Plant interactions for pollinator visits: a test of the magnet species effect

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Summary. From 1985–1987, patterns of fruit and seed set were studied in a population of mayapple *(Podophyllum peltatum)*, a clonal, self-incompatible herb found in deciduous woods in eastern North America. Mayapple flowers do not produce nectar, but depend on infrequent visits by nectar-seeking queen bumble bees for pollination. In all years female reproductive success in mayapple colonies was influenced by colony size (number of flowers), by the distance to neighbouring colonies and by proximity to lousewort plants *(Pedicularis canadensis)*, a prolific nectar producer heavily visited by bumble bees. In all years fruit and seed set were greater in mayapple colonies <25 m from lousewort flowers than in matched colonies which were >50 m from lousewort. In 1985 and 1987 the frequency of queen bumble bee visits to flowers in colonies close to lousewort was about four times greater than to distant colonies. In 1986 I removed about 80% of lousewort flowers to test whether the enhanced fruit and seed set in mayapples close to lousewort was pollinator mediated. Mayapple colonies close to flowerless lousewort patches did not differ in fruit or seed set from matched colonies >50 m from lousewort. In contrast, mayapples close to flowering lousewort patches had greater fruit and seed set compared with distant colonies. Over all years, a larger proportion of mayapples close to flowering lousewort patches had enhanced fruit and seed set compared with colonies close to louseworts without flowers. Though rarely documented, this type of facilitative interaction between plants that are highly attractive to pollinators ("magnet" species), and co-flowering species that are rarely visited by pollinators, may be widespread in plant communities.

Key words: Mayapple – *Podophyllum peltatum* – Lousewort – *Pedicularis canadensis* – Pollinator facilitation

Plant species flowering at the same time and place may interact for pollinator visits in a variety of ways (Rathcke 1983, 1988; Feinsinger 1987). If co-flowering plant species share the same pollinators they may compete for pollination services and seed and fruit set may be pollinator limited. Competitive interactions have been reported in some studies (Waser 1978, 1983; Campbell 1985a, b; Rathcke 1988; Galen and Gregory 1989) though other studies of natural plant communities have found little evidence for competition even when plants shared the same pollinators (Schemske et al. 1978; Thomson 1981, 1982; Motten 1986). A contrasting possibility is that co-flowering species could experience facilitation when one species attracts pollinators that also visit another species, or when the total attractiveness of the mixed species association enhances flower visitation rates relative to those any single species would experience in isolation.

Some of the most likely cases in which facilitation could operate include plant species that are rare and widely dispersed (e.g. Schemske 1981; Thomson 1982, 1983; Feinsinger et al. 1986) as well as species that depend on pollinator visits but do not offer attractive floral rewards (e.g. Brown and Kodric-Brown 1979; Nillson 1980; Pellmyr 1986; Laverty and Plowright 1988). In such species, fruit and seed set may often be pollinator limited and female reproductive success may be locally enhanced in areas where plants are associated with "magnet" species (Thomson 1978) that are highly attractive to pollinators.

A previous study (Laverty and Plowright 1988), found that proximity to lousewort *(Pedicularis canadensis)* plants was associated with enhanced fruit and seed set in mayapple *(Podophyllum peltatum)*. This suggested that lousewort might act as a magnet species to facilitate pollination in mayapple. In the study reported here, I assessed the effect of proximity to lousewort on mayapple fruit and seed set over several years and measured the response of mayapples to partial removal of lousewort flowers.

Ecology of mayapple and lousewort

Mayapple (*Podophyllum peltatum* L., Berberidaceae) is a common perennial herb found throughout eastern North

America (Meijer 1974). Individual plants form discrete colonies consisting of one to several thousand sexual and asexual stems. Sexual stems have a pair of leaves and a single large (3–4 cm diameter) white flower. The flowers are open, nectarless, have numerous stamens and last for about 6–9 days. Previous studies indicate that most colonies are self-incompatible clones that depend primarily on infrequent visits by queen bumble bees for cross-pollination and that fruit set is usually limited by insufficient pollination (Swanson and Sohmer 1976; Rust and Roth 1981; Laverty and Plowright 1988; Whistler and Snow 1990).

Lousewort (*Pedicularis canadensis,* Scrophulariaceae) is a perennial herb, occurring in upland woods throughout eastern North America. The yellow and red flowers are strongly zygomorphic and are presented on an upright spike of 10–25 flowers. The flowers produce large amounts of nectar and are pollinated exclusively by bumble bees (Macior 1976; pers. obs.).

Methods

Study area and sampling

From 1985–1987, I studied fruit and seed set in a population of 122 mayapple colonies in a strip (0.5 km by 1.5 km) of beech-maple woodland on Amherst Island (44° 07′ N; 76° 45′ W) at the northeast end of Lake Ontario (see Laverty and Plowright 1988). The central part of the wood also contained 13 patches of lousewort (Fig. 1). Other plant species that flowered at about the same time as lousewort and mayapple (mid-May to early June) included *Actea rubra, Phlox divaricata, Ribes* spp., *Smilacina racemosa, Tiarella cordifolia,* and *Viola* spp. The possible influence of these species on mayapple reproductive success was not assessed in this study, because in contrast to lousewort, they were widely dispersed throughout the study area and, with the exception of *Ribes,* they were not commonly visited by bumble bees.

In 1985, the locations of mayapple and lousewort patches were mapped and distances between patches were measured. Mayapple colonies were defined as groups of sexual and asexual stems growing closely together with no other stems within at least 3 m. Each year
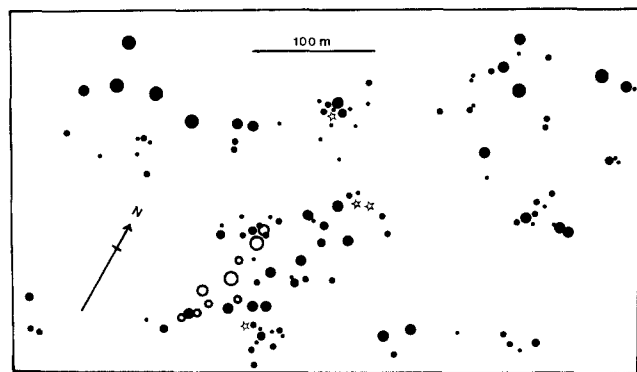

Fig. 1. Map of the central portion of the study area in 1987 showing the location of mayapple colonies (closed circles) and lousewort patches (open circles and stars). Circle diameter indicates patch size: five classes for mayapple (1–10, 11–50, 51–100, 101–500, and > 500 flowering stems); three classes for lousewort (10–50, 51–100, and 101–850 flowering spikes; the 4 patches indicated by stars ranged in size from 45 to 112 flowering spikes. All lousewort flower spikes were removed in 1986 except in starred patches

I censused every colony in the population in mid to late May and recorded the number of sexual stems (flowers) per colony. In 1986 and 1987 the number of sexual stems in very large colonies (> 300 flowers) was estimated by counting stems in m² subplots and multiplying the average by the approximate area of the colony. Fruit set was recorded in mid to late July using subsampling for very large colonies. Seed set per colony was estimated from a sample of ripe fruits from each colony. All fruits were collected from colonies setting fewer than 5 fruits; 5 or 10 fruits were sampled from colonies with 5–100 fruits and > 100 fruits, respectively. Samples were collected across the diameter of each colony.

Assessing the effect of lousewort

In 1985, 9 patches of lousewort were identified in the wood. Analysis of factors influencing intercolony variation in mayapple fruit and seed set (Laverty and Plowright 1988) indicated that fruit and seed set were enhanced in colonies close to lousewort. In May 1986, I tested this effect experimentally by removing all flower spikes from each of the 9 lousewort patches in the wood before mayapples began to flower. In 1987, I again monitored the mayapple population but without manipulating lousewort plants in the 9 patches. However, in 1987 I discovered 4 additional lousewort patches which had not been detected during 1985 or 1986 (Fig. 1, stars). These 4 patches were too large to have been newly established in 1987, and must have been present and flowering during 1985 and 1986.

I incorporated data on the 4 additional lousewort patches, recalculated distances from each mayapple colony to all 13 lousewort patches and reanalysed 1985 data on mayapple fruit and seed set. For 1986, the presence of the additional lousewort patches meant that only about 80% of lousewort flowers had been removed rather than 100%. This partial removal provided a means of testing whether enhanced fruit and seed set in mayapples close to lousewort were due to site effects (e.g. soil type) or to increased pollination (see below).

Pollinator activity

Observations of pollinator activity for 1985 (reported in Laverty and Plowright 1988) suggested that visit frequency to mayapple colonies increased as distance to lousewort patches decreased. No comparisons of pollinator visits to close and distant mayapple colonies were made in 1986 because I assumed that all lousewort flowers in the wood had been removed. In 1987, I compared the frequency of visitors to mayapple flowers in colonies (with > 10 flowers) that were close to and distant from lousewort patches. Visitors were sampled in 10 min observation periods made at different times during the day. Bumble bees were identified to species. I also sampled the frequency of visitors to lousewort as well as other common plant species in the study area.

Data analysis

I used one way ANOVA to compare characteristics of mayapple colonies among the three years. The effect of proximity to lousewort patches on sexual reproduction in mayapple was assessed in three separate analyses. First, I used multiple regression to determine which factors were important in accounting for intercolony variation in mayapple reproduction within each year. Dependent variables were fruit set per colony (fruits/flowers) and average seed set per colony. Independent variables tested included the number of flowers in a colony (FL = colony size), the average distance to the 5 nearest neighbouring mayapple colonies (NN5), and the distance from a mayapple colony to lousewort patches. The distance to lousewort was expressed in several ways: minimum distance, average distance of each mayapple colony to the 13 lousewort patches, and the sum of the reciprocal of the distance to each lousewort

patch weighted by the size (number of flowering spikes) of the patch (LDS). For the 4 additional lousewort patches discovered in 1987, I used the spike numbers recorded in 1987 when calculating LDS for 1985 and 1986. The rationale for calculating LDS was that the number of pollinators visiting a lousewort patch should be roughly proportional to the number of flowers in the patch; thus LDS should be a more sensitive measure of the probability of receiving pollinator visits than proximity to lousewort alone.

A second analysis made a more direct test of the hypothesis that mayapples benefit from being close to lousewort flowers. I compared fruit and seed set in colonies that were relatively close (<25 m) to lousewort with a matched set of colonies that were relatively distant (>50 m) from lousewort using nested ANOVAS. Within each year, I first ranked all mayapple colonies by the minimum distance to a lousewort patch. Each close colony was then paired with the most similar distant colony for neighbour distance (NN5) and colony size (FL), since these intraspecific variables were often significant in multiple regressions. Pairs of close and distant colonies among years rarely involved the same colonies because colony sizes changed among years.

A third analysis used several types of comparisons to assess the effect of lousewort on fruit and seed set in mayapple colonies in 1986. First, I used paired t tests to compare fruit and seed set in 13 mayapple colonies (manipulated group) that were within 25 m of flowerless lousewort patches, but >50 m from the 4 remaining patches, with matched colonies that were distant (>50 m) from lousewort plants. Second, I compared fruit and seed set in a group of 15 mayapple colonies (unmanipulated group) that were close (<25 m) to the 4 remaining flowering lousewort patches, with matched colonies that were more distant (>50 m). Third, I tested the effect on the manipulated group in relation to the difference in sexual reproduction between close and distant unmanipulated colonies in all three years. I calculated the difference between each pair of matched colonies in fruit or seed set (close – distant), and recorded the number of pairs in which the difference was positive (i.e. the close patch had greater fruit or seed set than the matched distant patch), or negative (including no difference between pairs). I then tested whether the frequency of positive and negative outcomes differed among manipulated and unmanipulated pairs using G tests.

Results

Population characteristics

Table 1 summarizes characteristics of mayapple colonies in the wood over the three years. Both the number of

Table 1. Mayapple population data for 1985–1987. Values indicate mean $\pm$ SD (range)

Variable	1985	1986	1987
Colonies Flowering	114	105	112
Colony size	141.7 $\pm$259.3 (1–1800)	94.0 $\pm$242.2 (1–1554)	102.8 $\pm$228.0 (1–1746)
Fruit set (%)	33.3 $\pm$23.1 (0–100)	24.2 $\pm$24.8 (0–100)	38.3 $\pm$25.6 (0–100)
Seed set	16.3 $\pm$8.4 (1–39.7)	10.8 $\pm$9.3 (1–31.0)	12.2 $\pm$7.4 (1–43.4)
Colonies With 0 Fruit Set (%)	7 (6.1)	34 (32.3)	14 (12.5)

flowers produced per colony and fruit set were significantly reduced in 1986 compared with the other two years (flowers/colony: $F_{2,333} = 8.32$, $P<0.001$, Scheffé multiple comparisons $P<0.05$; fruit set: $F_{2,333}=12.6$, $P<0.001$, Scheffé multiple comparisons $P<0.05$). Seed set also differed among years (ANOVA $F_{2,333}=10.95$ $P<0.001$) but 1985 had significantly greater seed set than in the other two years (Scheffé multiple comparisons $P<0.05$). In 1986 a larger proportion of colonies set no fruit compared to the other two years ($G=28.12$, df=2, $P<0.001$).

Flowering times

Both mayapple and lousewort began flowering in mid to late May during the three years of the study. Although lousewort always began flowering first (by 4, 3 and 5 days in 1985, 1986, and 1987, respectively) it had a more protracted flowering period (about 3 weeks) than mayapple (about 2 weeks). In 1985 and 1987 there was considerable overlap in peak flowering of the two species (9 days in 1985 and 7 days in 1987). In 1986, the start of flowering was delayed by about a week, probably due to aseasonally cold weather. A few lousewort spikes were just beginning to flower when the removal took place; mayapples first flowered about 3 days later. Although no direct observations of flowering in the 4 remaining lousewort patches were made in 1986, the dates of first flowering (May 22 for lousewort and May 25 for mayapple) indicate that the two plant species must have overlapped in flowering as in other years. Flowering within single mayapple colonies was more or less synchronous over a 1 or 2 day period. Most mayapple colonies began to flower within 2–3 days; the maximum difference in flower initiation observed among colonies was about 6 days. There were no obvious differences in flowering sequence among colonies in different areas of the wood.

Multiple regressions

Multiple regressions identified the most important factors explaining variation in fruit and seed set among mayapple colonies within each year (Table 2). In general, all three factors (colony size, near neighbour distance, and proximity to lousewort) were significant in accounting for some of the variation in fruit and seed set among colonies. The variable LDS (distance to each lousewort patch weighted by number of flower spikes in each patch) was always more highly correlated with mayapple fruit and seed set than the minimum or average distance to lousewort. The effect on mayapple fruit and seed set of NN5 and LDS was consistently positive (both variables were reciprocals so higher values indicate closer proximity to neighbours or lousewort). However, NN5 and LDS were significantly positively correlated in all years (1985 $r=0.63$; 1986 $r=0.55$; 1987 $r=0.65$; $P < 0.001$ in all cases) making it difficult to clearly separate their influence using regression.

Table 2. Multiple regression models for factors influencing fruit set and seed set in the mayapple population in 1985–1987. The factor with the highest correlation with the dependent variable was added to the model first, subsequent factors were added if significant at $P<0.05$. Values indicate: correlation coefficient when factor added to model first (r), partial correlation when effects of other factors held constant (r_p); partial F, P, and corrected coefficient of determination (r^2) for factors in best fit model. All variables log transformed except NN5 and seed set

Dependent variable	Factor	r	r_p	Best model		
				F	P	r^2
1985						
Fruit set	FL	−0.31**	−0.28**	112.27	0.0007	0.11
	NN5	0.34**	0.23*	9.91	0.0021	0.17
	LDS	0.26**	0.04			
Seed set	FL	−0.03	0.03			
	NN5	0.21*	0.01			
	LDS	0.33**	0.26**	113.67	0.003	0.10
1986						
Fruit set	FL	0.32**	0.35**	114.9	0.0002	0.090
	NN5	0.08	−0.07			
	LDS	0.24**	0.28**	9.6	0.0023	0.17
Seed set	FL	0.52**	0.55**	45.7	0.0001	0.30
	NN5	0.06	−0.02			
	LDS	0.13	0.19*	5.1	0.027	0.37
1987						
Fruit set	FL	0.34**	0.39**	19.1	0.0001	0.10
	NN5	0.31**	0.24*	16.6	0.0001	0.22
	LDS	0.21*	0.07			
Seed set	FL	0.33**	0.41**	21.9	0.0001	0.10
	NN5	0.27**	0.10			
	LDS	0.30**	0.25**	19.5	0.0001	0.24

* $P<0.05$
** $P<0.01$

Comparisons among matched pairs of colonies

Comparisons of fruit and seed set in close and distant unmanipulated mayapple colonies provided a more direct test of the influence of lousewort on mayapple female reproductive success (Tables 3, 4). Both fruit and seed set were lower in 1986 compared with the other two years (year main effect, Table 4) following the general trend in the entire mayapple population. In all years, colonies close to flowering lousewort had greater fruit and seed set compared with distant colonies matched for neighbour distance and size (distance main effect). The magnitude and direction of the difference in fruit and seed set between close and distant patches was consistent across the three years (non-significant year × distance interaction).

Removal of lousewort flowers

I tested the effect of removing lousewort flowers in 1986 in several ways. Colonies that were close to flowerless lousewort patches (manipulated group, $n=13$), were not significantly different in fruit or seed set from colonies > 50 m from lousewort (Table 3, fruit set, paired $t=1.16$,

Table 3. Fruit and seed set in mayapple colonies close to (<25 m) and relatively distant from (> 50 m) lousewort patches. Pairs of mayapple colonies were matched for colony size and average distance to nearest neighbours. Values indicate mean ± SD (range)

Year	N Pairs	Close	Distant	Difference
1985				
Fruit set	25	0.40± 0.21 (0.6 − 1.0)	0.28± 0.19 (0 − 0.75)	0.12
Seed set		21.7 ± 7.9 (5.5 −39.7)	14.3 ± 8.7 (0 −35.7)	7.4
1986				
Fruit set	15	0.34± 0.17 (0 −0.57)	0.19± 0.21 (0 − 0.58)	0.15
Seed set		14.5 ± 6.4 (0 −26.3)	10.2 ± 8.4 (0 −25.0)	4.3
1987				
Fruit set	25	0.50± 0.26 (0 − 0.93)	0.41± 0.26 (0 − 0.94)	0.09
Seed set		17.5 ± 9.8 (0 −43.0)	13.8 ± 7.8 (0 −36.4)	3.7
1986 (Manipulated)				
Fruit set	13	0.24± 0.26 (0 − 1.0)	0.16± 0.19 (0 − 0.57)	0.08
Seed set		7.9 ± 8.5 (0 −26.5)	7.3 ± 8.3 (0 −19.5)	0.6

Table 4. Analysis of variance of fruit and seed set in unmanipulated mayapple patches over three years. Year main effect tested with pair (year) as error term

Source	df	SS*	MS	F	P
Fruit Set[1]					
Year	2	0.38	0.190	5.45	0.0074
Distance	1	0.26	0.264	15.76	0.0003
Year*Distance	2	0.02	0.009	0.59	0.560
Pair (year)	62	2.17	0.035		
Error	62	1.04	0.017		

Source	df	SS	MS	F	P
Seed set					
Year	2	588.58	294.29	3.4	0.04
Distance	1	806.47	806.47	13.58	0.0005
Year*Distance	2	94.33	47.17	0.79	0.456
Pair (year)	62	5364.67	86.53		
Error	62	3681.07	59.37		

[1] Log (fruit set + 1)
* Type III SS

$df=12$, $P=0.27$; seed set, paired $t=0.43$, $df=12$, $P=0.67$). In this comparison, the fruit set mean for the close manipulated group (0.24, Table 3) is higher than mean for the distant colonies (0.16). However, this difference is due largely to a single pair; without this pair means are, close (0.19±0.22) vs. distant (0.17±0.19). Colonies that were close to flowering lousewort patches

Table 5. Comparison of differences in fruit and seed set between pairs of matched close and distant mayapple patches

Year	N Pairs	Difference between pairs	
		Close > Distant	Close ≤ Distant
Fruit set			
1985	25	17	8
1986	15	10	5
1987	25	15	10
1986 (manipulated)	13	4	9
Seed set			
1985	25	21	4
1986	15	10	5
1987	25	16	9
1986 (manipulated)	13	3	10

Table 6. Frequency of flower visits to common spring wildflowers in the study area in 1987. Values indicate means ± SD

Species	Visits/Flower/Hr	Samples	Visitors
Phlox divaricarpa	0	15	0
Smilacina racemosa	0	24	0
Podophyllum peltatum	0.037 ± 0.12	99	*Bombus*
Trillium # *grandiflorum*	0.042 ± 0.11	28	*Bombus*
Tiarella cordifolia	0.052 ± 0.09	16	*Bombus*
Viola spp.	0.71 ± 1.30	29	*Bombus*
Ribes spp.	1.92 ± 2.55	18	*Bombus*
Erythronium # *americanum*	2.97 ± 2.01	23	*Andrena, Bombus*
Pedicularis canadensis	3.53 ± 4.36	15	*Bombus*

* Nectarless; # Finished flowering before mayapples bloom

in 1986 (unmanipulated group, $n = 15$), had greater fruit and seed set than distant colonies (fruit set, paired $t = 2.74$, df = 14, $P = 0.008$; seed set, paired $t = 1.56$, df = 14, $P = 0.07$).

I also tested whether the distribution of positive and negative differences among matched pairs was similar across years, and whether there was an overall difference between all unmanipulated colonies and the manipulated colonies (Table 5). For unmanipulated pairs, the proportion of close colonies with enhanced sexual reproduction did not differ from year to year (fruit set $G = 0.37$, df = 2, $P > 0.05$; seed set $G = 2.83$, df = 2, $P > 0.05$). However, a significantly lower proportion of close manipulated pairs showed enhanced fruit and seed set compared with pooled data for all unmanipulated pairs (fruit set $G = 4.88$, df = 1, $P < 0.05$; seed set $G = 15.94$, df = 1, $P < 0.001$).

Pollinator visits

During 1987 the only visitors observed on mayapple and lousewort flowers were queen bumble bees of 4 different species. *Bombus vagans* accounted for 79% of bees visiting mayapple and 86% of those visiting lousewort. Single bees were observed visiting flowers in 10 of 40 observation periods at close mayapple colonies and in 4 of 44 periods at distant colonies (Fisher Exact Test, $P = 0.08$). The average visitation rate to mayapple flowers in colonies close to lousewort was about four times greater than in distant colonies (0.081 ± 0.18 visits/flower/hour vs. 0.018 ± 0.062; $t = 2.08$, df = 47.7, $P = 0.02$). On average bees visited 2.3 (range 1–6) flowers per colony in close colonies and 2.5 flowers (range 1–5) in distant colonies ($t = -0.19$, df = 12, $P = 0.86$). No bees were observed collecting pollen; 86% of bees probed around the stamen base apparently in search of nectar.

Bees were observed in 12 of 15 sampling periods at lousewort patches. Several queens (mean 3.9, range 0–8) were usually foraging continuously in a patch at the same time and a total of 58 bees (none with pollen loads) were counted over the 15 observation periods. The average

frequency of visits was 3.5 visits/flower/hour, about 100 times greater than the average to mayapple flowers (Table 6).

The frequency of insect visitors (mainly queen bumble bees) varied widely among the common plant species in the study area (Table 6). Lousewort enjoyed the highest visitation rate and mayapple one of the lowest. More than half the species had very low visitation rates (< 0.1 visits/flower/hour).

Discussion

Within years some of the variation in mayapple fruit and seed set was correlated with intraspecific factors (colony size and distance to neighbouring colonies) and with proximity to lousewort plants. The association between colony size and fruit and seed set depended on the year. In 1985 fruit set was proportionately greater in small colonies as has been reported for other clonal species (e.g. Handel 1983). However, in 1986 and 1987 larger colonies had proportionately greater fruit and seed set. Other studies have reported no relationship between colony size and fruit set in large mayapple populations (Whistler and Snow 1990). In all years colonies closer to neighbours and closer to lousewort had increased female reproductive success.

Because NN5 and LDS were correlated, separation of their influence on mayapple fruit and seed set was possible only by controlling for neighbour distance in paired comparisons and in the manipulation. Paired comparisons showed a consistent increase in fruit and seed set in mayapples close to lousewort in all years. The average increases in fruit set were 12%, 15% and 9% in 1985, 1986, and 1987 respectively. These values represent increases of 42%, 79%, and 22% when calculated as a percentage of the average fruit set recorded in distant colonies in each year. The average increase in seed set in close colonies was 7.4, 4.3, and 3.7 in 1985, 1986, and 1987 respectively, representing increases of 40%, 42% and 27% relative to average seed set in distant colonies.

The most likely explanation for enhanced fruit set in mayapples close to lousewort is the magnet species effect. Lousewort was very attractive to queen bumble bees, it flowered at about the same time as mayapple, the two species shared the same flower visitors, and mayapples close to lousewort received more visits than those further away. Mayapple is likely to benefit from even small increases in visit frequency because it is often pollinator limited. In 1985, for example, hand pollination increased fruit set from 25% to 100% and seed set from 13.2 to 34.2 relative to naturally pollinated flowers (Laverty and Plowright 1988).

The enhanced fruit set in mayapples close to lousewort patches could also be due to site effects such as physical properties of the soil, flowering time, or the genetic structure of mayapple colonies in the vicinity of lousewort. The removal experiment in 1986 tested this possibility. The strongest evidence against site effects is that 13 mayapple colonies close to flowerless lousewort patches did not show increased fruit or seed set relative to colonies > 50 m from lousewort. Only 3 of the 13 close colonies had greater seed set, and 4 had greater fruit set, relative to matched distant colonies. In contrast, the proportion of colonies close to flowering lousewort which had enhanced fruit and seed set was consistently higher in all years. These comparisons support a pollinator mediated explanation for the enhanced sexual reproduction in mayapples.

Mayapple appears to rely primarily on mistake pollination by nectar searching bumble bee queens, though the flowers are visited infrequently. Mayapple does not appear to mimic lousewort or any other co-flowering species. This type of mistake pollination, in which mimicry is not involved, has been documented in other nectarless plants (reviewed by Little 1983; Dafni 1984) including temperate orchids (Heinrich 1975; Nilsson 1980; Boyden 1982) and wind pollinated species (Melampy and Hayworth 1980).

The relationship between mayapple and lousewort is not necessarily specific and widespread across the ranges of the two species. Indeed, no association between these two species is mentioned in several studies of spring ephemeral plant communities in North America (Braun 1950; Struik and Curtis 1962; Rogers 1982; Motten 1986). Mayapple may benefit from loose associations with other magnet species in different parts of its range or even within the same population. Since reproduction in mayapples is primarily by vegetative growth (Rust and Roth 1981; Parker 1989) it is unclear how important association with magnet species may be. Sexual recruitment of new genotypes into mayapple colonies is apparently very rare. Rust and Roth (1981) found that 99% of seedlings within colonies failed to survive, probably because of susceptibility of young seedlings to pathogen attack (Parker 1989). However, fruit and seed production could be very important in the colonizing potential of existing clones (e.g. Braun and Brooks 1986).

Loose associations between nectar rich and nectarless plant species may be common in plant communities (e.g. Pellmyr 1985). Such effects would be difficult to detect if the magnet species were widely dispersed, and this may account for the few studies that have described this type of facilitative interaction.

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