Resource Partitioning in Two Sympatric Species of Subterranean Termites, *Reticulitermes flavipes* and *Reticulitermes hagenni* (Isoptera: Rhinotermitidae)

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**ABSTRACT** Landscape patterns of foraging activity in sympatric species of subterranean termites were examined. Foraging activity was observed biweekly within a grid of wooden monitoring stations covering an area of ~900 m². The number and spatial distribution of active monitoring stations within the grid were used to determine seasonal patterns of foraging activity for each species. Caps in the spatial distribution of occupied monitoring stations were quantified using the lacunarity index. *Reticulitermes flavipes* (Kollar) and *Reticulitermes hagenni* Banks were observed within monitoring stations throughout the study. The number and spatial distribution of occupied monitoring stations varied seasonally. Seasonal patterns of activity and spatial distribution also varied between species. Lacunarity was highest for *R. hagenni* during cool, wet months and highest for *R. flavipes* during hot, dry months. Seasonal changes in the number of active monitoring stations and their spatial distribution in the landscape were correlated with seasonal changes in soil temperature and soil moisture for both species. These patterns reflect differential degrees of adaptation to soil moisture and temperature extremes and could provide a mechanism for resource partitioning within the three-dimensional soil landscape.

**KEY WORDS** *Reticulitermes flavipes*, *Reticulitermes hagenni*, subterranean termites, foraging, resource partitioning, landscapes

Groups of closely related species having similar roles within an ecological community are called guilds (Ricklefs 1993). For example, herbivorous insects can be divided into several guilds including leaf-eaters, stem-borers, root-chewers, nectar-sippers, and bud-nippers. The increased similarity in ecological function within species guilds leads to competition for shared resources that are in limited supply. *Reticulitermes flavipes* (Kollar) and *Reticulitermes hagenni* Banks belong to the subterranean termite species guild, and their geographic distributions overlap in the southeastern United States (Snyder 1954). These ecologically similar species are likely to compete for wood as a food resource within landscapes.

Competition between ecologically similar species can lead to coexistence through resource partitioning. Resource partitioning is the division of shared resources between species so that each species uses the shared resource under different circumstances (Lawrence 1995). Coexistence between ecologically similar species is only possible if some degree of ecological separation is achieved between them. Ecological separation can be the result of several factors including: character displacement, habitat selection, microhabitat differences, temporal differences, or diet (Price 1997). Differences between ecologically similar species in any one of these factors may allow them to share a common resource. For example, two species may compete for the same food, but one species is nocturnal while the other is diurnal. Coexistence between the subterranean termites *R. flavipes* and *R. hagenni* within the soil landscape is likely due to a combination of these factors.

As a guild, subterranean termites function within ecological systems in the breakdown of woody plant materials (xylaphagy). Although the various termite species function in the breakdown of cellulotic materials, variation between species exists in the types of habitats they occupy and the behaviors they exhibit. It is well known that various kinds of termites differ from one another in their response to abiotic features of the environment (Collins 1969, Ettershank et al. 1980, Forschler and Henderson 1995) and that different kinds of termites occupy distinct geographic regions (Williams 1934) and unique habitats within landscapes (Weesner 1965, Howard et al. 1982). Differential adaptedness by termite species to distinct environmental conditions may reduce the level of competition between sympatric termite species foraging for woody plant materials.

Studies have identified differences between species of *Reticulitermes* Holmgren in their response to abiotic environmental conditions. Collins (1969) demon-
strated sharp differences in survival time between species when experimentally challenged by constant low humidity and high temperature. Survival time during experimental drying was influenced by the rate of water loss, body size, ability to retain water, group size, and behavioral reaction to adverse conditions (Dunmore and Collins 1951, Collins 1958, Collins and Richards 1963, Collins and Richards 1966). Forschler and Henderson (1995) showed differences in tolerance to inundation between species of Reticulitermes and stated that this may be an indication of unique resource utilization strategies. Macom (1999) also found differences in temperature preference between three species of Reticulitermes under experimental conditions.

Differences in termite biology and behavior are likely to influence seasonal foraging activity. Seasonal fluctuations in foraging activity have been reported for subterranean termites by several researchers (Haverty 1974, Jones et al. 1987, Haagsma and Rust 1995, Grace 1996, Haverty et al. 1999), but no one has discussed how seasonal fluctuations are related to ecological coexistence between competing species. The purpose of this study was to examine and compare seasonal and spatial changes in foraging activity between coexisting species of Reticulitermes in response to seasonal fluctuations in temperature and moisture and to discuss how this may be related to resource partitioning within the three-dimensional soil landscape.

Materials and Methods

Study Area. A location within Lick Creek Park, College Station, TX, was chosen for this study. The park covers ~500 acres and is associated with the Post Oak Savannah vegetation zone. Lick Creek, from which the park gets its name, is a major tributary of the Navasota River. Portions of Lick and Alum Creeks, and their associated flood plains, lie within the boundaries of the park. Several habitats exist within Lick Creek Park including riverine and alluvial hardwood forest, open marshland, sedge meadows, upland oak forests, and sandy prairies. Lick Creek Park has not been severely impacted by wetland drainage, therefore habitat and species diversity are high.

Naturally occurring populations of subterranean termites were discovered within the sedge meadow habitat, and a grid of monitoring stations was installed (Fig. 1). The sedge meadows lie within the moist bottomland floodplain. The meadows are covered extensively by Carex cherokeensis Schweinitz (Cherokee sedge) which grows under a closed canopy of native Ulmus crassifolia Nuttall (cedar elm). The canopy provides a high degree of shade during much of the year, minimizing temperatures within the landscape. A few grasses and a thistle, Cirsium engelmannii Rydberg, are also interspersed within the sedge meadow. Campsis radicans L. (trumpet creeper) vines are found growing on the trees. Because of periodic flooding, brushy undergrowth is kept to a minimum within the sedge meadow, however, clustered stands of Ilex vomitoria Aiton (Yaupon holly) are distributed throughout the landscape and are interspersed with seedlings of Fraxinus pennsylvanica Marsh (green ash) and a lowland variety of Quercus stellata Wangenhein (post oak). Several water channels and small oxbow lakes are found throughout the sedge meadows and represent former paths of Lick Creek and its tributaries. During the wet season, these channels and oxbows may hold water briefly, but during the dry season they are empty. None of these channels or oxbows were located within the grid of monitoring stations.

Termite Sampling Methods. The grid installed within the sedge meadows measured 27.5 by 27.5 m (~750 m²) and was composed of 144 monitoring stations in a 12 x 12 array (Fig. 1). The distance between individual monitoring stations was ~2.5 m (250 cm). A number corresponding to the row and column of the grid was assigned to each monitoring station and is written with the row number, followed with a period, then the column number (e.g., 3.4, 5.6, 10.4). Soil thermometers (PSG, Perkasie, PA) and soil moisture probes (Soil Moisture Equipment, Santa Barbara, CA) were placed in the center of each group of four monitoring stations (Fig. 1) to measure soil environmental changes in the surface layers (15 cm) of the soil profile. Soil thermometers were calibrated in the laboratory before field installation. Soil moisture was determined as percent saturation using time reflectometry and the Trace measurement system (Soil Moisture Equipment). Soil temperature and soil moisture readings were recorded at biweekly intervals and in conjunction with termite sampling between 15 December 1997 and 8 June 1999.

Monitoring stations were constructed from 4.5 by 4.5 by 15-cm pine stakes. Each pine stake had a 1-cm-diameter hole drilled lengthwise through the center. A single row of small holes, 2 mm in diameter, was drilled through the sides into the central cavity to act as termite entryways into the interior. Each monitoring station was placed in the soil to a depth of 15 cm by drilling a 4.5-cm-diameter hole with a soil auger and inserting the monitoring station into the hole. After the monitoring station was inserted into the soil and the exposed end of the center hole was capped with a rubber stopper. This rubber stopper was easily removed during sampling to observe termite activity within the station. Monitoring stations were replaced as needed during the course of the study. Replacement was considered necessary when >50% of the below ground portion of the station had deteriorated due to termite feeding or fungal growth and subsequent rotting. Stations were replaced by gently pulling the old station out of the ground and inserting a new station into the same hole.

Each monitoring station within the grid was inspected biweekly, between 11 April 1997 and 8 June 1999, for the presence or absence of subterranean termites by removing the rubber stopper and shining a flashlight into the interior cavity. The presence or absence of cruts or termites, along with the species in each monitoring station, were recorded for each sam-
Fig. 1. Spatial arrangement of monitoring stations (x) and temperature and moisture probes (○) within the 12 × 12 grid array. Distance between individual monitoring stations was 2.5 m and the distance along each side of the grid was 27.5 m. Spatial distribution of monitoring stations occupied by *R. flavipes* (black), *R. hageni* (gray), or both (white) between June 1997 and June 1999 is also shown. Numbers indicate monitoring stations occupied by a single colony or feeding group as identified by mark-release methods.

Placing interval. Termites or mud crusts below the stopper was recorded as presence for a sampling interval. The lack of mud crusts and termites was recorded as absence. Soldiers were removed for species identification during the first sampling interval after a station became occupied and also after any periods of inactivity lasting more than two consecutive sampling intervals. Because the size of the pseudergate varies between species of *Reticulitermes* recorded from Texas (Hostetler et al. 1995), consecutive weeks of
habitation in a station were assumed to be the same species when pseudergate size was consistent between consecutive sampling intervals.

To identify termite species, soldiers were removed from occupied monitoring stations using an aspirator. Species identifications using soldiers were made according to labrum morphology (Hostetler et al. 1995). Soldier labrums were removed under the microscope using a delicate razor blade and were mounted on microscope slides using Euparal (General Biological, Chicago, IL) as a slide-mounting medium. Termite alates were also used for species identifications (Snyder 1954) when collected from individual monitoring stations. Voucher specimens are deposited in the Enns Entomology Museum at the University of Missouri-Columbia.

The spatial location of individual colonies within the landscape was examined using mark-release methods. The methods were similar to those of Grace et al. (1989) and Grace (1990) except that population size was not estimated using recaptured termites. Bucket-block traps similar to those used by Su and Scheffran (1986) were installed within the grid to collect large numbers of foraging termites. These traps were installed by digging a hole ~18 cm in diameter and 25 cm deep. The rim of a plastic bucket (18 cm diameter) was placed around the top edge of the hole. This rim was ~10 cm wide and was obtained by cutting off the bottom portion of the bucket. The lid of the bucket was placed on the bucket rim lining the hole and covered with soil and surrounding debris.

Inside the bucket-block trap, a 2 by 9 by 12-cm piece of aged pine was placed in the soil in the bottom of the hole, with a removable wooden sandwich placed on top as a termite trap. The wooden sandwich was made of four 2 by 9 by 12-cm pieces of aged pine, each with a hole drilled in the center. A 15-cm bolt, wing nut, and six metal washers were used to assemble the wood pieces into a sandwich configuration. The wood pieces were stacked on the bolt by inserting the bolt through the holes in each piece, and two metal washers were placed between adjacent pieces. Four bucket-block traps were installed within the grid, early in the study, to minimize the disturbance to natural foraging activity.

Termites were collected from bucket-block traps and were taken to the laboratory to be marked using fat-soluble dyes (Grace and Abdallah 1989, Su et al. 1991, Oi and Su 1994). Unmarked termites were fed filter paper (Fisher, Pittsburgh, PA) impregnated with dye for a period of four days. Nile Blue dye (0.1%) and Sudan Red dye (0.1%) were both used throughout the cycle to distinguish between termites marked from different bucket-block traps. Marked termites were released back into the same bucket-block trap at the next biweekly sample. The location of colored termites within monitoring stations throughout the grid was recorded during subsequent biweekly sampling intervals. The spatial distribution of colored termites within the grid identified monitoring stations that were inhabited by termites from the same colony or feeding group.

Analysis. Seasonal changes in the number and spatial pattern of occupied monitoring stations were examined. Seasons were determined according to the months of the year, with March, April, and May being spring; June, July, and August summer; September, October, and November fall; and December, January, and February winter. Differences in soil temperature and soil moisture levels between these seasons were examined using analysis of variance (ANOVA). Differences in the average number of occupied stations were compared between seasons for the same species using ANOVA and a t-test was used to compare differences between species during each season.

To determine how the number of occupied foraging sites was related to changing soil environmental conditions, the number of occupied stations at each sampling interval was subjected to linear regression analysis against soil temperature and moisture levels for the same sampling interval. Soil temperature and moisture levels were calculated as the average of all locations within the grid. Polynomial regression also was used to determine if nonlinear models described more of the variation in occupied stations in response to soil temperature and moisture.

The spatial arrangement of occupied monitoring stations was compared with seasonal changes in soil moisture and temperature. Spatial arrangement was quantified for each biweekly sampling interval and termite species using the lacunarity index (Mandlebrot 1983, Plotnick et al. 1993). Lacunarity uses binary (presence-absence) data to measure the gaps in a spatial pattern using a moving window algorithm. To calculate lacunarity, a box containing a set number of cells (i.e., 2 × 2) is systematically moved across the rows and columns of the grid containing presence-absence (0, 1) data. After each move, a score is recorded as the sum of 0's and 1's within the box. After the moving box has covered the entire matrix, an algorithm calculates specific mean and variance values from the individual scores (Plotnick et al. 1993). The lacunarity index is the ratio of mean and variance values and is sensitive to the number of boxes with score 0 (gaps). The equation for calculating lacunarity is

$$\Lambda = Z^{(2)}/[Z^{(1)}]^2,$$

where $\Lambda$ is lacunarity, $Z^{(1)}$ is the sum of the proportion of the total number of boxes of score (S) multiplied by S, and $Z^{(2)}$ is the sum of the proportion of the total number of boxes of score (S) multiplied by $S^2$.

A 2 × 2 moving window size was used to calculate the lacunarity of subterranean termite presence-absence data in this study. Seasonal changes in lacunarity were examined for each species. A high lacunarity value indicates that there are large gaps within the spatial pattern of active monitoring stations. Large gaps are the result of having few active foraging sites within the landscape. Low lacunarity values are indicative of small gaps in the spatial pattern of active monitoring stations. Low lacunarity values result when several active feeding sites are distributed throughout the grid.
Lacunarity was compared between seasons for the same species using ANOVA and between species during the same season using a t-test. Lacunarity for each species was also regressed against seasonal changes in soil temperature, soil moisture and mean station activity to determine any significant relationships. SigmaStat 2.03 (SPSS, Chicago, IL) was used to perform all ANOVA, t-test and regression analyses. Finally, comparisons were made between regression models using the number of occupied stations and models using lacunarity to determine which variable was more correlated with soil environmental factors.

Results

Subterranean termites were observed in 61 different monitoring stations throughout the course of this study. The spatial location of these 61 stations is shown in Fig. 1. Two subterranean termite species, *Reticulitermes flavipes* (Kollar) and *Reticulitermes hagenii* Banks, were collected and identified from active monitoring stations. *Reticulitermes flavipes* inhabited 25 different stations, and *R. hagenii* inhabited 36. Mark-release activities delineated at least two different *R. flavipes* colonies within the grid (Fig. 1). *Reticulitermes hagenii* colonies were not delineated because this species was never collected in bucket-block traps.

Three stations within the grid, 8.9, 8.10, and 9.5 were inhabited by both species at different times throughout the study. In all three cases, *R. hagenii* initially inhabited the station during a warm, dry period, later abandoned the station when favorable conditions changed, and was replaced by *R. flavipes* during a cool, moist period. The period of inactivity between *R. hagenii* and *R. flavipes* in these three monitoring stations ranged from 12 wk (November to February) to 20 wk (October to March). This period of inactivity eliminates the possibility that direct antagonistic behavior by *R. flavipes* displaced *R. hagenii* from these monitoring stations. The displacement of *R. hagenii* by *R. flavipes* in these situations appears to be the result of species-specific activity patterns associated with seasonal changes in soil environmental factors.

There were significant differences (α = 0.05) in soil temperature and soil moisture between seasons (Fig. 2). Pairwise comparisons showed that summer soil temperatures were not significantly different (α = 0.05) from fall. Summer and fall soil temperatures were, however, significantly different (α = 0.05) from winter. Spring soil temperatures were only significantly different (α = 0.05) from summer. There were also significant differences (α = 0.05) in soil moisture between seasons. Summer and winter soil moisture levels were both significantly different (α = 0.05) from all other seasons. Soil moisture in spring and fall was not significantly different (α = 0.05).

**Number of Occupied Stations.** Initially, the number of monitoring stations located within the grid was equal to the number of occupied stations. Eventually, however, fewer monitoring stations were occupied than had been located. The cumulative number of monitoring stations located by each species within the grid increased at a relatively constant rate throughout the study, while the number of stations occupied during each sampling interval fluctuated seasonally (Fig. 3).

The number of monitoring stations occupied on any given sample date by *R. hagenii* within the grid fluctuated between two and 17 (mean = 9.9) and the number of stations occupied by *R. flavipes* fluctuated between four and 16 (mean = 9.7). ANOVA revealed

![Fig. 2. Mean values for soil temperature (°C) and % soil moisture in the top 15 cm of the soil profile calculated for each season of the year (1 = summer, 2 = fall, 3 = winter, 4 = spring).](image)

![Fig. 3. Cumulative number of monitoring stations located within the grid and the number of monitoring stations occupied during successive sampling dates for *R. flavipes* and *R. hagenii*.](image)
significant differences ($\alpha = 0.05$) in the mean number of occupied monitoring stations between seasons for each species (Fig. 4). Pairwise comparisons showed that the mean number of stations occupied by *R. flavipes* was lowest during the summer and was significantly different ($\alpha = 0.05$) from all other seasons. The mean number of stations occupied by *R. flavipes* during winter was also significantly different ($\alpha = 0.05$) from spring and summer. The mean number of stations occupied by *R. hageni* was lowest during winter and significantly different ($\alpha = 0.05$) from summer and fall.

The mean number of stations occupied by *R. flavipes* was higher that *R. hageni* during winter and spring, but lower than *R. hageni* during summer and fall. Comparisons between species for each season showed significant differences ($\alpha = 0.05$) in the number of occupied stations during spring and summer. No significant differences ($\alpha = 0.05$) in the number of occupied stations were found between species during fall or winter.

The number of stations occupied by *R. flavipes* and *R. hageni* on each sampling date was regressed against mean soil temperature and soil moisture from the same date (Fig. 5). Both soil variables were correlated with the number of occupied stations for *R. hageni* and *R. flavipes*. A linear model provided the best fit of these relationships for *R. hageni*. Linear regression showed a statistically significant relationship ($\alpha = 0.01$) between the number of stations occupied by *R. hageni* and values for soil temperature and moisture (Table 1). The number of occupied stations increased as soil temperatures increased above 23°C and soil moisture decreased below 30%. The general linear model containing both variables also showed reasonable correlation. This is probably due to the correlation between soil temperature and soil moisture ($R = 0.742$). The exponential model ($\alpha = 0.01$) provided the best fit of the relationships for *R. flavipes*. $R^2$ values were higher and $P$ values lower for both variables (Table 1) when using the exponential model. The number of occupied stations increased when soil moisture increased above 25%, and soil temperature decreased below 23°C.

Spatial Dispersion Patterns. Mean lacunarity values for all sampling intervals combined are lower for *R. hageni* ($L_\alpha = 5.94$) than for *R. flavipes* ($L_\alpha = 6.44$). This indicates a more uniform distribution of *R. hageni* activity, and a more clumped spatial distribution for *R. flavipes*. The distances between occupied stations were larger for *R. flavipes* than for *R. hageni* during every season of the year, except winter. The differences were statistically significant ($\alpha = 0.05$) when comparing lacunarity values between species during each season using a t-test. Spatial patterns were similar between species during the winter because this was the only season during the year when the distribution of *R. hageni* was disjunct.

Lacunarity values representing the spatial distribution patterns of both species changed seasonally (Fig. 6). The spatial distribution of *R. hageni* within the landscape was more uniform during summer and fall, and patchy during winter (Fig. 7). Spring was an intermediate season. The distribution pattern of stations occupied by *R. flavipes* was more extensive during winter and spring, and patchy during summer (Fig. 8). Fall was an intermediate season. ANOVA showed significant differences in seasonal spatial distribution patterns ($\alpha = 0.05$) for *R. hageni*, with winter being significantly different from the other seasons. The spatial dispersion of *R. flavipes* during the summer months was significantly different ($\alpha = 0.05$) from all other seasons (Fig. 8).

The lacunarity of termite distribution patterns was related to seasonal changes in soil temperature and moisture (Fig. 9). The spatial distribution patterns of each species were correlated with both soil environmental variables. Regression analysis revealed significant relationships ($\alpha = 0.01$) between lacunarity and soil temperature and moisture (Table 2) values from
R. hageni

The seasonal changes in lacunarity of R. flavipes and R. hageni spatial distribution plotted with corresponding changes in mean soil temperature (°C) and mean % soil moisture. Low lacunarity values reflect many active sites or small gaps in the spatial distribution pattern, while large values represent disjunct distribution patterns or large gaps.

The same sampling interval. Changes in the spatial distribution of R. hageni were predicted with a linear model, using either soil temperature or soil moisture as the predictor. An exponential model using either soil factor as the independent variable could predict changes in R. flavipes spatial patterns.

Table 1. Results of linear and polynomial regression analyses of the number of occupied monitoring stations in response to soil temperature and moisture values from the same sampling interval.

<table>
<thead>
<tr>
<th>Model</th>
<th>Variables</th>
<th>df</th>
<th>R²</th>
<th>F</th>
<th>P</th>
<th>R²</th>
<th>F</th>
<th>P</th>
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<td>0.290</td>
<td>7.15</td>
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* Moisture and temperature together.
NS = Not significant.
**Discussion and Conclusions**

This study provides evidence that *R. flavipes* (Kollar) and *R. hageni* Banks respond differently to changes in abiotic environmental factors at the soil surface. Termite activity by either species in the top 15 cm of the soil profile was related to seasonal changes in soil moisture and soil temperature. *Reticulitermes hageni* foraged actively and used woody resources at the soil surface during dry periods and was less active during moist periods. In contrast, *R. flavipes* used woody resources at the soil surface during moist seasons and was less active during dry seasons. Likewise, seasonal changes in soil temperature influenced foraging activity, with *R. hageni* being active during hot periods and *R. flavipes* being more active during cool periods. Because termite activity patterns in the surface 15 cm of soil are influenced by seasonal changes in soil temperature and moisture, the opportunity for each species to use wood at the soil surface may be limited to periods when soil temperature and soil moisture are favorable. These seasonal patterns of termite activity could play a role in resource parti-
Seasonal levels of foraging activity observed in this study complement these findings. Foraging activity of *R. flavipes* was higher during moist seasons and reduced during dry seasons. Tolerance to high soil moisture and susceptibility to water loss appear to enhance the ability of *R. flavipes* to use woody resources during moist seasons and limit their ability to use them during dry seasons. *Reticulitermes hagenni* is more susceptible to soil saturation during wet seasons and less susceptible to water loss during dry seasons, and is thus able to use woody resources during warmer, dry periods. The differential adaptedness to soil moisture and water loss between these species may influence resource utilization strategies within the landscape.

Moisture and temperature are inseparable as environmental factors, and termite behavior can be greatly influenced by temperature. Ueckert et al. (1976) found that in years of above normal precipitation, temperature was the most important factor in determining population densities of *Ctenotermes tubiformans* (Buckley). Haagsma and Rust (1995) also found that minimum soil temperature was the best predictor of *R. hesperus* Banks activity in both urban and natural landscapes. The temperature factor operates to limit termites at two extremes, the winter minimum and the summer maximum. Either extreme limits individuals that are not adapted to such temperatures either by killing them or by affecting their activity (Kofoid 1934).

Smith and Rust (1994) described the temperature preferences of *R. hesperus* Banks and examined seasonal soil temperatures conducive for foraging activity. They concluded that *R. hesperus* responds adaptively to unfavorable soil temperatures by moving to areas more conducive to their temperature preferences. It seems reasonable to assume that *R. flavipes* and *R. hagenni* also minimize the effects of unfavorable temperature extremes through appropriate adaptive responses. Macom (1999) examined temperature preferences and the effects of temperature on caste differentiation and secondary colony formation in *R. flavipes*, *R. hagenni* and *R. virginicus*. Caste differentiation and secondary colony formation occurred more readily at lower temperatures for *R. flavipes* and at higher temperatures for *R. hagenni*. *Reticulitermes hagenni* was very sensitive to lower temperatures and no caste differentiation occurred in less than 28 wk at 15°C. Caste differentiation and the formation of supplemental reproductives always occurred in less than 24 wk for *R. flavipes* colonies held at 15°C. Temperature preference studies showed that *R. flavipes* preferred lower temperatures, whereas *R. hagenni* preferred higher temperatures. Foraging activity levels of *R. flavipes* and *R. hagenni* in this study support these observations. *Reticulitermes hagenni* foraging activity was highest during warm seasons, whereas *R. flavipes* occupied more monitoring stations during cooler seasons. It seems reasonable that these species are foraging when soil temperatures are within their preferred range.

Observations of foraging activity represent the adaptive response of *R. flavipes* and *R. hagenni* to chang-
Fig. 9. Relationship between lacunarity of *R. flavipes* and *R. hageni* spatial distribution within the grid, mean soil temperature (°C), and mean % soil moisture on the same sampling date.

Table 2. Results of linear and polynomial regression analyses of lacunarity in response to soil temperature and moisture data taken during the same sampling intervals.

<table>
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<th>Model</th>
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<th>Reticulitermes hageni</th>
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* Moisture and temperature together.

NS = Not significant.
each species would influence vertical migrations along soil temperature and moisture gradients. This hypothesis is consistent with studies by Ettershank et al. (1980), who concluded that subterranean termites detect and respond to temperature differences within the soil profile, and Forschler and Henderson (1995), who showed that subterranean termites move in response to soil moisture changes.

Vertical gradients in temperature and moisture occur within the soil profile as a result of climatic variables operating at the soil surface. The temperature of the soil depends on the ratio of energy absorbed to that being lost (Brady and Weil 1996). Variations in soil temperature occur seasonally with increases and decreases in surface soil temperatures generally following changes in atmospheric temperatures. Soil surface temperatures affect soil temperatures, but there is a lag between temperature changes in surface soil and concomitant changes in subsoil temperatures. These lags create a thermal gradient within the soil profile that changes seasonally (Fig. 10). Fluker (1958) examined thermal gradients within the soil profile in College Station, TX, and found that subsoil temperatures were cooler than surface temperatures from March through October when energy absorption was high at the surface. During periods when energy loss at the soil surface was high (November through February), subsoil temperatures were warmer than surface temperatures.

Vertical soil moisture gradients are greatly influenced by the timing and rate of precipitation. Precipitation saturates surface soil layers and then penetrates into the subsoil. This creates a transition zone from saturated surface soils to dry subsoils above the water table (Fig. 11). The lower limit of infiltration by water into the subsoil depends on the rate of saturation in the surface soil. Heavy rainfall within a short period of time (within an hour) can exceed the absorptive capacity of many surface soils and can result in reduced penetration into the subsoil and increased runoff (Brady and Weil 1996). Steady precipitation over long periods of time results in increased penetration of moisture into the subsoil and a deeper transition zone. It is important to note that the area below the lowest level of infiltration by precipitation, but above the water table, remains relatively dry.

*Reticulitermes flavipes* and *R. hageni* appear to be responding to soil moisture and temperature gradients in the soil profile. Temperature was a good predictor of foraging activity for both species in this study. Based on temperature preferences (Macom 1999), *R. flavipes* would follow temperature gradients toward cooler temperatures while *R. hageni* would follow temperature gradients toward warmer temperatures. Following these preferences along soil temperature gradients would bring *R. flavipes* near the soil surface, and into the monitoring stations, during seasons when surface soil is cooler than the subsoil (Fig. 10), whereas *R. hageni* would move into the monitoring stations during seasons when surface soil is warmer than the subsoil. Conversely, foraging activity within the top 15 cm of the soil surface would decrease for *R. flavipes* when the subsoil is cooler than the surface and for *R. hageni* when the subsoil is warmer than the surface. These vertical movements would explain the patterns of activity observed in this study.

Soil moisture was also a good predictor of the number and spatial pattern of occupied monitoring stations in this study, and the response of *R. flavipes* and *R. hageni* to the soil moisture gradient compliments the vertical movements of these species along temperature gradients. Based on the ability of *R. flavipes* to withstand higher levels of moisture present in the surface soil during the cooler seasons, this species would not be restricted when seeking preferred soil...
temperatures at the soil surface. When seeking warmer soils during cooler seasons, *R. hageni* foragers would encounter the relatively dry soil below the zone of infiltration (Fig. 11), thus reducing their susceptibility to inundation. During warmer seasons when the driest soils are near the surface, *R. hageni* would not be inhibited from following the temperature gradient to the soil surface. In seeking cooler temperatures at greater depths during warmer seasons, *R. flaviipes* would find relatively moist soils to offset its susceptibility to water loss.

In summary, seasonal partitioning of resources between *R. flaviipes* and *R. hageni* is based in part on their differential response to seasonal changes in soil moisture and soil temperature. Although wood resources are present at the soil surface throughout the year, each of these species utilizes the resource when favorable environmental conditions exist. *Reticulitermes hageni* is able to use the resource during warm, dry seasons because it prefers warm temperatures, is less tolerant to soil saturation, and may be less susceptible to water loss through its cuticle. *Reticulitermes flaviipes* is adapted to use the wood resource during cool, wet seasons based on its preference for cooler temperatures and an increased tolerance to soil saturation. The unique seasonal responses of *R. hageni* and *R. flaviipes* to changing soil environmental conditions within the landscape may be an important mechanism that allows these sympatric species to coexist while performing a similar ecological function.

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