

**A Study of Floral Morphologies Promoting Outcrossing in Plant Species at Litzsinger Road  
Ecology Center**

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## Abstract

Outcrossing in plants is important for genetic diversity in a species. Plants that self-pollinate are prone to inbreeding depression, which reduces biological fitness in changing environments. While there are some advantages to self-pollination, such as still being able to reproduce in the absence of pollinators, outcrossing promotes genetic diversity which is beneficial for the species to adapt to changes in their environments. Plants can promote outcrossing in many unique ways. This study aims to observe the different ways flowers promote outcrossing morphologically. Over the course of 6 weeks of the summer, many prairie and woodland plant species were observed. A list of 23 species with unique morphological barriers to self-pollination were observed. The results showed many different mechanisms for increasing outcrossing, such as herkogamy, dichotomy, dioecious and monoecious species.

## Introduction

Genetic outcrossing increases gene flow, which supports biodiversity. In plants, outcrossing occurs when a flower is fertilized through the transfer of pollen from a flower of a different individual. This allows for an exchange of genetic material to create a genetically diverse population. The opposite of this, called self-fertilization, or “selfing”, occurs when a flower fertilizes itself. Selfing limits the exchange of genetic material among individuals, which can negatively impact biodiversity in populations over time and increase homozygosity. This can reduce offspring fitness and fertility by increasing the expression of lethal recessive traits, which in turn negatively affects plant stature, vigor, and yield (Merrick et al., 2023).

Evolutionarily, there is a strong selection for preventing self-pollination. Many flowering species have self-incompatibility systems which are designed to reject pollen from the same flower during fertilization, a process that is biochemically complex (Wright et al., 2013). However, this is difficult to observe physiologically. This study focuses on physical and observable ways that flowering plants promote outcrossing. There are many physiological mechanisms flowers may exhibit that prevent self-fertilization. One effective mechanism is dioecy, in which the species has separate male (staminate) flowers and female (pistillate) flowers on different individuals. Spicebush (*Lindera benzoin*) and box elder (*Acer negundo*) are dioecious species. This makes it impossible for individuals to breed with themselves, promoting outcrossing. Another common mechanism is monoecy, in which the individual plant has both separate pistillate and staminate flowers on the same individual. These flowers are separate structures (i.e., imperfect) but can be found on the same plant. This prevents the pollen of a flower from fertilizing the stigma of the same flower. (Slafer et al., 2003). A common example of this mechanism is seen in cattail flowers (*Typha*). In cattails the female flowering spike is located below the male flowering spike on the inflorescence stalk. Another example of this seen in the area is Oak trees (*Quercus*). On oaks, male flowers are arranged as hanging catkins, female flowers are separated on the branch and are typically solitary or in small clumps (Yatskievych, 2013).

However, most flowers are perfect, meaning they contain both male and female parts within the same flower. Morphological and temporal barriers in reproduction have evolved in perfect flowers to prevent selfing. One mechanism is herkogamy. Herkogamy is the spatial separation of anthers and stigmas within a flower. Often this is seen as the style of a flower protruding away from the anthers so that they are less likely to touch and fertilize itself. Curvature of the style to the left or right is called enantiostyly and is seen in many flowering species. Another type of herkogamy is heterostyly. This is the

variation of style and filament heights in different flowering individuals. For example, in heterostylous species, one individual plant would exhibit flowers with long styles and short filaments, (called a pin flower) which presents pollinators the stigma of the flower. Other individuals in the species would exhibit flowers with short styles and long filaments (called a thrum flower), presenting the pollinators with anthers (Simpson, 2019). This mechanism decreases the chance of the flower to pollinate itself due to the spatial separation of the reproductive parts. This also affects pollen deposition on pollinators. In heterostylous species, pollinators typically collect pollen in a way that promotes transfer between different floral morphs (such as from pin to thrum flowers) rather than between flowers of the same type, which increases the likelihood of cross-pollination (Slafer et al., 2003). An example of this is winged loosestrife (*Lythrum alatum*).

Another common mechanism to promote outcrossing is the temporal differences of maturation of anthers and stigmas, named dichotomy. In this mechanism, flowers exhibit both male and female parts, however they mature at different times. Protandry is the term for flowers that have earlier development of the androecium, before the gynoecium. Protogyny is the term for flowers with earlier development of the gynoecium (Master Gardeners of Northern Virginia, 2023).

This project aims to survey the different types of flower morphology that promotes outcrossing at Litzsinger Road Ecology Center, which types are more commonly found, and which plant families commonly exhibit these adaptations.

## Methods

Surveys were performed at the Litzsinger Road Ecology Center, a 39-acre area featuring 35-year-old bottomland woodland and prairie restoration alongside Deer Creek, an urban creek in Ladue, Missouri. Survey dates were between June and July of 2025. The surveying process started with looking at what was in bloom within the prairie and woodland areas. Flowers that exhibited types of herkogamy (i.e. enantiostyly, heterostyly), dichogamy, monoecy, or dioecy were compiled in an observation list. Each species was documented on iNaturalist for reference, which includes the date and location of the observation as well as photos of the flower. Photos were taken using a Canon EOS Rebel T5 camera with a 0.25m/0.8ft macro lens to get magnified photos of the floral parts of interest. For smaller flowers, such as disk florets of *Heliopsis helianthoides*, a microscope was used to enlarge the small florets at different stages for a clearer image of the floral parts of interest. These photos were taken with an iPhone camera.

## Results

This study resulted in an observation list of flowering plants that have physical barriers to self-pollination. One of the most common barrier types seen was herkogamous flowers. 10 observed species had styles that significantly protruded away from the anthers. Examples of this kind of morphology include *Hemerocallis fulva*, *Calystegia sepium*, *Blephilia hirsuta*, *Solanum carolinense*, *Campanula americana*, *Monarda fistulosa*, *Teucrium canadense*, and *Scrophularia marilandica*. Another type of herkogamous flower, heterostyly, is seen in *Lythrum alatum*, which is found commonly throughout the prairies at LREC. Many individuals of both pin and thrum morphologies are found, commonly near each other.

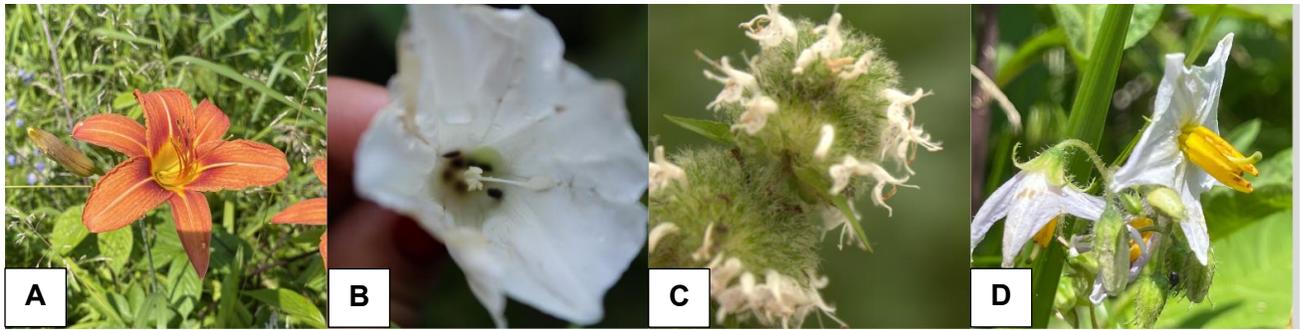


Figure 1. (A) *Hemerocallis fulva*, (B) *Calystegia sepium*, (C) *Blephilia hirsuta*, (D) *Solanum carolinense*.

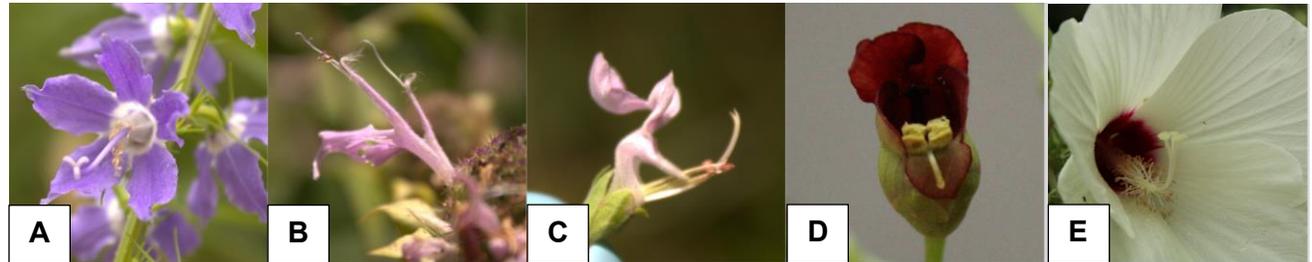


Figure 2. (A) *Campanula americana*, (B) *Monarda fistulosa*, (C) *Teucrium canadense*, (D) *Scrophularia marilandica*, (E) *Hibiscus lasiocarpus*.

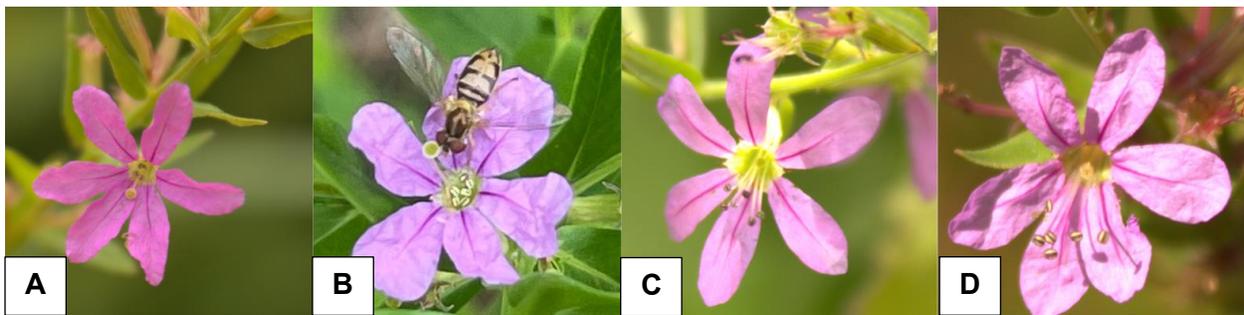


Figure 3. (A, B) *Lythrum alatum* pin flowers, (C, D) *Lythrum alatum* thrum flowers.

Another type of mechanism observed was monoecious species. Examples of this flower type include *Tripsacum dactyloides* and *Typha angustifolia*. In *T. dactyloides*, the staminate flowers are above the pistillate flowers. *Typha angustifolia* also has staminate flowers above the pistillate, but these are compact spikelets on a stalk. Directly below the staminate spikes are the pistillate spikes.

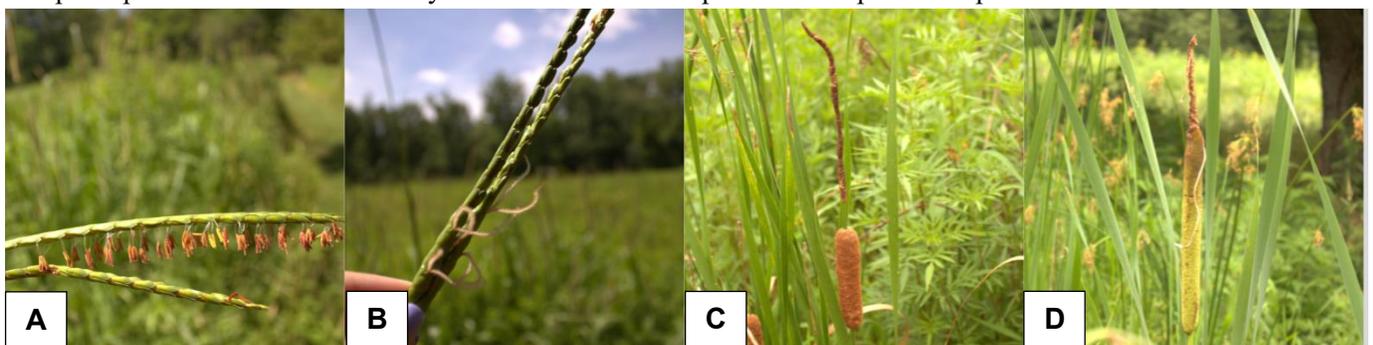


Figure 4. (A) *Tripsacum dactyloides* staminate flowers (B) *T. dactyloides* pistillate flowers, (C, D) *Typha angustifolia*.

10 species with floral dichotomy were observed. Examples include *Heliopsis helianthoides*, *Silphium integrifolium*, *Vernonia missurica*, *Ratibida pinnata*, *Rudbeckia subtomentosa*, *Rudbeckia hirta*, *Helianthus mollis*, *Eryngium yuccifolium* and *Liatris pycnostachya*. The only example of observed protogyny was *Plantago lanceolata*.

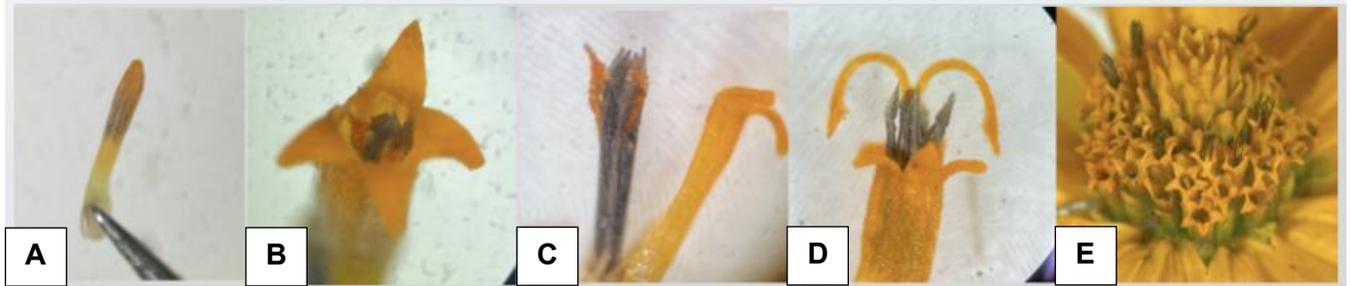


Figure 5, *Heliopsis helianthoides* disk flower stages under microscope. (A) closed floret, (B) opened floret with anthers producing pollen, (C) stamen view with petals removed and emerging style (not yet receptive), (D) style branches parted and receptive of pollen, (E) entire capitulum, disk flowers at different stages.



Figure 6. (A) *Silphium integrifolium*, (B) *Vernonia missurica*, (C) *Ratibida pinnata*, (D) *Rudbeckia subtomentosa*.



Figure 7. (A) *Rudbeckia hirta*, (B) *Helianthus mollis*, (C) *Liatris pycnostachya*, (D) *Plantago lanceolata*.

The last type of mechanism observed is dioecious species. The only observable species on site with dioecious flowers (that was flowering at the time of the study) is *Buchole dactyloides*. However, the known patch of this species had been mowed before observing and was not showing any flowers. Photos were taken from an iNaturalist observation from the previous year located at LREC.



Figure 8. *Buchole dactyloides* staminate flowers (left) and pistillate flowers (right).

Table 1. List of observed species that have a physical mechanism for promoting outcrossing at Litzsinger Road Ecology Center. The list includes the species, its mechanism for promoting outcrossing, location, family, C- value, description of flower, flowering phenology (the months it flowers on average), pollinators observed, a link to the iNaturalist observation, and any extra notes (such as common name, if it was introduced, etc.). Species with a C-value listed as “\*” are introduced to Missouri and do not have an associated C- value.

Species	Mechanism	Location	Family	C Value	Description of flower	Phenology	Pollinators observed	Notes	Link to iNat Observation
<i>Lythrum alatum</i>	Heterostyly; Dimorphic lengths of stamen and pistils	Prairies	Lythraceae	6	Actinomorphic; the hypanthium much longer than wide; stamen 6, anthers usually dark purple, variable in length; pistils with nectary disk, also variable in length due to its dimorphism.	May-September	Toxomerus marginatus (Margined calligrapher fly) on a pin flower	2 flower forms: pin and thrum, both populations found; common name Winged Loosestrife	<a href="https://www.inaturalist.org/observations/292625716">https://www.inaturalist.org/observations/292625716</a> <a href="https://www.inaturalist.org/observations/292626229">https://www.inaturalist.org/observations/292626229</a>
<i>Tripsacum dactyloides</i>	Monoecious; Pistillate and staminate flowers separate on stalk	Prairies	Poaceae	5	Staminate spikelets paired along 1 side of the flattened axis; Pistillate spikelets single, the lowermost usually sterile and reduced, the uppermost fertile.	May-September		Common name Gama Grass	<a href="https://www.inaturalist.org/observations/292625546">https://www.inaturalist.org/observations/292625546</a>
<i>Hemerocallis fulva</i>	Enastioistyly	Center of south prairie	Liliaceae	*	Petals 3 Sepals 3, Stamens 6, the filaments arched and all positioned on one side of the flower. Style 1, parallel to the filaments of the stamens but extending away from stamens.	May-August		Introduced species; common name Orange Daylily	<a href="https://www.inaturalist.org/observations/288757704">https://www.inaturalist.org/observations/288757704</a>
<i>Calystegia sepium</i>	Style protruding away from stamens	Prairies	Convolvulaceae	1	Stamens 5, alternating with corolla lobes, not exerted. Pistil 1 per flower, of 2 fused carpels. Ovary superior, one style 2	May-September		Common name Hedge Bindweed	<a href="https://www.inaturalist.org/observations/292180822">https://www.inaturalist.org/observations/292180822</a>

					stigmas higher out than the stamens.			
<i>Blephilia hirsuta</i>	Stamens are tucked into the flower until mature	Woodlands and garden beds	Lamiaceae	7	Clustered towards ends of the stems with pointed bracts and hairy fringes; have an upper and a 3-lobed lower lip, asymmetrical; 2 stamens tucked into the flower until maturity; style protruding out.	May-September		Also a possible timing difference in maturity between the male and female parts; common name Hairy Wood Mint <a href="https://www.inaturalist.org/observations/292181232">https://www.inaturalist.org/observations/292181232</a>
<i>Solanum carolinense</i>	Enantiostyly, extends out and away from anther ring	Roadside and prairies	Solanaceae	0	Stamens 5, alternating with corolla lobes; thick banana shaped anthers surrounding the protruding style.	May-October		Common name Horse Nettle <a href="https://www.inaturalist.org/observations/294837078">https://www.inaturalist.org/observations/294837078</a>
<i>Campanula americana</i>	Strongly exerted and curved style	Woodlands and prairies	Campanulaceae	4	Saucer shaped corolla with 5 petal lobes, elongate calyx tube, stigma 3 lobed, style exerted and curved, about double the length of filament.	July-September		Common name Tall Bell Flower <a href="https://www.inaturalist.org/observations/296054371">https://www.inaturalist.org/observations/296054371</a>
<i>Monarda fistulosa</i>	Style longer and protrudes out from stamens	Prairies	Lamiaceae	4	Light purple/pink 2 lipped flowers, upper lip straight and hairy, lower slender and often toothed; stamen and style viable and extend past corolla.	May-August		Common name Wild Bergamot <a href="https://www.inaturalist.org/observations/296845920">https://www.inaturalist.org/observations/296845920</a>
<i>Typha angustifolia</i>	Monecious; male flower stalk directly above female	Savannah and creek	Typhaceae	0	Thousands of staminate flowers densely packed on stalk, separated by a couple inches of stem from the female flowers, which	May-August		Invasive in the Midwest; flowers seen may have been done flowering and in <a href="https://www.inaturalist.org/observations/297982261">https://www.inaturalist.org/observations/297982261</a>

					are also densely packed.			the process of fruiting, many staminate flowers have dropped; common name Narrowleaf Cattail	
<i>Eryngium yuccifolium</i>	Dichogamy; protandrous, pollen is shed before stigma is receptive	Prairies	Apiaceae	8	Stamens 5, distinct, folded back on themselves at first and then erect and exerted.	June-September	Xylocopa virginica; Eastern Carpenter Bee	Appears that styles emerge first, but don't become receptive until staminate flowers are done releasing pollen; common name Rattlesnake Master	<a href="https://www.inaturalist.org/observations/296845607">https://www.inaturalist.org/observations/296845607</a>
<i>Teucrium canadense</i>	Protruding styles	Prairies	Lamiaceae	2	Corolla flower with no upper lip, stamen long and arching, style strongly exerted.	June-September		Common name American Germander	<a href="https://www.inaturalist.org/observations/292180177">https://www.inaturalist.org/observations/292180177</a>
<i>Heliposis helianthoides</i>	Protandry	Prairies	Asteraceae	5	Ray florets pistillate, 10-80 disk florets perfect brownish or greenish yellow; style branches with the sterile tip somewhat elongate and tapered.	May-October		Common name False Sunflower	<a href="https://www.inaturalist.org/observations/296844818">https://www.inaturalist.org/observations/296844818</a>
<i>Plantago lanceolata</i>	Protogyny	Open disturbed areas	Plantaginaceae	*	Terminal elongate spikes coming out from basal rosette, stamens 4, flowers bloom from bottom to top, female matures first.	April-October		Common name Narrow Leaf Plantain	<a href="https://www.inaturalist.org/observations/299864291">https://www.inaturalist.org/observations/299864291</a>
<i>Buchloe dactyloides</i>	Dioecious	Roadside	Poaceae	5	Produces pollen or seeds on separate plants, reproduces by stolon's so large patches of just one	May-August		Common name Buffalo grass; couldn't find it flowering myself	<a href="https://www.inaturalist.org/observations/216381182">https://www.inaturalist.org/observations/216381182</a>

					flower type may form.			due to mowing but there is an iNat identification from last year by Caity that includes both flowering sexes.	
<i>Liatrix pycnostachya</i>	Protandry	Prairies	Asteraceae	6	Ray florets absent, disk florets pink, stamens 5 connate around style, style exerted.	July-October		Common name Prairie Blazing Star	<a href="https://www.inaturalist.org/observations/298768792">https://www.inaturalist.org/observations/298768792</a>
<i>Silphium integrifolium</i>	Protandrous; ray florets pistillate, disks staminate (has nonfunctional pistils)	Prairies	Asteraceae	4	Ray florets (20-35) pistillate and fertile; yellow corolla; disk florets staminate with nonfunctional pistils (undivided).	July-September		Disk flowers have exerted styles but are undivided and nonfunctional, ray flowers have fertile pistils; common name Rosinweed.	<a href="https://www.inaturalist.org/observations/292180612">https://www.inaturalist.org/observations/292180612</a>
<i>Vernonia missurica</i>	Protandry	Prairies	Asteraceae	5	32-60 disk florets per head, deeply lobed purple corolla.	July-September		Common name Missouri Ironweed	<a href="https://www.inaturalist.org/observations/298506377">https://www.inaturalist.org/observations/298506377</a>
<i>Scrophularia marilandica</i>	Exserted style	Woodlands and roadside	Scrophulariaceae	3	Darker staminode present higher than fertile stamen, style exerted and bends below stamen.	July-October	Hummingbirds	Common name Fig Wort	<a href="https://www.inaturalist.org/observations/302182390">https://www.inaturalist.org/observations/302182390</a>
<i>Helianthus mollis</i>	Protandry	Prairies	Asteraceae	6	Sterile ray florets (17-30), disk florets perfect, 5 stamens, anthers connate around style, style exerted beyond anthers.	July-October		Common name Ashy Sunflower, started blooming right before observations completed	<a href="https://www.inaturalist.org/observations/303614435">https://www.inaturalist.org/observations/303614435</a>

<i>Hibiscus lasiocarpus</i>	Exserted style, anthers fused to style below stigma	Prairies and roadside	Malvaceae	5	Numerous stamens on staminal column, 5 parted style.	July-October		Common name Hairy Rose Mallow	<a href="https://www.inaturalist.org/observations/302431556">https://www.inaturalist.org/observations/302431556</a>
<i>Ratibida pinnata</i>	Protandry	Prairies	Asteraceae	4	Sterile ray florets (6-15) yellow and drooping, disk florets numerous.	May-September		Common name Grey-headed Coneflower	<a href="https://www.inaturalist.org/observations/296845535">https://www.inaturalist.org/observations/296845535</a>
<i>Rudbeckia subtomentosa</i>	Protandry	Prairies	Asteraceae	5	Ray florets sterile (12-20), disk florets numerous and perfect, stamens 5 connate around style.	July-October		Common name Sweet Coneflower	<a href="https://www.inaturalist.org/observations/299872629">https://www.inaturalist.org/observations/299872629</a>
<i>Rudbeckia hirta</i>	Protandry	Prairies	Asteraceae	1	Ray florets sterile 8-21; disk florets numerous and perfect; stigma lobes elongate and pointed at tip.	May-October		Common name Black Eyed Susan	<a href="https://www.inaturalist.org/observations/298505233">https://www.inaturalist.org/observations/298505233</a>

## Discussion

The results of this survey show the diversity of morphologies and mechanisms that flowering plants use to promote outcrossing with other individuals. 23 examples were observed on site, including herkogamy, dioecy, monoecy, and dichotomy. The results suggest that there is not one adaptation to promote outcrossing, but many unique ones that serve the plant and its pollinators best. Eight examples of protandry were observed, specifically all in the Asteraceae family. Many of the species in the Asteraceae family evolved protandrous flowers to promote outcrossing with other individuals (Simpson, 2019). Protandrous flowers were the highest observed adaptation, likely due to the timing of composite flowers blooming during the study period. The Asteraceae family is the most speciose plant family in North America and is morphologically diverse as well. The Asteraceae's ability to promote outcrossing could be a factor in this trait. Within the composite head of Asteraceae flowers, there are numerous tube-shaped florets (disc florets) that have a unique blooming method. As the style elongates within the floret, it lifts the pollen out of the tube where it can be accessed by pollinators. At this stage, the stigma is not yet receptive to pollen since it is not yet matured. The style remains shut for enough time to pass for the pollen to be collected by pollinators. Then the style will separate, and each side will curl backward once the stigma is receptive to pollen (In Defense of Plants, 2019). This process is seen in Figure 5 of *Heliopsis helianthoides*.

All Asteraceae composite head florets observed matured from the outside in, likely to prevent nearby florets from pollinating each other. This also was observed in *Plantago lanceolata*. Florets matured from the bottom to top of the stalk, with the pistils maturing before the anthers ensuring successful outcrossing. This maturation pattern may ensure that florets that are near each other are in the same stage of maturity and cannot pollinate each other.

There were 10 species observed that exhibited herkogamous floral morphologies, making it the most observed floral adaptation. This shows that it is a simple yet effective mechanism to promote outcrossing. Three of which are in the family Lamiaceae (*B. hirsuta*, *M. fistulosa*, *T. canadense*), which may imply that the Lamiaceae family flower type promotes outcrossing in other species as well. There are likely many more herkogamous species at LREC that were not observed or in bloom at the time of the study.

The lack of monoecious flowers suggests the importance of considering phenology in this project. Since the observations were restricted to late June-August, it does not account for many early spring flowers that are monoecious. Many trees are monoecious, including oaks and some maples. Although this paper outlines the importance of outcrossing, there are still benefits for a plant to self-pollinate. Self-pollination reduces pollen wastage, maintain useful genetic traits, and does not need to rely on pollinators to facilitate fertilization. However, self-pollination reduces genetic diversity, which is important for populations to adapt to a changing environment and withstand disease (Advantages & Disadvantages of Self- vs. Cross-Pollination | Pollination Education, 2022). The Litzsinger Road Ecology Center is prone to disturbance by flooding and prescribed fire, therefore having high genetic diversity is useful for plants to adapt to these changes.

Various forms of herkogamy, such as heterostyly and enantiostyly, can strategically deposit pollen on a specific area of the pollinator's body. This allows for pollen from the anthers of one flower to

transfer on to the stigma of a complementary floral morph in another individual. This floral adaptation ensures that different flower morphs on different individuals are exchanging genetic material (Slafer et al., 2003). For example, the curvature of the stigma of *Scrophularia marilandica* will pick up pollen from the bill of a hummingbird as it reaches for the nectar inside the flower (Personal observation, Maddie Wood, 2025). Another observed example is of *Lythrum alatum*. A pollinator, such as a bee, that visits a thrum flower morph will get pollen deposited on the lower abdomen as it collects the flowers nectar. Then, if it visits a pin flower morph, the lower abdomen will brush against the stigma of exerted style as it collects flower nectar. This deposition of pollen strategy helps promote outcrossing of different individuals and limits pollen wastage.

It is important to acknowledge that this survey does not include every flowering species with barriers to self-pollination. This is likely only a handful of species that exhibit a unique morphological barrier. The time constraints of this study limits this to about 6 weeks of observations. A further study should observe the flora of the site for an entire year to fully represent all species. Another study could observe pollinator interactions, as many of these flowers with herkogamy deposits pollen on a specific spot on the pollinator.

## Conclusion

There are various ways that flower morphology at the Litzsinger Road Ecology Center promotes outcrossing. Separating male and female structures and shifting the orientation of the style are unique and fascinating ways that plants encourage outcrossing. Although many plants have a physiological self-incompatibility system to reject pollen from itself, physical barriers are the first line of defense to prevent inbreeding. These floral strategies contribute to the beauty and importance of flowers.

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