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# Ant–seed mutualisms: can red imported fire ants sour the relationship?

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## Abstract

Invasion by the red imported fire ant, *Solenopsis invicta*, has had negative impacts on individual animal and plant species, but little is known about how *S. invicta* affects complex mutualistic relationships. In some eastern forests of North America, 30% of herbaceous species have ant-dispersed seeds. We conducted experiments to determine if fire ants are attracted to seeds of these plant species and assessed the amount of scarification or damage that results from handling by fire ants. Fire ants removed nearly 100% of seeds of the ant-dispersed plants *Trillium undulatum*, *T. discolor*, *T. catesbaei*, *Viola rotundifolia*, and *Sanguinaria canadensis*. In recovered seeds fed to ant colonies, fire ants scarified 80% of *S. canadensis* seeds and destroyed 86% of *V. rotundifolia* seeds. Our study is the first to document that red imported fire ants are attracted to and remove seeds of species adapted for ant dispersal. Moreover, fire ants might damage these seeds and discard them in sites unfavorable for germination and seedling establishment. © 2001 Elsevier Science Ltd. All rights reserved.

**Keywords:** *Solenopsis invicta*; Red imported fire ant; Ant–plant mutualism; Myrmecochory; Seed dispersal; Invasive species

## 1. Introduction

Worldwide, representatives from at least 70 plant families are known to have ant-dispersed (myrmecochorous) seeds (Beattie, 1985). In some eastern forests of North America, approximately 30% of herbaceous species are myrmecochores (Beattie and Culver, 1981; Handel et al., 1981). These seeds bear a lipid-rich appendage (elaiosome) that is attractive to ants. Ants consume the externally attached elaiosomes, but the seeds are discarded intact in refuse heaps or in nest chambers (Handel, 1976). Myrmecochory might benefit ants directly, since elaiosomes provide a nutrient-rich resource early in the season (Marshall et al., 1979). In addition, ants might benefit indirectly. Morales and Heithaus (1998) found that *Aphaenogaster rudis* colonies have significantly more female reproductives when fed elaiosomes of *Sanguinaria canadensis*. Likewise, myrmecochory can benefit plants. Seeds dispersed by ants may escape rodent predation (Heithaus, 1981) and avoid interspecific (Handel, 1978) and parent–seedling

competition (Pudlo et al., 1980). Seeds dispersed by ants might also benefit in that their seedlings have access to additional nutrients (e.g. phosphorus, potassium, and nitrogen) contained in ant nests (Czerwinski et al., 1971). Accordingly, the relationship between ants and elaiosome-bearing plants is considered to be a mutualism (Handel and Beattie, 1990). In mesic forests of eastern North America, many native ant genera, including *Crematogaster*, *Prenolepis*, and *Aphaenogaster*, are attracted to elaiosome-bearing seeds (e.g. Gaddy, 1986).

The red imported fire ant, *Solenopsis invicta* Buren, became established in the United States in the 1930s (Lofgren, 1986). By 1995, *S. invicta* had invaded more than 114 million ha in the southeastern USA (Calcott and Collins, 1996). In areas where fire ants have become established, overall ant species richness has declined by as much as 70% (Porter and Savignano, 1990). *S. invicta* might also have negative impacts on myrmecochores. This could result from fire ants (1) decreasing populations of native ants that disperse seeds, and (2) damaging elaiosome-bearing seeds directly, or indirectly by dispersing seeds to unfavorable sites for germination and establishment. The purpose of this study is to assess

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potential interactions between the red imported fire ant and ant-dispersed seeds.

*S. invicta* inhabits disturbed sites with full to partial sun. While fire ants tend to occur in forest openings (Tschinkel, 1988), individuals may forage up to 40 m into closed-canopy forests (Forys et al., 2001). Therefore, the impact of fire ants on the biota may extend from forest openings to intact forest. In this study, we address two basic questions: (1) are red imported fire ants attracted to elaiosome-bearing seeds and (2) if so, how do they handle and discard such seeds? To address these questions, we first determined the removal rates of seeds from six elaiosome-bearing species presented to fire ants. We then assessed seeds for scarification or damage done by *S. invicta*.

## 2. Methods

### 2.1. Seed species

We collected elaiosome-bearing seeds of six native plant species of eastern deciduous forests. Seeds of *Trillium undulatum* Willd., *T. catesbaei* Ell., *T. discolor* Wray, *Sanguinaria canadensis* L., *Iris cristata* Aiton, and *Viola rotundifolia* Michaux were collected in the Blue Ridge Mountains of North and South Carolina. For *V. rotundifolia*, we used seeds from cleistogamous (closed, obligate self-pollinating) flowers. Seeds were collected from May to August 1999, refrigerated at 4°C, and were used in experiments conducted in August and September 1999. Elaiosome-bearing seeds remain attractive to ants for up to 1 year (Hughes and Westoby, 1990, Ruhren, 1994), so seed preference was unlikely to have been influenced by seed age.

### 2.2. Seed removal rates

We established a 35×45 m plot in a heavily infested ( $\geq 1333$  fire ant mounds/ha) lawn in Clemson, SC, which was divided into an 80-cell grid with 5-m intervals. At random grid locations, an index card with 10 seeds of one species was placed on the ground. Index cards were folded twice so that when unfolded, seeds rested securely in the center crease, preventing them from rolling off the cards. This experiment was done in the morning when the air was calm so that seeds were not blown off cards. For each of the six plant species tested, we used 10 replicate cards with 10 seeds each. Seeds taken from an index card by *S. invicta* were recorded as removed. We continuously monitored index cards by pacing transects, and we observed that only *S. invicta* removed seeds. After 1 h, the remaining seeds were counted. Differences among plant species in seed removal rates were analyzed by a one-way analysis of variance (ANOVA) and a Tukey's multiple comparison test.

### 2.3. Seed damage in laboratory colonies

Five *S. invicta* mounds (containing queen, brood, and workers) were collected in August 1999 from the Clemson Experimental Forest (Clemson, SC) and maintained in 19-l buckets in a laboratory with an average temperature of 22°C. Colonies were fed a diet of crickets, honey, and tuna. Ten seeds of each of the six species (60 seeds total) were presented to each of the five colonies. Seeds were placed on feeding platforms made from index cards glued to 0.30-m dowels. Fire ants moved all seeds from index cards to their mounds within 12 h. Trash piles on the soil surface were searched daily for discarded seeds for 30 days. The total number of seeds recovered in trash piles was recorded, and each seed was examined microscopically for evidence of scarification or damage (seeds with at least 1/4 of the seed consumed were considered destroyed). Seed-recovery rates and numbers of scarified or destroyed seeds were analyzed using Kruskal–Wallis ANOVA, and a significant result ( $P < 0.05$ ) was examined further using the Student–Newman–Keuls method.

### 2.4. Seed damage in field colonies

In September 1999, two *S. invicta* colonies located along a roadside in Pendleton, SC, were offered 10 seeds of each of the six same species (60 seeds total). All seeds were taken into the mounds within 2 h, and after 24 and 48 h, discarded seeds were collected in trash piles. The experiment was terminated prematurely because a rain-storm disrupted the mounds and trash piles. Recovered seeds were classified as scarified or destroyed as described above.

## 3. Results

### 3.1. Seed-removal rates

Nearly all (95–99%) seeds from five species (*T. undulatum*, *T. catesbaei*, *T. discolor*, *V. rotundifolia*, and *S. canadensis*) were removed by *S. invicta* (Table 1). The sixth species, *I. cristata*, had 30% of its seeds removed by fire ants (Table 1).

### 3.2. Seed damage in laboratory experiment

More than 55% of the seeds removed by fire ants in laboratory colonies were recovered, except for *V. rotundifolia* for which only 28% of the seeds were recovered (Table 2). Of the recovered *V. rotundifolia* seeds, 86% were destroyed by fire ant feeding (Fig. 1). Fire ants removed elaiosomes from nearly all recovered seeds (92–100%), except for *I. cristata*, which had relatively few (24%) elaiosomes consumed. We recovered

all *S. canadensis* seeds, 80% of which had been scarified by fire ants (Table 2). The fate of unrecovered seeds is unknown; they could have been discarded within the nest or been consumed. Because these ant colonies were used in an unrelated experiment, the soil could not be searched for undiscarded seeds.

### 3.3. Seed damage in field experiment

Recovery rates of seeds fed to field colonies of fire ants were low (5–70%) probably because the experiment was ended prematurely (Table 2). Only *S. canadensis* seeds had high (70%) recovery rates, 93% of which were scarified (Table 2). All recovered seeds had elaiosomes removed by *S. invicta*, except *I. cristata* which had relatively few (33%) elaiosomes consumed.

Table 1  
Removal rates of elaiosome-bearing seeds by the red imported fire ant in Clemson, SC, USA, in September 1999<sup>a,b</sup>

| Seed species           | % Seed removed <sup>c</sup> |
|------------------------|-----------------------------|
| <i>S. canadensis</i>   | 99 (9.9±0.1)a               |
| <i>T. catesbaei</i>    | 99 (9.9±0.1)a               |
| <i>T. undulatum</i>    | 99 (9.9±0.1)a               |
| <i>T. discolor</i>     | 95 (9.5±0.2)a               |
| <i>V. rotundifolia</i> | 99 (9.9±0.1)a               |
| <i>I. cristata</i>     | 30 (3.0±1.1)b               |

<sup>a</sup> Numbers in parentheses are the means ±S.E.

<sup>b</sup> Means with the same letter are not significantly different ( $P > 0.05$ ).

<sup>c</sup> Ten replicates of 10 seeds for each plant species.

## 4. Discussion

To our knowledge, this is the first study to document that red imported fire ants remove seeds of spring herbs. We found that fire ants remove seeds, consume elaiosomes, and scarify or destroy seeds. As a result, invasion by *Solenopsis invicta* is a potential threat to spring ephemerals. Nearly 100% of the seeds of *T. undulatum*, *T. catesbaei*, *T. discolor*, *Sanguinaria canadensis*, and *V. rotundifolia* were removed by *Solenopsis invicta*. An exception was the elaiosome-bearing *I. cristata* seeds, which had relatively low (30%) removal rates and relatively few elaiosomes consumed in both laboratory and field experiments (24 and 33%, respectively). Although *Iris* is documented as an ant-dispersed genus (Beattie 1983), *I. cristata* is not a known myrmecochore.

The continuing range expansion of *Solenopsis invicta* throughout the southeast and the Pacific coast of the United States (Calcott and Collins, 1996) renders myrmecochorous plants vulnerable to seed predation. Although fire ants feed primarily on invertebrates, *Solenopsis invicta* is considered an omnivore (Hays and Hays, 1959). In a study by Tennant and Porter (1991), non-elaiosome-bearing seeds made up at least 4.8% of the diet of *Solenopsis invicta*. Moreover, fire ants are known to consume sorghum seeds in agricultural fields (Drees et al., 1991). Because fatty acid composition of elaiosomes is similar to that of insect hemolymph (Hughes et al., 1994), elaiosome-bearing seeds may be particularly attractive to fire ants. In a preliminary experiment, fire ants were significantly ( $P < 0.05$ ) more attracted to elaiosome-bearing seeds of myrmecochores than to seeds of *Sorghum vulgare* (which lacks elaiosomes; unpublished data).

Table 2  
Percent of seeds recovered in trash piles of laboratory and field colonies of red imported fire ants in Clemson, SC, USA, in September 1999<sup>a</sup>

|                            | % Seeds recovered <sup>b</sup> | % Recovered seeds scarified | % Recovered seeds destroyed <sup>c</sup> |
|----------------------------|--------------------------------|-----------------------------|--|
| <i>Laboratory colonies</i> |                                |                             |  |
| <i>V. rotundifolia</i>     | 28 (2.8±1.3)b                  | 14 (0.4±0.2)b               | 86 (2.4±1.2)a                            |
| <i>I. cristata</i>         | 58 (5.8±0.7)bc                 | 3 (0.2±0.2)b                | 0 (0.0±0.0)a                             |
| <i>T. catesbaei</i>        | 68 (6.8±1.2)ac                 | 6 (0.4±0.2)b                | 29 (2.0±1.1)a                            |
| <i>T. undulatum</i>        | 70 (7.0±1.1)ac                 | 6 (0.4±0.2)b                | 3 (0.2±0.2)a                             |
| <i>T. discolor</i>         | 56 (5.6±0.9)bc                 | 0 (0.0±0.0)b                | 39 (2.2±0.8)a                            |
| <i>S. canadensis</i>       | 100 (10.0±0.0)a                | 80 (8.0±1.5)a               | 4 (0.4±0.4)a                             |
| <i>Field colonies</i>      |                                |                             |  |
| <i>V. rotundifolia</i>     | 5 (0.5±0.5)                    | 0 (0.0±0.0)                 | 100 (0.5±0.5)                            |
| <i>I. cristata</i>         | 15 (1.5±0.5)                   | 7 (0.5±0.5)                 | 33 (0.5±0.5)                             |
| <i>T. catesbaei</i>        | 35 (3.5±2.5)                   | 57 (2.0±2.0)                | 0 (0.0±0.0)                              |
| <i>T. undulatum</i>        | 30 (3.0±1.0)                   | 67 (2.0±2.0)                | 0 (0.0±0.0)                              |
| <i>T. discolor</i>         | 30 (3.0±2.0)                   | 50 (1.5±1.5)                | 0 (0.0±0.0)                              |
| <i>S. canadensis</i>       | 70 (7.0±1.0)                   | 93 (6.5±1.5)                | 7 (0.5±0.5)                              |

<sup>a</sup> Of the recovered seeds, the percent scarified and destroyed are given. Numbers in parentheses are the means ±S.E. Within-column means with the same letter are not significantly different ( $P > 0.05$ ).

<sup>b</sup> Laboratory colonies; five replicates of 10 seeds for each plant species. Field colonies; two replicates of 10 seeds for each plant species.

<sup>c</sup> Seeds with at least a quarter of the seed consumed were considered destroyed.



Fig. 1. Five seeds of *Viola rotundifolia* destroyed by laboratory colonies of the red imported fire ant, *Solenopsis invicta*. An intact seed in the lower corner is for reference since it was not presented to *S. invicta*. Scale on tool measures 5 mm total.

We found that 86% of *V. rotundifolia*, 29% of *T. catesbaei*, and 36% of *T. discolor* seeds recovered in trash piles were destroyed. In contrast, *S. invicta* destroyed less than five percent of *T. undulatum* and *S. canadensis* seeds. One possible explanation for the observed variation in predation rates is a difference among species in seed coat thickness or strength (Rodgers, 1998). In addition, species with lower seed predation rates might contain chemical compounds that repel predators. *S. invicta* is not a natural seed-disperser of these plant species, and the damage they inflict is not typically found in seeds dispersed by native ants. For example, 70% of cleistogamous seeds of *V. papilionacea* fed to colonies of native ants in the genus *Aphaenogaster* were scarified, but no seeds were destroyed (Culver and Beattie, 1978).

The native fire ant, *S. geminata*, is a known seed predator of some myrmecochorous species. For example, Beattie and Lyons (1975) found that laboratory colonies destroyed 67% of recovered seeds of violets (*V. pedata*, *V. canadensis*, and *V. papilionacea*). However, *S. geminata* populations are being replaced by the red imported fire ant (Porter et al., 1988) as the latter species expands its range (Calcott and Collins, 1996), and the prevalence

of polygynous (multiple queen) colonies increases (Porter and Savignano, 1990). Higher densities and prevalence of *S. invicta* likely will amplify negative impacts of seed predation by fire ants.

In addition to destroying seeds through predation, fire ants might have other effects on seeds. We found that a high percentage (80 and 93% in laboratory and field colonies, respectively) of recovered *S. canadensis* seeds were scarified by fire ants. If fire ants scarify seeds too deeply, the embryo could be damaged directly or indirectly due to desiccation. The seed coat, which is three times thicker than other seed parts, under the elaiosome of *Fremontodendron decumbens* probably protects the seed from ant-feeding damage (Boyd, 1996). Although scarification with fine sandpaper enhances (though not significantly) germination of *V. odorata* and *V. hirta* seeds (Culver and Beattie, 1980), it is unknown if scarification by *S. invicta* promotes seed germination. Scarification of some ant-dispersed seeds [e.g. *S. canadensis* (Barton, 1944), *T. erectum* (Barton, 1944), and *Erythronium albidum* (Baskin and Baskin, 1985)] probably has little effect on germination due to a morphophysiological dormancy mechanism that is broken by stratification.

Seed germination and establishment rates in fire ant mounds might be less than in native ant nests. Nests of *Aphaenogaster* average 12 cm deep, but the upper nest chambers often consist of a thick layer of leaves (Talbot, 1951). Dispersed seeds are found most commonly in the upper chambers near the soil surface or in trash piles under the leaf litter (Culver and Beattie, 1980). Fire ant mounds, in contrast, often occur in open disturbed areas with bare soil (Tschinkel, 1986), and trash piles of fire ants occur on the soil surface (Howard and Tschinkel, 1976). Such conditions could result in a diminution in seed germination and seedling establishment.

The continuing spread of *S. invicta* might adversely affect ant-dispersed plants. Increasing fragmentation of forests due to urbanization, logging, and roads will almost surely increase the abundance of fire ants in forests. This, in turn, could exacerbate the impact of fire ants on myrmecochores. In addition, more open forests such as longleaf pine-wiregrass savannas in the southern coastal plain are especially vulnerable to fire ant invasion. While such forests have fewer ant-dispersed plants than eastern deciduous forests, those that occur may be particularly susceptible to seed predation by fire ants.

In South Africa, the introduction of non-native ants has had a negative impact on myrmecochores. For example, when an introduced ant displaced native seed-dispersing ants, emergence of *Mimetes cucullatus* seedlings was reduced (Bond and Slingsby, 1984). Bond and Slingsby (1984) suggest that introduction of non-native ants can change plant community composition by reducing seedling recruitment. Therefore, non-native

ants can potentially impact both individual species and communities. Our study has shown that fire ants are both attracted to and damage the seeds of several ant-dispersed plants. However, long-term effects of fire ant invasions on ant–seed mutualisms have yet to be determined.

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### References

- Barton, L.V., 1944. Some seeds showing special dormancy. Contributions from Boyce Thompson Institute 13, 259–271.
- Baskin, J.M., Baskin, C.C., 1985. Seed germination ecophysiology of the woodland spring geophyte *Erythronium albidum*. Botanical Gazette 146, 130–136.
- Beattie, A.J., 1983. Distribution of ant-dispersed plants. Sonderbande des Naturwissenschaftlichen Vereins in Hamburg 7, 249–270.
- Beattie, A.J., 1985. The Evolutionary Ecology of Ant–Plant Mutualisms. Cambridge University Press, Cambridge.
- Beattie, A.J., Culver, D.C., 1981. The guild of myrmecochores in the herbaceous flora of West Virginia forests. Ecology 62, 107–115.
- Beattie, A.J., Lyons, N., 1975. Seed dispersal in *Viola*: adaptations and strategies. American Journal of Botany 62, 714–722.
- Bond, W.J., Slingsby, P., 1984. Collapse of an ant–plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. Ecology 65, 1031–1037.
- Boyd, R.S., 1996. Ant-mediated seed dispersal of the rare chaparral shrub *Fremontodendron decumbens* (Sterculiaceae). Madroño 43, 299–315.
- Calcott, A.A., Collins, H.L., 1996. Invasion and range expansion of imported fire ants (Hymenoptera: Formicidae) in North America from 1918–1995. Florida Entomologist 79, 240–251.
- Culver, D.C., Beattie, A.J., 1978. Myrmecochory in *Viola*: dynamics of seed-ant interactions in some West Virginia species. Journal of Ecology 66, 53–72.
- Culver, D.C., Beattie, A.J., 1980. The fate of *Viola* seeds dispersed by ants. American Journal of Botany 67, 710–714.
- Czerwinski, Z., Jakubczyk, H., Petal, J., 1971. Influence of ant hills on meadow soils. Pedobiologia 11, 277–285.
- Drees, B.M., Berger, L.A., Cavazos, R., Vinson, S.B., 1991. Factors affecting sorghum and corn seed predation by foraging red imported fire ants (Hymenoptera: Formicidae). Journal of Economic Entomology 84, 285–289.
- Forsy, E.A., Quistorff, A., Allen, C.R., in press. Potential fire ant (Hymenoptera: Formicidae) impact on the endangered Schaus swallowtail (Lepidoptera: Papilionidae). Florida Entomologist.
- Gaddy, L.L., 1986. Twelve new ant-dispersed species from the southern Appalachians. Bulletin of the Torrey Botanical Club 113, 247–251.
- Handel, S.N., 1976. Dispersal ecology of *Carex pedunculata* (Cyperaceae), a new American myrmecochore. American Journal of Botany 63, 1071–1079.
- Handel, S.N., 1978. The competitive relationship of three woodland sedges, and its bearing on the evolution of ant dispersal of *Carex pedunculata*. Evolution 32, 151–163.
- Handel, S.N., Beattie, A.J., 1990. Seed dispersal by ants. Scientific American 263, 76–83.
- Handel, S.N., Fisch, S.B., Schatz, G.E., 1981. Ants disperse a majority of herbs in a mesic forest community in New York State. Bulletin of the Torrey Botanical Club 108, 430–437.
- Hays, S.B., Hays, K.L., 1959. Food habits of *Solenopsis saevissima richteri* Forel. Journal of Economic Entomology 52, 455–457.
- Heithaus, E.R., 1981. Seed predation by rodents on three ant-dispersed plants. Ecology 62, 136–145.
- Howard, D.F., Tschinkel, W.R., 1976. Aspects of necrophoric behavior in the red imported fire ant, *Solenopsis invicta*. Behavior 56, 157–180.
- Hughes, L., Westoby, M., 1990. Removal rates of seeds adapted for dispersal by ants. Ecology 71, 138–148.
- Hughes, L., Westoby, M., Jurado, E., 1994. Convergence of elaiosomes and insect prey: evidence from ant foraging behaviour and fatty acid composition. Functional Ecology 8, 358–365.
- Lofgren, C.S., 1986. The economic importance and control of imported fire ants in the United States. In: Vinson, S.B. (Ed.), Economic Impact and Control of Social Insects. Praeger, New York, pp. 222–251.
- Marshall, D.L., Beattie, A.J., Bollenbacher, W.E., 1979. Evidence for diglycerides as attractants in an ant–seed interaction. Journal of Chemical Ecology 5, 335–344.
- Morales, M.A., Heithaus, E.R., 1998. Food from seed-dispersal mutualism shifts sex ratios in colonies of the ant *Aphaenogaster rudis*. Ecology 79, 734–739.
- Porter, S.D., Savignano, D.A., 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. Ecology 71, 2095–2106.
- Porter, S.D., Van Eimeren, B., Gilbert, L.E., 1988. Invasion of red imported fire ants (Hymenoptera: Formicidae): microgeography of competitive replacement. Annals of the Entomological Society of America 81, 913–918.
- Pudlo, R.J., Beattie, A.J., Culver, D.C., 1980. Population consequences of changes in an ant–seed mutualism in *Sanguinaria canadensis*. Oecologia 146, 32–37.
- Rodgers, L., 1998. Mechanical defense in seeds adapted for ant dispersal. Ecology 79, 1669–1677.
- Ruhren, S., 1994. Seed Dispersal Dynamics of *Erythronium americanum*, a Deciduous Forest, Spring Ephemeral Myrmecochore. Master's thesis. University of Maryland. College Park, MD.
- Talbot, M., 1951. Populations and hibernating conditions of the ant *Aphaenogaster (Attoymyrmex) rudis* Emery. Annals of the Entomological Society of America 44, 302–307.
- Tennant, L.E., Porter, S.D., 1991. Comparison of diets of two fire ant species (Hymenoptera: Formicidae): solid and liquid components. Journal of Entomological Science 26, 450–465.
- Tschinkel, W.R., 1986. The ecological nature of the fire ant: some aspects of colony function and some unanswered questions. In: Lofgren, C.S., Vander Meer, R.K. (Eds.), Fire Ants and Leaf-cutting Ants: Biology and Management. Westview, Boulder, pp. 72–87.
- Tschinkel, W.R., 1988. Distribution of the fire ants *Solenopsis invicta* and *S. geminata* (Hymenoptera: Formicidae) in southern Florida in relation to habitat and disturbance. Annals of the Entomological Society of America 81, 76–81.