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Floral Visitation of the Invasive Stinking Ash in Western Suburban Chicago

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ABSTRACT

Ailanthus altissima (the stinking ash) is an invasive tree that has spread to most states in the continental U.S. No formal study has yet documented the *Ailanthus* pollination ecology. We observed the insects visiting *Ailanthus* at four sites in a western suburb of Chicago over several weeks during the summer. Numerous insects visited the flowers, with flies and bees most common, though there was significant heterogeneity among sites in the composition of the local pollinator assemblage. Over half of the pollen carried on the legs of large bees was similar to the *Ailanthus* morphotype pollen. These results suggest generalist pollination mediated by geographically wide-spread insect vectors, which would facilitate range expansion. Moreover, the reliance on both bees and flies may help explain the species' preference for disturbed sites and its ability to expand into northern latitudes. Ants also were frequent floral visitors and potential symbionts, though they are unlikely pollinators of this dioecious species.

INTRODUCTION

The invasive tree *Ailanthus altissima* Swingle (stinking ash, Tree-of-Heaven, Chinese sumac) is an increasing component of U.S. forests and is a common weed tree in many cities where it is noted for its capacity to thrive in the cracks in concrete and asphalt nearly as readily as at a forest edge (Pan and Bassuk 1986). Its tenacity inspired the book *A Tree Grows in Brooklyn* (Smith 1943), and later a movie and musical by the same title. A deciduous member of the tropical family Simaroubaceae (Quassia), *A. altissima* [Mill] Swingle was first imported from China through England in 1784 by William Hamilton, a Philadelphia gardener (Hu 1979). Additional introductions into the west coast are thought to have occurred with Chinese immigrants during the 1800s. Although other species of the genus exist, *Ailanthus altissima* (hereafter, *Ailanthus*) has spread to most states in the United States (USDA-NRCS 2008) by following human disturbances (Hu 1979, Huebner 2003), often along transportation right-of-ways (Burch and Zedaker 2003).

Ailanthus presents large pinnately compound leaves with indeterminate growth, often yielding large swooping leaves that suggest its tropical origin (Fig. 1). It incorporates many of the strategies employed by invasive species including (a) early and profuse reproduction (Feret 1973) wherein a single adult can produce a million seed in a year

(California Invasive Plant Council 2008), (b) long-distance seed dispersal (Matlack 1987), (c) aggressive clonal reproduction (Miller 2000), and (d) a reliance on high sunlight (Grime and Jeffrey 1965). Moreover, (*e*) *Ailanthus* produces toxins that inhibit plant growth and appear to render it unpalatable to many U.S. herbivores (Heisey 1990a, b, De Feo et al. 2003). For a recent review of the biology of *Ailanthus altissima* see Kowarik and Saumel (2007).

Much less studied are the interactions between *Ailanthus* and its mutualists, such as pollinators. Some claim that *A. altissima* is wind-pollinated (Ballero et al. 2003) but the strong fetid odor of its flowers is thought to attract honey bees as well as beetles and other insects (Hu 1979, Miller 1990). In fact, *Ailanthus* honey is made in some quarters of Europe (Dalby 2000). There it is reported that bee keepers with hives located near large *Ailanthus* stands produce a smokey, greenish honey that some consider bitter and undesirable, though pleasant once sufficiently aged. The flowers appear to fit a generalist insect pollination syndrome as they are small and actinomorphic with white to yellowish or greenish petals, presented in dense clusters of racemose cymes (Fig. 1) in April through June and into July. The species is dioecious, though hermaphrodites do exist (Gleason and Cronquist 1993). Flowers of both genders emit a strong fetid odor at times compared to burnt peanut butter (California Invasive Plant Council 2008, Global Invasive Species Database 2008), though some descriptions emphasize the male flowers as particularly odoriferous.

Here, we report on the floral visitors of *Ailanthus* in the western suburbs of Chicago. Information to date on *Ailanthus* pollination draws largely on anecdotal records and casual observations. Our study provides quantitative information on the putative pollinator assemblage of this invasive species near its northernmost extent in the Midwestern U.S.

STUDY AREA & METHODS

We conducted the study in the Naperville area, a western suburb of Chicago, Illinois, between the months of June and August 2006. The western suburbs are a mosaic of predominantly urban-suburban habitat intermingled with a large network of forest reserves. We selected four roughly 1-hectare patches of forest that contained *Ailanthus*, with distances between sites ranging from 0.4 to 3 km. Site 1 contained three large (> 10 cm dbh) female *Ailanthus* residing in contiguous canopy edge habitat adjacent to a parking lot and a major highway. Site 2 was roughly two km away and contained a single, large, freestanding female *Ailanthus* in a small park of both prairie (mostly non-native species) and forest habitat. Sites 3 and 4 were another km away and only 0.4 km apart in riparian edge habitat adjoining a major road (site 3) and a parking lot (site 4). Both of these sites held several large *Ailanthus*, (site 3, N = 7; site 4, N = 5), with both males and females present. Note that population size estimates are only approximate since *Ailanthus* can propagate clonally (Kowarik 1995) and so in several instances it was unclear what was a ramet versus a genet.

Field observations and collections were made as follows. We marked a single, large *Ailanthus* inflorescence per tree with string and made insect observations and collections at these during a period of 45 minutes to an hour per site between 9 AM and 2 PM. Most time was allotted per site to detailed observations and collections at a single female focal tree, though we also surveyed and collected from other marked inflorescences at each site every 10-15 minutes. Our goal in conducting the study was to produce a list of candidate pollinators for *Ailanthus*, and since an effective pollinator must visit both male and female trees to move pollen between genders, one should be able to sample either (or both) genders and capture the subset of visitors that are the truly effective pollinators. Some have noted that the male flowers emit a stronger odor than the female flowers (e.g., Global Invasive Species Database 2008) and this might attract a larger assemblage of floral visitors, though the male-specific visitors are of less interest to our study. We visited all of the four sites every two to three days over the course of two months with exceptions made for rainy and windy weather (total hours of observation, 36). We rotated the order in which we visited the sites so as not to conflate site effects with temporal variation in insect activity.

Insects visiting *Ailanthus* flowers were collected with a net after they were observed interacting directly with the flowers, rather than simply being present in the vicinity or resting on the inflorescence. A few exceptions to this rule were some of the smaller insects that were captured via an aspirator, some directly from the flowers and some from the net following a sweep. All specimens were stored in a freezer until identification. Specimens were pinned, labeled, mounted, and identified down to the family level of classification using two keys (Borror et al. 1989, Romoser and Stoffolano 1998). Visitation rates were calculated for important taxonomic groups (flies, bees, etc.) and a Pearson chi-square (SPSS program) was used to test for differences in visitor classes among the sites.

During identifications we found that several specimens, particularly the larger bees, carried pollen loads on their legs, which were assayed as follows. Pollen was removed from the leg of eleven bees (family Apidae; ten bees from site 1, one bee from site 3) and placed, separately, into microcentrifuge tubes containing Calberla's stain (2 drops of saturated aqueous solution of basic fuchsin, 5 ml glycerol, 10 ml 95% ethanol, and 15 ml distilled water). These were vortexed and examined under a compound microscope. As a control, we examined the treated pollen from *Ailanthus* and used this morphotype to compare against the pollen carried by the insects. For each sample we determined the frequency of grains that were like and unlike the *Ailanthus* morphotype with sample sizes ranging from 50 to 77 grains per bee. A Pearson chi-square test was used (SPSS program) to determine if the putative *Ailanthus* pollen load varied across bees. Note that we also found pollen dusted on many of the other insects, including flies, though it was unclear to what extent this was a byproduct of the net capture process. As a result, these were not quantified.

RESULTS

Flies and bees were the most common insects visiting the *Ailanthus* flowers. A total of 118 insects were collected representing five orders and more than sixteen families (Table 1, Figure 2). The Dipterans (flies) accounted for nearly half of the collections (48.3%) with Hymenopterans second most abundant overall (32.2%), and roughly 2/3 of these bees and the remaining 1/3 ants. Other orders were rare including Hemiptera (true bugs, 10.2%), Coleoptera (beetles, 7.6%), and Lepidoptera (butterflies, 1.7%).

The composition of the insect communities visiting the *Ailanthus* flowers varied across the four sites, with bees dominant at one site and flies dominant at two other sites. The single tree at site 2 received very low visitation rates and so it was removed from the formal analysis of site heterogeneity. At site 1, bees comprised a larger fraction of the visitor pool (44.7%) than did flies (23.4%). In contrast, the visitor pools at the other sites were dominated by flies while bees represented only a minor component (site 3: 2.7% bees, 56.8% flies; site 4: 3.7% bees, 77.8% flies). A Pearson chi-square test showed that the bee and fly numbers were significantly different when comparing site 1 with pooled data of the adjacent sites 3 and 4 ($\chi^2 = 32.78$, 1 df, $P < 0.001$).

Morphotype analysis of the pollen carried by bees indicated that bees were indeed actively collecting *Ailanthus* pollen, not simply visiting the flowers for nectar or by happenstance. The large bees visiting *Ailanthus* flowers (predominantly at site 1 with all female *Ailanthus*) carried on their legs a large percentage (58.5%) of pollen that was indistinguishable from *Ailanthus* pollen collected from a known source (Table 2). The remaining pollen (41.5%) clearly derived from several other unidentified species. Differences in the ratio of *Ailanthus* versus non-*Ailanthus* pollen morphotypes were not significant across bees ($\chi^2 = 13.26$, $P = 0.104$). Allowing for the fact that the pollen of some other species might appear morphologically similar to that of *Ailanthus*, the 58.5% is an upper bound on our estimate of the percent of *Ailanthus* pollen carried by these bees. But assuming that these were indeed *Ailanthus* pollen grains, we have further promoted the status of bees as effective pollinators of *Ailanthus* since these large bees carrying *Ailanthus* pollen were collected visiting female *Ailanthus* flowers, thereby establishing a male – female link.

DISCUSSION

These data support the notion that *Ailanthus* is pollinated by a variety of generalist insects, most notably flies and bees. Although these visitation data cannot prove effective pollination by these insects, we have nevertheless circumscribed the list of candidates. This list includes taxa recognized as likely pollinators in less formalized studies of *Ailanthus* reproduction (e.g., bees noted by Dalby 2000). Moreover our list includes many insect taxa known to be generalist pollinators that associate with other invasive plant species (reviewed by Richardson et al. 2000). Plants that maintain more obligate associations with particular pollinators are more bound to the geography of those pollinators and therefore less likely to become invasive. A partial reliance on fly pollination (myophily) in a north-temperate zone is reasonable given other studies of floral visitation that have shown an increase in the importance of fly pollination with increasing altitude and elevation (reviewed in Kearns 2001). The infestation of *Ailanthus* in the Chicago area is near the northernmost extent of the range of *Ailanthus* in the Midwestern U.S., where it reaches into Wisconsin and Michigan but only sparingly with concentrations near Chicago and in Milwaukee and Detroit (USDA - NRCS 2008).

Our list of floral visitors of *Ailanthus* is largely distinct at the family level from the list of arthropods known to associate with *Ailanthus* in China. This latter list reported by Siling (1997, cited and described in Zheng et al. 2004) is comprised mostly of natural herbivore pests, not necessarily floral visitors. Some of these associates may serve to keep *Ailanthus* in check and prevent it from becoming locally invasive. A total of 32 arthropod species are noted as associating with *Ailanthus* in China: Lepidoptera (12 species of mostly moths and some butterflies), Coleoptera (10 species of beetles), Homoptera and Hemiptera (8 species of true bugs, cicadas, and planthoppers), and Acariformes (2 species of mites). By contrast, these groups form only a small part of our list of floral visitors, with only a single species of butterfly along with a few beetles and true bugs present in our survey of *Ailanthus* in the Chicago area. The bulk of the floral visitors in our dataset (flies, bees and ants) were not mentioned in the China survey, which is not surprising, geography aside, as the two studies appear to have focused on different modes of insect-plant interactions.

As for flies, despite their generalist behavior and at times inefficient transfer of pollen, flies often contribute to plant reproduction and can rival bees as important pollinators in many circumstances in part due to their sheer ubiquity (Motten 1986, Kearns and Inouye 1994, Kearns 2001, Larson et al. 2001). There are two main types of fly pollination, myophily and sapromyophily. Myophily entails several fly groups that regularly visit flowers for nectar and pollen and can be important pollinators. Families included here are the Anthomyiidae, Bombyliidae, Calliphoridae, Muscidae, Syrphidae, and Tachinidae (Kearns 2001); all but the Bombyliidae were detected at *Ailanthus* flowers in this study.

The sapromyophilous group of flies, on the other hand, regularly visits dead animals and dung, though they may also visit flowers that emit similar fetid odors, as do the flowers of *Ailanthus*. If proximity plays a role, the sapromyophilous flies should cross paths with *Ailanthus* as both have a habit in urban settings of frequenting the less-groomed portions of a city, areas in which it is not uncommon to find garbage lying about (Aldrich, personal observation). In our study, the sarcophagidae (flesh flies) were well-represented at each site. Although their visits may have been largely cases of ‘mistaken identity’, repeated albeit inefficient visitations may in the balance have led to effective pollination, especially at sites 3 and 4 where bees were less common.

Several factors could explain the among-site heterogeneity of the insect assemblages. First and foremost, the number of sites surveyed was small and so we must be conservative in generalizing the pattern of heterogeneity, though the heterogeneity that we did observe is readily explained. Studies of fly visitation rates often show high spatial heterogeneity in fly numbers and species by site (Herrera 1988, Kearns and Inouye 1994). For example, in our study sites 3 and 4 were near a stream which might have attracted a novel assemblage of insects including more flies compared to the other sites, perhaps due to sewer runoff, goose feces, and various other aquatic sources of carrion and detritus. Another possible factor is the gender differences between sites, as sites 3 and 4 included some male trees that conceivably could have been more attractive to flies, although they would then be less efficient pollinators if they failed to visit females.

The prevailing wisdom has been that bees are an important pollinator of *Ailanthus* judging from a variety of anecdotal reports and observations (e.g., Miller 1990, Dalby 2000). Our quantitative studies of visitation rates and pollen morphotypes carried on bee legs support this contention. The large bees that we captured visiting *Ailanthus* flowers carried more *Ailanthus* morphotype pollen than pollen from other sources (average for 11 bees, 58.5% *Ailanthus* morphotype pollen). These bees also carried a very similar proportion of *Ailanthus* morphotype pollen suggesting they were interacting with *Ailanthus* with some sort of regularity. Moreover, since we captured bees at female trees we are able to establish a male – female connection, further supporting the role of bees as effective pollinators of *Ailanthus*, not just floral visitors. Bees, like flies, are widespread and important generalist pollinators that likely have facilitated the spread of *Ailanthus*. However, the decline of bee and other pollinator populations in many areas of the globe (Kearns et al. 1998, Biesmeijer et al. 2006) may lead to a rise in the importance of less efficient yet ubiquitous pollinators such as flies.

Several of the other insect groups visiting the *Ailanthus* flowers in this study may contribute to pollination (e.g., butterflies, Lepidoptera), though likely not all of these groups. Several of the beetles (Coleoptera), true bugs (Hemiptera), and the ants (Hymenoptera, Formicoidea) may have been casual or predatory visitors rather than pollinators, and some of these groups are well-represented in the survey of natural enemies of *Ailanthus* in China (Siling 1997, Zheng et al. 2004). Those unable to fly (ants) were further unlikely as pollinators because *Ailanthus* is dioecious and the insect would have had to travel a large surface distance to the next *Ailanthus* to affect pollination. These less vagile floral visitors might prove more effective as pollinators should gender determination prove to be more flexible or certain modes of bisexuality more common in *Ailanthus* than is normally reported.

Even though ants are unlikely pollinators of a dioecious *Ailanthus*, ants may nevertheless be a symbiont. Ants commonly patrol the leaves of *Ailanthus*, removing nectar from the flowers and from extra-floral nectaries that occur at the leaf margins and stipules (Aldrich, personal observation). Chemical analysis has shown that the extra-floral nectaries of *Ailanthus glandulosa* produce sucrose, rhamnose, and several amino acids, mostly serine, threonine, and proline (Bory and Clair-Maczulajtys 1986). These resources may serve as a reward to the ants for protection from herbivores, augmenting *Ailanthus'* defenses, although ants might also deter potential pollinators as well. The interaction is reminiscent of the symbiosis in the Central American tropics between the bullhorn acacia (*Acacia cornigera*, Fabaceae) and an ant (*Pseudomyrmex ferruginea*) that guards the plant against herbivores and in return eats protein nodules from the leaf tips and nectar from petiolar glands, and lives in the hollowed out *Acacia* thorns (Janzen 1983). Casual observations (Aldrich) of the *Ailanthus* – ant system in West Lafayette, Indiana revealed that ants behave aggressively toward other insects as they patrol the leaves, and will take up residence in the hollow boles of large adults, in which heart rot is commonplace (Hu 1979).

These data demonstrate that bees, flies, and ants are frequent visitors to the flowers of *Ailanthus* in the Chicago area. A dependence on generalist pollinators would make colonization of new environments predictably easier, and is a trait manifest by many invasive plants. We have made a case for bees as effective pollinators, and proposed that flies may be important as well although it is conceivable that fly pollination might be less prevalent in lower latitudes. We also submit that ants may be part of a broader generalist symbiosis that includes floral rewards but whose influence may extend into protection from herbivory, further augmenting the chemical defenses possessed by *Ailanthus*. Such matters deserve further study.

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Table 1. Insect visitation frequencies at *Ailanthus altissima* flowers at four sites in suburban Naperville, IL between June and August 2006.

Order	Family	Common name	Site 1	Site 2	Site 3	Site 4	Total
Coleoptera	Total	beetles	3	1	5	0	9
	Cantharidae	soldier beetles	0	1	0	0	1
	Cerambycidae	longhorn beetles	0	0	1	0	1
	Coccinellidae	ladybugs	2	0	2	0	4
	Other		1	0	2	0	3
Diptera	Total	flies	11	4	21	21	57
	Anthomyiidae	flies	3	0	0	1	4
	Asilidae	flies	0	0	0	1	1
	Calliphoridae	flies	2	0	6	0	8
	Helcomyzidae	flies	0	0	1	0	1
	Muscidae	flies	0	0	3	0	3
	Sarcophagidae	flies	4	4	5	3	16
	Syrphidae	flies	0	0	5	4	9
	Tachinidae	flies	1	0	0	0	1
	Other	flies	0	0	1	12	13
Hemiptera	Total	true bugs	8	0	1	3	12
Hymenoptera	Total	bees / ants	25	1	10	2	38
	Apoidea	bees	21	1	1	1	24
	Andrenidae	bees	1	0	1	0	2
	Apidae	bees	1	0	0	0	1
	Colletidae	bees	2	0	0	0	2
	Halictidae	bees	2	0	0	0	2
	Other	bees	15	1	0	1	17
	Formicoidea	ants	4	0	9	1	14
	Formicidae	ants	4	0	9	1	14
Lepidoptera	Total	butterflies	0	1	0	1	2
TOTAL			47	7	37	27	118

* "Other" indicates specimens that were identified to order but remained ambiguous at the familial level.

Table 2. Counts of pollen morphotypes collected from the limbs of bees visiting *Ailanthus* flowers. A-morph = *Ailanthus*-like pollen, N-morph = Non-*Ailanthus* pollen.

Specimen	A-morph	N-morph	Total
AB007	37	26	63
AB008	33	22	55
AB009	29	27	56
AB031	33	29	62
AB042	30	20	50
AB043	32	20	52
AB053	35	16	51
AB056	50	27	77
AB063	23	31	54
AB077*	30	26	56
AB090	38	19	57
TOTAL	370	263	633

* Collected at site 3, all others collected at site 1.

Figure 1. Flowers and leaves of a male *Ailanthus altissima*.

Figure 2. Insect visitations to *Ailanthus altissima* organized by site.