Feeding, Uptake, and Utilization of Carbohydrates by Western Subterranean Termite (Isoptera: Rhinotermitidae)

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ABSTRACT Western subterranean termite, *Reticulitermes hesperus* (Banks), prefers various mono-, di-, and trisaccharides, total feeding being the greatest on paper disks treated with 5% ribose followed by 3% xylose, 2% maltose, 2% fructose, 2% arabinose, and 2% ribose. In multiple choice tests, termites were not able to discriminate between 2% ribose, 2% fructose, 2% xylose, and 2% maltose. Termites readily take up [^{14}C]sucrose in feeding studies. Most of the sucrose is used as an energy source for respiration (89.2%), a very small proportion remains within the termite (9.3%), and an even smaller amount is excreted as solid waste (1.5%). The amount of ^{14}C label transferred to other colony members via trophallaxis, body contact, or grooming is small and directly dependent upon the time and numbers of donors and recipients. At day 15 postmixing, the percentage of transfer was highest, 14.4 and 15.1% for both 1:1 and 2:1 donor to recipient mixing ratios, respectively. The mean amount of labeled ^{14}C received by recipients increased from seven disintegrations per minute (dpm) on day 2 to 30 dpm on day 15 for 1:1. Overall mean radioactivity recovered from recipient termites when mixed with donor termites at 1:1 ratio (20 dpm) was significantly less than (28 dpm) when mixed with donor termites at 2:1 ratio. Sugars act as phagostimulants to the termites at concentrations much higher to those that termites naturally encounter in wood. Termites readily metabolize carbohydrates such as sucrose, and thus their use in bait matrices may increase consumption and retention at bait stations.

KEY WORDS carbohydrates, phagostimulants, baits, subterranean termites

BAITS CONTAINING SLOW-ACTING TOXICANTS and insect growth regulators (IGRs) to control termites are promising both in terms of efficacy and minimizing environmental impact. The amount and rate by which these compounds enter a termite colony, however, are not easily controlled. The effectiveness of baits depends on termites locating the bait and the rate at which they consume and distribute it to other colony members. Consequently, a considerable amount of research over years has focused on devising more attractive baiting systems and bait matrices (Mauldin and Rich 1975; Becker 1976; Esenther and Beal 1974, 1978; Lenz et al. 1991; Chen and Henderson 1996; Suoja et al. 1999; Rojas and Morales-Ramos 2001; Reinhard et al. 2002; Cornelius 2003; Morales-Ramos and Rojas 2003). Baiting systems are more effective if termites feed more regularly on the baits (Su 1991, 1994; Haagsma and Bean 1998). Subterranean termites show a wide range of feeding preferences toward synthetic and natural substances (Mishra 1992, Chen and Henderson 1996, Morales-Ramos and Rojas 2001, Reinhard et al. 2002, Cornelius 2003). The subterranean termite *Reticulitermes santonensis* De Feytaud preferred filter paper treated with secretions from the labial glands, different sugar-like components, and amino acids (Reinhard and Kaib 2001). Waller and Curtis (2003) found an increased consumption of filter paper treated with solution of glucose, sucrose, and xylose in *Reticulitermes flavipes* (Kollar) and *Reticulitermes virginicus* (Banks). Even though termites show an increased consumption when offered filter paper treated with simple carbohydrates, their fate and exchange between the termites are not clear. Lower termites with the help of protozoans in their gut have the ability to digest cellulose and hemicelluloses (polysaccharides) from wood that serves as the natural food source for termites. In our study, we determined the feeding preferences of western subterranean termites, *Reticulitermes hesperus* (Banks), for different simple carbohydrates. In addition, we examined the fate of a simple carbohydrate, sucrose, and its exchange among termites after ingestion by using [^{14}C]sucrose.

Materials and Methods

Termites. Termites were collected on University of California, Riverside campus, in polyvinyl chloride traps provisioned with rolls of corrugated cardboard. Termites were gently removed and maintained in lab in rectangular Rubbermaid containers (3.78 liter, Wooster, OH) at 24°C and 98% RH. Pieces of brown paper towel (Fort James Corp., Deerfield, IL) were regularly provided as a food source. Undifferentiated

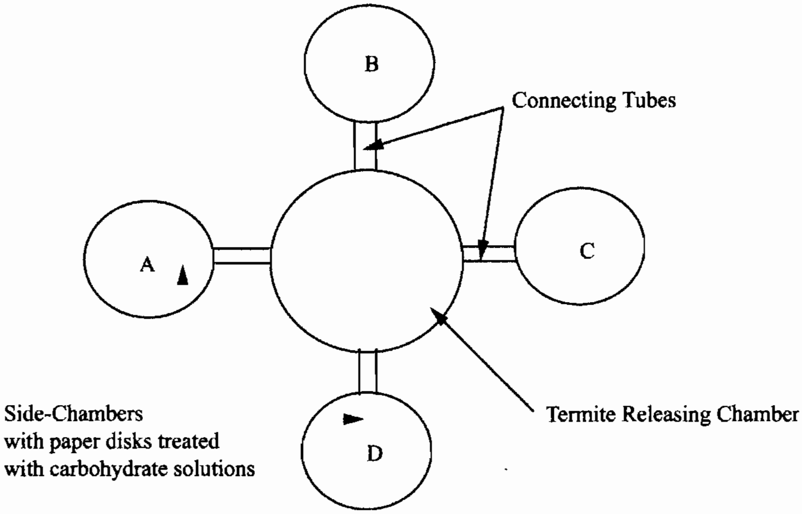

Fig. 1. Multiple choice feeding arena with termites released in the center chamber and side chambers A, B, C, and D containing paper disks treated with different carbohydrate solutions DIH_2O.

larval termites, the average worker weighing 1.6 ± 0.44 mg, were used for bioassays and radiolabel studies (Thorne 1996).

Chemicals. All of the following technical grade carbohydrates were obtained from Sigma (St. Louis, MO): pentose-monosaccharides ribose, xylose, and arabinose; hexose-monosaccharides glucose, fructose, and mannose; disaccharides sucrose and maltose; and trisaccharides melezitose, and raffinose. These carbohydrates were selected because they were at least partially soluble in water (Merck 1976). Gatorade powder (The Gatorade Co., Chicago, IL) containing sucrose, dextrose, citric acid, and sodium and potassium salts [86.7% of sugars (wt:wt)] was also tested. Carbohydrate solutions were prepared in deionized (DI) water (wt:vol).

Simple Choice Feeding Tests. To test the feeding preference of termites for different carbohydrates, termites were confined to disks of treated paper in choice tests. Initially paper disks were treated with 1, 2, 3, and 5% solutions of each carbohydrate and tested. Solutions to which termites showed the highest amount of feeding were ultimately selected. Two percent solutions were applied for all carbohydrates, except ribose for which both 5 and 2% and xylose for which 3% were applied. Small disks of brown paper towel (2.5 cm in diameter) were cut in half, and both halves were weighed. One half was dipped in a carbohydrate solution, and the other half was dipped in DI water. They were dried in a laminar flow hood for 24 h and were then weighed again. Dipping disks into 1, 2, 3, and 5% sugar solutions resulted in ≈20, 40, 50, and 75 μg of sugar per milligram of paper disk, respectively.

After drying, a treated and untreated half disk were adhered back together with a small strip of Scotch tape (3M, St. Paul, MN). The intact disk was placed in the bottom of a plastic petri dish (3.5 cm in diameter by 1.0 cm, Falcon, BD Biosciences, Franklin Lakes, NJ) with the tapped side facing downwards. Petri dishes and discs placed inside a plastic container (43.2 by 29.9 by 17.7 cm, Rubbermaid Inc., Wooster, OH) were maintained at 100% RH with DI water. Humidity indicator strips (Sud-Cheme Performance Packaging, Colton, CA) were taped to the walls of the container to ensure it was at 100% RH throughout the studies. The disks were allowed to condition for 48 h. Forty termites of similar size and weight were transferred to each petri dish. The petri dishes with termites were covered with a lid to keep moisture high and held in the container for 5 d. Appropriate controls also were used to check for mortality. Five replicates were conducted for each concentration and carbohydrate. At day 5, the termites were removed. The two halves of the disk were separated, cleaned by gently brushing the fecal material and dirt from them, and dried in a laminar flow hood for 24 h. The half disks were weighed again.

Multiple Choice Feeding Arena Tests. To determine whether termites discriminated between different carbohydrates, termites were tested in a four-way choice arena. Carbohydrates (5% ribose, 2% glucose, and 2% fructose) that showed the greatest amount of net feeding in two-choice feeding tests were tested. Choice-arena had a central chamber (5.0 cm in diameter by 1.0-cm petri dish) connected to four side-chambers (3.5 cm in diameter by 1.0-cm-diameter petri dishes) every 90° by 1.5-cm-long Tygon tubing (Saint-Gobain Performance Plastic Corp., Akron, OH) (Fig. 1). Paper disks treated with different carbohydrate solutions (5% ribose, 2% glucose, and 2% fructose) were randomly placed in the side chambers A, B, C, and D for each replicate. Circular disks (2.5 cm in diameter) of brown paper towel were weighed and dipped in selected carbohydrate solutions or DI water. The disks dried for 24 h and were weighed again.

After placing the disks in each of the side chambers of the choice arena, 5 g of sterilized play sand (Oglebay Norton Industrial Sands, San Juan Capistrano, CA) was added to the center releasing chamber and moistened with 1 ml of DI water. The choice arena setup was then transferred to plastic container described above to condition for 48 h. Sixteen replications for each test were made of this choice arena study. After 48 h, 100 workers of similar age and weight from same colony were placed in the central releasing chamber. Termites were observed until they settled down in different chambers and began feeding. Termites were allowed to feed for 7 d. After 7 d, the disks were removed, gently brushed to remove fecal material and dirt, dried for 24 h in a laminar flow hood, and weighed.

Radiolabeled [^{14}C]Sucrose Study. A stock solution was prepared by adding 40 μl of radiolabeled [^{14}C]sucrose (516 μCi/mmol and 110 μCi/ml) in a 20-ml sucrose solution (1.93%) so that the final concentration was 2%. Disks were prepared by dipping the filter paper disks (4.5 cm in diameter, Whatman no. 1) in 2 to 3 ml of 2% [^{14}C] sucrose solution and shaking off any extra solution. The disks were dried under laminar flow hood for 24 h. The final deposit of sucrose on the filter paper disks was 4.13% (wt:wt).

Background counts were determined by preparing termite samples and NaOH-treated paper similarly from a control setup without any radio label feeding substrate. Cytocint and Hionic-fluor scintillation fluid were tested separately for any background counts. All disintegrations per minute (dpm) counts were corrected for 54 dpm average background counts, and the liquid scintillation counting (LSC) efficiency was 95% for most of the radiolabel.

Uptake of [^{14}C]Sucrose. Filter paper disks (4.5 cm in diameter, Whatman no. 1, Whatman, Maidstone, England) were dipped in a 2% [^{14}C]sucrose solution, prepared as described above, and excess solution was gently removed. The disks were dried under a hood for 24 h and weighed. The difference in the weight [40 μg mg^{-1} (wt:wt)] represented the amount of sucrose on the disk. The [^{14}C]sucrose labeled filter paper disk was transferred to bottom of a 250-ml Erlenmeyer flask. Exactly 250 workers were placed on the paper disk. A filter paper strip saturated with 0.5 ml of a 1 M NaOH solution to absorb CO_2 produced by termites was suspended by a stainless steel insect pin from the rubber flask stopper. The flask also was provisioned with a filter paper (4.5 cm in diameter, Whatman no. 1) glued to the side and saturated with 1 ml of a 1 M H_2SO_4 solution to ensure constant humidity of ≈97% RH (Weast 1988, Haagsma 2003). Four replicates were tested.

To determine the amount of sucrose uptake by termites, a group of five termites were removed each day from each flask and placed in individual 20-ml scintillation vials. Termites were digested for 24 h in 100 μl of 15.8 N nitric acid. Ten milliliters of Cytoscint scintillation fluid (MP Biomedicals, Irvine, CA) was added to each vial and the vials were vigorously shaken. After 1 h, samples were placed in a scintillation counter (LS 3801, Beckman Coulter, Inc., Fullerton, CA) and counted for 1 h or until the dpm had a σ value of 2.

The amount of sucrose consumed and used in respiration was measured by determining the amount of [^{14}C]CO_2 trapped in the NaOH strips. Each day, the filter paper saturated with NaOH was removed and replaced with a new piece of NaOH-treated filter paper. Each filter paper strip was placed in a 20-ml scintillation vial and 10 ml of Hionic-fluor scintillation fluid (PerkinElmer Life and Analytical Sciences, Boston, MA) was added. Filter paper strips were then counted by LSC. Hionic-fluor scintillation fluid was used because it gives more precise counts on a solid substrate like filter paper. Data for CO_2 collection were adjusted for the number of termites within each replicate per sampling time. After 16 d, the labeled substrate was removed and replaced with untreated filter paper disk (4.5 cm in diameter).

To determine the amount of [^{14}C] label in the solid waste, all the fecal material on the top of the paper disk and at the bottom of the flask was gently brushed and transferred to a 20-ml scintillation vial. Ten milliliters of Hionic-fluor scintillation fluid was added to it and analyzed by LSC as described above.

To account for the [^{14}C]sucrose that might be present on outside of the cuticle of termites confined on [^{14}C]sucrose labeled filter paper, ≈200 termite workers were allowed to feed on 2% [^{14}C]sucrose treated paper (9.0 cm in diameter). At days 5, 10, and 15, four samples of five termites were collected, two samples being designated as unwashed and two as washed termites. The unwashed samples were digested 24 h in 15.8 M nitric acid (100 μl). The washed samples were rinsed three separate times with 2 ml of hexane to remove the [^{14}C]sucrose from the cuticle. Cytoscint scintillation fluid (10 ml) was added (MP Biomedicals) to each vial with washed and unwashed samples, and the vials were vigorously shaken. After, 1 h, samples were placed in a scintillation counter (LS 3801, Beckman Coulter, Inc.) and counted for 1 h or until the dpm had a σ value of 2.

To determine whether sucrose or its by-products were passed between workers by trophallaxis, contact or mutual grooming, termites (donors) were confined to 2% [^{14}C]sucrose treated paper and then held with unexposed workers (recipients). Two hundred worker termites were held on a [^{14}C]sucrose treated filter paper for 15 d. The disk was prepared as described above. Untreated termites (recipients) were marked by applying a small drop of pink paint (Painty paint pens, EK Success Co., Clifton, NJ) diluted with acetone (1:1 vol) and applied with a camel's-hair brush to the dorsal side of the termite abdomens. Recipient and donor termites were held together in a plastic petri dish (5.0 cm in diameter) provisioned with untreated filter paper disk (4.5 cm in diameter, Whatman no. 1) for 2, 5, 10, and 15 d. Two different ratios of donors to recipients (1:1 and 2:1) were used. Tests were replicated four times for each ratio and time period combination. At the end of days 2, 5, 10, and 15, four groups of five donor and recipient

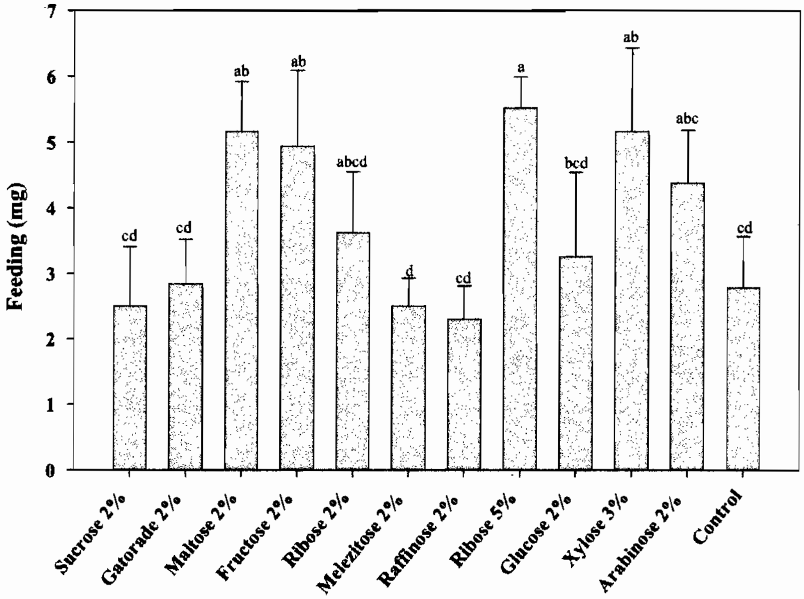

Fig. 2. Total feeding (milligrams) of treated paper and control paper disks together by termites over 5 d in simple choice test. Columns with same letter are not significantly different at $P < 0.05$.

termites from each treatment were placed in 20-ml scintillation vials and analyzed for [^{14}C]sucrose as described above.

Data Analysis. Results of termite feeding tests were analyzed with PROC GLM analysis of variance (ANOVA) procedure (SAS Institute 1999). Means were analyzed using Tukey's honestly significant difference (HSD) test for significance at $P < 0.05$.

Data for surface contamination and trophallaxis were analyzed by two-way ANOVA (SAS Institute 1999). Average values for unwashed minus washed individuals were added to background dpm (average 54 dpm), and subtracted from dpm data in subsequent analysis for trophallaxis and [^{14}C]sucrose utilization.

Results

Simple Choice Feeding Tests. The carbohydrates and Gatorade powder tested were selected based on initial screening of these chemicals at four different concentrations (1, 2, 3, and 5%). At three and 5% concentration, except for 5% ribose and 3% xylose, there was higher amount of moisture and mold on the paper disks, resulting higher mortality of termites. Two percent was selected for most sugars because of optimum feeding and survival of termites. There were significant differences in the total amount of feeding on both treated and untreated paper combined with various carbohydrate solutions ($F = 9.44$, df = 48, $P =$ 0.0001), with feeding being greatest on 5% ribose-, 3% xylose-, 2% maltose-, 2% fructose-, 2% arabinose-, and 2% ribose-treated paper. The total feeding on control (2.78 mg/40 termites/5 d) was not significantly different from feeding on 2% arabinose, 2% ribose, 2% glucose, 2% Gatorade, 2% melezitose, 2% sucrose, and 2% raffinose. The least amount of total feeding was on 2% raffinose (2.3 mg/40 termites/5 d) (Fig. 2).

Net feeding on the test compounds was determined by subtracting the amount of feeding on control half of the disk from the total amount of feeding (feeding on both halves). There were significant differences in the amount of net feeding on paper towel disk halves treated with various 2% carbohydrate solutions, 5% ribose, and 3% xylose ($F = 5.35$, df = 44, $P = 0.0001$). Mean net feeding was significantly higher on 5% ribose, 2% fructose, 3% xylose, 2% ribose, 2% maltose, and 2% glucose (Fig. 3). Lowest amount of net feeding was on raffinose (1.5 mg/40 termites/5 d)-treated paper (Fig. 3).

Multiple Choice Feeding Arena Tests. There were significant differences in the amount of feeding on paper disks treated with 5% ribose, 2% glucose, 2% fructose, and control paper disk ($F = 5.12$, df = 16, $P =$ 0.0113). Mean amount of feeding on 5% ribose (6.10 mg/100 termites/7 d), 2% glucose, and 2% fructose was not significant from one another (Tukey's HSD, $\alpha =$ 0.05) (Fig. 4). However, feeding on 5% ribose and 2% glucose was significantly higher than it was on control disk (Tukey's HSD, $\alpha = 0.05$) (Fig. 4).

In a similar test when given a choice between 2% ribose, 2% fructose, 2% xylose, and 2% maltose, mean feeding on disks treated with 2% carbohydrates was not significantly different from each other (Tukey's HSD, $\alpha = 0.05$).

Uptake of [^{14}C]Sucrose. Termites were allowed to feed on [^{14}C]sucrose labeled filter paper for 16 d. The radiolabeled filter paper was then replaced with clean filter paper and termites were allowed to feed on it for the next 15 d. Thus, a sample of five termites for each replication was analyzed for radioactivity on each con-

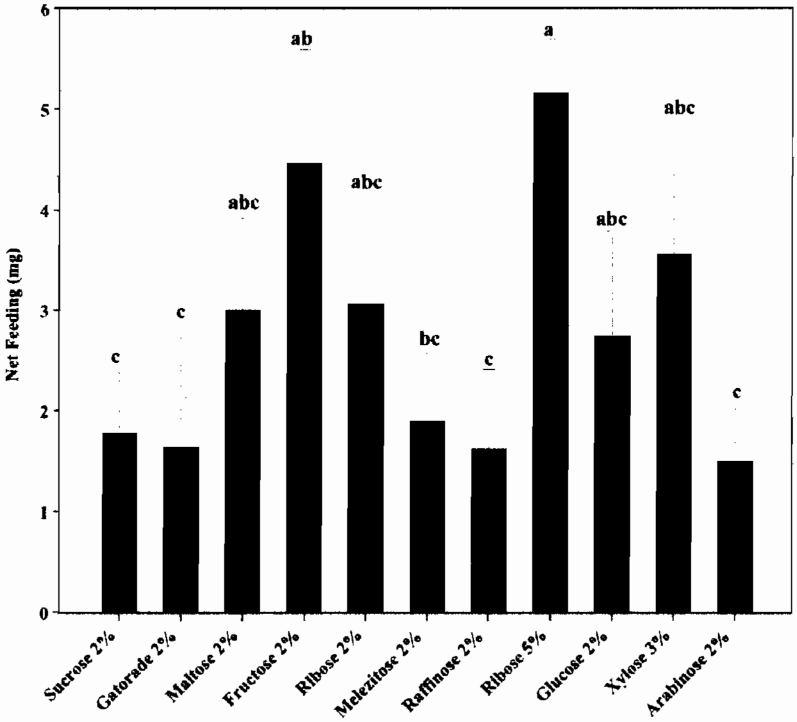

Fig. 3. Net feeding (milligrams of treated paper disks by termites over 5 d in simple choice tests. Net feeding = total feeding -feeding on control half of disk (n = 40 termites). Columns with same letter are not significantly different at $P < 0.05$.

secutive day for 31 d. The dpm counts for five termites increased from 71 on day 1 to 223 on day 12. Between days 13 and 16, the average activity counts stabilized at ≈233 dpm, suggesting a possible equilibrium between the intake, excretion, metabolism, and incorporation of label substrate into termite tissues (Fig. 5).

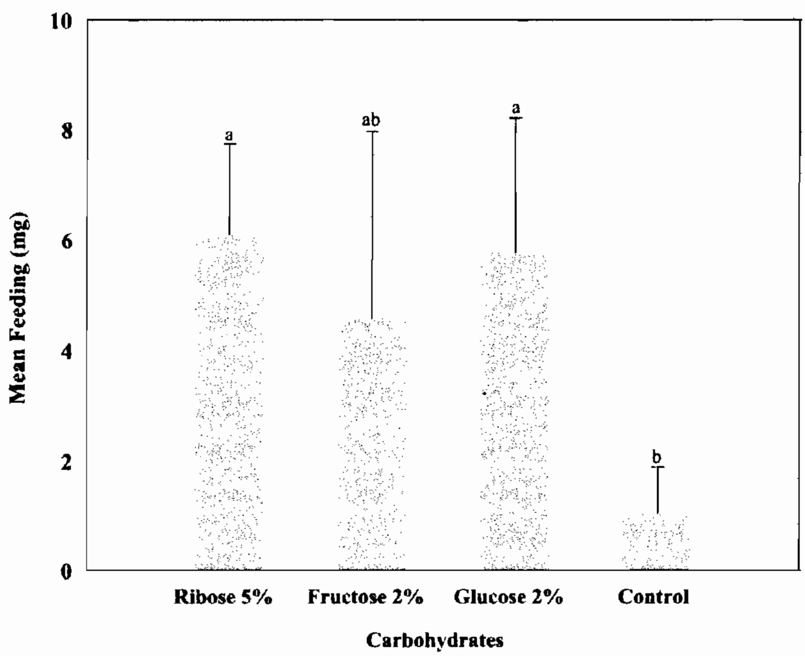

Fig. 4. Mean amount of feeding (milligrams) of treated paper by termites over 7-d period in a multiple choice feeding study with three different carbohydrates and one control (n = 100 termites). Columns with same letter do not differ significantly at $P < 0.05$.

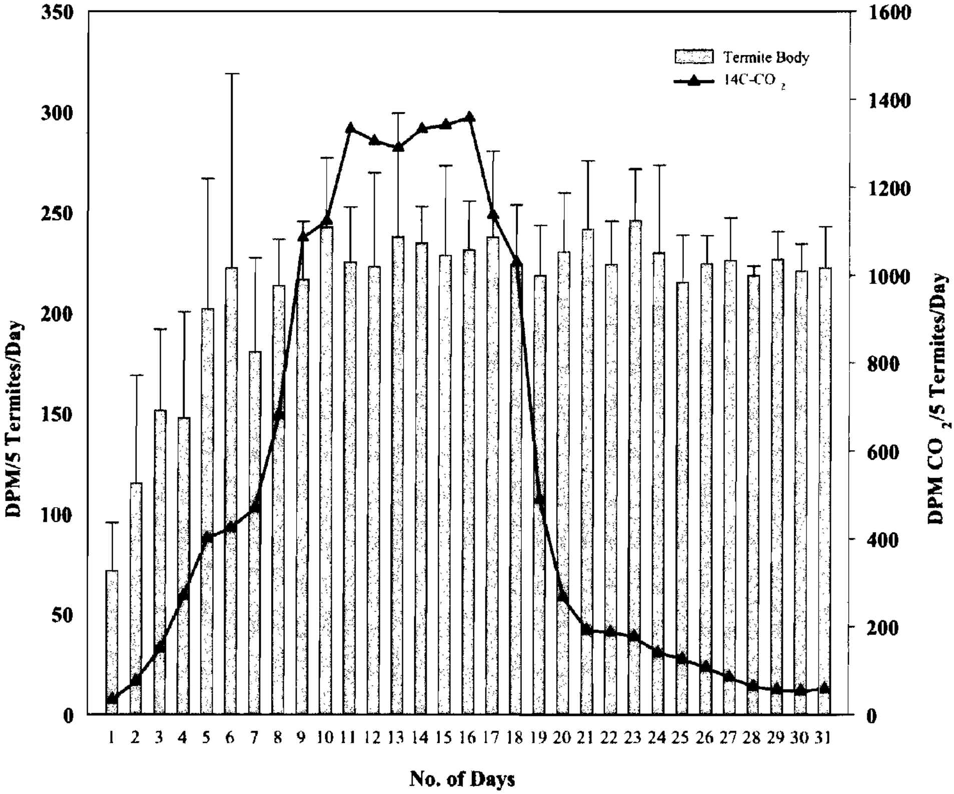

Fig. 5. Uptake and respiration of [14C]sucrose by termites feeding on treated filter paper for 16 d and then provided with untreated filter paper. Recovery of ^{14}C both from the termites (bars) and as CO_2 (line graph) produced by termites was recorded over 31 d. Bars indicate standard deviations.

The amount of $[^{14}C]CO_2$ produced increased steadily from an average of 33 dpm per five termites on day 1 to a high of 1,305 dpm on day 12 (Fig. 5). After day 12, the $[^{14}C]CO_2$ production stabilized with an average at ≈1,330 dpm counts between days 13 and 16 (Fig. 5). From day 14 to 16, no increase in the $[^{14}C]CO_2$ level was observed. It was assumed that the CO_2 production level reached to a saturation level. After replacing with a clean feeding substrate (day 17), $[^{14}C]CO_2$ production level dropped to 1,138 and 1,029 dpm counts on 17 and 18 d. On day 19, the drop was 489 dpm and remained <150 dpm after day 23. The study was culminated at day 31 when $[^{14}C]CO_2$ level decreased to an average of 59 dpm counts (Fig. 5).

The percentage of the total [14C]sucrose used for different metabolic processes, respiration, building body mass, and excretion, was calculated by the formula total amount ingested = amount used in respiration (%) + average amount in body mass (%) + amount excreted (%). Of the total amount of sucrose ingested, 89.2% (1.21 mg/16 d) was used in respiration, 9.3% was retained in body tissues, and only 1.5% was excreted. Most of the sucrose was used as a fuel for respiration process by the termites.

The unwashed termites had significantly higher dpm counts than did the washed termites over 15 d ($F = 79.16$, df = 5, $P = 0.0001$). The mean amount of [14C]sucrose radioactivity recorded in unwashed and washed termite workers on day 5 was significantly less than that on days 10 and 15 (Fig. 6). The surface contamination of unwashed termite workers ranged from 274 to 343 dpm, whereas the level of contamination in washed worker termites ranged from 194 on to 245 dpm (Fig. 6). The differences being attributed to surface contamination of the cuticle wash.

The mean amount of [14C]sucrose increased in recipient from seven (lowest on day 2) to 30 dpm (highest on day 15) for 1:1 donor to recipient ratio (Table 1). Overall mean radioactivity recovered from recipient termites when mixed with donor termites at 1:1 ratio (20 dpm) was significantly less than when (28 dpm) mixed with donor termites at 2:1 ratio. However, there were no significant differences in the radioactivity recovered from termites due to the ratios in which termites were mixed (donor:recipient) for a given sampling day ($F = 0.38$, df = 3, $P = 0.7667$). Higher amounts of radioactivity was recovered from recipient termites at day 15 for 2:1 (donor: recipient) compared with 1:1 (donor:recipient), but means were not significantly different (Table 1). The mean amount of donor dpm was highest 247 and 255 at day 2 and decreased significantly to 174 and 207 at day 15 for 1:1 and 2:1 donor to recipient ratios, respectively (Table 1). There was a significant effect of time and

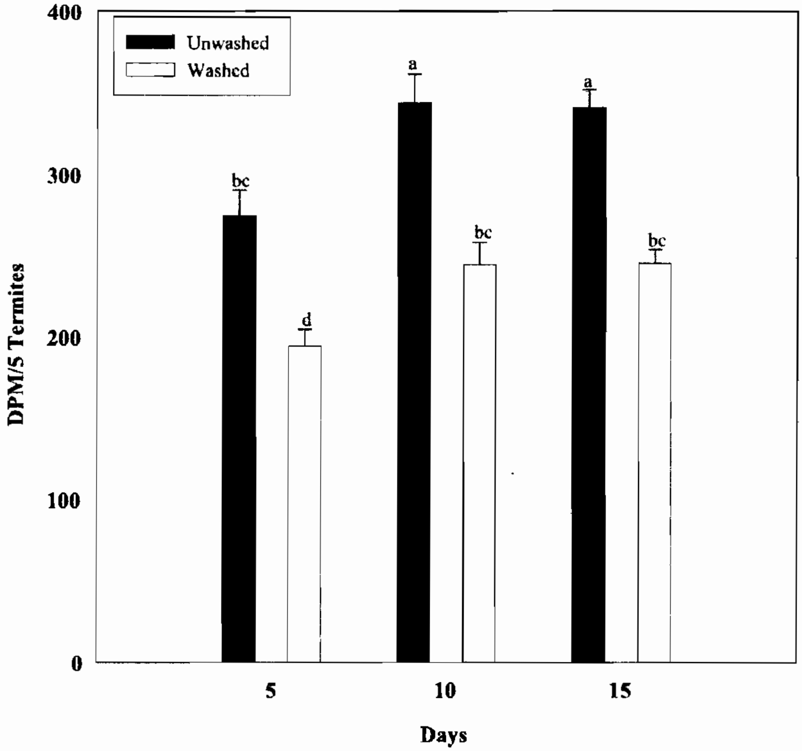

Fig. 6. Cuticular contamination due to surface contact during feeding on radiolabeled substrate. Columns with same letter are not significantly different at $P < 0.05$.

mixing ratios on the radioactivity recovered from the donor termites at the end of the study ($F = 4.94$, df = 7, $P = 0.0014$). There was a significant difference in the mean amount of [^{14}C]sucrose recovered from recipient termites for different ratio and days postmixing ($F = 11.52$, df = 7, $P = 0.0001$), (Table 1). However, differences in DPM means were attributable more to days postmixing ($F = 22.16$, df = 3, $P = 0.0001$) rather than mixing ratio ($F = 13.04$, df = 1, $P = 0.0014$).

Discussion

Sugars are phagostimulants for many insects (Bartlet et al. 1994), especially for all phytophagous insects studied. *R. hesperus* consumed significantly greater amounts of brown paper towel disks when it was treated with solutions 5% ribose, 3% xylose, 2% maltose, 2% fructose, 2% arabinose, 2% ribose, and 2% glucose than they did on untreated paper. In a similar study to ours, Waller and Curtis (2003) showed that *R. flavipes* and *R. virginicus* consumed more filter paper treated with 1% glucose and sucrose and 3% xylose, compared with water-treated paper. Workers of *Microtermes traegardhi* (Sjöstedt) consumed significantly larger amount of millet disks soaked in sugars in preference to discs soaked in water (Abushama and Kamal 1977). Contrary to these above-mentioned studies, a recent study (Swoboda et al. 2004) did not find different sugars to be phagostimulants. Their study suggests a preferential feeding on sugar-treated disks only in the presence of a competing food source. These differences may be due to the manner in which

Table 1. **Donor and recipient levels of [^{14}C]sucrose after mixing termite workers in two different ratios**

	dpm/5 termites[b]							
Days postmixing[a]	2		5		10		15	
Ratio (donor:recipient)	Donor	Recipient	Donors	Recipient	Donors	Recipient	Donor	Recipient
1:1	247 ± 35.3	7 ± 3.5d	216 ± 34.0	15 ± 2.6cd	174 ± 18.4	26 ± 6.6abc	178 ± 22.9	30 ± 8.7ab
% transfer		2.75		6.49		13		14.42
2:1	255 ± 34.1	12 ± 4.6d	228 ± 25.2	26 ± 8.3abc	210 ± 20.5	38 ± 8.5a	208 ± 17.9	37 ± 8.3a
% transfer		4.49		10.23		15.32		15.10

[a] All the radioactivity counts are in dpm per five termites. Percentage of transfer calculated as (dpm recipients * 100/dpm donors + recipients).

[b] Mean ± SD amount of radioactivity in recipients at different times represented with same letters is not significantly different from one another at $P < 0.05$.

feeding was determined. Swoboda et al. (2004) determined the area fed upon as an indicator of the total feeding. However, we have observed termites feeding on the top thin layer of the treated disk resulting in a decrease in the disk weight without any obvious increase in the visual area fed upon by termites.

Results from net feeding demonstrated a similar trend as total feeding in terms of preference toward carbohydrate-treated paper disks. Higher net feeding on the paper disk treated with a specific carbohydrate suggests greater phagostimulatory effect of that carbohydrate compared with total feeding and feeding on controls. Total feeding takes into account both treated and control part of disk together.

When offered several carbohydrates at the same concentrations simultaneously, termites did not show a preference toward pentose sugars (2%) over hexose sugars (2%). Xylose (2%), ribose (2%), fructose (2%) and maltose all at 2% were used to determine whether termites could differentiate the sugars. However, termites clearly showed stronger preference toward 5% ribose compared with 2% fructose, 2% glucose, and control. Net and total feeding was not significantly different in all the four sugars tested in simple choice experiments. The results suggest that termites have limited ability to discriminate between the carbohydrates based on their individual phagostimulatory effects. Amino acids and sugars have been proposed as additives to bait matrices for control of subterranean termites. *R. santonensis* showed a clear feeding preference for certain sugars, including glucose and sucrose (Reinhard and Kaib 2001). Morales-Ramos and Rojas (2003) reported that the total amino acid, sugar, and fatty acids concentrations in eight common wood species were highest in birch (0.0011%), ash (0.0004%), and Douglas-fir (0.0014%), respectively. As observed in our experiments and pervious studies (Waller and Curtis 2003), these compounds are only active at very high concentrations, and termites under natural conditions probably never encounter such high concentrations of freely available carbohydrates.

It has been widely reported that termites are attracted to wood decayed by certain fungi. Brown-rot fungi and white-rot reduce the degree of polymerization of cellulose and hemicellulose during decaying process (Highely and Kirk 1979). This leads us to speculate that the attractiveness of fungi degraded wood may be attributable to the presence of monosaccharides and disaccharides in wood as by-products of fungal decay.

The radiolabeled [^{14}C]sucrose studies suggest that termites are able to digest the sucrose on the treated paper and use it in respiration producing [^{14}C]CO_2. Termites used most of the sucrose in respiration (89.2%), in body tissues (9.3%) and only a very small fraction is excreted (1.5%). The [^{14}C]label in the termite body remained approximately constant once it reached an equilibrium point even after termites were feeding on the clean filter paper. This suggests that excess sucrose was probably stored as reserve in fat bodies. Incorporation of excess [^{14}C]sucrose in the termite is responsible for a constant amount of ^{14}C label recovered and not readily available for respiration or trophallaxis. The percentage of [^{14}C]sucrose used studies agree with the hypothesis that the three acetate formed per glucose monomer are absorbed from the hind gut and oxidized by the termite to support up to 100% of the insect's respiration requirement (Brauman et al. 1992).

Termites can acquire the radiolabeled sucrose from the donor termites by trophallaxis, grooming or body contact. The external contamination of body surfaces from the radioisotope impregnated food can occur (MacMahan 1969). In a review by MacMahan (1969), it was suggested by Alibert (1959) and Gosswald and Kloft (1963) such contamination by surface contact can be minimized by covering the radioactive filter paper, used as food, with plastic screens and allowing termites to feed only through small holes. In one of our preliminary trials with *R. hesperus*, the mortality in such a setup was very high (>10%). We used an established technique in our laboratory (Haagsma 2003) to account for external contamination by washing the donor termites and comparing with unwashed donors. There were significant amount of contamination on the body of termites exposed to [^{14}C]sucrose-treated surfaces. When termites were allowed to feed on a filter paper treated with [^{14}C]sucrose ≈43% of the [^{14}C]sucrose from individual termites is due to the contamination of the body surface. However, the differences between the washed and unwashed individuals reached a steady state on day 10 and 15. In general, the rate at which social insects acquire radioactivity in tracer studies may differ considerably based on feeding habits, properties of food source, size, age, and caste of the individual insects (MacMahan 1969, Hooper 1998). Therefore, there are differences in terms of time and amount of radioactive matter acquired by termites can be found in different studies. In *Incisitermes minor* (Hagen), it took 3 d for adequate uptake of a rubidium (radioactive solution)-impregnated food source to study feeding relationship (Cabrera and Rust 1999).

The amount of [^{14}C]sucrose transferred within termites ranged from 3% on day 3 to 17% on day 15, depending on the ratio of donors to recipients. In a similar study, donors transferred ≈20% of the isotope to the recipient groups in three termite species (Suarez and Thorne 2000). In the same study, uptake of ^{60}Co isotope was similar in two species of *Reticulitermes* and peaked at ≈14 d.

In a study (K. Haagsma and M.K.R., unpublished data) with [^{14}C]cellulose, there was a relatively lower transfer (5–8%) of radiolabeled cellulose between termite workers held in situations similar to this study. Any differences in such transfers can be attributed both to the nature of radiolabeled feeding material used ([^{14}C]sucrose in current study) and also the ratio of the donor to recipient used in the study. As described below, most of the sucrose taken up by termites was readily available for own use, and there was little sharing with nestmates without undergoing further extensive digestive processes, as later may be the case with cellulose. However, when the ratio of the donor to recipient was two-fold there was no significant increase in terms of final transfer of radioactive material from donor to recipient, suggesting that the grooming and food sharing activity between the termite members have a limitation in terms of the amount of material that can be shared. But overall mean amount of food shared at two-fold donor to recipient ratio suggests that collectively, the effect may be significant because the individual termites have more opportunity to share food with larger number of nestmates. Our aim in this study was to observe the trophallaxis behavior ability in termites workers when offered a readily available "unnatural" energy source such as sucrose and therefore, we did not look into other trophallaxis process between workers and soldiers or nymphs.

The results of trophallaxis suggest that when the carbohydrate is offered as more readily available form to termites as opposed to "natural" form in wood or cellulose, it is more readily and directly used by termites without much of sharing with other workers. Thus, most of the radiolabel acquired by recipient termites may be just a result of body contact and mutual grooming. It may be possible that as soon as such readily available excessive carbohydrate is ingested, it can be acted upon by esterases very easily, readily oxidized, and broken to acetate molecules for fueling respiration. Thus, excess carbohydrate is no longer available in the form of food normally exchanged during trophallaxis.

This research affirms the potential use of simple carbohydrates in termite baits to make them more palatable and increase consumption of slow-acting IGRs or metabolic inhibitors. Field evaluations of such feeding stimulants will provide better insight of their importance. In situations where the rate of abandoned bait stations is very high, the use of carbohydrates may help increase station fidelity and the amount of toxicant incorporated into the colony.

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