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Natural Wood-Consumption Rates and Survival of a Dry-Wood and a Subterranean Termite at Constant Temperatures[1,2]

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ABSTRACT

Groups of 2 species of termites, *Paraneotermes simplicicornis* (Banks) and *Heterotermes aureus* (Snyder), were separately confined on each of 3 or 4 wood species for 28 days at constant temperatures ranging from 16 to 36°C. Wood consumption was measured in milligrams wood consumed per group per 28 days and milligrams wood consumed per hour per gram dry-weight of termite. *P. simplicicornis* groups consumed more wood at all temperatures than did those of *H. aureus*. Wood consumption was highest at 28°C for *P. simplicicornis,* and at 36°C for *H. aureus*. Survival of *P. simplicicornis* decreased with increasing temperature, while it increased for *H. aureus*. When corrected for survival, consumption measured as milligrams wood consumed per hour per gram dry-weight of termite, for both species, gave a quadratic regression with temperature within the range of 16–36°C. The order of increasing or decreasing consumption of wood species, for either termite, varies with the method of measurement. Hourly rates of wood consumption based on unit dry-weights of termite, and expressed as a function of temperature, provide realistic expressions needed in computer models for the long-term prediction of wood removal from an ecosystem, as well as an absolute basis for interspecific comparisons.

Termites play an important role in the detritus cycle in many ecosystems and, along with microorganisms, function to break down and recycle dead, woody plant material. For purposes of developing a computer model to analyze the role of subterranean termites in desert ecosystems, we have concluded that rate of wood consumption as a function of temperature and termite biomass is fundamental to estimating the quantity of wood which a given termite species can process. *Paraneotermes simplicicornis* (Banks) and *Heterotermes aureus* (Snyder) were chosen for study because they are among the major processors of buried and superficial dead wood in desert and grasslands over much of southern Arizona.

Becker (1969) has recently reviewed the role of temperature and other variables on laboratory-rearing of termites for testing purposes. The influence of temperature on wood consumption has been examined for *Heterotermes indicola* Wasmann (Becker 1962), and for 6 other species (Becker 1967); for *Coptotermes formosanus* Shiraki and *Reticulitermes flavipes* (Kollar) (Smythe and Williams 1972), and for *Reticulitermes virginicus* (Banks) (Smythe 1972).

Factors affecting wood consumption by termites are numerous and complexly interrelated. Among the most important of these are wood species and hardness, presence of toxic substances, feeding inhibitors or deterrents, presence or absence of fungi and degree of fungal decay, moisture content of wood and soil, and temperature. Because of the state of our knowledge of this complex subject, and for simplicity, most of these studies deal with the consumption of various species of timber at 1 or 2 temp. However, Becker (1965) and Smythe et al. (1971) have also considered the influence of fungal attack and moisture on wood consumption by several species of termites. Our concern here is with temperature and wood species.

METHODS AND MATERIALS

Termites.—Two foraging groups of *P. simplicicornis* were collected near Tucson, the 1st in a mesquite stump, and the 2nd from the base of a dead cholla cactus. Three foraging groups of *H. aureus* were collected at the Santa Rita Experimental Range, ca. 40 km S of Tucson, using rolls of toilet paper as bait (LaFage et al. 1973). All termites were held at 25°C for 3 weeks, on filter paper with a piece of 4% agar as a moisture source.

Woods.—Three species of wood which *P. simplicicornis* commonly attacks in the Tucson area were chosen: catclaw acacia, *Acacia Greggii* Gray; jumping cholla, *Opuntia fulgida* Engelm.; and mesquite, *Prosopis juliflora* var. *velutina* (Wooton) Sarg. *Cercidium floridum* Benth., blue palo verde, was added to the list of host woods used for *H. aureus,* since this termite attacks all of these conspicuous

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trees in the local plant communities. Blocks were cut from sound, dead branches of each species, 6×25×25 mm for *P. simplicicornis* and 6×12×12 mm for *H. aureus.* Before testing, blocks were oven-dried at 105°C for 24 h, and weighed. Although we cannot say that this wood had not been attacked by fungi, it did not appear to be altered significantly.

Test Procedures.—Experimental units consisted of groups of termites in closed containers with blocks of wood on moistened sand. Group size and caste composition varied somewhat with termite species and replication. The group size for *P. simplicicornis* was 44, and for *H. aureus,* 100. The caste composition of the test groups was varied to match the caste proportions of the foraging groups from which they were taken, and the resulting composition of each replication for each species is shown in Table 1. Dry-weights of termites were obtained by drying at 60°C for 24 h in a vacuum oven. Average dry-weights for each caste were determined at the end of the experiment, by using the live specimens from ½ of the experimental units. These average caste-weights were then used to estimate the dry-weight of the termites per experimental unit.

Each experimental unit for *P. simplicicornis* consisted of 1 pint jar containing 40 ml sterile, washed sand, 16 ml distilled water, and a block of wood gently pressed into the sand; for *H. aureus,* each unit was a 5-dr, snap-cap vial, 10 ml sand, and 4 ml distilled water. The termite groups were then immediately added to each container. Each experimental unit was held at an assigned temperature of 16, 20, 24, 28, 32 or 36°C, in a temperature cabinet adjusted to ± 1.0°C and ca. 100% RH. The limits of the temperatures used in our experiments are known to be well within the foraging limits of *H. aureus* (LaFage et al. 1973), and are probably within the foraging limits of *P. simplicicornis.* Each combination of variables received 3 replications.

Containers were examined daily with minimal disturbance, to see that the groups were still active. If all the termites in a group had died, the container was placed in a freezer to prevent decay of the wood. At the end of the test period (28 days), the termites of each surviving group were counted, the blocks were oven-dried for 24 h and reweighed for calculating weight loss due to feeding. Wood consumption was determined either by measuring the total amount of wood removed by each group of termites during the test period, regardless of survival, or by calculating the amount of wood consumed per hour per gram dry-weight of termites. The latter calculation was made by dividing the amount of wood consumed per group by the number of hours survived (if less than 28 days, number of days was multiplied by 24 to give number of hours survived), then dividing by the estimated dry-weight of the termites in grams.

Data Analysis.—The wood-consumption data were examined by an analysis of variance, utilizing a randomized complete-block design with a factorial selection of treatments. The survival data were transformed to square root of arc sine before analysis. Means were tested for significance at the 5% level, and separated using the Student-Newman-Keuls' test. Regression equations were determined by the method of orthogonal polynomials.

RESULTS AND DISCUSSION

Groups of *P. simplicicornis* consumed more of each species of wood at all temperatures than did those of *H. aureus* (Table 2, Fig. 1). The temperature at which each species of termite consumed the most wood varied with the wood species. With *P. simplicicornis,* the amount consumed generally increased with increasing temperature to 28 or 32°C, and decreased at 36°C. For *H. aureus,* wood consumption generally increased with increasing temperature from 16 to 36°C. Combining values for all woods, *H. aureus* showed a linear relationship for wood consumption, $Y = 8.37 + 2.61X$, while *P. simplicicornis* showed a quadratic relationship, $Y = -563.38 + 61.18X - 1.03X^2$, within the chosen extremes (Fig. 1). Becker (1969) showed that the amount of wood eaten by 6 species of termites in 3 families increased linearly to an optimum temperature, then decreased rapidly. Wood consumption was optimum between 30 and 34°C, and fell off rapidly between 32 and 36°C, for all 6 species. Smythe and Williams (1972) and

Table 1.—Group weights and caste composition of each replication for each species of termite used in wood-consumption tests. Individual caste weights are means determined by drying at 60°C for 24 h in a vacuum oven.

	P. simplicicornis				*H. aureus*			
Caste	Caste wt, mg	Rep. 1	Rep. 2	Rep. 3	Caste wt, mg	Rep. 1	Rep. 2	Rep. 3
Larvae	0.967	21	6	6	0.336*	99	99	98
Soldiers	3.091	2	1	1	0.479	1	1	2
Nymphs (short wing pads)	2.224	4	6	6	—	—	—	—
Nymphs (long wing pads)	3.131	14	20	20	—	—	—	—
Pseudergates	2.344	3	11	11	—	—	—	—
Group wt, mg		86.251	110.641	110.641		33.743	33.743	33.886

* Undifferentiated larvae of at least the 3rd instar, or workers.

Table 2. — Wood consumption by 2 species of termites at several temperatures and on various species of wood. Duration of tests, 28 days.

Treatment	$\overline{X}$ % survival* all woods	Mg wood consumed/group (Survival disregarded)					Mg wood consumed/h per gram dry-weight of termite (Survival considered)				
		OPUFUL**	PROJUL	ACAGRE	CERFLO	All woods	OPUFUL	PROJUL	ACAGRE	CERFLO	All woods
				Paraneotermes simplicicornis (group size = 44)							
16°C	91 a	107.3 b	200.9 a	145.2 b	—	151.1 b	1.63 c	2.87 a	2.14 b	—	2.21 c
20°	96 a	178.0 ab	259.7 a	293.6 a	—	243.8 a	2.65 bc	3.80 a	4.23 ab	—	3.56 bc
24°	92 a	260.2 ab	364.6 a	339.7 a	—	321.5 a	3.77 ab	5.28 a	5.04 ab	—	4.70 ab
28°	61 ab	257.2 ab	400.1 a	314.8 a	—	324.0 a	3.75 ab	9.39 a	6.97 a	—	6.70 a
32°	67 ab	313.3 a	349.7 a	374.3 a	—	345.8 a	4.73 ab	7.15 a	5.59 ab	—	5.82 a
36°	54 b	278.4 ab	245.1 a	370.5 a	—	298.0 a	5.56 a	8.71 a	5.34 ab	—	6.54 a
All temperatures on:											
OPUFUL	84 a	232.4 b					3.68 c				
PROJUL	69 a		303.4 a					6.20 a			
ACAGRE	78 a			306.4 a					4.88 b		
				Heterotermes aureus (group size = 100)							
16°	26 a	23.5 a	21.2 a	50.9 a	105.1 b	50.2 c	1.04 c	1.29 a	2.24 a	4.77 b	2.34 b
20°	48 a	51.5 a	22.9 a	40.5 a	107.2 b	55.5 bc	2.27 bc	2.06 a	2.66 a	4.72 b	2.93 b
24°	59 a	76.7 a	32.0 a	50.4 a	152.3 a	77.9 ab	3.68 ab	3.52 a	2.32 a	6.71 a	4.06 a
28°	45 a	65.1 a	37.1 a	41.3 a	169.4 a	78.2 ab	5.12 a	3.83 a	3.51 a	7.46 a	4.98 a
32°	59 a	88.4 a	60.2 a	76.0 a	165.5 a	97.5 a	4.62 ab	5.11 a	3.35 a	7.29 a	5.09 a
36°	56 a	88.9 a	78.8 a	79.1 a	145.1 ab	98.0 a	3.92 ab	3.47 a	3.49 a	6.43 ab	4.33 a
All temperatures on:											
OPUFUL	59 a	65.7 b					3.44 b				
PROJUL	39 a		42.0 c					3.21 b			
ACAGRE	43 a			56.4 bc					2.93 b		
CERFLO	54 a				140.8 a					6.23 a	

* Means in a column or diagonal followed by the same letter are not significantly different at the 5% level by Student-Newman-Keuls' test.
** Species of wood: ACAGRE, *Acacia Greggii;* CERFLO, *Cercidium floridum;* OPUFUL, *Opuntia fulgida;* PROJUL, *Prosopis juliflora* var. *velutina.*

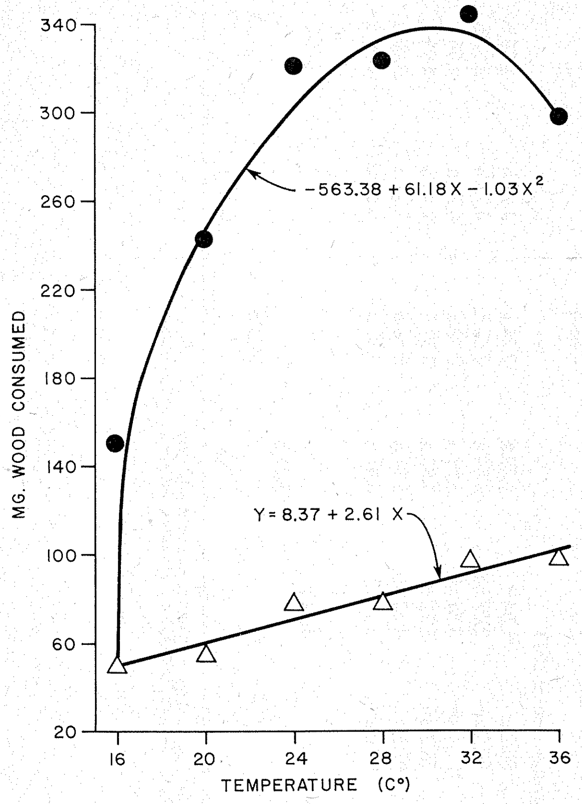

FIG. 1.—Mean wood consumption by groups of *Paraneotermes simplicicornis* (3 wood species, upper curve) and *Heterotermes aureus* (4 wood species, lower curve) at 6 temp over a 28-day period. Data for supper curve based on 9 replications; for lower curve, 12 replications.

Smythe (1972), working with *Reticulitermes flavipes* and *R. virginicus,* reported increased consumption up to 30 or 31.5°C, with a rapid decline thereafter.

Survival of *P. simplicicornis* decreased with increasing temperature. Using a similar range of temperatures and high humidity, Sen-Sarma (1965) found such a decrease in group longevity of pseudergates of *Kalotermes flavicollis* (F.) with increased temperature. *H. aureus* appeared to follow an opposite trend with respect to temperature; that is, survival increased with increasing temperature, although no significant differences were found. Smythe and Williams (1972) showed that *Coptotermes formosanus* was able to survive 4-week periods at tempertures of 15–35°C, near the range of our experiments, while *R. flavipes* and *R. virginicus* (Smythe 1972) did not survive well at 35°C. The differences in survival with increasing temperature between *P. simplicicornis* and *H. aureus* are probably related to the differences in foraging methods between the 2 species. Although both species have underground nests, *P. simplicicornis* attacks buried or partially buried wood (Light 1937) while *H. aureus* regularly attacks superficial as well as buried wood (Haverty and Nutting, unpublished data). Differences between maximum surface and 15-cm soil temp may reach as high as 22° (38–60°C) on a dry, sunny summer day on the Santa Rita Experimental Range (Cable 1969), where much of our field work has been done. Although *H. aureus* was never found foraging in situations where temperatures rose above 47°C (LaFage et al. 1973), it can withstand brief exposure to 53°C with very little effect on survival (Collins et al. 1973). The upper foraging limit for *P. simplicicornis* is not known, but is likely much lower.

Survival, particularly of *H. aureus,* presented a problem during the course of the experiments. Active, and apparently healthy, groups occasionally died, but their rather sudden demise did not seem to result from attacks by the usual mites, nematodes or fungi. Nineteen of the 72 groups of *H. aureus* terminated before the end of the 28-day period, but only 6 of the 54 groups of *P. simplicicornis* terminated early. The consumption rates for each wood species in milligrams wood consumed per hour per gram dry-weight of termite are presented in Table 2 and plotted in Fig. 2. When all species of wood are combined, rates regressed as a function of temperature give $Y = -8.63 + 0.87X - 0.013X^2$ for *P. simplicicornis,* and $Y = -6.89 + 0.75X - 0.012X^2$ for *H. aureus.*

When all temperatures are combined, the 2 termite species demonstrated definite differences in wood-consumption rates with respect to plant species. With consumption rate expressed as milligrams wood consumed per group per 28 days, the order of consumption for *P. simplicicornis* was: catclaw acacia > mesquite > jumping cholla, and for *H. aureus:* blue palo-verde > jumping cholla > catclaw acacia > mesquite. With consumption rate expressed as milligrams of wood consumed per hour per gram dry-

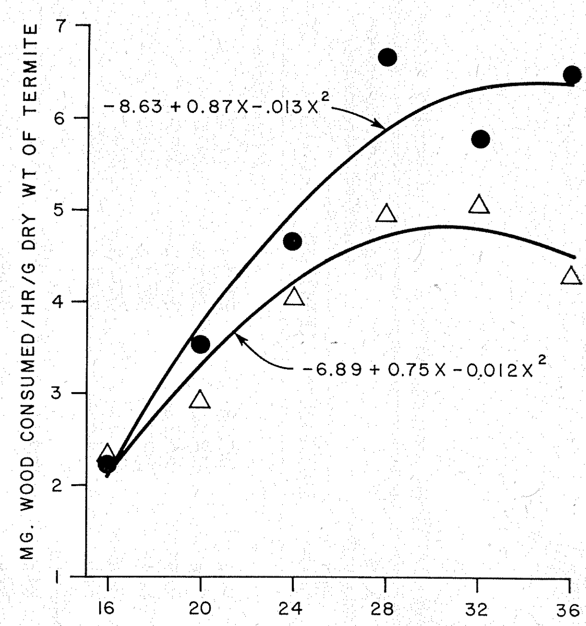

FIG. 2.—Mean wood-consumption rates for *Paraneotermes simplicicornis* (3 wood species, upper curve) and *Heterotermes aureus* (4 wood species, lower curve) at 6 temp. Data for upper curve based on 9 replications; for lower curve, 12 replications.

weight of termite, the order of consumption for *P. simplicicornis* is changed to: mesquite > catclaw acacia > jumping cholla, and for *H. aureus,* to: blue paloverde > jumping cholla > mesquite > catclaw acacia.

Wood consumption by termites has most often been reported as milligrams of particular wood species consumed over a given experimental period at 1 or more temp., either by a specified number of termites (Smythe and Williams 1972; Becker 1962) or by a given live-weight of termites (Gay et al. 1955). It has also been expressed as percent of wood weight lost under specified conditions (Behr et al. 1972). These expressions are not readily interconvertible, nor do they provide a common basis for comparing wood consumption between species. Further, since mortality at higher temperatures is 1 reason for low wood consumption when measured over long periods (Smythe and Williams 1972; Smythe 1972), and since some desert termites forage at rather high temperatures (Collins et al. 1973), we feel that an hourly rate expressed as a function of temperature and termite biomass is a more realistic measure of wood consumption. Thus, such a rate is particularly desirable in computer modeling, for example, in predicting the amount of wood a termite population might remove from an ecosystem on a long-term basis, while it also provides a common basis for comparing wood consumption between termite species.

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