

Odor-Mediated Push-Pull Pollination in Cycads

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Cycads are dioecious gymnosperms, with male and female individuals, of Permian origin. Cycads share obligate mutualisms with specialist insect pollinators, almost universally beetles (1). The known exception involves thrips of the genus *Cycadotherips* (1, 2), which participate in obligate pollination mutualisms with endemic Australian *Macrozamia* cycads. *Cycadotherips* are in a basal thysanopteran family, proposed as arising by at least the Cretaceous (3). Thrips are primarily found on male cones, which provide food (pollen) for adults and larvae (2, 4). During pollination, male and female *Macrozamia lucida* cones self-heat daily, up to 12°C above ambient temperatures between the hours of ~1100 and 1500, when nearly a million-fold increase in male volatile emissions occurs [females reach ~one-fifth that amount (4)]. In

concert, adult *Cycadotherips chadwicki* leave male and female cones en masse (movie S1) (4), and larvae move to the exterior of their male cone habitat. Pollination is mediated by pollen-laden thrips that enter female cones.

We tested thrips' electrophysiological and behavioral responses to cone volatiles. A two-way choice between male sporophyll volatiles or air in a Y-tube olfactometer (5) demonstrated that thrips are attracted (or neutral) to sporophylls early in the day, repelled at midday, and attracted at later times (Fig. 1A). These phases parallel field results; cones retain (morning, low volatile emissions), repel (midday high emissions), and later attract (low emissions) thrips (4).

Electrophysiological tests (5) with volatiles from cones and their specific chemical components revealed that *Cycadotherips* respond to

three components (Fig. 1, B and C): β -myrcene (>90% of total emissions during thermogenesis) and (*E*)- β -ocimene (2%), which change postthermogenesis (4, 5), and allo-ocimene (~2%) (5). Y-tube tests at ecological concentrations of these chemicals (5) showed that ocimenes attract thrips (fig. S1), whereas β -myrcene attracts thrips at low concentrations but repels them at higher levels (Fig. 1D). When control and high-concentration β -myrcene vessels (5) were switched after thrips had entered the control arm, 77% moved directly into the new control arm. Most that remained died within 10 min, suggesting that by leaving cones thrips avoid toxic β -myrcene levels.

These cone volatile changes sufficiently explain the diel thrips behavior observed in situ (4), although temperature and light may modulate their effects. We characterize this as a "push-pull" pollination strategy. Flowers are generally portrayed as only "pulling" pollinators via visual or odor cues. Some orchids, though, chemically repel pollinators after pollination (6). Driving thrips from male cones increases pollen-laden thrips attendance at female cones, which presumably attract by deceit because their volatile components match those of males (4). Parallel attraction to male cones allows thrips to accrue pollen for the next day's cycle. This obligate pollination mutualism stands out for its push-pull behavior and because it involves an ancient gymnosperm lineage and a basal thrips clade (2). Floral scent may have originally evolved to deter herbivores (7), and this system may represent a conserved early intermediary in the evolution of seed plant pollination.

References and Notes

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Supporting Online Material

www.science.org/cgi/content/full/318/5847/70/DC1

Materials and Methods

Fig. S1

Movie S1

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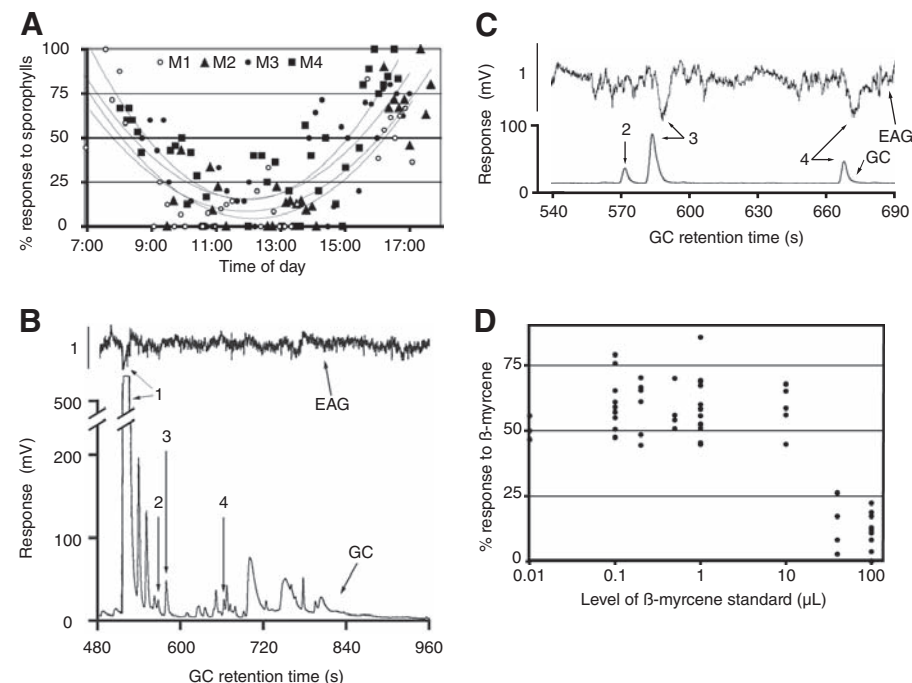


Fig. 1. *Cycadotherips* responses to *M. lucida* volatiles. (A) The % of insects going to sporophylls of four mid-pollination-stage male cones (M1 to M4) versus controls (Y-tube tests). Lines are quadratic fits to data from separate cones; fit parameters are not statistically different (5). (B and C) Male thrips physiologically respond [gas chromatography electroantennographic (EAG) detection, GC-EAD] (B) to β -myrcene (peak 1) from male cone volatiles and (C) to (*E*)- β -ocimene (peak 3) and allo-ocimene (peak 4) but not to (*Z*)- β -ocimene (peak 2) from ocimene standard. (D) The % of insects attracted to different concentrations of β -myrcene standard versus controls (Y-tube tests).

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