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Pollen viability and germination in some neotropical aroids

Denis Barabé, Karine Lavallée, and Marc Gibernau

Abstract: Pollen viability and germination were observed in six species of neotropical Araceae. In *Anaphyllopsis americana* (Engl.) A. Hay, 50% of pollen grains remain viable after 70 h following dehiscence, and it takes over 210 h for total loss of viability to occur. In *Montrichardia arborescens* (L.) Schott, approximately 50% of pollen grains are not viable after 24 h, and no germination occurs after 36 h. *Monstera adansonii* Schott and *Philodendron pedatum* (Hook.) Kunth have the lowest initial pollen viability (40%–55%) and lose half of this viability after approximately 30 h. Pollen grains of *Monstera adansonii* remain viable for at least 60 h and that of *P. pedatum* for approximately 40 h, and constitute another group with a similar viability pattern. In *Philodendron melinonii* Brongn. ex Regel and *Philodendron solimoesense* A.C. Sm., pollen loses 50% of its viability after 24 h, but remains viable for at least 48 h. The percentage of viability decreases in a pattern from species having a long flowering cycle and small pollen grains (*A. americana*) to species with a short flowering cycle and large pollen grains (*M. arborescens*).

Key words: pollination, flower, flowering cycle, French Guiana.

Résumé : Les auteurs ont examiné la viabilité du pollen et sa germination, chez six espèces d'Araceae tropicales. Chez l'*Anaphyllopsis americana* (Engl.) A. Hay, 50 % des grains de pollen demeurent viables 70 heures après la déhiscence, et il faut compter 210 h pour atteindre la perte totale de viabilité. Chez le *Montrichardia arborescens* (L.) Schott, environ 59 % du pollen n'est plus viable après 24 h, et l'on observe aucune germination après 36 h. Le *Monstera adansonii* Schott et le *Philodendron pedatum* (Hook.) Kunth possèdent la plus faible viabilité initiale (40–55 %) et perdent 50 % de cette viabilité après environ 30 h. Les grains de pollen du *Monstera adansonii* demeurent viables pendant environ 60 h et ceux du *P. pedatum* pendant environ 40 h, ce qui en fait un autre groupe ayant un patron de viabilité similaire. Chez le *Philodendron melinonii* Brongn. ex Regel et le *P. solimoesense* A.C. Sm., le pollen perd 50 % de sa viabilité après 24 h et demeure viable pendant au moins 48 h. Le pourcentage de viabilité diminue selon un patron allant d'espèces ayant un long cycle de floraison et de petits grains de pollen (*A. americana*), à des espèces ayant un court cycle de floraison et de gros grains de pollen (*M. arborescens*).

Mots-clés : pollinisation, fleur, cycle de floraison, Guyane française.

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Introduction

In flowering plants, floral characters are linked to pollination mechanisms and have coevolved to maximize the probability of reproduction (Cruden 2000; Fenster et al. 2004). Various relationships among floral characters (stigma depth, style length, diameter of the stigma) and pollen/ovule ratio have been studied in many families of angiosperms, including the Araceae (Chouteau et al. 2006*a*, 2006*b*). However, among characters that are involved in reproductive efficiency, pollen viability remains a poorly known factor in general, and in family Araceae in particular (Hesse 2006*a*, 2006*b*). Recently, it has been observed in the temperate species, *Arum italicum* P. Mill. and *Arum maculatum* L., which have a flowering cycle of 2 d, that pollen grains are viable for 2(–3) days after dehiscence (Gibernau et al. 2003*b*). However, the relationship between the flowering cycle and the viability of pollen in the Araceae remains unknown.

In regard to this question, Hesse formulated the hypothesis that "ephemeral spathes and the absence of sporopollenin are the consequence of an adaptive syndrome for a short pollination time window, where short-lived pollen, rapid germination, and brief receptivity of stigma work together." (Hesse 2006*a*, p.148). The Araceae, a family that has a great floral diversity linked with particular pollination syndromes, constitutes very good material for testing this hypothesis.

Family Araceae contains 107 genera and more than 3300 species (Mayo et al. 1997). Two main types of inflorescence

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Table 1. Pollen characteristics: length, width, volume, and germination time at anthesis.

Species	Pollen grain length (μm)	Pollen grain width (μm)	Pollen grain volume (μm^3) $\times 10^3$	Statistical groups	Germination time* (h)
Anaphyllopsis americana (n = 30)	30.4±1.7	30.4±1.7	14.8±2.4	a	2.0±0
Monstera adansonii (n = 40)	55.8±1.9	47.6±0.6	66.1±9.6	b	1.1±0.6
Montrichardia arborescens (n = 40)	122.6±8.6	90.8±5.4	532.7±92.3	c	0.6±0.2
Philodendron melinonii (n = 50)	59.4±3.4	42.5±1.3	56.4±6.4	b	0.4±0.1
Philodendron pedatum (n = 50)	60.1±2.5	40.9±1.6	52.8±6.3	b	0.5±0
Philodendron solimoesense (n = 65)	64.3±1.2	42.6±1.2	61.1±4.6	b	0.5±0.3

Note: Pollen grain volume varied significantly among species (Anova: $F_{5,279} = 564.2$, $P = 7 \times 10^{-12}$), and species with different letters were statistically different (Bonferroni adjustments $P = 1.5 \times 10^{-14}$); n, number of samples; asterisk indicates 3–7 replicates depending on the species.

can be identified in the family: (*i*) those with only bisexual flowers represented by the genus *Anthurium*, and (*ii*) those with unisexual flowers represented by the genus *Philodendron*. On inflorescences of the *Philodendron* type, the female flowers are located in the lower portion and the male flowers in the upper portion. An intermediate zone of sterile, male flowers is also present in certain genera (e.g., *Caladium*, *Philodendron*).

In tropical aroids, inflorescences with bisexual flowers are associated with a long flowering cycle (14–21 d), for example in *Anaphyllopsis* and *Anthurium* or, to use Hesse's terminology, with a long "pollination time window". On the contrary, inflorescences with unisexual flowers such as *Philodendron* or *Montrichardia*, are linked to a short flowering cycle (2 d). One may also find inflorescences with bisexual flowers (*Monstera*; M. Chouteau, D. Barabé, and M. Gibernau, unpublished data, 2004) or unisexual flowers (*Anchomanes*; Beath 1993) possessing an intermediate flowering cycle (6–8 d).

To test Hesse's hypothesis (2006*a*, 2006*b*), we used data collected on two bisexual species (*Anaphyllopsis americana* (Engl.) A. Hay, *Monstera adansonii* Schott) and four unisexual species (*Montrichardia arborescens* (L.) Schott, *Philodendron melinonii* Brongn. ex Regel, *Philodendron pedatum* (Hook.) Kunth, *Philodendron solimoesense* A.C. Sm.). These species have either long (*Anaphyllopsis*), intermediate (*Monstera adansonii*), or short flowering cycles (*Montrichardia arborescens*, *Philodendron melinonii*, *P. pedatum*, *P. solimoesense*).

In the general context of pollination time window, the purposes of our paper are (*i*) to determine the rate of pollen germination in species belonging to genera with bisexual flowers versus genera with unisexual flowers in the Araceae; (*ii*) to analyze the viability of pollen with respect to the pollination time window.

Material and methods

Material used in this study was collected in French Guiana between May and August 2003. Voucher specimens of the six species studied are deposited at the Marie-Victorin Herbarium (MT): *Anaphyllopsis americana* (Engl.) A. Hay (*Barabé et al.* 258), *Monstera adansonii* (*Chouteau & Lavallée 5*), *Montrichardia arborescens* (*Barabé et al. 263*), *Philodendron melinonii* (*Barabé et al. 261*), *Philodendron pedatum* (*Barabé et al.* 259), *Philodendron solimoesense* (*Barabé 42*).

Pollen characteristics

The size of pollen grains was estimated by measuring the diameter of the polar (i.e., length) and equatorial (i.e., width) axes of the grains from dehisced anthers. Measurements were made with an ocular micrometer at 630×. Between 30 and 65 pollen grains per species were measured (see Table 1 for the exact sample sizes). For each species the pollen was collected on at least three different inflorescences. 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. Pollen volume means were compared among species using Anova after log-transformation of the data (Systat 1998). A post-hoc test with a Bonferroni adjustment was performed to determine which pairs of means differ significantly.

Germination

Pollen grains of different species were collected at anther dehiscence during the flowering cycle. For each species, the pollen was collected on at least three different inflorescences and stored in Eppendorf tubes at room temperature (27.5 ± 4.3 °C). To test pollen grain viability, germination tests were performed. Every 12 h for 9 consecutive days (0, 12, 24...216 h), pollen grains (100–200) were taken from the stored tubes, placed into a fresh growing solution on a haemocytometer slide, and observed under a microscope. The growing medium was a modified Brewbaker and Kwack solution (BK Solution) with 10% sucrose (Brewbaker and Kwack 1963). The pollen began to germinate 15–30 min (e.g., *P. melinonii*, *Montrichardia arborescens*) to 120 min (*Anaphyllopsis americana)* after its deposition in the growing solution. We counted the proportion of pollen grains that had germinated by using a sample of 100 to 200 grains depending on the species. For each period of time, the number of counts per species varies from 3 to 7 depending on material availability.

The comparison of germination rates among species was performed using a generalized linear model analysis (GLIM 1986) with a binomial error (proportion data, χ^2 statistics). First, the 6-level factor "species" was fitted to the data (full model). Afterwards, simplified models grouping certain species were adjusted to the data and only the one which was

Fig. 1. Variation in germination percentage in relation to time (i.e., age) since pollen dehiscence for the six studied aroids.

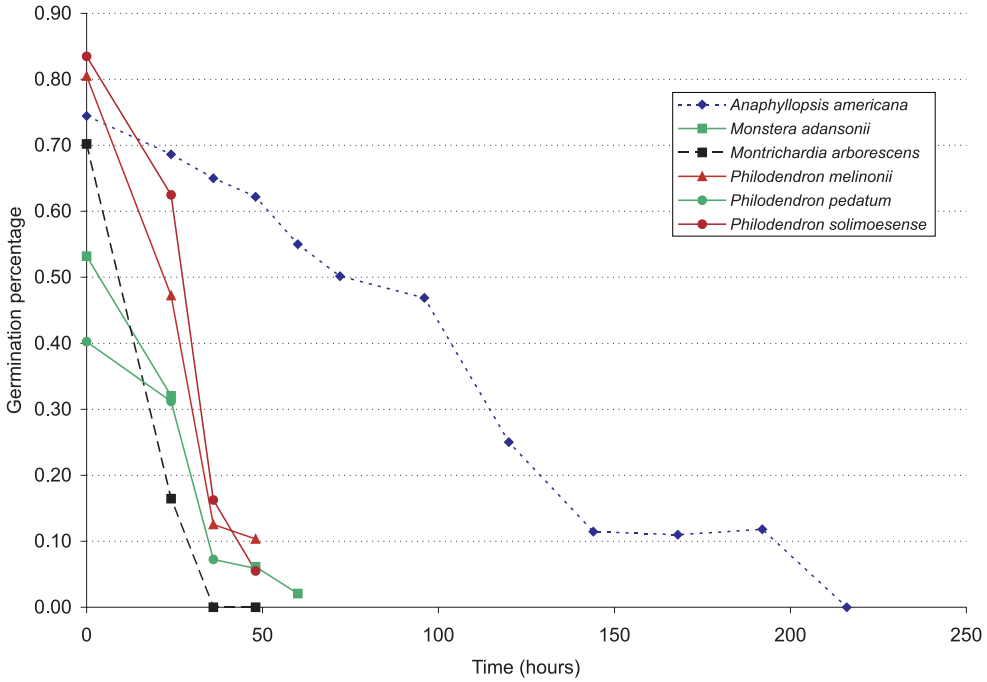

Table 2. Regression equations and squared multiple *R*'s for each aroid studied between pollen germination rate and age.

Species	Regression	R^2	Group
Anaphyllopsis americana	$Y = -0.0038X + 0.7639$	0.82	a
Monstera adansonii	$Y = -0.0088X + 0.5207$	0.72	c
Montrichardia arborescens	$Y = -0.0158X + 0.6484$	0.82	d
Philodendron melinonii	$Y = -0.0159X + 0.8776$	0.71	b
P. pedatum	$Y = -0.0076X + 0.4210$	0.33	c
P. solimoesense	$Y = -0.017X + 0.8808$	0.65	b

Note: The generalized linear model analysis indicates that the negative relationships between pollen germination rate and age vary among species (full model: $\chi^2_{11} = 200$, $P < 10^{-5}$). Species with different letters show significant different negative regressions (simplified model: $\chi^2_7 = 199.6$, $P < 10^{-5}$). The simplified model is not statistically different from the full model ($\chi^2_4 = 1$, $P > 0.10$).

not significantly different from the main model (χ^2 test) was retained (Crawley 1993).

Results

Pollen characteristics

Pollen volume varied among genera and species and three groups were statistically recognizable (Table 1). The smallest pollen volume was observed in *Anaphyllopsis americana*, and the largest in *Montrichardia arborescens*. The third group contained *Monstera adansonii*, *Philodendron melinonii*, *P. pedatum*, and *P. solimoesense*. These species were characterized by a similarity in pollen volume, which was intermediate between those of *Anaphyllopsis americana* and *Montrichardia arborescens* (Table 1).

Germination

There was a significant negative relationship between the germination rate and the age of the pollen grain (Table 2, Fig. 1). However, the rate of viability loss varied among genera and species. The generalized linear model analysis showed that there were four significantly different groups (i.e., slopes and intercepts) among the species studied in terms of initial pollen viability and its loss in relation to time.

In *Anaphyllopsis americana*, 75% of the initial pollen germinated, 50% of pollen grains remained viable after 70 h (Fig. 1), and more than 210 h (almost 9 d) are required to obtain a total loss of viability. Contrary to *Anaphyllopsis*, in *Montrichardia arborescens* with a comparable initial germination proportion (70%), approximately 50% of pollen grains were not viable after 24 h, and no germination occurred after 36 h. *Monstera adansonii* and the *Philodendron* species occupied a position intermediate between *Anaphyllopsis* and *Montrichardia*. *Monstera adansonii* and *P. pedatum*, which belong to the same group, had the lowest initial pollen viability (40%–55%) and lost half of this viability after approximately 30 h. However, the pollen grains of *Monstera* remained viable for at least 60 h and that of *P. pedatum* for approximately 40 h. *Philodendron melinonii* and *P. solimoesense* form another group with a similar pattern of viability and the highest initial pollen germination

(80% and more). In these species, pollen lost 50% of its viability after 24 h, and remained viable for at least 48 h. These two *Philodendron* species belong statistically to a different group than *M. arborescens,* even if the regression slopes are very close (Table 2), because their initial germination proportions were different (82% vs. 70%, respectively).

Discussion

In all species studied, except *Anaphyllopsis americana* and *Monstera deliociosa*, pollen germinated within the growing medium almost immediately, i.e., in less than 1 h (Table 1). Although the pollen volume of *Montrichardia arborescens* is significantly greater than that of the other species, this did not affect the speed of germination. In *A. americana* however, the smaller pollen volume seems to be linked to a lower speed of germination.

It has been shown that pollen hydration influences pollen viability and germination (Nepi et al. 2001; Franchi et al. 2002; Pacini et al. 2006). In regard to the analysis of Pacini et al. (2006), one may hypothesize that pollen of species with a short pollination time window, such as *Philodendron* and *Montrichardia*, lose water more rapidly than pollen of *Anaphyllopsis* and *Monstera*. Therefore, in *Philodendron* and *Montrichardia*, the transfer of pollen grains to a receptive stigma must be fast and efficient to avoid desiccation.

Partially hydrated pollens (pollen with a water content greater than 30%, Franchi et al. 2002) are associated with a rapid pollen-tube emission, because the rehydration phase is shorter (5–30 min) than for partially dehydrated pollens (>60 min; pollen with a water content less than 30%) (Nepi et al. 2001; Franchi et al. 2002; Pacini et al. 2006). In our study, the germination time (Table 1) indicates that in *Anaphyllopsis*, and maybe also in *Monstera*, the pollen corresponds to partially dehydrated pollen, unlike *Philodendron* and *Montrichardia* in which partially hydrated pollen is found.

Among the species studied, the longest pollen viability and the smallest pollen volume were found in *A. americana*. It is also the only species studied where the pollen is released progressively along the inflorescence over a long period of time (2–3 weeks; M. Chouteau, D. Barabé, and M. Gibernau, unpublished data, 2003). This geophytic species with bisexual flowers is also characterized by the highest ratio of pollen number / ovule number (P/O ratio) per flower and the longest flowering cycle (3–4 weeks) (Chouteau et al. 2006*a*). Thus, such high pollen viability could compensate for a more or less efficient pollination system by increasing the time during which a pollen grain can germinate on a receptive stigma.

The largest pollen volume and the lowest pollen viability were found in *Montrichardia arborescens*. This species, with unisexual flowers, is also characterized by facultative xenogamy (Gibernau et al. 2003*a*; Chouteau et al. 2006*a*). One might think that large pollen and short viability would be associated with a short flowering cycle (2 d) and presence of facultative xenogamy. However, these characters may also be linked to the particular morphofunctional anatomy of *M. arborescens*. Bringing pollen grains in contact with water leads to a rapid swelling of the intine followed by an explosive opening of the exine, with no protective coating around the damageable pollen protoplast (Weber and Halbritter 2007). This might, therefore, explain why the pollen of *Montrichardia arborescens* does not have a long viability time.

Monstera adansonii is characterized by bisexual flowers and an intermediate flowering cycle of 6 d (M. Chouteau, D. Barabé, and M. Gibernau, unpublished data, 2003). Anthesis occurs on the last day of the flowering cycle, and pollen is released simultaneously along the inflorescence as in *Philodendron* species. This mode of release and the size of pollen may explain why the pollen of *Monstera adansonii* behaves differently from the pollen of *Anaphyllopsis americana*. *Monstera adansonii* has a P/O ratio per inflorescence significantly different from that of all *Philodendron* species examined in this study (Chouteau et al. 2006*a*). This indicates that P/O is associated with pollen viability. Although the differences are not very strong in the group characterized by the same average pollen volume (*Monstera adansonii*, *Philodendron* spp.), there are two subgroups with regard to pollen germination rate (Table 2): *M. adansonii – Philodendron pedatum* and *P. melinonii – P. solimoesense*.

Monstera adansonii and *P. pedatum* share the same growth habit. Both species grow primarily as climbing vines producing long internodes. However, in their reproductive phase, the architectural structure of both species is different. When the first mature functional inflorescences appear, *M. adansonii* loses its climbing structure (long internodes) to adopt a rosette habit, contrary to *P. pedatum*, which maintains a climbing form even during its mature phase. *Philodendron solimoesense* and *P. melinonii* are two hemiepiphytic species growing just below the canopy. Both species have short internodes, but the mode of ramification is different (D. Barabé, unpublished results, 2003). Therefore it is very difficult to find a unique character explaining the cluster formed by these four species belonging to two morphologically different genera. In fact, these four species are linked by two characters that are not present together in *Anaphyllopsis americana* or *Montrichardia arborescens*: intermediate pollen size and mode of release of pollen.

There is a trend with regard to pollen viability among the six species analyzed. The percentage of viability decreases as we go from species having a long flowering cycle and small pollen grain (*Anaphyllopsis americana*) to species with a short flowering cycle and large pollen grain (*Montrichardia arborescens*). By including the species in an intermediate position, the trend can be represented in the following way: *Anaphyllopsis americana* → (*Monstera adansonii – Philodendron pedatum*) → (*P. melinonii – P. solimoesense*) → *Montrichardia arborescens*. This trend indicates that reproductive characters such as pollen germination and flowering cycle are integrated in a functional way to ensure the efficiency of pollination mechanisms.

Germination of pollen is generally most successful immediately after anthesis, and viability deteriorates rapidly in most species (Kearns and Inouye 1993). In *Erythronium grandiflorum* Pursh (Liliaceae), pollen viability decreases significantly within 1 h of exposure to air after dehiscence (Kearns and Inouye 1993). However, not all pollen is short-lived; some Rosaceous and Liliaceous pollen can remain viable for 100 d (Leduc et al. 1990). Our results confirm a rapid loss of pollen viability for species with a short flower-

ing cycle (*Montrichardia arborescens* and *Philodendron* spp.) This is in accordance with what has been observed in the temperate aroid species *Arum italicum* and *A. maculatum* (Gibernau et al. 2003*b*). Under natural conditions, pollen grains of these species are viable for 2(–3) d. These species have a flowering cycle of 2 d, as is the case in *Montrichardia* and *Philodendron*, two tropical genera.

When the viability of pollen is short under natural conditions, it must be dispersed quickly among receptive inflorescences in order for pollination to be efficient. In the case of *Philodendron* for example, it should happen during the same evening when pollinators leave the inflorescence in the male phase to find an inflorescence in the female phase (Gibernau et al. 1999). However, if pollinators find an inflorescence in the female phase only on the second day, they will still carry some viable pollen grains. By contrast, pollinators that find an inflorescence on the third day would probably carry nonviable pollen and thus, would not pollinate the inflorescence they visit.

The pollination mechanism of *Anaphyllopsis* is unknown. However the long flowering cycle suggests that the pollination mechanism is not as efficient as that in *Philodendron*. To compensate for a less efficient pollen transfer mechanism, long pollen viability is required. Even if the pollinator carrying pollen does not find a receptive inflorescence for many days, the pollen will still be viable.

Our results confirm Hesse's hypothesis (2006*a*, 2006*b*) that low pollen viability (e.g., *Arum*, *Montrichardia*, *Philodendron*) is linked to the lack of a stable, sporopolleninous outer pollen wall, which indeed characterizes the Araceae. However, with regard to the floral biology of *Monstera adansonii*, pollen viability could be linked to the mode of release of pollen at anthesis instead of the life time of the spathe (early or late collapsing). To test this hypothesis it would be interesting to study species with unisexual flowers having a long flowering cycle, such as is found in the genera *Anchomanes* or *Arisaema*.

Further experiments are needed to investigate whether pollen viability deteriorates rapidly in other species of Araceae, and whether the length of the flowering cycle is associated with duration of pollen viability.

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