Subterranean flowers of Aspidistra elatior are mainly pollinated by not terrestrial amphipods but fungus gnats

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(Citation)
Ecology,99(1):244-246

(Issue Date)
2018-01

(Resource Type)
journal article

(Version)
Version of Record

The Scientific Naturalist

Ecology, 99(1), 2018, pp. 244–246

Subterranean flowers of *Aspidistra elatior* are mainly pollinated by not terrestrial amphipods but fungus gnats

The genus *Aspidistra* (Asparagaceae) comprises over 130 species of herbaceous plants (Chase et al. 2009), most of which are distributed in Southeast Asia (Vislobokov et al. 2013). However, even though most *Aspidistra* species are common, they are also inconspicuous, and the leaf litter of forest habitats usually covers their flowers and fruits, both of which are found close to ground level (Fig. 1A). Therefore, the *Aspidistra* flower is often considered cryptic (Phonsena and De Wilde 2010). Nevertheless, the flowers are extraordinarily diverse, and their morphology is considered critical to species delimitation (Vislobokov et al. 2013, Tillich 2008).

The pollination of biology of *Aspidistra* is interesting because of the extreme diversity in its floral morphology, its inconspicuous appearance, and the forest litter which covers them (Vislobokov et al. 2013). Because of these

Fig. 1. (A) *Aspidistra elatior* flower in forest litter. (B) Longitudinal section of *A. elatior* flower. (C) The fungus gnat *Cordyla sixi* (Mycetophilidae) exiting gaps between the stigma lobes and the perianth tube and carrying a lot of *A. elatior* pollen grains. (D) Diaprid wasp exiting a gap between the stigma lobes and the perianth tube and carrying a few *A. elatior* pollen grains.

reasons, little is known about the pollinators of almost all the species. Nevertheless, the unusual flowers suggest biotic pollination, since pollen grains are hidden under each flower's stigma and because the flowers look like insect traps (Vislobokov et al. 2013). The stamens of *A. elatior* positioned within a perianth chamber under a large stigma (Fig. 1B) that has a receptive upper surface, thereby rendering self-pollination impossible (Buchenau 1867). One researcher, Delpino (1868) provided compelling evidence for cross-pollination in cultivated *A. elatior*; he located *Aspidistra* pollen grains along the trajectories of floral visitors exiting a small opening formed between the stigmatic margin and the perianth tube. In addition, Wilson (1889) suggested that *A. elatior* was pollinated by slugs, a hypothesis subsequently adopted by numerous studies as a rare example of angiosperm flowers being pollinated by mollusks (e.g., Richards 1986).

More recently, Kato (1995) conducted the first investigation of *A. elatior* visitors in the species' native habitat and failed to find any evidence of pollination by slugs. Instead, the author observed *Platorchestia japonica* (Amphipoda) feeding on pollen, which suggested that *A. elatior* could be pollinated by the terrestrial crustaceans (Kato 1995). Pollination by crustaceans and collembolans has also been suspected in the introduced population of *A. elatior* (Conran and Bradbury 2007). Taken together, Vislobokov et al. (2013) noted that the information known about the floral ecology of *A. elatior* suggests it has the most unusual pollination ecology among all angiosperms. However, the novel observations by Kato (1995) and Conran and Bradbury (2007) relied on collected flowers that were studied through dissection. Therefore, without direct observations in the field, the study could have underestimated the role of more quickly moving visitor groups.

In order to further elucidate the pollination biology of *A. elatior*, we conducted the first direct observation of *A. elatior* visitors in the species' natural habitat. *Aspidistra elatior* is widely cultivated in both China and Japan but is indigenous to only a few small islands in the southern part of Japan (Liang and Tamura 2000). Therefore, we made direct observations of pollinators visiting *A. elatior* flowers in evergreen oak forests at altitudes between ca. 300–600 m on Kuroshima Island, Kagoshima Prefecture, Japan, where *A. elatior* is abundant in the understory. We performed the observations of floral visitors for ca. 30 h in mid- to late April of 2015–2016, covering all periods of a 24 h cycle, and red light was used during nocturnal observations to minimize the effect of light on the visitors. We also tagged 253 flowers in mid-April 2016 and assessed the fruit sets under natural condition in late October 2016.

We observed that five individuals of fungus gnats visited and penetrated thorough the gaps between the stigma lobes and perianth tube, three of which were captured for the precise identification. They were identified as *Cordyla sixi* (Mycetophilidae), newly recorded from Japan, and *Bradysia* sp. (Sciaridae; Table 1). In addition, all captured fungus gnats were male, thereby providing no evidence that the flowers serve as brood sites. When a fungus gnat visited a flower, it landed on the upper surface of the stigma so that, if the fungus gnat had previously visited another flower, cross-pollination would occur. The fungus gnats often penetrated under the stigma by entering small openings between the stigma lobes and perianth tube. Therefore, when the fungus gnats exited, they were covered with pollen grains (Fig. 1C). The fungus gnats would often try to penetrate under the stigma several times before succeeding and, then, would remain there for up to dozens of seconds, before exiting through the gaps. Because flowers of *Aspidistra* do not produce nectar and adult fungus gnats do not feed on pollen grains, we concluded that fungus gnats did not receive any benefits from this interaction.

TABLE 1. Composition of floral visitors to *Aspidistra elatior.*

Order	Species	No. individuals on the flowers	No. individuals entering into the flowers
Amphipoda	*Platorchestia japonica*	4	1
Blattodea	*Opisthoplatia orientalis*	1	–
Collembola	*Ceratophysella denticulata*	17	8
Diptera	*Cordyla sixi*	2	2
	Mycetophilidae (genus and species undetermined).	2	2
	Bradysia sp.	1	1
	Ctenosciara insolita	2	–
	Ctenosciara sp.	2	–
	Trichosia morio	1	–
	Phoridae (genus and species undetermined)	1	–
Hymenoptera	Diapriidae (genus and species undetermined)	1	1
	Nylanderia flavipes	11	1
	Pachycondyla nakasujii	2	–

Interestingly, a wasp in the family Diapriidae was also documented as a potential pollinator. We observed only one, but the wasp penetrated under the stigma through the gaps between the stigma lobes and perianth tube, and when the wasp exited, it was covered with pollen grains (Fig. 1D). The diaprid wasps are parasitoids that attack the larvae of fungus gnats (Gauld et al. 1988), and they have also been documented to pollinate *Cypripedium fasciculatum*, the morphology of which is similar to species pollinated primarily by fungal gnats (Lipow et al. 2002). Therefore, the similar appearance of *A. elatior* and mushroom fruit bodies may help attract fungus gnats, as well as their natural enemies (Tillich 2005). In fact, larva of both *C. sixi* and *Bradysia* sp. are known as the fungivore.

As reported by previous studies (Kato 1995, Conran and Bradbury 2007), we also observed small soil invertebrates, such as *Ceratophysella denticulata* and *Platorchestia japonica*, in the *A. elatior* flowers. Therefore, we cannot exclude the role of soil invertebrates as supplemental pollinators. However, these visitors would play relatively minor roles as pollinators since they are only able to carry a few pollen grains, even after penetrating the stigma. The flowers were also visited by two species of ants (e.g., *Pachycondyla nakasujii* and *Nylanderia flavipes*), but the behavior of the ants observed in the field was much less focused than that of the fungus gnats. Instead, the ants primarily appeared to walk around the perianth lobe and stigma, and the ants were rarely observed penetrated under the stigma using the gaps used by the fungus gnats.

We predicted that the fungus gnats are the most effective pollinator of *A. elatior* since (1) they were observed on multiple occasions departing from *Aspidistra* flowers with a lot of pollen grains on their bodies, (2) they were the dominant flying insects that visited the *Aspidistra* flowers, and (3) the flowers that they visited often developed fruits (2 fruits/5 flowers) despite the population's overall low fruit set (12 fruits/253 flowers). Since experienced insects usually avoid non-rewarding plants due their associative learning ability, the deceptive pollinator attraction strategy could account for the low pollination visitation rate (Tremblay et al. 2004), and this could contribute to the low reproductive success of these plants. In addition, the size of the fungus gnats allows them to pass through the gaps between the stigma lobes and perianth, enter the chamber, and locate the stamens. Therefore, we speculate that the methodology used by Kato (1995) may have been insufficient for detecting dipteran visitors, likely owing to their short duration of their visitations.

Indeed, several aspects of *A. elatior*'s floral morphology, such as its superficial similarity to mushroom fruit bodies, suggest that *Aspidistra* species are pollinated by fungus gnats (Tillich 2005). We also found that the *A. elatior* in our study site emitted a strong musty odor, while other *Aspidistra* flowers are often described as odorless. Therefore, the fungus gnats may be attracted by both visual and chemical mimicry. It is also interesting to note that *Cordyla* species, that are the main pollinators of *A. elatior*, also pollinate *Heterotropa* which is also considered a mushroom mimic (Sugawara 1988).

Vislobokov et al. (2013, 2014) also observed that flies pollinate some species of the genus *Aspidistra.* Therefore, in combination with the results of the present study, we suspected that dipteran pollination would be common among *Aspidistra* species. However, pollination biology of each *Aspidistra* species will still be very diverse. For example, the pollinators of the two other species observed so far belong to different dipteran families; *A. phanluongii* is pollinated by flies of genus *Megaselia* (Phoridae) (Vislobokov et al. 2013), whereas *A. xuansonensis* is pollinated by gall midges, whose larvae are able to grow in the pollen mass (Vislobokov et al. 2014). Further study is needed to elucidate the diversity of unique pollination systems in *Aspidistra*.

ACKNOWLEDGMENTS

We thank Drs Taizo Nakamori, Kyohei Watanabe and Shigeko Fukumoto for their assistance with insect identification. This work was financially supported by the JSPS KAKENHI (Grant Number 17H05016).

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Manuscript received 1 June 2017; revised 31 August 2017; accepted 1 September 2017. Corresponding Editor: John Pastor.

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