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Short-term dynamics of an acacia ant community in Laikipia, Kenya

Received: 24 June 1999 / Accepted: 3 December 1999

Abstract In monospecific stands of *Acacia drepanolobium* in Laikipia, Kenya, virtually all but the smallest trees are occupied by one of four species of ants. Although trees are a limiting resource, all four ant species are maintained in this system. Three separate lines of evidence confirm a linear dominance hierarchy among these four ants: (1) experimentally staged conflicts, (2) natural transitions among 1773 tagged trees over a 6-month period, and (3) the average sizes of trees occupied by ants of different species. Short-term dynamics during a drying period reveal that many smaller trees (<1 m) occupied by dominant ants were subsequently abandoned, and that abandoned trees had grown more slowly than those that were not abandoned. Height growth increments over 6 months were generally independent of ant occupant, but increased with tree height. Among taller trees (>1 m), changes in ant occupation congruent with the dominance hierarchy (i.e., transitions from more subordinate ant species to more dominant ant species) occurred on trees that grew faster than average. In contrast, the (less frequent) changes in ant occupation “against” the direction of the dominance hierarchy occurred on trees that grew more slowly than average. Observed correlations between tree vigor and takeover

direction suggest that colony growth of dominant ant species is either favored in more productive microhabitats, or that such colonies differentially seek out healthier trees for conquest. Colonies of dominant species may differentially abandon more slowly growing trees during (dry) periods of retrenchment, or suffer higher mortality on these trees. Subordinate ant species appear to move onto these abandoned trees and, to a lesser extent, colonize new recruits in the sapling class. These data reveal that within a simple linear dominance hierarchy, short-term variations exist that may reveal underlying mechanisms associated with coexistence.

Key words Species coexistence · Dominance hierarchy · *Acacia drepanolobium* · *Crematogaster* · *Tetraponera*

Introduction

Unraveling the mechanisms underlying species coexistence remains a central goal for ecology, and is a crucial link for our understanding how biodiversity is maintained. At broad spatial scales, coexistence of potentially competing species may readily be explained by geographic separation, or by large-scale gradients such as climate, productivity, or resources (Ricklefs and Schluter 1993). More vexing is how a number of competitors can coexist at smaller spatial scales while sharing a limited resource (Hutchinson 1961). Theoretical approaches to this question have included both conceptual (e.g., Connell 1978) and mathematical (e.g., Chesson 1986) models, and empirical studies have addressed species coexistence in laboratory, mesocosm, and field settings (reviewed in Tokeshi 1999).

Despite this rich literature, we are still far from a consensus on the relative importance of different factors in promoting species coexistence (e.g., spatial structure; reviewed in Tilman and Kareiva 1997), or even agreement on the specific mechanisms for coexistence in well-studied systems (e.g., Tilman 1999). In part, this problem stems from the complexity of many natural systems, for

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which long-term, large-scale studies (e.g., Hubbell et al. 1999) may be necessary to elucidate the mechanisms underlying coexistence. Other studies have focused on simpler, more tractable systems (e.g., tree hole communities: Schreiber et al. 1988; Fincke 1992; freshwater rock pool communities: Pajunen 1986; Pajunen and Pajunen 1993; Laurila 1998), but these systems are often very minor ecosystem components. Powerful generalizations about species coexistence will emerge from studies of systems that are widespread, important to ecosystem function, yet reasonably tractable.

We have initiated a long-term study of a system that provides unique opportunities to examine the nature of species coexistence. The acacia-ant community occurring on *Acacia drepanolobium* trees in East Africa (Young et al. 1997) is in many ways an ideal study system for research on species coexistence. (1) The species richness (four) is simple enough for explicit analysis, but complex enough for more general tests of theory. (2) There is a clearly defined shared limiting resource in the form of swollen-thorn acacia trees. (3) As all four ants are specialists, these acacia trees represent a critical resource to which success of an ant colony is explicitly tied. (4) The system is readily amenable to both experimental manipulation and large-scale, long-term descriptive studies. (5) *A. drepanolobium* dominates millions of hectares of semiarid highland in East Africa, and its ant associates comprise a large proportion (>25%) of the animal biomass in these ecosystems (Hocking 1970).

We report here on an initial set of competition experiments, and 6 months of ant occupancy dynamics in 1773 permanently tagged trees. These short-term data include both patterns that are consistent with equilibrium coexistence, and non-equilibrium community dynamics that reveal underlying mechanisms of species interactions.

Materials and methods

Study site and species

This research was carried out at the Mpala Research Centre in Laikipia, Kenya. Although rainfall averages 500–600 mm/year, the year previous to the start of the study (1997–1998) was one of the wettest on record (>1200 mm). The study plots are located at an elevation of 1800 m above sea level (0°17' N, 37°52' E). The vegetation at the study plots is *A. drepanolobium* bushed grassland, characteristic of heavy clay “black cotton” soils of impeded drainage (Ahn and Geiger 1987; Taiti 1992). The dominant tree, *A. drepanolobium*, accounts for >95% of the woody vegetation (Young et al. 1997, 1998). The understory is dominated by five species of grasses. Further details of the study ecosystem can be found in Young et al. (1998).

A. drepanolobium is a small tree defended by stipular spines (Young 1987; Milewski et al. 1991; Young and Okello 1998), symbiotic ants (Madden and Young 1992; Young et al. 1997), and perhaps leaf chemistry (D. Ward and T.P. Young, unpublished data). Its population size structure is L-shaped, implying healthy recruitment (Young et al. 1997, 1998). A pair of straight sharp spines is produced at each node. Approximately 1 node out of every 10–20 has a swollen structure up to 5 cm in diameter, located at the base of the spine pair, that usually houses resident ants that feed in part from extrafloral nectaries at the leaf bases (Hocking 1970; Young et al. 1997). Virtually all trees more than 1 m tall

have a single resident ant colony, although the colony may occupy multiple trees.

Four ant species are common residents on these trees (Young et al. 1997; Stanton et al. 1999). Vouchers of all ant species found in this system have been examined by Phil Ward of the University of California at Davis and are on deposit there. *Crematogaster* is a difficult and diverse genus currently under review, and our specimens have been assigned provisional designations (P. Ward, personal communication). The following summary is based on Young et al. (1997), Stanton et al. (1999), and personal observation.

Crematogaster mimosae Santschi is the most common resident ant species. It actively defends the tree, especially at the young shoots. It also tends scale insects both inside the swollen thorns and on the undersides of young branches. *C. sjostedti* Mayr is less active when disturbed. Uniquely among the four ants, it does not raise brood inside the swollen thorns, preferring cavities of dead wood on older plant parts or on the ground around the bases of trees. Nonetheless, it defends its trees against the other three ant species. It tends scale insects, and is tolerant of a variety of other insects and epiphytes. *C. nigriceps* Emery is a more active ant. It has the peculiar behavior at our study site of removing virtually all axillary buds except at swollen thorns, effectively sterilizing the tree. This and the next species are most common on smaller trees. *Tetraponera penzigi* Mayr is slow to respond to disturbance, but is the only species with a (painful) sting. It eats the extrafloral nectaries on its leaves, and the swollen thorns on its trees have entry holes that are smaller (and more numerous) than for the *Crematogaster* spp., which must widen them to gain entry.

Experimentally staged conflicts

We staged conflicts for all six possible pairwise combinations of the four ant species. For each species combination, we located 10–12 pairs of adjacent trees, matched for similar height and canopy volume, and occupied by the appropriate species. We then pulled individual branches on each tree toward the other, and tied them together using steel wire. A total of 63 tree pairs were tied together. We then revisited each tree pair at 24-hour intervals for 3 days, then at 1-month intervals for the next 2 months, and afterwards at 2-month intervals for the next 10 months. At each resurvey, we noted whether active conflict was occurring at the point of canopy contact, and whether either ant species had partially or completely taken over the opponent's tree. Partial takeovers were scored when we found workers of one species patrolling branch systems and occupying some but not all swollen thorns on the opponent's tree. Complete takeovers were scored when only a single ant species could be found on branches and within swollen thorns on both trees. A tie was scored where no continuing conflict between ant species was observed on the focal trees, and no encroachment by either ant onto the competitor's tree was noted. At the end of the 12-month experiment, all conflicts had either resulted in complete takeovers or ties.

Census of trees

In January and February 1998, we established five permanent, 200-m transects within the study area. We marked the beginning of each transect with a short post, and its position was recorded with a portable GPS by taking ten readings at 1-min intervals, and averaging them. Additional posts were placed regularly along the transect line, whose compass direction was recorded. Every tree found within 10 m of each of these transect lines was measured to the nearest 10 cm, and its ant occupant (if any) was identified. Although locating shorter trees was hampered by the tall grass at the time, this survey represents a complete sample of trees >0.5 m tall.

Stratified sample of trees for long-term monitoring

We also permanently tagged 1773 individual *A. drepanolobium* trees along these transects. We defined five ant occupancy states

(uninhabited, *T. penzigi*, *C. nigriceps*, *C. mimosae*, *C. sjostedti*) and five tree size classes (height <0.50 m, 0.50–0.99 m, 1.00–1.49 m, 1.50–2.99 m, ≥3.00 m). There were therefore 25 possible combinations of tree size and ant occupant. We attempted to tag at least 100 trees for each combination. However, some of these combinations were rare (e.g., taller trees occupied by *T. penzigi* or *C. nigriceps*, or uninhabited). Permanently tagged trees were generally within 20 m of the transect line.

The sampling was stratified in two additional ways. First, we sampled similar numbers of ant/tree combinations along each of the five transects. Second, the tagged trees were further spatially stratified within transects, so that abundant ant/tree combinations were not concentrated at the beginnings of individual transects.

Each reference tree was scored for species of ant occupant, and its height was initially measured to the nearest 5 cm for smaller trees and 10 cm for taller trees. Cartesian coordinates were recorded with respect to the marked transect line, and maps were made to facilitate relocation of the trees.

In July–August 1998, the tagged trees were resurveyed for height (now measured to the nearest centimeter for all trees) and species of ant occupant. Whenever there was a change in the species of ant occupant, or a large change in tree height, the tree was carefully rechecked to ensure accuracy. Although intraspecific transitions among colonies may occur on trees, we were unable to detect them.

Statistical analyses

All data were analyzed using standard parametric statistical tests in JMP (SAS 1996). All growth data were log ($x+1$) transformed for parametric analyses, except where indicated in the text. All figures show untransformed growth data. We tested for homogeneity of variances among samples using the Brown-Forsythe test for unequal variance. Post hoc multiple comparisons were made using Tukey's post hoc methods.

Results

Experimentally staged conflicts

With the exception of staged conflicts involving *T. penzigi*, battles between adjacent colonies ensued immediately following the connection of tree canopies. *Crematogaster* spp. rapidly recruited to the point of canopy contact, waving their abdomens and releasing a pungent alarm pheromone. Within minutes, workers from all parts of the tree were in a high state of activity, and hundreds of workers occupied the branches that were tied together. When heterospecific workers met, they immediately began biting and spraying/stinging one another with their gasters, usually falling off the tree together in a tightly entwined grip. Approximately half the time that workers fell, they separated on landing and returned to their respective trees. In remaining conflicts, workers

either continued fighting to the death, or separated, but were too badly wounded to return to the tree and subsequently died. Intense fighting between colonies often occurred for several days.

Staged conflicts involving *T. penzigi* were considerably less dramatic. While *Crematogaster* spp. workers temporarily moved onto *T. penzigi*-occupied trees, almost three-quarters of these conflicts ended in ties. In encounters, *T. penzigi* workers would assume a prostrate posture and freeze. After several seconds of antennal contact of the *T. penzigi* ant by the *Crematogaster* ant, the latter would move on, and the former would then resume activity. After several minutes of forays onto the *T. penzigi*-occupied tree, *Crematogaster* spp. ants usually returned to their own trees, and were rarely noted making subsequent forays. Ties were omitted from further analysis in this study.

We generated a hierarchy in competitive dominance by constructing a dominance matrix that minimized the number of competitive reversals (numbers below the diagonal, see Lehner 1979 and Isbell and Pruetz 1998). Our measure of dominance is akin to Schoener's (1983) behavioral dominance, where dominant species prevail in interspecific encounter competition due to superior fighting and/or recruitment ability (Davidson 1998). In the resultant putative competitive hierarchy among the four ant species, *C. sjostedti* was the most dominant, followed by *C. mimosae*, *C. nigriceps*, and *T. penzigi* (Table 1). Eighty-four percent of observed transitions in experimental conflicts were consistent with this hierarchy.

Outcomes of 30% of experimental conflicts were determined within 3 days of initiation. Of these rapidly determined conflicts, 73% were won by *C. sjostedti*, and the remainder by *C. mimosae*, both competitively dominant species. Increases in takeover rates corresponded with the onset of the short rains in early October 1998 (Fig. 1). Competitive outcomes were never reversed during the 1-year observation period for experimental trees. After 1 year, trees were monitored for another 3 months, during which no further changes in outcome were noted.

Survey data

Relative abundances of the four ant species on trees differed from one another and varied with tree height. Figure 2 shows the relative abundances of different ants on 4141 trees of different heights, but over 0.5 m tall. This survey differed from a similar survey done in 1993

Table 1 Winners and losers from experimentally staged conflicts. Trees used in these experiments ranged from 1.0 to 3.5 m in height ($n=8-12$ per ant species pair). Conflicts resulting in ties are not shown here

Winner	Loser				Total wins
	<i>C. sjostedti</i>	<i>C. mimosae</i>	<i>C. nigriceps</i>	<i>T. penzigi</i>	
<i>C. sjostedti</i>	–	11	8	2	21
<i>C. mimosae</i>	0	–	7	2	9
<i>C. nigriceps</i>	0	3	–	1	4
<i>T. penzigi</i>	2	1	0	–	3

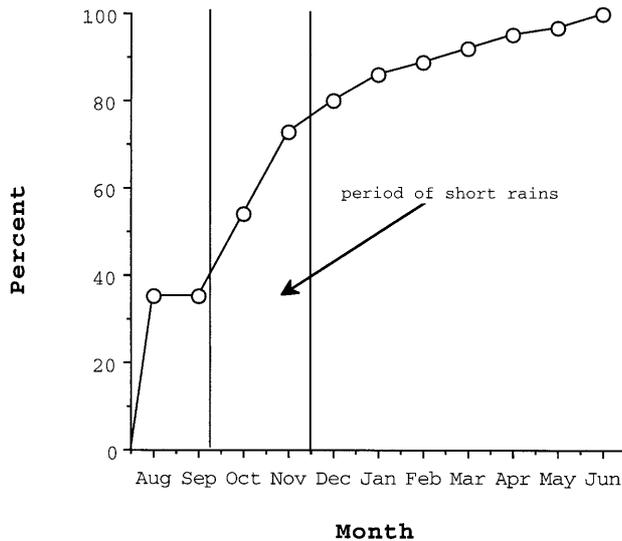


Fig. 1 The cumulative proportion of total resolved conflicts won over the course of a 1-year competition experiment, beginning August 1997, and ending June 1998. Vertical bars denote timing and duration of short rains

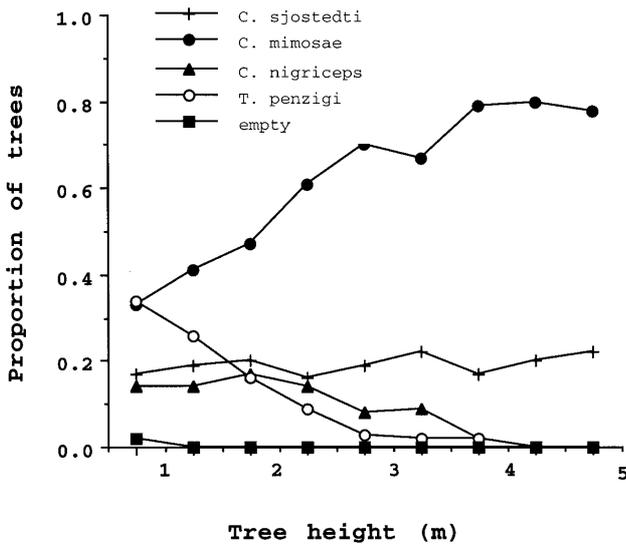


Fig. 2 The relative abundances of different ant species on randomly sampled *Acacia drepanolobium* trees of different heights ($n=4141$ trees total)

in the same area (Young et al. 1997). First, the 1993 survey included trees <0.5 m. Second, in the 1998 survey, far fewer taller trees were occupied by *C. sjostedti*.

Relationships among tree growth, tree height, and ant occupant

The proportion of trees that we were unable to relocate declined steeply with tree height. We were able to locate almost all tagged trees taller than 0.6 m. The proportion of located trees that died between February and August 1998 also declined steeply with tree height. Mean mor-

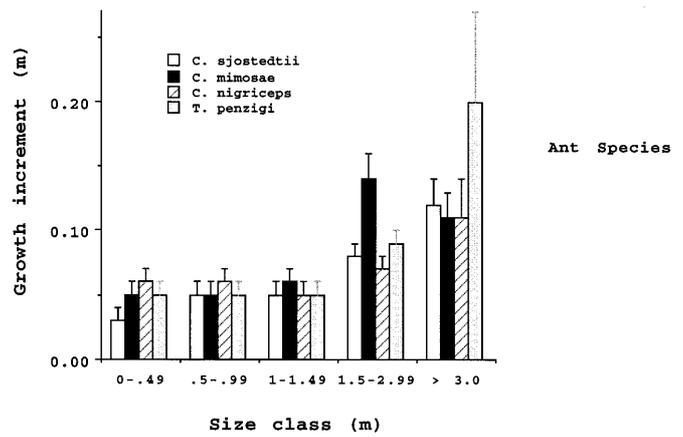


Fig. 3 Average growth increments of *A. drepanolobium* trees in five size classes with different ant occupants. Error bars show SEs for height growth over a 6-month interval. There were only three trees over 3 m tall that were occupied by *Tetraponera*. Otherwise, sample sizes ranged from 21 to 103 (median 93)

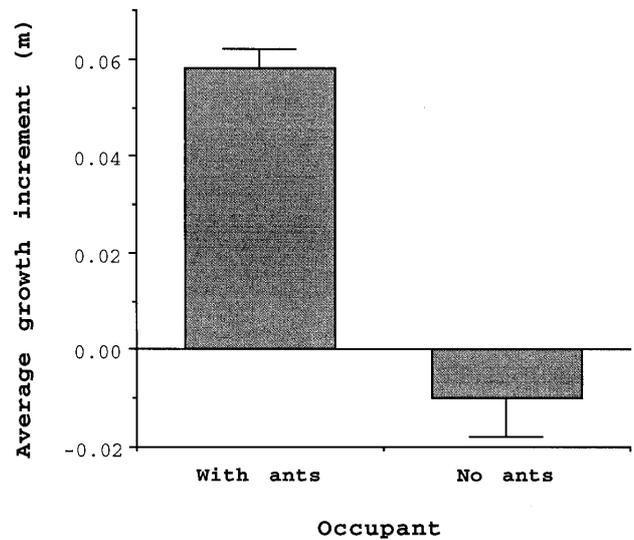


Fig. 4 Average growth increment for continually occupied ($n=651$) vs uninhabited ($n=126$) *A. drepanolobium* trees in size classes 1 and 2. Continually occupied trees were defined as trees occupied by ant colonies at both the initial and 6-month surveys. Uninhabited trees are defined as trees that were vacant at the time of both surveys. Error bars show SEs

tality across trees of all size classes was 0.8% over this 6-month period, and 0.5% for trees taller than 1.0 m. Average height growth increments were similar in the first three size classes, but increased strongly in trees >1.5 m tall (Fig. 3).

Changes in tree height growth over 6 months were strongly influenced by tree height, but did not depend upon the species identity of the ant occupant. To decouple the influence of these two variables on tree height growth, we analyzed growth increments of 1338 occupied trees that did not undergo interspecific ant transitions using ANCOVA with tree height in January 1998 as the covariate. Change in height over 6 months was

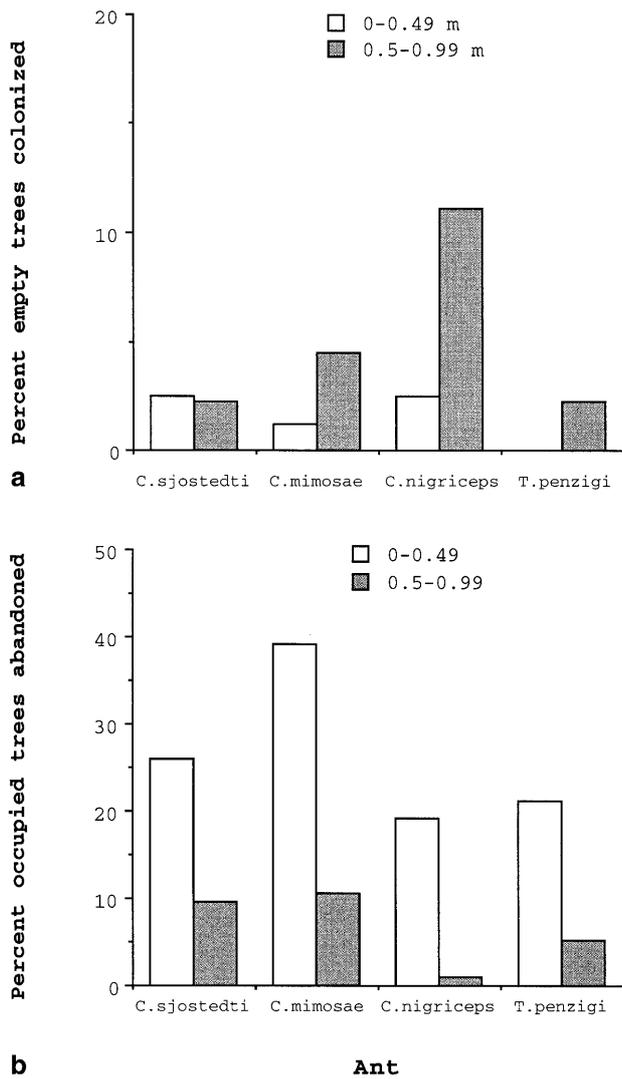


Fig. 5 **a** Percentage of initially vacant trees in size classes 1 and 2 colonized by ants after 6 months. Sample sizes are 81 and 45 for size class 1 and 2, respectively. **b** Percent of initially occupied trees in size classes 1 and 2 abandoned after 6 months. Sample sizes for size class 1 are 77, 84, 57, and 80, and for class 2 are 94, 95, 97, and 97 for *C. sjostedti*, *C. mimosae*, *C. nigriceps*, and *T. penzigi*, respectively

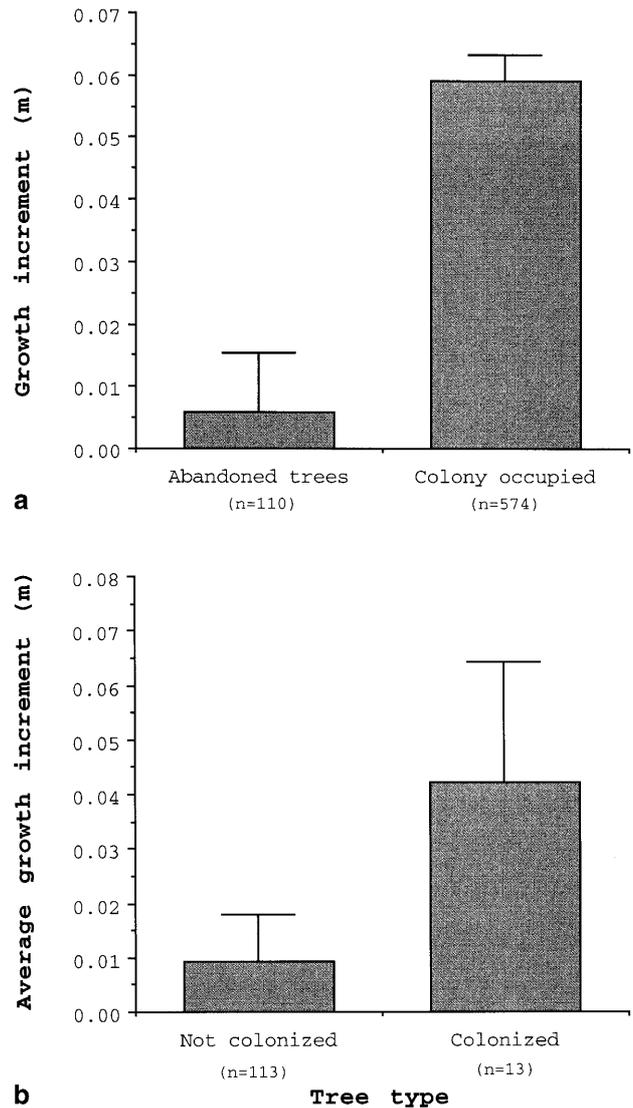


Fig. 6 **a** Average (+SE) growth increments for initially occupied trees in size classes 1 and 2, where trees were abandoned ($n=110$) or retained ant colonies ($n=574$) over a 6-month period. **b** Average (+SE) growth increments for initially vacant trees in size classes 1 and 2, where trees were colonized ($n=13$) or remained uninhabited ($n=113$) over a 6-month period

significantly greater in taller trees ($F=17.28$, 1 *df*, $P<0.0001$), but was similar across different species of ant occupant ($F=1.32$, 3 *df*, $P=0.26$). There was no significant interaction between tree height and ant occupant ($F=1.27$, 3 *df*, $P=0.28$).

Growth of uninhabited versus ant-occupied trees

Changes in tree height over a 6-month period were correlated with the presence or absence of ant occupants. Fewer than 1% of *A. drepanolobium* trees at our study site were unoccupied at the time of the first survey. While we were able to locate and tag 81 vacant trees in size class 1, and 42 trees in size class 2, uninhabited

trees in larger size classes were extremely rare. Thus, we present only growth rate data for uninhabited trees in the smallest two size classes (<1.0 m). On these small trees, growth increments were significantly higher for ant-occupied than for uninhabited trees (Fig. 4; ANOVA $F_{1,683}=44.27$, $P<0.0001$). In contrast, uninhabited trees decreased in height over the 6-month period, on average, probably through stem breakage from trampling or tissue removal by browsers.

Colonization and abandonment of small trees

Trees ≥ 1.0 m in height (size classes 3–5) were never initially vacant and subsequently colonized, and were rarely

occupied and subsequently abandoned (less than 0.5% of all occupied trees); thus, we analyzed colonization and abandonment of trees only in the two smallest size classes, where colonization and abandonment occurred far more frequently. Within these shorter trees, overall colonization rates were higher on larger trees. Figure 5a shows the percentage of initially uninhabited trees that were colonized over the 6-month survey period for trees in the two smallest size classes. Only 6.2% of uninhabited trees in size class 1 were colonized after 6 months, compared to 20% colonization of uninhabited trees in size class 2 ($\chi^2=6.38$, $P<0.02$). The competitively subordinate *C. nigriceps* showed the strongest colonization of vacant trees between 0.5 and 1.0 m tall.

Within these shorter size classes, larger trees were less likely to be abandoned than were small trees (Fig. 5b; $\chi^2=53.96$, $P<0.001$). More competitively dominant *C. mimosae* and *C. sjostedti* showed the highest abandonment of small trees, while the more subordinate *C. nigriceps* and *T. penzigi* abandoned trees less frequently ($\chi^2=13.68$, $P<0.001$).

Abandonment of occupied trees and colonization of uninhabited trees were correlated with tree growth rate (Fig. 6a,b). Initially occupied trees retaining ant colonies had tenfold higher average growth increments than trees that were abandoned ($F_{1,682}=25.14$, $P<0.0001$). Initially vacant trees that were colonized by ants over the 6-month census interval grew about four times as much in height as did vacant trees that were not colonized ($F_{1,126}=12.39$, $P<0.001$).

Concordance between observed transitions and the putative competitive hierarchy

Interspecific transitions among ant occupants occurred on 7.5% of all marked trees (134 of 1773 trees total). Tables 2 and 3 show transitions between ant species on

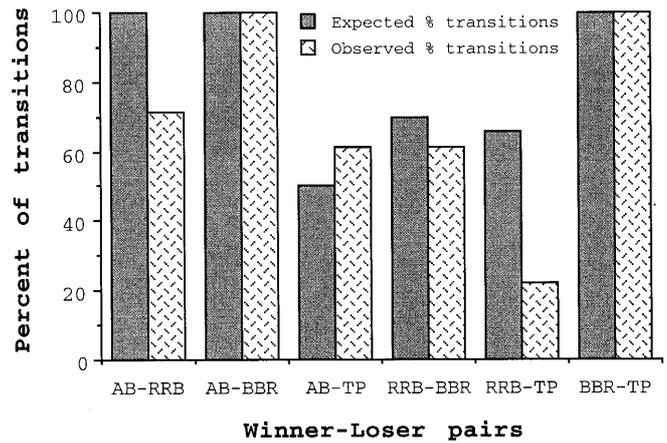


Fig. 7 Comparisons of percentage expected (from experimentally staged conflicts) and observed (from natural transition data) transitions on trees for all six possible pairwise combinations of ant species (AB=*C. sjostedti*, RRB=*C. mimosae*, BBR=*C. nigriceps*, TP=*T. penzigi*). Observed values reflect naturally occurring transitions on trees ≥ 1.0 m in height. Calculation of expected and observed values is explained in the text

trees shorter than 1.0 m ($n=68$ transitions) and taller than 1.0 m ($n=66$ transitions), respectively. Pooling transitions across all tree height classes, the identity of ants colonizing trees previously occupied by a different species parallels the putative competitive hierarchy established in the experimental ant conflicts (47, 21, 17, and 15% of transitions to *C. sjostedti*, *C. mimosae*, *C. nigriceps*, and *T. penzigi* occupancy, respectively; $n=134$ transitions in all tree height classes).

To assess whether the pattern of natural transitions between particular ant species was predicted by the outcomes of experimental conflicts between species, we compared the proportion of conflicts won by each species in each species pairing from the experimentally staged conflicts ("expected" transitions) to the propor-

Table 2 Transitions on trees 0.1–0.99 m in height. Only trees marked in January 1998 and relocated in July 1998 are included

July 1998	January 1998				Uninhabited
	<i>C. sjostedti</i>	<i>C. mimosae</i>	<i>C. nigriceps</i>	<i>T. penzigi</i>	
<i>C. sjostedti</i>	132	18	5	10	3
<i>C. mimosae</i>	4	104	3	5	3
<i>C. nigriceps</i>	2	11	133	2	7
<i>T. penzigi</i>	4	3	1	138	1
Uninhabited	29	43	12	22	112

Table 3 Transitions on trees ≥ 1.0 m in height. Only trees marked in January 1998 and relocated in July 1998 are included

July 1998	January 1998				Uninhabited
	<i>C. sjostedti</i>	<i>C. mimosae</i>	<i>C. nigriceps</i>	<i>T. penzigi</i>	
<i>C. sjostedti</i>	253	15	7	8	0
<i>C. mimosae</i>	6	249	8	2	0
<i>C. nigriceps</i>	0	5	208	3	0
<i>T. penzigi</i>	5	7	0	177	0
Uninhabited	1	1	0	2	2

tion of natural transitions “won” by the same species (“observed” transitions; Fig. 7). As was the case with the experimentally staged conflicts, we assume that natural transitions occurred as a result of interspecific conflict between adjacent colonies for the possession of trees. For this comparison, we used only natural transition data from trees ≥ 1.0 m, since experimentally staged conflicts were conducted on trees larger than 1.0 m. To calculate the proportion of conflicts won by each ant species in pairwise experimental conflicts, we used the formula: (number of conflicts won by species X over species Y) \div (number of conflicts won by X over Y + number of conflicts lost by X to Y), and the proportion of naturally occurring transitions “won” by a given species in a particular species pair was calculated as: (number of transitions from species Y to species X) \div (number of transition from Y to X + number of transitions from X to Y). The pattern of naturally occurring transitions was in fairly good agreement with the outcome of experimentally induced conflicts between species (Fig. 7); there were no significant differences between expected and observed outcomes for any of the six species pairs (χ -tests, 1 *df*, all $P > 0.20$).

However, two striking (albeit non-significant) departures from experimental predictions were noted in naturally occurring transitions. First, transitions from *C. sjostedti* to *C. mimosae* occupation, not predicted by experimentally staged conflicts, occurred as roughly 30% of transitions between these two species. Second, transitions from *C. mimosae* to either of the two subordinate species *C. nigriceps* and *T. penzigi* occurred more commonly than expected (Tables 2, 3, Fig. 7).

Relationship between transition “direction” and growth rate

Transitions occurred in one of two directions: (1) in the direction of the competitive hierarchy (i.e., more dominant species replacing more subordinate species) and (2) against the competitive hierarchy (i.e., more subordinate species replacing more dominant species). We examined whether there was a relationship between tree growth and transition direction.

To do this, we calculated a “differential height growth increment” for trees on which transitions occurred in the direction of the hierarchy, and against the hierarchy. We calculated differential height growth increments by subtracting the mean growth increment in the appropriate ant by tree size class for the displaced species (on trees occupied by that species that did not undergo transition) from the growth increment for the tree that underwent transition. This allowed us to assess whether trees that underwent transitions to another species had grown faster or more slowly than the average tree for that ant by tree size class that did not undergo transition. Because the number of trees undergoing transitions in any given size class was low, we aggregated data for size classes 1 and 2, and size classes 3–5 to increase statistical power.

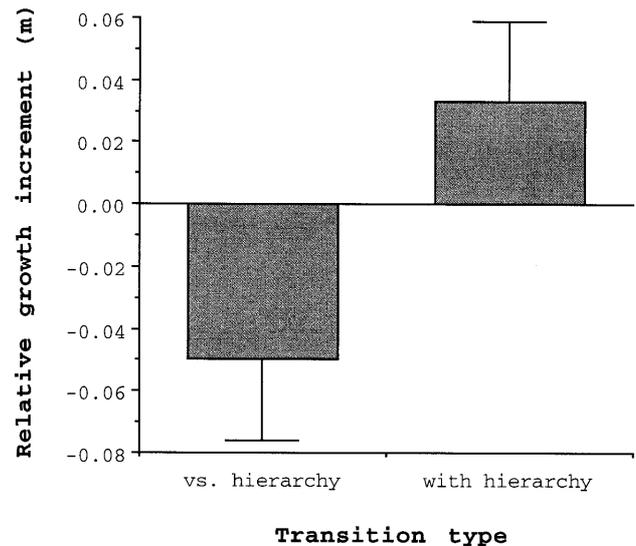


Fig. 8 Relative growth increments for taller trees undergoing transitions in the direction of ($n=85$) or against ($n=48$) the putative competitive hierarchy. Calculation of relative growth increment is explained in the text. Error bars show SEs

er. We pooled data for size classes 1 and 2 because tree abandonment was substantial in these smaller size classes, suggesting that competition for saplings was less intense than was competition for larger trees, where only 0.41% of trees occupied in January were vacant in July.

Trees ≥ 1.0 m in height that underwent transitions in the direction of the putative competitive hierarchy had significantly greater relative growth increments than did trees on which transitions occurred against the hierarchy (Fig. 8; $F_{1,63}=4.16$, $P < 0.05$). In the two smallest size classes (trees < 1.0 m), there were no significant differences in tree growth increments between transitions occurring with and against the putative competitive hierarchy ($F_{1,66}=0.0038$, $P=0.95$).

Discussion

Competitive hierarchy among ant species

Results from this study indicate that the demography of *A. drepanolobium* trees and the dynamics of their ant associates are closely linked. Although this system of four competing ant species is highly dynamic and variable, several clear patterns emerge. The first is the coincidence of several independent measures of a linear competitive hierarchy among the ants. The experimental and the natural takeovers reveal a similar dominance hierarchy: *C. sjostedti* $>$ *C. mimosae* $>$ *C. nigriceps* $>$ *T. penzigi*.

Resource competition and agonistic interactions at territory boundaries are common among ant species (reviewed in Hölldobler and Wilson 1990), often giving rise to linear dominance hierarchies (Vepsäläinen and Pisarski 1982; Fellers 1987; Savolainen and Vepsäläinen 1988; Morrison 1996). However, dominance relations

are usually inferred through patterns of territory occupation or by interactions at baits. Experiments are rarely conducted between entire adjacent colonies to examine dominance hierarchies in competition for nest sites. To our knowledge, this study represents the first experimental confirmation of a dominance hierarchy in competition for nest sites among sympatric plant ants.

This competitive hierarchy matches the natural occurrences of ants on trees of different heights in a 1993 survey of our study site (Young et al. 1997). In that survey, *T. penzigi* occupied the smallest trees, followed by *C. nigriceps*, *C. mimosae*, and *C. sjostedti*, occupying increasingly taller trees on average. The height data gathered at virtually the same locations in 1998 differed from the earlier study in that the trees occupied by *C. sjostedti* were on average shorter than those occupied by *C. mimosae* (Fig. 1). The reasons for this difference are not yet clear.

Differences in ant species occupancy associated with differences in tree height have been documented elsewhere. For example, Longino (1991) reported that although *Cecropia obtusifolia* saplings often contain a number of queens of different *Azteca* species, large trees in the forest canopy contained only *Azteca constructor* or *Azteca xanthochroa* colonies. While the swollen thorns of an *A. drepanolobium* sapling may contain foundress queens of several different ant species (M.L. Stanton, T.P. Young, T.M. Palmer, unpublished data), results from the present study indicate that many small trees are occupied by subordinate species and most large trees are occupied by colonies of *C. sjostedti* or *C. mimosae*. Our results indicate that this succession of ant species with increasing tree height may be driven by competition: as trees grow more rapidly and to larger sizes, subordinate species are replaced by competitive dominants.

Colonization and abandonment of small trees

The high turnover of ant occupants among smaller trees may be part of a complex interplay between colonization of this limiting resource and energetic decisions by larger colonies. The rarity of unoccupied *A. drepanolobium* trees (<1%; see Fig. 2) suggests that nesting sites strongly limit ant colonies in this community. Abandonment was only prominent in the two smallest size classes, and was highest among the competitively dominant *C. sjostedti* and *C. mimosae*. Surveys (M.L. Stanton, T.P. Young, T.M. Palmer, unpublished data) indicate that few saplings are occupied by queens, suggesting that many saplings are used for nest space by colonies occupying nearby trees. Both *C. sjostedti* and *C. mimosae* are strongly polydomous species (i.e., both maintain multiple-tree colonies), and may abandon small "satellite" trees during periods of low resource availability.

Trees may become more valuable as resources to ant colonies as trees grow larger. We observed decreased abandonment of previously colonized trees and increased colonization of initially vacant trees in size class 2 rela-

tive to size class 1 (Fig. 5). In contrast to trees larger than 0.5 m, most saplings in the smallest size class had very few or no swollen thorns, and often had very few or no leaves and extrafloral nectaries. Unoccupied trees larger than 1.0 m were very rare in this system.

Tree growth rates and ant presence were strongly and positively correlated in the smallest size classes, but it is difficult to determine the direction of causality for this relationship. Increased growth on continuously occupied trees relative to abandoned trees may represent ant-conferred benefits to trees, differential colonization/abandonment of slow-growing trees, or some combination of the two. Other studies have shown that ant colonies may facilitate plant growth in a number of ways, including protection from herbivory (Janzen 1966; Tilman 1978; McKey 1988; Madden and Young 1992), fertilization (Rickson 1979; Rico-Gray et al. 1989; Treseder et al. 1995; Wagner 1997), and pruning of nearby vegetation (Janzen 1969; Schupp 1986). However, it is unlikely that the small colonies (between 5–40 individuals on saplings <0.5 m tall) observed on trees in the smallest size class would effectively deter larger insect and vertebrate herbivores; workers were seldom aggressive when we manipulated these trees for measurements. Yet despite their low numbers, colonies on small saplings may contribute to the fertilization of small trees; with seasonal waterlogging, black cotton vertisol soils may lose nitrogen via denitrification (Coulombe et al. 1996), so even small additions of excreta may constitute an important nitrogen supplement to these young trees. However, it seems more likely that differences in tree quality are being effectively tracked by ant colonies, which may only occupy smaller trees that are relatively productive.

Similar difficulties exist in assessing causality for growth differences between uninhabited trees that were colonized versus those that remained vacant. Ants may influence growth on trees that they colonize (see above) or, alternatively, ants may selectively colonize faster-growing saplings. Ongoing experiments at this study site are aimed at determining the effectiveness of incipient colonies in influencing the growth rates of their sapling hosts.

Trends in colonization and abandonment of small saplings varied strongly among the four ant species. We observed higher rates of colonization by the subordinate *C. nigriceps* and lower rates of abandonment for both *C. nigriceps* and *T. penzigi* relative to the competitively dominant *C. sjostedti* and *C. mimosae*. Higher persistence of competitive subordinates on smaller trees may represent an important component in the maintenance of these inferior competitors in the system.

Transitions in ant occupancy

Although the majority of transitions on unmanipulated, adult trees occurred in a direction consistent with the competitive hierarchy inferred from staged conflicts (Table 3), transitions occurring against the hierarchy were

not uncommon, and occurred twice as frequently in natural versus experimental transitions (35% vs 16%, respectively). Transitions in experimentally staged conflicts involved at least initial conflict. The increase in natural relative to experimental transitions against the hierarchy may in part represent abandonment by dominants, followed by colonization by subordinates. Our data indicate that for the two smallest size classes, dominants are more likely to abandon trees, while subordinates are more likely to persist on or colonize these trees. This may explain the high number of transitions from *C. mimosae*, which had the highest rates of tree abandonment, to *C. nigriceps*, which had the highest rates of tree colonization (Table 2). Transitions against the hierarchy may form an important component of the persistence of subordinates in this ecosystem, especially in areas where sapling recruitment is low.

Correlations between transition direction and tree growth increments

Correlations between tree growth rate and transition direction indicate that more subordinate species are being replaced by dominants on their faster-growing trees, while more dominant species are replaced by subordinates on their slower-growing trees (Fig. 8). These data suggest that the mechanisms underlying transitions in the direction of and against the dominance hierarchy may differ.

If tree growth increments and rates of resource production for resident ants (e.g., production of swollen thorns and extrafloral nectar) are correlated, more rapidly growing trees may represent more highly contested resources among competitive dominants. Higher growth of trees where transitions occurred in the direction of the hierarchy may indicate that dominant species assess tree quality and then choose higher-quality trees for takeover. We have often observed workers of dominant species exploring trees occupied by colonies of more subordinate species. This interpretation is consistent with Davidson et al. (1991), who hypothesized that poor competitors with slow colony development will persist on more slow growing hosts, but be displaced on fast-growing plants by superior competitors.

Alternatively, tree growth rates may correlate with the productivity of off-tree resources used by ants. For example, if high productivity areas supporting rapid tree growth also have high invertebrate densities, protein intake by colonies in these areas may be higher. Because ant colony growth depends on the availability of protein (Hölldobler and Wilson 1990; Tobin 1995), while tree-provisioned resources (e.g., extrafloral nectar) are typically carbohydrate rich and nitrogen and protein poor (Baker et al. 1978; Davidson and Patrell-Kim 1996), local habitat availability of nitrogen-rich resources may constrain rates of colony growth. In rich microsites, colony growth may be more rapid, necessitating takeovers of neighboring trees as space becomes limiting. If strong

competitors for nest sites are also strong competitors for off-tree resources, then we might expect dominant colonies to expand onto neighboring trees wherever local productivity is high.

In contrast, dominants are replaced on their more slowly growing trees by subordinates. There are several possible interpretations of this pattern. A first explanation is that these transitions represent true competitive reversals, where subordinate colonies have actively supplanted more dominant species from trees. These reversals almost certainly occur, since transitions against the hierarchy did sometimes occur in experimentally staged conflicts. Reversals may reflect differences in factors such as colony size; for example, incipient colonies of dominant species may be competitively subordinate to larger colonies of subordinates until they grow to larger sizes (Fellers 1987; Savolainen and Vepsäläinen 1988; T.M. Palmer, unpublished data). Experimental manipulations in other ant species have shown that competitive outcomes may depend on worker number (Adams 1990; T.M. Palmer, unpublished data). In the black cotton ecosystem, poor-quality habitats may inhibit the growth of colonies of dominant species and/or favor the growth of subordinate species, resulting in competitive reversals in these areas.

A second explanation is that slow-growing trees may have lower rates of resource supply, increasing the chance of abandonment/colony failure on these trees. If dominant species have higher resource demands than subordinates (i.e., because of more active foraging, territorial defense, or more rapid colony growth; Davidson 1997), then colonies of dominants may disproportionately abandon or fail on trees with lower rates of resource renewal. This abandonment may be followed by successful colonization of these trees by subordinate species with lower energetic demands. Alternatively, the more polydomous dominant species may be more likely to relinquish smaller trees that were occupied during productive periods since their colonies have other trees, whereas subordinate species (especially *T. penzigi*) may have little option but to continue to occupy less productive trees during stressful periods.

Coexistence in the ant community of *A. drepanolobium* appears to be mediated by a number of mechanisms that operate simultaneously. Rapid colonization of emerging saplings and abandoned trees by the subordinate *C. nigriceps* and *T. penzigi* may contribute to the persistence of these species, sensu fugitive/competitor models (MacArthur and Wilson 1967; Horn and MacArthur 1972). Trade-offs in competitive and colonization ability play a role in species coexistence in a number of other assemblages (e.g., Werner and Platt 1976; Roughgarden et al. 1988; Gleason and Tilman 1990). Furthermore, variation in tree quality appears to be closely linked to the dynamics of interspecific competition among ants for trees; regardless of whether tree growth rates are a cause or a correlate of the direction of transitions, environmental heterogeneity appears to be a crucial determinant of coexistence among the four ant species. Environmental heterogeneity can play an important role in species co-

existence, as demonstrated both in theoretical (e.g., Shigesada et al. 1979; Pacala 1986) and empirical (e.g., Huffaker 1958; Keats et al. 1994; Vivian-Smith 1997) studies. We are currently investigating the underlying causes for heterogeneity in *A. drepanolobium* growth rates, and examining the relationships between environmental gradients and ant community structure.

Acknowledgements We wish to thank John Lemboi, Lizzie King, Amanda Evans, and Frederick Erei for assistance in the field, and the Mpala Research Centre, Segera Ranch, the National Science Foundation (DEB 9726663) and the Bridge Grant Program at the University of California at Davis for logistical and financial support. Helpful comments were made by Pete Coppolillo, Kimber Haddix and three anonymous reviewers.

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