionema* 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 result 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). Many studies have more or less confirmed the relationship between P/O and 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/O of Neotropical aroids are only known from two studies (Ramirez and Seres 1994; Chouteau et al. in press). 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 different 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/O than hemiepiphytic species (Chouteau et al. 2006).

Based on 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 maximise 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 both 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 allocation into male and female functions are possible. According to this author, genetic variation in sex allocation (negative correlation) is often small compared with variation in traits related to resource acquisition and vigour (positive correlation), perhaps because flowers can use different resource pools for male and female parts, as suggested by a physiological study (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 hemi-epiphytic and epiphytic types of growth (Ramirez and Seres 1994; Chouteau et al. 2006). In this perspective, the Araceae family (105 genera, more than 3,300 species), which possesses a great variability of reproductive mechanisms, constitutes very good material for studying the relationships presented in figure 2.1. Aroids have the particularity of possessing compact inflorescences with bisexual flowers (e.g. *Anthurium*) or unisexual flowers (e.g. *Philodendron*), exhibiting very different floral cycles. In the present study, two genera, *Philodendron* and *Anthurium*, with different inflorescence structures and pollination mechanisms, will be compared.

The genus *Philodendron* is the second largest in the Araceae, with about 400 species present in the Neotropics (Govaerts and Frodin 2002), but estimated to up to 750 species (Croat 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. 2.2). The pistillate flowers occupy the lower portion of the spadix, whereas the male flowers are located on 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 hour flowering cycle (Gibernau et al. 1999, 2000; Gibernau and Barabé 2002), beginning with the receptivity of the female flowers (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 (e.g. 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 body of the beetles that are leaving the inflorescence. This quite complex inflorescence morphology and cycle has the particularity of preventing self-pollination (sexual phases temporally separated, e.g. 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 as many as 1,000 species (Croat cited in Govaerts and Frodin 2002). The inflorescences bear only bisexual flowers and do not have any distinct morphological zones. The bisexual flowers consist of 4 tepals and 4 stamens surrounding a pistil (Mayo et al. 1997). In the genus *Anthurium*, the flowering cycle can last for more than 2 weeks (Croat 1980; Chouteau et al. 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 the complex pollination function of *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 (see Gibernau 2003 for a review, Anenexe I). Moreover, in *Anthurium*, the inflorescence has no floral chamber and thus pollinators come and go repeatedly during the pollination cycle. The efficiency of pollination may be reduced by the fact that at least two visits are required, first to bring pollen to a receptive inflorescence and 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 certain of the relationships presented in figure 2.1 remain the same in genera of the same family having different floral morphologies and pollination mechanisms.

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

2.2 Materials and methods

This study was conducted on 23 species of *Philodendron* (Table 2.1) and 20 species of *Anthurium* (Table 2.2) from the living collections of the Montreal Botanical Garden and the Montreal Biodôme, or collected in the field (French Guiana). Voucher specimens (see Annexe II) 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 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 cylindric and its height was measured with a digital calliper (0.01 mm resolution). *Anthurium* inflorescences were collected 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 days at ambient air temperature. Once dried, the stamens of each single 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 ten flowers and the number of ovules per locule for ten 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, 3 groups of 5 stamens were collected on inflorescences of *Philodendron* and 3 groups of 4 stamens (i.e. one flower) were collected for *Anthurium*. Each group of stamens was digested in 300 µl of 95% sulphuric acid, for 5 days 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 X 5 or 4 stamens per inflorescence). Standard deviations were calculated by using the total number of pollen grains counted for the 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 20X magnification under a dissecting microscope equipped with an ocular micrometer and using the formula $\pi D^2/4$ where D is the diameter measured. To obtain the total stigmatic area of an inflorescence, the mean stigmatic area is multiplied by the mean number of flowers bearing stigma for each species.

Style length and stigma height (Fig. 2.3) were measured on 10 female flowers for each inflorescence using the same microscopic technique used for the stigmtic 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 630X. 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 the equatorial axis diameter. Generally, 10 pollen grains per inflorescence were measured from 3 independent inflorescences (n=30).

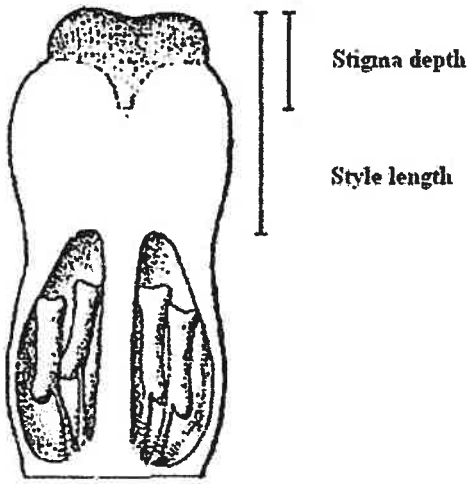


Figure 2.3. Schematic representation of a longitudinal section of a *Philodendron* female flower showing the measures used in the analysis.

The inflorescence peduncle diameter was measured on all inflorescences collected (generally 3) about 2-3 cm under the base of the spathe. This measure will be used in the present study to evaluate the different species capacity for resource acquisition (specific vigour).

A minimum of 3 inflorescences for each of the species listed in tables 2.1 and 2.2 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; 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*.

2.3 Results

2.3.1 Philodendron

The inflorescence peduncle diameter only varied by a fourfold range in the *Philodendron* species studied (Table 2.1). The style length varied from 0.68 to 1.86 mm, except for *P. melinonii* (3.10 mm), and stigma height ranged from 0.11 mm 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 flower had a tenfold range, varying from 47,230 in *P. bipinnatifidum* to 4,941 in *P. cannifolium.* The number of male flowers per inflorescence also varied by a tenfold range from 245 to 2,574. Ovule number per flower showed a huge variation. The highest ovule count was found in *P. 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 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 under 5 mm^2 and as low as 0.28 mm^2. Finally, the number of female flowers ranged from 232 to 1,458.

The inflorescence P/O in *Philodendron* is the number of male flowers multiplied by the number of pollen grains per flower over 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 (Table 2.1). The highest P/O was found in *P. bipinnatifidum*, mostly due to the inflorescence's huge quantity of pollen that characterizes the selected species of *Philodendron* sect. *Meconostigma*. All species of *Philodendron* studied are considered to be self-incompatible due to the lack of fructification in bagged inflorescences (Table 2.1).

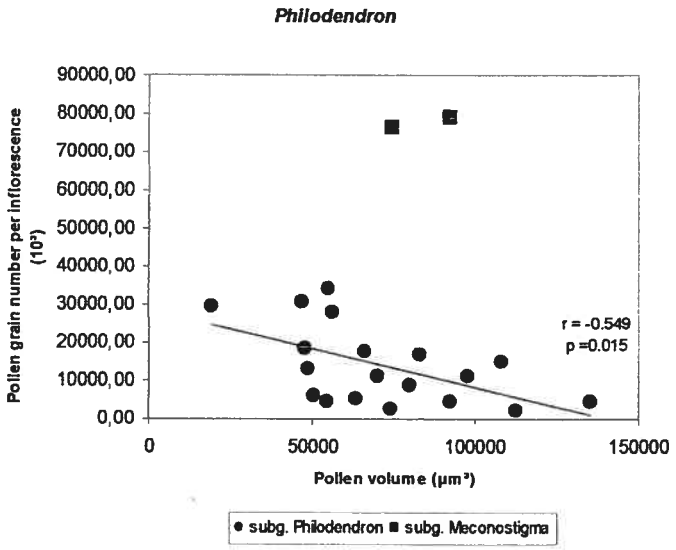
Table 2.1. Floral traits and self-pollination capacity for 23 *Philodendron* species. *: smaller sampling n ≤ 2 inflorescences. —: data not available.

	Inflorescence peduncle diameter (cm) N ≥ 3	Style length (mm) N ≥ 30	Stigma height (mm) N ≥ 30	Pollen grain volume (µm³) N ≥ 30	Pollen grain number per stamen N ≥ 27	Stamen per flower N ≥ 30	Ovule number per flower N ≥ 30	Stigma area per flower (mm²) N ≥ 30	Stamen number per inflorescence N ≥ 3	Female flower number per inflorescence N ≥ 3	P/O of inflorescence N ≥ 3	Self-pollination capacity
P. acutatum Schott	—	—	—	—.	4,286 ± 1,476	4.76 ± 0.60	77.9 ± 16.8	2.63 ± 0.74	7,987 ± 1,254	737 ± 79	630 ± 275	no
P. bipinnatifidum Schott	3.40 ± 0.50	1.86 ± 0.15	0.79 ± 0.02	74,749 ± 10,777	9,839 ± 1,546	4.30 ± 0.48	16.6 ± 0.2	5.73 ± 0.50	7,792 ± 465	411 ± 43	11,418 ± 3,065	no
P. cannifolium (Dryander ex Sims) G. Don	1.60 ± 0.10	0.97 ± 0.04	0.38 ± 0.30	50,346 ± 5,557	2,353 ± 1,413	2.10 ± 0.32	17.6 ± 3.9	0.99 ± 0.20	2,603 ± 629	1,070 ± 30	308 ± 4	no
P. distantilobum K. Krause	1.47 ± 0.06	1.27 ± 0.11	0.63 ± 0.04	79,915 ± 8,304	1,703 ± 787	4.70 ± 0.48	32.4 ± 3.8	1.55 ± 0.45	5,135 ± 1,040	688 ± 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	2,713 ± 1,335	2.60 ± 0.52	15.7 ± 0.9	1.04 ± 0.12	1,989 ± 105	775 ± 129	469 ± 292	no
P. glaziovii Hook. f.	1.07 ± 0.06	0.80 ± 0.12	—	54,649 ± 5,446	4,139 ± 2,998	4.00 ± 0.66	26.4 ± 1.2	1.34 ± 0.15	1,143 ± 40	695 ± 122	239 ± 150	no
P. gloriosum Andre	1.28 ± 0.05	1.00 ± 0.02	0.27 ± 0.04	—.	4,389 ± 1,951	5.40 ± 0.51	100.2 ± 7.1	1.75 ± 0.08	4,203 ± 785	478 ± 106	454 ± 381	no
P. grandifolium Schott	—	—	—	135,327 ± 33,322	1,279 ± 824	—.	13.6 ± 0.1	2.04 ± 0.97	3,664 ± 156	717 ± 61	474 ± 162	no
P. insigne Schott	1.16 ± 0.06	1.02 ± 0.04	—	74,319 ± 7,945	1,289 ± 547	4.10 ± 0.32	15.4 ± 0.2	0.28 ± 0.01	2,212 ± 44	1,197 ± 102	152 ± 26	no
P. linnaei Kunth	1.05 ± 0.05	0.83 ± 0.09	0.35 ± 0.03	69,937 ± 5,474	3,086 ± 1,116	3.80 ± 0.42	24.2 ± 0.2	0.99 ± 0.17	3,632 ± 167	1,424 ± 166	327 ± 37	no
P. melanochrysum Linden & Andre	1.69 ± 0.03	1.22 ± 0.37	0.75 ± 0.01	54,928 ± 5,949	5,313 ± 2,665	5.90 ± 0.64	284.1 ± 31.1	1.63 ± 0.52	6,457 ± 1,781	761 ± 78	153 ± 74	no
P. megalophyllum Schott	1.00 ± 0.10	0.88 ± 0.02	0.21 ± 0.03	112,719 ± 9,072	2,416 ± 1,362	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 ± 5,636	6,209 ± 2,304	4.64 ± 0.12	52.8 ± 3.4	3.25 ± 0.86	4,937 ± 1,113	394 ± 56	1,487 ± 529	no
P. microstictum Standley & L. O. Williams	1.06 ± 0.06	0.68 ± 0.08	0.11 ± 0.01	48,686 ± 8,552	2,516 ± 1,172	4.10 ± 0.52	8.2 ± 0.1	0.90 ± 0.08	5,126 ± 419	680 ± 58	2,300 ± 657	no
P. Sp. aff. megalophyllum	1.28 ± 0.02	1.03 ± 0.08	0.68 ± 0.06	92,449 ± 13,019	2,610 ± 775	3.20 ± 0.42	3.8 ± 0.1	0.76 ± 0.08	1,724 ± 791	564 ± 15	2,157 ± 1,240	no
P. ornatum Schott	1.30*	0.86 ± 0.01	0.30 ± 0.02	19,250 ± 1,075	7,354 ± 2,000	4.90 ± 0.87	68.4 ± 0.2	0.91 ± 0.10	4,033 ± 1,749	708 ± 291	608 ± 48	no
P. pedatum Kunth	1.29 ± 0.03	1.10 ± 0.05	0.43 ± 0.02	83,061 ± 39,695	2,893 ± 1,276	6.00 ± 0.30	34.1 ± 2.0	1.28 ± 0.09	5,789 ± 2,140	1,060 ± 76	484 ± 297	no
P. radiatum Schott*	2.13 ± 0.13	1.78 ± 0.09	—	56,357 ± 3,309	6,386 ± 1,810	4.20 ± 0.41	43.1 ± 6.0	2.30 ± 0.21	4,377	647	1002	no
P. ruizii Schott	1.33 ± 0.15	1.67 ± 0.33	0.47 ± 0.01	107,823 ± 6,946	2,729 ± 1,308	3.50 ± 0.71	23.1 ± 1.8	1.86 ± 0.17	5,563 ± 719	1,458 ± 80	448 ± 53	no
P. solimoesense A. C. Smith	2.83 ± 0.15	0.95 ± 0.09	0.72 ± 0.03	92,215 ± 6,116	6,169 ± 1,992	5.00 ± 0.28	169.8 ± 24.7	10.44 ± 0.20	12,872 ± 2,742	232 ± 34	2,065 ± 989	no
P. squamiferum Poepp. & Endl.	0.86 ± 0.05	0.90 ± 0.11	0.32 ± 0.03	47,680 ± 26,117	3,863 ± 1,171	3.80 ± 0.42	25.8 ± 3.4	1.06 ± 0.54	4,783 ± 1,313	641 ± 36	1,081 ± 86	no
P. talamancae Engl.*	—	—	—	—	4,746 ± 300	—	43.3 ± 6.3	4.81 ± 0.30	4,29	458	—	no
P. tripartitum Schott	1.15 ± 0.05	—	—	65,929 ± 15,992	5,406 ± 977	—	15.2 ± 3.1	1.12 ± 0.32	3,294 ± 303	782 ± 83	1,579 ± 638	no

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. 2.7). At both flower and inflorescence levels, pollen grain number was negatively correlated with pollen volume, but only when the two species of section *Meconostigma* (*P. bipinnatifidum* and *P. solimoesense*), which have much higher quantities of pollen grains, were removed from the analysis (figs. 2.4A, 2.7). Pollen number was positively correlated with ovule number in a logarithmic manner at both the flower and the inflorescence levels when species of subgenus *Meconostigma* were removed (fig. 2.5A,B). Correlations were found between the inflorescence peduncle diameter and (1) the pollen grain number per flower (r=0.671, p=0.002, fig. 2.6), (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 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, $p<10^{-3}$).

The negative relation found by Cruden (1997) between the stigmatic area and the number of pollen grain per flower was not found in *Philodendron* species (fig. 2.7). Instead, a positive interspecific linear relation was found between the stigma area of a flower and the pollen grain number per inflorescence (calculated as the mean number of male flowers x the mean pollen number per flower). A more accurate measure of investment in pollen is the pollen volume per flower (pollen number per flower x pollen grain volume) or per inflorescence (pollen volume per flower x number of male flowers). A strong positive linear relation was found between the stigmatic area of the inflorescence (stigma area per flower x number of female flowers) as well as the stigma area of one flower and the pollen grain volume per inflorescence and per flower (Table 2.3).

A



B

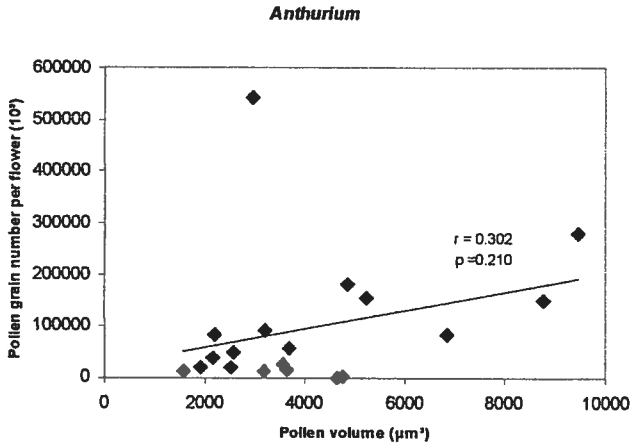


Figure 2.4. Relationship between pollen volume and pollen grain number per flower for 21 species of *Philodendron* in 2 subgenera (A) and 19 species of *Anthurium* (B). The two species of *Philodendron* subg. *Meconostigma* in (A) are plotted but were not included in the regression analysis.

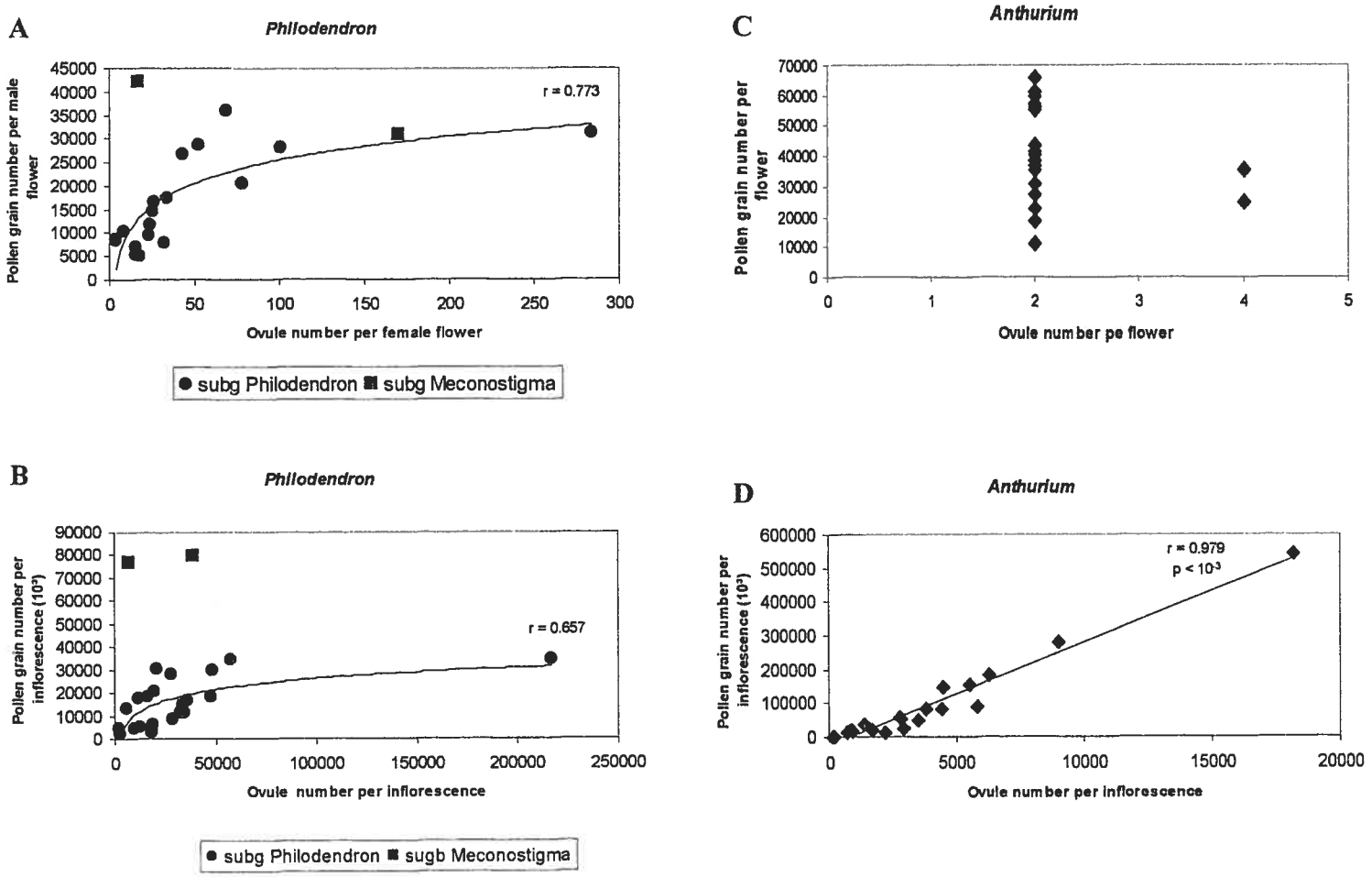


Figure 2.5. Relationship between ovule number and pollen grain number at the flower and inflorescence level for the species of *Philodendron* (A, B) and *Anthurium* (C, D) studied. The two species of *Philodendron* subg. *Meconostigma* are plotted but were not included in the regression analysis

2.3.2 Anthurium

At the inflorescence level, the peduncle diameter varied from 0.26 mm to 2.03 mm (Table 2.2). *Anthurium fendleri* had the smallest style length (0.56 mm) while *A. 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 mm to 0.46 mm. Pollen grain number per flower ranged from 65,999 (*A. barclayanum*) to 8,733 (*A. divaricatum*). Pollen grain volume ranged from 1,583 μm^3 (*A. barclayanum*) to 9,452 μm^3 (*A. clavigerum*). The variable with the least variation was ovule number per flower, which was 2 for most of the species studied, and 4 in *Anthurium trinerve* and *A. crystallinum*. The most variable character was the flower stigmatic area. The smallest stigma was found in the small *A. trinerve* (0.13 mm^2) while the largest 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 of 43, while the gigantic *A. salviniae* had a mean of 9,087 flowers. The pollen-ovule ratios ranged from 5,674 (*A. trunciculum*) to 31,225 (*A. barclayanum*) in the studied species. Due to the lack of variability of the number of ovules per flower (2 or 4), the variations of the P/O closely followed the variation of the number of pollen grains per flower. Among all bagged *Anthurium* inflorescences, 9 species produced seeds and therefore are considered able to self-pollinate (Table 2.2). No significant difference was found between the P/O of the group able to self-pollinate and that of the group 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. 2.7). Contrary to *Philodendron*, pollen size was positively related to pollen grain number at the flower level but not at the inflorescence level (figs. 2.4B, 2.7). In the genus *Anthurium*, no correlation was found between pollen number and ovule number at the flower level, while a strong correlation was found at the inflorescence level (figs. 2.5C,D, 2.7). An interspecific positive correlation was found between the inflorescence peduncle diameter and the flower number (r=0.906, $p<10^{-3}$), as well as with the pollen grain number per flower (r=0.679, p=0.001, fig. 2.6).

Table 2.2.. Floral traits and self-pollination capacity for 20 *Anthurium* species. —: data not available.

	Inflorescence peduncle diameter (cm) N ≥ 3	Pistil length (mm) N ≥ 30	Stigma height (mm) N ≥ 30	Pollen grain volume (µm³) N ≥ 30	Pollen grain number per flower N ≥ 27	ovule number per flower N ≥ 30	Stigma area per flower (mm²) N ≥ 30	flower number per inflorescence N ≥ 3	P/O of inflorescence N ≥ 3	self-pollination capacity
A. acaule Schott	0.78 ± 0.10	0.61 ± 0.06	0.26 ± 0.03	1,923 ± 274	22,966 ± 12,684	2 ± 0	0.27 ± 0.04	861 ± 230	11,482 ± 6,387	yes
A. barclayanum Engl.	0.88 ± 0.13	0.77 ± 0.03	0.18 ± 0.01	8,768 ± 929	65,999 ± 4,104	2 ± 0	0.13 ± 0.02	2,235 ± 97	31,225 ± 2,038	no
A. clavigerum Poepp.	1.26 ± 0.06	1.05 ± 0.05	0.46 ± 0.01	9,452 ± 1,163	61,565 ± 29,787	2 ± 0	0.80 ± 0.05	4,522 ± 102	30,782 ± 18,173	no
A. crystallinum Linden & André	0.52 ± 0.10	0.73 ± 0.08	0.34 ± 0.01	3,550 ± 505	35,465 ± 9,787	4 ± 0	0.32 ± 0.05	733 ± 84	8,866 ± 3,016	yes
A. truncicolum Engl. *(divericatum)*	0.40 ± 0.09	0.83 ± 0.07	0.25 ± 0.02	1,583 ± 179	11,349 ± 6,855	2 ± 0	0.29 ± 0.05	1,102 ± 469	5,674 ± 1,850	no
A. fendleri Schott	0.70 ± 0.10	0.56 ± 0.09	0.19 ± 0.10	2,200 ± 338	43,415 ± 16,068	2 ± 0	0.20 ± 0.02	1,903 ± 394	21,707 ± 10,005	yes
A. harrisii (Grah.) G. Don	0.49 ± 0.09	0.94 ± 0.05	0.37 ± 0.01	3,172 ± 794	35,488 ± 6,683	2 ± 0	1.08 ± 0.17	369 ± 55	17,743 ± 2,284	no
A. jenmanii Engl.	1.53 ± 0.15	1.01 ± 0.06	0.34 ± 0.01	4,854 ± 1,380	57,566 ± 8,679	2 ± 0	0.76 ± 0.06	3,134 ± 458	28,783 ± 2,238	no
A. longistamineum Engl.	0.73 ± 0.25	0.85 ± 0.07	0.23 ± 0.02	2,579 ± 334	27,499 ± 10,143	2 ± 0	0.57 ± 0.07	1,742 ± 326	14,166 ± 5,279	yes
A. ornatum Schott	0.65 ± 0.06	—	—	—	38,349 ± 4,925	2 ± 0	—	1,409 ± 73	19,174 ± 2,038	no
A. pedatoradiatum Schott	0.49 ± 0.10	1.36 ± 0.11	0.33 ± 0.02	3,648 ± 605	36,932 ± 2,701	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	1,399 ± 201	20,282 ± 16,664	no
A. polyschistum R. E. Schult. & Idrobo	0.42 ± 0.03	1.02 ± 0.04	0.41 ± 0.01	2,522 ± 453	41,799 ± 4,029	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	—	4,748 ± 871	18,616 ± 2,455	2 ± 0	0.19 ± 0.04	104 ± 7	8,460 ± 1,540	no
A. salviniae Hemsl.	2.03 ± 0.25	1.71 ± 0.87	—	2,953 ± 823	59,632 ± 20,800	2 ± 0	0.19 ± 0.04	9,087 ± 155	29,815 ± 5,279	yes
A. schlechtendalii ssp. schlechtendalii Kunth	0.73 ± 0.03	0.82 ± 0.04	0.25 ± 0.01	6,858 ± 1,233	36,882 ± 3,269	2 ± 0	0.33 ± 0.05	2,215 ± 54	18,441 ± 1,001	yes
A. spectabile Herincq	1.10 ± 0.18	3.30 ± 0.32	0.23 ± 0.02	5,238 ± 938	56,182 ± 26,000	2 ± 0	1.68 ± 0.12	2,761 ± 649	28,091 ± 16,557	yes
A. tatoense K. Krause	0.96 ± 0.15	1.54 ± 0.08	0.29 ± 0.03	2,163 ± 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	4,645 ± 823	24,749 ± 1,990	4 ± 0	0.13 ± 0.04	43 ± 17	5,916 ± 612	yes
A. upalahense Croat & R. A. Baker	1.08 ± 0.13	1.16 ± 0.07	0.21 ± 0.02	3,202 ± 438	31,016 ± 7,798	2 ± 0	0.43 ± 0.06	2,917 ± 378	15,507 ± 4,373	yes

As in *Philodendron*, these results suggest that an interspecific increase of peduncle diameter is correlated with an increase in 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 a surrogate of inflorescence size suggesting that larger inflorescences produce more pollen. Also, stigmatic area and pollen grain number among *Anthurium* species were positively correlated at the inflorescence level but not at the flower level (fig. 2.7). The pollen grain volume 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 2.3). As in *Philodendron*, P/O values were positively correlated with inflorescence peduncle diameter ($r=0.703$, $p=0.001$) and the number of flowers per inflorescence ($r=0.650$, $p=0.002$). *Philodendron* P/O were significantly smaller than *Anthurium* P/O ($t_{41}=10.05$, $p\leq 0.0001$).

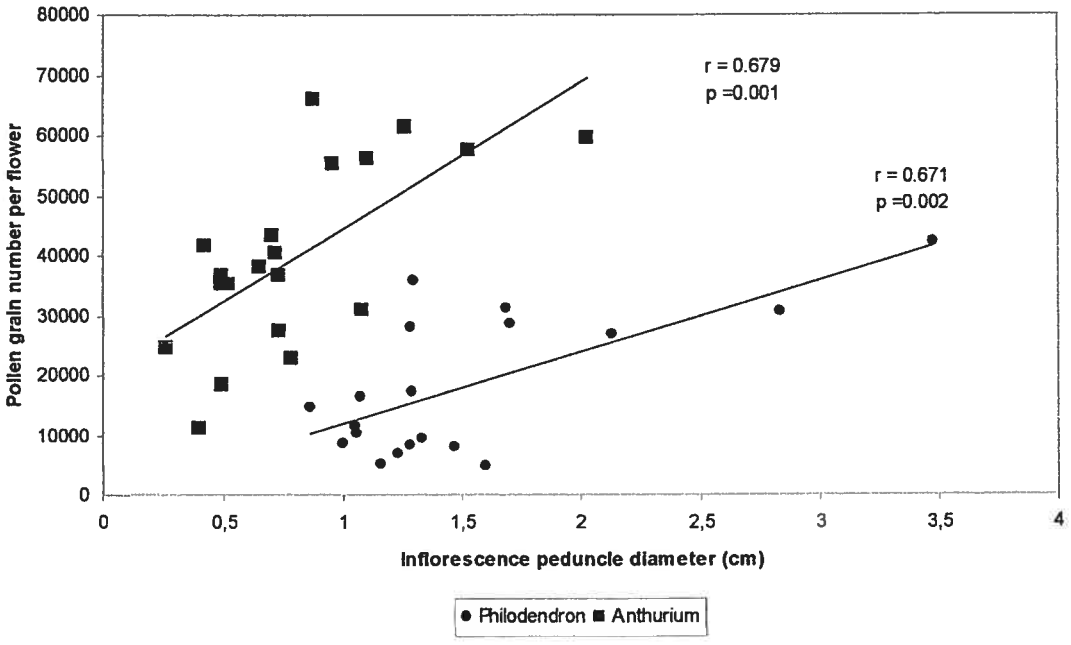


Figure 2.6. Correlation analysis between inflorescence peduncle diameter and pollen grain number per flower for 19 species of genus *Philodendron* and 20 of genus *Anthurium*.

Table 2.3. 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*. Significance level: * ≤0,05 and **≤0,01.

Philodendron

	Flower stigma area	Inflorescence stigma area
Pollen volume per flower	r = 0.843**	r = 0.706**
Pollen volume per inflorescence	r = 0.949**	r = 0.725**

Anthurium

	Flower stigma area	Inflorescence stigma area
Pollen volume per flower	r = 0.146	r = 0.516*
Pollen volume per inflorescence	r = 0.081	r = 0.651**

2.4 Discussion

2.4.1 Relationship between style length or stigma height and pollen size

Among the 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 plant groups at both the inter- and intra-specific 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 greater 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 the non-random fertilisation success of large pollen grains in pistils with a long style (Sarkissian and Harder 2001).

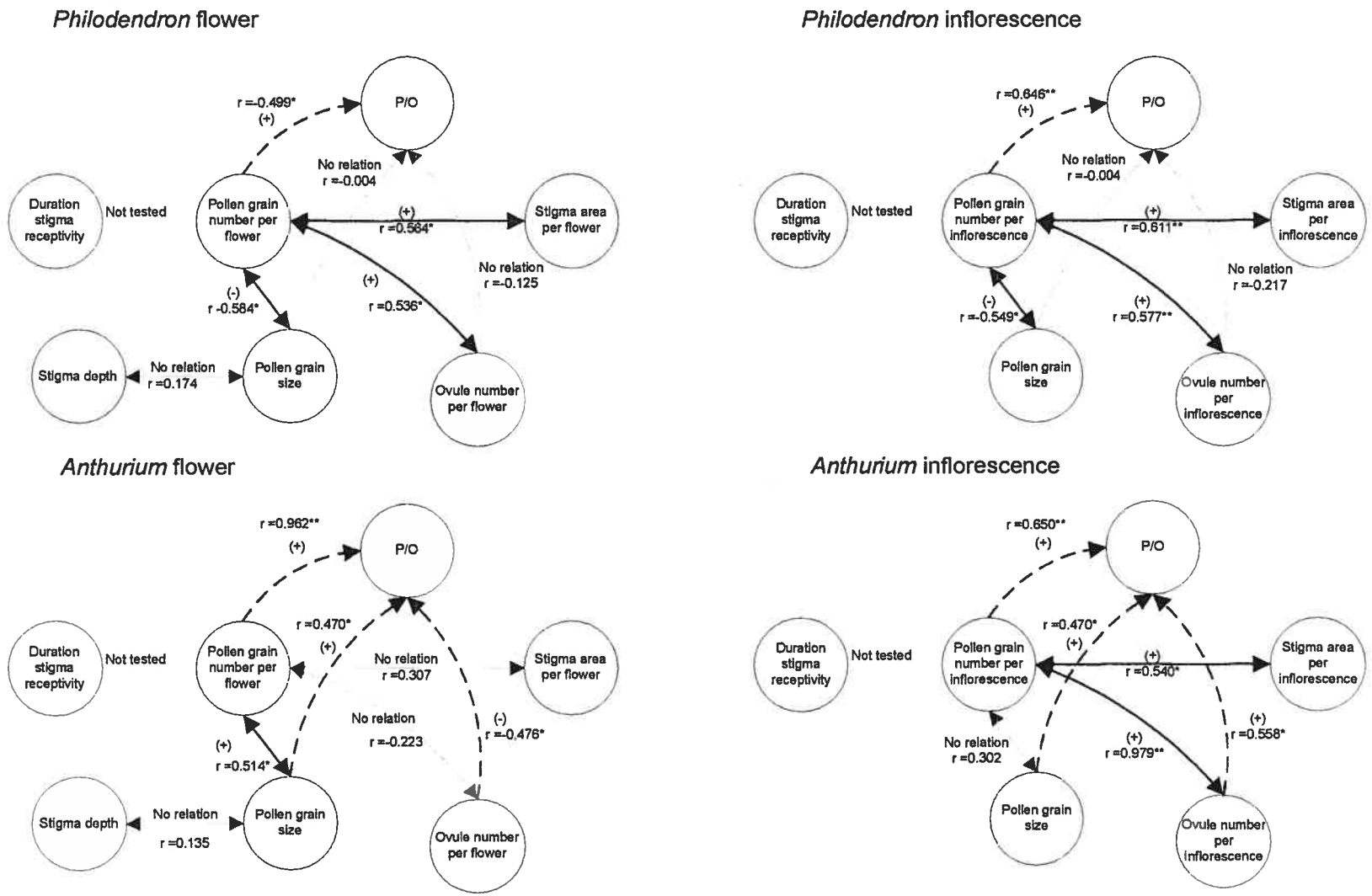


Figure 2.7. Relationships among floral traits based on Cruden (2000) (see also fig. 2.1) in the genera *Philodendron* (A) and *Anthurium* (B) at both flower and inflorescence levels. Correlations are indicated for each relationship. Significance level: * ≤0,05 and **≤0,01.

Cruden and Lyon (1985) argued that pollen size is functionally linked to stigma depth and not to 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 stabilise pollen size and style/stigma length in different species. The pollen would have the necessary prerequisite size to grow its pollen tube in order to reach the ovules. The extra volume (i.e. not necessary for the pollen tube growth) would then be explained by exogenous or endogenous factors. Exogenous factors might 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 1897; Cruden 2000), or pollen reserve type (López et al. 2005). Moreover, larger pollen grains might be associated with faster pollen tube growth in the context of pollen competition (Ottaviano et al. 1983; Lord and Eckard 1984) or even with stronger and larger pollen tubes (Plitmann and Levin 1983).

2.4.2 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; Yuang and Guo 2004 but see Cruden and Miller-Ward 1981). Such a trade-off 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, while 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 between number of pollen grain per flower and inflorescence peduncle diameter in both *Anthurium* and *Philodendron* confirms this hypothesis. This could be particularly true for tropical, long-lived Aroids. The *Anthurium* species studied vary greatly in size and growth speed (pers. obsv.) and should therefore have different capacities for resource acquisition, which may be 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 20001; Yang and Guo 2004). This relationship could be explained by the similar mode of growth and size (as indicated by the small range of variation of the peduncle diameter), and similar inflorescence structure 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 subgenus *Philodendron* also appears in subgenus *Meconostigma*, which corresponds to the outlier points excluded from certain analyses (figs. 2.4A, 2.5).

The results suggest that there is 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; Yuang and Guo 2004) indicating that there is a trade-off between size and number, but only among closely related species with perhaps approximately the same capacity for resource acquisition. When studying species with a large range of variation in the capacity for resource acquisition (e.g. *Anthurium*), the difference in the amount of energy available to the reproductive structures may influence floral traits such as

pollen number, consequently masking the negative relationship between pollen size and number.

2.4.3 Flower trait evolution with respect to floral cycle and inflorescence structure

The relationship between 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 grains in two groups of plants (*Synphionema* and *Isopogon*). This relationship has been explained as a trade-off between the investment in pollen versus 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. On the contrary, plants producing a large number of pollen grains would have a smaller stigma due to 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 x pollen grain volume) and per inflorescence (pollen volume per flower x number of male flowers) and the stigmatic area at both the flower and the inflorescence levels (stigma area per flower x number of female flower). Those relationships can be explained by the flowering cycle of this genus and its inflorescence morphology. *Philodendron* has a 24-hour flowering cycle. Female and male flowers are synchronous over two successive nights during the female and male phases, respectively. Thus, the inflorescence of *Philodendron* behaves functionally as if it were made of only a single female and male flower each. 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. Each cycle lasts for 2 to 3 weeks depending on the species. It begins with the simultaneous stigmatic receptivity of all the hermaphrodite flowers along the whole inflorescence. The receptivity lasts for about half the flowering cycle. *Anthurium* flowers are dichogamic (i.e. sexual phases temporally separated). There is a full day (24 hours) when no sexual function is active between the end of stigma receptivity and the beginning of pollen release. After this inter-phase, the stamens begin to release pollen. In some species, female and male phases overlap shortly, allowing self-pollination to occur in the absence of visits by pollinators (Croat, 1980). Contrary to *Philodendron,* the pollen of which is released in an explosive way (all at the same time) along the inflorescence, *Anthurium* stamens open sequentially, beginning at 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, since 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 is on the inflorescence, the higher the number of pollen grains per flower.

Inflorescences of *Philodendron* and *Anthurium* are integrated structures in which most floral traits are linked in order to optimize the inflorescence level as the main pollination unit and not individual flowers.

2.4.4 Pollen and ovule number

Recent studies on sex allocation theory have revealed an intraspecific intra-flower positive genetic correlation between male (pollen) and female (ovule) functions (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 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 (2 or 4) 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 implies that the *Philodendron* inflorescence is a well-integrated 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 that can be produced. This maximum 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 stamen morphology and consequently inflorescence architecture, which is closely linked to pollinators. In *Anthurium* inflorescences, a strong positive linear correlation was found between pollen and ovule number at the inflorescence level. This is due to the additive effect of flower number, the flowers being bisexual, and thus all similar equivalent. We found a positive interspecific correlation between the number of pollen grains and ovules for two genera having compact inflorescences, suggesting that their inflorescence must be considered the effective pollination unit.

2.4.5 Pollen-ovule ratio and breeding system

Our results clearly show that the breeding system is 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 have a higher P/O in comparison to *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 specialised. 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 hours), with floral rewards (sterile flowers rich in protein) for the beetle pollinator, the secretion of resin to secure pollen to the pollinator, and the production of odours and heat which attract pollinators (Gibernau et al. 1999, 2000; Seymour et al. 2003). On the contrary, in *Anthurium*, the flowering cycle is much longer (up to 2 weeks), the spathe is generally open and spreading (i.e. 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; pers. obsv.)

Among the *Anthurium* species studied no significant difference in P/O values was found between species able to self-pollinate, and those unable to self-pollinate which 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 to 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.

2.4.6 Conclusion

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 pollen-ovule ratios in Aroids may not be an indicator of breeding system as 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 in understanding variations in floral traits.

2.5 Acknowledgements

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Chapitre 3

Relationships between Floral Characters, Pollination Mechanisms, Life Forms and Habitats in Araceae

Botanical Journal of the Linnean Society: Soumis

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Abstract

The floral traits of the inflorescences of angiosperms have co-evolved to ensure and maximise pollination. Other factors believed to influence floral architecture are factors external (e.g. ecological) to the inflorescence, which have been insufficiently studied in the context of floral structures. In order to understand the relationships between such factors and floral characters, we measured 12 floral traits in 54 species of Araceae. We analysed how these traits are linked to 1) self-pollination capacity, 2) life form (evergreen *versus* seasonally dormant), 3) climatic conditions, and 4) type of pollinator (i.e., flies, bees, or beetles). We found a significant difference between the pollen-ovule ratio (P/O) of the self- pollinated Aroids and those unable to do so. Evergreen and tropical Aroids produced a higher number of gametes than seasonally dormant and temperate Aroids. Finally, several floral traits such as pollen volume and number, number of female flowers, and flower sexual type (unisexual or bisexual) showed clear differences among the three pollinator types. The P/O cannot be considered an accurate measurement of breeding systems in Aroids because of the particular pollination ecology of the family. Variations in floral traits between the different life forms and climatic conditions are discussed with respect to pollination efficiency and properties of the growing season.

Keywords

bee- beetle- fly-pollination, P/O, pollination syndrome, life cycle, climatic conditions.

3.1 Introduction

Angiosperms have evolved a complex reproductive structure. the flower, which functionally ensures their reproduction. Floral architecture is directly linked to pollination and therefore presents characters that have co-evolved in order to ensure and maximize pollen transfer to the ovule (reviewed in Cruden 2000) and, thus, the probability of reproduction (Cruden 2000; Fenster et al. 2004). The relationship between floral characters and breeding system has been well studied (reviewed in Cruden 2000), but other factors not physically linked to the inflorescence (i.e., extrinsic to it) may also influence the floral architecture. Such external (e.g. ecological) factors include, for example, pollinator types, life form and habitats. However, contrary to the "internal" relationships (i.e., within the inflorescence) between the floral characters, these external relationships have rarely been properly studied in Angiosperms at the family level (Raven 1979; Plitmann and Levin 1990; Ramirez and Seres 1994; Jürgens et al. 2002; Chouteau et al. 2006).

After studying 80 different species, Cruden (1977) concluded that the pollen-ovule ratio (P/O) was related to the plant breeding system and pollination efficiency. "The more efficient the transfer of pollen is, the lower the P/O should be" (Cruden 1977). Some recent studies have more or less confirmed the relationship between P/O, breeding system, and pollination efficiency (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, 2005), while others have not found such relationships (Gallardo et al. 1994; Ramirez and Seres 1994; Wyatt et al. 2000; Chouteau et al. 2006, unpublished results). These studies have mentioned other factors such as habitat, pollen vectors, and pollination mechanisms that could also influence floral morphology and pollen-ovule ratio, without producing evidence in support (Small 1988; Cruden 2000; Jürgens et al. 2002; Chouteau et al. 2006). According to Cruden (2000), variations in floral traits reflect variations in pollinator efficiency in different habitats. Such variations in P/O and floral traits for a given pollinator have been documented (Plitmann and Levin 1990; Ramirez and Seres 1994). Also, factors such

as arboreal or terrestrial habits, or perennial or annual life cycles, appear important in understanding floral architecture and the ranges of P/O in relation to breeding system (Raven 1979; Plitmann and Levin 1990; Ramirez and Seres 1994; Jürgens et al. 2002; Chouteau et al. 2006). In the present study we propose to investigate such factors in the Aroid family.

The Aroid family comprises 105 genera and more than 3,300 species (Mayo et al. 1997). Two main types of inflorescences are found in this family: (1) with only bisexual flowers represented in the genus *Anthurium*; and (2) with unisexual flowers, represented in the genus *Philodendron*.

In inflorescences of the *Philodendron* type, the female flowers are located in the lower portion and the male flowers in the upper. An intermediate zone of sterile male flowers is also present in certain genera (e.g. *Caladium*, *Philodendron*), and in others a terminal appendix without flowers (e.g. *Arum*) is present above the male flowers, with diverse functions such as odour and heat production (Vogel and Martens 2000). Aroids are present on all continents between the latitudes 50° North and 35° South (Mayo et al. 1997). They can be epiphytic, hemi-epiphytic, terrestrial, geophytic, helophytic, or free floating, and evergreen or seasonally dormant (Mayo et al. 1997). Pollination is mainly accomplished by insect vectors as diverse as beetles, bees, and flies (Gibernau, 2003).

To date, the relationships between breeding systems and floral characters in Aroids have been studied at the intra-genus level only in *Anthurium* and *Philodendron* (Chouteau et al. unpublished results). This study showed no relationship between P/O and breeding systems, and it is believed that P/O is not an indicator of breeding system at this level for Aroids. On the other hand, the only study available at the family level (Chouteau et al. 2006) was conducted on a limited number of species (i.e. nine French Guianese Aroids) and clearly showed that the relation of P/O to breeding systems was contrary to the findings of Cruden (1977). In *Araceae*, it is thought that a link exists between P/O and type of pollination mechanism, habitat, and growth mode. The more complex the pollination mechanism, the lower the P/O. Terrestrial, helophytic and geophytic species had higher P/O ratios than hemi-epiphytic species (Chouteau et al. 2006).

In order to understand floral architecture in relation to ecological factors (i.e., extrinsic to the inflorescence), we address the following questions. (1) Are P/O and capacity for self-pollination linked in Aroids at the family level? (2) Are floral traits influenced by life form or (3) by climatic zone? And (4) do floral traits and P/O vary in relation to pollinator type (i.e. pollination syndromes)?

3.2 Materials and methods

This study was conducted on 54 species belonging to 32 genera of *Araceae* sampled from the living collections of the Montreal and Missouri Botanical Gardens, the Montreal Biodôme, as well as from the field in French Guiana (Annexe III). The species listed in Table 3.1 were sampled during their flowering period. Voucher specimens were deposited at the Marie-Victorin Herbarium (MT).

For species with unisexual flowers, inflorescences were collected during the first day of the flowering cycle, when the spathe is open but before the pollen is released. For each inflorescence, the total numbers of female, male and bisexual flowers were counted; in cases where male flowers could not be isolated, the total number of male flowers was estimated. To do so, a 5 mm slice was cut in the middle of the male zone and the number of stamens over the entire surface was counted. 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 calliper (± 0.01mm). 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 as measured on at least 30 flowers from three separate inflorescences.

For species with bisexual flowers, inflorescences were collected on the first day of pollen release. In the case of *Monstera* and *Stenospermation*, which have a short flowering cycle of approximately 7 days (Chouteau et al. 2006), the inflorescences were collected just after the spathe had opened. For all these species, the total number of flowers was determined by counting flowers individually.

For both types of inflorescences, the number of ovules per flower was estimated by counting the number of locules on ten flowers and the number of ovules per locule for ten locules for each inflorescence collected. Ovule number per inflorescence was obtained by multiplying the mean number of ovules per flower by the mean number of flowers per inflorescence.

To estimate the number of pollen grains per inflorescence, three groups of five stamens were collected on inflorescences where flowers could not be isolated, and three groups of one flower on inflorescences where flowers could be isolated. Each group of stamens or each flower was dissolved 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 on a microscope slide. The number of pollen grains was counted for three independent replicates of 1 µl.

When three groups of five stamens were used, the total number of pollen grains per flower was obtained by multiplying the mean of the triplicate count by 300, dividing the result by 5 and multiplying that by the number of stamens per flower. When three groups of one flower were used, the number of pollen grains per flower was obtained by multiplying the mean of the triplicate by 300. A complete pollen count was performed in triplicate for each inflorescence (3 x 5 stamens or 3 x one flower per inflorescence). Standard deviations were calculated by using the total number of pollen counts (generally n = 9) of the same species. The number of pollen grains per inflorescence was obtained by multiplying the mean number of pollen grains per flower by the mean number of flowers. In the same way, the pollen grain volume per inflorescence was obtained by multiplying the mean number of pollen grains per inflorescence by the mean pollen volume of the concerned species (see below).

The size of the 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 630x. The volume of a single pollen grain was estimated using the formula $\pi PE^2/6$ (Harder 1998), where P is the polar axis and E the equatorial axis diameter. Ten pollen grains per inflorescence were measured from three independent inflorescences (generally n=30). For a few species, pollen grain

volume was estimated by using Grayum's (1992) data on pollen diameter and applying the formula $(4/3)\pi(D/2)^3$ where D is the diameter.

The pollen-ovule ratio was calculated for the inflorescence by dividing the mean number of pollen grains per inflorescence by the mean number of ovules per inflorescence. For the dioecious *Arisaema triphyllum*, the P/O was calculated by dividing the mean number of pollen grains per inflorescence of male plants by the mean ovule number per inflorescence of female plants. For all species, standard deviations were calculated using all the inflorescences from the same species (generally n = 3).

For each inflorescence, the stigma area (approximated to a circle) of 10 flowers was calculated using the diameter (0.01mm resolution) of the stigmas measured at 20x magnification under a dissecting microscope equipped with an ocular micrometer and using the formula $\pi D^2/4$ where D is the measured diameter. To obtain the total stigmatic area of the inflorescences, the mean stigmtic area was multiplied by the mean number of flowers bearing stigma for each species. When inflorescences bore fewer than 10 female flowers, all the stigmas were measured.

A minimum of three inflorescences per species (Table 3.1) were bagged at the bud stage. After anthesis, if at least one inflorescence had set fruits, the species was considered to be able to self-pollinate; if all inflorescences withered without producing seeds, it was considered unable to self-pollinate.

Life form, growth mode and climatic region were obtained from Mayo et al. (1997) and from personal observations. Species are considered seasonally dormant (seasonal) when they have an annual dormant stage associated with the loss of the aerial vegetal system, while evergreen species do not show dormant stage and the aerial vegetal system is present year-round. For growth mode, species were categorized as epiphytic (non-parasitic plants growing on another plant, without roots in contact with the ground), hemi-epiphytic (plants growing on a host plant with feeder roots in contact with the ground), terrestrial (plants growing on the ground and lacking underground stems), geophytic (plants with underground stems, either a tuber or a rhizome), helophytic (marsh or swamp plants growing in flooded ground with the foliage above the water), or free-floating (aquatic plants floating above the water

without anchor roots). Finally, the species were divided into two climatic regions: temperate or tropical (including subtropical, tropical and equatorial regions).

T-test analyses were used to determine differences between groups for the variable measured (self-pollination capacity, life form, climatic zone and growth mode) for all the species studied (SPSS 11.0.0, 2001). Differences in floral traits between the different types of pollinators were tested using ANOVA (Systat 8.0, 1998). Prior to the analysis, the P/Os were log-transformed and the numbers of ovules were square-root transformed. In order to study the relationships between floral traits and type of pollinating insect, a stepwise backward discriminate analysis was performed (Systat 8.0, 1998). The analysis was conducted for three types of pollinators (grouping variable) - bees, beetles and flies – according to the data available in the literature (see Gibernau 2003 for a review, Annexe I). Twenty species were coded as beetle-pollinated, fourteen as fly-pollinated, seven as bee-pollinated and thirteen as unknown (Table 3.1). Species with unknown pollinator were used as complementary data and, after analysis, were classified into one of the three defined groups. The twelve floral traits (variables) available for all species were selected in order to test discrimination among the three pollinator groups: flower stigma area, stigma per inflorescence, mean pollen grain volume, pollen volume per inflorescence, pollen number per inflorescence, number of ovules per flower and per inflorescence, pollen-ovule ratio, number of female flowers, sexual type of the flower, growth mode, and life form.

Table 3.1. Climatic region, Life form, growth mode, pollinator, floral traits measured and self-pollination capacity for 54 aroids species in 32 genera.

	Climatic region	Life form	Growth mode	Pollinator	Stigma area per flower (mm^2)	Pollen grain volume (μm^3)	Male flower number per inflorescence	Female flower number per inflorescence	Pollen grain number per male flower	Pollen grain number per inflorescence	Ovule number per flower	Ovule number per inflorescence	P/O ratio of inflorescence	self-pollination capacity
					N ≥ 30	N ≥ 30	N ≥ 3	N ≥ 3	N ≥ 27	N ≥ 3	N ≥ 30	N ≥ 3	N ≥ 3	
Alocasia sp.	Trop	E	T	fly	3.14 ± 0.43	22,449*	153 ± 11	51 ± 2	11,399 ± 3,482	1,739,446 ± 6,599	9.3 ± 0.9	459 ± 25	3,795 ± 196	
Alocasia macrorhizos (L.) G. Don	Trop	E	T	fly	1.68 ± 0.05	33,944 ± 1,973	162 ± 23	110 ± 15	47,310 ± 5,591	7,679,920 ± 1,266,074	11.8 ± 0.7	1,303 ± 201	5,885 ± 98	no
Alocasia portei Schott	Trop	E	T	fly	1.93 ± 0.49	45,293 ± 6,595	491 ± 33	111 ± 11	18,910 ± 4,240	9,257,149 ± 437,165	6.3 ± 0.6	707 ± 44	13,129 ± 1,129	yes
Anaphyllopsis americana (Engl.) A. Hay	Trop	S	H	.	0.29 ± 0.01	14,847 ± 2,405	129 ± 30	129 ± 30	106,324 ± 34,724	17,074,965 ± 53,995,780	1.0 ± 0.0	129 ± 30	106,324 ± 34,724	no
Anchomanes difformis (Blume) Engl.	Trop	S	G	.	0.50 ± 0.11	26,521*	.	141 ± 133	.	4,686,303 ± 5,494,704	1.0 ± 0.0	141 ± 133	29,232 ± 11,222	.
Anthurium harrisii (Grah.) G. Don	Trop	E	E	bee	1.08 ± 0.17	3,172 ± 794	369 ± 55	369 ± 55	35,488 ± 6,683	13,106,904 ± 2,208,933	2.0 ± 0.0	738 ± 110	17,743 ± 2,284	no
Anthurium longistamineum Engl.	Trop	E	E	bee	0.57 ± 0.07	2,579 ± 334	1,742 ± 326	1,742 ± 326	27,499 ± 10,143	47,904,129 ± 13,316,890	2.0 ± 0.0	3,484 ± 652	14,166 ± 5,279	yes
Anthurium schlechtendalii ssp. schlechtendalii Kunth	Trop	E	E	bee	0.33 ± 0.05	6,858 ± 1233	2,215 ± 54	2,215 ± 54	36,882 ± 3,269	81,725,717 ± 4,616,231	2.0 ± 0.0	4,430 ± 108	18,441 ± 1,001	yes
Anubias barteri Schott	Trop	E	H	beetle	0.56 ± 0.02	7,238*	105 ± 41	54 ± 9	55,782 ± 23,413	6,397,989 ± 5,057,274	37.8 ± 1.5	2,060 ± 347	3,360 ± 3,021	no
Anubia heterophylla Engl.	Trop	E	H	beetle	0.07 ± 0.01	15,598*	62 ± 36	54 ± 12	86,699 ± 23,685	5,725,785 ± 4,326,564	20.7 ± 0.8	1,129 ± 264	4,749 ± 2,718	no
Arisaema dracontium (L.) Schott	Temp	S	G	fly	0.01 ± 0.01	5,575*	27 ± 9	185 ± 37	47,832 ± 12,065	1,346,202 ± 674,186	3.5 ± 0.5	640 ± 126	2,172 ± 1,044	.
Arisaema triphyllum (L.) Schott	Temp	S	G	fly	0.62 ± 0.01	8,768 ± 829	41 ± 7	68 ± 6	34,299 ± 6,207	1,385,094 ± 2,910	5.3 ± 0.4	365 ± 38	3,793	no
Arum cylindraceum Gasp.	Temp	S	G	fly	.	17,157*	69 ± 15	51 ± 10	6,830 ± 1,161	510,620 ± 95,040	3.8 ± 0.4	199 ± 39	2,512 ± 424	no
Arum italicum Mill.	Temp	S	G	fly	.	17,157*	144 ± 26	52 ± 12	7,496 ± 1,109	1,048,468 ± 260,598	5.8 ± 1.6	311 ± 138	4,221 ± 1,323	no
Aum maculatum L.	Temp	S	G	fly	.	12,770*	106 ± 31	31 ± 11	5,485 ± 1,198	550,345 ± 257,435	4.8 ± 1.4	161 ± 108	4,596 ± 1,910	no
Caladium bicolor (Aiton) Vent.	Trop	S	G	beetle	0.83 ± 0.06	35,494 ± 7,882	152 ± 43	194 ± 16	7,649 ± 2,577	1,136,430 ± 118,013	8.0 ± 0.0	1,556 ± 130	729 ± 14	no
Cercestis stigmaticus N.E. Br.	Trop	E	HE	beetle	1.85 ± 0.02	95,322 ± 3,824	221 ± 78	46 ± 10	11,087 ± 2,931	2,409,590 ± 632,299	1.0 ± 0.0	46 ± 10	51,610 ± 1,825	no
Colocasia esculenta (L.) Schott	Trop	S	G	fly	0.76 ± 0.07	6,027 ± 799	490 ± 59	207 ± 51	18,199 ± 7,513	9,112,362 ± 4,291,846	41.6 ± 8.5	8,646 ± 2,264	1,023 ± 228	no
Colocasia fallax Schott	Trop	S	G	fly	0.01 ± 0.01	27,198 ± 4,761	165 ± 7	123 ± 9	36,615 ± 3,974	6,067,225 ± 753,821	.	3,782 ± 441	1,626 ± 389	no
Culcasia saxatilis A. Chev.	Trop	E	T	beetle	0.48 ± 0.04	17,157*	114 ± 17	22 ± 4	13,932 ± 1,384	1,599,376 ± 300,207	1.0 ± 0.0	22 ± 4	72,735 ± 381	no
Dieffenbachia oerstedii Schott	Trop	E	T	beetle	7.06 ± 0.67	508,047*	210 ± 33	39 ± 6	8,421 ± 2,375	1,722,299 ± 357,475	1.0 ± 0.0	39 ± 6	45,577 ± 14,878	yes
Dieffenbachia seguine (Jacq.) Schott	Trop	E	T	beetle	.	258,154*	286 ± 47	39 ± 6	9,788 ± 1,379	2,754,300 ± 205,628	2.2 ± 0.1	85 ± 18	33,276 ± 6,453	yes
Dracontium polyphyllum L.	Trop	S	G	Fly	0.38 ± 0.03	11,312 ± 4,243	127 ± 8	127 ± 8	138,632 ± 60,282	21,111,163 ± 3,360,695	3.0 ± 0.0	381 ± 25	55,238 ± 5,130	no
Dracunculus vulgaris Schott	Trop	S	G	Fly	0.63 ± 0.12	47,712*	.	211 ± 110	.	3,546,327 ± 2,092,984	3.9 ± 0.3	844 ± 441	4,116 ± 327	.
Gonatopus angustus N.E. Br. [1]	Trop	S	G	.	2.26 ± 0.09	229,847*	49	40	4,499 ± 436	220,451	2.0 ± 0.0	80	2,756	no
Gonatopus bovinii (Decne.) Engl.	Trop	S	G	.	1.76 ± 0.13	229,847*	195 ± 19	101 ± 2	3,192 ± 1,282	677,820 ± 20,858	2.0 ± 0.0	202 ± 5	3,345 ± 96	.
Homalomena rubescens Kunth	Trop	E	T	.	1.34 ± 0.06	3,156 ± 1,469	563 ± 5	135 ± 20	40,565 ± 9,410	22,855,411 ± 3,732,359	39.7 ± 3.2	10,907 ± 836	2,114 ± 504	no
Homalomena philippinensis Engl. [1]	Trop	E	T	.	0.12 ± 0.01	3,053*	125	66	1,300 ± 225	162,557	55.0 ± 1.0	3630	44	.
Monstera adansonii Schott	Trop	E	HE	bee	0.57 ± 0.05	51,870 ± 10,621	230 ± 44	230 ± 44	57,203 ± 8,289	12,985,938 ± 219,9319	4.0 ± 0.0	922 ± 179	14,300 ± 2,072	no
Montrichardia arborescens (L.) Schott	Trop	E	H	beetle	11.16 ± 0.22	720,667 ± 129,288	448 ± 118	73 ± 12	19,445 ± 5,316	8,727,761 ± 3,394,104	1.0 ± 0.0	73 ± 12	119,020 ± 42929	yes

Table 3.1. (continued)

	Climatic region	Life form	Growth mode	Pollinator	Stigma area per flower (mm²) N ≥ 30	Pollen grain volume (µm³) N ≥ 30	Male flower number per inflorescence N ≥ 3	Female flower number per inflorescence N ≥ 3	Pollen grain number per male flower N ≥ 27	Pollen grain number per inflorescence N ≥ 3	Ovule number per flower N ≥ 30	Ovule number per inflorescence N ≥ 3	P/O ratio of inflorescence N ≥ 3	self-pollination capacity
Montrichardia linifera (Arruda) Schott	Trop	E	H	beetle	.	434,892*	649 ± 38	122 ± 22	17,251 ± 8,292	11,397,606 ± 5,920,738	1.0 ± 0.0	122 ± 22	923,55 ± 45,682	.
Peltandra virginica (L.) Schott	Temp	S	H	fly	0.57 ± 0.02	11,494*	185 ± 13	43 ± 21	19,666 ± 5,630	3,656,094 ± 491,645	3.2 ± 0.4	142 ± 74	28,744 ± 11,568	no
Philodendron erubescens C. Koch & Augustin	Trop	E	HE	beetle	1.04 ± 0.12	63,218 ± 11,383	765 ± 40	775 ± 129	7,054 ± 3,471	5,331,093 ± 2,265,953	15.7 ± 0.9	12,234 ± 2,806	469 ± 292	no
Philodendron pedatum Kunth	Trop	E	HE	beetle	1.28 ± 0.09	83,061 ± 39,695	964 ± 356	1,060 ± 76	17,359 ± 7,656	17,840,873 ± 1,162,0431	34.1 ± 2.0	36,148 ± 3,163	484 ± 297	no
Philodendron squamiferum Poepp. & Endl.	Trop	E	HE	beetle	1.06 ± 0.54	47,680 ± 26,117	1,258 ± 345	641 ± 36	14,679 ± 4,450	17,768,841 ± 90,404	25.8 ± 3.4	16,478 ± 1,231	1,081 ± 86	no
Pinellia tripartita (Blume) Schott	Temp	S	G	fly	0.017 ± 0.01	12,770*	.	67 ± 8	.	856,848 ± 5,159	1.0 ± 0.0	67 ± 8	6,443 ± 777	.
Pistia stratiotes L.	Trop	E	FF	.	1.61 ± 0.17	10,305*	1 ± 0	1 ± 0	2,033 ± 1,464	2,033 ± 1,464	22.3 ± 1.5	22 ± 1	90 ± 66	no
Pseudodracontium fallay Serebr.	Trop	S	G	.	0.50 ± 0.05	57,905*	94 ± 5	95 ± 33	17,582 ± 3,049	1,671,158 ± 251,408	1.0 ± 0.0	94 ± 33	18,642 ± 3942	.
Rhaphidophora shottii Hook[1]	Trop	E	HE	beetle	0.19 ± 0.02	18,816*	991	991	98,766 ± 7,750	97,877,106	1.0 ± 0.0	991	98,766	.
Spathiphyllum friedrichsthalii Schott	Trop	E	T	bee	0.77 ± 0.07	10,865 ± 929	171 ± 32	171 ± 32	25,932 ± 9,602	4,545,879 ± 1,851,630	9.0 ± 0.0	1,539 ± 293	2,881 ± 833	no
Spathiphyllum patinii (Mast.) N.E. Br.	Trop	E	T	bee	0.64 ± 0.06	18,470 ± 1,266	118 ± 12	118 ± 12	21,987 ± 10,934	2,598,082 ± 1,292,262	9.0 ± 0.0	1,065 ± 109	2,467 ± 1211	no
Spathiphyllum wallisii Regel	Trop	E	T	bee	0.56 ± 0.11	12,198 ± 865	126 ± 31	126 ± 31	38,455 ± 7,213	4,917,462 ± 1,774,087	9.0 ± 0.0	1,141 ± 279	4,235 ± 892	no
Stenospermation longipetiolatum Engl.	Trop	E	E	.	0.77 ± 0.05	75,123 ± 11,638	179 ± 5	179 ± 4	2,599 ± 433	465,291 ± 63,295	5.4 ± 0.5	969 ± 26	481 ± 78	no
Stenospermation sessile Engl.[1]	Trop	E	E	.	0.50 ± 0.03	38,792*	206	206	9,399 ± 721	2,609,196	4.0 ± 0.0	824	3,166	no
Synandrospadix vermitoxicus (Griseb.) Engl.[1]	Trop	S	G	.	0.19 ± 0.04	61,600*	275	28	16,466 ± 2,106	4,528,160	4.0 ± 0.0	112	40,429	.
Syngonium angustatum Schott	Trop	E	HE	beetle	0.53 ± 0.01	76,335 ± 5,819	158 ± 32	52 ± 4	12,799 ± 4,823	2,111,784 ± 1,287,717	2.0 ± 0.0	104 ± 8	19,868 ± 10,760	no
Syngonium auritum (L.) Schott	Trop	E	HE	beetle	6.22 ± 0.77	27,012 ± 4,052	554 ± 222	91 ± 26	70,541 ± 14,704	39,737,310 ± 18,838,639	1.0 ± 0.0	91 ± 26	42,2107 ± 85,191	no
Syngonium ruizii Schott	Trop	E	HE	beetle	0.78 ± 0.11	47,712*	75 ± 19	353 ± 49	8,090 ± 3,175	594,886 ± 4,729	4.0 ± 0.0	1,413 ± 197	428 ± 70	.
Syngonium schottianum H. Wendl. ex Schott[1]	Trop	E	HE	beetle	10.06 ± 1.32	220,893*	868	173	17,933 ± 3,564	15,853,152	2.0 ± 0.0	346	45,818	no
Typhonium trilobatum (L.) Schott	Trop	S	G	beetle	0.12 ± 0.01	24,429*	.	174 ± 16	.	837,676 ± 189,880	1.0 ± 0.0	174 ± 16	4,783 ± 624	.
Typhonium violifolium Gagnep.	Trop	S	G	beetle	0.19 ± 0.03	17,157*	.	16 ± 2	.	234,064 ± 50,668	1.0 ± 0.0	16 ± 2	15,210 ± 5,293	.
Xanthosoma corpuscatum Schott[1]	Trop	S	G	beetle	0.78 ± 0.08	38,792*	103	76	8,865 ± 737	913,095	16.6 ± 0.9	1,261	723	no
Zamioculcas zamiifolia (Lodd.) Engl.	Trop	S	G	.	2.59 ± 0.24	145,683 ± 43,782	94 ± 14	50 ± 6	5,415 ± 376	513,985 ± 109,275	2.0 ± 0.0	101 ± 12	5,060 ± 444	no
Zomicarpella amazonica Bogner	Trop	E	G	.	0.07 ± 0.01	3,591*	.	8 ± 1	.	273,891 ± 19,952	3.5 ± 0.5	28 ± 1	9,607 ± 466	.

[1]: smaller sampling n ≤ 2 inflorescences.
*: data was obtained from Grayum's (1992) data on pollen diameter (see Materials and methods).
Climatic region was coded: Trop = Tropical, Temp = Temperate. Life form was coded: E = Evergreen, S = Seasonally dormant. Growth mode was coded: T = Terrestrial, H = Helophyte, G = Geophyte, E = epiphyte, HE = Hemiepiphyte, FF = Free floating.

3.3 Results

Table 3.1 summarizes the floral traits, climatic region, life form, growth mode, pollinator type, and capacity for self-pollination for 54 species of Aroids. Among the species studied, 41 had unisexual flower inflorescences and 13 had bisexual flower inflorescences. Thirty-two species were evergreen and all were tropical or subtropical taxa with varying growth modes (8 terrestrial, 4 helophytic, 13 hemi-epiphytic, 5 epiphytic, 1 free floating, and 1 geophytic species). All the 22 seasonally dormant species were geophytes, seven were from temperate regions and 15 were tropical.

3.3.1 Pollen-ovule ratio and self-pollination capacity

Among the 39 species bagged for the self-pollination capacity test, only six set fruits and were therefore considered able to self-pollinate (Table 3.1). A significant difference in P/O (*t*-test: $t_{37} = 2.182$, $P = 0.036$) was found between the group able to self-pollinate (log mean ± s.d. = 9.89 ± 0.55) and that unable to do so (log mean ± s.d. = 8.12 ± 0.34), with the species unable to self-pollinate having lower P/O.

3.3.2 Floral traits with respect to life form

Evergreen taxa had a significantly higher pollen grains volume (*t*-test: $t_{31.49} = 2.872$, $P = 0.007$) and ovule number per inflorescence (*t*-test: $t_{46.37} = 2.183$, $P = 0.034$) than seasonally dormant taxa (Fig. 3.1A, 3.1B). This was mainly due to more numerous male (*t*-test: $t_{34.60} = 3.381$, $P = 0.002$) and female flower (*t*-test: $t_{32.25} = 2.699$, $P = 0.011$) per inflorescence in evergreen taxa. Also, the stigmatic area of a single flower (*t*-test: $t_{33.67} = 2.266$, $P = 0.030$) and of the inflorescence (*t*-test: $t_{29.68} = 3.792$, $P = 0.001$) was larger in evergreen than in seasonally dormant taxa (Fig. 3.1C). Finally, P/O was not significantly different between evergreen and seasonal taxa (*t*-test: $t_{51.89} = 0.243$, $P = 0.809$; Fig. 3.1D).

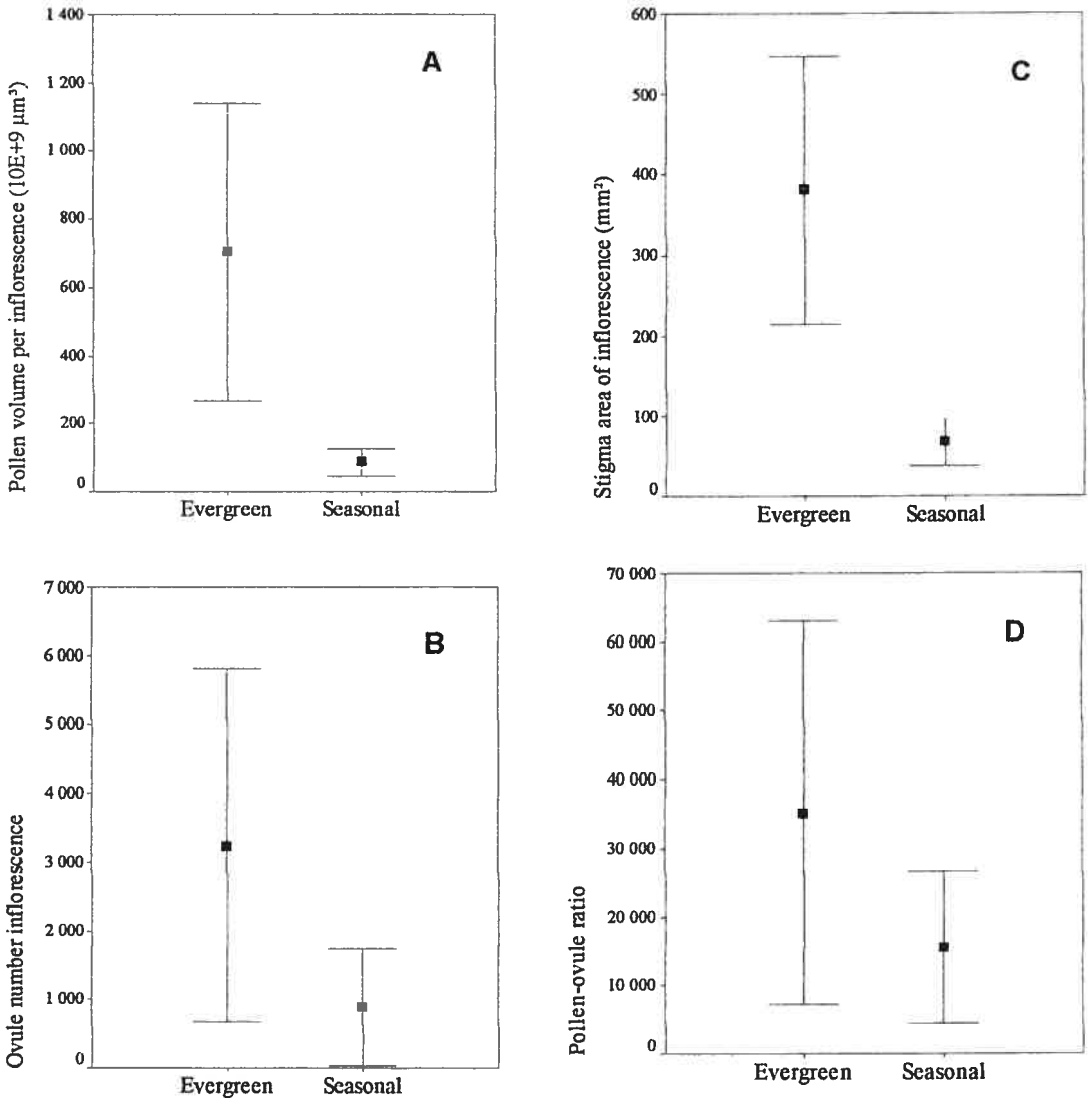

Figure 3.1. Differences in floral traits between evergreen and seasonally dormant taxa in the Aroids studied. Means and 95% confidence intervals for pollen volume per inflorescence (A), ovule number per inflorescence (B), stigmatic area of inflorescence (C) and pollen-ovule ratio (D).

3.3.3 Floral traits with respect to climatic zone

A similar pattern of differences in floral traits was found between tropical and temperate, seasonally dormant geophytic taxa (Fig. 3.2). Because evergreen taxa all come from tropical regions, no analysis was performed. Tropical geophytes (15 species) had higher pollen grain volumes (*t*-test: $t_{14.19} = 2.721$, P = 0.016) and per inflorescence (*t*-test: $t_{15.09} = 4.338$, P = 0.001; Fig. 3.2A), while the number of ovules per inflorescence did not differ (*t*-test: $t_{16.87} = 1.392$, P = 0.182; Fig. 3.2B); they also had a larger stigmatic area per inflorescence (*t*-test:$t_{15.22} = -3.418$, P = 0.004; Fig. 3.2C) than temperate geophytic taxa (7 species). No significant difference was found for the numbers of male (*t*-test: $t_{15} = 1.396$, P = 0.183) or female flowers (*t*-test: $t_{20} = 1.543$, P = 0.138) nor for the number of ovules per inflorescence (*t*-test: $t_{20} = 1.022$, P = 0.319; Fig. 3.2B), nor for P/O (*t*-test: $t_{19.44} = -0.513$, P = 0.614; Fig. 3.2D) between tropical and temperate geophytes.

No significant difference in any of the floral traits was found between different growth modes in the Aroid species studied, suggesting that there is no clear relationship between the measured floral traits and the growth modes. It is noteworthy that growth modes were not independent from climatic zones and life forms, as in our sampling epiphytes and hemi-epiphytes are evergreen and tropical taxa, terrestrials and geophytes are mainly seasonally dormant and temperate taxa. More data are necessary to further study the influence of these characters on floral traits.

3.3.4 Floral traits with respect to pollinator type

The stepwise backward discriminate analysis retained five variables, even if a few other variables showed significant differences between pollinator types (Table 3.2): pollen volume and number per inflorescence, number of female flowers, sexual type of the flower, and life form. The jackknifed classification matrix resulted in 78% of the data being correctly classified (75% for beetle pollination, 71% for fly pollination, and 100% for bee pollination). The three pollinator groups are distinct with no overlapping (see Fig. 3.3), but some species were misclassified (see below).

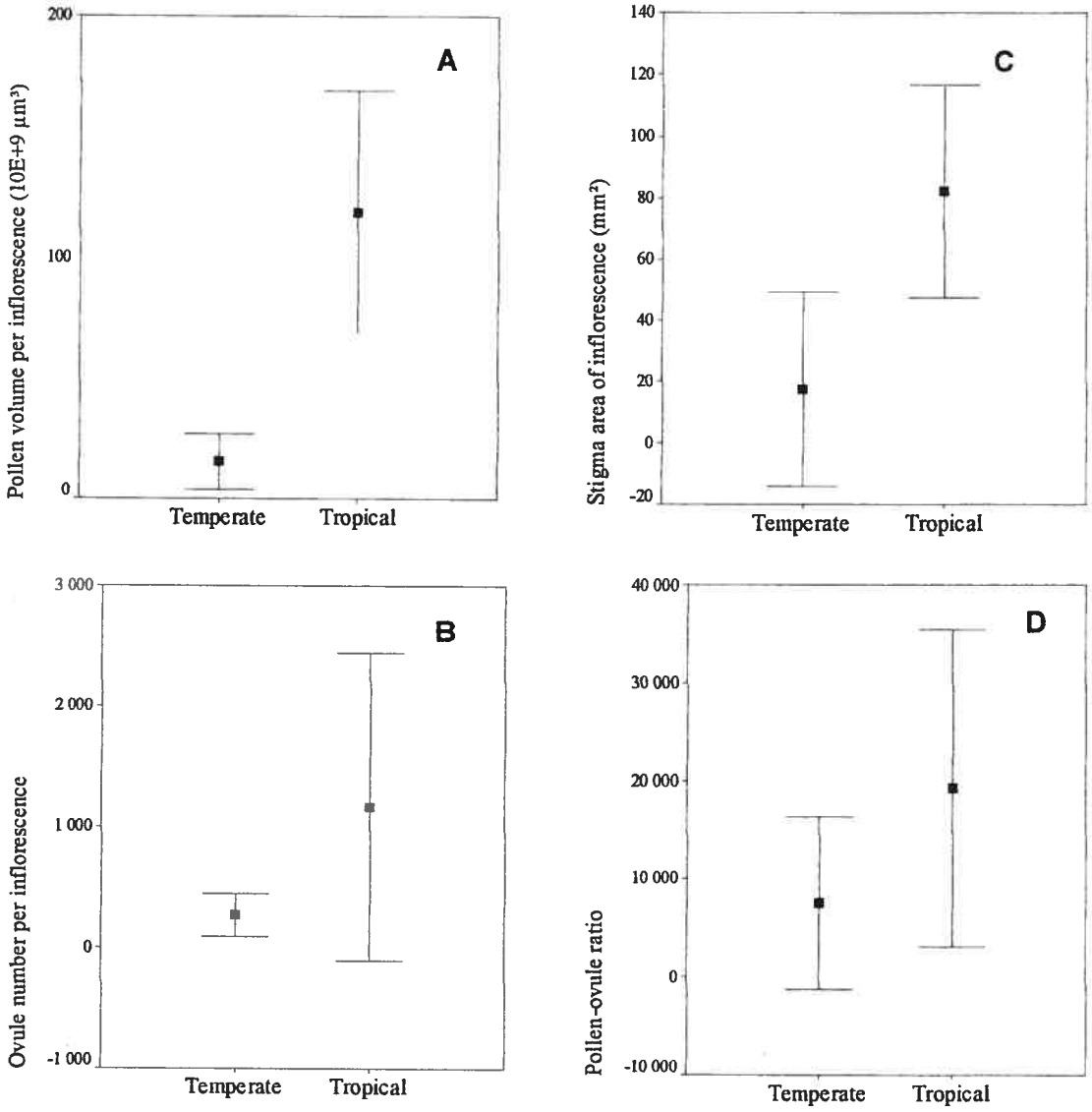

Figure 3.2. Differences among floral traits between temperate and tropical seasonally dormant Aroids studied. Means and 95%confidence intervals for pollen volume per inflorescence (A), ovule number per inflorescence (B), stigmatic area of inflorescence (C) and pollen-ovule ratio (D).

The bee-pollinated group is characterised by species with bisexual flowers, an evergreen life form type, and a high number of female-flowers (Table 3.2). Beetle-pollinated species are characterised by a high pollen volume per inflorescence, a medium number of female flowers, and almost always unisexual flowers (Table 3.2). Fly pollination is associated with species with low female flower numbers and a relatively low number of pollen grains per inflorescence (Table 3.2).

Now we shall consider species classification according to pollinator type. Eight of 41 species were misclassified. Four beetle-pollinated species were classified among fly-pollinated species, namely: *Typhonium trilobatum* and *T. violifolium*, *Caladium bicolor* and *Xanthosoma corpuscatum* (Fig. 3.3). Conversely, the three *Alocasia* fly-pollinated species were classified among beetle-pollinated species (Fig. 3.3). The fly-pollinated *Dracontium podophyllum* was classified as bee-pollinated, close to *Anaphyllopsis americana*, an "unknown taxon", that clearly is intermediate between the fly- and bee- pollinated groups (Fig. 3.3). The other species with unknown pollinators were classified as follows: the two *Stenospermation* species are considered to be bee-pollinated; the two *Homalomena* species, *Pistia stratiotes* and *Zomicarpella amazonica* appear beetle-pollinated; and *Synandrospadix vermitoxicus*, *Pseudodracontium fallay*, the two *Gonatopus* species, and *Zamioculcas zamiifolia* may be fly-pollinated (Fig. 3.3). The two *Gonatopus* species appear to be marginally separate (like *Zamioculcas zamiifolia*) from the other fly-pollinated species (Fig. 3.3).

The P/O was much higher in beetle-pollinated species (mean: 51,657) compared to fly- (mean: 9,807) and bee-pollinated (mean: 10,605) species, but these differences were not significant (Table 3.2). Pollen grain volume in relation to pollinator class displayed the same kind of difference, with pollen volume of beetle-pollinated species being significantly larger (mean: 123,595 μm^3) than the fly- (mean: 19,973 μm^3) and bee-pollinated (mean: 15,145 μm^3) species (Table 3.2). In the same way, the flower stigmatic surface was significantly larger in beetle-pollinated (mean: 3.06 mm^2) than in fly- (mean: 0.85 mm^2) or bee-pollinated (mean: 0.65 mm^2) taxa (Table 3.2).

Table 3.2. Group means (± standard error) used in the discriminate analysis for the different floral characters according to type of pollinator. The level of significance of the ANOVA results is coded as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Group means with different letters are significantly different (post-hoc test $P < 0.05$).

Floral character	Beetle pollination (N = 20)	Fly pollination (N = 14)	Bee pollination (N = 7)	Statistic values $F_{2,38}$ =
Flower stigma area	3.06 ± 0.87^{a}	0.85 ± 0.23^{b}	0.65 ± 0.09^{b}	3.44*
Stigma area per inflorescence	431 ± 115^{a}	76.4 ± 20.3^{b}	453 ± 137^{a}	3.84*
Mean pollen grain volume	$123{,}595 \pm 35{,}614^{a}$	$19{,}973 \pm 3{,}674^{b}$	$15{,}144 \pm 6{,}467^{b}$	4.43*
Pollen volume per inflorescence	$10 \pm 3.24 \times 10^{11\,a}$	$1.04 \pm 0.34 \times 10^{11\,b}$	$2.22 \pm 1.03 \times 10^{11\,b}$	3.59*
Pollen number per inflorescence	$1.2 \pm 0.5 \times 10^{7}$	$0.48 \pm 0.15 \times 10^{7}$	$2.39 \pm 1.12 \times 10^{7}$	2.13
Ovule number per flower	8.89 ± 2.67	9.59 ± 3.14	5.28 ± 1.34	0.38
Ovule number per inflorescence	$3{,}719 \pm 1962$	$1{,}286 \pm 620$	$1{,}903 \pm 548$	0.64
Pollen-ovule ratio	$51{,}657 \pm 21{,}224$	$9{,}807 \pm 3{,}977$	$10{,}605 \pm 2{,}695$	1.93
Female flower number	252 ± 74^{a}	103 ± 16^{a}	853 ± 321^{b}	7.99**
Flower sexual type [1]	1.95 ± 0.05^{a}	1.93 ± 0.07^{a}	1 ± 0^{b}	52.1***
Growth mode [2]	2.8 ± 0.28^{a}	1.5 ± 0.23^{b}	4 ± 0.38^{c}	13.3***
Life form [3]	1.2 ± 0.09^{a}	1.79 ± 0.11^{b}	1 ± 0^{a}	13.5***

[1] The flower sexual type was coded: 1 = bisexual, 2 = unisexual.

[2] The growth mode was coded: 1 = geophyte, 2 = helophyte, 3 = ground, 4 = hemiepiphyte, 5 = epiphyte.

[3] The life form was coded: 1 = evergreen, 2 = seasonally dormant.

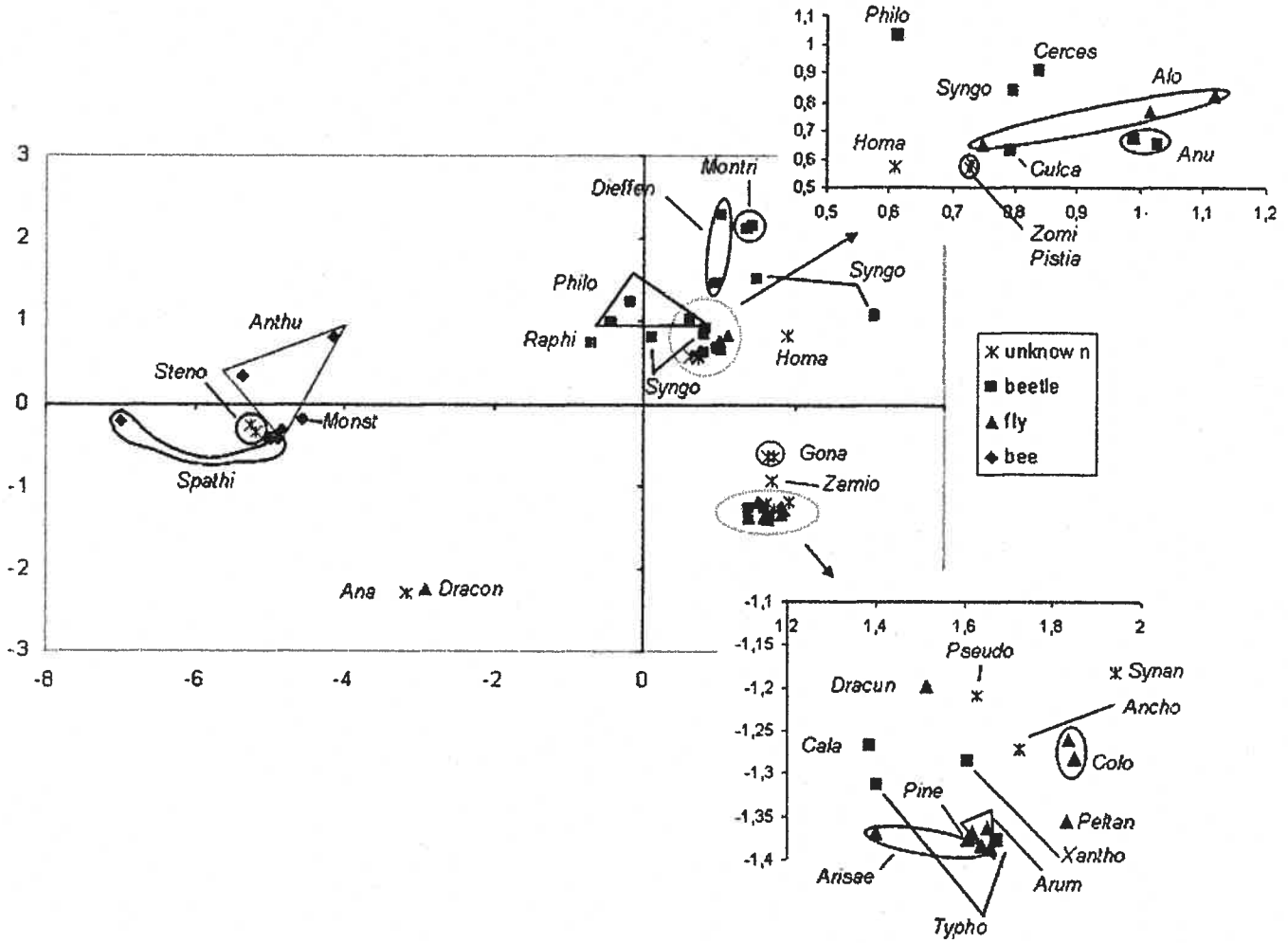

Figure 3.3. Graphic result of the discriminate analysis with two point clouds detailed (bottom and top). Species from the same genera are grouped together. Genera names are coded by the first 3-6 letters of their name (see Table 1).

3.4 Discussion

3.4.1 Pollen-ovule ratio and breeding system

Aroids seem to be a family with inflorescences that are adapted for out-breeding. Among all the species studied, only six showed an ability to self-pollinate. This result is confirmed by the fact that Aroid inflorescences are dichogamous, with stigmas receptive before pollen release (Mayo et al. 1997). Self-pollination in some Aroids could be a mechanism for eventually ensuring fertilisation when pollinator frequency is limiting. Also, genera such as *Alocasia* (Yafuso 1993; Miyake and Yafuso 2003; pers. observ.), *Dieffenbachia* (Young 1986; Beath 1999) and *Montrichardia* (Gibernau et al. 2003), which are able to self-pollinate, present distinctive traits such as thermogenesis, odour production, nectar production and even movements of the spathe during the flowering cycle to attract entomophilous pollinators and ensure pollination. Because self-pollination is most likely a secondary mechanism in the Aroid family, the assumption that the P/O reflects the breeding or the compatibility system is not found to be true in this family. As suggested by Chouteau et al. (2006), in Araceae, a higher P/O is most likely due to a less efficient pollination mechanism and, therefore, to ensure seed production, the plant could have evolved self-pollination mechanisms.

3.4.2 Floral traits with respect to life forms

Little is known about floral traits with respect to life form. Jürgens et al. (2002) found significant differences between perennial and annual *Caryophylloideae* in terms of various floral traits. Perennial flowers had higher numbers of pollen grains and ovules, and higher P/Os than annual flowers. In the Aroids studied, there were significant differences between seasonally dormant (perennial) and evergreen taxa. Evergreen taxa may invest more resources in the male reproductive function by producing a higher number of male flowers and larger pollen volumes than seasonally dormant taxa (which are all geophytic). Ovule numbers per inflorescence were also higher in evergreen taxa.

Two non-exclusive, main hypotheses could explain these differences between evergreen and seasonally dormant taxa:

1) Evergreen taxa are able to photosynthesize all year around and therefore can acquire more resources to be invested in male and female functions compared to seasonally dormant taxa.

2) As seasonally dormant taxa produce very few inflorescences each year (generally one per growing season), they should have more efficient pollen transfer mechanisms in order to achieve pollination. The stigmatic area per flower and per inflorescence is much smaller in seasonally dormant than in evergreen taxa, which may support the hypothesis of higher pollination efficiency (Cruden 2000).

3.4.3 Floral traits with respect to climatic zones

Among the seasonally dormant species studied, the temperate taxa, which are true perennials, had fewer pollen grains volume per inflorescence (mostly due to smaller pollen volumes) than their related tropical taxa. The mean pollen grain number per flower of the temperate (perennial) group is consistent with data published for *Caryophylloideae* (Jürgens et al. 2002). On the other hand, we found lower ovule numbers per flower and thus a higher P/O than for *Caryophylloideae* even if both perennial *Araceae* and *Caryophylloideae* are xenogamous (Jürgens et al. 2002). In the same way, differences between evergreen and seasonally dormant taxa, with lower gamete production and smaller stigma area per inflorescence for temperate (perennial) compared to tropical taxa, might result from a greater efficiency in pollen transfer (Cruden 1977, 2000) due to the harsh climatic conditions and the shortness of the flowering season at temperate latitudes. Among seasonally dormant taxa, all temperate species are known to be pollinated by flies while tropical species are pollinated by beetles and bees.

3.4.4 Floral traits with respect to pollinator types

The selective pressure of the different types of pollinators has led to a convergence of floral traits adapted to functional groups according to pollinator; i.e., pollination syndromes (reviewed in Fenster et al. 2004). A few studies dealing with the subject

have focused on the P/O to explain the difference in pollination efficiency of the different types of pollinators. It was found that in a tropical cloud forest community the P/O was higher in beetle- and fly-pollinated species compared to bee-, bird- and bat-pollinated species (Ramirez and Serez 1994). On the other hand, no difference in P/O ratios was found among the species pollinated during the day (Lepidoptera, Hymenoptera and Diptera) and those pollinated at night (Lepidoptera) in *Caryophylloideae* (Jürgens et al. 2002). Another floral trait that has been studied in relation to pollinator is pollen grain size, which is believed to be optimal for collection and transportation by the pollinator without being lost (Wodehouse 1935; Harder 1998; Cruden 2000). Our results show clearly that the P/Os of bee- and fly-pollinated species were similar, which is consistent with the literature (Cruden 2000) suggesting that bees and flies have similar pollination efficiencies. The much higher P/O of beetle-pollinated species compared to other types of pollinators lends credence to the hypothesis that beetles may be less effective pollinators. Pollen size was also much higher for beetle-pollinated species compared to the other classes of pollinators, which reinforces the hypothesis of pollen size being related to pollinator in order to maximise its transportation. The much higher P/O and pollen grain volume of beetle-pollinated species suggest a much higher investment in pollen production by beetle-pollinated plants. Many beetles eat pollen which is in fact part of the plant's rewards for its pollinators (Bernhardt 2000). Therefore, plants with pollen rewards would tend to have a higher pollen production to counterbalance the disadvantage of pollen loss by direct consumption in beetle pollinations. Even if bees are known to harvest a pollen "reward", the lower P/O of this group could be explained by the bees being more efficient pollinators (Webb 1984). Also, the bee-pollinated Aroids studied all provide other types of rewards that could be favoured by the pollinator, such as the stigmatic secretions and sweet scents that could be collected from *Anthurium* (Croat 1980; Schwerdtfeger et al. 2002) and *Spathiphyllum* (Lewis et al. 1988; Gerlach and Schill 1991; Yong 1993), or the resin known to be harvested for nest construction from *Monstera* (Ramirez and Gómez 1978).

3.4.5 Conclusion

Floral traits appear correlated to the type of pollinator (i.e., pollination syndromes, Fenster et al. 2004), life form, climatic conditions and self-pollination capacity, while growth mode has no apparent influence. The floral characters retained for the characterisation of the pollinator type are: pollen volume per inflorescence, pollen number per inflorescence, number of female flowers, sexual type of the flower and life form. The number of male flowers could also be an important character, as suggested by the two male characters retained in the discriminate analysis: pollen number and volume. This aspect was not included in the analysis since it was not available for all species studied. Further data are needed to verify this hypothesis. These results provide new insight into and understanding of specialised floral architecture in relation to pollinator type and could help in identifying the pollination syndrome for a specific species. Also, life form and climatic region are factors affecting investment in male and female functions in Aroids. Temperate and seasonally dormant species had lower gamete productions and smaller stigma areas, suggesting more efficient pollination mechanisms in comparison to tropical and evergreen species. These differences could be attributed to the length and condition of the growing season, which would directly influence the energy pool of plants allocated to inflorescence production. The less energy plants have to invest in an inflorescence, the more efficient the pollination system is. Finally, in aroids, pollen-ovule ratio in relationship with breeding system behave contrary to what has been found in other plant groups, suggesting it might not be linked to breeding system. It seems more likely that the pollen-ovule ratio is a measure of pollen transfer efficiency.

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Chapitre 4

Conclusion générale

Cette maîtrise a permis d'étudier les relations quantitatives existant entre les caractères floraux chez les Aracées dans 2 types d'inflorescence distinctes, soient les inflorescences à fleurs unisexuées (e.g *Philodendron*) et à fleurs bisexuées (e.g *Anthurium*), et de comprendre la relation entre certains facteurs externes au système reproductif et la morphologie de l'inflorescence.

Dans un premier temps, l'étude des relations quantitatives entre les caractères floraux a permis de déterminer que, dans les genres *Anthurium* et *Philodendron*, la profondeur du stigmate ainsi que la longueur du style ne sont pas liés à la taille du pollen comme cela a été trouvé dans d'autres groupes (Baker & Baker 1982; Plitmann & Levin 1983; Cruden & Lyon 1985; William & 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 & Harder 2001; Aguilar et al. 2002; Yang & Guo 2004). Cette situation pourrait s'expliquer par le fait que, dans ces genres, le grain de pollen possède un volume (réserve énergétique) supérieur à celui qui est nécessaire à la croissance du tube pollinique jusqu'à l'ovule. Ce volume en surplus pourrait refléter l'influence d'autres facteurs comme le type de pollinisateur (Taylor & Levin 1975; Lee 1978; Muller 1979; Harder 1998), la protection du grain contre le climat humide tropical (Kerner 1897; Cruden 2000) ou encore la largeur (Plitmann & Levin 1983) et la vitesse de croissance du tube (Ottaviano et al. 1983; Lord & Eckard 1984).

La capacité d'acquisition des ressources (taux d'accumulation des éléments essentiel à la croissance représenté entre autre par la taille adulte de la plante), spécifique à chaque espèce, influence fortement l'investissement de l'espèce dans ses structures reproductives. Ainsi, plus une espèce aura une capacité importante d'acquisition des ressources, plus son inflorescence possèdera un grand nombre de

fleurs et plus la quantité de pollen par fleur sera importante. De fait, le compromis entre la taille et le nombre de grains de pollen (Mione & Anderson 1992; Knudsen & Olesen 1993; Vonhof & Harder 1995; Yuang & Guo 2004) dans les 2 genres étudiés peut être relégué au second plan devant l'importance de la capacité d'acquisition des ressources sur le nombre de grains de pollen. Dans le genre *Philodendron*, le compromis (relation négative) entre la taille et le nombre de grains de pollen ressort clairement, car la capacité d'acquisition des ressources entre les espèces est relativement similaire et, influence donc moindrement le nombre de grains de pollen. Par contre, les espèces d'*Anthurium* étudiées montrent une grande variation dans la capacité d'acquisition des ressources, ce qui se reflète par l'absence de corrélation entre la taille et le nombre de grains de pollen. Ainsi, les gènes contrôlant l'acquisition des ressources peuvent camoufler les corrélations génétiques entre les entités en compétition comme la taille et le nombre des grains de pollen (Young et al. 1994; Fenster & Carr 1997).

Une relation fonctionnelle positive entre la surface stigmatique et la production de pollen (quantité et volume) a été mise en évidence au niveau de l'inflorescence. Cette relation, établie pour la première fois chez les angiospermes, dépend aussi du cycle floral de la plante (i.e. l'agencement temporel de la réceptivité des stigmates et du relâchement du pollen ainsi que de la proportion de chaque fonction sexuelle active à un moment donné). Ainsi, dans le genre *Philodendron*, plus la surface stigmatique de l'inflorescence est grande, plus celle-ci produira une grande quantité de pollen (nombre et/ou taille des grains) ce qui reflète bien le cycle floral du genre (i.e. tous les stigmates réceptifs simultanément suivis de toutes les étamines relâchant leur pollen au même moment). Chez *Anthurium*, qui a un cycle floral différent du *Philodendron*, la relation fonctionnelle positive entre la surface stigmatique et la quantité de pollen est présente, mais à des niveaux fonctionnels (fleur vs. inflorescence) différents. Chez *Anthurium*, la surface stigmatique de l'inflorescence augmente en relation avec la quantité de pollen de chaque fleur, ce qui reflète le cycle floral du genre (i.e. tous les stigmates réceptifs simultanément suivis de quelques fleurs relâchant leur pollen chaque jour sur une période de plusieurs semaines). Cette relation fonctionnelle positive entre la surface stigmatique de l'inflorescence et la

quantité de pollen liée avec le cycle floral permettrait à la plante d'optimiser la quantité de pollen relâché par l'inflorescence en fonction de la surface stigmatique réceptive chez une autre inflorescence, à un moment donné, et d'augmenter ainsi son efficacité de pollinisation. Enfin, les inflorescences des genres *Philodendron* et *Anthurium* sont des structures complexes et intégrées dans lesquelles la majorité des traits floraux sont liés afin d'optimiser l'inflorescence comme étant la principale unité de pollinisation au lieu d'une fleur individuelle.

Dans un deuxième temps, l'étude du ratio pollen-ovule au niveau du genre et au niveau de la famille a permis de déterminer que cette mesure n'est pas adéquate pour déterminer le système de reproduction chez les Aracées. Normalement, plus une plante a un P/O bas, plus elle sera autogame (auto-compatible), et plus son P/O sera élevé, plus la plante sera xenogame (Cruden 1977). Dans la famille des Aracées, on trouve une tendance contraire à celle trouvée chez les autres familles de plantes : les espèces auto-compatibles ont un P/O plus élevé que les espèces xenogames. Il est suggéré que chez les Aracées, le P/O serait un indicateur de la complexité et de l'efficacité des mécanismes de pollinisation et non du système de reproduction (Chouteau et al. 2006). Ainsi, les espèces auto-compatibles étudiées avaient toutes des adaptations propres à la pollinisation par les insectes (thermogenèse, odeur, nectar, chambre florale), ainsi qu'un cycle floral dichogamique empêchant normalement l'auto-fécondation. Ces attributs suggèrent que l'auto-compatibilité chez les Aracées permettrait à la plante d'assurer la fructification lorsque la pollinisation par les insectes a échoué; il s'agirait donc d'un mécanisme de remplacement.

Finalement, ce travail a permis de mieux comprendre comment certains facteurs externes à l'inflorescence influencent l'architecture florale. La forme de vie ainsi que la zone climatique semblent influencer grandement l'investissement de la plante dans ses structures reproductives. Ainsi, les espèces saisonnières, autant tropicales que tempérées investissent moins de ressources dans l'inflorescence que les espèces à feuilles persistantes. C'est-à-dire qu'elles auront peu de fleurs, peu d'ovules, peu de

grains de pollen et de plus petites surfaces stigmatiques comparativement aux espèces à feuilles persistantes. Le même schéma de variation se retrouve entre les espèces tropicales et les espèces tempérées, ces dernières investissant moins de ressources dans leur inflorescence. Ces différences pourraient être attribuables à la durée et à la rigueur des saisons de croissance qui influenceraient l'accumulation des réserves et leur investissement dans l'inflorescence. La période de croissance est moins longue pour les plantes saisonnières que pour les plantes à feuilles persistantes, et les conditions de croissance sont plus dures sous les latitudes tempérées que tropicales. Ces différences d'investissement dans les structures reproductives pourraient aussi s'expliquer par l'efficacité de pollinisation qui est plus grande et demande moins de ressources à la plante (Cruden 2000). Ainsi, plus les contraintes liées à la saison de croissance seraient élevées, plus l'efficacité de pollinisation des espèces concernées serait grande afin d'assurer la reproduction.

Chez les Aracées, les caractéristiques de la saison de croissance (climat, durée) ainsi que la forme de vie de l'espèce influenceraient les ressources disponibles pour l'inflorescence et l'efficacité du transfert du pollen. Plus la croissance de la plante est difficile et limitée dans le temps, moins elle aura de ressources à investir dans l'inflorescence et plus sa pollinisation sera efficace afin de maximiser sa fructification.

Les Aracées sont majoritairement pollinisées par 3 groupes de pollinisateurs : les coléoptères, les diptères et les hyménoptères (Gibernau 2003). L'étude au niveau de la famille des Aracées a révélé que certains traits floraux sont directement liés au type de pollinisateur. Ainsi, les différences de ratio pollen-ovule expliquent que les coléoptères (associé a des P/O hauts) sont des pollinisateurs moins efficaces que les diptères et les hyménoptères (associé a des P/O bas) puisque la plante a besoin d'un nombre de grains de pollen beaucoup plus important pour parvenir à féconder chaque ovule (Cruden 1977, 2000). Un autre caractère floral lié au type de pollinisateur est la taille des grains de pollen. La taille du pollen serait liée au type de pollinisateur afin de maximiser son transport (Wodehouse 1935; Harder 1998; Cruden 2000). Ainsi, les Aracées pollinisées par les coléoptères ont des grains de pollen beaucoup plus gros que les espèces pollinisées par les diptères et les hyménoptères. Enfin, nos résultats

ont permis de mieux comprendre la spécialisation de l'architecture florale en fonction du type de pollinisateur, ce qui pourrait permettre d'identifier les syndromes de pollinisation pour une espèce spécifique. Les principaux traits floraux identifiés chez les Aracées permettant de catégoriser les pollinisateurs sont les suivants : le volume de pollen et le nombre de grains de pollen par inflorescence, étroitement reliés, le nombre de fleurs femelles, le type sexuel de la fleur (unisexué ou bisexué) et la forme de vie de la plante (espèce saisonnière et espèce à feuilles persistantes).

Les inflorescences spadiciformes comme celles que l'on trouve dans la famille des Aracées ont une architecture complexe influencée par les différentes relations entre les traits floraux et les facteurs écologiques afin d'optimiser le transfert du pollen. Mon projet de maîtrise a permis d'établir un modèle expliquant comment un changement dans un caractère floral influence les autres caractères. Aussi, l'étude des facteurs externes aux structures reproductives a permis d'identifier et de comprendre comment la plante adapte son inflorescence aux différentes contraintes environnementales afin de maximiser la pollinisation. Enfin, une perspective future dans la compréhension de l'architecture florale serait de cartographier les différents caractères floraux sur la phylogénie au niveau des espèces et des genres. Une telle étude permettrait entre autres de mieux comprendre les variations qui existent entre les caractères floraux dans un taxon donné.

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Annexes

Annexe I Revue de littérature concernant les pollinisateurs/visiteurs des *Araceae* (Gibernau, 2003)

Subfamily / tribe	Genera	Bees	Beetles	Flies	Others
Orontioideae	*Lysichiton*		Staphylinidae	Anthomyiidae Lauxaniidae Various flies	
Orontioideae	*Symplocarpus*	"hive bees"	Staphylinidae	Drosophilidae Psychodidae Chloropidae Ceratopogonidae Chironomidae Simuliidae Cecidomyiidae Muscidae	Wind (self-pollination) Various invertebrates
Pothoideae / Anthurieae	*Anthurium*	Euglossine	Curculionidae Staphylinidae		Self-pollination (wind?) Hummingbird
Monsteroideae / Monstereae	*Monstera*	Trigone	 Scarabaeidae		
Monsteroideae / Monstereae	*Rhaphidophora*		Scarabaeidae		
Monsteroideae / Monstereae	*Rhodospatha*		"beetles"		
Monsteroideae / Spathiphylleae	*Spathiphyllum*	Euglossine Trigone Halictidae	Chrysomelidae	Drosophilidae Tephritidae	
Lasioideae	*Cyrtosperma*		Nitidulidae		
Lasioideae	*Dracontium*			"myiophilous"	
Lasioideae	*Urospatha*		Nitidulidae		
Calloideae	*Calla*			"small flies"	
Aroideae / Dieffenbachieae	*Dieffenbachia*		Scarabaeidae		
Aroideae / Philodendreae	*Philodendron*		Scarabaeidae		
Aroideae / Homalomeneae	*Furtadoa*			Drosophilidae	
Aroideae / Homalomeneae	*Homalomena*		Scarabaeidae (neotropics) Chrysomelidae In Malaya	 Drosophilidae (Asia)	
Aroideae /	*Montrichardia*	"bees"			

Montrichardieae			Scarabaeidae		
Aroideae / Anubieae	*Anubias*		Nitidulidae Scarabaeidae		
Aroideae / Schismatoglottideae	*Aridarum*		Nitidulidae		
Aroideae / Schismatoglottideae	*Piptospatha*		Staphylinidae		
Aroideae / Schismatoglottideae	*Schismatoglottis*			Drosophilidae	
Aroideae / Caladieae	*Caladium*		Scarabaeidae		
Aroideae / Caladieae	*Chlorospatha*		Staphylinidae		
Aroideae / Caladieae	*Syngonium*		Scarabaeidae		
Aroideae / Caladieae	*Xanthosoma*	Euglossine	Scarabaeidae (Nitidulidae)	Drosophilidae	
Aroideae / Thomsonieae	*Amorphophallus*	Trigone	Asilidae Cetoniidae Nitidulidae Scarabaeidae Silphidae Staphylinidae Hybosoridae Histeridae	Calliphoridae Platystomatidae	
Aroideae / Aglaonemateae	*Aglaonema*			Drosophilidae	
Aroideae / Zantedeschieae	*Zantedeschia*		Scarabaeidae Scydmaenidae		
Aroideae / Nephthytideae	*Anchomanes*	Trigone	Nitidulidae	Lonchaeidae	
Aroideae / Nephthytideae	*Nephthytis*		Nitidulidae	Drosophilidae	
Aroideae / Nephthytideae	*Pseudohydrosme*		Scaphidiidae Staphylinidae	Choridae Sphaeroceridae	
Aroideae / Culcasieae	*Cercestis*		Nitidulidae	Drosophilidae	
Aroideae / Culcasieae	*Culcasia*		Nitidulidae	Drosophilidae	
Aroideae / Colocasieae	*Alocasia*		Nitidulidae Scarabaeidae Staphylinidae	Drosophilidae Anthomyiidae Neurochaetidae	
Aroideae / Colocasieae	*Colocasia*			Drosophilidae	
Aroideae / Cryptocoryneae	*Cryptocoryne*			Centropogonidae Ephydridae Phoridae	
Aroideae / Peltandreae	*Peltandra*			Chloropidae Syrphidae	
Aroideae / Arisamateae	*Arisaema*			Sciaridae Mycetophilidae Dolichopodidae Phoridae Keroplatidae	Thrips
Aroideae /	*Pinellia*			"fungus gnat"	

Arisamateae				Ceratopogonidae	
Aroideae / Arisareae	*Arisarum*			Mycetophilidae Sciaridae Psychodidae Chironomidae Drosophilidae	
Aroideae / Ambrosineae	*Ambrosina*			"flies"	Mites?
Aroideae / Pistieae	*Pistia*		"Curculionids"		
Aroideae / Areae	*Arum*			Psychodidae Centropogonidae Ceratopogonidae Sphaeroceridae Sciaridae Simuliidae	
Aroideae / Areae	*Biarum*		Scarabaeidae Staphylinidae	Flies? Sepsidae Empididae Drosophilidae	
Aroideae / Areae	*Dracunculus*		Staphylinidae Dermestidae Histeridae Sylphidae	Calliphoridae Muscidae Sarcophagidae	
Aroideae / Areae	*Eminium*		Scarabaeidae Staphylinidae	Sphaeroceridae Sepsidae Ortidae Muscidae Ulidiidae Heleomyzidae Ephydridae	
Aroideae / Areae	*Helicodiceros*			Calliphoridae	
Aroideae / Areae	*Sauromatum*		Scarabaeidae Bruchidae	Sepsidae Muscidae Otitidae Sarcophagidae Calliphoridae	
Aroideae / Areae	*Theriophonum*			Ceratopogonidae	
Aroideae / Areae	*Typhonium*		Scarabaeidae Staphylinidae Nitidulidae Ptiliidae Scydmaenidae		

Annexe II Location collection and list of voucher specimens used in Chapter 2

Specie	Location (Identification number)	Voucher number (Herbarium)
A. acaule Schott	Montreal Botanical Garden (No 2240-1957)	*Barabé 223* (MT)
A. barclayanum Engl.	Montreal Botanical Garden (No 3375-1988)	*Chouteau 3* (MT)
A. clavigerum Poepp.	Montreal Botanical Garden (No 2150-1952)	*Barabé 221* (MT)
A. crystalinum Linden & André	Montreal Botanical Garden (No 1645-1942)	*Barabé 241* (MT)
A. truncicolum Engl. *(divaricatum)*	Montreal Botanical Garden (No 2097-1956)	*Chouteau 2* (MT)
A. fendleri Schott	Montreal Botanical Garden (No 2317-1953; No 2727-1951)	*Barabé 220* (MT)
A. harrisii (Grah.) G. Don	Montreal Botanical Garden (No 635-1942)	*Barabé 253* (MT)
A. jenmanii Engl.	Montreal Botanical Garden (No 3554-1987; No 908-1999)	*Barabé 248* (MT)
A. longistamineum Engl.	Montreal Botanical Garden (No 1554-1958; No 3038-1959)	*Barabé 233* (MT)
A. ornatum Schott	Montreal Botanical Garden (No 1176-1956)	*Barabé 237* (MT)
A. pedatoradiatum Schott	Montreal Biodôme (No 7074-1998)	*Barabé 240* (MT)
A. polyrhizum (polyrhizon) K. Koch & Augustin	Montreal Botanical Garden (No 2288-1951; No 1868-1948)	*Barabé 226* (MT)
A. polyschistum R. E. Schult. & Idrobo	Montreal Botanical Garden (No 3037-1959)	*Barabé 182* (MT)
A. radicans K. Koch & A. Haage	Montreal Biodôme (No 7165-1995)	*Barabé 185* (MT)
A. salviniae Hemsl.	Montreal Botanical Garden (No 2042-1968)	*Chouteau 4* (MT)
A. schlechtendalii ssp. schlechtendalii Kunth	Montreal Botanical Garden (No 2463-1954)	*Barabé 219* (MT)
A. spectabile Herincq	Montreal Botanical Garden (No 2044-1968)	*Barabé 234* (MT)
A. fatoense K. Krause	Montreal Biodôme (No 7024-1998)	*Chouteau 1* (MT)
A. trinerve Miq.	Montreal Botanical Garden (No 979-2004)	*Barabé 243* (MT)
A. upalahense Croat & R. A. Baker	Montreal Botanical Garden (No 2061-1968)	*Barabé 245* (MT)
P. acutatum Schott	French Guyana	*Chouteau 5* (MT)
P. bipinnatifidum Schott	Montreal Botanical Garden (No 1856-1955; No 2875-1982)	*Gauthier 4* (MT)
P. cannifolium (Dryander ex Sims) G. Don	Montreal Botanical Garden (No 2424-1946)	*Chouteau 6* (MT)
P. distantlobum K. Krause	Montreal Botanical Garden (No 2601-1959)	*Gauthier 12* (MT)
P. erubescens C. Koch & Augustin	Montreal Botanical Garden (No 2798-1950; No 1892-1957)	*Chouteau 12* (MT)
P. glaziovii Hook. f.	Montreal Biodôme (No 7014-1998)	*Chouteau 13* (MT)
P. gloriosum Andre	Montreal Biodôme (No 7168-1995)	*Chouteau 7* (MT)
P. grandifolium Schott	Montreal Botanical Garden (No 3549-1987; No 2415-1992)	*Gauthier 15* (MT)
P. insigne Schott	Montreal Botanical Garden (No 168-2000; No 2909-2001)	*Barabé 75* (MT)
P. linnaei Kunth	Montreal Botanical Garden (No 2228-1986; No 2221-1986)	*Barabé 76* (MT)
P. melanochrysum Linden & Andre	Montreal Botanical Garden (No 83-2003)	*Chouteau 8* (MT)
P. megalophyllum Schott	Montreal Botanical Garden (No 194-1997)	*Chouteau 9* (MT)
P. melinonii Brongn. ex Regel	French Guyana	*Gauthier 13* (MT)
P. microstictum Standley & L. O. Williams	Montreal Botanical Garden (No 2122-1951)	*Chouteau 14* (MT)
P. Sp. aff. moonenii	Montreal Botanical Garden (No 2032-1997)	*Gauthier 16* (MT)
P. ornatum Schott	Montreal Botanical Garden (No 1511-1996)	*Chouteau 11* (MT)
P. pedatum Kunth	French Guyana	*Barabé 259* (MT)
P. radiatum Schott	Montreal Botanical Garden (No 2740-1951)	*Gauthier 6* (MT)
P. ruizii Schott	Montreal Botanical Garden (No 1638-1953)	*Chouteau 10* (MT)
P. solimoesense A. C. Smith	French Guyana	*Barabé 203* (MT)
P. squamiferum Poepp. & Endl.	Montreal Botanical Garden (No 2365-1992; No 2201-1986)	*Barabé 136* (MT)
P. talamancae Engl.	Montreal Botanical Garden (No 2576-1954)	*Gauthier 18* (MT)
P. tripartitum Schott	Montreal Botanical Garden (No 2347-1992)	*Gauthier 3* (MT)

Annexe III Location collection and list of voucher specimens used in Chapter 3

Species	Location (Identification number)	Voucher number (Herbarium)
Alocasia sp.	Missouri Botanical Garden (No 90145)	*Croat 90145* (UMO)
Alocasia macrorrhizos (L.) G. Don	Montreal Botanical Garden (No 1774-1956)	*Chouteau 15* (MT)
Alocasia portei Schott	Montreal Botanical Garden (No 1643-1953)	*Chouteau 16* (MT)
Anaphyllopsis americana (Engl.) A. Hay	French Guiana	*Barabé 258* (MT)
Anchomanes difformis (Blume) Engl.	Missouri Botanical Garden (No Knecht.1)	*Knecht 1* (UMO)
Anthurium harrisii (Grah.) G. Don	Montreal Botanical Garden (No 635-1942)	*Barabé 253* (MT)
Anthurium longistamineum Engl.	Montreal Botanical Garden (No 1554-1958; No 3038-1959)	*Barabé 233* (MT)
Anthurium schlechtendalii ssp. schlechtendalii Kunth	Montreal Botanical Garden (No 2463-1954)	*Barabé 219* (MT)
Anubias barteri Schott	Montreal Botanical Garden (No 3548-1985)	*Chouteau 17* (MT)
Anubias heterophylla Engl.	Montreal Botanical Garden (No 1941-1999; No 1909-1999)	*Barabé 197* (MT)
Arisaema dracontium (L.) Schott	Missouri Botanical Garden (No 69905)	*Croat 69905* (UMO)
Ariseama triphyllum (L.) Schott	Montreal Botanical Garden (No 1984-2000)	*Barriault 25* (MT)
Arum cylindraceum Gasp.	Corsica	
Arum italicum Mill.	Corsica	*Barabé 182* (MT)
Arum maculatum L.	Corsica	
Caladium bicolor (Aiton) Vent.	Montreal Botanical Garden (No 2364-1992; No 1590-1995)	*Barabé 96* (MT)
Cercestis stigmaticus N.E. Br.	Montreal Biodôme (No 7078-1998)	*Barabé 239* (MT)
Colocasia esculenta (L.) Schott	Montreal Botanical Garden (No 1412-1998; No 1143-1999)	*Barabé 175* (MT)
Colocasia fallax Schott	Montreal Botanical Garden (No 1416-2002)	Chouteau 18 (MT)
Culcasia saxatilis A. Chev.	Montreal Botanical Garden (No 4094-1984)	*Barabé 91* (MT)
Dieffenbachia oerstedii Schott	Montreal Botanical Garden (No 1834-1955)	*Chouteau 19* (MT)
Dieffenbachia seguine (Jacq.) Schott	French Guiana	*Chouteau & Lavallée* 3 (MT)
Dracontium polyphyllum L.	Montreal Botanical Garden (No 484-1987; No 2464-1954)	*Barabé 50* (MT)
Dracunculus vulgaris Schott	Missouri Botanical Garden (No 942193)	*Croat 942193* (UMO)
Gonatopus angustus N.E. Br.	Montreal Botanical Garden (No 4106-1984)	*Barabé 101* (MT)
Gonatopus bovinii (Decne.) Engl.	Missouri Botanical Garden (No 69740)	*Croat 69740* (UMO)
Homalomena rubescens Kunth	Montreal Botanical Garden (No 1721-1955)	*Barabé 108* (MT)
Homalomena philippinensis Engl.	Missouri Botanical Garden (No 52988)	*Croat 52988* (UMO)
Monstera adansonii Schott	French Guiana	*Chouteau & Lavallée* 5 (MT)
Montrichardia arborescens (L.) Schott	French Guiana	*Barabé 263* (MT)
Montrichardia linifera (Arruda) Schott	French Guiana	*Chouteau & Lavallée* 4 (MT)
Peltandra virginica (L.) Schott	Missouri Botanical Garden (No 96738)	*Croat 96738* (UMO)
Philodendron erubescens C. Koch & Augustin	Montreal Botanical Garden (No 2798-1950; No 1892-1957)	*Chouteau 12* (MT)
Philodendron pedatum Kunth	French Guiana	*Barabé 259* (MT)
Philodendron squamiferum Poepp. & Endl.	Montreal Botanical Garden (No 2365-1992; No 2201-1986)	*Barabé 136* (MT)
Pinellia tripartita (Blume) Schott	Missouri Botanical Garden (No 78128)	*Croat 78128* (UMO)
Pistia stratiotes L.	Montreal Botanical Garden (2627-1993)	*Chouteau 20* (MT)
Pseudodracontium fallay Serebr.	Missouri Botanical Garden (No 79452)	*Croat 79452* (UMO)
Rhaphidophora schottii Hook	Missouri Botanical Garden (No Kew 478-65-47801)	*Kew 478-65-47801*(UMO)
Spathiphyllum friedrichsthalii Schott	Montreal Botanical Garden (No 2577-1954)	*Chouteau 21* (MT)
Spathiphyllum patinii (Mast.) N.E. Br.	Montreal Botanical Garden (No 1779-1949; No 2229-1960)	*Barabé 189* (MT)
Spathiphyllum wallisii Regel	Montreal Botanical Garden (No 2471-1954; No 1231-1986)	*Barabé 105* (MT)
Stenospermation longipetiolatum Engl.	Montreal Biodôme (No 7267-1992; No 7057-1998)	*Barabé 251* (MT)
Stenospermation sessile Engl.	Montreal Biodôme (No 7003-2000)	*Chouteau 22* (MT)
Synandrospadix vermitoxicus (Griseb.) Engl.	Missouri Botanical Garden (No 62836)	*Croat 62836* (UMO)
Syngonium angustatum Schott	Montreal Botanical Garden (No 1891-1942)	*Barabé 217* (MT)

Syngonium auritum (L.) Schott	Montreal Biodôme (No 7342-1992)	*Barabé 216* (MT)
Syngonium ruizii Schott	Missouri Botanical Garden (No 85-1656 Atwood)	*Atwood 85-1656* (UMO)
Syngonium schottianum H. Wendl. ex Schott	Montreal Biodôme (No 7013-1998)	*Barabé 212* (MT)
Typhonium trilobatum (L.) Schott	Missouri Botanical Garden (No 53260)	*Croat 53260* (UMO)
Typhonium violifolium Gagnep.	Missouri Botanical Garden (No HAR194)	*HAR194* (UMO)
Xanthosoma corpuscatum Schott	Montreal Botanical Garden (1510-2003)	
Zamioculcas zamiifolia (Lodd.) Engl.	Montreal Botanical Garden (No 7324-1939)	*Barabé 84* (MT)
Zomicarpella amazonica Bogner	Missouri Botanical Garden (No 71763)	*Croat 71763* (UMO)