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CONSEQUENCES OF THE TIMING OF SEED RELEASE OF *ERYTHRONIUM AMERICANUM* (LILIACEAE), A DECIDUOUS FOREST MYRMECOCHORE¹

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Myrmecochores are plants with seeds adapted for ant dispersal. This specialized dispersal syndrome may provide *Erythronium americanum* seeds with protection from predators within the eastern deciduous forests. To determine the adaptive significance of myrmecochory in *E. americanum*, seed removal rates and seed predation in relation to seed release date and location along the Potomac River in Langley, Virginia, were examined. The number of seeds removed from four enclosure treatments were monitored two times in 1992 and three times in 1993 within floodplain and hilltop populations of *E. americanum*. Overall, seed removal was greatest from control depots, and *E. americanum* seeds were removed at nearly the same rate from predator-exclusion depots, indicating that removal from open depots is largely due to ant removal. Ants removed significantly more seeds than predators in the first 48 h of seed exposure and could potentially remove all *E. americanum* seeds before nightfall. *Aphaenogaster rudis* was identified as the primary disperser of *E. americanum*. Seeds placed in depots after the natural seed release period were discovered more quickly and removed by ants at a significantly higher rate than seeds released at the natural date. These results suggest that ant dispersal of *E. americanum* seeds reduces the likelihood of seed predation.

Key words: Ant dispersal; deciduous forests; *Erythronium americanum*; *Jeffersonia diphylla*; Liliaceae; myrmecochores; seed release.

Myrmecochory, the dispersal of seeds by ants, is a widespread phenomenon documented in more than 70 plant families (Beattie, 1985) and numerous habitats including deciduous forests (e.g., Holland, 1974; Culver and Beattie, 1978; Muller, 1978, 1990), dunes (Öostermeijer, 1989), tropical epiphyte communities (Kleinfeldt, 1978), and sclerophyllous shrub (Bond and Slingsby, 1984; Hughes and Westoby, 1990). Examples of myrmecochory are most abundant in Australia and South Africa (Hughes and Westoby, 1990; Westoby et al., 1991), but this syndrome is well represented in the eastern deciduous forests of North America where myrmecochores may constitute up to 40% of the herbaceous layer (Handel, Fisch, and Schatz, 1981).

Many of these myrmecochores are co-occurring spring ephemerals, herbaceous plants that grow rapidly following snowmelt and begin to senesce as the canopy closes. The prevalence of this syndrome in the spring flora of the eastern deciduous forests may be maintained by the paucity of lipid-rich foods (Carrol and Janzen, 1973). Therefore, seed-dispersing ants are attracted to the lipids contained in most elaiosomes (e.g., Carrol and Janzen

1973; Öostermeijer, 1989). Within the eastern deciduous forests many myrmecochores release their ant-dispersed seeds during a relatively short period. Some myrmecochores exhibit overlapping seed release phenologies during this time, with the less abundant seeds often preferred by dispersers and predators (e.g., Smith et al., 1989). For other myrmecochores, however, there appears to be some temporal separation of release dates (e.g., Beattie and Culver, 1981; Handel, Fisch, and Schatz, 1981; Heithaus, 1986; Ruhren, 1994). For example, *Erythronium americanum* Ker. (Gleason and Cronquist, 1991) is a typical ephemeral myrmecochore exhibiting an elaiosome (Holland, 1974; Muller, 1978; Harder et al., 1985; Wein and Pickett, 1989) and a synchronous seed release period that occurs after *Viola* spp. yet before several other sympatric myrmecochores in northern Virginia (e.g., *Jeffersonia diphylla* and *Trillium sessile*) (Lobstein and Rockwood, 1993; Ruhren, 1994). This temporal separation of seed release among myrmecochores may maximize exposure to seed-dispersing ants.

It is theorized that myrmecochory may provide seeds with several benefits, including protection from seed predators (e.g., Culver and Beattie, 1978; O'Dowd and Hay, 1980; Heithaus, 1981; Turnbull and Culver, 1983), avoidance of interspecific competition (e.g., Handel, 1976, 1978), deposition in a nutrient-enriched safe site (Culver and Beattie, 1980, 1983) and protection from fire (e.g., Berg, 1975). Within the eastern deciduous forests of North America, a driving force in this plant-animal interaction is seed predation. The elaiosomes that attract the ants also attract predators including rodents, primarily *Peromyscus leucopus* (e.g., Heithaus, 1981), birds (Milewski, 1982), and many arthropods (e.g., Bond and Slingsby, 1984; Anderson, 1988). Most of the arthropod seed predators are nocturnal ground beetles (e.g., Ohara

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and Higashi, 1987; Higashi and Ito, 1991). Rodents are assumed to be destructive because they do not cache seeds in the spring and early summer (Barry, 1976). Heithaus (1981) discovered that *P. leucopus* may cue in on the natural seed depots formed under dehiscing capsules and frequently destroy predehiscent fruits. However, it also was revealed that seeds are less detectable by *P. leucopus* after ants strip seeds of their elaiosomes within their nests. Therefore seeds discovered and collected by ants should exhibit reduced predation.

The goals of our study were to examine factors affecting *E. americanum* seed dispersal and to evaluate the theoretical benefit of this dispersal mechanism in reducing predation and its response to an artificially extended seed release phenology. First, we tested this with a series of treatments designed to exclude either ants, rodents, or both from seeds placed in two sites in both 1992 and 1993. Second, we extended the seed release period of *E. americanum* to evaluate the effect of timing on seed dispersal and predation rates. Third, we compared removal rates of *E. americanum* to *Jeffersonia diphylla*, a sympatric myrmecochore, to determine if any preference was exhibited by ants and predators. Finally, to explore the nutrient-enriched safe site hypothesis, we analyzed ant nest and control soil to determine if *E. americanum* seeds were present in ant nests and whether ant nest soil provided an enhanced germination site.

MATERIALS AND METHODS

Study organism—*Erythronium americanum* Ker. (Liliaceae) is a common spring ephemeral herb that occurs in eastern North America from Nova Scotia west to Minnesota and south to northern Florida (Holland, 1974). This perennial herb exhibits rapid aboveground growth during April and May in northern Virginia, with two-leafed ramets producing a single flower. After a highly synchronized anthesis, fruits are formed as the aboveground portion of the plant begins to senesce. At the end of May, the capsules begin to open on the ground and the hard, crescent-shaped seeds lay exposed. Each seed is equipped with an elaiosome that attracts ant seed dispersers as well as seed predators. When ants bring myrmecochorous seeds into their nests, they remove the elaiosome and discard the intact seed in underground burrows or on the mound (e.g., Culver and Beattie, 1978). *Erythronium americanum* elaiosomes appear to degrade within 1–2 wk when exposed to heat and humidity (Ruhren, 1994). Like other myrmecochores examined by Lobstein and Rockwood (1993) (*Asarum canadense*, *Jeffersonia diphylla*, *Dicentra cucullaria*, and *Viola striata*), *E. americanum* seeds do not require scarification by ants to enhance germination (Ruhren, 1994).

Study site—All *E. americanum* seeds were collected from native populations at Turkey Run Park (TRP) in Langley, Fairfax County, Virginia, ≈ 8 km northwest of Washington, DC. TRP is a mixed deciduous forest habitat situated along the Potomac River. Transects were placed in two habitats within TRP: the river floodplain and a dry upland hilltop site 30 m above the Potomac River, ≈ 300 m from the floodplain. Both sites were chosen because they contained dense patches of *E. americanum*, represented distinct habitats, and were relatively undisturbed by human activity.

In addition to *E. americanum*, other spring ephemeral sympatric herbs at the floodplain included the myrmecochores *Trillium sessile*, *Asarum canadense*, and *Claytonia virginica*. The *E. americanum* patch within the floodplain was $\approx 12 \times 27$ m. This patch was dissected by an intermittent stream that flowed into the river during heavy rainfall.

The hilltop community was characterized by a dense shrub layer of *Asimina triloba* saplings. The herb layer was composed of a patch of

E. americanum $\approx 9 \times 15$ m mixed with *Galium* spp. and the myrmecochores *C. virginica* and *A. canadense*.

Plant analysis/seed collection—All ramets were counted and the flowering ramets were marked with plastic stakes and monitored to determine dates of opening, onset of senescence, and cessation of fruit and seed production. These individuals were checked in 1992 and 1993 to determine reproductive output. All capsules within the floodplain and hilltop were bagged in bridal veil, a fine mesh fabric, to prevent pre-dispersal predation and dispersal by ants and to facilitate recovery of seeds. All seeds were counted and weighed. Seeds were pooled within sites, and additional seeds were collected and weighed from adjacent nonstudy populations within TRP. Seeds were refrigerated for several days to prevent lipid degradation until sufficient seed was available to begin field manipulations and observations. Seeds of this species that had been refrigerated for 1 yr were detected and quickly removed by ants in 1993 (Ruhren, 1994).

Monitoring seed dispersal—In 1992 two transects were placed 5 m apart in both the floodplain and hilltop study sites to determine *E. americanum* seed removal rates by ants and predators. The linear transects contained seven replicates. Each replicate contained four exclusion treatments randomly placed. The depots, constructed of 5-cm diameter polyvinyl chloride (PVC) pipe sections driven into the soil, received six seeds and were evenly placed 1 m apart in blocks that were spaced 1 m apart from adjacent blocks. This arrangement simulated natural seed densities. Within the floodplain and the hilltop study sites, a mean of 5.4 and 7.5 seeds were produced, respectively, per fruit. The PVC pipe was painted brown to blend in with the soil and leaf litter. Approximately 2 cm of each pipe were left unburied, and this surface was treated to provide one of four simulations: (1) untreated pipe allowing access by ants and predators, (2) pipe with a Tanglefoot® (The Tanglefoot Company, Grand Rapids, MI) barrier allowing mammalian seed predator access only, (3) pipe with 0.6-cm wire mesh cover allowing ant access, and (4) pipe with Tanglefoot® and wire mesh providing total exclusion. Transects were designated for natural and delayed seed placement. Therefore, all treatments were replicated within sites and times.

Beginning 3 June 1992 (natural seed release period), the first series of exclusion treatments were initiated in the floodplain and hilltop sites. To test for an effect of seed release timing on seed removal rates, the initial transect was followed 5 d later (day 6) by another transect within the floodplain and hilltop sites. In both periods seeds were placed in depots at 0800 and each depot was checked approximately every half hour for 8 h daily for 1 wk following release. After this intensive monitoring period, observations were reduced as removal activity declined. Overall, exclusion depots were monitored for ≈ 3 mo. Overnight seed removal from exclusion-free depots was assumed to be by rodents (primarily *P. leucopus*), seed-eating arthropods, as well as nocturnally foraging ants.

In 1993, the transects were placed in the same locations in the floodplain and hilltop sites and monitored for the same period of time beginning on 2 June. Treatments were rerandomized within transects in each block. Another transect was added to simulate a 15-d delay of seed release (day 16) in each site. Thus, there were three seed release dates in 1993. Additionally, six *E. americanum* seeds were placed on the soil surface within each block of exclusion treatments to simulate natural seed placement and test for any pipe effect. In 1993 only, all seeds were marked with a small dot of enamel paint, color coded to correspond to the three release dates. This was done in an attempt to determine the fate of seeds removed during the study. Because seed tracking was found to be ineffective in the dense leaf litter at TRP, ant nests were marked during the monitoring phase and subsequently exhumed at the end of the 1993 season. Ant nests were not marked during the natural *E. americanum* seed release period because of time constraints. While tabulating seed removal rates, we monitored arthropod visitors and several were captured for identification. Also, ant density and activity were

TABLE 1. Results of three-way ANOVA showing the effect of site, timing, and exclusion treatments and interactions on *Erythronium americanum* cumulative seed removal for the first 48 h in 1992 and 1993.

Source	Year							
	1992				1993			
	df	MS	F	P	df	MS	F	P
Site (S)	1	0.003	0.01	0.92	1	0.44	0.95	0.34
Temporal (T)	1	6.45	19.13	0.0001	2	5.04	10.91	0.0001
Exclusion Treatment (ET)	3	16.06	47.62	0.0001	3	22.12	47.91	0.0001
S × T	1	0.37	1.11	0.29	2	0.45	0.98	0.38
S × ET	3	0.13	0.40	0.75	3	1.48	3.20	0.03
T × ET	3	1.29	3.84	0.01	3	0.93	2.00	0.07
S × T × ET	3	0.50	1.49	0.22	3	0.72	1.55	0.16
Error	96	0.34			144	0.46		

monitored with tuna baits and pitfall traps randomly placed within both sites.

The cumulative amounts of seed removed from each exclusion treatment were compared for the first 48 h of seed removal. These totals were analyzed assigning exclusion treatment, seed release date, and site as fixed effects in the analysis of variance (ANOVA) using SAS (1989). Cumulative seed removal was square-root transformed to meet the assumptions of ANOVA. Tukey posthoc comparisons identified significant differences among treatments. Interpretations were based on the first 48 h of seed exposure in exclusion depots because additional seeds placed on the soil in 1993 were frequently removed within 8 h and usually within 48 h. Also long-term monitoring revealed no significant change in removal rates after 48 h (Ruhren, 1994). With the addition of a third transect and additional seed placed on the soil surface in 1993, data from the 2 yr were analyzed separately.

Sympatric myrmecochores—In 1992, within an *E. americanum* population ≈200 m downstream from the floodplain, we tested for ant seed preference between *E. americanum* and *Jeffersonia diphylla* during the natural dispersal period of *J. diphylla*, which occurred ≈7 d after the natural seed dispersal phase of *E. americanum*. This other myrmecochores occurred sympatrically with several patches of *E. americanum* within TRP. Because of limited seed supply, only two treatments replicated seven times were used: rodent exclusion and our control with no exclusion. Six seeds of either species were placed in separate depots within a single transect. Both treatments of each species were placed within each square metre. Cumulative amounts of seed removal were analyzed assigning species and exclusion treatment as fixed effects with ANOVA using SAS (1989). This experiment was not replicated in 1993 because of insufficient seed supply following the addition of the 15-d delay release period.

Soil analyses—To determine if *E. americanum* seed were deposited in ant nests, soil from nests and reference soil were separated using the chemical extraction and flotation method described by Malone (1967). Organic debris was then dried and examined under a light microscope. The method was tested by spiking six soil samples with previously collected *E. americanum* and *Dicentra cucullaria* seeds. We recovered 96% of the *E. americanum* and 98% of the *D. cucullaria* spiked seeds.

To test the nest-enrichment hypothesis (Culver and Beattie, 1980, 1983) soil collected from 12 ant nests and 12 randomly located reference locations in 1992 was analyzed for nutrients and chemical characteristics (Mg, P₂O₅, K₂O, Cu, Mn, NO₃, SO₄, Zn, and pH) and physical characteristics (sand, silt, clay, and organic matter). All ant nests sampled were in the soil. The University of Maryland Soil Testing Laboratory conducted these analyses. The effects of soil type (ant nest or reference) and site (floodplain or hilltop) were analyzed using MANOVA of log-transformed data on SAS (1989). One-way ANOVAs for each soil characteristic were performed to determine variation in individual soil components.

RESULTS

Population monitoring—The floodplain population was composed of ≈1 100 and 2 400 ramets in 1992 and in 1993, respectively. Thirty (7.7%) and 80 (11%) flowering individuals were counted in 1992 and 1993, respectively. Flowers began to open on 30 March 1992, and 6 April 1993, with seeds naturally releasing between 27 May and 2 June 1992, and 29 May and 3 June 1993. Significantly more rainfall occurred during the flowering period of *E. americanum* in 1993 than in 1992 (27 mm compared to 13 mm), causing heavy flooding at this site.

Approximately the same number (3 660) of ramets was at the hilltop in both years. Three percent of the ramets flowered in 1992 compared to 2% in 1993 at this site. *Erythronium americanum* flowers began opening at the hilltop on 3 April 1992, and 6 April 1993. Seeds were released between 31 May and 2 June 1992, and 30 May and 3 June 1993.

Seed dispersal vs. predation—Seed removal from both sites in 1992 and 1993 was rapid in the initial phase (≈48 h) of seed exposure, followed by a near cessation of activity for the remainder of the observations. The seed supply was never entirely depleted within any transects or treatments by August 1992 and 1993 (Ruhren, 1994). However, all of the *E. americanum* seeds placed on the soil surface in 1993 were removed within 48 h, indicating the potentially high natural removal rate.

In 1992 and 1993 no significant difference in removal was observed between the floodplain and hilltop for the first 48 h (Table 1). Consequently, the sites were pooled within 1992. However, in 1993 there was a significant interaction between site and exclusion treatment (Table 1); consequently, the two sites were not pooled in the analysis.

Based on the comparison of seed removal rates from the four exclusion treatments, ants removed significantly more seeds (≈25%) than predators (1%) in the first 48 h of the 1992 monitoring (Table 1; Fig. 1). Ants were the only organism observed removing *E. americanum* seeds. In 1993, a period of rapid discovery and removal in the first 48 h occurred once again in the floodplain and hilltop (Fig. 2a, b).

It appears that removal by predators occurred primarily at night in both years. Seven chewed *E. americanum* seeds and empty seed coats were discovered in three depots within the floodplain and hilltop transects on four

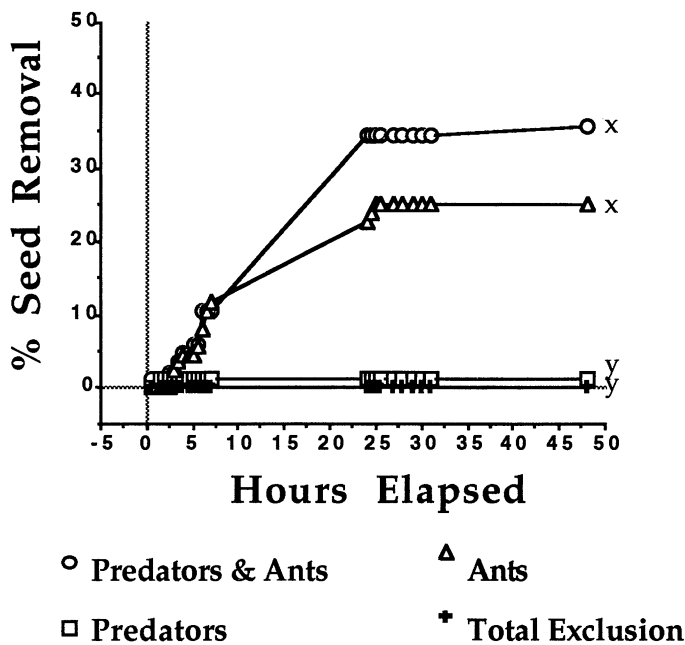


Fig. 1. Comparison of natural seed removal rates from all exclusion treatments, pooled across floodplain and hilltop sites for the first 48 h during 1992 ($N = 84$ seeds/exclusion treatment). Symbols represent *E. americanum* seed removal by suspected organisms. Each point represents the percentage of seeds removed from 14 replicates. Exclusion treatments followed by the same letter are not significantly different at the $P < 0.05$ level.

mornings in 1992 and 1993. We also occasionally detected evidence of burrowing around the depots in the morning when arriving at TRP. During the day, few if any vertebrates were observed in and around the transects. Chipmunks (*Tamias striatus*) sometimes investigated the floodplain area, but they normally confined their activities to the rocky slope above the floodplain transects and were never seen at the depots during the day.

Timing effects—The timing of seed release had a highly significant influence (Table 1; Fig. 3) on seed removal rates within the first 48 h of seed exposure in 1992. Seeds released after a 5-d delay were removed $\approx 40\%$ more rapidly by ants than seed released at the natural date. The exclusion treatments significantly interacted with timing of seed release date in 1992 (Table 1).

Variable results were observed between sites in 1993 (Fig. 4a, b). Seeds released 5 d later were again removed significantly more quickly ($\approx 60\%$ and $\approx 15\%$ increases at the floodplain and hilltop, respectively) within the first 48 h of exposure (Table 1). Seeds released 15 d later did not result in any significant increase beyond the already significant 5-d delay period in the floodplain. However a 15-d delay did enhance seed removal by $\approx 40\%$ in the hilltop, perhaps because the hilltop was not as wet as the floodplain. Overall, seed removal plateaued as observed in 1992.

Sympatric myrmecochores—Significantly more *J. di-phylla* seeds were removed by ants in the first 24 h of seed exposure (ANOVA, $F = 61.63$, $P < 0.0001$) than

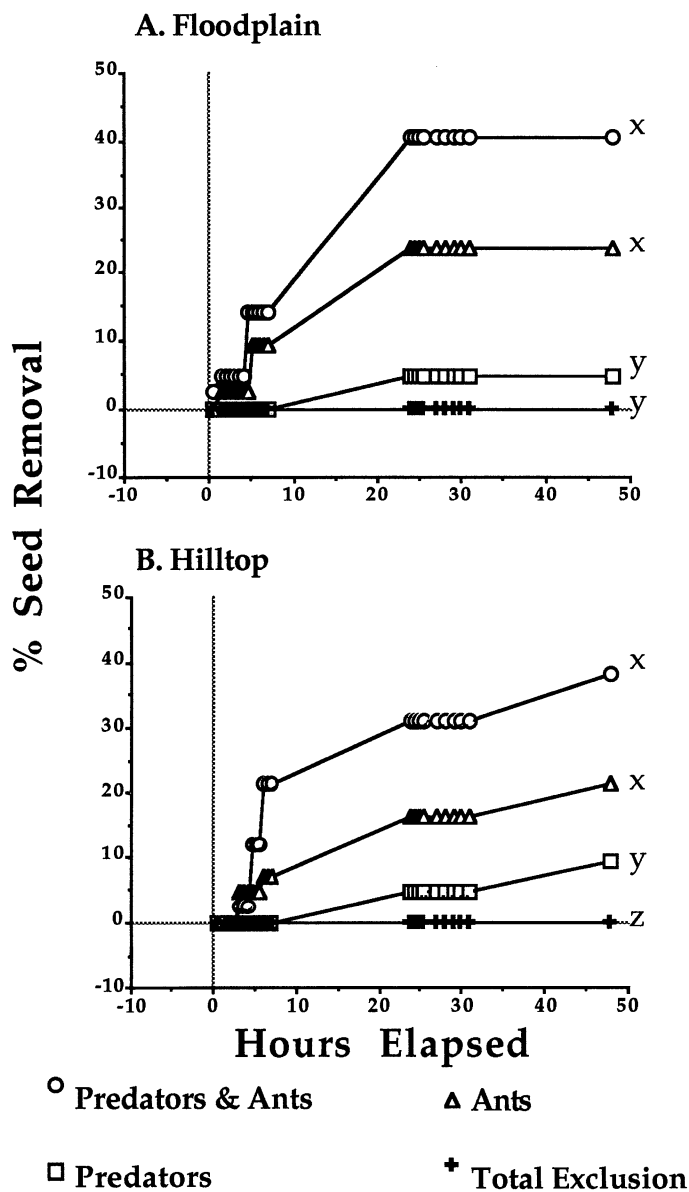


Fig. 2. Comparison of natural seed removal rates from all exclusion treatments within the transects of (A) floodplain and (B) hilltop sites for the first 48 h during 1993 ($N = 42$ seeds/exclusion treatment). Symbols represent *E. americanum* seed removal by suspected organisms. Each point represents the percentage of seed removal from seven replicates. Exclusion treatments followed by the same letter are not significantly different at the $P < 0.05$ level.

E. americanum seeds in 1992. Seventy percent of these seeds were removed after 8 h (Fig. 5), compared to $\approx 21\%$ removal of *E. americanum* seeds. Neither species' seeds were removed completely from the depots. There was no significant difference between 48-h seed removal from either exclusion treatment.

Soil and seed separation—No *E. americanum* seeds were detected in any of the *Aphaenogaster rudis* nests and reference soil samples inspected in 1993. However, *Dicentra canadensis* seeds, also known to be dispersed by ants in early May, were discovered in both soil sample

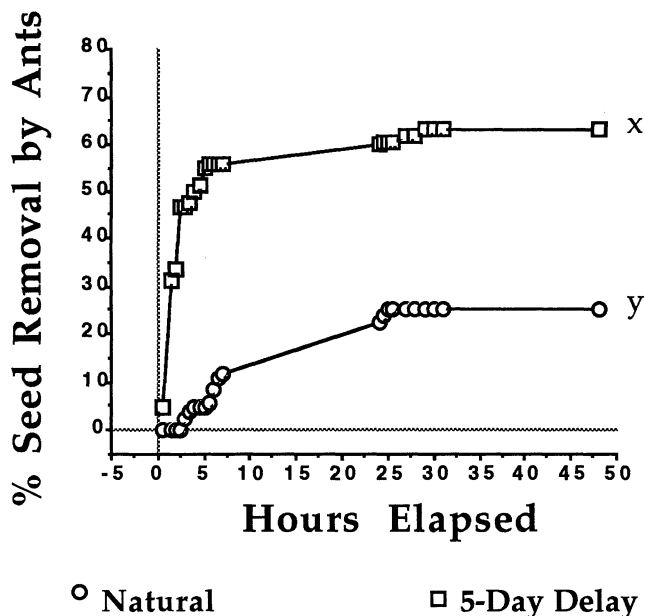


Fig. 3. Comparison of seed removal by ants after different seed release dates pooled across sites for the first 48 h of 1992 ($N = 84$ seeds/exclusion treatment). Each point represents the percentage of seed removal from 14 replicates. Plots followed by the same letter are not significantly different at the $P < 0.05$ level.

types (63 in nests and 19 in reference soil). These seeds occurred significantly more frequently in ant nest soil from both the floodplain ($X^2 = 7.35, P < 0.01, df = 1$) and the hilltop ($X^2 = 10.39, P < 0.01, df = 1$) than in reference soil.

Soil analyzed in 1992 revealed no significant trend in nutrient content of ant nests according to Wilks' Lambda test of the MANOVA, ($F_{13,10} = 2.026, P > 0.10$) except organic matter ($F_{1,22} = 4.73, P < 0.05$). However, nest soil was found to be significantly greater than reference soil according to the ANOVA of separate variables ($F_{39,12} = 5.734, P < 0.0009$): a mean of 155.3 parts per million (ppm) K_2O in the nest soil vs. 124.2 ppm in the reference soil ($F_{3,16} = 6.97, P = 0.0007$); 20.9 ppm Zn (nest), 17.7 ppm Zn (reference) ($F_{3,16} = 23.66, P = 0.0001$); and 19.2% clay (nest) and 17.7% clay in the reference ($F_{3,16} = 12.74, P = 0.0002$).

Ant activity—*Aphaenogaster rudis* was assumed to be the primary disperser of *E. americanum* because it was the most frequent ant species observed at exclusion depots, baits, and pitfall traps within the floodplain and hilltop in 1992 and 1993 (Ruhren, 1994). Out of all observed ant visits to seed depots in 1992, *A. rudis* were 77% of the visitors within the floodplain, 94% within the hilltop, and 69% and 65%, respectively, in 1993. The remainder of the ant visitors were primarily *Prenolepis imparis*; however, they never were seen removing seeds. In fact, several *P. imparis* were found eating the elaiosomes within the pipe enclosures. *Lasius alienus* and *Camponotus pennsylvanicus* were less frequently observed at the seed depots, baits, and pitfall traps, and they were not seen removing seeds.

Several harvestmen (*Leiobunum bimaculatum*) also

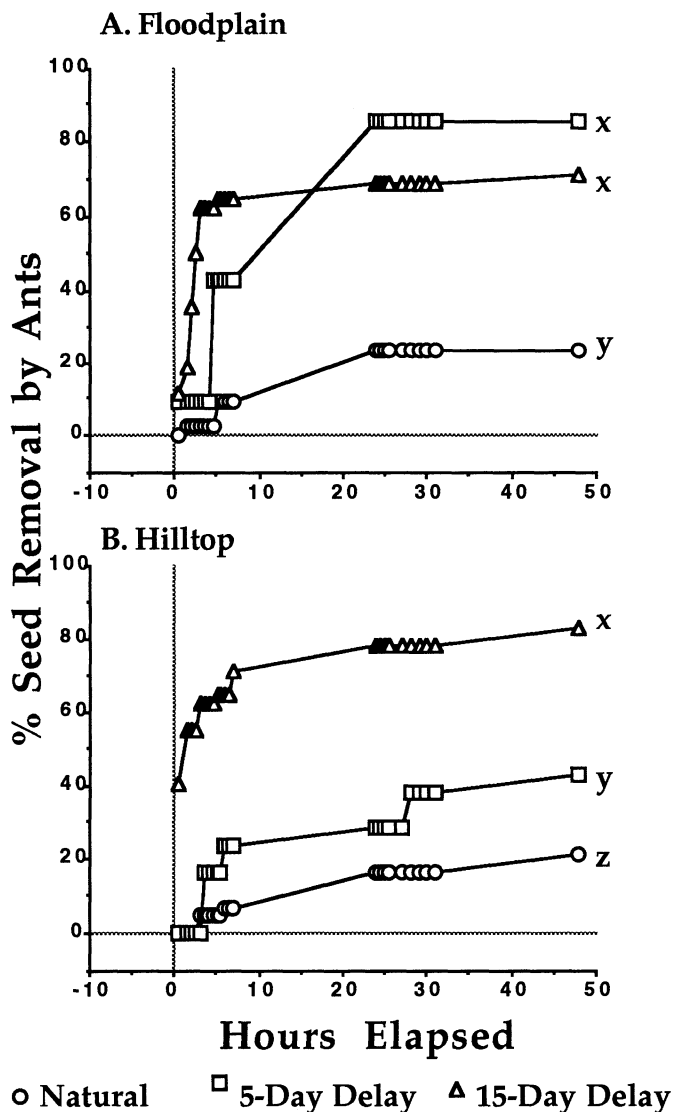


Fig. 4. Comparison of seed removal by ants after natural, 5 d and 15 d delay seed release dates in (A) floodplain and (B) hilltop for the first 48 h of 1993 ($N = 42$ seeds/date of release). Each point represents the percentage of seed removal from seven replicates. Seed release times followed by the same letter are not significantly different at the $P < 0.05$ level.

were observed on *E. americanum* seeds in the hilltop in both years. Although their visits to the exclusion treatments were infrequent, they appeared to be eating the elaiosomes in situ.

DISCUSSION

Ants were the primary removers of *E. americanum* seeds and removed significantly more *E. americanum* seeds than predators in the first 48 h of seed release. Seed removal rates did not vary by site (floodplain or hilltop) but increased significantly when *E. americanum* seed release was delayed for 5 d past the natural seed release date in both 1992 and 1993. A further delay of 15 d in 1993 continued to enhance significantly seed removal rates by ants in only the hilltop site. In both 1992 and

○*Erythronium americanum* □*Jeffersonia diphylla*

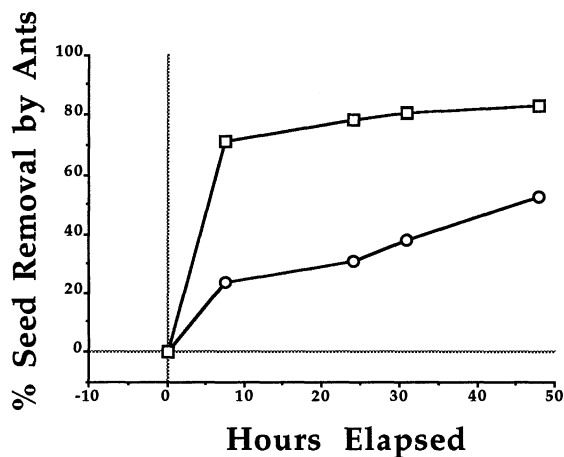


Fig. 5. Comparison of seed removal by ants of *E. americanum* and *J. diphylla* seeds for the first 48 h of 1993 ($N = 42$ seeds/species). Each point represents the percentage of seed removal from seven replicates. There was an initial significant difference in seed removal at 8 h that disappeared within the overall analysis at 48 h.

1993 there was a slowing of ant activity after 48 h regardless of site, timing, dispersal, or predation. Estimates of seed removal by ants actually are conservative because some overnight seed removal, attributed to predation in this study, may be the result of nocturnally foraging ants (e.g., Lynch, Balinsky, and Vail, 1980; Post and Jeanne, 1982). The results suggest an initially low risk of predation followed by nearly complete seed removal outside the depots.

Based on field observations and ant trapping, there is no shortage of ants during the seed dispersal phase of *E. americanum*. Seeds left in the depots, therefore, could indicate some satiation of the ants as well as an inhibitory effect of the artificial depots. *Erythronium americanum* appears to be visited by a guild of generalist scavenging ants that probably do not exhibit host specificity, a fact supported by previous research on other myrmecochores (Beattie and Culver, 1981; Lobstein and Rockwood, 1993). *Aphaenogaster rudis* is the most frequent visitor and most likely disperser of *E. americanum* within TRP. This species, also identified as the disperser of *E. americanum* by Wein and Pickett (1989), is a common ant in Virginia and Maryland (Lynch, Balinsky and Vail, 1980). *Aphaenogaster rudis* disperses several other spring ephemerals including *Viola* spp. (Culver and Beattie, 1978) and *Asarum canadense* (Heithaus, 1986). Although *A. rudis* is behaviorally subordinate to the less frequent ants, *L. alienus*, *P. imparis*, and *C. pennsylvanicus* (Lynch, Balinsky, and Vail, 1980; Fellers, 1987, 1989), they frequently can exploit food resources because they tend to discover food and recruit workers much more quickly than other ant species (Fellers, 1987). This may explain why *E. americanum* seeds placed on the soil surface were almost entirely removed within 8 h.

Another habit of *A. rudis* that may be beneficial for *E. americanum* is its shallow, temporary nests under fallen leaves and next to decaying logs within the floodplain and hilltop sites. According to soil analyses, these nests

may provide an enhanced germination site while reducing predation. Also, *A. rudis* colonies are normally nomadic, reducing the likelihood that *E. americanum* seed collections will become too dense. This habit of relocating nests often after 20 d (Culver and Beattie, 1978) was observed in the floodplain and hilltop and may explain the absence of *E. americanum* seeds in exhumed ant nests. Also, nests were marked after the natural seed release period of *E. americanum* because of time constraints.

The timing of seed release exerted a major influence on *E. americanum* seed removal rates in this study. If indeed dispersal by ants confers an advantage to *E. americanum* seeds, it may be inferred that extending the restricted seed release period could be favored by natural selection if it increases the period of exposure to ants. In 1992 and 1993, *E. americanum* seeds released 5 d later were removed significantly faster than those released at the natural time. A further delay of 5 d may continue to enhance seed removal in some sites. This initial increase in seed removal may be due to ant learning, an increase in ant colony size, or changes in ant activities. Thus, after an initial period of acclimation and learning at the two sites, ant activity appears to have stabilized at the floodplain, perhaps resulting in avoidance of seeds, leaving some *E. americanum* seeds in the exclusion depots. Dispersers did at first appear to be slow to respond in this system, but this was because of an inhibitory treatment effect, preventing the rapid and complete removal observed with *E. americanum* seeds placed on the soil. Furthermore, ants may prefer less common sympatric seeds within densely seeded plots (Smith et al., 1989). Smith et al. (1989) revealed that the probability of seed removal often depends on density and species composition of available seeds.

The slight separation of the dispersal phase of the various sympatric myrmecochores present at these sites may be favored by natural selection to maintain as well as maximize the rate of dispersal of these ant-seed relationships. For example, within both the floodplain and hilltop, dense patches of ant-dispersed *A. canadense* and *Trillium sessile* often were interspersed with *E. americanum*. *Asarum canadense* seeds are naturally released 2–3 wk after *E. americanum*, while *T. sessile* capsules dehisce in mid-July in northern Virginia. Another myrmecochore, *J. diphylla*, releases its seeds in mid-June \approx 1 wk after *E. americanum* at TRP. When placed in treatment depots, *J. diphylla* seeds were rapidly detected and were removed by *A. rudis* significantly faster in the first 8 h than seeds from *E. americanum* but at 48 h no difference was detected. The cause of this preference has not been quantified but may be influenced by variation in elaiosome chemical composition (e.g., Carrol and Janzen, 1973; Marshall, Beattie, and Bollenbacher, 1979; Brew, O'Dowd and Rae 1989). Lanza, Schmitt, and Awad (1992) discovered that the variation in fatty acid composition of elaiosomes of three *Trillium* species elicited different behavior in seed-dispersing ants. Also, ants could have been satiated with the more abundant *E. americanum* seeds within a population of *E. americanum*. Still, this overlap of *E. americanum* and *J. diphylla* seeds does not occur naturally. Actually, *E. americanum* seeds presented with *J. diphylla* seeds were still removed at

rates comparable to the unmixed seed exclosures at the floodplain and hilltop sites ($\approx 40\%$). Based on our observations of natural populations, *E. americanum* seeds will be removed by the time *J. diphylla* capsules dehisce at both sites.

The abundance of myrmecochores within TRP is not unique. In many other eastern deciduous forests (e.g., Handel, Fisch, and Schatz, 1981), the potential for competition among myrmecochores seems apparent. However, most of these species, including *E. americanum*, stagger their seed release throughout the spring and early summer. Because ant dispersers may be the only mechanism of escaping predation and seed predation appears to be rapid on seed remaining on the soil surface, mechanisms that maximize exposure to effective dispersers should be selected. Perhaps, as suggested in numerous sympatric pollination studies (e.g., Schemske 1981), temporal partitioning and sharing could evolve in this seed dispersal scenario. Among the myrmecochores of the eastern deciduous forest, seed predation appears to be very intense, and ant-dispersed seeds in this system appear to be released over a period of several months, possibly reducing competition for seed dispersers.

Although total seed depletion did not occur in either year from any of the transects, a result supporting Wein and Pickett's (1989) conclusion that *E. americanum* seeds may be dispersed at a slower rate than other myrmecochores, this may not represent the natural seed removal rates. In this study, incomplete removal of *E. americanum* seeds occurs most likely because of two factors. First, an inhibitory effect of the pipes was detected when seeds were placed on the soil, outside of treatment pipes. This motivated our emphasis on the first 48 h of seed removal in the final analyses. Second, seeds introduced into the *E. americanum* populations were the predominant myrmecochore seeds present and may have increased the density enough to satiate the fatty acid requirements of foraging ant colonies.

In this system, predation and timing seem to be major ecological forces on this ant-plant mutualism. Predators such as nocturnal ground beetles (Ohara and Higashi, 1987; Higashi and Ito, 1991), or more commonly *P. leucopus* (Heithaus, 1981) could remove any *E. americanum* seeds remaining after the diurnal ant foraging. Consequently, the lack of specificity in this ant-plant interaction is favored by natural selection to maximize protection from nocturnal seed predation in a guild of sympatric myrmecochores. This complements other forces that discourage specialization, such as maximizing the effect of the dispersal guild and increasing dispersion of seeds into the habitat.

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