

Thrips: the primeval pollinators?

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Introduction

From their presumed beginnings as fungal hyphae feeders in detritus, thrips have diversified into grass, herb and floral herbivory, pollenivory, carnivory, and sporophagy. Among these, pollenivory is quite common (see review by Kirk 1997). Pollen of many plant species is very nutritional, containing essentials for development such as starches (up to 22% by dry weight), proteins (2.5-61%), lipids (1-20%) and vitamins (Roulston and Cane 2000).

Certainly with so many species of Thysanoptera known to utilize pollen, the potential for thrips to effect pollination is possible. However, thrips have been systematically overlooked by pollination biologists. These small insects have generally been considered only a minor or secondary contributor to pollination of some plants, many of which are crops. In part this attitude is due to thrips lacking a number of characters that are deemed essential to be an “efficient pollinator” (Kirk 1997): 1) thrips are tiny and have no specific organs or structures that carry pollen; 2) they carry only a small number of pollen grains per individual; and 3) they are assumed to be poor fliers with little directed flight, and rarely leave their flowers. But these traits are not always true for thrips, nor are these traits always limitations. Thrips do have some directed flight, and some species do move between flowers very often. Members of both *Frankliniella* and *Thrips* genera are considered important pollinators of some crops. Finally, even though individual thrips only carry a few grains, sometimes up to hundreds of grains (Kirk 1997), they can move between plants and flowers in high numbers. Even Darwin (1876, 1877) observed the movement of thrips carrying pollen between convolvulus flowers and noted how they could interfere with pollination experiments. Until recently, though, there have been no definitive studies showing that thrips are

essential for pollination of any plant species. As more attention is being paid to thrips activities and behaviors, more discoveries are being made that speak to their potential as pollinators.

Thien *et al* (2000) reviewed the characteristics of the pollination biology of 29 basal angiosperm families, including all the basal dicots (e.g., Magnoliaceae, Lauraceae, Monimiaceae, Annonaceae, and Nymphaeaceae) and one basal monocot (Araceae). One common feature of these basal families is that most of their species are insect pollinated, with wind pollination a rarity. The dominant pollinators in these 29 basal angiosperm families are members of Coleoptera and Diptera, these two orders being involved in pollination of species in 17 and 14 families, respectively. Hymenoptera (mostly bees) and thrips are secondary pollinators, found in 7 and 9 of these families, respectively. One implication of these results is that Coleoptera and Diptera, being associated commonly with basal angiosperms, as well as pollinators of some gymnosperms, are possibly the more primitive pollinators and have shifted to and become more specialized on higher angiosperms. Other pollinators, such as moths, butterflies, birds, and bats, likely evolved later. However, Thien *et al.* (2000) caution that thrips importance in pollination is often overlooked.

Pollination syndrome

Although the utility of the term “pollination syndrome” (i.e., plants, sometimes unrelated, with similar floral traits and similar types of pollinator) has been questioned (Johnson and Steiner 2000), it may serve as a good starting point for analyzing particular associations of pollinators with their floral hosts. Flowers that tend to be associated with ‘thripophily’ (as reviewed by Kirk 1997) are medium sized, with white to yellow color, they are sweetly scented with or without nectar, their structure is compact, globose, or urceolate, with pollen chamber or shelter, and their pollen grains are small and dry.

Some of these traits do fit the floral morphologies of some recently reported subtropical plants (and some are in basal angiosperm families), where thrips play a role in pollination. 1) Webber and Gottsberger (1995) found thrips visitors carrying pollen between flowers on two species of Amazonian Annonaceae, *Bocageopsis multiflora* and *Oxandra euneura*. Flowers are small and white (< 4 mm across) with a tiny pollen chamber formed by overlapping petals and stamens. Other members of this family have medium to large sized flowers and are pollinated by beetles. The sweet odors were stronger during the day. 2) Two species of *Macaranga* (Family Euphorbiaceae) trees are likely pollinated by thrips: *M. velutiniflora*, a newly described species in Borneo (Davies 1999), and *M. hullettii*, a common species in southeast Asia (Moog *et al.* 2002). A phlaeothripid species of the genus *Neoheegeria* has been found on both male and female flowers of *M. hullettii* carrying pollen. The trees are dioecious, and both male and female inflorescences are tiny and hidden. The staminate flowers are about 1 mm long, and multiples of these flowers are enclosed by a greenish bracteole. Female flowers are slightly larger but subglobose. A vanilla-like odor is emitted from flowers of *M. hullettii*. 3) *Thrips setipennis* were the only insects found on both male and female flowers, and are the likely pollinators, of *Wilkiea huegeliana* (Monimiaceae), a rainforest tree in Queensland, Australia (Williams, *et al.* 2000). Individual flowers are tiny (<4.5mm), white and have only a tiny ostiole by which these insects enter the flower.

In these studies, thrips use tiny and sometimes hidden flowers rather than medium to large flowers, but globose and urn-like shapes and small openings are common. Because thrips have been widely overlooked, pre-conceived notions about thripophily should not be taken as complete, and the focus should be placed on searching for thrips on plant species where pollinators are not known, regardless of their floral traits.

Discovery of thrips pollination of cycads

One unusual thrips pollination system has been discovered on cycads in Australia that should bring much more focus on thrips as pollinators. Cycads (Cycadales) are dioecious plants of Paleozoic origin, and are considered the basal

clade among extant gymnosperms (Bowe *et al.* 2000, Chaw *et al.* 2000). Cycads were most diverse during the Mesozoic Era - Jurassic period (144-213 MYA), when the first flowering plants were evolving (Friis *et al.* 1987, Thomas and Spicer 1987). During most of the 20th century, cycads were thought to be wind-pollinated like other gymnosperms. The first study to show that cycads were insect pollinated was by Norstog *et al.* (1986). They observed pollen laden weevils, *Rhopalotria mollis* (Sharp), moving from male cones to female cones of *Zamia furfuracea*, and they demonstrated that seed set significantly declined when beetles were excluded from female cones. Strong mutualisms between specialist beetles in the weevil superfamily (Coleoptera, Curculionioidea) (Oberprieler 1995a, Oberprieler 1995b), and their cycad hosts are now known across most cycad-bearing continents.

The cycad genus *Macrozamia* (Zamiaceae) is found only in Australia, and there are approximately 40 extant species. Most of these species are found near the east coast, with three species being found in the southwestern coastal area near Perth. However, one species, *M. macdonnellii*, is found in the central desert interior, in scattered isolated populations throughout the Macdonnell and Hart Ranges, at least 1400 km in all directions from all other *Macrozamia* species. Numerous insect species have been found on male and female cones of *Macrozamia* (Forster, *et al.* 1994), but only beetles, primarily *Tranes* spp. (Coleoptera, Curculionidae), and wind were thought to be pollen vectors, even though thrips in the genus *Cycadothrips* (Terebrantia: Aeolothripidae) had been observed by the thousands in male cones of several species. *Cycadothrips chadwicki* Mound was reported on male cones of *M. communis* (Mound 1991, Chadwick 1993) and *C. emmaliami* Mound & Marullo was found on both male and female cones of *M. riedlei* in southwestern Australia (Mound, *et al.* 1998). During October through December 1999, a study was undertaken to examine the potential for *C. chadwicki* to pollinate *Macrozamia communis*, a cycad found on the southeastern coast of New South Wales, using exclusion experiments as well as determining pollen loads and behavioral observations (Terry 2001).

In this study, thrips were observed moving between cones, including from male to female cones, during the day time only. Average pollen loads of thrips were determined by counting the pollen grains around thrips bodies caught on sticky traps as they were leaving male cones or arriving on female cones. Those leaving male cones had slightly higher loads than those arriving at female cones (Table 1). Thrips visited and carried pollen to female cones. Seed set was high in cycad cones where weevils were excluded and was not significantly different from open controls (62% versus 59.9%, controls versus beetle exclusion, respectively). Further, excluding wind from vectoring pollen did not significantly reduce seed set (62% versus 57.7%, control versus wind exclusion, respectively). Total pollen grains delivered to each female ovule was estimated to be over 1000 grains, more than sufficient to achieve fertilization.

While this study was underway, a new species, *Cycadothrips albrechti* Mound and Terry, was discovered on male cones of *Macrozamia macdonnellii*, the desert cycad of central Australia. Mound and Terry (2001) examined the interaction between this thrips species and its cycad host, to determine the potential for the thrips to pollinate *M. macdonnellii*. A brief summary of the results of the observations on this desert cycad and a discussion of the significance of other cycad studies follows.

Cycadothrips albrechti was the only potential pollinator species found on cones in a survey of several different *M. macdonnellii* populations. As many as 50,000 thrips per male cone were estimated on some male cones during pollen dehiscence, based on subsamples of individual sporophylls from male cones. Thrips mated and oviposited on male cones, and both adults and larvae fed on pollen inside sporangia. During pollen dehiscence, male cones emitted

a very strong and pungent odor that humans could detect at least 10 m away from cones. Thrips moved out of *M. macdonnellii* male cones daily *en masse* in the late afternoon. Female *M. macdonnellii* cones were receptive (had tiny gaps between sporophylls, emitted odor similar to male cone, attracted thrips) for perhaps only one day. Over 5000 thrips were caught on one sticky trap collar (2cm wide and 45 cm diameter) around a receptive female cone in a single afternoon. Pollen loads per thrips leaving male cones averaged around 20 grains per thrips, and averaged slightly over 15 grains on thrips arriving at female cones (Table 1). Pollen loads and estimates of total thrips visitation at the female cone indicated a pollen delivery of >5700 grains per ovule in a single afternoon (Table 1). Thus *C. albrechti* appears to be the sole pollinator of this species.

Implications of thrips pollination of cycads

Surveys of insects on *Macrozamia* cones (see review by Terry 2001) suggest that at least four *Macrozamia* species are pollinated by only *Cycadothrips* spp.; eight species are pollinated only by *Tranes* spp. weevils (Coleoptera: Cuculionidae); and three species have both insects. More than 20 other *Macrozamia* species have not been surveyed for cone visitors. On other continents, only beetles are associated with cycads, although researchers have not specifically looked for thrips and may have overlooked them. If a thrips/cycad association is found only on Australian *Macrozamia*, then thrips association with cycads may be recent. *Macrozamia* genus is at least late Cretaceous in origin (Pole and Douglas 1999) based on fossil records, but fossils of thrips on cycads are lacking. However, biogeographical information can be used in lieu of fossil evidence to establish a possible age of thrips associated with *Macrozamia*.

Pollen grains per thrips or ovule	<i>M. communis</i>	<i>M. macdonnellii</i>
Leaving male plant	41.9 (6.3)	20.5 (3.8)
Arriving at female plant	20.5 (2.8)	15.1 (3.2)
Ovule ¹	1218	5700

¹ Pollen grains per ovule estimate based on average estimate of thrips arriving at female cones (number caught on sticky traps corrected for trap size relative to cone size) multiplied by the pollen load per individual thrips arriving at female cones, all divided by the average number of ovules per cone.

Table 1. Pollen loads of *Cycadothrips* spp. (SE) and estimate of pollen grains per ovule in *Macrozamia communis* and *Macrozamia macdonnellii*

The cycad genus *Macrozamia* is found on both east and west coasts of Australia as well as in a small area within the central desert region. These cycads probably had a continent wide distribution during a previous geological period, and species now survive only in a few areas as relicts. *Cycadotherips* is the only pollinator found in all three regions, and this thrips is not found on other plants. Marine incursions and subsequent drying in the southern part of Australia during the Eocene 50 MYA may have isolated the eastern and western species of the southern *Macrozamia* populations and their pollinators (Ladd and Connell 1993), but even earlier vicariance events are possible. The massive marine intrusion during the Cretaceous ~114-119 MYA (Cranston and Naumann 1991, Beynon, *et al.* 1992) fragmented the continent into eastern, central, and western islands. These islands match the current *Macrozamia* and *Cycadotherips* distributions and endemism. Thus, one possibility is that thrips mutualism with *Macrozamia* existed before these events. Because this argument is circumstantial, however, further corroborating evidence is needed to give more validity to this time frame.

It is possible that thrips were involved in early cycad pollination systems before weevil involvement. Cycads are at least Permian in origin (Table 2) and the earliest *Macrozamia*

fossil is dated at 65 MYA. This is from New Zealand, which separated from Australia around 85 MYA. The earliest fossil of the weevil superfamily, Curculionoidea, is from the Late Jurassic, represented by Nemonychidae, and the modern families (Brentidae and Curculionidae) in the early Cretaceous, although the modern weevil genera such as *Tranes* spp. that are associated with cycad pollination did not evolve until the Cenozoic Era, in the Paleocene or Eocene (Oberprieler 1995b). Evidence suggests that weevil pollinators of modern cycads are derived from angiosperm dwelling ancestors that developed in reproductive organs or bored in wood, rather than from the older gymnosperm feeding weevil lineage, Nemonychidae, which has never been found on either fossil or extant cycads (Oberprieler 1995a, Oberprieler 1995b). It is now believed that each cycad bearing continent has had an independent evolution of its weevil pollinators. If this is true, then other pollinators of cycads presumably existed before these weevils evolved.

The insect order Thysanoptera is Paleozoic in origin (Kukalova-Peck 1991, Labandeira and Seposki 1993); thus ancestors in the basal groups of Thysanoptera predate angiosperms and some of the modern genera of cycads. Finally, the genus *Cycadotherips* has been placed in its own sub-family, Cycadotheripinae within one of the basal thysanopteran families, Aeolothripidae.

ERA	Period	MYA ¹	Plant evolution	Insect evolution
Cenozoic	Eocene	38		Rise of true/modern weevils, including the genus <i>Tranes</i> ²
	Paleocene	55		Rise of modern weevil genera?
Mesozoic	Cretaceous	65	1 st record of <i>Macrozamia</i> 1 st record of a modern cycad family	Diversification of weevils; rise of modern weevil families
	Jurassic	144	1 st angiosperms?	1 st Cucurlioidea
	Triassic	213	Cycad dominance	1 st beetles
Paleozoic	Permian	244	Many extinct cycads	1 st thrips / endopterygote insects
	Carboniferous	280	1 st cycads?	

¹ approximate first year of the period, million years ago

² *Tranes* is one of the modern weevil genera whose members are pollinators of *Lepidozamia* spp. and some *Macrozamia* spp. Cycades

Table 2. Time of appearance of particular insect and plant groups

Although the exact relationships among these basal families and of the Cycadthripinae among its sister taxa are unresolved, this genus is among the basal clades of Thysanoptera (Marullo and Mound 1995), suggesting that ancestors of this clade were likely around during the evolution of some gymnosperms and before angiosperms. Based on this information, thrips may be among the oldest pollinators of plants.

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