

Biology and Management of the Texas Leafcutting Ant (Hymenoptera: Formicidae)

T. D. Schowalter¹ and D. R. Ring

Entomology Department, Louisiana State University Agricultural Center, Baton Rouge, LA 70803 (tschowalter@agcenter.lsu.edu; dring@agcenter.lsu.edu), and ¹Corresponding author, e-mail: tschowalter@agcenter.lsu.edu

Subject Editor: Boris Castro

Received 5 April 2017; Editorial decision 18 May 2017

Abstract

Leafcutting ants are primarily a tropical group, but three species, particularly the Texas leafcutting ant, *Atta texana* (Buckley) (Hymenoptera: Formicidae), occur in the southern United States. Leafcutting ants provide an example of the complexity of ecological interactions. As a result of extensive defoliation and nest excavation, these ants influence vegetation cover, soil structure, and water fluxes over a significant portion of the landscape. They also can be severe forest and crop pests, and collapse of their extensive underground colonies can undermine roads and structures. In Texas, they are considered the second most important pest in pine plantations, following southern pine beetle, *Dendroctonus frontalis* Zimmerman (Coleoptera: Curculionidae). Leafcutting ants can defoliate a wide variety of plants, but some plant species are unpalatable because of defensive chemicals or endophytic fungi growing within foliage. Leafcutting ant populations also are regulated naturally by the availability of suitable nest sites and by predators, parasites, and antagonists of their fungal gardens. Relatively few management options are available. One bait and one fipronil product are labeled for leafcutting ant control.

Key words: forest management, defoliator, fungus garden, soil excavation, bait

Leafcutting ants provide one of the most interesting examples of ecological interactions but also cause severe losses to crop and forest yields and can cause collapse of roads and structures. Leafcutting ants belong to the genera *Atta* F. and *Acromyrmex* Mayr (Hymenoptera: Formicidae), which include at least 48 species common to tropical and subtropical North and South America. The two genera are distinguished by three pairs of spines on the promesonotum for *Acromyrmex* and two pairs for *Atta* (Fisher and Cover 2007). Three species occur in the United States. *Atta texana* (Buckley), the Texas leafcutting ant or “town ant,” is the most widespread species in the United States, occurring primarily in forested areas of east Texas, Louisiana, and northeastern Mexico (Moser 2006, Sanchez-Peña 2010). *Atta mexicana* inhabits arid regions of Mexico, crossing into extreme southern Arizona (Mintzer 1979, 1980; Mintzer and Mintzer 1988). In the United States, *A. texana* can be distinguished from *A. mexicana* by having long pronotal spines and hair on posterior cephalic lobes on the first gastral tergite; *A. mexicana* lacks these features. However, these two species do not overlap geographically. *Acromyrmex versicolor* Pergrande is most common in the Sonoran Desert of southern Arizona but can be found from west Texas to southern California and south into Mexico (Mintzer 1980, Fisher and Cover 2007, Shattuck and Cover 2016). Where *A. mexicana* and *A. versicolor* overlap in the Sonoran

Desert, they are known to share foraging trails without showing aggressive behavior (Mintzer 1980).

Leafcutting ants have been studied extensively because of their unique cultivation of mutualistic fungi in underground fungal gardens (Currie et al. 1999, Currie and Stuart 2001, Barnett et al. 2013, Mighell and Van Bael 2016). The fungi are cultivated as food for the colony. Fungal cultivation requires defoliation of nearby plants for necessary detrital substrate. Leafcutting ants also have received attention for their trail pheromones that facilitate foraging (Tumlinson et al. 1971), for their responses to host chemistry and endophytic fungi (fungi that live mutualistically within leaf tissues; Waller 1982a,b; Howard et al. 1989; Saverschek and Roces 2011), and for their symbiotic association with a wide variety of myrmecophilous nest associates (Moser 2006, Hooper-Bui and Seymour 2007, Barnett et al. 2013). As a result of extensive defoliation and nest excavation, these ants increase biodiversity and soil health and alter vegetation cover, structure and composition, soil structure, and water fluxes over a significant portion of the landscape (Cahal et al. 1993, Moser 2006, Barnett et al. 2013), thereby functioning as ecosystem engineers. However, leafcutting ants also have negative impacts on commercial crops or plantations in the vicinity of their nests (Cherrett 1986, Moser 1986, Cahal et al. 1993, Montoya-Lerma et al. 2012, Fischer 2015).

The Texas leafcutting ant is considered the second most important pest in pine plantations, following southern pine beetle, *Dendroctonus frontalis* Zimmerman (Coleoptera: Curculionidae) (Fischer 2015). Fischer (2015) estimated that costs of control and seedling replacement average US\$2.3 million per year. These ants also become severe pests when they defoliate ornamental plantings or crops and when collapse of their colonies causes structural damage to homes or roads (Cherrett 1986, Moser 1986, Cahal et al. 1993, Dash et al. 2005, López-Riquelme et al. 2006, Hooper-Bui and Seymour 2007, Fischer 2015, Merchant and Drees 2015, Montoya-Lerma et al. 2012). Although leafcutting ants can defoliate a wide variety of plants, populations are regulated naturally by the availability of suitable nest sites and host plants and by predators, parasites, and antagonists of their fungal gardens (Disney 1980; Waller 1982a,b; Cahal et al. 1993; Currie et al. 1999; Zavala-Hurtado et al. 2000; Reynolds and Currie 2004; Rodrigues et al. 2009). The following description of biology and management will focus on the Texas leafcutter ant, also commonly known as the “town ant,” supplemented with information for other leafcutting ant species.

Description

Leafcutting ants typically are reddish-brown in color, with 11-segmented antennae that lack a club, three pairs of spines on the thorax, and a two-segmented petiole (Fig. 1; Fisher and Cover 2007). Leafcutting ants are highly polymorphic with numerous castes, with *Atta* showing a higher degree of polymorphism than does *Acromyrmex* (Fig. 2; Wetterer 1999, Fisher and Cover 2007). Workers range from 1.5 to 15 mm in length (Dash et al. 2005). Queens and drones are disproportionately large and are likely to be confused with large wasps (Fig. 2). Only dispersing queens and drones are winged. Winged reproductives swarm in late spring.

Leafcutting ants have powerful mandibles used to cut foliage fragments for use in their fungal gardens (Fig. 3A). Although these ants cannot sting (Hermann et al. 1970), they are capable of inflicting painful bites (Fig. 3B).

The Texas leafcutting ant occurs primarily in forest gaps west of the Mississippi alluvial plain (Dash et al. 2005, Fisher and Cover 2007). Nests typically are constructed in sandy or sandy loam soils, especially on ridges where the water table is deep (Cahal et al. 1993, Dash et al. 2005), and can cover up to 1,200 m² (12,000 ft.²) surface area and extend >7 m (22 ft.) deep (Cahal et al. 1993, Moser 2006). The surface is marked by numerous crescent-shaped mounds about 15–30 cm (6–12 in.) in height and about 30 cm (12 in.) in diameter (Fig. 4; Cahal et al. 1993, Moser 2006). Nest structure is characterized by numerous tunnels and galleries containing fungus gardens upon which the ants feed (Cahal et al. 1993, Moser 2006). Colonies can become immense, with up to several million workers, often include small satellite colonies within the bounds of the primary colony, and are typically polygynous, i.e., including multiple queens (Echols 1966a, Jonkman 1980, Moser and Lewis 1981, Mintzer and Vinson 1985, Mintzer 1987).

Ecology

The Texas leafcutting ant is the northernmost species of leafcutting ants and persists because its mutualistic fungi are more cold-tolerant than are fungal species cultivated by more tropical and subtropical ant species (Mueller et al. 2011). Consequently, warming temperatures are likely to promote northward spread of this ant and its



Fig. 1. Texas leafcutting ant. Photo by Susan Ellis, courtesy of Bugwood.org.



Fig. 2. Texas leafcutting ant castes. Photo by R. Scott Cameron, Advanced Forest Protection, Inc., courtesy of Bugwood.org.

fungal associates. The establishment of Texas leafcutting ant colonies depends on the availability of forest gaps with sandy soils (Cahal et al. 1993, Fisher and Cover 2007), availability of suitable host plants (Cahal et al. 1993, Saverschek and Roces 2011), and on colony ability to initiate and sustain their fungal garden (Currie et al. 1999, Currie and Stuart 2001, Mighell and Van Bael 2016).

Leafcutting ants are unique in their use of cut foliage to support the growth of mutualistic fungi, *Leucocoprinus* spp. and *Leucoagaricus* spp. (Basidiomycota), on which the ants feed (Fig. 5; Currie et al. 1999, Currie and Stuart 2001) and on which they depend for digestive proteinases (Boyd and Martin 1975). Foliage is cut from various plant species (Fig. 6A) and returned along distinct foraging trails to the colony (Fig. 6B, C), where the leaf fragments are cut into smaller pieces to maximize surface area (Garrett et al. 2016), cleaned to remove microbes that would compete with or parasitize their garden fungi (Mighell and Van Bael 2016), deposited in chambers and inoculated with the mutualistic fungus (Currie et al. 1999). The ants tend these fungal gardens by pruning to increase productivity and weeding competitive fungi and pathogenic microbes, and feed on the fungus (Bass and Cherrett 1994, 1996; Currie and Stuart 2001; Mighell and Van Bael 2016).

Such mutualistic interdependence would seem to favor a high degree of specificity among partners. Recent studies involving exchange of fungal symbionts among leafcutting ant species or preference among cultivars indicate that *Atta texana* is capable of surviving on gardens composed of fungi from multiple leafcutting ant species (Seal and Tschinkel 2007, Sen et al. 2010). Nevertheless,



Fig. 3. (A) Close up of Texas leafcutting ant, worker head; (B) injury inflicted by mandibles. Photos by J. Moser, USDA Forest Service, courtesy of Bugwood.org.

the degree of mutualism between attine ant species and their garden fungi, including ant foraging to optimize carbohydrate:protein ratio for the fungi, has been proposed as an explanation for the success of these ants in the Neotropics (Shik et al. 2016).

Foundress queens carry fungus inoculum when they establish new colonies. However, fungus gardens often host competing fungi, as well as a virulent fungal pathogen, *Escovopsis weberi* J. J. Muchovej & Della Lucia (Hypocreales: incertae sedis), capable of destroying the fungus garden and the dependent ant colony (Currie et al. 1999, Reynolds and Currie 2004, Rodrigues et al. 2009). Pinto-Tomás et al. (2010) reported that >80 tropical leafcutting ant colonies contained bacteria in the genera *Klebsiella* and *Pantoea* that fix nitrogen within the fungal gardens and provide a vital source of this limiting nutrient. The ants have additional mutualistic



Fig. 4. Texas leafcutting ant colony ("town") in forest, east Texas. Photo by Ronald F. Billings, Texas A&M Forest Service, courtesy of Bugwood.org.



Fig. 5. Excavated chamber of Texas leafcutting ant colony showing fungus garden. Photo by John Moser, USDA Forest Service, courtesy of Bugwood.org.

associates, including an actinomycete bacterium, *Pseudonocardia* sp., other bacteria, *Burkholderia* sp., and yeasts, that produce specialized antibiotics with potent inhibitory activity against *E. weberi*, competing fungi and ant pathogens, *Beauveria bassiana* (Bals.-Criv.) Vuill. (Hypocreales: Clavicipitaceae), necessary to protect the ants and their fungus gardens (Currie et al. 1999, Rodrigues et al. 2009, Barke et al. 2010). Colony survival depends on protection of the fungus garden from parasites or competing fungi.

Fungal cultivars have specific nutritional requirements that influence leafcutting ant foraging choices (Shik et al. 2016). Leafcutting ants show a preference for grasses, forbs, and hardwood foliage, compared to conifers (Cahal et al. 1993) and for shorter plants, compared to taller plants that require longer foraging distances (Vasconcelos 1997), as well as strong preferences within and among plant species (Rockwood 1976, Howard 1990) that reflect differences in leaf toughness, sugar content, plant defenses, and endophytic fungi (Waller 1982a,b; Howard et al. 1988, 1989; Van Bael et al. 2009; Bittleston et al. 2011; Saverschek and Roces 2011; Estrada et al. 2013, 2015). Foraging generally declines with distance from nests, but is not evenly distributed among available trees (Rockwood 1976). Levels of herbivory by leafcutting ants are higher in monocultures of palatable crops than in more diverse vegetation (Blanton and Ewel 1985, Cahal et al. 1993, Varón et al. 2007, Montoya-Lerma et al. 2012).

Foraging is strongly dependent on recruitment of foragers to suitable foliage resources. *Atta texana* was the first ant for which a trail

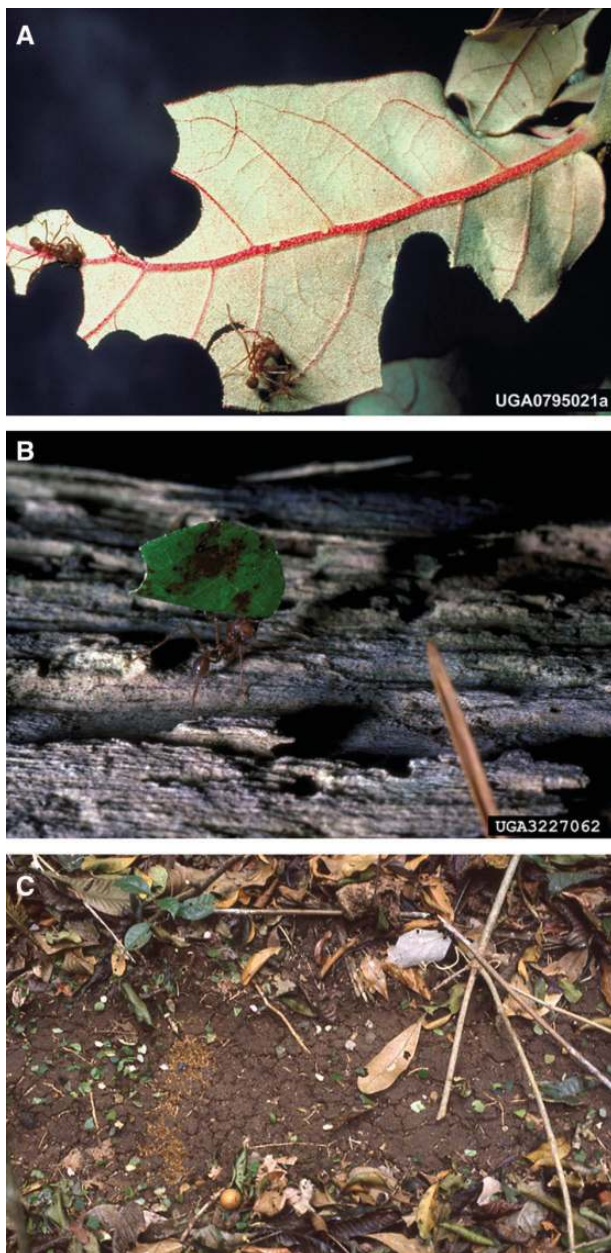


Fig. 6. (A) Workers cutting leaf disks; (B) worker carrying leaf disk; (C) foraging trail. Photo A by Herbert A. 'Joe' Pase III, Texas A&M Forest Service; photo B by Ronald F. Billings, Texas A&M Forest Service; both courtesy of Bugwood.org.

pheromone, 4-methylpyrrole-2-carboxylate, was identified (Tumlinson et al. 1971). Morgan et al. (2006) reported that ability of leafcutting ants to follow foraging trails depends on pheromone concentration, with workers following the trail with greater pheromone concentration at branches.

Atta texana foraging, in particular, is determined by leaf toughness and foliage quality (Waller 1982a, Howard et al. 1989, Clark 2006, Saverschek and Roces 2011). Foliage of some tree species is unpalatable, whereas foliage of other species is palatable but too tough to cut. Foliage of some tree species becomes too tough to cut as it matures. Waller (1982b) found foraging varied widely among southern live oak, *Quercus virginiana* Mill., surrounding a nest in central Texas. Comparison of foliage characteristics among foraged and nonforaged trees indicated that foliage was palatable

throughout the year, but leaf toughness deterred foraging, and ants preferred mature leaf disks from foraged trees to those from nonforage trees, indicating differences in palatability. Ants cut significantly more mature live oak leaves that had been coated with sugar, indicating that foraging is influenced by a toughness \times palatability interaction. Clark (2006) found that *Atta columbica* Guérin-Méneville showed differential foraging by castes in Costa Rica, with larger castes harvesting tougher foliage material.

Palatability also is influenced by plant defensive compounds. Howard et al. (1988, 1989) reported that foraging declined as terpenoid concentrations in foliage increased. Bioassays indicated that terpenoids were toxic to both the ants and their mutualistic fungi. Saverschek and Roces (2011) reported that leafcutting ants learn to avoid foliage that contain defenses toxic to their mutualistic fungi. Howard (1990) noted that leafcutting ants typically abandon plants before they are completely defoliated, suggesting avoidance of induced defenses. However, comparison of foliage quality among preferred and nonpreferred foliage indicated that induced defenses were not responsible for host abandonment but rather depletion of high-value resources. Herz et al. (2008) and Saverschek et al. (2010) reported that some leafcutting ants initially forage for foliage that is unsuitable for their garden fungi but subsequently reject this foliage.

Finally, endophytic fungi reduce ant foraging (Van Bael et al. 2009; Bittleston et al. 2011; Estrada et al. 2013, 2015; Coblenz and Van Bael 2013). Endophytic fungi are known to reduce foliage suitability for herbivores (Clay 1990, Van Bael et al. 2009), but their effect on leafcutting ant foraging appears to reflect primarily their negative effects on the ants' fungal gardens (Van Bael et al. 2009, 2012; Estrada et al. 2014; Mighell and Van Bael 2016). Foliage fragments with higher abundances of endophytic fungi required greater effort to clean prior to incorporation into fungal gardens, but foliage freed of endophytic fungi appeared to be more suitable for growth of garden fungi, perhaps due to reduced concentration of antimicrobial defenses (Estrada et al. 2014). Garden fungi also showed stronger inhibitory effects on endophytic fungal species that were more capable of outgrowing garden fungi (Estrada et al. 2014). However, Van Bael et al. (2012) found that endophytic fungi were capable of reducing garden development during the earliest stages of colony establishment, when few workers were available to clean fragments.

Although the fungus gardens are the primary food source for leafcutting ants, other materials also are eaten. Echols (1966b) noted that soybean oil attracts leafcutting ants. Killion (1991) reported that Texas leafcutting ants may feed on vertebrate tissues under at least some circumstances. Leafcutting ants were observed feeding on rodents (captured in traps) that may have been dead when discovered by the ants. Furthermore, he suggested that ant feeding on animal tissue may have been in response to drought-induced attraction to moisture sources.

Leafcutting ant nests provide resources for a variety of associated species. At least 80 species of myrmecophilous arthropods are known from leafcutting ant nests (Dash et al. 2005, Barnett et al. 2013), including cockroaches, *Attaphila fungicola* Wheeler (Blattaria: Blattidae) (Waller and Moser 1990), fungus-feeding flies, *Pholeomyia texensis* Sabrosky (Diptera; Milichiidae), and a variety of other Diptera, Orthoptera, and Coleoptera (Moser 1963, Waller 1980, Waller and Moser 1990). In addition, leafcutting ant nests have served as nurseries for some species of frogs and snakes (Schlüter and Regós 1981, Velásquez-Múnera et al. 2008, Baer et al. 2009, Bruner et al. 2012).

Predators and parasitoids affect foraging patterns in leafcutting ants. Texas leafcutting ant populations are subject to predation by birds and arthropods (Montoya-Lerma et al. 2012) and especially to

parasitism by scuttle flies, *Myrmosicarius texanus* (Greene) (Diptera: Phoridae) and *Apocephalus wallerae* Disney (Disney 1980, Waller and Moser 1990), which attack ants along foraging trails (Waller and Moser 1990, Erthal and Tonhasca 2000). The effect of predators and parasitoids on foraging by Texas leafcutting ants has not been investigated. Phorids attacking other *Atta* species have been shown to cause about 1% mortality but to reduce ant foraging (Brança et al. 1998, Erthal and Tonhasca 2000). Waller and Moser (1990) noted that leafcutting ant workers responded to *M. texanus* attack by rearing up on their hind legs with mandibles open and abdomens tucked forward, by vigorously cleaning their heads and mandibles with their forelegs, and by reduced foraging. In some *Atta* species, the smallest workers ride atop foliage fragments carried by larger foragers, primarily to defend against phorid attacks along foraging trails (Feener and Moss 1990), but this behavior apparently does not occur in the Texas leafcutting ant (Waller and Moser 1990).

Leafcutting ants are relatively immune to microbial pathogens (Hughes et al. 2009), although high mortality of queens prior to successful colony establishment likely reflects a variety of entomopathogenic fungi that can be cultured from dead queens (Marti et al. 2015). Leaf-cutting ants defend themselves and their nestmates against generalist entomopathogens such as *Metarhizium* spp. and *Ophiocordyceps* spp., as well as against pathogens of their fungus gardens (see above), by grooming secretions from paired metapleural glands that produce broad-spectrum antibiotics (Jaccoud et al. 1999, Fernández-Marín et al. 2006, Cremer et al. 2007). These defenses have contributed to the Texas leafcutting ant's ecological success.

Although leafcutting ant nests may become a nuisance in human-dominated systems, in natural systems they increase landscape and plant diversity and can accelerate succession (Jonkman 1978, Cahal et al. 1993, Kulhavy et al. 2001, Meyer et al. 2011). The large surface area and volume of soil excavated significantly increase surface clay content, nutrient availability for plants, and water infiltration rates (Jonkman 1978, Cahal et al. 1993, Kulhavy et al. 2001, Sternberg et al. 2007). Cahal et al. (1993) reported that nests covered 1.3% of the landscape area, and ant foraging beyond the nest resulted in defoliation of >20% of the landscape area measured in their study. Cahal et al. (1993) reported that clay content of surface soil was threefold higher on mounds than at sites not affected by mounds ($P < 0.05$). Kulhavy et al. (2001) found that plant diversity was increased by the dominance of unpalatable tree and shrub species on leafcutting ant mounds. Meyer et al. (2011) reported that canopy opening over leafcutting ant mounds in the tropics increased light and temperature and decreased moisture to an extent that can alter seedling recruitment and vegetation dynamics.

Management

Leafcutting ants are favored by the availability of disturbed areas, such as roadsides and clearcuts, which provide suitable habitats for colony establishment and spread (Cahal et al. 1993, Vasconcelos et al. 2006). Although Texas leafcutting ants often are viewed as pests, their positive effects on vegetation diversity and soil structure and fertility should be recognized and control initiated only when warranted (Cahal et al. 1993, Kulhavy et al. 2001).

Leafcutting ants are frequent pests in pine plantations, as a result of monoculture cropping and soil disturbance (Blanton and Ewel 1985, Moser 1986, Cahal et al. 1993, Fischer 2015, Merchant and



Fig 7. Defoliation of pine plantation by Texas leafcutting ants. Photo by Ronald F. Billings, Texas A&M Forest Service, courtesy of Bugwood.org.

Drees 2015), and also in crops and ornamental plantings (Buckley 1860, Dash et al. 2005, Louisiana Insect Pest Management Guide 2016). Texas leafcutting ants kill pine seedlings over 5,000 ha (12,000 acres) per year, on average, with control and seedling replacement costs averaging US\$2.3 million (Fig. 7; Fischer 2015). In addition, collapsing nest cavities can cause extensive subsidence and damage to neighboring roads or buildings (Dash et al. 2005, Hooper-Bui and Seymour 2007, Montoya-Lerma et al. 2012).

Relatively few options are available for control of *A. texana* (Cherrett 1986, Montoya-Lerma et al. 2012). Most options are not effective in keeping populations below economic thresholds and have adverse effects on human and environmental health (Cherrett 1986). The size and depth of nests and large numbers of workers require massive efforts and materials to ensure successful control. Biocontrol options have proven to be ineffective, as these ants have few effective predators or parasites (Waller and Moser 1990) and generally are protected from entomopathogens by antimicrobial secretions (Hughes et al. 2009). Introduction of fungal antagonists into colonies has not been effective (Montoya-Lerma et al. 2012). Although leafcutting ants rely on trail pheromones for foraging, disruption of foraging with pheromone treatment has not been tested, nor are formulations available. Chemical options remain the most effective means of management for these ants, but most effective insecticides, e.g., methyl bromide, are no longer approved for treatment. Alternative means of control are needed.

Cultural controls can mitigate yield losses from leafcutting ant foraging. Cherrett (1986), Saverschek and Roces (2011), and Montoya-Lerma et al. (2012) recommended interplanting of unpalatable trees or shrubs as a cultural tactic for reducing leafcutting ant

foraging. Diversifying crops also can reduce losses to leafcutting ants (Blanton and Ewel 1985, Cherrett 1986, Varón et al. 2007). Blanton and Ewel (1985) reported that defoliation of cassava, *Manihot esculenta* Crantz, by leafcutting ants in Costa Rica was twice as high in monocultures and crop mixtures, compared to more diverse plantings, although overall rates were <3% in all treatments. No data are available for cultural control of *A. texana*. Obviously, these approaches require planning in advance of leafcutting ant appearance.

Chemical repellents or insecticides have been successful in protecting targeted plants from leafcutting ants. Repellents include both biogenic and manufactured products. For example, plants targeted by foraging ants can be protected temporarily by spreading refuse from leafcutting ant nests (Montoya-Lerma et al. 2012). However, refuse may be difficult to obtain, treatments are species-specific, and effects are short-lived (Farji-Brener and Sasal 2003). Dust or granular formulations of contact insecticides, such as acephate, carbaryl, or permethrin, can be spread around targeted plants, but such treatments must be reapplied frequently (Merchant and Drees 2015). Although these methods may reduce foraging, they will not eliminate underground nests.

Options for eliminating colonies are limited and their efficacy variable. Fumigants (such as methyl bromide) were ineffective because the fumigant could not penetrate satellite nests that could quickly reinfest treated areas (Echols 1966a,b). Fumigants also have serious side effects on soil communities that regulate litter decomposition. Two current control methods are baits and nest injection with insecticide. However, ants from neighboring colonies may quickly reinvade treated sites (Mann 1968).

PTM (BASF, Research Triangle Park, NC), is available for leafcutting ant control in pine plantations, including Christmas trees (Wilent 2015). The active ingredient is 9% fipronil. This product must be injected at least 7.5 cm (3 inches) into each leafcutting ant exit hole, per label instructions. The insecticide must reach all portions of nests that can extend at least 7 m (22 ft.) deep in order to eliminate colonies.

Leafcutting ants do not respond well to most conventional ant baits, because they feed only on their fungus gardens (Fischer 2015, Merchant and Drees 2015). However, one bait can be used for control of leafcutting ants, a special formulation of hydramethylnon, Amdro Ant Block (Ambrands, Atlanta, GA). This bait was originally formulated for control of red imported fire ants, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), but showed improved activity against leafcutting ants when sugar was added (Fischer 2015, see Waller 1982b). The bait also contains soybean oil that acts as an attractant (Echols 1966b).

Baits have several advantages over other control methods. First, baits attract the target insect and have fewer nontarget effects than do fumigation or injected insecticides. Second, baits are carried into the nest and shared with other colony members through trophallaxis, thereby reaching the entire colony, including portions difficult to reach with fumigants or injected insecticides. Third, baits will be carried to satellite nests that have proven difficult to identify or reach with other methods.

Bait can be used in most urban and suburban settings, such as lawns, landscaped areas, golf courses, ornamental gardens, roadsides, commercial grounds, etc. (Merchant and Drees 2015, Louisiana Insect Pest Management Guide 2016) and forests (Fischer 2015). Bait should be applied around all mounds of a colony while ants are foraging to ensure the best control. Applications can be made any time of year but should be postponed until after rain or freezing weather. Initial evidence of control is a reduction in

foraging and excavation activity, usually within 5–7 d after bait application. Ant activity will continue to decline over 4–6 wk, but activity may recover in 4–6 mo (in about 50% of cases), requiring a second treatment. This bait should not be used in vegetable gardens or agricultural sites (Fischer 2015, Merchant and Drees 2015). Reducing bait granule size and incorporating alarm pheromones has improved the efficacy of baits for other leafcutting ant species (Hughes and Goulson 2002).

Conclusions

The Texas leafcutting ant provides a unique example in the United States of the complexity of ecological interactions involving the ants, their preferred hosts, endophytic and symbiotic fungi and bacteria, and associated invertebrates and vertebrates. Their abundance is promoted by soil disturbance and canopy removal. Their nest structure increases biodiversity and improves soil conditions, but their presence may reduce crop and forest production and undermine roads and structures in the vicinity of their nests. Relatively few options are available or effective for reducing their foraging or eliminating nests. The two primary options that are effective are a bait and an insecticide that can be injected into nests.

Acknowledgments

Natalie Clay and Sunshine Van Bael provided constructive comments on the manuscript. Mention of specific products in this paper does not constitute an endorsement. This manuscript is published with approval of the Director of the Louisiana Agricultural Experiment Station, as manuscript number 2017-234-31213.

References Cited

- Baer, B., S.P.A. den Boer, D.J.C. Kronauer, D. R. Nash, and J. J. Boomsma. 2009. Fungus gardens of the leafcutter ant *Atta colombica* function as egg nurseries for the snake *Leptodeira annulata*. *Insectes Sociaux* 56: 289–291.
- Barke, J., R. F. Seipke, S. Grünschow, D. Heavens, N. Drou, M. J. Bibb, R.J.M. Goss, D. W. Yu1, and M. I. Hutchings. 2010. A mixed community of actinomycetes produce multiple antibiotics for the fungus farming ant *Acromyrmex octospinosus*. *BMC Biology* 8: 109. (<http://www.biomedcentral.com/1741-7007/8/109>) (accessed 4 April 2017).
- Barnett, J. P., D. A. Streett, and S. R. Blomquist. 2013. Town ants: The beginning of John Moser's remarkable search for knowledge, p. 53. *In: Gen. Tech. Rep. SRS-182*. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC.
- Bass, M., and J. M. Cherrett. 1994. The role of leaf-cutting ant workers (Hymenoptera: Formicidae) in fungus garden maintenance. *Ecological Entomology* 19: 215–220.
- Bass, M., and J. M. Cherrett. 1996. Leaf-cutting ants (Formicidae, Attini) prune their fungus to increase and direct its productivity. *Functional Ecology* 10: 55–61.
- Bittleston, L. S., F. Brockmann, W. Weislo, and S. A. Van Bael. 2011. Endophytic fungi reduce leaf-cutting ant damage to seedlings. *Biology Letters* 7: 30–32.
- Blanton, C. M., and J. J. Ewel. 1985. Leaf-cutting ant herbivory in successional and agricultural tropical ecosystems. *Ecology* 66: 861–869.
- Boyd, N. D., and M. M. Martin. 1975. Faecal proteinases of the fungus-growing ant, *Atta texana*: their fungal origin and ecological significance. *Journal of Insect Physiology* 21: 1815–1820.
- Brança, M.A.L., A. Tonhasca, Jr., and T.M.C. Della Lucia. 1998. Reduction in the foraging activity of the leaf-cutting ant *Atta sexdens* caused by the phorid *Neodohrniphora* sp. *Entomologia Experimentalis et Applicata* 89: 305–311.
- Bruner, G., H. Fernández-Marín, J. C. Touchon, and W. T. Weislo. 2012. Eggs of the blind snake, *Liotyphlops albirostris*, are incubated in a nest of

- the lower fungus-growing ant, *Apterostigma* cf. *goniodes*. *Psyche* 2012: 532314–532315. doi:10.1155/2012/532314.
- Buckley, S. B. 1860. The cutting ant of Texas. *Proceedings of the Academy of Natural Sciences of Philadelphia* 12: 233–236.
- Cahal, R. R., D. L. Kulhavy, W. G. Ross, W. D. Tracey, and W. D. Hacker. 1993. Forest pest management on typic quartzsammits: a management dilemma, pp. 541–546. *In* Proceedings of the Seventh Biennial Southern Silvicultural Research Conference, Nov 17–19, 1992, Mobile, AL.
- Cherrett, J. M. 1986. The economic importance and control of leaf-cutting ants, pp. 165–192. *In* S. B. Vinson (ed.), *The Economic Impact and Control of Social Insects*. Praeger Publishers, New York, NY.
- Clark, E. 2006. Dynamic matching of forager size to resources in the continuously polymorphic leaf-cutter ant, *Atta colombica* (Hymenoptera, Formicidae). *Ecological Entomology* 31: 629–635.
- Clay, K. 1990. Fungal endophytes of grasses. *Annual Review of Ecology and Systematics* 21: 275–297.
- Coblentz, K. E., and S. A. Van Bael. 2013. Field colonies of leaf-cutting ants select plant materials containing low abundances of endophytic fungi. *Ecosphere* 4: 66. <http://dx.doi.org/10.1890/ES13-00012.1>
- Cremer, S., S. A. O. Armitage, and P. Schmid-Hempel. 2007. Social immunity. *Current Biology* 17: R693–R702.
- Currie, C. R., and A. E. Stuart. 2001. Weeding and grooming of pathogens in agriculture by ants. *Proceedings of the Royal Society of London B*. 268: 1033–1039.
- Currie, C. R., U. G. Mueller, and D. Malloch. 1999. The agricultural pathology of ant fungus gardens. *Proceedings of the National Academy of Sciences* 96: 7998–8002.
- Dash, S. T., L. M. Hooper-Búi, and M. A. Seymour. 2005. *The Pest Ants of Louisiana: a Guide to Their Identification, Biology and Control*. LSU AgCenter, Baton Rouge, LA.
- Disney, R.H.L. 1980. A new species of *Apocephalus* (Diptera: Phoridae) that parasitizes *Atta texana* (Hymenoptera: Formicidae) in Texas. *Zeitschrift Für Angewandte Entomologie* 67: 47–50.
- Echols, H. W. 1966a. Compatibility of separate nests of Texas leaf-cutting ants. *Journal of Economic Entomology* 59: 1299–1300.
- Echols, H. W. 1966b. Texas leaf-cutting ant controlled with pelleted mirex bait. *Journal of Economic Entomology* 59: 628–631.
- Erthal, M., Jr., and A. Tomhasca Jr. 2000. Biology and oviposition behavior of the phorid *Apocephalus attophilus* and the response of its host, the leaf-cutting ant *Atta laevigata*. *Entomologia Experimentalis et Applicata* 95: 71–75.
- Estrada, C., W. T. Wcislo, and S. A. Van Bael. 2013. Symbiotic fungi alter plant chemistry that discourages leaf-cutting ants. *New Phytologist* 198: 241–251.
- Estrada, C., E. I. Rojas, W. T. Wcislo, and S. A. Van Bael. 2014. Fungal endophyte effects on leaf chemistry alter the in vitro growth rates of leaf-cutting ants' fungal mutualist, *Leucocoprinus gongylophorus*. *Fungal Ecology* 8: 37–45.
- Estrada, C., E. C. Degner, E. I. Rojas, W. T. Wcislo, and S. A. Van Bael. 2015. The role of endophyte diversity in protecting plants from defoliation by leaf-cutting ants. *Current Science* 109: 55–61.
- Farji-Brener, A. G., and Y. Sasal. 2003. Is dump material an effective small-scale deterrent to herbivory by leaf-cutting ants? *Ecoscience* 10: 151–154.
- Feener, D. H., Jr., and K.A.G. Moss. 1990. Defense against parasites by hitchhikers in leaf-cutting ants: a quantitative assessment. *Behavioral Ecology and Sociobiology* 26: 17–29.
- Fernández-Marín, H., J. K. Zimmerman, S. A. Rehner, and W. T. Wcislo. 2006. Active use of the metapleural glands by ants in controlling fungal infection. *Proceedings of the Royal Society B* 273: 1689–1695.
- Fischer, M. 2015. Forest Health: Leaf-cutting Ant. Texas A&M Forest Service, Lufkin, TX. (<http://texasforests.tamu.edu/LeafCuttingAnt/>)
- Fisher, B. L., and S. P. Cover. 2007. *Ants of North America: a Guide to Genera*. University of California Press, Berkeley.
- Garrett, R. W., K. A. Carlson, M. S. Goggans, M. H. Nesson, C. A. Shepard, and R.M.S. Schofield. 2016. Leaf processing behavior in *Atta* leafcutter ants: 90% of leaf cutting takes place inside the nest, and ants select pieces that require less cutting. *R. Soc. Open Science*. 3: 150111. <http://dx.doi.org/10.1098/rsos.150111>.
- Hermann, H. R., J. C. Moser, and A. N. Hunt. 1970. The hymenopterous poison apparatus. X. morphological and behavioral changes in *Atta texana* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* 63: 1552–1558.
- Herz, H., B. Hölldobler, and F. Roces. 2008. Delayed rejection in a leaf-cutting ant after foraging on plants unsuitable for the symbiotic fungus. *Behavioral Ecology* 19: 575–582.
- Hooper-Bui, L. M., and M. A. Seymour. 2007. Leaf-cutting ants: miniature town builders. *Louisiana Agriculture* 50(4): 18–19.
- Howard, J. J. 1990. Infidelity of leafcutting ants to host plants: resource heterogeneity or defense induction? *Oecologia* 82: 394–401.
- Howard, J. J., J. Cazin, Jr., and D. F. Wiemer. 1988. Toxicity of terpenoid deterrents to the leafcutting ant *Atta cephalotes* and its mutualistic fungus. *Journal of Chemical Ecology* 14: 59–69.
- Howard, J. J., T. P. Green, and D. F. Wiemer. 1989. Comparative deterrence of two terpenoids to two general of attine ants. *Journal of Chemical Ecology* 15: 2279–2288.
- Hughes, W.O.H., and D. Goulson. 2002. The use of alarm pheromones to enhance bait harvest by grass-cutting ants. *Bulletin of Entomological Research* 92: 213–218.
- Hughes, D. P., H. C. Evans, N. Hywel-Jones, J. J. Boomsma, and S.A.O. Armitage. 2009. Novel fungal disease in complex leaf-cutting ant societies. *Ecological Entomology* 34: 214–220.
- Jaccoud, D. B., W.O.H. Hughes, and C. W. Jackson. 1999. The epizootiology of a *Metarhizium* infection in mini-nests of the leaf-cutting ant *Atta sexdens rubropilosa*. *Entomologia Experimentalis et Applicata* 93: 51–61.
- Jonkman, J.C.M. 1978. Nests of the leaf-cutting ant *Atta vollenweideri* as accelerators of succession in pastures. *Zeitschrift Für Angewandte Entomologie* 86: 25–34.
- Jonkman, J.C.M. 1980. Average vegetative requirement, colony size and estimated impact of *Atta vollenweideri* on cattle raising in Paraguay. *Zeitschrift Für Angewandte Entomologie* 89: 135–143.
- Killion, M. J. 1991. Use of vertebrate tissue by the leaf-cutting ant *Atta texana* (Hymenoptera: Formicidae: Attini). *Southwestern Naturalist* 36: 116–117.
- Kulhavy, D. L., L. A. Smith, and W. G. Ross. 2001. Impact of the Texas leaf-cutting ant (*Atta texana* (Buckley)) (Order Hymenoptera, Family Formicidae) on a forested landscape, pp. 85–90. *In* A. M. Liebhold, M. L. McManus, I. S. Otvos, and S.L.C. Fosbroke (eds.), *Proceedings: Integrated Management and Dynamics of Forest Defoliating Insects*. USDA Forest Service Gen. Tech. Rep. NE-277. USDA Forest Service Northeastern Research Stn., Newtown Square, PA.
- López-Riquelme, G. O., E. A. Malo, L. Cruz-López, and M. L. Fanjul-Moles. 2006. Antennal olfactory sensitivity in response to task-related odours of three castes of the ant *Atta mexicana* (hymenoptera: formicidae). *Physiological Entomology* 31: 353–360.
- Louisiana Insect Pest Management Guide 2016. Louisiana State University Agricultural Center. Baton Rouge, LA.
- Mann, W. F. Jr. 1968. Reinfestation of forest sites by the Texas leaf-cutting ant. *Journal of Economic Entomology* 61: 1460–1461.
- Marti, H. E., A. L. Carlson, B. V. Brown, and U. G. Mueller. 2015. Foundress queen mortality and early colony growth of the leafcutter ant, *Atta texana* (Formicidae, Hymenoptera). *Insectes Sociaux* 62: 357–363.
- Merchant, M., and B. Drees. 2015. *Insects in the City: Texas Leaf Cutting Ant*. Texas A&M Agrilife Extension Fact Sheet. (<http://citybugs.tamu.edu/factsheets/landscape/ants/ent-1002/>)
- Meyer, S. T., I. R. Leal, M. Tabarelli, and R. Wirth. 2011. Ecosystem engineering by leaf-cutting ants: Nests of *Atta cephalotes* drastically alter forest structure and microclimate. *Ecological Entomology* 36: 14–24.
- Mighell, K., and S. A. Van Bael. 2016. Selective elimination of microfungi in leaf-cutting ant gardens. *Fungal Ecology* 24: 15–20.
- Mintzer, A. 1979. Foraging activity of the Mexican leafcutting ant *Atta mexicana* (F. Smith), in a Sonoran Desert habitat (Hymenoptera: Formicidae). *Insectes Sociaux* 26: 364–372.
- Mintzer, A. C. 1980. Simultaneous use of a foraging trail by two leafcutter ant species in the Sonoran Desert. *New York Entomological Society* 88: 102–105.
- Mintzer, A. C. 1987. Primary polygyny in the ant *Atta texana*: number and weight of females and colony foundation success in the laboratory. *Insectes Sociaux* 34: 108–117.

- Mintzer, A., and S. B. Vinson. 1985. Cooperative colony foundation by females of the leafcutting ant *Atta texana* in the laboratory. *Journal of the New York Entomological Society* 93: 1047–1051.
- Mintzer, A. C., and C. L. Mintzer. 1988. Population status of the Mexican leafcutting ant, *Atta mexicana* (Formicidae), in the Sonoran Desert of Arizona. *Southwestern Naturalist* 33: 250–251.
- Montoya-Lerma, J., C. Giraldo-Echeverri, I. Armbrecht, A. Farji-Brener, and Z. Calle. 2012. Leaf-cutting ants revisited: Towards rational management and control. *International Journal of Pest Management* 58: 225–247.
- Morgan, E. D., S. J. Keegans, J. Tits, T. Wenseleers, and J. Billen. 2006. Preferences and differences in the trail pheromone of the leaf-cutting ant *Atta sexdens sexdens* (Hymenoptera: Formicidae). *European Journal of Entomology* 103: 553–558.
- Moser, J. C. 1963. Contents and structure of *Atta texana* nest in summer. *Annals of the Entomological Society of America* 56: 286–291.
- Moser, J. C. 1986. Estimating timber losses from a town ant colony with aerial photographs. *Southern Journal of Applied Forestry* 10: 45–47.
- Moser, J. C. 2006. Complete excavation and mapping of a Texas leafcutting ant nest. *Annals of the Entomological Society of America* 99: 891–897.
- Moser, J. C., and J. R. Lewis. 1981. Multiple nest queens of *Atta texana* (Buckley 1860) (Hymenoptera: Formicidae). *Turrialba* 31: 256–257.
- Mueller, U. G., A. S. Mikheyev, E. Hong, R. Sen, D. L. Warren, S. E. Solomon, H. D. Ishak, M. Cooper, J. L. Miller, K. A. Shaffer, et al. 2011. Evolution of cold-tolerant fungal symbionts permits winter fungiculture by leafcutter ants at the northern frontier of a tropical ant–fungus symbiosis. *Proceedings of the National Academy of Sciences* 108: 4053–4056.
- Pinto-Tomás, A. A., M. A. Anderson, G. Suen, D. M. Stevenson, F. S. T. Chu, W. W. Cleland, P. J. Weimer, and C. R. Currie. 2010. Symbiotic nitrogen fixation in the fungus gardens of leaf-cutter ants. *Science* 326: 1120–1123.
- Reynolds, H. T., and C. R. Currie. 2004. Pathogenicity of *Escovopsis weberi*: The parasite of the attine ant–microbe symbiosis directly consumes the ant-cultivated fungus. *Mycologia* 96: 955–959.
- Rockwood, L. L. 1976. Plant selection and foraging patterns in two species of leaf-cutting ants (*Atta*). *Ecology* 57: 48–61.
- Rodrigues, A., R. N. Cable, U. G. Mueller, M. Bacci, Jr., and F. C. Pagnocca. 2009. Antagonistic interactions between garden yeasts and microfungus garden pathogens of leaf-cutting ants. *Antonie Van Leeuwenhoek* 96: 331–342.
- Sanchez-Peña, S. R. 2010. Some fungus-growing ants (Hymenoptera: Formicidae), from northeastern Mexico. *Florida Entomologist* 93: 501–504.
- Saverschek, N., and F. Roces. 2011. Foraging leafcutter ants: olfactory memory underlies delayed avoidance of plants unsuitable for the symbiotic fungus. *Animal Behavior* 82: 453–458.
- Saverschek, N., H. Herz, M. Wagner, and F. Roces. 2010. Avoiding plants unsuitable for the symbiotic fungus: learning and long-term memory in leaf-cutting ants. *Animal Behavior* 79: 689–698.
- Schlüter, A., and J. Regős. 1981. *Lithodytes lineatus* (Schneider 1799) (Amphibia: Leptodactylidae) as a dweller in the nests of the leaf cutting ant *Atta cephalotes* (Linnaeus, 1758) (Hymenoptera: Attini). *Amphibia-Reptilia* 2: 117–121.
- Seal, J. N., and W. R. Tschinkel. 2007. Co-evolution and the superorganism: switching cultivars does not alter the performance of fungus-gardening ant colonies. *Functional Ecology* 21: 988–997.
- Sen, R., H. D. Ishak, T. R. Kniffin, and U. G. Mueller. 2010. Construction of chimaeric gardens through fungal intercropping: a symbiont choice experiment in the leafcutter ant *Atta texana* (Attini, Formicidae). *Behavioral Ecology and Sociobiology* 64: 1125–1133.
- Shattuck, S., and S. Cover. 2016. Taxonomy of some little-understood North American ants (Hymenoptera: Formicidae). *Zootaxa* 4175: 10–22.
- Shik, J. Z., E. B. Gomez, P. W. Kooij, J. C. Santos, W. T. Wcislo, and J. J. Boomsma. 2016. Nutrition mediates the expression of cultivar–farmer conflict in a fungus-growing ant. *Proceedings of the National Academy of Sciences USA* 113: 10121–10126.
- Sternberg, L.S.L., M. C. Pinzon, M. Z. Moreira, P. Moutinho, E. I. Rojas, and E. A. Herre. 2007. Plants use macronutrients accumulated in leaf-cutting ant nests. *Proceedings of the Royal Society of London B* 274: 315–321.
- Tumlinson, J. H., R. M. Silverstein, J. C. Moser, R. G. Brownlee, and J. M. Ruth. 1971. Identification of the trail pheromone of a leaf-cutting ant, *Atta texana*. *Nature* 234: 348–349.
- Van Bael, S. A., H. Fernández-Marín, M. C. Valencia, E. I. Rojas, W. T. Wcislo, and E. A. Herre. 2009. Two fungal symbioses collide: endophytic fungi are not welcome in leaf-cutting ant gardens. *Proceedings of the Royal Society B* 276: 2419–2426.
- Van Bael, S. A., C. Estrada, S. A. Rehner, J. F. Santos, and W. T. Wcislo. 2012. Leaf endophyte load influences fungal garden development in leaf-cutting ants. *BMC Ecology* 12: 23. (<http://www.biomedcentral.com/1472-6785/12/23>)
- Varón, E. H., S. D. Eigenbrode, N. A. Bosque-Pérez, and L. Hilje. 2007. Effect of farm diversity on harvesting of coffee leaves by the leaf-cutting ant *Atta cephalotes*. *Agricultural and Forest Entomology* 9: 47–55.
- Vasconcelos, H. L. 1997. Foraging activity of an Amazonian leaf-cutting ant: Responses to changes in the availability of woody plants and to previous plant damage. *Oecologia* 112: 370–378.
- Vasconcelos, H. L., E.H.M. Vieira-Neto, and F. M. Mundim. 2006. Roads alter the colonization dynamics of a keystone herbivore in Neotropical savannas. *Biotropica* 38: 661–665.
- Velásquez-Múnera, E., A. Ortiz-Reyes, V. P. Páez, and G. E. Guzmán-Restrepo. 2008. Oviposition of *Stenorrhina degenhardtii* (Serpentes: Colubridae) in a nest of *Acromyrmex octospinosus* (Hymenoptera: Formicidae). *Actualidades Biológicas* 30: 193–195.
- Waller, D. A. 1980. Leaf-cutting ants and leaf-riding flies. *Ecological Entomology* 5: 305–306.
- Waller, D. A. 1982a. Leaf-cutting ants and avoided plants: Defences against *Atta texana* attack. *Oecologia* 52: 400–403.
- Waller, D. A. 1982b. Leaf-cutting ants and live oak: the role of leaf toughness in seasonal and intraspecific host choice. *Entomologia Experimentalis Et Applicata* 32: 146–150.
- Waller, D. A., and J. C. Moser. 1990. Invertebrate enemies and nest associates of the leaf-cutting ant *Atta texana* (Formicidae, Attini), pp. 256–273. *In* R. I. Vander Meer, K. Jaffe and A. Cedeno (eds.), *Applied Myrmecology: a World Perspective*. Westview Press, Boulder, CO.
- Wetterer, J. K. 1999. The ecology and evolution of worker size-distribution in leaf-cutting ants (Hymenoptera: Formicidae). *Sociobiology* 34: 119–144.
- Wilent, S. 2015. Beetle-killing pesticide is one of TFS Cooperative’s success stories. *Forestry Source* 20(3): 12.
- Zavala-Hurtado, J. A., P. L. Valverde, M. del Carmen Herrera-Fuentes, and A. Díaz-Solis. 2000. Influence of leaf-cutting ants (*Atta mexicana*) on performance and dispersion patterns of perennial desert shrubs in an inter-tropical region of Central Mexico. *Journal of Arid Environments* 46: 93–102.