17

COMMON MILKWEED

(*Asclepias syriaca*)

Common milkweed thrives just outside Center City but not inside, despite wind-blown seeds that disperse downtown.

Figure 17.1 Common milkweed (*Asclepias syriaca*) along railroad tracks by the Schuylkill River at Locust Street in 2008. This plant was part of a sprawling colony destroyed in 2011 by railroad maintenance crews.

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In 1803 Benjamin Smith Barton described entrapment of houseflies in flowers of common milkweed, which he concluded is a kind of "muscipula," or flytrap. Barton, professor of materia medica, natural history, and botany at the University of Pennsylvania, presented his findings to the American Philosophical Society in Philadelphia:

> In the summer of 1801, I discovered a vegetable muscipula in the vicinity of Philadelphia. Having collected some branches, in flower, of the Asclepias syriaca, or Syrian Swallow-wort, well known in the United States by the names of Wild-cotton, cotton-plant, &c; with the view of making some experiments with the milky juice of this plant, I was not a little surprised to find in the course of a few hours, a number of the common houseflies strongly attached to the flowers; being secured, some by their proboscis, and others by their legs: the greater number, however, by their legs. I, at first, imagined, that the flies were merely retained by the viscous juice of the flowers of this Asclepias: but I soon found, that this was not the case. They were detained by the small valves of the flower, and I observed, that the irritability of the valves seemed to reside exclusively in one particular spot, not larger than the point of a common sized pin. Neither in this spot nor in any other part of the valve, could I observe the least vestige of a glutinous or viscous quality. I think it sufficiently evident, that the valve is endued with the irritable principle.
>
> In the genus Asclepias, the valves which I have noticed, are ten in number, being situated in pairs, so as to form five little foviae, the structure and uses of which are not sufficiently known to botanists.
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> A considerable number of flies, not less perhaps than sixty or seventy, which alighted upon the flowers of my Asclepias, were detained in the manner I have mentioned…Many of the flies, particularly the larger ones, were enabled, after some time, to disengage themselves from their prison, without the loss of any of their limbs or organs, or any perceptible injury whatever. Many others effected their escape, not however, without the loss of one or more of their legs, or their proboscis. Not a few, after making long and repeated efforts to regain their liberty, perished in their vegetable prisons.[1]

Milkweed pollination

Barton's "valves" are *pollinia,* or agglutinated masses of pollen. Paired pollinia linked together are *pollinaria*. Barton was the first to observe pollinia adhere to the legs and mouthparts of insects visiting flowers of common milkweed, but he misconstrued their functional significance as entrapment akin to that of Venus flytraps (*Dionaea muscipula*) and sundews (*Drosera*).

From the perspective of bees, Barton correctly perceived milkweed's behavior as less mutualistic than that of, say, clover, which rewards bees with nectar and pollen. Milkweed offers bees only nectar. Bees visiting milkweed do collect pollen—in the form of pollinia stuck to their feet and other body parts—but they are unable to use such pollen as food. Douglass H. Morse at Brown University found that pollinia of common milkweed slowed down the foraging of bumblebees by 25 percent; pollinia entangled their mouthparts and their appendages, and caused loss of body parts, including claws and segments of legs,[2] much as Barton described for houseflies.

By the end of the nineteenth century European botanists demonstrated that pollinia contain pollen. They showed that pollinia in common milkweed flowers adhere to insects' legs and feet and other body parts as they take nectar, and that milkweed flowers later snag pollinia off the insects when the insects incidentally insert the pollinia into flower chambers containing the stigma, the flower's receptive female structure.[3]

Figure 17.2 Leg of honeybee (*Apis mellifera*) entangled by orange pollinia containing milkweed pollen.

Figure 17.3 Honeybee struggling to extricate herself from milkweed flowers that have snagged pollinia stuck to her feet.

Scarcity of milkweed downtown

In 1818, William P. C. Barton, a relative of Benjamin Smith Barton, published the first systematic inventory of plants in the vicinity of Philadelphia. About common milkweed, his *Compendium Florae Philadelphicae* states:

> The commonest species of this genus in this neighbourhood. From three to four feet high. On the banks of the Schuylkill, Delaware, and all our creeks, very frequent. Perennial. June.[4]

Common milkweed currently blooms in scattered colonies along the west bank of the Schuylkill River beside Martin Luther King Drive just outside Center City. Here I watched a honeybee struggling to extricate herself from a common milkweed flower that had snared her in a tangle of pollinia. After five minutes she finally liberated herself. She flew about 10 centimeters away only to turn around and return to the same cluster of flowers that had just trapped her. She drank nectar for a minute until, still free, she flew away.

Milkweed thrives in Philadelphia despite over two centuries of urbanization. The plant's success, however, has been uneven. In Fairmount Park just outside Center City, it makes sprawling, multistemmed perennial colonies with abundant flower heads and seed-bearing pods. By contrast, in Center City it typically produces just a few stalks that last only one or two seasons and yield no pods. For the past several decades in Center City, I have found it to be absent or rare. In 2011 along tracks by the Schuylkill River, railroad maintenance crews destroyed the last big colony here. Its scarcity in Center City is surprising, since it tolerates a broad range of conditions, including drought and soil ranging from alkaline to acidic.[5]

Figure 17.4 Rare example of common milkweed in Center City. It is on the edge of a parking lot near 22nd and Sansom Streets. It never produced seedpods, and was gone the following year. Concrete prevented the roots from spreading and establishing a colony. Photographed August 31, 2008.

Figure 17.5 Colony of common milkweed off Martin Luther King Drive along the Schuylkill River about a kilometer from Center City. Space sufficient to accommodate such a large colony is scarce in Center City.

Baker's Law

What might account for the absence of a plant that is generally regarded as a weed? In 1955 Herbert George Baker observed that plants that disperse long distances typically reproduce vegetatively, or by self-fertilization.[6] This observation was later dubbed Baker's Law.[7] Baker's Law offers a possible explanation for the rarity of common milkweed in Center City. Seeds of common milkweed disperse on strands of silk blown by the wind. In Center City I have watched common milkweed seeds floating in the air far from milkweed patches. Common milkweed violates Baker's Law in the sense that it is a long-distance colonizer that reproduces predominantly by outcrossing.[8] Perhaps the reason common milkweed is rare in Center City is its violation of Baker's Law.

Common milkweed does make vegetative clones from its roots, but these clones do not disperse over long distances unless the roots are broken into pieces that can travel as independent propagules, as in agricultural fields that have been tilled.[9] Self-pollination in common milkweed does produce seedpods, but the rate is low—only 4 percent in experiments in which milkweed was pollinated by hand.[10] In theory, common milkweed's poor compliance with Baker's Law might account for its rarity in Center City: a milkweed that colonized Center City would be far away from potential mates required for outcrossing.

Figure 17.6 Seed of common milkweed about to disperse from a colony of milkweed along railroad tracks in Center City. Wind can carry these seeds long distances. The red insect is a young nymph of the large milkweed bug (*Oncopeltus fasciatus*).

Milkweed's trouble obtaining mates downtown would constitute an Allee effect, named after the same Allee who investigated aggregation of pillbugs. Allee effects occur when low population densities impede sexual reproduction. As distances separating members of a population increase, their access to mates decreases, potentially causing reproductive failure and collapse of the population.[11] In theory, the proportion of Center City covered with concrete and asphalt is so high that it depresses population densities of milkweed and impedes sexual reproduction.

Tatyana Livshultz, pollination biologist and botanist at the Academy of Natural Sciences of Drexel University in Philadelphia, and her colleagues at the Royal Botanical Gardens, Kew, found evidence that Allee effects due to drought and thinning of milkweed populations in Africa influenced the evolution of milkweed flowers, particularly of pollinia.[12] Pollinia improve chances that pollen grains carried by pollinators reach their destination—the stigma of a milkweed plant of the same species.[13] In addition, pollinia package pollen in quantities optimized for reproduction.[14]

The evolutionary experience of milkweeds coping with Allee effects in Africa may have prepared common milkweed for Allee effects in Center City. Before railroad crews destroyed it, the colony of milkweeds growing along the railroad tracks produced abundant seedpods. Common milkweed has demonstrated that in Center City it can overcome reproductive barriers due to low population densities. Pollinia and self-fertilization both may have contributed to this success.

Light pollution

Pollinia protect pollen from becoming fodder for bees, and they facilitate pollination; but they may be vulnerable to light pollution. In 1957, Stuart W. Frost at Penn State University found milkweed pollinia attached to 290 banded tussock moths (*Halysidota tessellaris*) that had flown into light traps, mostly during the first few weeks of July. He reported that no milkweed grew near the light traps.[15] The following year he replicated these findings. He noted that the pollinia could have come from any of three milkweed species, including common milkweed.[16] I have found the banded tussock moth and its larvae in Center City. Specimens probably collected in Philadelphia are included in Titian Ramsey Peale's nineteenth-century moth collection housed at the Academy of Natural Sciences in Philadelphia.[17] The larvae feed on many kinds of shade trees, shrubs, and vines.[18]

Urban light pollution might undermine milkweed reproduction by diverting moths carrying milkweed pollinia. Such diversion would disrupt pollination and deplete stores of pollinia. Common milkweed has been shown to produce four times more nectar and double the amount of sugar during the night compared to the day.[19] Per visit to a milkweed flower, nighttime pollinators are twice as likely to produce a milkweed pod than are daytime pollinators.[20]

Despite these findings, light pollution does not explain the rarity of milkweed in Center City. In a study comparing pollination during the day and night, flowers of common milkweed exposed only to daytime pollinators produced eight times more pods than did flowers exposed only to nighttime pollinators.[21] The greater abundance of daytime pollinators of milkweed more than offsets their lower efficiency of pollination.[22]

Ozone

In theory, air pollution could disrupt milkweed pollination. Ozone destroys volatile floral hydrocarbons that attract pollinators.[23] Common milkweed in the laboratory begins to develop purple stipling when exposed to concentrations of ozone below ozone concentrations measured in Philadelphia.[24] Detrimental effects of ozone on plants, however, have been found to be greater outside core urban areas than inside.[25] The absence of purple stipling on the common milkweed that I have observed in Center City suggests that ozone is not a cause for the failure of this species to establish itself in Center City.

Pollinator scarcity

Scarcity of pollinators downtown could prevent common milkweed from making pods, especially since the railroad intensified suppression of weeds. Common milkweed requires insect pollinators even for self-pollination; neither wind nor gravity is capable of depositing milkweed's pollinia into its flowers' stigmatic chambers.

Gerald A. Mulligan and Judy N. Findlay at the Canada Department of Agriculture placed bags over flower heads of common milkweed to exclude insect pollinators; these flower heads produced no seed. They obtained similar results for a handful of other widespread weedy species, none of which is common in downtown Philadelphia.

In contrast, they did obtain seeds from bagged flowers of many of Center City's most abundant weeds. Examples are: dandelion (*Taraxacum officinale*), pigweed (*Amaranthus retroflexus*), lambsquarters (*Chenopodium album*), horseweed (*Erigeron canadensis*), fleabane (*Erigeron annuus*), purslane (*Portulaca oleracea*), smartweeds (*Polygonum persicaria, P. aviculare, P. lapathifolium,* and *P. pensylvanicum*), groundsel (*Senecio vulgaris*), foxtails (*Setaria viridis* and *S. glauca*), chickweed (*Stellaria media*), bull thistle (*Cirsium vulgare*), St. John's wort (*Hypericum perforatum*), evening primrose (*Oenothera biennis*), broadleaf plantain (*Plantago major*), and common mullein (*Verbascum thapsus*).[26]

Among the weeds Mulligan and Findlay tested, dandelion is one of the most conspicuous in Center City, where it grows in cracks in pavement and in almost any kind of soil. Dandelion makes seed asexually without insect pollinators, even though it produces showy flowers containing nectar and pollen.[27] Dandelion and common milkweed are both perennials that disperse seeds on fine strands of silk blown by wind. At first glance, dandelion's success compared to milkweed's failure in Center City might be attributed to dandelion's capacity to produce seed without pollinators.

Figure 17.7 Dandelion, like milkweed, uses silk strands to disperse seeds long distances.

Figure 17.8 Dandelion blooming in sidewalk crack on Locust Street in Center City. It produces seed asexually, eliminating dependence on insect pollinators.

On closer examination, pollinator scarcity in Center City does not offer a compelling explanation for the scarcity of common milkweed, as plants dependent on insects for pollination do produce seed in Center City. A conspicuous example is northern catalpa (*Catalpa speciosa*);[28] ailanthus is probably another, despite claims of pollination by wind.[29] Male and female ailanthus flowers reside on separate trees.[30] One survey found that a diverse group of insects, especially bees and flies, pollinate ailanthus;[31] another identified a soldier beetle (*Chauliognathus marginatus,* Cantheridae) as a principal pollinator.[32] This soldier beetle is common in Center City. I have observed it taking nectar at milkweed blossoms in Fairmount Park just outside Center City.

Figure 17.9 Ailanthus altissima in bloom. In one study, a soldier beetle was found to be a principal pollinator of ailanthus. Figure 17.10 shows this beetle on flowers of common milkweed.

Figure 17.10 Soldier beetle (*Chauliognathus marginatus*) on common milkweed off Martin Luther King Drive in Fairmount Park. Pollinia from milkweed are attached to tarsi of two legs. This species also pollinates ailanthus trees.

In Center City white clover (*Trifolium repens*) is another wild plant that produces seed only after insect pollination.[33] Its flowers here attract bumblebees and honeybees.

Scarcity of space

By increasing the number of its flower-bearing stalks, common milkweed can increase the number of flowers that it presents to pollinators; but lack of growing space in Center City limits such expansion. A milkweed seedling normally spreads vegetatively before it flowers. During its initial year of growth, it does not flower, but first sends off horizontal roots that produce new shoots from root buds. By the time it flowers the second year, it has already established vegetative clones with many stems, each producing three to seven heads of flowers. During four years, one common milkweed seedling produced fifty-six stalks vegetatively and ninety-six seedlings in an area of 9 square meters.[34] In Center City, space big enough to accommodate such reproductive sprawl is rare.

Ailanthus and catalpa, as trees, can offer pollinators nectar and pollen on a large scale.

White clover, spreading vegetatively in lawns, produces carpets of flowers, presenting pollinators with bountiful offerings of food. In contrast, lack of space constrains the mass of flowers that common milkweed can muster for pollinators in Center City compared to areas just outside, as in Fairmount Park.

Figure 17.11 Honeybee with pollen basket filled with pollen from white clover (*Trifolium repens*). Pollen baskets of honeybees visiting milkweed remain empty.

Figure 17.12 A carpet of white clover on a lawn offers pollinators a bountiful source of nectar and pollen. Flowers grow just below the height of lawn mower blades.

Persecution

Concrete and asphalt are the primary physical barriers to formation of big colonies of common milkweed in Center City, but other barriers may be more important in impeding its establishment downtown. Seedlings of common milkweed take two growing seasons to mature, typically in full sun.[35] Pod-bearing stems grow to a height of a meter or more. To produce seed, the conspicuous stalks of common milkweed must, for two consecutive years, escape the scrutiny of hostile property owners, landscape maintenance crews, and others who would regard them as unsightly intruders. In Center City, I can think of few places where common milkweed could escape persecution.

Other wild herbaceous plants in Center City are better adapted for evading detection. Seedlings of tall annual weeds like pigweed (*Amaranthus hybridus*) mature in half the time that it takes milkweed, and biennials (which take two years to mature) typically keep a low profile their first year, when they form rosettes, as in the case of Queen Anne's lace (*Daucus carota*). White clover is a perennial like milkweed, but in Center City it keeps its flower heads below the height of lawn mower blades. Lambsquarters (*Chenopodium album*) produces seed on intrusive-appearing plants a meter tall, like common milkweed, but in Center City lambsquarters also makes seed on plants whose height is a tenth of a meter. Grasses, plantains (*Plantago*), and other denizens of pavement in Center City hide below pedestrians' sight lines, and they tolerate trampling. Lawn pennywort (*Hydrocotyle sibthorpioides*), a perennial like milkweed that produces flowers in umbels and spreads vegetatively, completes its life cycle completely within cracks between the bricks of our front sidewalk.

Herbicide

In 1999 Robert G. Hartzler at Iowa State University found that common milkweed was present in 51 percent of fields of corn and soybean in Iowa. Ten years later, the number had dropped to 8 percent. Hartzler blamed the declines on glyphosate, an herbicide whose use increased after introduction of corn and soybeans genetically engineered to resist this herbicide.[36] John M. Pleasants and Karen S. Oberhauser, also at Iowa State University, found that declines in populations of common milkweed coincided with an 81 percent decline in Midwestern production of monarch butterflies, whose larvae feed on milkweed. They concluded that widespread agricultural use of glyphosate reduced populations of monarch butterflies and made them more vulnerable to other threats.[37] In 2011 railroad crews used herbicide to kill Center City's only seed-producing colony of milkweed.

In 1784 John and William Bartram sent common milkweed to a European patron,[38] presumably for a garden. Currently in Center City, gardeners cultivate tropical milkweed (*Asclepias curissavica*), swamp milkweed (*Asclepias incarnata*), and butterfly weed (*Asclepias tuberosa*); common milkweed would probably thrive in Center City if left alone with space to grow.