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Influence of Elaiosome Removal on Germination in Five Ant-Dispersed Plant Species

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ABSTRACT

Seed dispersal by ants is a common phenomenon in Eastern deciduous forests of the United States. Among the proposed benefits to the plant of seed manipulation by ants is enhancement of the germination rate. Since 1984 we have investigated the hypothesis that elaiosome removal enhances germination rate on eight different ant-dispersed species. Preliminary results have shown a significant increase in germination rate with elaiosome removal in only one species, *Sanguinaria canadensis*. We report here the results of two years of laboratory experiments. Intact (control) seeds, and seeds whose elaiosomes have been removed were incubated on moistened foam pads in petri dishes. Seeds were exposed to three months each of temperature regimes meant to simulate summer, fall, and winter (5°C) conditions. High germination rates were obtained for *S. canadensis*, *Asarum canadense*, *Jeffersonia diphylla*, and *Viola striata*. Only in *S. canadensis* did elaiosome removal significantly enhance germination ($p < 0.001$). Germination rates were poor in *Dicentra cucullaria* and the effects of elaiosome removal were inconclusive. The results strongly suggest that elaiosome removal does enhance germination in *S. canadensis*.

INTRODUCTION

The dispersal of seeds by ants is a common phenomenon in the herbaceous understory of the temperate forests of Europe and North America, in the shrublands of South Africa and Australia, and even in alpine and tropical locations (Beattie, 1985). Ants are attracted to a lipid-rich structure, known as an elaiosome, aril, or caruncle which is externally attached to the seed coat. Ants carry the seeds to their nest where the elaiosome, but not the seed itself, is consumed, usually by the larvae. The seeds are then carried to another location in or near the nest. Chemical analyses of elaiosomes from several plant species, including species from North America and Australia, have shown that oleic acid is the most common fatty acid present, and a common diglyceride is 1,2-diolein, both of which have been shown to be ant attractants (Marshall et al., 1979; Kusmenoglu et al., 1989; Skidmore and Heithaus, 1988; Brew et al., 1989). Worker ants from a large number of species are attracted to elaiosome-bearing seeds. In Loudoun County, Virginia, Rockwood (unpublished results) has found 15 species of ants carried the seeds of *Sanguinaria canadensis*, *Viola papilionacea*, and *Trillium sessile* (nomenclature used in this paper follows Radford et al., 1968) . Beattie and Culver (1981) have reported that nine species of ants carried seeds when they tested 10 elaiosome-bearing species in West Virginia, and Hanzawa et al. (1988) have found that nine ant species dispersed the seeds of *Corydalis aurea* in Colorado.

The benefits of this interaction to the ants seem evident in that the elaiosomes provide a temporary high quality source of lipids. What remains problematic, however, is exactly how the interaction benefits the plants. When Beattie (1985) reviewed the literature, he has found little evidence that seeds were moved far enough by the ants to support a "dispersal for distance" hypothesis. Some researchers have stressed the advantages of seeds being rapidly removed from the forest floor by the ants once they are shed from the fruit. Ants quickly locate and move the seeds to sites within or near the nest. This prevents predation by rodents or snails (Heithaus, 1981). Other ecologists have shown that, though ants may not move seeds very far, they place them in a microhabitat (near an ant nest) where the soil is inherently rich in nutrients and relatively free of competition from other plants (Hanzawa et al., 1988).

It has also been proposed that ant manipulation of seeds results in an increase in the rate of germination. As explained by Horowitz and Beattie (1980), "if ant manipulation of seeds is adaptive, then one could expect that removal of the elaiosome or aril would enhance the probability or speed of germination." The process of seed handling could effectively scarify the seed and thereby enhance germination. The elaiosome may also contain chemicals which suppress germination. Removal of the elaiosome could be interpreted as an environmental cue for germination, and thought of as part of the ant-seed dispersal syndrome evolved by the plant.

Data in support of this hypothesis are not strong. For example, Horowitz and Beattie (1980) collected 20 seeds of *Calathea microcephala* (Marantaceae) from the forest floor in Vera Cruz, Mexico and incubated them on moist filter paper. Of 13 seeds with intact arils, none germinated, while three seeds germinated of the seven whose arils were removed. The sample size was small and the age of the seeds was unknown. Subsequently, Horowitz (1981) collected 185 seeds of *C. microcephala* and 61 seeds of *C. ovandensis* from freshly opened capsules. Arils were removed, either by ants or by the use of a razor blade. Some seeds were immediately placed on moist filter paper and others were held two days before being placed on filter paper. The rate of germination was actually higher in *C. microcephala* when arils were left intact if the seeds were immediately placed on moist filter paper. With two days delay, aril removal resulted in a higher germination rate (75.0% versus 43.9%). None of the *C. ovandensis* seeds germinated. When Culver and Beattie (1978) tested the effects of elaiosome removal on *Viola papilionacea* seeds they found no significant effect on germination rate, though 33% of the ant-handled seeds had reached the seedling stage after 25 days, as compared to only 14% of the control plants. Later, Culver and Beattie (1980) examined germination rates of *V. odorata* and *V. hirta*, and found that elaiosome removal had a positive, but statistically insignificant, effect. In most of these studies the sample sizes were small, there were no replicates, and the time-frame allowed for germination was usually no more than 35 days.

In a series of papers on the germination ecophysiology of herbaceous plants from Eastern Deciduous forests, Baskin and Baskin (1985a, 1985b, 1986, 1989) have studied several ant-dispersed plant species. They have found two basic patterns. Some species (*Erythronium albidum*, *Hepatica acutiloba*, and *Asarum canadense*) have epicotyl dormancy. In such species the radicles of seeds sown in the soil

emerge in the autumn, but emergence of the cotyledons is delayed until late winter or early spring. Radicle dormancy is broken by autumn-like temperatures (20° C and 10°C for 12 hours each) and chilling is necessary to break the dormancy of the epicotyl. In a second, though similar pattern, shown by the ant-dispersed *Jeffersonia diphylla* (Baskin and Baskin, 1989), when seeds are produced in late May or early June, they have underdeveloped embryos. High summer temperatures are necessary for maturation of the embryos. Once embryos have attained a length of at least one mm, seed dormancy can be broken by a period of cold stratification. Seeds kept at 5° C for 180 days had a germination rate of 85-96% (Baskin and Baskin, 1989).

Although Baskin and Baskin worked on a number of ant-dispersed species, in none of their papers did they remove the elaiosomes. The fact that they still obtained high germination rates casts doubt on the hypothesis that elaiosome removal stimulates germination. Furthermore, the fact that germination requires specific temperature regimes does not lend credence to the idea that removal of the elaiosome by an ant is a significant environmental cue, at least in Eastern Deciduous forest ecosystems.

Nevertheless, in several preliminary experiments, we have found that germination rates in *Sanguinaria canadensis* were significantly improved if the elaiosomes were removed, though this effect was not evident in other species tested (Blois and Rockwood, 1985, 1986, 1987; Rockwood and Blois, 1986; Lobstein and Rockwood, 1991). The purpose of the work reported here was to test the effect of elaiosome removal of a number of ant-dispersed plants common to Northern Virginia. We also repeated the work of Baskin and Baskin (1986, 1989) on two species while using their germination protocol on three additional species.

STUDY SITES

Plants of the spring blooming native species used in this study were collected at two sites in Loudoun County and at one site in Prince William County, Virginia.

Lake Jackson Road

The Lake Jackson Road study site is in Prince William County, 0.5 km south of the intersection with Route 234. *Sanguinaria canadensis* was collected on a steep slope along the edge of the road. The overstory is made up of mixed oak *(Quercus)* species.

Ball's Bluff Site

Ball's Bluff National Cemetery is located in Loudoun County, 1.6 kilometers north of Leesburg, VA off Route 15. The *Asarum canadense* and *Viola striata* collection sites are on a siltstone bluff above the floodplain of the Potomac River. This study site is an oak *(Quercus* spp.), beech *(Fagus grandifolia)* and tulip poplar *(Liriodendron tulipifera)* forest with an understory of *Lindera benzoin* and *Asimina triloba*. The other primary herbaceous species in the area are *Podophyllum peltatum*, *Caulophyllum thalictroides*, *Osmorhiza longistylis*, *Dicentra cucullaria*, *Viola papillionacea*, *Allaria offinalis*, *Arisaema triphyllum*, *Hydrophyllum virginianum*, *Trillium sessile*, *Smilacina racemosa*, *Impatiens capensis*, *Veronica hederacea*, and *Galium aparine*.

Point of Rocks Site

The Point of Rocks study site is in Loudoun County, 17.6 km north of Leesburg, VA off Route 15 near the bridge over the Potomac River. The *Asarum canadense*, *Sanguinaria canadensis*, *Dicentra cucullaria*, and *Jeffersonia diphylla* collection sites are located on a steep rocky outcropping. This collection site is an oak, maple (*Acer* spp.), and beech forest with an understory of *Cornus florida*. The other primary herbaceous species in the general study area are *Podophyllum peltatum*, *Canlophyiium thalictroides*, *Erythronium albidum*, *Arisaema triphyllum*, *Viola papillionacea*, *V. pensylvanica*, *Erigenia bulbosa*, *Hydrophyllum virginianum*, *Polygonatum biflorum*, *Osmorhiza claytonia*, *O. longistylis*, *Phlox divaricata*, *Claytonia virginica*, *D. canadensis*, *Smilacina racemosa*, *Allaria officinalis*, and *Galium aparine*.

SPECIES DESCRIPTIONS

Sanguinaria canadensis (Papaveraceae) is a spring blooming perennial herbaceous species of mesic deciduous forests. This species blooms from late March to early April in Northern Virginia. The flower is 5-10 cm in diameter with 8-12 white petals, 2 green sepals, 24 stamens, and a single ovary with 40-45 ovules. The primary pollinators are bees and syrphid flies. The flower remains receptive to cross-pollination for two days after which autogamy may occur (Schemske, 1978). Fruit set begins shortly after fertilization. The fruit is an elongated capsule that reaches a length of 5-8 cm at maturity. The capsule splits along two longitudinal sutures, releasing 20-25 seeds. Each dark brown seed is 2-3 mm long with an elaiosome and is ant-dispersed (Gates, 1942). The primary single leaf is 5-20 cm in length, and is reniform with distinctive scalloped edges. The leaves of individual plants may persist into late summer. The underground storage structure is a large fleshy rhizome that exudes an orange-red exudate if damaged.

Jeffersonia diphylla (Berberidaceae) is a spring blooming perennial herbaceous species, usually located in mesic deciduous forests, often with calcareous soils. In Northern Virginia, this species often begins to bloom early in April and fruit set begins two days to one week after blooming. The solitary flowers are approximately 4 cm in diameter with 8 white petals, 8 stamens, and a pistil with 15-60 ovules within a single ovary. Bees are the primary pollinators. There is some evidence that if cross-pollination is not effective that autogamy may occur (Smith et al., 1986). The fruit is a pear-shaped capsule that is 2-5 cm long at functional maturity (late June in northern Virginia). The top of the fruit dehisces like an urn lid at maturity, releasing 20 or more chestnut-brown, 7-8 mm long seeds. The seeds have elaiosomes and are ant-dispersed (Smith et al., 1986). The leaves are 6-14 cm wide, 3-7 cm long, and are two-parted, resembling the wings of a butterfly. Each plant produces 2-17 leaves, which may persist until late summer. The underground storage structures are rhizomes.

Dicentra cucullaria (Fumariaceae) is a spring ephemeral of mesic deciduous forests. The flowers have 4 petals that form bilaterally symmetrical sac-like corollas, 2 green sepals, 6 stamens, and a bicarpellate ovary. Bumblebees are the primary pollinators. Fruit set begins several weeks after flowering. The fruit is a 2.5-3.0 cm long capsule which matures by early May. As the fruit matures it begins

to disintegrate, releasing an average of 15-20 shiny black seeds, each 2-3 mm long. The seeds have elaiosomes and are ant-dispersed. Each plant has several finely divided leaves which begin to senesce as the fruits are maturing. The underground storage structures are corms.

Asarum canadense (Aristolochiaceae) is a spring ephemeral of mesic deciduous forests. In Northern Virginia, this species begins to bloom in mid-April. The flowers have three maroon sepals, twelve stamens, and an inferior ovary. The primary pollinators are mushroom gnats, ground-walking flies, and beetles. There is some evidence that autogamy may occur if cross-pollination does not take place. Fruit set begins several weeks after flowering. The fruit is a 6-8 mm long capsule that matures in mid-June in Northern Virginia. As the fruit matures it begins to disintegrate, releasing an average of 15-20 russet-colored seeds 4-5 mm long. These seeds have elaiosomes and are ant-dispersed (Beattie and Culver, 1981). Each plant has a pair of cordate leaves with the single flower developing at the base between these two leaves. The leaves remain photosynthetic into late autumn. The underground storage structures are rhizomes.

Viola striata (Violaceae) is a spring ephemeral of mesic deciduous forests. This species begins to bloom in early to mid-April in Northern Virginia. The flowers of *V. striata* have 5 white petals, 5 green sepals, 5 stamens, and a tricarpellate pistil. Bees are the primary pollinators. Fruit set begins soon after flowering. The fruit is a 7-11 mm long three-chambered capsule that matures in early to mid-May in Northern Virginia. As the fruit matures it begins to dehisce, releasing an average of 12-15 seeds, each 2-2.5 mm long. These seeds have elaiosomes and are ant-dispersed (Culver and Beattie, 1978). Each plant has both stem and basal cordate leaves. The leaves may begin to senesce after the fruits mature or may remain photosynthetic well into summer. The underground storage structures are rhizomes.

METHODS

Seeds were collected from the field when fruits were ripe and beginning to shed their seeds (Table 1). Elaiosomes were carefully removed from half of the seeds under a dissecting microscope using forceps. Care was taken to avoid damaging the seeds or scarifying them. In most cases the elaiosomes separated cleanly from the seed coat.

Seeds were placed in petri dishes lined with a gray foam pad (8 cm in diameter, 5 mm thick) which fits into a standard petri dish. Ten seeds were placed in each dish, which was kept moist with distilled water. In the 1989-90 experiments, filter paper discs were placed on top of the foam pads and the seeds were placed on the filter paper. However, the filter paper seemed to encourage fungal contamination of the seeds. The filter paper was removed at the end of August, 1989. Thereafter, and in the 1990-91 experiments, seeds were germinated directly on the foam pads.

Germination was defined as penetration of the seed coat by the radicle of the embryo. Thus, we did not concern ourselves with breaking the dormancy of the epicotyl, though, in fact, radicle emergence was usually followed by emergence of the cotyledons at a later date. All petri dishes were inspected at least weekly with a dissecting microscope. Germination was clearly evident on the foam pads, an

advantage over our previous experiments in which we had germinated seeds on sphagnum moss or on soil (Blois and Rockwood, 1985).

Five species were used in 1989-90: *Senguinaria canadensis*, *Asarum canadense*, *J.effersonia diphylla*, *Dicentra cucullaria*, and *Viola striata*. In the 1990-91 experiments only *S. canadensis*, *A. canadense*, and *D. cucullaria* seeds were used.

Seasonal temperature and day length regimes were adapted from Baskin and Baskin (1989) as shown in Table 1. In the 1989-90 experiments we put the seeds through a simulated spring season (15°C for 12 hours and 5°C for 12 hours) before exposing them to at least three months of "summer" temperatures (28°C and 15°C for 12 hours each). In 1990-91 the seeds were placed directly into the "summer" temperatures as the experiment began. In both years the incubators were then set on "fall" temperature conditions (20°C and 10°C, 12 hours each) for three months. At this point the incubators were set at 5°C ("winter"), 24 hours per day, until the experiment was concluded (Table 1). During the entire experiment the photoperiod was kept constant at 14 hours of light, 10 hours of darkness per day.

The germination rates of plants whose elaiosomes were experimentally removed were compared to controls using the X^2 test.

RESULTS

Of the five species examined, two (*Asarum canadense* and *Sanguinaria canadensis*) showed epicotyl dormancy as previously reported by Baskin and Baskin (1986) for *A. canadense*. The radicles of these two species emerged 30-60 days after the incubators were set at "fall" conditions (Figs. 1-2). Elaiosome removal did not affect the percentage of seeds which germinated in *A. canadense* in either 1989-90 or 1990-91 (Table 2, Fig. 1). The average seed of *A. canadense*, however, germinated 9-10 days sooner in both years if the elaiosome was removed. Average time to germination was 89.4 and 42.4 days for experimentals and 98.4 and 52.9 days for controls in 1989-90 and 1990-91, respectively.

Elaiosome removal did significantly affect the final percentage of *S. canadensis* which germinated in both years of the experiment (Table 2, p, X^2 test). Germination also began earlier when elaiosomes were removed, especially in the 1990-91 experiment (Fig. 2).

Two species required cold stratification for germination. That is, after being kept in "fall" temperatures for three months, germination began only after exposure to temperatures of 5°C. *Dicentra cucullaria* seeds began germinating 30 days after being exposed to 5°C temperatures (Fig. 3). *Jeffersonia diphylla*, however, required over 100 days at 5°C for germination (with the exception of one seed which germinated earlier).

In neither of these two species did elaiosome removal have a consistent effect. The results for *D. cucullaria* are contradictory. In 1989-90 none of the experimental seeds germinated as compared to 11.7% of the controls. In 1990-91, 20.0% of the experimentals germinated, while the germination rate for controls fell to 6.7%. Therefore, although the X^2 test is significant for each year, the overall result is inconclusive. In the *J. diphylla* experiment (Table 2, Fig. 4), the germination rate was somewhat higher for controls, but the difference was not significant (0.10).

Viola striata does not show a consistent germination pattern, and elaiosome removal does not significantly affect germination (Table 2, Fig. 5). Germination

TABLE 1. Dates and temperature regimes for seed germination experiments conducted in 1989-90 and 1990-91 in which elaiosomes were removed from half of the seeds. All seeds were germinated on foam pads moistened with distilled water and kept in an incubator. Day length equal 14 hours in all experiments; high and low temperatures were for 12 hours each per day.

Asarum canadense. Seeds were collected at Ball's Bluff on June 2, 1989 and at Point of Rocks site on June 6, 1990.

Dates	Temperature Regime(°C)		Simulated
1989-90	Day	Night	"*Season*"
6/2-8/21	15	5	Spring
8/21-11/20	28	15	Summer
11/20-2/20/90	20	10	Fall
2/20-8/3	5	5	Winter
1990-91			
6/7-9/7	28	15	Summer
9/7-1/10/91	20	10	Fall
1/10-6/17	5	5	Winter

Sanguinaria canadensis. Seeds were collected at Lake Jackson site on May 29, 1989 and at Point of Rocks on May 22, 1990.

Dates	Temperature Regime(°C)		Simulated
1989-90	Day	Night	"*Season*"
5/29-6/15	15	5	Spring
6/15-11/20	28	15	Summer
11/20-2/20/90	20	10	Fall
2/20-8/3	5	5	Winter
1990-91			
5/22-8/22	28	15	Summer
8/22-11/29	20	10	Fall
11/29-3/8/91	5	5	Winter

Dicentra cucullaria. Seeds were collected at Point of Rocks on May 4, 1989 and at Point of Rocks on May 2, 1990.

Dates	Temperature Regime(°C)		Simulated
1989-90	Day	Night	"Season"
5/5-6/22	15	5	Spring
6/22-11/29	28	15	Summer
11/29-2/20/90	20	10	Fall
2/20-8/3	5	5	Winter
1990-91			
5/4-8/3	28	15	Summer
8/3-11/3	20	10	Fall
11/3-3/8/91	5	5	Winter

TABLE 1. CONTINUED

Jeffersonia diphylla. Seeds were collected at Point of Rocks on June 12, 1989.

Dates 1989-90	Temperature Regime(°C) Day	Night	Simulated "Season"
6/12-8/21	15	5	Spring
8/21-11/20	28	15	Summer
11/20-2/20/90	20	10	Fall
2/20-8/3	5	5	Winter

Viola striata. Seeds were collected at Ball's Bluff on June 28, 1989.

Dates 1989-90	Temperature Regime(°C) Day	Night	Simulated "*Season*"
6/30-8/21	15	5	Spring
8/21-11/20	28	15	Summer
11/20-2/20/90	20	10	Fall
2/20-8/3	5	5	Winter

TABLE 2. Final results of germination experiments in which elaiosomes were removed from half of the seeds while intact seeds served as controls. Percent germination is followed in parenthesis by the number germinated/sample size. Significant X^2 values are noted.

Species	Year	Controls		Elaiosomes Removed		X^2
Asarum canadense	1989-90	46.7%	(28/60)	51.7%	(31/60)	0.30
	1990-91	88.3%	(53/60)	91.7%	(55/60)	0.37
Sanguinaria canadensis	1989-90	30.0%	(18/60)	81.7%	(49/60)	32.6[1]
	1990-91	13.3%	(8/60)	46.7%	(28/60)	16.0[1]
Dicentra cucullaria	1989-90	11.7%	(7/60)	0.0%	(0/30)	4.42[2]
	1990-91	6.7%	(4/60)	20.0%	(12/90)	0.62[2]
Jeffersonia diphylla	1989-90	41.1%	(37/90)	34.4%	(31/90)	0.85
Viola striata	1989-90	60.0%	(9/15)	80.0%	(12/15)	1.40

[1] $p < 0.001$
[2] $0.025 < p < 0.050$

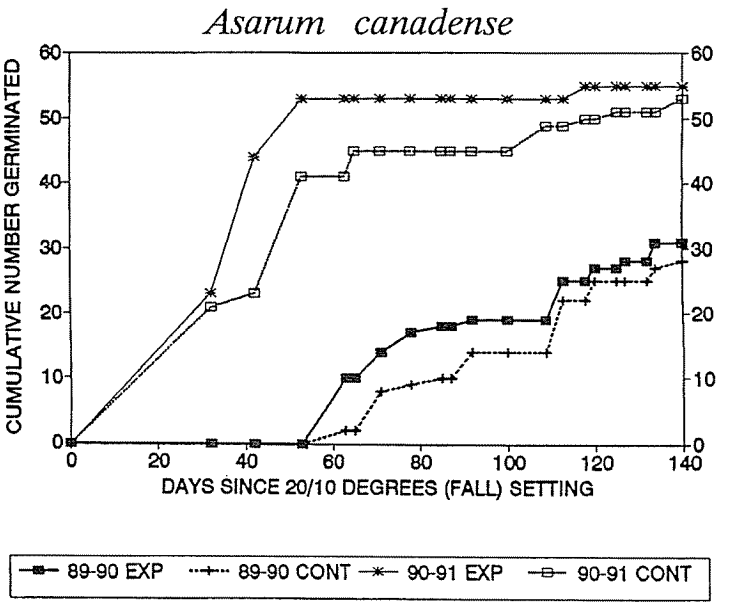

FIGURE 1. Cumulative number of *Asarum canadense* seeds which germinated after the incubator temperatures were set to simulate fall conditions. Exp represents seeds whose elaiosomes had been removed.

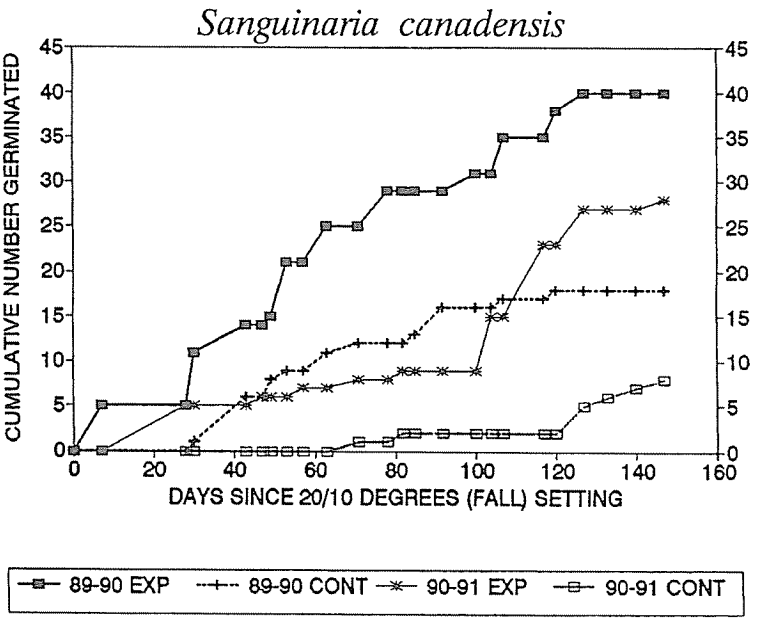

FIGURE 2. Cumulative number of *Sanguinaria canadensis* seeds which germinated after the incubator temperatures were set to simulate fall conditions. Exp represents seeds whose elaiosomes had been removed.

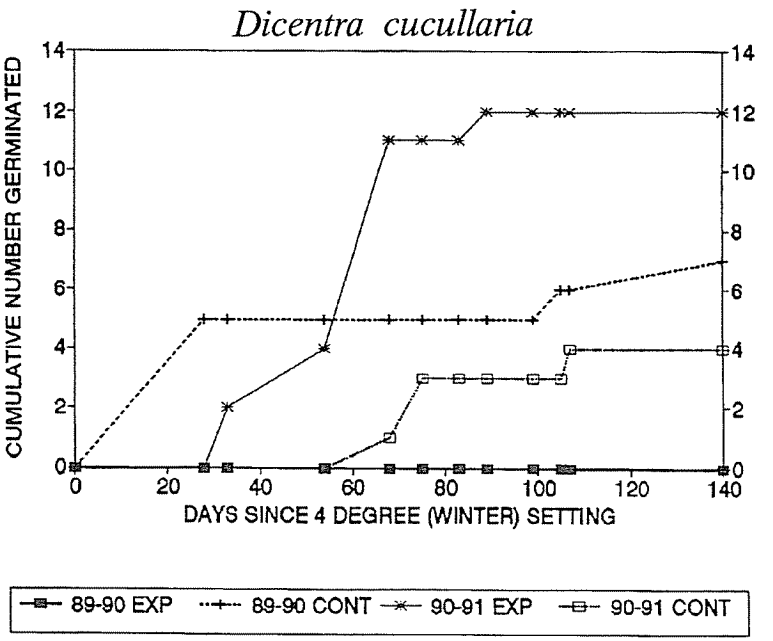

FIGURE 3. Cumulative number of *Dicentra cucullaria* seeds which germinated after the incubator temperatures were set to simulate winter conditions. Exp represents seeds whose elaiosomes had been removed.

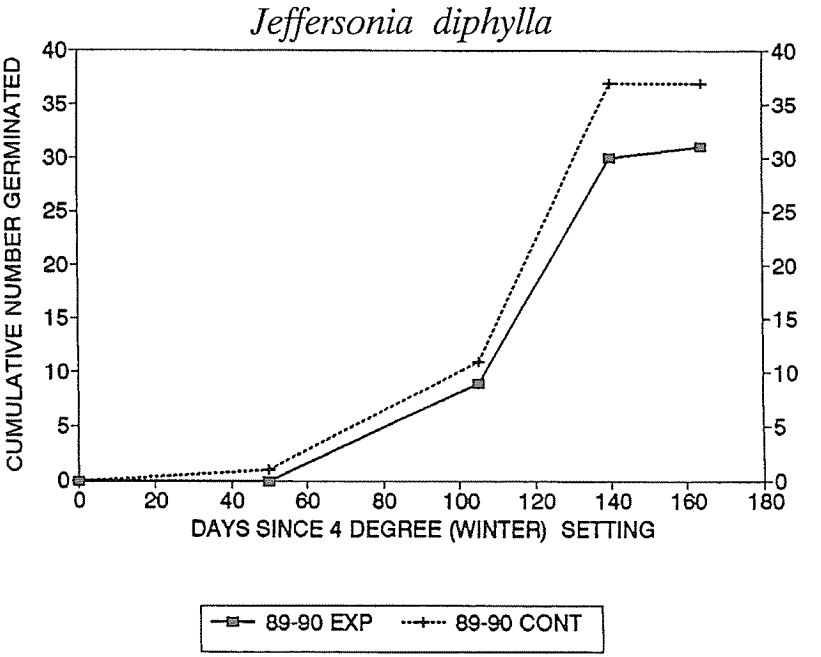

FIGURE 4. Cumulative number of *Jeffersonia diphylla* seeds which germinated after the incubator

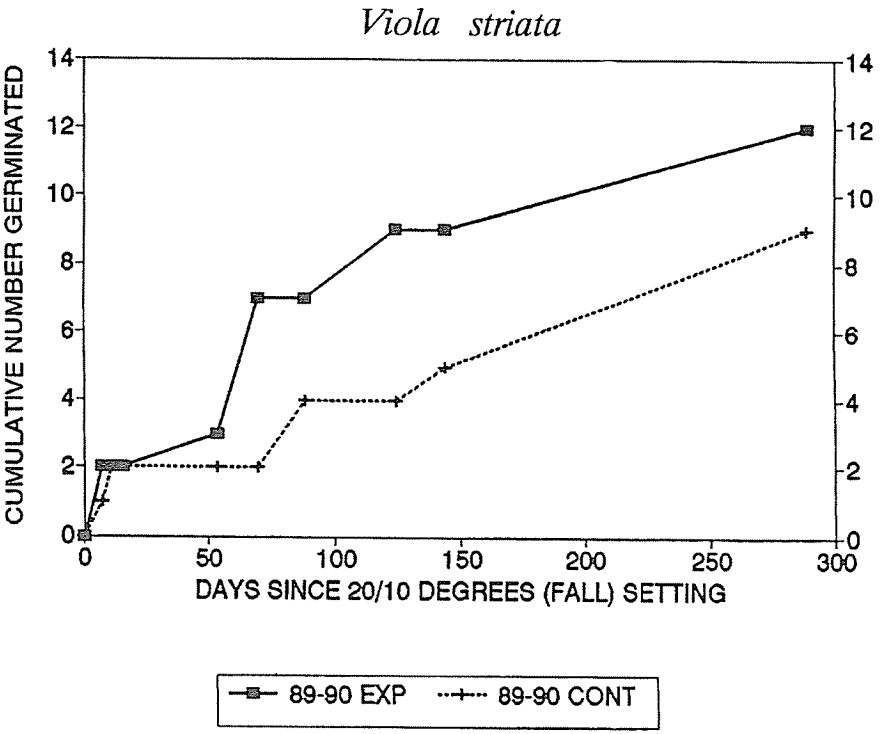

FIGURE 5. Cumulative number of *Viola striata* seeds which germinated after the incubator temperatures were set to simulate fall conditions. Exp represents seeds whose elaiosomes had been removed.

began 7-10 days after the incubator was switched to "fall" temperatures, but then ceased for over a month. Four months later there was additional germination. Three months after being shifted to "winter" temperatures (289 days after being exposed to "fall" temperatures) another group of seeds germinated (Fig. 5). Seeds whose elaiosomes had been removed germinated at a higher rate (80.0% vs. 60.0%, Table 2), but the difference is not statistically significant (X^2 = 1.4, 0.10).

DISCUSSION

Our results support previous findings (Blois and Rockwood, 1985, 1986, 1987; Lobstein and Rockwood, 1991) in that, of the species tested, only *S.anguinaria canadensis* clearly showed significant enhancement of germination when elaiosomes are removed. Though germination rate was not affected in either *Jeffersonia diphylla* or *Asarum canadense*, the time for germination to begin was reduced in A. *canadense* with elaiosomes removal. The data suggest a weak positive effect of elaiosome removal in *Dicentra cucullaria* and *Viola striata*, but the results are contradictory or insignificant. Furthermore, we have previously reported (Blois and Rockwood, 1987) that elaiosome removal, either by hand or by a laboratory ant colony, had no effect on the germination rate of *D. cucullaria*. In that experiment we obtained a germination rate of over 90% for control seeds as

well as for both sets of experimental seeds. In experiments with *V. pensylvanica* (Blois and Rockwood, 1986, 1987) we also found that elaiosome removal did not enhance germination.

As found by Baskin and Baskin (1986), the radicles of *A. canadense* seeds began to appear after being exposed for 12 hours per day to temperatures of 20°C and 10°C. We found that this was also true of *S. canadensis*. As previously reported (Baskin and Baskin, 1989), *J. diphylla* seeds only germinated after three months of "summer" temperatures, three months of "fall" temperatures, and about 100 days at 5°C (Fig. 4). *D. cucullaria* needed a similar treatment, but began germinating 30 days after exposure to 5°C. We do not understand the environmental cues needed for germination of *V. striata* seeds.

Given that elaiosome removal enhances germination in *S. canadensis* seeds, what is the mechanism, and what is the adaptive significance of this inhibition? As for the mechanism, at present we can only speculate as to whether the elaiosome physically prevents the imbibition of water needed for germination or whether there is a chemical in the elaiosome which prevents germination. Detailed microscopic studies and further chemical analysis of the *S. canadensis* elaiosome are needed. At present we only have information on the lipid portion of the elaiosome (Kusmenoglu et al., 1989).

Given the ecophysiology of seed germination in *S. canadensis*, radicles would be expected to emerge in October in the field, as was found for *A. canadense* by Baskin and Baskin (1986). If ants have not yet removed the elaiosome, would it still be present 4-5 months after being shed from the fruit, or would it have decomposed? In our laboratory the elaiosomes turned black but were still present at the conclusion of the experiment. In the soil, bacteria and fungi would presumably decompose the elaiosome, thereby removing any inhibition to germination. Still, is there adaptive significance to germination enhancement after elaiosome removal? Perhaps elaiosome removal, either by ants or by decomposition, would be correlated with favorable conditions for growth of the *S. canadensis* seedling, and elaiosome presence would be a signal that conditions are not yet favorable for germination. If a *S. canadensis* seed does not begin germination within six months of dispersal, would it still be viable twelve months later? That is, how long can a seed wait to germinate before it loses its viability? No data exist on this last question, to our knowledge.

The interesting possibility exists, then, that the evolutionary syndrome of seed dispersal by ants includes enhancement of germination as one of the benefits for the plants. Though only *S. canadensis* shows a consistent germination effect, we believe there remains a great deal to learn about this aspect of myrmecochory.

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