The red imported fire ant, *Solenopsis invicta*, in early-successional coastal plain forests: tests of distribution and interaction strength

by

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ABSTRACT

The red imported fire ant, *Solenopsis invicta*, is an abundant and aggressive component of early-successional communities in the southeastern United States. After disturbance, it rapidly invades new habitats, and once there, it has strong competitive and predatory effects on the existing arthropod community. In upland coastal plain pine forests at the Savannah River Site in South Carolina, I conducted two studies of fire ant ecology. In my first study (chapter 1), I investigated the way in which fire ants colonize early-successional road and powerline cuts through forests, and I tested whether some of these linear habitats provided better fire ant habitat than others. I found that fire ant mound density (#/ha) was similar in narrow dirt roads and in wider roads with the same intermediate level of mowing disturbance, and that density was lower in wide powerline cuts where the vegetation is only removed every five years. Furthermore, mound density was greatest near the edges of cleared roads and powerline cuts and was also greater on the northern sides of roads and powerline cuts where there was less shading from the adjacent forest. Results from this study suggest that allowing increased shading from adjacent forest vegetation, especially along northern roadside edges, would limit the suitability of road and powerline cuts as fire ant habitat, thereby slowing invasion. In my second study (chapter 2), I examined the impact of fire ants on arthropod and plant species in early-successional forest gaps. In a tritrophic system, I tested whether the top-down effect of insect herbivore consumption by fire ants was strong enough to cascade through two trophic levels and improve plant productivity. I compared this potential effect to that of other arthropod predators in the community. I found that fire ants controlled the level of damage to plant leaves by herbivores, but that the damage was not severe enough to influence plant growth or fitness. Fire ants had stronger negative interactions with insect herbivores than other predators in the community, and

for this reason, fire ants can be considered keystone predators. This project provides further evidence that fire ants successfully invade even small patches of early-successional habitat that exist within larger matrices of uninhabitable, late-successional forest, and that once there, they have a dramatic effect on the arthropod community. Restricting the amount of early-successional habitat within southeastern forests, either as permanent road and powerline cuts or as temporary gaps, would limit the potential detrimental effects by the invasive fire ant.

ACKNOWLEDGEMENTS

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INTRODUCTION

It has often been recognized that "the world is green" and that plants provide the bottom-up forces that control the abundance and distribution of other trophic levels in the community (Hairston et al. 1960). In terrestrial communities, predator (i.e., top-down) control over community patterns is thought to be rare (Polis and Strong 1996, Strong 1992). However, it has been shown that some animals and microbes can contribute to succession and community composition (McBrien et al. 1983, Brown 1994, Brown et al. 1988, Brown 1984, Van der Putten et al. 1993). The relationship between animals and plant community patterns is reciprocal: animals may have an impact on plant species distribution, and plant species distribution may have a strong impact on the animals present within any community. Whether one process drives the other is dependent on the life-history characteristics of the species present and the abiotic conditions of the particular habitat involved (Brown 1984).

Disturbance regimes are key determinants of succession and community patterns. Small-scale disturbances may have little effect on community structure. For example, gaps created by low-level disturbance are usually filled by growth of existing plants or by establishment of species whose propagules are already present in the community. Large-scale disturbance, however, has the potential to drastically change the community and return the successional process to an earlier stage. In this situation, early-successional plants and animals that are not able to establish in small patches may find both the abiotic and biotic conditions necessary for successful growth.

Largely because of human intervention, the southeastern United States is a mosaic of large-scale, frequent disturbance. Agricultural fields and land cleared for human habitation are disturbed frequently enough to arrest progression from an early-successional stage. Furthermore, reticulate patterns of frequently-disturbed linear habitats, formed by road and powerline cuts, fragment most natural, later-successional communities. Logging within late-successional forest communities routinely opens new early-successional gaps that are spatially large even though temporally short-lived. In both frequently-disturbed and newly-disturbed communities, early successional or "weed" species (Tschinkel 1986) are successful across the landscape.

A significant new early-successional member of disturbed communities in the southeastern U.S. is the red imported fire ant, *Solenopsis invicta* Buren. *Solenopsis invicta* was accidentally introduced into Alabama from Brazil approximately 75 years ago (Vinson 1997). The ants have spread rapidly, and now occupy a range as far north as Maryland and as far west as Texas. Their spread may be reaching its macro-geographical limit, but fire ant populations continue to invade new habitats on a micro-geographical scale (Porter et al. 1988). The ability of fire ants to successfully invade and affect new habitats is dependent on both abiotic and biotic factors. The ant is most successful in areas where disturbance is frequent, such as pastures or roads (Tschinkel 1987). Competition with other ants and predation of newly-landed fire ant queens limits initial invasion rates (Brown 1980), but over time, *S. invicta* becomes a dominant member in the community and diversity of other arthropods declines (Porter and Savignano 1990). In areas of frequent disturbance, fire ant mound density may reach 600 mounds/ha (Maxwell 1982), and a single, monogynous colony may contain 200,000-300,000 individuals (Lofgren et al. 1975). Over a long period of time, as colony density increases and as available resources decrease, density will stabilize and average 50-75 mounds/ha (Vinson and Greenberg, 1986).

Much is known about role of fire ants in pasture, crop, and yard communities, but its role in natural communities is still poorly researched. Fire ants are considered pests in agricultural areas and in human habitats, and most fire ant research has focused on eradicating or at least controlling fire ant populations. However, successful methods of control have not yet been found, and fire ants are and will most likely continue to be integral members of most early-successional communities in the southeast. For this reason, it is necessary to understand the ecology of the red imported fire ant, not only as a pest, but also as a community member. Fire ants play a dominant role in the food web through direct predation of arthropods and competitive displacement of native ants (Reagan 1986, Tedders et al. 1990, Porter and Savignano 1990, Camilo and Phillips 1990, Morris and Steigman 1993). It is not known whether its strong interactions with other trophic levels produce an effect that cascades to primary producers. How this dominant species is able to invade natural communities and, once there, how it contributes to the plant community patterns by impacting growth and survival of individual plants are two questions that will be addressed in this thesis.

More specifically, this research will first determine if the imported fire ant utilizes early-successional linear habitats to penetrate later-successional forest habitats, and if its spread is

influenced by the structure of the linear habitat (chapter 1). Second, it will determine if the

characteristics that account for the successful invasion of the imported fire ant (e.g., large

population size, rapid dispersal, aggressiveness) make the fire ant a keystone species that is able

to exert top-down control on the abundance and distribution of species in other trophic levels

(chapter 2).

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CHAPTER 1

Distribution of the red imported fire ant, *Solenopsis invicta*, in road and powerline habitats[1]

1. ABSTRACT

For early-successional species, road and powerline cuts through forests provide refugia and source populations for invading adjacent forest gaps. Within an 800 km^2 forest matrix in South Carolina, I determined if width, disturbance frequency or linear features of road and powerline cuts influenced the mound distribution of the red imported fire ant, *Solenopsis invicta* Buren. For each of five linear habitat types, differing in width and disturbance frequency, I mapped all mounds located within ten 500 m segments. Mean mound density was lowest in narrow, infrequently-disturbed closed-canopy dirt road habitats (8.8 mounds/ha). For types with an opening in the forest canopy (i.e., open dirt road, gravel road, paved road and powerline cut), mean mound density was highest in narrow habitats where disturbance was intermediate (open dirt roads, 86.5 mounds/ha). It was lowest in wide habitats where disturbance was infrequent (powerline cuts, 27.6 mounds/ha). Mean mound size was greater in infrequently-disturbed powerline cuts than in frequently-disturbed paved roads. Mounds were located significantly closer to road or forest edges than expected by random. In all types except dirt roads, mounds were more common toward northern edges, and more so as the orientation of the linear habitat changed from north/south to east/west. These data suggest that narrow, disturbed habitats are more suitable for fire ant establishment and success than wider ones, and that the distribution of fire ants in linear habitats is not as uniform as it has been shown to be in pastures. A decrease in roadside disturbance and an increase in shade, especially along the northern edge, may result in lower fire ant mound density in these linear habitats.

Keywords: ant abundance, corridor, exotic species, invasion, powerline cuts, roads, *Solenopsis invicta*, spatial pattern

2. INTRODUCTION

Linear habitats, such as road and powerline cuts, embedded within a forest matrix may provide suitable habitat for early-successional or disturbance-oriented plants and animals amidst an otherwise uninhabitable landscape (Bennett 1991, Forman 1995, DeMers 1993, Warner 1992). They may also serve as barriers (Merriam et al. 1989, Mader 1984), dispersal corridors (DeMers 1993, Vermeulen 1994, Getz et al. 1978), and invasion routes (Lewis 1991, Amor and Stephens 1976) for many species. For the red imported fire ant, *Solenopsis invicta* Buren, road and powerline cuts may provide not only primary habitat but also a refugia or source population for dispersal into adjacent forest gaps.

Southeastern U.S. forests are fragmented by a shifting mosaic of early-successional forest gaps caused by logging practices and by a reticulate pattern of linear, early-successional habitat, or corridors (Forman 1995, Rich et al. 1994, Kroodsma 1982), in the form of road and powerline cuts. Unlike forest gaps, these linear habitats are maintained in an early-successional stage by anthropogenic disturbance such as mowing or burning. Additionally, they are typified by higher degrees of edge environments and shading than those of non-linear gaps (Reed et al. 1996, Kroodsma 1982). *Solenopsis invicta* frequently colonizes both logged gaps and road and powerline habitats. In logged gaps, populations persist for the first five to ten years of reforestation (personal observations). The prevalence of the more permanent road and powerline habitats ensures that few logged gaps lack nearby refugia or source populations of fire ants. However, if some road and powerline cuts provide better fire ant habitat than others, then the structure of the linear habitat network may determine the rate and degree of fire ant invasion into forest gaps.

Solenopsis invicta is a notorious pest species that has strong effects on other organisms. Native ants are frequently displaced through competition (Tschinkel 1987, Porter and Savignano 1990, Camilo and Phillips 1990, Morris and Steigman 1993, Porter et al. 1988), and total arthropod diversity and abundance are often reduced when *S. invicta* is abundant (Tedders et al. 1990, Reagan 1986). Fire ants are also predators of the young of birds, small mammals, and reptiles (Allen et al. 1994).

The potential impacts of *S. invicta* are exacerbated in areas where mounds are abundant (W.R. Tschinkel, personal communication). Because mound volume is positively related to the number and biomass of ants in a mound (Tschinkel 1993), the impacts are also stronger where mounds are large. Fire ants have been shown to be abundant in open habitats where the soil has been disturbed by agricultural practices, logging, or vehicles (Tschinkel 1986, Porter and Savignano 1990) and where direct sunlight can reach the soil surface (Brown 1980). They are rare in shaded or undisturbed habitats such as forests (Tschinkel 1987, Summerlin 1976, Maxwell 1982).

The objectives of my study were to determine whether the abundance, size, or spatial distribution of *S. invicta* mounds varied among five linear habitat types. I hypothesized that mound density and volume are related to habitat width and to the frequency of direct mound disturbance, and I predicted that mound density and volume would increase with width but would decrease with increasing disturbance frequency. I also hypothesized that the spatial distribution of mounds is related to linear features of the habitat such as edges and would therefore be less uniform than the mound distribution in pastures.

Wide road and powerline cuts may be preferred by fire ants for two reasons. First, wide habitats have a larger area that is not shaded by the adjacent forest canopy. Secondly, dispersing alates respond to reflectance and vegetation cues from the ground (Maxwell, 1982). Therefore, wide habitats may be easier to locate than narrow ones.

Although initial large-scale disturbances such as logging, burning, mowing or tilling often precede fire ant establishment, extremely frequent and direct disturbance to the mound as a result of continued burning or mowing may limit the size and abundance of mounds. For this reason, early-successional habitat with low levels of direct disturbance to the mounds may have higher mound density and volume than those that are mowed or burned more often.

Studies of the spatial distribution of *S. invicta* mounds are few and have been performed mainly in pastures, where mature mounds have an approximately uniform distribution due to intraspecific competition (Adams and Tschinkel 1995, Baroni Urbani and Kannowski 1974). Edges, which predominate in linear habitats, are often areas where levels of light, temperature, litter moisture, humidity, and species diversity change abruptly (Matlack 1993, Yahner 1988, Wales 1972). Fire ants may be attracted to or repelled by the edge environment and either target it for mound construction or avoid it. For this reason, the spatial distribution of mounds within

linear habitats may be related to the presence or orientation of edges and be less uniform than it is in pastures. Furthermore, like mound density and mound volume, mound distribution may vary with habitat width and disturbance frequency.

3. METHODS

This study was conducted at the Savannah River Site (SRS) in the coastal plain of South Carolina. SRS is an 800 km^2 national environmental research park forested primarily by longleaf (*Pinus palustris*), slash (*Pinus elliottii*), and loblolly (*Pinus taeda*) pines. The area was probably invaded by *S. invicta* in the mid 1970's (Buren et al. 1974, Wojcik 1983). A network of several linear habitat types fragments the forest matrix. In this study, I examined five types distinguished by width and disturbance frequency: powerline cuts, paved roads, gravel roads, open dirt roads (i.e., the forest canopy did not extend into the center of the road), and closed-canopy dirt roads. The roadsides (i.e., the vegetated strip between the road edge and the forest edge) of the paved, gravel and open dirt roads were predominantly grassy. The roadsides of the closed-canopy dirt roads were sparsely vegetated and were covered with pine needles or leaves, and the powerline cuts were vegetated primarily by tall herbaceous species.

Disturbance regimes in each habitat type were obtained from the USDA Forest Service Savannah River Forest Station and verified by observation. In powerline cuts, vegetation was burned or sprayed with herbicide once every five years. Vegetation in the paved roadsides was mowed as needed (usually three or more times per year). Gravel and open dirt roadsides were mowed approximately twice per year. Closed-canopy dirt road habitats were disturbed only by occasional vehicular traffic. Because of the disturbance regimes, the height of the vegetation in October 1996 averaged 12 cm in the paved roadsides, 25 cm in the gravel roadsides, 30 cm in the open dirt and closed-canopy dirt roadsides, and 100 cm in the powerline cuts.

The habitat types varied in their suitability for fire ant establishment. The powerline cuts used in this study did not contain service roads. Therefore, the entire cut was equally available for fire ant colonization. In paved and gravel road habitats, fire ants were not able to colonize the asphalt or gravel and were therefore restricted to the roadsides. The roads in the dirt road habitats consisted of two compacted tire tracks interrupted by a less-compacted, vegetated median. Fire ants could colonize the roadsides and the median but not the tire tracks.

For each habitat type, I randomly chose ten vectors radiating from the center point of the roughly circular SRS and located the 500 m road or powerline segment closest to the end of each vector. Segments that intersected or were adjacent to forest stands younger than fifteen years or other early-successional habitats were disqualified and new segments were chosen. All chosen segments were located in upland, sandy soils dominated by Fuquay and Blanton sands (USDA 1990).

During October 1996, I surveyed each of the fifty segments (ten segments per type) for all active *S. invicta* mounds greater than 10 cm in diameter. I excluded smaller mounds because their size suggested recent establishment. New colonies experience high rates of attrition (Lofgren et al. 1975, W.R. Tschinkel, personal communication), and I chose to exclude mounds that might not persist through the year. Mound activity was determined by observing loose dirt on the mound and by digging into the mound and noting the presence of ants. Temperatures during sampling were moderate (20°-30° C), and ants were active and near the surface of the mounds. I measured the dimensions of each mound surveyed, and I estimated mound volume using the formula for half of a sphere (Porter et al. 1992, $v=(2/3)(\pi abc)$ where a=length of the mound's long axis/2, b=length of the mound's short axis/2 and c=mound height). I also measured the distance of each mound (to the nearest 0.1 m) from three points: the forest edge, the road edge, and the starting point of each 500 m segment. Powerline cuts did not contain road edges so distances were measured from the forest edge and from the starting point of the 500 m segment only.

Forest edges were defined as borders where soil disturbance from the original construction of the road or powerline cut ended. In almost all cases, this border was clearly denoted by a small ridge of soil. In cases where a distinct ridge was not present, the forest edge was delineated at the trunks of trees in the treeline. The treeline almost always coincided with a visible shift in vegetation and was easily identified. Some mounds were located just inside the forest, and I included these in my study if their distance into the forest from the forest edge did not exceed two meters. These mounds received insolation similar to mounds opposite the edge, and their proximity suggested a relationship between their presence and that of the adjacent open habitat. Road edges were defined as the border where the vegetation in the roadside abutted the asphalt, gravel or compacted tire track.

The width of each segment was measured at 50 m intervals. In the four road habitat types, I measured the width of the road, the width of each roadside, and the width of the dirt road median. There were no roads in powerline cuts, so I measured the total width only. In addition to width, the orientation of the long axis of each segment was measured using a compass. Some small dirt roads curved moderately, and their orientation was considered the average compass heading.

Analysis. I estimated the area of each site in two ways. The "total area" was defined as the area of the entire segment, and the "inhabitable area" was defined as the area assumed to be available for *S. invicta* colonization (i.e., total area minus the area of the asphalt, gravel, or tire tracks). Mound density for each segment was calculated per total area and per inhabitable area before analysis.

Differences in mound density among linear habitat types were compared using a one-way ANOVA and Tukey's HSD (Sokal and Rohlf 1995). Differences in mound volume were analyzed using a nested ANOVA where mounds were nested within segments, and by Tukey's HSD.

I examined the spatial patterns of mounds perpendicular to the long axis of a habitat in two ways. For both these analyses, I excluded all mounds located in the median of the dirt roads. I first determined whether mounds were distributed randomly throughout the inhabitable area by calculating the distance of each mound to the nearest edge (i.e., road edge or forest edge). I compared the distances observed with those expected by a random distribution using a one-sample Kolmogorov-Smirnov test for goodness of fit (Sokal and Rohlf 1995).

Second, I determined whether mound density and volume were greater in some regions than others. I divided each roadside into two linear strips of equal width parallel to the long axis, for a total of four strips per segment (Figure 1a). In powerline cuts, I divided each segment into four linear strips of equal width parallel to the long axis (Figure 1b). All strips were designated A, B, C, and D from north to south respectively.
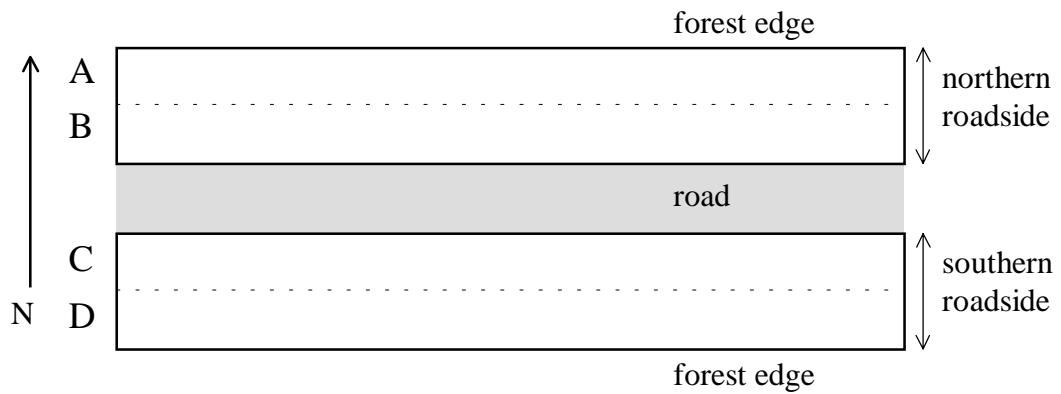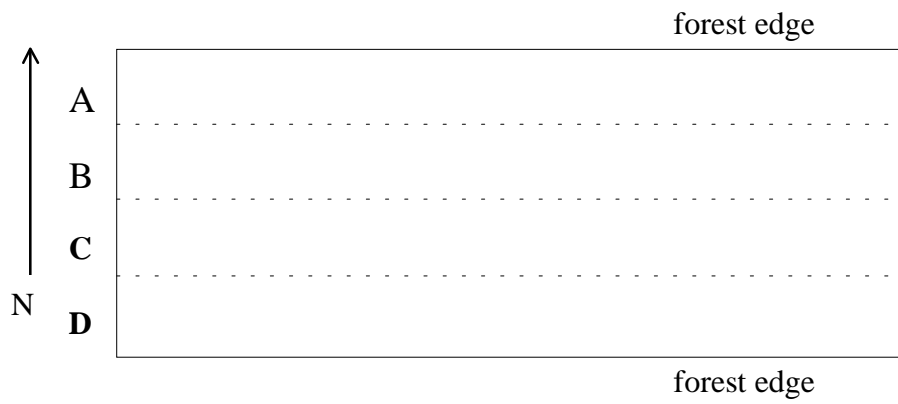
Figure 1. Division of a 500 m segment into linear strips (A, B, C, D) in road (a) and powerline cuts (b).

I compared the densities among strips by fitting the data to a Poisson distribution using SAS Proc Genmod with a model for overdispersion since variances were large (SAS Institute 1996). The number of mounds within most areas was large so I was also able to analyze my results using a one-way ANOVA and Tukey's HSD. These results did not differ greatly from those generated using the Poisson distribution. Since the ANOVA was the more conservative test, I will report only the ANOVA results. I compared mound volume among strips using a nested ANOVA and Tukey's HSD. I determined whether the orientation of the road or powerline cut (i.e., degrees from 0° N) was related to the difference in mound density between the northern and southern roadsides (or halves in powerline cuts) using a weighted regression analysis where segments were weighted according to total mound density.

To examine the spatial patterns parallel to the long axis of a segment, I used the Kolmogorov-Smirnov test to determine whether mounds were distributed randomly along the 500 m length. I divided the 500 m distance into 10 m sections and compared the densities observed in each section with those expected by a random distribution.

4. RESULTS

4.1 Comparison of habitat types

Results of my analyses were similar using either total or inhabitable area; therefore, I report only those for inhabitable area. Habitat types differed significantly in width: powerline cuts were widest, followed by paved and gravel, then open dirt, and closed-canopy dirt roads (Figure 2). Mound density differed among habitat types, but not as predicted. Density was relatively low in the narrowest type (closed-canopy dirt roads) as predicted. However, for the four open canopy types, density was higher in the narrowest type (open dirt roads) than in the widest type (powerline cuts), and there was a trend for decreasing mean density as width increased (Figure 3a). Furthermore, mound density was greater in habitat types with intermediate to frequent disturbance (open dirt and paved roads) than types with infrequent disturbance (powerline cuts and closed-canopy dirt roads; Figure 3b). Mound density was most variable (i.e., largest standard error) in open dirt road habitats (Figure 3).

Mound volume was not clearly related to habitat width (Figure 3c), but mounds were largest
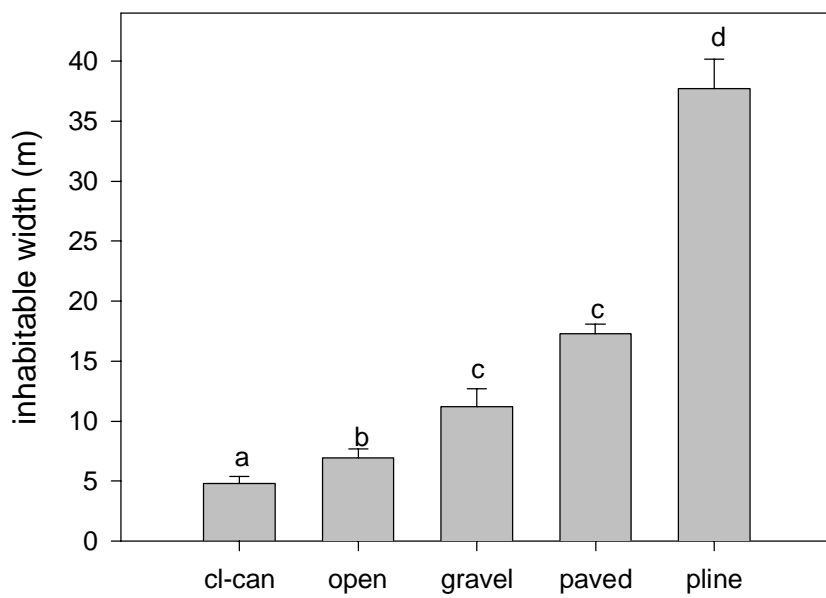
Figure 2. Mean width of closed-canopy (cl-can) and open dirt roadsides+median, gravel and paved roadsides, and powerline (pline) cuts (n=10 for each type, + standard errors). Bars with different letters are significantly different ($p < 0.05$) using Tukey's HSD.
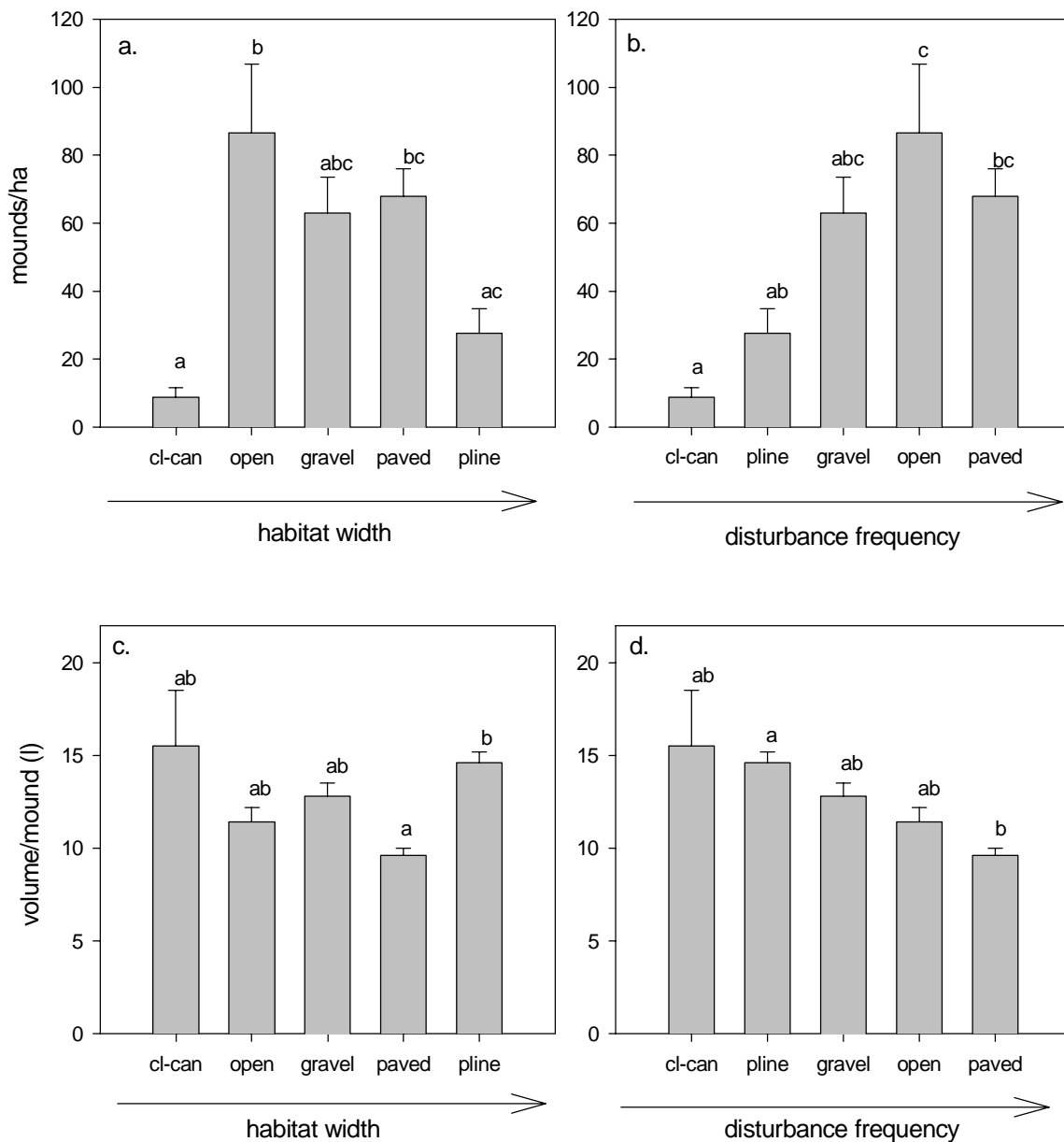
Figure 3. Mean mound density in closed-canopy (cl-can) and open dirt roadsides+median, gravel and paved roadsides, and powerline (pline) cuts (n=10 for each type, + standard errors) in order of increasing width (a) and disturbance frequency (b). Mean mound volume per mound by habitat type (n=10 for each type, + standard errors) in order of increasing width (c) and disturbance frequency (d). Bars with different letters are significantly different (p<0.05) using Tukey's HSD.

in the un-mowed powerline cuts and smallest in the frequently-mowed paved roadsides (Figure 3d). The trend (not significant) in mound volume may indicate an inverse relationship with disturbance frequency. Mound volume was most variable in closed-canopy dirt road habitats (Figure 3).

4.2. Spatial distribution within habitats

Distributions perpendicular to the long axis of the habitat. Within four habitat the types, mounds were closer to either the forest edge or the road edge than expected by a random distribution (Figure 4). Closed-canopy dirt road habitats were not included in this analysis because the number of mounds (n=28) was too low. Most mounds (26%) were located within 2 m of the forest edge in powerline cuts and within 1 m of either edge in paved and gravel roadsides (49% and 64% respectively). Along the road edge, mounds were commonly located so close to the edge that a portion of the mound actually spilled over on to the asphalt or gravel. More mounds were located close to the forest edge than road edge in gravel (204 vs. 114 mounds), open dirt (206 vs. 80), and closed-canopy dirt (25 vs. 3) roadsides. In paved roadsides, more mounds were located close to the road edge (318 vs. 259).

Solenopsis invicta preferred some linear strips of the habitat for colonization over others. In all fifty segments combined, mound density was greater in strip A than D (Figure 5). This trend was evident in all habitat types except open dirt roads, but the differences were significant in gravel roads only. In all fifty segments combined, mound volume was higher in strip A than in strips B and C (Figure 6). Within each habitat type, however, differences in mound volume among strips were not significant.

A wide and frequently traveled road may act as a barrier to colony movement. If fire ants cannot move the colony across the asphalt or gravel expanse, then each roadside may have a functional northern region (i.e., strips A and C). I combined the mound density in strips A and C and compared it with the combined density in strips B and D. The density in A+C was larger than the density in B+D in paved (74.2 mounds/ha, SE=10.2 vs. 43.9 mounds/ha, SE=7.8, $p<0.05$) and gravel roadsides (66.3, SE=11.6 vs. 29.3, SE=10.4, $p<0.05$). The density in A+C was not different from the density in B+D in powerline cuts (35.2, SE=9.3 vs. 14.8, SE=4.6,
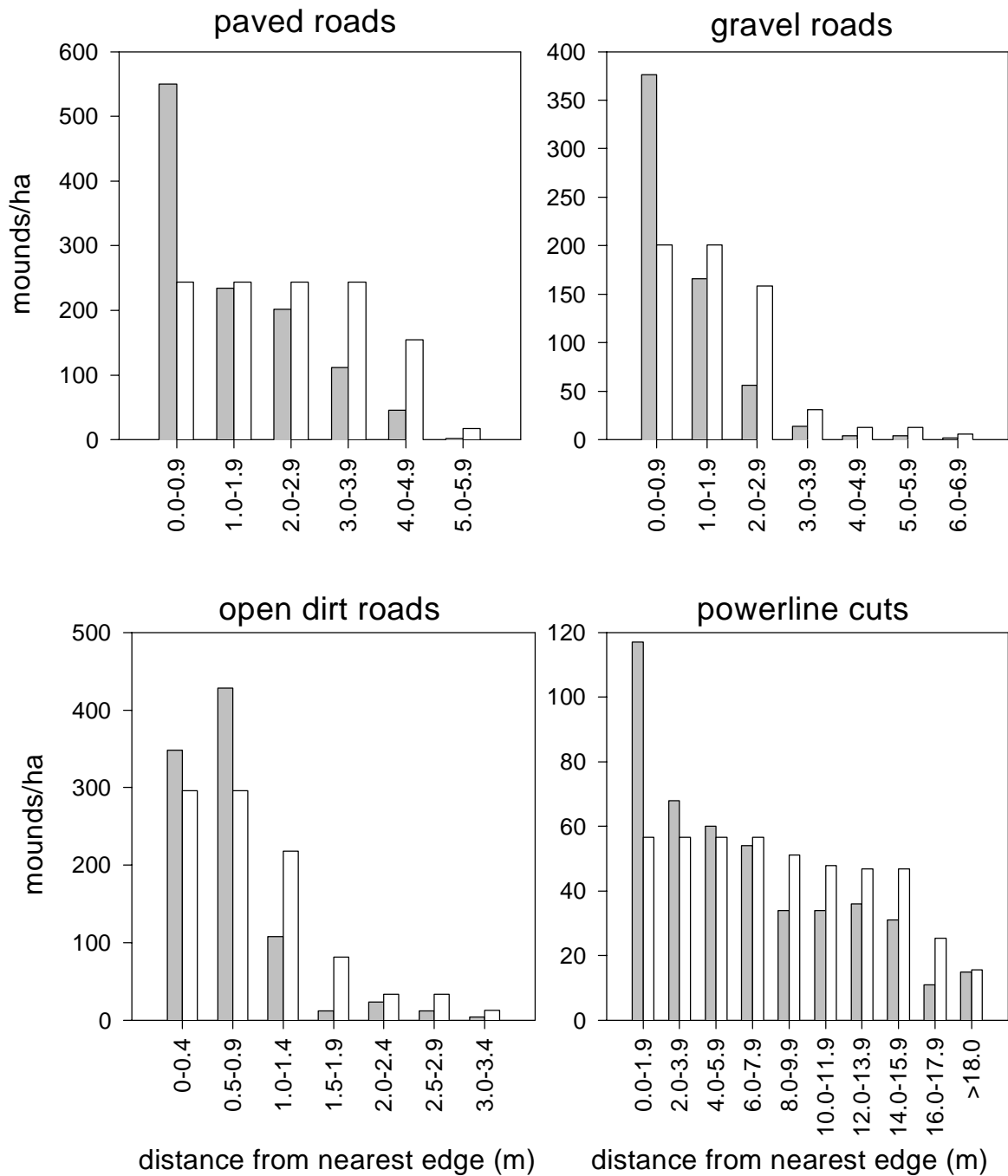
Figure 4. Mound distribution relative to forest or road edges in four linear habitat types. Gray bars represent the observed mound density and white bars represent the density expected by random. All distributions are significantly closer to edges than expected (p<0.01) using a one-sample Kolmogorov-Smirnov test for goodness of fit.

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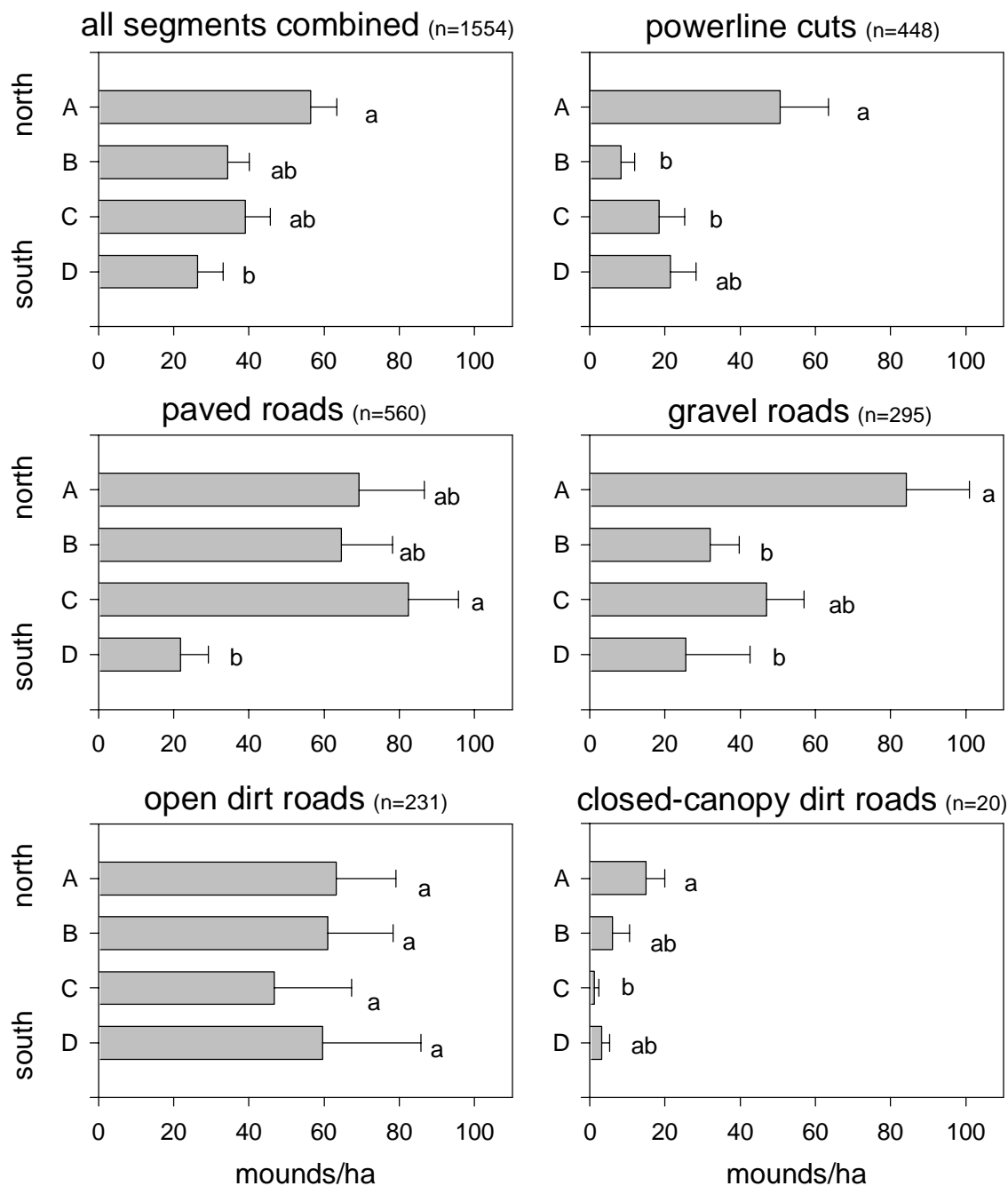
Figure 5. Mound distribution perpendicular to the long axis of the linear habitat by density in all segments combined (n=50) and in each habitat type (n=10 for each, + standard errors). A, B, C, and D denote linear strips located in the northernmost to southernmost sides of the habitat respectively. Bars with different letters are significantly different (p<0.05) using Tukey's HSD.

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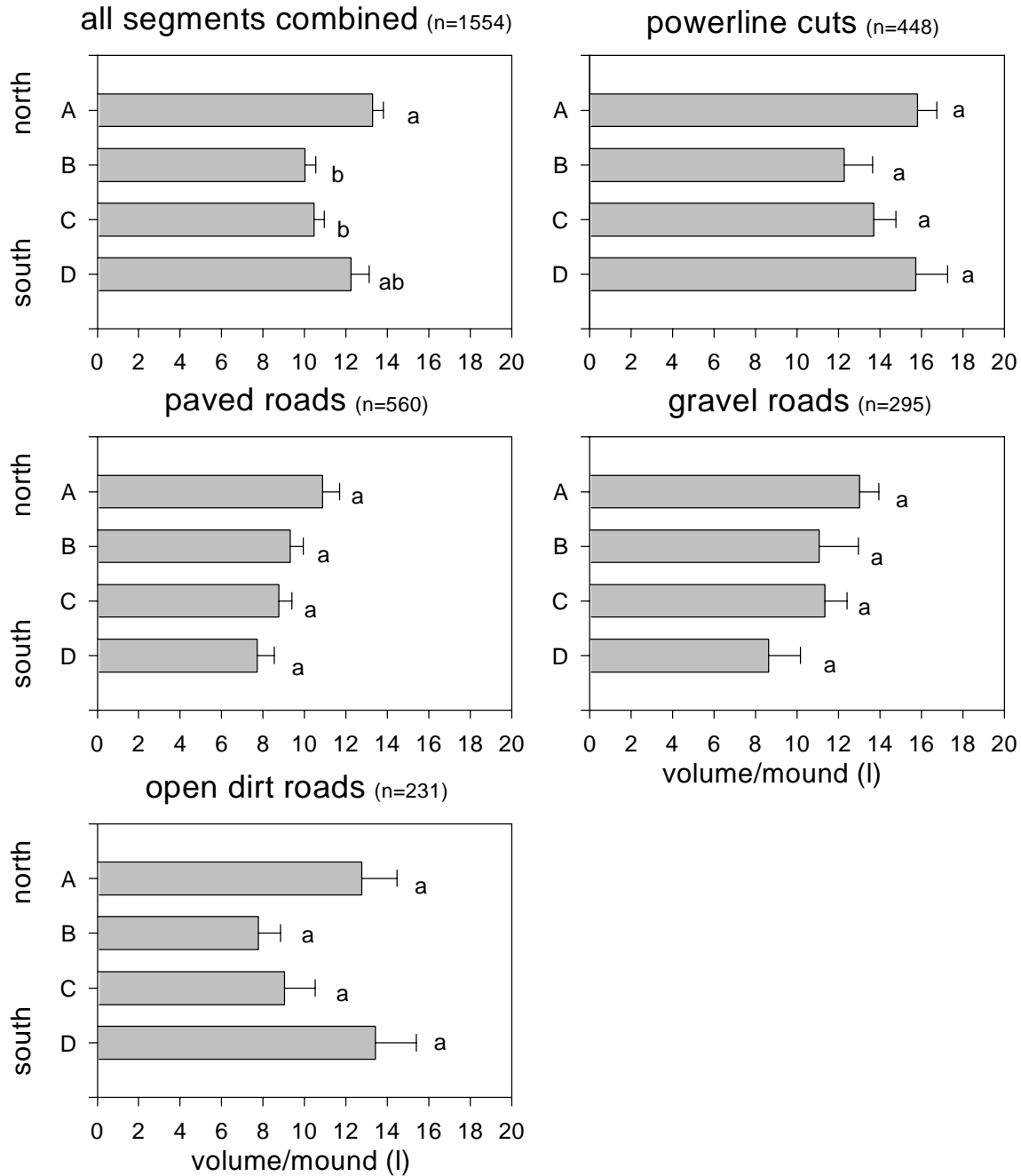
Figure 6. Mound distribution perpendicular to the long axis of the linear habitat by volume in all segments combined (n=50) and in each habitat type (n=10 for each, + standard errors). A, B, C, and D denote linear strips located in the northernmost to southernmost sides of the habitat respectively. Bars with different letters are significantly different (p<0.05) using Tukey's HSD.

p>0.05), open dirt (57.3, SE=14.7 vs. 62.4, SE=17.6, p>0.05) or closed-canopy dirt roadsides (7.4, SE=2.4 vs. 4.4 mounds/ha, SE=2.4, p>0.05).

The difference between the mound density in the northern and southern roadsides (or halves in powerline cuts) was related to the orientation of the habitat (Figure 7). The difference between the mound density in the northern and southern roadsides (or halves) was negative or small in roads or cuts oriented more north/south. This difference increased as the orientation of the road or cut shifted from north/south to east/west (R^2=0.19, p=0.003). Most of the high-density habitats, however, had orientations within 40° of north (Figure 7).

Distributions parallel to the long axis of the habitat. Along the 500 m axis of the segments, mounds in the roadsides or powerline cuts were not randomly distributed. Mounds in the ten closed-canopy dirt road segments were not analyzed because of low numbers. For the remaining forty segments surveyed, mound density in each of the fifty 10 m sections was similar across the entire 500 m in only four segments: one gravel and three paved road habitats. In the other thirty-six cases, mound density differed more among 10 m sections than would be expected by a random distribution (p<0.05).

5.   DISCUSSION

5.1. Effects of linear habitat type

Fire ant mound density differed among habitat types; however, the density was not related to habitat width or disturbance frequency in the ways that I predicted. The narrowest habitat type (closed-canopy dirt roads) did indeed have the fewest mounds, as predicted, but among the four open-canopy types, density was highest in the narrowest type (open dirt roads) and lowest in the widest type (powerline cuts; Figure 3a). My results suggest that direct sunlight is a requirement for fire ant colonization. Mound densities were non-existent in five of the ten closed-canopy dirt road segments and extremely low in the other five. Thus, our original prediction that greater width leads to greater density is correct; however, once the habitat exceeds a critical width (i.e., one that allows for some direct sunlight at the soil surface) other factors are more important. My evidence suggests that disturbance is one of those key factors. Frequent direct disturbance seems to increase rather than decrease fire ant mound density. Mowing or burning decreases vegetative
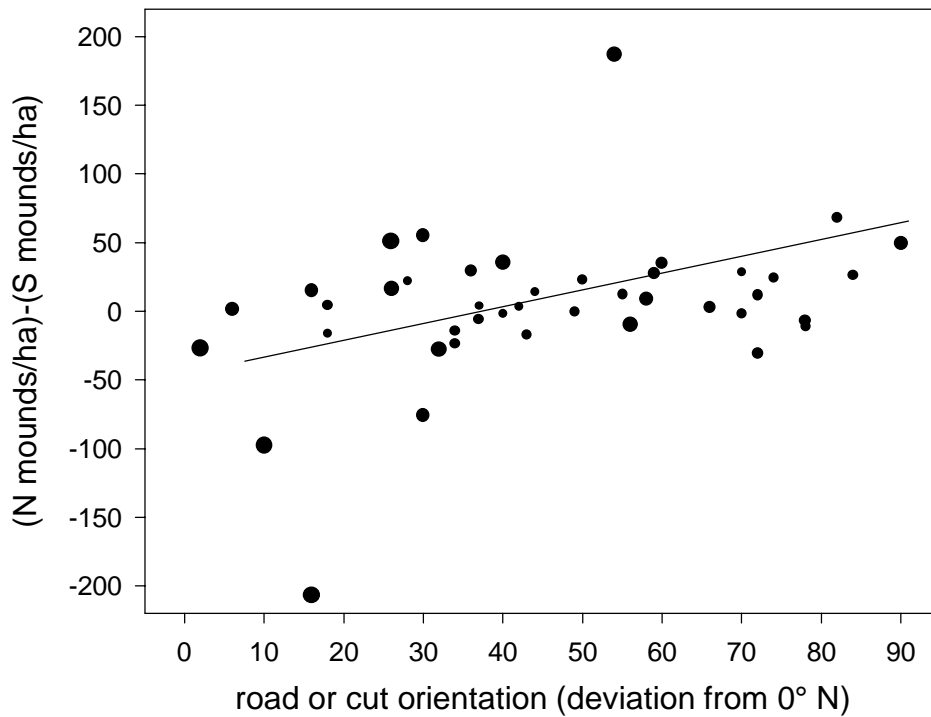
Figure 7. Difference between the mound density in the northern (N) and southern (S) roadsides (or halves in powerline cuts) as a function of road or cut orientation (R^2=0.19, p=0.003) using a weighted regression. Larger symbols denote segments with greater total mound density.

height and exposes or disturbs soil. The increased insolation and soil disturbance may stimulate fire ant colonization or population growth more than the decrease in growth I expected from direct, physical disruption of the existing mounds. Other key factors that may determine differences in mound density among habitat types include the availability of resources and the abundance of predators of fire ant queens, but my data cannot provide information about these hypotheses.

The differences in fire ant densities suggested by my mound density data may be partly offset by a different trend in mound volume. Mounds were smaller in habitats that were disturbed more frequently, and the difference between the extreme disturbance regimes in open habitats (i.e., paved roadsides vs. powerline cuts) was significant (Figure 3d). Mounds in paved roadsides may be run over by mowing machinery several times a year. Colonies may be forced to move or rebuild each time, and thus, their smaller size may reflect a transition phase. Abandoned mounds, many marked by tire tracks, were often seen within 2-4 m of active mounds. Mean mound volume in powerline cuts, however, may have been larger because mounds may escape physical destruction for up to five years. I observed more evidence of mound relocation in paved and gravel roadsides than in powerline cuts. The demonstrated relationship between mound volume and ant abundance (Tschinkel 1993) may not be as strong for frequently-disturbed mounds as it is for infrequently-disturbed mounds; however, my results suggest that powerline cuts have more fire ants per mound than paved roadsides. The impact of fire ants on their community depends on both mound density and volume because both contribute to ant abundance. However, differences in mound volume among habitat types are not nearly as large as differences in mound density. Therefore, it is likely that mound density plays a larger role in determining the impact of fire ant invasion.

5.2 Spatial distribution within habitats

Fire ant mounds were more abundant near the northern side of linear habitats (i.e., strip A), and the disparity between the density in the northern and southern roadsides (or halves) increased in roads or cuts oriented more east/west. Mounds near the northern side may receive more insolation than those near the southern side, especially during winter months. In winter, the area close to the southern edge of a linear habitat (i.e., strip D) is shaded for at least part of the day. Optimal temperatures for colony growth of *S. invicta* are between 24° and 32° C

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(Porter 1988, Lofgren et al. 1975), and the location of the mound may influence thermoregulation. Individual mounds are often oriented so that the long axis of the mound runs north/south for more effective thermoregulation (Hubbard and Cunningham 1977). It is likely that the location of the mound would serve this same purpose.

Fire ants usually move their mounds at least once per year for reasons that are not apparent (Hays et al. 1982). I sampled all segments in October and did not replicate my study in other seasons. Therefore, I do not know whether ants move their mounds northward as the southern roadside becomes more shaded or whether colonies that initially established near the northern side experience lower attrition.

The structure of the linear habitat type affects the north/south mound distribution (Figure 5). In paved and gravel roadsides, mound density was higher in strips A and C than strips B and D. For fire ants, the road constitutes a wide, uninhabitable expanse. Colonies in the southern roadside may not be able to establish mounds further northward than strip C. The mound densities in strips A and B were different in gravel roadsides, but they were the same in paved roadsides. Since paved road habitats are wider, a larger area may receive more sunlight. Colonies in the northern roadside may not need to be close to the northern edge to receive sufficient insolation. Open dirt road habitats, which had the same mound density in all strips, may not be wide enough to provide insolation along any consistent edge. This does not help explain the high mound density in this habitat type, but it may help explain the high variability in mound density among segments. In powerline cuts, fire ants favored the strips near the forest edges (i.e., A and D). Mound density was low in strips B and C even though the adjacent forest never shades these regions.

Mounds were largest towards the northern side of the linear habitats (Figure 6). However, they were not significantly different from those near the opposite forest edge (i.e., strip D). Colonies in strip A may grow larger as a result of more effective thermoregulation, or when close to edges, or both. Additionally, mounds near the forest may escape direct physical disturbance from mowing machinery.

My results suggest that ants prefer edges in general regardless of orientation (Figure 4). Mounds located in any strip were frequently built close to the road or forest edge. Several hypotheses may explain this distribution. For example, fire ants may be responding to the distribution of other species, or the soil structure near edges may be important. Soil near forest

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edges contains more tree roots and decomposing wood; soil near paved and gravel roads contains more gravel. Both edge soils may be easier to excavate. Banks et al. (1990) documented numerous potholes resulting from the tunneling of *S. invicta* under highways in Florida and North Carolina. Edges may also provide microsites where humidity, temperature, foraging efficiency, vegetative cover, or the frequency of direct disturbance changes.

The spatial distributions of mounds differ between linear and non-linear early-successional patches. Mature mounds in pastures with high mound density are regularly distributed (Adams and Tschinkel 1995). Baroni Urbani and Kannowski (1974) found that mounds were somewhat aggregated at a small scale, but over an entire pasture, mounds were roughly uniform. Similarly, I have observed that mounds in forest gaps are not associated with edges. The spatial distribution of mounds within pastures, agricultural fields, and forest gaps may reflect a response to small-scale environmental heterogeneity such as tree stumps, fence posts (Hays et al. 1982), slight variation in topography (Maxwell 1982), or other mounds (Adams and Tschinkel, 1995). In contrast, the spatial distribution of mounds within linear habitats (Figures 4 and 5) may reflect a response to large-scale environmental heterogeneity such as the level of insolation, soil compaction, or temperature found along a consistent edge.

Solenopsis invicta is an exotic species whose effects on native ants and other arthropods are detrimental. Furthermore, its abundance and distribution throughout the southeastern U.S. is growing (Vinson 1994, Porter et al. 1988). In order to prevent or slow further fire ant invasion into newly-disturbed areas, the spatial distributions of mounds and the use of different linear habitat types need to be considered. To limit the suitability of road and powerline cuts as primary habitat for the red imported fire ant, my study suggests that a reduction in roadside disturbance (i.e., less mowing) and an increase in the amount of forest canopy allowed to shade roadsides, especially towards northern edges, may result in lower fire ant mound density.

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CHAPTER 2

Top-down control by the red imported fire ant: a test of tritrophic interaction

strength

1. ABSTRACT

Top-down control by predaceous insects has rarely been demonstrated in terrestrial communities, but invasive species may be particularly suited to exert such control. The red imported fire ant, *Solenopsis invicta*, has strong interactions with spiders, other ants, and phytophageous insects, and I predicted that it would exert top-down, cascading control in early-successional plant communities in the southeastern U.S. In a forest gap in South Carolina, I measured levels of herbivory, growth and fecundity for five common herbaceous plant species in plots where ants were present vs. excluded (ant exclusion experiment) and in plots with varying abundance of fire ants and sympatric ants (ant substitution experiment). For all plant species in the ant exclusion experiment, herbivory was greater when fire ant abundance was low ($p<0.01$). Light levels, spider abundance, and herbivore density were also related to folivory for some plant species in both experiments ($p<0.01$). Mean folivory over the growing season was low for all plant species (mean amount of leaf tissue removed for most-chewed species=11%). Variation in growth and fecundity were not well explained or consistent for any plant species in either experiment (partial $R^2 \leq 0.10$ for eight significant variables related to aboveground vegetative biomass and three significant variables related to reproductive biomass). My results indicate that fire ants play an important role in determining the level of herbivory on early-successional plants; however, their top-down influence is not strong enough to cascade and impact plant growth or fecundity.

Keywords: ants, fire ants, herbivores, interaction strength, invasive species, keystone predators, *Solenopsis invicta*, top-down control, tritrophic, trophic cascades

2. INTRODUCTION

In tritrophic communities, top-level predators may have positive, indirect effects on primary producers via their direct consumption of primary consumers (Hairston et al. 1960, Fretwell 1977, Oksanen et al. 1981). If primary and secondary consumers feed solely on the level directly below them, there is potential for efficient predators to exert cascading, top-down control and improve growth and fitness of producers. However, in natural terrestrial communities, many top-level, invertebrate predators are generalists and consume from several trophic levels including their own (Schoener 1989). These complex linkages dilute the potential for trophic cascades and make them difficult to identify (Strong 1992, Polis and Strong 1996).

Nevertheless, several studies in terrestrial communities have demonstrated top-down control on plants via primary consumers (Spiller and Schoener 1994, Marquis and Whelan 1994, Dial and Roughgarden 1995, Moran et al. 1996). To better predict which species may be able to exert top-down control, Spiller and Schoener (1990) propose a graphical model that incorporates interaction strength. According to their model, predators that have strong interactions with other species, both within and among trophic levels, have potential for top-down control over plant productivity, especially when other interactions within the web are comparatively weak.

Invasive species may be particularly suited to exert top-down control. Many exotics have few competitors or predators, and therefore often become highly abundant. They may also possess characteristics (e.g., aggressiveness, efficient dispersal, rapid reproduction, and polyphagy) that create strong interactions with potential competitors and prey (Erhlich 1986, Jones and Phillips 1987). With a competitive and predatory edge over other secondary consumers and few clear checks on their population growth, successful invasive species may be able to competitively displace other predators, monopolize resources, and consume prey to such a degree that the effects cascade to plants. These strong interactions with other species may allow some exotics to become keystone predators once they have established within a community.

The invasive and highly abundant red imported fire ant, *Solenopsis invicta* Buren (hereafter referred to as fire ant), is a generalist predator that interacts strongly with both the second and third trophic levels. *Solenopsis invicta* was accidentally introduced from Brazil into Alabama approximately 75 years ago and is now widely distributed and abundant throughout the southeastern U.S. as far north as Maryland and as far west as Texas (Vinson 1997). Fire ants

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feed on predatory arthropods such as spiders (Wilson and Oliver 1969, Tennant and Porter 1991) and on other invertebrates such as decomposers (Vinson 1991, Stoker et al. 1995). They also feed on plant material such as seeds (Morrison et al. 1997) and nectar (Lanza et al. 1993). However, their primary food source consists of insect herbivores at any stage of development from egg to adult (Wilson and Oliver 1969, Ali et al. 1984, Reagan 1986, Lee et al. 1990, Porter and Savignano 1990, Cherry and Nuessly 1992). They prefer insects to other food items (Tennant and Porter 1991), and arthropod consumption is necessary for colony growth (Porter 1989).

Fire ants are efficient and aggressive predators, and most importantly, they are highly abundant. A single mound often contains 200,000-300,000 workers (Lofgren et al. 1975, Vinson 1997). In coastal plain forests in South Carolina, density can average 27 mounds/km along the forest edges of roads (Stiles and Jones 1998) and can number over 100 mounds/ha in forest gaps (Stiles, unpublished data). Because of their prevalence and their efficiency, the effects of fire ants on the community may overpower those of other arthropod predators such as spiders, mantids, or other generalist ants. In fact, fire ants often displace or restrict many native ant populations through competition (Whitcomb et al. 1972, Camilo and Phillips 1990, Porter and Savignano 1990, Morris and Steigman 1993) and replace them with populations that are usually larger (Hölldobler and Wilson 1990). Additionally, fire ants have been shown to reduce the abundance and diversity of insect herbivores in some agroecosystems and have been proposed as biological control agents (Reagan 1986, Tedders et al. 1990, Way and Khoo 1992). They and other members of their genus have demonstrably reduced levels of folivory in monocultures of plants (Risch and Carroll 1982, Reagan 1986). Fire ants have been shown to have strong interactions in relatively simplified communities such as pastures or agricultural fields, but little is known about their effect on the first, second or third trophic levels in more complex, natural communities. Additionally, as an invasive species, little is known about their effect in comparison with sympatric species.

My study tested a graphical model of fire ant interaction strength (Figure 1). Specifically, I focused my test on the indirect, positive interaction between fire ants and plants. To test this
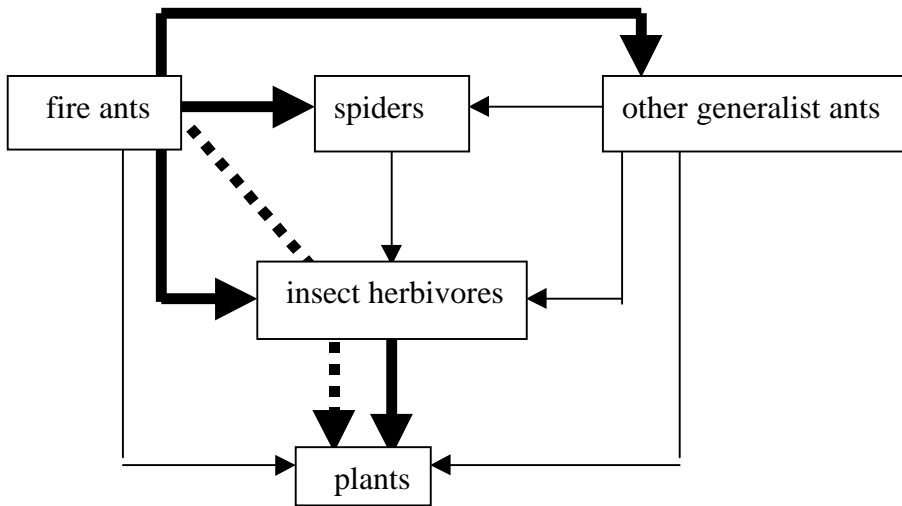
Figure 1. Hypothesized model of tritrophic interactions in gaps within pine forests in the coastal plain of the southeastern U.S. Wide arrows represent direct, strong interactions. Narrow arrows represent direct, weak interactions. Solid arrows indicate competitive or predatory interactions and point from the group causing the effect to the group experiencing the effect. Dashed arrow represents hypothesized, positive indirect interaction tested by my study.

model, I measured herbivory and herbivore impacts on plant growth and fitness in the presence of fire ants and when fire ants were experimentally removed. I also compared herbivore impacts in the presence of fire ants and in the presence of other predaceous ants whose interaction strengths are less well documented. I tested two hypotheses. First, fire ants exert strong top-down control and have indirect effects on primary producers via direct effects on insect herbivores. I predicted that removal of plant tissue would be greater and plant biomass and seed production would be less when fire ants were excluded than when present. Second, fire ants exert stronger top-down control than other ant species. I predicted that plants within areas dominated by fire ants would have greater biomass and seed production and less tissue removed than plants within areas dominated by other ant species.

3. METHODS

3.1 Study site

My study was conducted at the Savannah River Site (SRS) in the coastal plain of South Carolina from March-October 1997. SRS is an 800 km^2 national environmental research park forested primarily in longleaf (*Pinus palustris* Miller), loblolly (*Pinus taeda* L.) and slash (*Pinus elliottii* Englm.) pines, and it was invaded by fire ants during the mid 1970's (Vinson 1997, Wojcik 1983). The study site was a 35-yr-old plantation of *P. elliottii*. Two gaps, totaling approximately 1.1 ha and delineated by scattered overstory trees, were created within the site by salvage logging approximately three years before the study began. At the time my study was initiated, the gaps were vegetated with early-successional herbaceous species and a few small pine and hardwood trees (<5 m in height). Fuquay sand (a loamy, kaolinitic, thermic Ultisol) is the predominant soil series in the gaps (USDA 1990). Fire ant density within the study site was approximately 100 large mounds/ha (volume>10 liters and over one year in age). Other abundant ant species included *Dorymyrmex pyramicus* Roger, *Linepithema humile* Mayr (formerly *Iridomyrmex humilis*, Shattuck 1992), and *Pogonomyrmex barbatus* Mayr. *Dorymyrmex pyramicus* (the pyramid ant) is a highly aggressive native ant that feeds on arthropods and honeydew (Smith 1965). *Linepithema humile* (the Argentine ant) is an aggressive, invasive ant with feeding behavior similar to that of *S. invicta* (Cole et al. 1992), and *P. barbatus* (a harvester ant) is primarily granivorous (Gordon and Kulig 1996). Less-abundant

genera included *Paratrechina*, *Monomorium*, *Neivamyrmex*, *Crematogaster*, *Ponera*, *Pheidole*, *Strumigenys*, and *Trachymyrmex*.

3.2   Study species

From preliminary field observations, I chose herbaceous plant species for experimental manipulations based on three criteria: that the leaves were attractive to phytophageous insects and removal of tissue was visible, that they were abundant in early-successional sites within SRS, and that ants were observed on them. Study species included three annual legumes, *Chamaecrista fasciculata* (Michx.) Greene*, Chamaecrista nictitans* (L.) Moench (both formerly *Cassia*, Tucker 1996), and *Crotalaria spectibilis* Roth; an annual vine, *Jacquemontia taminifolia* (L.) Grisebach; a perennial vine, *Passiflora incarnata* L.; a perennial shrub, *Sida rhombifolia* L.; and a clonal forb, *Pityopsis graminifolia* (Michx.) Nutt. *Chamaecrista fasciculata*, *C. nictitans*, and *P. incarnata* have extrafloral nectaries, which are attractive to many ant genera including *Solenopsis* (Kelly 1986, Barton 1986, McLain 1983). Seeds of these plant species were collected from SRS in the fall of 1996, and were propagated in a greenhouse in Blacksburg, Virginia. While in the greenhouse, seedlings were fertilized three times with a 20-20-20 mix fertilizer to promote growth. Seedlings were transplanted into the study site in April 1997. The number of seedlings that germinated and survived to planting determined my final plot design.

3.3   Plot design

I tested my first hypothesis (that fire ants exert top-down control) using an ant exclusion experiment within a small gap (<0.5 ha, Figure 2). Grasses and forbs dominated the ground cover, and the area contained over fifteen large fire ant mounds and relatively few colonies of other ant species. I tested my second hypothesis (that fire ants exert stronger top-down control than other generalist ants) using an ant substitution experiment distributed throughout an irregular 0.8 ha gap fragmented by scattered overstory trees (Figure 2). This area contained over sixty fire ant mounds and numerous colonies of other ant species.   Shading from overstory trees and height of the understory vegetation were more variable in this area than in the area designated for the ant exclusion experiment. Ground cover ranged from dense pine needles to bare sand to grass.

ant exclusion   ant substitution
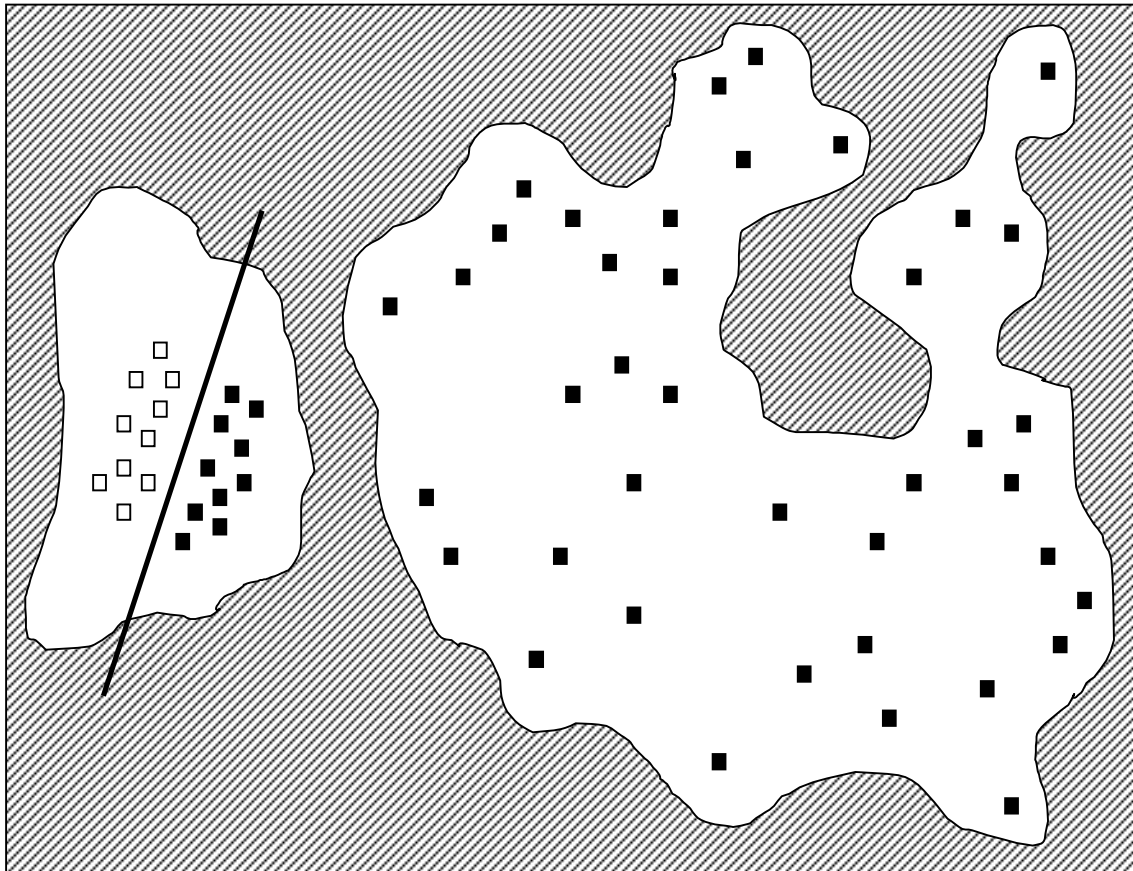
Figure 2. Map of the study site (1.1 ha) showing the approximate layout of plots in both experiments. In the ant exclusion experiment, white squares show plots treated with a toxic bait and black squares show untreated plots. The line dividing the gap shows the location of an ant barrier. In the ant substitution experiment, black squares show approximate location of all plots.

In February 1997, I divided the ant exclusion gap longitudinally by an ant barrier constructed of 60 m of metal flashing buried 12 cm into the ground (Figure 2). Few fire ant foraging tunnels are constructed deeper than 10 cm (Markin et al. 1975), so the barrier prevented most, if not all, underground movement by ants. The aboveground 12 cm portion of the flashing was painted monthly with Fluon® (Northeast Chemical Co., Woonsocket, RI) which dries into a slick surface that ants cannot cross. I treated the area on one side of this barrier monthly beginning in March 1997 with the toxic bait Amdro® (hydramethylnon, American Cyanamid, Princeton, NJ) to eliminate all ant colonies. In addition, I searched every three weeks for colonies that did not respond to the bait and doused them with 2-5 gallons of boiling water until no living ants were left. I left the area on the opposite side of the ant barrier untreated.

Twenty permanent 1x1.4 m plots were established towards the center (i.e., the sunniest part) of the gap. All plots were located at least 5 m from the barrier. Ten of the plots were randomly placed in the bait-treated area. The other ten were placed directly opposite in the untreated area so that the arrangement of plots on either side of the barrier was identical (Figure 2).

Plots in the ant substitution experiment were distributed over a much larger area (Figure 2) and their location depended on the location of ant colonies. I randomly chose twenty fire ant mounds from all those within the area and placed a 1x1.4 m plot within 3 m of each mound. The locations of these twenty plots were designed to maximize the number of fire ant foragers present. Twenty additional plots were established in order to minimize fire ant foraging and maximize the foraging of other species. These were placed in randomly-chosen locations at least 25 m from any visible fire ant colonies but close to nests of other ant species.

In both experiments, each plot was planted with thirty-five seedlings. Seven seedlings of each of *C. nictitans*, *C. spectabilis*, *J. taminifolia*, *S. rhombifolia*, and *P. graminifolia* were planted in each of the twenty plots in the ant exclusion experiment. Eight seedlings of *C. spectabilis*, seven of *J. taminifolia*, five to six of *P. incarnata*, and six to seven of *C. fasciculata* and *P. graminifolia* were planted in each of the forty plots in the ant substitution experiment. Individuals were planted randomly within the plots at the intersections of a 20x20 cm grid. The grid was used to minimize competition among the experimental plants. Competing vegetation (non-study individuals) was clipped periodically, but the plots were not trenched to prohibit root competition. Seedlings were watered a total of five times during dry periods in May and June to promote establishment.

Each plant was monitored monthly from May 1997 until harvest (October for the last species) for percent leaf tissue removed by insects. In preliminary trials, leaves and leaf holes were measured and proportions of tissue removal were calculated. Percent tissue removal of the entire plant was estimated from these calculations and from the number of leaves. After several trials, percent removal was estimated visually from the standards set by these earlier measurements. Senescing leaves were excluded. To ensure consistency, all estimates were made by the same person (J. Stiles) throughout the growing season.

In addition to estimates of herbivory, each plant was censused monthly for the number of ants, insect herbivores, insect eggs, and arthropod predators found on the plant. All observed arthropods were identified to family, and ants were identified to species in the field. A representative of each common species was collected to confirm field identifications. For analysis, the numbers of ants, spiders, and insect herbivores on a plant were divided by aboveground plant biomass (measured at harvest) to correct for the possible bias that larger plants attract more arthropods.

To estimate the number of ants foraging within the plots during the growing season, five pitfall traps were placed within each of the sixty plots. Traps were made by burying plastic cups so that the rim was level with the soil surface. Traps were open (i.e., filled with 20 ml ethylene glycol) for a period of 48 hours in June, July, August and September 1997. When collected, contents of each of the five traps in each plot were pooled into one sample. Arthropods in the samples were counted and identified, ants to genus or species and others to order or family. The Insect Identification Laboratory in the Virginia Polytechnic Institute and State University Department of Entomology confirmed the identifications of insects in pitfall traps and those collected from plants. Voucher specimens of common species were placed in the entomology collection of the Virginia Museum of Natural History at Virginia Polytechnic Institute and State University.

Fruits of all plant species were harvested as they matured. The aboveground portion of the plants (stems and leaves) was harvested after seed set and just preceding senescence. Harvest date varied by species: *J. taminifolia* was harvested in late July, followed by *C. fasciculata* in late August, *C. nictitans* and *S. rhombifolia* in early October, and *C. spectabilis* in late October. *Pityopsis graminifolia* and *P. incarnata* were not harvested due to high mortality and extremely slow growth. I recorded total shoot length, basal diameter, number of fruits, and number of

seeds of all harvested plants. Leaf area was estimated from a random subset of harvested leaves.

Stems, leaves, fruits, and seeds were dried and weighed separately as measures of growth and

fecundity.

Differences in light levels among plots can contribute greatly to differences in plant biomass.

Although light regimes within the gap did not vary greatly, some plots were more heavily

shaded than others, especially in the ant substitution experiment. For this reason, I took a

hemispherical canopy photo from the center of each plot in October 1997. Photos were scanned

and analyzed for amount of total light penetration using FishEye software (FEW 4.0 by M.

Ishizuka 1997) to derive a seasonal gap light index (Canham 1988). This software estimated and

averaged light levels over the entire growing season (May-October).

3.4   Analyses

Plots in each experiment were initially established as replicates within treatments.

However, because ant abundance, ant species distribution, herbivore abundance, and light

penetration varied within treatments, I analyzed the data using multiple regressions with step-

wise elimination of non-significant variables (Sokal and Rohlf 1995). For each plant species in

each experiment, regression models were constructed for the three response variables: herbivory,

growth, and fecundity of the harvested plants. A total of ten explanatory variables included the

mean number of fire ants, pyramid ants, Argentine ants, or spiders collected from pitfall traps,

the mean number (per gram plant biomass) of fire ants, pyramid ants, Argentine ants, spiders, or

herbivores observed on plants, and the amount of light reaching the plot. Means were calculated

as the number of insects in traps or on plants averaged over the entire growing season (2-4 pitfall

trapping dates and 3-6 census dates depending on time of harvest). Herbivory measurements (%

plant tissue removed) were arcsine transformed. To ensure that the models fit the data

reasonably well without violating assumptions of colinearity of independent variables, residuals

were plotted and colinearity of explanatory variables was tested according to Philippi (1993).   I

also computed product-moment correlation coefficients among the explanatory variables to

further determine their level of independence and p-values for the large number of coefficients

were corrected using the Bonferroni method (Sokal and Rohlf 1995). In contrast to ANOVA,

multiple regression is not as powerful for testing hypotheses of cause and effect. A compromise

approach suggested by Philippi (1993) for testing hypotheses is to use a random subset of the

data to develop a model (i.e., select the set of significant explanatory variables) and then test that

model using the remaining data. I performed this split data test for the three response variables in order to support the standard multiple regression tests performed using the full data. All statistical procedures were conducted using SAS (SAS Institute 1988).

4. RESULTS

4.1   Plant survival

The majority of plants survived, produced seeds, and were harvested (Table 1). June and July were unusually wet months for SRS (USDA 1990). USDA Forest Service records from the SRS forest station reported 16.7 cm of rain in June (vs. a 10 yr average of 10.9 cm) and 18.6 cm in July (vs. a 10 yr average of 12.3 cm). May and August 1997, however, were unusually dry (5.3 cm in May vs. a 10.6 cm average and 6.3 cm in August vs. an 11.5 cm average). Water stress was the most common cause of mortality, and in the ant exclusion experiment, most individuals of *P. graminifolia* died (Table 1). By the end of the growing season, survivors of *P. graminifolia* and *P. incarnata* had not grown much larger than their initial size when transplanted in the spring, and I did not harvest them. In eight of the forty ant substitution plots, rodents clipped all *C. fasciculata* at the base and ate the seeds. *Jacquemontia taminifolia* was harvested in mid-growing season (July) because seed set and senescence occurred earlier than expected.

4.2   Explanatory variables: the biotic and abiotic environment

Overall, I were not able to control the distribution or abundance of ant species in the plots; however, differences among plots occurred naturally. Applications of toxic bait and boiling water worked well to reduce ant abundance, but foragers could not be eliminated completely. Additionally, in both experiments, the proximity of visible colonies to the plots did not always correspond with ant abundance or foraging patterns, especially for fire ants. Furthermore, the

Table 1. Fate (%) of plants in each experiment.

experiment			mortality caused by				
species	N	harvested	water stress	insects[1]	rodents[1]	unknown	little/no growth
ant exclusion							
C. nictitans	140	71.4	15.0	7.9	2.9	2.9	0
C. spectabilis	140	83.6	5.0	0.7	2.9	7.9	0
J. taminifolia	140	96.4	0.7	0	0	2.9	0
P. graminifolia	140	0	85.7	0	0	1.4	12.9
S. rhombifolia	140	68.6	18.6	1.4	5.7	5.7	0
ant substitution							
C. fasciculata	260	63.3	3.1	4.3	18.9	7.0	0
C. spectabilis	320	79.9	4.1	2.8	0	7.2	0
J. taminifolia	280	79.9	0	0.4	0	17.9	0
P. graminifolia	250	0	14.8	2.0	0	4.0	78.4
P. incarnata	220	0	18.6	1.4	0	5.7	68.6

abundance of a single ant species within a plot varied throughout the growing season. This variability of ant abundance and species distribution required use of the multiple regression analyses explained earlier.

In the ant exclusion experiment, fire ants were the most consistently trapped ants (Table 2). In the ant substitution experiment, mean fire ant abundance was less than the abundance of all other ant species collected (Table 2). However, fire ants were the most abundant single species (35.8% of all ants collected in pitfall traps), followed by Argentine ants (30.7%), and pyramid ants (21.7%). The remaining 11.8% was composed of mixed species (mostly *Pogonomyrmex*, *Crematogaster*, and *Paratrechina*). The dominant ants observed foraging on plants were also fire ants, Argentine ants and pyramid ants. Furthermore, these same three were the dominant species observed on the ground throughout the growing season.

The number of ants of any species observed foraging on the plants was low in both experiments regardless of the number of ants collected from pitfall traps (Table 2). The few workers observed on plants were usually pyramid ants, and they were found almost exclusively (99%) on *C. nictitans* and *C. fasciculata*. Additionally, the numbers of herbivores and spiders (the only common arthropod predator observed on plants) were low (Table 2). The most common herbivores observed included several species of short-horned grasshoppers (Acrididae), leafhoppers (Cicadellidae), beetle larvae, and two caterpillars (tiger moths [Arctiidae] and bagworm moths [Psychidae]). *Peucetia viridans* Hentz (Oxyopidae) was the most common spider observed on plants, and wolf spiders (Lycosidae) were the most common spiders collected in pitfall traps. Relatively few insects were observed on plants overall, but observations were conducted only once every three weeks at mid-day.

Few of the explanatory variables were correlated (Table 3). In the ant exclusion experiment, the number of herbivores observed on plants was positively correlated with the mean number of Argentine ants found on plants ($p<0.05$). In the ant substitution experiment, the amount of light reaching a plot was positively correlated with the mean number of fire ants collected in pitfall traps ($p<0.05$). The number of other ant species collected was not related to the light environment ($p>0.05$).   The amount of light was also negatively correlated with the mean number of herbivores observed on plants ($p<0.05$).

The level of co-linearity for all tests was within tolerance limits for regression analyses of

Table 2. Summary of explanatory variables (biotic and abiotic) measured in each experiment.

experiment			
variable	mean	range	std. dev.
ant exclusion			
fire ants in pitfall traps[1]	17.45	3.75 – 35.25	10.14
other ants in pitfall traps[1]	15.10	0.25 – 144.00	31.82
spiders in pitfall traps[1]	7.21	3.5 – 11.25	2.23
fire ants on plants[2]	0.01	0 – 0.33	0.04
other ants on plants[2]	0.01	0 – 0.67	0.04
herbivores on plants[2]	1.30	0 – 76.00	6.75
spiders on plants[2]	0.02	0 – 0.60	0.08
% total light reaching plot[3]	75.32	54.74 – 83.68	9.18
ant substitution			
fire ants in pitfall traps[1]	20.34	1.5 – 42.50	10.30
other ants in pitfall traps[1]	34.67	1.5 – 155.00	31.44
spiders in pitfall traps[1]	5.83	1.25 – 19.00	3.53
fire ants on plants[2]	0.13	0 – 5.67	0.52
other ants on plants[2]	0.42	0 – 14.83	1.28
herbivores on plants[2]	0.73	0 – 41.00	2.02
spiders on plants[2]	0.04	0 – 0.60	0.10
% total light reaching plot[3]	57.18	28.12 – 80.71	13.51

[1]mean number for each plot (4 trapping dates), [2]mean number for each plant (6 census dates), [3]estimation over growing season (May-October) based on hemispherical photos taken October 23 1997

Table 3. Pearson product-moment correlation coefficients (r) for explanatory variables. Values above the diagonal line are from the ant exclusion experiment, values below the diagonal line are from the ant substitution experiment. ***bold** values are significant (p<0.05 using Bonferroni's correction).

variable	fire ants[1]	pyr. ants[1]	Arg. ants[1]	spi-ders[1]	fire ants[2]	pyr. ants[2]	Arg. ants[2]	spi-ders[2]	herbi-vores[2]	light[3]
fire ants[1]		0.38	0.38	0.36	0.02	0.12	0.03	-0.06	-0.03	-0.08
pyr. ants[1]	0.18		-0.02	0.01	-0.02	0.01	0.30	-0.03	0.04	0.14
Arg. ants[1]	-0.35	-0.32		-0.23	0.01	-0.05	-0.02	-0.03	-0.06	-0.04
spiders[1]	0.16	0.08	-0.04		0.00	0.13	-0.01	0.04	0.08	0.03
fire ants[2]	-0.01	0.03	-0.08	0.01		-0.01	-0.01	-0.01	-0.01	-0.10
pyr. ants[2]	0.07	0.12	-0.08	0.00	0.40		-0.01	-0.01	-0.02	0.03
Arg. ants[2]	-0.06	-0.10	0.05	-0.03	0.05	0.11		-0.01	***0.33**	0.05
spiders[2]	0.01	0.02	0.04	0.01	0.00	0.17	0.12		-0.02	0.05
herbi-vores[2]	-0.04	-0.01	0.01	0.06	0.07	0.21	-0.02	-0.01		0.02
light[3]	***0.47**	0.03	-0.03	-0.13	-0.15	-0.06	-0.05	-0.01	***-0.23**	

[1]mean number in pitfall traps (4 trapping dates), [2]mean number on plants (6 census dates), [3]estimation of percent total light reaching a plot over growing season (May-October) based on hemispherical photos taken (October 1997)

herbivory, growth, and fecundity. All calculated condition numbers (SAS proc reg, SAS Institute 1985) ranged between 0-25, which were lower than the minimum cut-off point for concern (i.e., 30; Philippi 1993). Plots of residuals provided evidence that relationships were linear and interaction terms were not important.

4.3 Herbivory

The mean level of herbivory over the entire growing season was low for all species in both experiments (Table 4). In the ant exclusion experiment, mean percent tissue removed was highest for *S. rhombifolia*, less for *C. nictitans* and *C. spectabilis*, and lowest for *J. taminifolia*. In the ant substitution experiment, *C. fasciculata* had the highest mean tissue loss, *C. spectabilis* had less, and *J. taminifolia* was hardly eaten at all.

For all plant species in the ant exclusion experiment, the mean amount of leaf tissue removed was significantly related to fire ant density (Table 5), and regression slopes showed that herbivory declined as fire ant abundance increased (Figure 3a). For some plant species, herbivory was more strongly related to fire ant abundance than it was for other species. *Sida rhombifolia* had the steepest slope, while *J. taminifolia*, which had the lowest mean tissue loss of all species, had the flattest slope. The abundance of Argentine ants, pyramid ants, and insect herbivores did not have effects on the level of herbivory for any plant species ($p > 0.01$). For *S. rhombifolia*, herbivory was related to the amount of light reaching the plot (Figure 3b), and for both *C. nictitans* and *S. rhombifolia*, tissue removal was higher when spiders were abundant (Figure 3c).

The level of herbivory on plant species in the ant substitution experiment was not related to fire ant density, but for some species, it was related to other factors (Table 5). The mean proportion of tissue removal of *C. fasciculata* was positively related to the number of herbivores found on the plants (Figure 3d). For both *C. spectabilis* and *J. taminifolia*, the mean proportion of tissue removal was related to the amount of light reaching the plot, but the slope was steeper for *C. spectabilis* (Figure 3e). Light was both positively and negatively related to tissue removal depending on the species and the experiment (Figure 3).

Table 4. Means and standard errors for level of herbivory (mean % leaf tissue removed by insect herbivores over growing season), aboveground vegetative biomass harvested (g), and reproductive biomass harvested (g) for each species in each experiment.

experiment species	N	leaf tissue removed (%)		aboveground vegetative biomass (g)		reproductive biomass (g)	
		mean	S.E.	mean	S.E.	mean	S.E.
ant exclusion							
C. nictitans	100	9.54	0.55	11.43	0.73	11.33	0.80
C. spectabilis	117	7.02	0.35	24.77	1.45	15.37	1.12
S. rhombifolia	94	11.02	0.65	0.235	0.013	0.026	0.005
J. taminifolia	134	2.43	0.22	0.231	0.010	0.209	0.013
ant substitution							
C. fasciculata	164	8.31	0.65	6.10	0.43	3.95	0.33
C. spectabilis	255	6.85	0.25	12.36	0.60	5.46	0.46
J. taminifolia	223	1.35	0.09	0.090	0.003	0.068	0.004

Table 5. Relationships explaining level of herbivory (mean % leaf tissue removed by insect herbivores over growing season). Herbivory levels were arcsine transformed before analyses.

experiment species	N	explanatory variables	partial R^2	p-value	relationship
ant exclusion					
C. nictitans	100	fire ants[1]	0.15	0.0001	-
		spiders[1]	0.11	0.0002	+
C. spectabilis	117	fire ants[1]	0.26	0.0001	-
S. rhombifolia	94	fire ants[1]	0.16	0.0001	-
		spiders[1]	0.11	0.0003	+
		light[2]	0.09	0.0006	+
J. taminifolia	134	fire ants[1]	0.06	0.006	-
ant substitution					
C. fasciculata	164	herbivores[3]	0.06	0.002	+
C. spectabilis	255	light[2]	0.12	0.0001	-
J. taminifolia	223	light[2]	0.06	0.0002	-

[1]mean number in pitfall traps (2-4 trapping dates), [2]estimation of percent total light reaching plot over growing season (May-October) based on hemispherical photos taken in October 1997, [3]mean number on plants/g plant biomass (5 census dates)
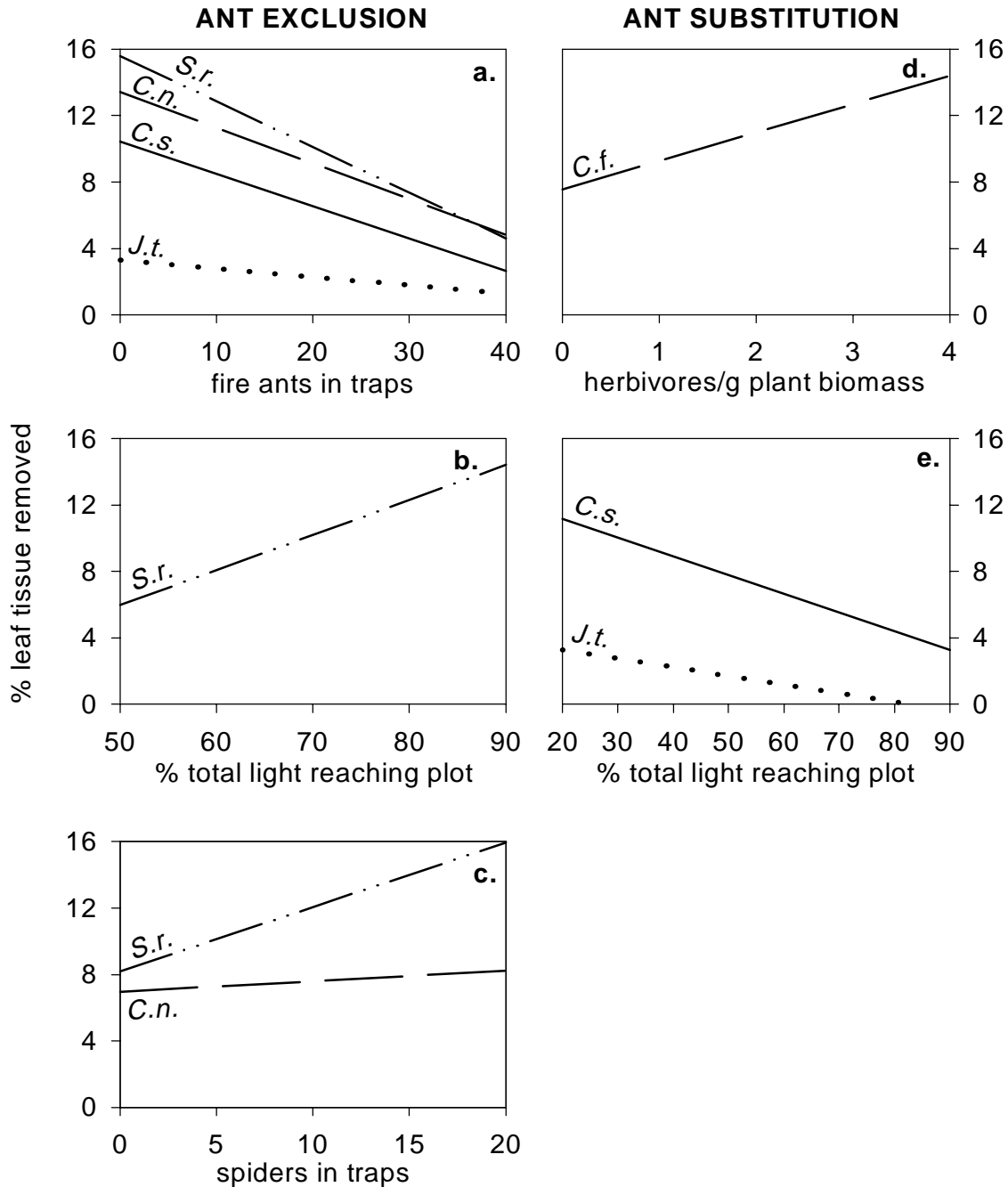
Figure 3. Significant explanatory variables (mean abundance or light, p<0.01) and their predicted impact on foliar herbivory. Lines for species not shown were not significant (p>0.01). Plots show results from the ant exclusion experiment (a-c) and the ant substitution experiment (d-e). Lines are labeled *S.r.* for *Sida rhombifolia*, *C.n.* for *Chamaecrista nictitans*, *C.s.* for *Crotalaria spectabilis*, *J.t.* for *Jacquemontia taminifolia*, and *C.f.* for *Chamaecrista fasciculata*.

4.4 Growth

Separate analyses of various growth parameters (stem weight, leaf weight, leaf area, total stem length, and basal diameter) produced results similar to those of total aboveground vegetative biomass (g dry wt of stem+leaves). Therefore, I present results for total, aboveground vegetative biomass only. Overall, the aboveground vegetative biomass within a single plant species did not vary greatly within each experiment (Table 4). In both experiments however, the existing variation was largely unexplained by the variables tested (i.e., note the low R^2 values in Table 6).

In the ant exclusion experiment, relationships between spiders and aboveground vegetative biomass had opposite slopes for *C. spectabilis* and *J. taminifolia* (Figure 4b and c). Pyramid ant abundance was negatively related to the growth of *S. rhombifolia*, and fire ant abundance was negatively related to the growth of *J. taminifolia*. Overall, however, ant or spider abundance explained only a small amount of the variation in plant growth (Table 6). For *C. nictitans*, growth was not significantly related to any of the variables measured (p>0.01).

In the ant substitution experiment, the number of pyramid ants collected in pitfall traps had a positive relationship with the growth of *C. fasciculata*, but the number of fire ants on the plants had a negative relationship with plant growth (Figure 4d and e). Herbivore abundance was negatively related to growth of *C. spectabilis* and light was positively related to it (Figure 4e and f). Biomass of *J. taminifolia* was not significantly related to any of the variables (p>0.01).

4.5 Fecundity

I analyzed fruit number, fruit weight, seed number, seed weight, the number of fruits eaten by insects, and the number of seeds eaten by insects separately. Results were either non-significant or identical to those obtained when I grouped all reproductive material together, so I will report results for reproductive biomass (g dry wt of fruit+seeds) only. Most of the plants produced reproductive material (Table 4). Insect abundance explained some of the variation in the amount of reproductive biomass produced in one species in the ant exclusion experiment and one species in the ant substitution experiment, but R^2 values were low (Table 7). In the ant exclusion experiment, regression slopes for *J. taminifolia* showed a negative relationship

Table 6. Relationships explaining aboveground vegetative plant biomass (g).

experiment species	N	explanatory variables	partial R^2	p-value	relationship
ant exclusion					
C. nictitans	100	none			
C. spectabilis	117	spiders[1]	0.06	0.008	-
S. rhombifolia	94	pyramid ants[2]	0.10	0.002	-
J. taminifolia	134	fire ants[2]	0.05	0.006	-
		spiders[2]	0.05	0.006	+
ant substitution					
C. fasciculata	164	fire ants[1]	0.07	0.001	-
		pyramid ants[2]	0.06	0.001	+
C. spectabilis	255	herbivores[1]	0.05	0.0002	-
		light[3]	0.03	0.006	+
J. taminifolia	223	none			

[1] mean number on plants/g plant biomass (5-6 census dates), [2] mean number in pitfall traps (2-4 trapping dates), [3] estimation of % total light reaching plot over growing season (May-October) based on hemispherical photos taken in October 1997
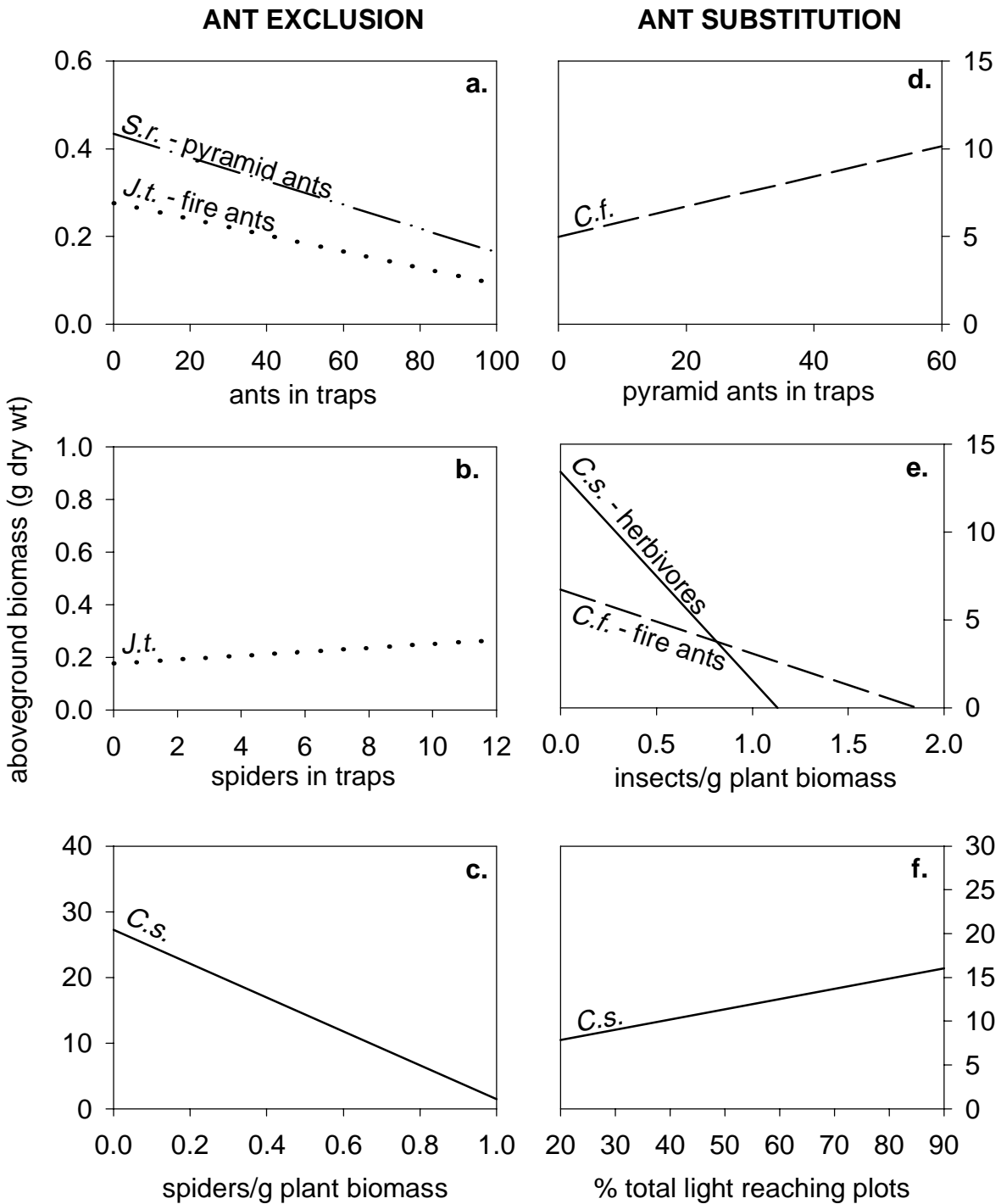
Figure 4. Significant explanatory variables (mean abundance or light, p<0.01) and their predicted impact on aboveground vegetative plant biomass. Lines for species not shown were not significant (p>0.01). Plots show results from the ant exclusion experiment (a-c) and the ant substitution experiment (d-f). Lines are labeled *S.r.* for *Sida rhombifolia*, *C.s.* for *Crotalaria spectabilis*, *J.t.* for *Jacquemontia taminifolia*, and *C.f.* for *Chamaecrista fasciculata*.

Table 7. Relationships explaining reproductive biomass (g).

experiment species	N	explanatory variables	partial R^2	p-value	relationship
ant exclusion					
C. nictitans	100	none			
C. spectabilis	117	none			
S. rhombifolia	94	none			
J. taminifolia	134	fire ants[1]	0.08	0.002	-
		spiders[1]	0.06	0.004	+
ant substitution					
C. fasciculata	164	none			
C. spectabilis	255	herbivores[2]	0.03	0.008	-
J. taminifolia	223	none			

[1]mean number in pitfall traps (2-3 trapping dates), [2]mean number on plants/g plant biomass (6 census dates)

between fire ant density and reproductive biomass, and a positive relationship between spiders and reproductive biomass (Figure 5a). For *C. nictitans*, *C. spectabilis*, and *S. rhombifolia*, significant relationships did not exist (p>0.01). In the ant substitution experiment, fecundity of *C. spectabilis* was negatively related to the abundance of insect herbivores found on the plants (Figure 5b); fecundity for *C. fasciculata* and *J. taminifolia* was not significantly related to any explanatory variables (p>0.01).

4.6   Split data tests

For herbivory, split data tests were in agreement with the full data models; i.e., fire ants had a significant, negative impact on percent plant tissue consumed. When each half of the random data was compared, 95% confidence interval estimates for slope parameters overlapped in all cases except one: the number of fire ants in pitfall traps for *J. taminifolia* in the ant exclusion experiment. Furthermore, significant models generated from one half of the data were the same as those identified using the full data (i.e., those listed in table 5) for all species in both experiments.

For growth, the split data tests were in less agreement with the full data models, but they support the result that variation in aboveground vegetative biomass was largely unexplained for any species. When each half of the random data was compared, confidence interval estimates for slope parameters overlapped in three cases: *J. taminifolia* (ant exclusion), *C. fasciculata* (ant substitution) and *C. spectabilis* (ant substitution). They did not overlap for *S. rhombifolia* or *C. spectabilis* in the ant exclusion experiment. Significant models generated from one half of the data were quite different from those generated using the full data (i.e., those listed in table 6). Models for *S. rhombifolia* and *C. spectabilis* contained completely different explanatory variables, and the model for *C. spectabilis* contained only herbivores.

For fecundity, the split data tests were in agreement with the full data models in that measures of arthropod abundance and light did not have significant impacts on the reproductive biomass of most plants. When each half of the random data was compared for *J. taminifolia* (ant exclusion experiment), confidence interval estimates for slope parameters overlapped. Furthermore, a significant model generated from one half of the data was the same as that identified using the full data (i.e., listed in table 7) for *J. taminifolia*. No other fecundity

ANT EXCLUSION

ANT SUBSTITUTION
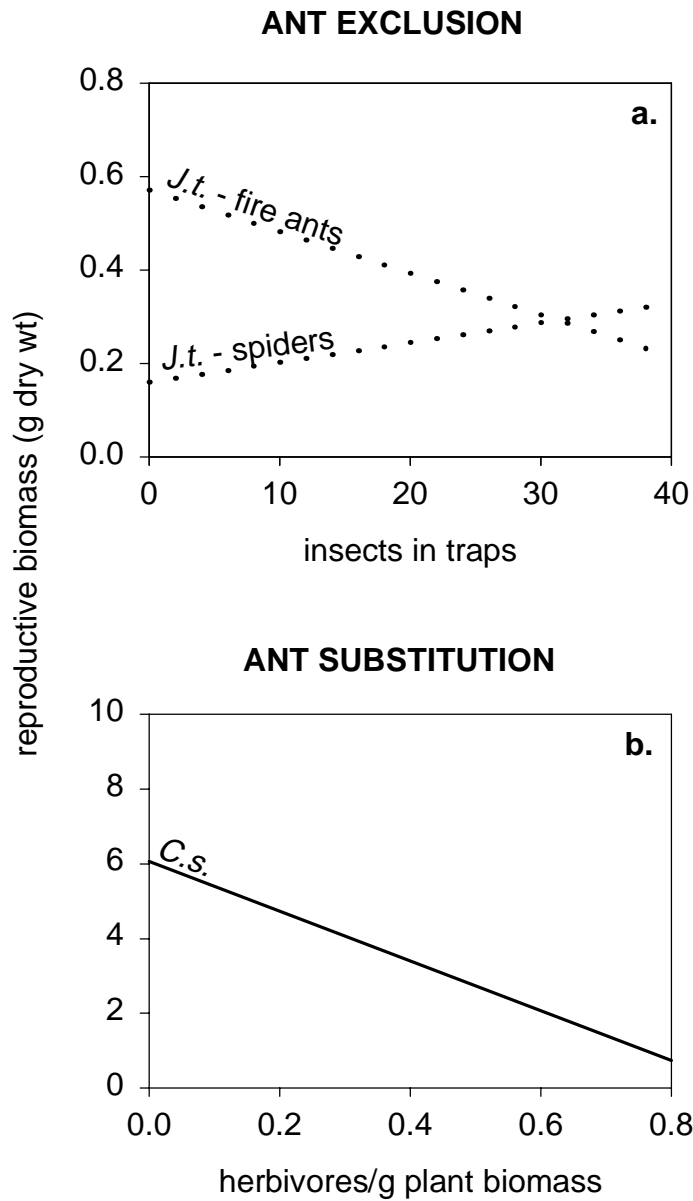
Figure 5. Significant explanatory variables (mean abundance, p<0.01) and their predicted impact on reproductive biomass. Lines for species not shown were not significant (p>0.01). Plots show results from the ant exclusion experiment (a) and the ant substitution experiment (b). Lines are labeled *J.t.* for *Jacquemontia taminifolia* and *C.s.* for *Crotalaria spectabilis*.

models generated using one half of the data were significant (p>0.05), and they cannot be compared.

5. DISCUSSION

My results suggest that fire ants exert top-down control on the second trophic level. In the ant exclusion experiment, fire ants were important in determining the level of folivory; tissue removal by insects increased when the number of fire ants within a plot decreased. I did not see a direct reduction in the number of insect herbivores present on the plants when fire ants were abundant, but the number of insects that I observed was low on all plants. Based on the limited abundance and diversity found during my census, I do not feel that I observed the entire insect herbivore community. Furthermore, fire ants forage both on the ground and in the vegetation (Tedders et al. 1990), and they consume insects as eggs, larvae, pupae and adults. My observations were focused on the clearly visible portions of the plants, and with the exceptions of a few caterpillars and beetle larvae, I observed mostly adult forms. I hypothesize that fire ants interacted with portions of the insect community that I did not observe.

Fire ants produced a visible effect on folivory, but the effect was not strong enough to cascade and strongly impact the plant community. For true top-down cascades, plant growth and fitness must change relative to predator abundance (Power 1992, Strong 1992, Menge 1995). Plant biomass and seed production remained largely unaffected by the density of fire ants in my experiments. Similar results (i.e., effects on herbivores but not on primary producers) have been documented for fire ants in agricultural fields (Ali et al 1984, Reagan 1986, Tedders et al 1990) and for a native fire ant, *S. geminata*, in squash fields.

The lack of evidence for a cascade in my study probably stems from the low levels of herbivory observed. Plant growth and fecundity are often not negatively affected by low or moderate tissue removal (Belsky 1986). Mean herbivory levels ranged from 1–11%, and were low compared with levels previously reported for our study species (Barton 1986, Gillett et al. 1991). These low levels suggest that there were not many insect herbivores of these plant species present in the community and that other predators, which I did not attempt to eliminate, still had an effect in areas where fire ant density was low. For a cascade to occur, the interaction between insect herbivores and plants must be strong (Spiller and Schoener 1990), and in my study, the interaction appeared to be relatively weak.

Despite their inability to improve plant productivity for my study species, fire ants may still be a keystone predator in these early-successional forest gaps. Keystone predators may be defined as consumers that reduce the number of individuals or species within a trophic level and have large effects on community composition (Risch and Carroll 1982). My results show that, not only do fire ants interact strongly with insect herbivores, their effect is stronger than that of other predaceous ant species present in the gap. Pyramid ants had some weak and inconsistent relationships growth, but it is not clear whether the interactions were direct, indirect, or behavioral. Argentine ant abundance was not related to plant response for any species. Like fire ants, Argentine ants are invasive generalists, and they have been shown to have strong interactions with other arthropods (Majer 1994, Human and Gordon 1996). Argentine ants were abundant in my study site, but I saw no evidence of such effects. The stronger effect of fire ants that I observed may have resulted from higher fire ant density in my study site. The abundance of Argentine ants collected in pitfall traps was large, but unlike fire ants, Argentine ants often contaminated individual traps with extremely high numbers when traps were adjacent to their nests. This may have skewed my estimate of their overall mean abundance. Based on observations of colony density and presence of ant foragers, I feel that Argentine ants were distributed patchily throughout the site and probably had a limited range for potential effects. In contrast, the distribution of fire ant foragers appeared much more even. Within the assemblage of ants in my study site, fire ants had the strongest control over the insect herbivores that consumed my plants and are therefore key determinants of herbivore abundance in my early-successional community.

The presence of many weak and inconsistent relationships (Tables 6 and 7) may indicate a relatively complex web of different kinds of interactions (e.g., direct, indirect, predatory, competitive, or behavioral). Fire ants and pyramid ants have been shown to have some direct interactions with plants. For example, they tend aphids and other insects for honeydew (Smith 1965, Tedders et al 1990) and they consume extrafloral nectar (Kelly 1986, Barton 1986). In addition to possibly interacting with plants, ants may have interacted with insect predators that I did not observe in abundance but still may have influenced my model (Figure 1) more than I originally predicted (e.g., ladybugs, Wilson and Oliver 1969). Ants, spiders or herbivores may have been attracted to plants of different sizes for nutritive, foraging, defensive, or other behavioral reasons. Additionally, arthropods and plants may have both been responding, either

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directly or inversely, to microsites of abiotic variables (e.g., moisture). Because of the myriad of complex linkages and indirect effects possible in this early-successional community, it is difficult to predict which interactions led to the weak relationships observed between arthropods and plant growth and fecundity.

Plant species had differential responses to insect abundance (Figures 4, 5, and 6). Because of extrafloral nectaries, I expected the relationship between ants and the two *Chamaecrista* species to be stronger than those of the other plant species tested. Relationships, especially those for herbivory, existed between ants and *Chamaecrista*, but they did not explain more of the variation than they did for other plant species. Ants foraging on plants were found almost exclusively on *Chamaecrista* in both experiments, and all three dominant ant species in the community were observed at nectaries. However, again because of the paucity of herbivores, ant presence did not translate into more protection from herbivory for these species compared to those without nectaries. Fire ants were not often observed on plants which suggests that fire ants limited the herbivore population at several levels (e.g., on the ground, on other plants) and this effect translated into overall protection for many species in the area rather than protection for distinct individuals.

Site productivity may determine the strength of top-down control (Oksanen et al. 1981, Stiling and Rossi 1997). In our study, greater productivity at the ant exclusion gap may explain the differences in results between the two experiments. Within the same species (*C. spectabilis* and *J. taminifolia*), plants in the ant exclusion experiment grew larger and produced more fruit than they did in the ant substitution experiment (i.e., note differences in means for aboveground and reproductive biomass in Table 5, p<0.0001 using a two-sample t-test). Additionally, after heavy rains, water pooled in the ant exclusion site while the ant substitution site remained drier, suggesting that plants in the ant exclusion side had access to more water throughout the growing season. Vegetation patterns also differed between sites: vegetation was dense and grassy in the ant exclusion area and it ranged from grassy to pine needles to relatively bare sand in the ant substitution area. Productive sites with dense vegetation support larger insect herbivore populations and provide better foraging for fire ants over smaller areas (Ali et al. 1984, Showler et al. 1989). My apparent productivity gradient may have concentrated, and therefore strengthened, the top-down control by the fire ant on folivory in the ant exclusion experiment.

My study does not support the hypothesis that fire ants exert top-down control that cascades to some plant species within this tritrophic community. My study does, however, support previous work that has demonstrated a strong interaction between fire ants and primary consumers. Furthermore, interactions between the invasive fire ant and other secondary consumers in the system do not limit the fire ants' ability to interact strongly with insect herbivores. The lack of an apparent cascading effect on the plant community in my study most likely results from a weaker top-down interaction between the primary consumers and the primary producers than has been demonstrated for other early-successional communities (Brown et al. 1988). Without that strong interaction present, plant growth and fitness are more strongly determined by bottom-up forces than by pressure from above. *Solenopsis invicta* is notorious for its invasibility and arthropod community dominance. It possesses many attributes that would make it a successful candidate for top-down, cascading control. However, although I should continue to be concerned about its ability to negatively impact the arthropod community as a keystone predator, I find no evidence to suggest that I should be concerned about its influence on early-successional plant community composition.

6. ACKNOWLEDGEMENTS

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