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ORIGINAL ARTICLE

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Feeding responses of the western dry-wood termite *Incisitermes minor* (Hagen) (Isoptera: Kalotermitidae) against ten commercial timbers

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Abstract Five Japanese timbers, four timbers from the USA, and one Malaysian timber were evaluated for their resistance to the invasive dry-wood termite *Incisitermes minor* (Hagen) using laboratory choice and no-choice feeding tests with holed specimens. The highest survival rates of *I. minor* in both the heartwood and sapwood no-choice feeding tests were more than 70% after 3 months. When offered sapwood and heartwood choice feeding tests and the combined choice feed·ing tests, the highest survival rates of *I. minor* were more than 75% after 3 months. With regards to the percentage of wood mass losses in the no-choice and choice feeding tests, karamatsu (*Larix leptolepsis*), buna (*Fagus crenata*), and Douglas fir (*Pseudotsuga menziesii*) were classified as "resistant" species among the ten sapwood specimens. In the heartwood no-choice and choice feeding tests, the resistant species were buna, karamatsu, Douglas fir, sugi (*Cryptomeria japonica*), akamatsu (*Pinus densiflora*), and western red cedar (*Thuja plicata*). The ranking of the resistance of the ten commercial timbers against *I. minor* was buna > karamatsu > sugi > western red cedar > Douglas fir > rubber > western hemlock > hinoki > spruce.

Key words Feeding responses · Commercial timbers · Western dry-wood termite · *Incisitermes minor* (Hagen)

Introduction

The factors affecting wood consumption by termites are numerous and highly interrelated. It has been widely accepted that wood species palatability is one of the influential parameters of termite wood consumption. Studies have shown that each species of termite has its own preference for different wood species, which may play a role in wooden structure damage.[1–7]

The western dry-wood termite, *Incisitermes minor* (Hagen), is one of the five important dry-wood termite species causing serious damage in wooden structures and wood products in the United States,[8] and has been sporadically reported in Japan.[9–11] *Incisitermes minor* has been reported to attack timbers in the USA such as eucalyptus, willow, sycamore, oak, alder, Monterey cypress, redwood, California laurel, buckeye, peach, pear, almond, walnut, cherry,[12] and Douglas fir.[4] A study of the infestation of houses by *I. minor* in the Kansai and Hokuriku areas in Japan also revealed that American timbers such as Douglas fir and western hemlock and Japanese timbers such as hinoki and sugi, were mostly found to be the type of timbers that were attacked.[11] Kofoid and Bowe[13] and Rust and Reierson[3] suggested that the factor determining wood selection by termites in nature included the differences between heartwood and sapwood.

Morales-Ramos and Rojas[14] mentioned that laboratory choice feeding tests were more appropriate to determine termite wood preference than no-choice tests. No-choice feeding tests with termitary composed of different species of wood veneer showed a 46% survival rate for the dry-wood termite *Cryptotermes brevis* (Walker) in preferred woods (maple, yellow poplar, tupelo, sycamore, sweet gum, and ash) and 4% in less preferred woods (Spanish oak, cherry, African mahogany, white pine, black walnut, and white oak) after 12–15 months.[15] Rust and Reierson[3] have conducted forced wood preference tests with *I. minor* using paper towels treated with extractives of various wood species, resulting in the highest survival rate of 97.8% in ponderosa pine and the lowest of 75.6% in red oak after 13 days. In another study, no-choice feeding tests were conducted using flat surface small wood blocks, measuring 20 (R) × 20 (T) × 10 mm (L), against the dry-wood termite *Cryptotermes cynocephalus* (Light), and the lowest survival rate of 50.67% was recorded with southern yellow pine and

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the highest of 68.67% with jabon [*Anthocephalus chinensis* (Lam.) Rich. Ex Walp.] wood after 10 weeks.[16] However, to our knowledge, no study on the wood preference of dry-wood termites with the choice feeding test method using wood blocks has been reported so far, and there is no standard choice feeding test method for dry-wood termites.

The objectives of this study were to design choice and no-choice feeding test methods using holed specimens to study the wood preferences of *I. minor*, and to determine the resistance of ten commercial wood species commonly used in Japan against *I. minor*.

Materials and methods

Termites

Incisitermes minor pseudergates were collected from infested timbers in Yokohama city, Kanagawa Prefecture, Japan, and were used as test organisms. The termites were extracted from the timbers and kept in plastic containers with lids containing small wood blocks of Douglas fir as both food sources and harborage. The containers with the termites were kept in a termite culturing room of the Research Institute for Sustainable Humanosphere (RISH), Kyoto University, at 28° ± 2°C and greater than 85% relative humidity (RH) in a dark room for at least 1 week before testing to ensure that only healthy termites would be used in the experiment.

Wood specimens

Five commercial Japanese timbers, four commercial timbers from the USA, and one Malaysian timber were used for the feeding tests (Table 1).

Two different sizes of timbers were designed for the test. Wood specimens of 30 (R) × 30 (T) × 50 mm (L) were used for experiment I (no-choice feeding tests). For experiments II-A and II-B (choice feeding tests), test specimens measuring 30 (R) × 30 (T) × 15 mm (L) were employed. A hole measuring 40 (depth) × 10 mm (diameter) for the no-choice feeding tests, or 15 (depth) × 12.5 mm (diameter) for the choice feeding tests, was drilled in the center of each wood specimen to accommodate the termites. Before the tests, each wood specimen was oven-dried at 60ºC for 3 days and then weighed to measure its oven-dried mass.

Bioassays

Experiment I: no-choice feeding tests

For the no-choice feeding tests, twenty pseudergates of *I. minor* with no external evidence of wing buds or eyes were put into the hole of a test wood specimen, and then the hole was covered with a fine mesh screen tightened by two stainless steel wires (Fig. 1). Three replicates were employed for each sapwood and heartwood specimen.

Experiment II: choice feeding tests

Part A: choice feeding tests of each sapwood and heartwood sample. In the choice feeding tests of each sapwood and heartwood specimen, all wood specimens were combined into one block with randomly selected positions. One hundred pseudergates of *I. minor*, with similar descriptions as in the no-choice feeding tests, were put into the hole of the combined wood blocks, and then both sides of the hole were covered with fine mesh screens that were held by two stainless steel wires (Fig. 2). Ten different positions from ten

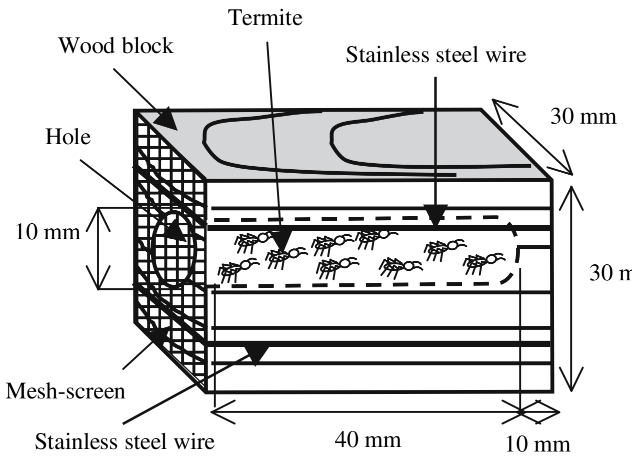

Fig. 1. Experimental setup of the no-choice feeding tests

Table 1. Timbers used for the feeding test

Source of timber	Common name	Scientific name	Part of wood
Japan	Karamatsu	*Larix leptolepis* Gord.	Sapwood and heartwood
	Sugi	*Cryptomeria japonica* D. Don	Sapwood and heartwood
	Buna	*Fagus crenata* Blume	Sapwood and heartwood
	Hinoki	*Chamaecyparis obtusa* Endl.	Sapwood and heartwood
	Akamatsu	*Pinus densiflora* Sieb. et Zucc.	Sapwood and heartwood
USA	Douglas fir	*Pseudotsuga menziessi* Mirbel	Sapwood and heartwood
	Western red cedar	*Thuja plicata* Donn ex D. Don	Sapwood and heartwood
	Western hemlock	*Tsuga heterophylla* Sarg.	Sapwood and heartwood
	Spruce	*Picea abies* Karst.	Sapwood and heartwood
Malaysia	Rubber	*Hevea brasiliensis* Willd. Muell.	–[a]

[a] No consideration given to whether the sample was sapwood or heartwood

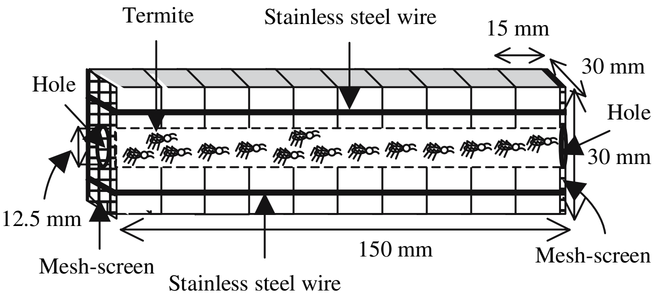

Fig. 2. Experimental setup of the choice feeding tests (sapwood and heartwood samples)

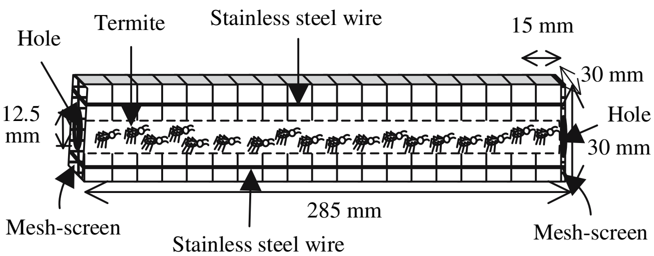

Fig. 3. Experimental setup of the combined choice feeding tests

wood species were randomly selected as replications in this test.

Part B: choice feeding tests of combined sapwood and heartwood specimens. For the combined choice feeding tests, an experimental setup similar to that used for the choice feeding tests was employed for both the sapwood and heartwood specimens, except for the number of pseudergates (200 individuals) and the number of replications (five) (Fig. 3).

All test units (experiments I and II) were kept in the culturing room for 3 months. The numbers of live termites were counted monthly to calculate the survival rates. At the end of the tests, the blocks were recovered, oven-dried at 60°C for 3 days, and reweighed to measure their oven-dried masses after exposure to the termites to calculate wood consumption rate (the amount of wood consumed per live termite per day) and the percentage of wood mass loss (total percentage of wood consumed by termites). The pellets produced were also oven-dried at 60°C for 3 days prior to being reweighed to measure the wood utilization. Wood utilization rate (Wu), which is defined as the amount of wood consumed and converted into termite biomass or used for metabolism per live termite per day, was calculated by the following equation:[17]

$$\text{Wood utilization rate (Wu) (mg/termite per day)} = \frac{\text{Mass loss} - \text{Mass of pellet}}{\text{Number of live termite days}}$$

From the percentage mass losses of the test wood blocks, the ten timbers were classified into five levels of resistance, as shown in Table 2.

Table 2. Categorization of level of resistance based on percent mass loss

Mass loss (%)		Level of resistance
No-choice test	Choice test	
0 < 0.1	0 < 0.1	Highly resistant (HR)
0.10–0.50	0.10–3.00	Resistant (R)
0.51–1.50	3.01–10.00	Moderately resistant (MR)
1.51–3.00	10.01–20.00	Nonresistant (NR)
>3.00	>20.00	Susceptible (S)

Table 3. Percentage mass losses of ten commercial timbers and their level of resistance against *Incisitermes minor* in no-choice feeding tests after 3 months

Wood species	Mass loss (%)[a]	Level of resistance
Sapwood		
Karamatsu	0.278 ± 0.137 a	R
Sugi	1.108 ± 0.634 ab	MR
Douglas fir	1.238 ± 0.694 ab	MR
Buna	1.289 ± 0.125 ab	MR
Western red cedar	1.633 ± 1.344 ab	NR
Hinoki	1.654 ± 0.680 ab	NR
Western hemlock	2.146 ± 0.717 ab	NR
Spruce	2.935 ± 1.859 b	NR
Akamatsu	3.516 ± 0.969 b	S
Heartwood		
Western red cedar	0.066 ± 0.085 a	HR
Buna	0.582 ± 0.217 a	MR
Akamatsu	0.661 ± 0.342 a	MR
Hinoki	1.088 ± 0.243 ab	MR
Karamatsu	1.294 ± 0.933 ab	MR
Sugi	1.771 ± 0.699 ab	NR
Douglas fir	1.919 ± 0.976 ab	NR
Western hemlock	2.389 ± 1.041 bc	NR
Spruce	2.450 ± 0.628 bc	NR
Rubber[b]	1.696 ± 0.248	NR

[a] Values are means ± standard deviations from three replications. Means followed by the same letter within a column are not significantly different (Tukey's test: $P < 0.05$)
[b] Not statistically analyzed because no consideration was made whether it was from sapwood or heartwood

Results

No-choice feeding tests

Mass loss

Table 3 shows the average percentage mass losses of the ten wood species in both the sapwood and heartwood no-choice feeding tests after 3 months. In the sapwood no-choice feeding tests, karamatsu had the highest resistance to *Incisitermes minor*, with a 0.278% mean mass loss, and was classified as "resistant". Sugi, Douglas fir, and buna were classified as "moderately resistant," showing 1.108%, 1.238%, and 1.289% mean mass losses, respectively (Table 3). Four wood species, western red cedar, hinoki, western hemlock, and spruce, which showed 1.633%, 1.654%, 2.146%, and 2.935% mean mass losses, respectively, were classified as "nonresistant." Akamatsu was the only "susceptible" wood among the ten wood species (3.516% mean mass loss). Although the level of resistance in akamatsu and spruce was different, no statistically significant difference was observed between these two species (Tukey's test: $P < 0.05$) (Table 3), and they were indicated to be the most preferred wood species for *I. minor*.

As shown in the table, the lowest mean mass loss (0.066%) was observed in the heartwood of western red cedar, which was classified as resistant. Moderately resistant species were buna, akamatsu, hinoki, and karamatsu with 0.582%, 0.661%, 1.088%, and 1.294% mean mass losses, respectively. Sugi, Douglas fir, western hemlock, and spruce were classified as nonresistant, with mean mass losses of 1.771%, 1.919%, 2.389%, and 2.450%, respectively. Western hemlock and spruce showed significantly higher mass losses than western red cedar, buna, and akamatsu (Tukey's test: $P < 0.05$). However, no significant difference was observed among hinoki, karamatsu, sugi, and Douglas fir (Tukey's test: $P < 0.05$) (Table 3). Rubber, which was not used in the statistical analysis, was classified as nonresistant from the mean mass loss of 1.696% (Table 3).

Survival rates

All wood species in the sapwood no-choice feeding tests tended to show similar mean survival rates (73.3%–83.3%) after 1 month and no significant difference was observed (Tukey's test: $P < 0.05$) (Fig. 4). At 2 and 3 months, the survival rates were in the ranges of 55.0%–76.7% and 26.7%–75.0%, respectively. However, no significant difference was observed in the survival rates after 2 months and after 3 months among the ten wood species (Tukey's test: $P < 0.05$) (Fig. 4).

In the heartwood no-choice feeding tests, all wood species except western red cedar permitted more than 60.0% survival rates of *I. minor* after 1 month (Fig. 5). After 2 months, Douglas fir and western red cedar showed the highest and lowest mean survival rates of 78.3% and 0% (no survival), respectively. The remaining wood species, excluding rubber (i.e., buna, karamatsu, spruce, hinoki, akamatsu, western hemlock, and sugi) had no significant difference in survival rates (Tukey's test: $P < 0.05$), showing 71.7%, 63.3%, 58.3%, 40.0%, 38.3%, 38.3%, and 16.7% mean survival rates, respectively. The survival rates in hinoki, akamatsu, and sugi decreased rapidly during the second and third months and finally reached 0%–5%. After 3 months, the mean survival rate of *I. minor* fed on buna wood (56.7%) was higher than those of spruce, western hemlock, karamatsu, and Douglas fir (41.7%, 35.0%, 31.7%, and 28.3%, respectively), but no significant difference was observed among those species (Tukey's test: $P < 0.05$) (Fig. 5). In the case of rubber, after 3 months, the mean survival rate of *I. minor* was highest (73.3%) among the ten wood species tested.

Wood consumption

The results of wood consumption in the sapwood no-choice feeding tests are shown in Fig. 6A. Karamatsu was significantly less preferred by *I. minor* among the ten wood species, with a mean wood consumption of 0.049 mg/termite per day (Tukey's test: $P < 0.05$) (Fig. 6A). The most preferred group consisted of akamatsu, spruce, western hemlock, and hinoki, which were consumed at means of 0.366, 0.337, 0.322, and 0.304 mg/termite per day by *I. minor*, respectively, and showed no significant differences at $P < 0.05$ (Tukey's test). Douglas fir, western red cedar, buna, and sugi showed moderate mean consumption (0.274, 0.205, 0.158, and 0.153 mg/termite per day, respectively), and no significant difference was observed among the species (Tukey's test: $P < 0.05$).

As shown in Fig. 6B, western red cedar heartwood showed the lowest mean wood consumption (0.011 mg/termite per day) (Tukey's test: $P < 0.05$). The mean wood

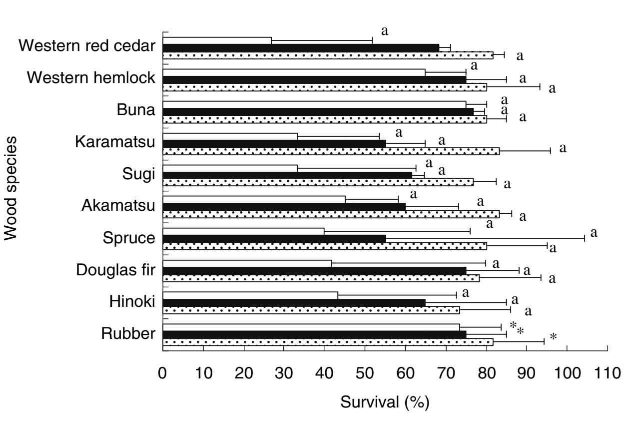

Fig. 4. Mean percent survivals of *Incisitermes minor* in the sapwood no-choice feeding tests. *Dotted bars*, after 1 month; *filled bars*, after 2 months; *open bars*, after 3 months. *Same letters* represent no significant difference by Tukey's test. *Asterisk* indicates no statistical analysis because no consideration was made whether the sample was sapwood or heartwood. *Error bars* show standard deviations

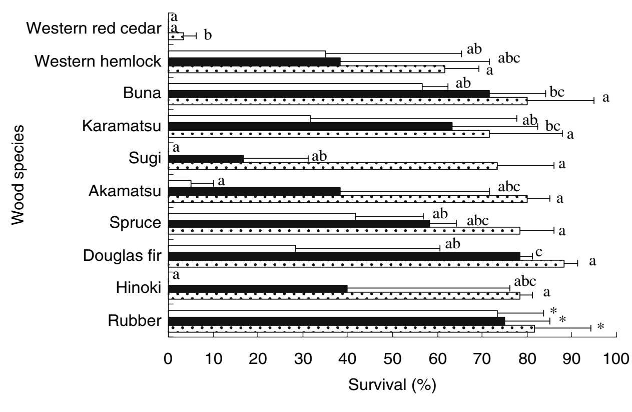

Fig. 5. Mean percent survivals of *I. minor* in the heartwood no-choice feeding tests. *Dot bars*, after 1 month; *filled bars*, after 2 months; *open bars*, after 3 months. Bars in the group of wood species with different letters (a, b, c) are statistically different by Tukey's test ($P < 0.05$). *Asterisk* indicates no statistical analysis because no consideration was made whether the sample was sapwood or heartwood. *Error bars* show standard deviations

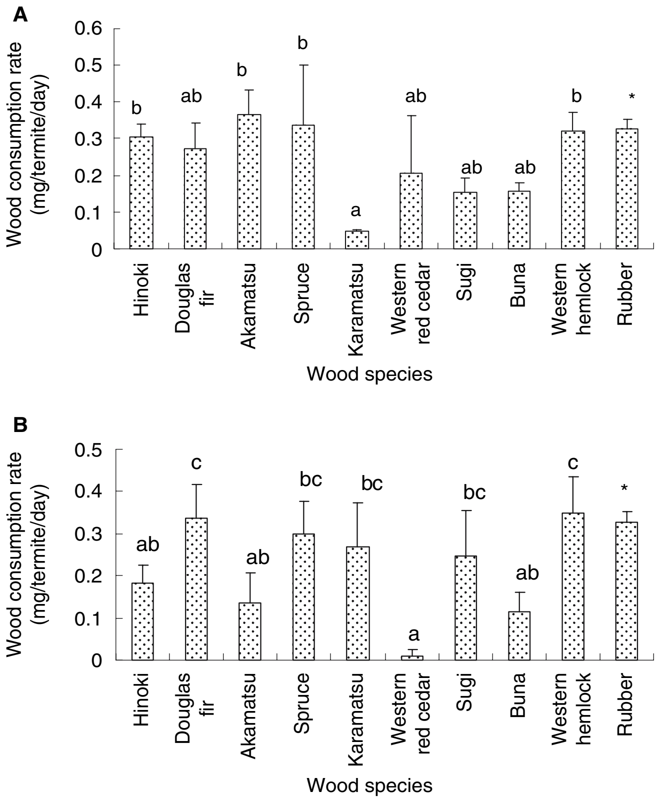

Fig. 6A, B. Mean wood consumption of ten wood species after 3-month exposure to *I. minor*. **A** Sapwood no-choice feeding tests; **B** heartwood no-choice feeding tests. Different letters (a, b, c) are statistically different by Tukey's test ($P < 0.05$). *Asterisk* indicates no statistical analysis because no consideration was made whether the sample was sapwood or heartwood. *Error bars* show standard deviations

consumptions of the heartwood samples of western hemlock, Douglas fir, spruce, karamatsu, and sugi (0.348, 0.336, 0.301, 0.268, and 0.248 mg/termite per day, respectively) were significantly higher among the ten wood species; the mean wood consumptions for these five heartwood samples were not significantly different (Tukey's test: $P < 0.05$). Hinoki, akamatsu, and buna were found to be moderately preferred by *I. minor* with mean consumptions of 0.183, 0.135, and 0.115 mg/termite per day, respectively. The mean wood consumption rate of rubber was 0.328 mg/termite per day. Rubber was noted as the most preferred wood by *I. minor* among the ten wood species, either in the sapwood or heartwood no-choice feeding tests (Fig. 6).

Wood utilization

Table 4 shows the amount of wood utilization by *I. minor* in the sapwood no-choice feeding tests after 3 months. As shown in the table, karamatsu was significantly less consumed among the ten wood species (Tukey's test: $P < 0.05$). The mean wood utilizations (Wu) were higher in akamatsu, spruce, and western hemlock (0.225, 0.224, and 0.220 mg/termite per day, respectively), and lower in karamatsu, sugi, buna, and western red cedar (–0.029, 0.041, 0.065, and 0.074 mg/termite per day, respectively). Moderate mean Wu values were observed in hinoki and Douglas fir, showing Wu values of 0.164 and 0.175 mg/termite per day, respectively.

Table 4. Mean of wood utilized by *Incisitermes minor* in the no-choice feeding tests after 3 months

Wood species	Wood utilization (mg/termite per day)[a]
Sapwood	
Karamatsu	–0.029 ± 0.015 a
Sugi	0.041 ± 0° ab
Buna	0.065 ± 0.019 abc
Western red cedar	0.074 ± 0.115 abc
Douglas fir	0.164 ± 0.078 bcd
Hinoki	0.175 ± 0.019 bcd
Western hemlock	0.220 ± 0.014 cd
Spruce	0.224 ± 0.114 cd
Akamatsu	0.225 ± 0.050 cd
Heartwood	
Western red cedar	0.003 ± 0.015 a
Buna	0.005 ± 0.044 a
Akamatsu	0.085 ± 0.047 ab
Hinoki	0.141 ± 0.047 abc
Karamatsu	0.173 ± 0.085 bc
Sugi	0.176 ± 0.056 bc
Spruce	0.191 ± 0.042 bc
Douglas fir	0.195 ± 0.061 bc
Western hemlock	0.203 ± 0.032 bc
Rubber[b]	0.260 ± 0.002

[a] Values are means ± standard deviations from three replications. Means followed by the same letter within a column are not significantly different (Tukey's test: $P < 0.05$)
[b] Not statistically analyzed because no consideration was made whether it was from sapwoo day)a d or heartwood

In the heartwood no-choice feeding tests, the lower mean Wu values were observed in both western red cedar and buna (0.003 and 0.005 mg/termite per day, respectively) (Tukey's test: $P < 0.05$) (Table 4). Akamatsu, hinoki, karamatsu, sugi, spruce, Douglas fir, and western hemlock were highly utilized (0.085, 0.141, 0.173, 0.176, 0.191, 0.195, and 0.203 mg/termite per day on average, respectively), without significant differences at $P < 0.05$ by Tukey's test. As shown in Table 4, rubber was the most utilized by *I. minor* (0.260 mg/termite per day) among the wood species tested in both the sapwood and heartwood no-choice feeding tests.

Choice feeding test

Mass loss

Table 5 shows the average percentage mass losses of ten wood species after 3 months in the choice feeding tests of both sapwood and heartwood, and the combined choice feeding tests. In the sapwood choice feeding tests, buna and karamatsu were classified as resistant, showing 0.743% and 2.173% mean mass losses, respectively. A six-species group consisting of sugi, rubber, western red cedar, western hemlock, Douglas fir, and akamatsu was classified as moderately resistant, with 4.960%, 5.660%, 5.842%, 6.045%, 7.005%, and 8.601% mean mass losses, respectively. Nonresistant

Table 5. Percentage mass losses of ten commercial timbers and their level of resistance against *Incisitermes minor* in choice feeding tests

Methods	Wood species[a]	Mass loss (%)[b]	Level of resistance
Choice feeding tests (sapwood)	Buna	0.743 ± 0.533 a	R
	Karamatsu	2.173 ± 1.782 ab	R
	Sugi	4.960 ± 2.162 abc	MR
	Rubber[c]	5.660 ± 2.701 abc	MR
	Western red cedar	5.842 ± 2.883 abc	MR
	Western hemlock	6.045 ± 4.466 abc	MR
	Douglas fir	7.005 ± 4.131 abc	MR
	Akamatsu	8.601 ± 4.413 bcd	MR
	Hinoki	10.645 ± 8.359 cd	NR
	Spruce	14.121 ± 9.101 d	NR
Choice feeding tests (heartwood)	Sugi	0.590 ± 0.370 a	R
	Western red cedar	0.649 ± 0.494 a	R
	Buna	1.142 ± 1.010 a	R
	Akamatsu	1.696 ± 1.121 a	R
	Karamatsu	3.042 ± 1.352 ab	MR
	Douglas fir	3.166 ± 3.343 ab	MR
	Hinoki	3.221 ± 1.301 ab	MR
	Rubber[c]	6.528 ± 3.707 bc	MR
	Western hemlock	10.503 ± 5.371 c	NR
	Spruce	20.583 ± 5.298 d	S
Combined choice feeding tests	Buna (H)	0.451 ± 0.576 a	R
	Sugi (H)	0.578 ± 0.449 a	R
	Akamatsu (H)	0.727 ± 1.029 a	R
	Karamatsu (S)	0.777 ± 0.672 a	R
	Western red cedar (H)	0.926 ± 0.637 a	R
	Buna (S)	1.354 ± 1.814 a	R
	Karamatsu (H)	1.681 ± 2.311 a	R
	Douglas fir (S)	2.712 ± 1.379 ab	R
	Douglas fir (H)	2.960 ± 1.986 ab	R
	Hinoki (H)	3.377 ± 1.584 ab	MR
	Sugi (S)	3.889 ± 3.021 ab	MR
	Western red cedar (S)	4.651 ± 2.637 ab	MR
	Rubber[c]	5.294 ± 3.001 ab	MR
	Western hemlock (S)	6.128 ± 3.251 ab	MR
	Western hemlock (H)	6.652 ± 1.431 ab	MR
	Akamatsu (S)	12.068 ± 9.642 bc	NR
	Spruce (H)	12.872 ± 10.973 bc	NR
	Hinoki (S)	17.789 ± 7.904 c	NR
	Spruce (S)	18.831 ± 4.502 c	NR

[a] S, Sapwood; H, heartwood
[b] Values are means ± standard deviations from ten replications for choice feeding tests and five replications for combined choice feeding tests. Means followed by the same letter within a column are not significantly different (Tukey's test: $P < 0.05$)
[c] No consideration was made whether it was from sapwood or heartwood

wood species were noted in both hinoki and spruce, with higher wood mass losses of 10.645% and 14.121%, respectively, without significant differences between these two species (Tukey's test: $P < 0.05$) (Table 5).

In the heartwood choice feeding tests, sugi, western red cedar, buna, and akamatsu were significantly less preferred by *I. minor* (0.590%, 0.649%, 1.142%, and 1.696% mean mass losses, respectively) and were classified as resistant (Tukey's test: $P < 0.05$). The mean mass losses of karamatsu, Douglas fir, hinoki, and rubber were in the same level (Tukey's test: $P < 0.05$), and showed 3.042%, 3.166%, 3.221%, and 6.528% resistance, respectively, and these timbers were classified as moderately resistant. Western hemlock was classified as nonresistant, with a 10.503% mean mass loss, which was significantly higher than those of the resistant and moderately resistant species except for rubber (Tukey's test: $P < 0.05$) (Table 5). The termites consumed the spruce specimen with a higher mean mass loss (20.583%) than the other species, and the wood was classified as susceptible.

As shown in Table 5, out of 19 wood specimens in the combined choice feeding tests, buna heartwood, sugi heartwood, akamatsu heartwood, karamatsu sapwood, western red cedar heartwood, buna sapwood, karamatsu heartwood, and Douglas fir sapwood and heartwood appeared to be the most resistant or least preferred by *I. minor* with 0.451%, 0.578%, 0.727%, 0.777%, 0.926%, 1.354%, 1.681%, 2.712%, and 2.960% mean mass losses, respectively, and were classified as resistant without significant difference among those species (Tukey's test: $P < 0.05$). The moderately resistant species were hinoki heartwood, sugi sapwood, western red cedar sapwood, rubber, western hemlock sapwood, and heartwood with mean mass losses of 3.377%, 3.889%, 4.651%, 5.294%, 6.128%, and 6.652%, respectively, and no significant difference was seen either among these wood species or between resistant wood, as described above (Tukey's test: $P < 0.05$). The highest mean mass losses were obtained in akamatsu sapwood, spruce heartwood, hinoki sapwood, and spruce sapwood, showing 12.068%, 12.872%, 17.789%, and 18.831% mean mass losses, respectively, and they were classified as nonresistant. However, all nonresistant wood species except for hinoki sapwood and spruce sapwood had no significant difference in mass losses compared with the moderately resistant wood species (Tukey's test: $P < 0.05$).

Survival rate

The mean survival rates of *I. minor* in both the sapwood and heartwood choice feeding tests were more than 75.0% after 3 months, while in the combined choice feeding tests they were more than 80.0% (Fig. 7). In general, each sapwood and heartwood choice feeding test and combined choice feeding test showed that the survival rates of *I. minor* after 1 month and 2 months did not differ as much as after 2 months and 3 months (Fig. 7). On the other hand, the mean survival rates of termites were significantly different after 1 month and after 3 months according to Tukey's test ($P < 0.01$) for both the sapwood and heartwood choice feeding tests, and at $P < 0.05$ for the combined choice feeding tests (Fig. 7). The mean survivals of *I. minor* after 1, 2, and 3 months for both the sapwood and heartwood choice feeding test and combined choice feeding test were 87.0%, 82.2%, and 77.5%; 90.4%, 85.0%, and 75.6%; 88.2%, 85.1%, and 83.4%, respectively.

Wood consumption

The wood consumption of the ten wood species calculated from the survivals and mass losses in the sapwood choice feeding tests are shown in Fig 8A. Wood consumptions were strongly varied among the wood species. Buna had the lowest mean wood consumption (0.006 mg wood/termite per day), while the highest was noted in spruce (0.074 mg/termite per day). The remaining wood species, rubber, hinoki, Douglas fir, akamatsu, western hemlock, western red cedar, sugi, and karamatsu, showed moderate mean wood consumptions (0.057, 0.057, 0.457, 0.044, 0.041, 0.028, 0.021, and 0.021 mg/termite per day, respectively), and no signifi-

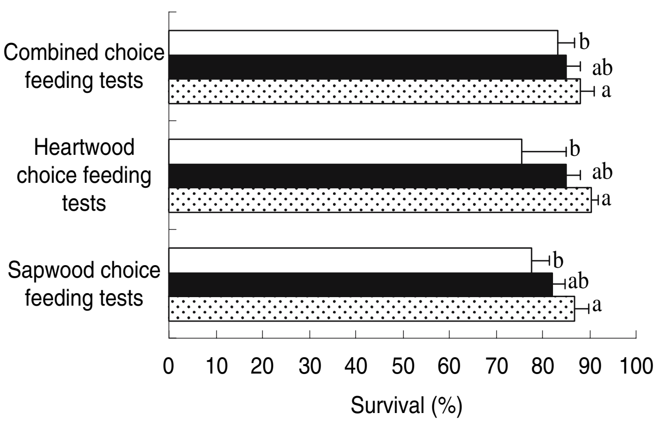

Fig. 7. Mean percentage survivals of *I. minor* in the choice feeding tests. *Dot bars*, after 1 month; *filled bars*, after 2 months; *open bars*, after 3 months. Bars in the group of wood species with different letters (a, b) are statistically different by Tukey's test ($P < 0.05$). *Error bars* show standard deviations

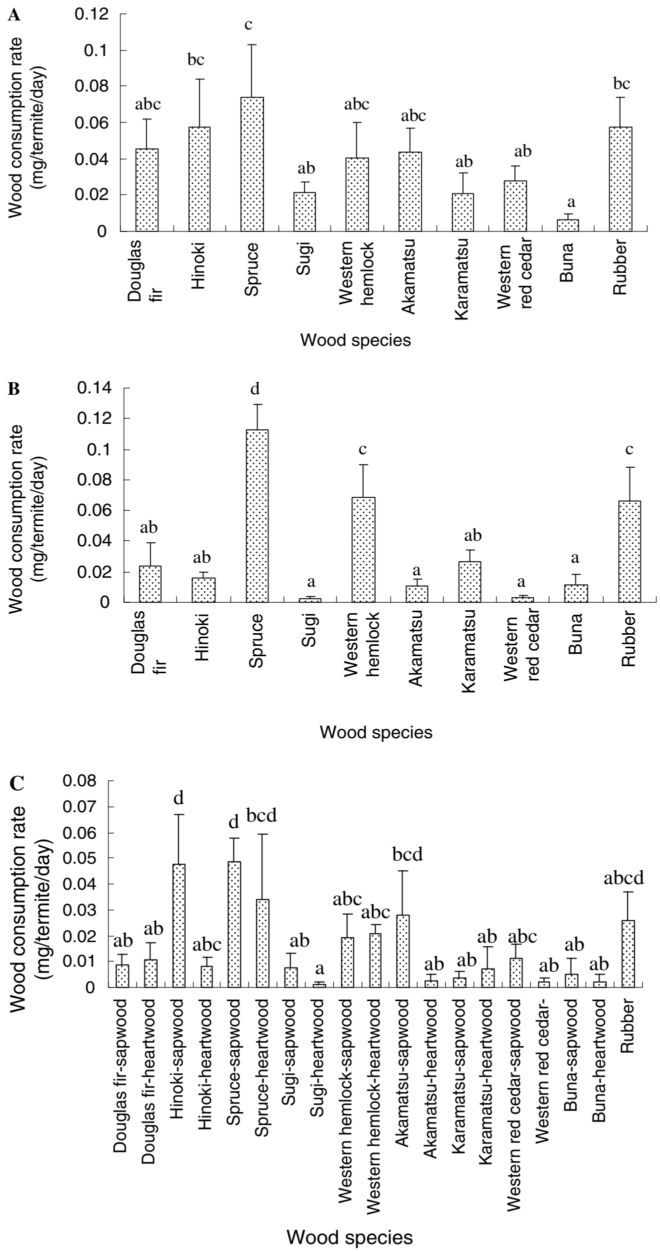

Fig. 8A–C. Mean wood consumption of ten wood species after 3-month exposure to *I. minor*. **A** Sapwood choice feeding tests; **B** heartwood choice feeding tests; **C** combined choice feeding tests. Different letters (a, b, c) are statistically different by Tukey's test ($P < 0.05$). *Asterisk* indicates no statistical analysis because no consideration was made whether the sample was sapwood or heartwood. *Error bars* show standard deviations cant difference was observed among these species by Tukey's test ($P < 0.05$) (Fig. 8A).

As shown in Fig. 8B, strong differences in mean wood consumption were observed in the heartwood choice feeding tests. The spruce wood specimen showed the significantly highest mean wood consumption (0.113 mg/termite per day) followed by western hemlock (0.068 mg/termite per day) and rubber (0.066 mg/termite per day) (Tukey's test: $P < 0.01$). The mean wood consumptions did not differ in karamatsu, Douglas fir, and hinoki (0.027, 0.024, and 0.016 mg/termite per day, respectively). Sugi, western red cedar, akamatsu, and buna wood specimens showed significantly low mean wood consumptions (0.003, 0.003, 0.011, and 0.012, mg/termite per day, respectively) (Tukey's test: $P < 0.01$) (Fig. 8B).

In the combined choice feeding tests (Fig. 8C), a 13-specimen group consisting of western hemlock heartwood, western hemlock sapwood, western red cedar sapwood, Douglas fir heartwood, Douglas fir sapwood, sugi sapwood, hinoki heartwood, karamatsu heartwood, buna sapwood, karamatsu sapwood, akamatsu heartwood, western red cedar heartwood, and buna heartwood showed lower mean wood consumptions (0.021, 0.019, 0.011, 0.011, 0.009, 0.008, 0.008, 0°, 0.005, 0.004, 0.002, 0.002 and 0.002 mg/termite per day, respectively) than hinoki sapwood, spruce sapwood and heartwood, akamatsu sapwood, and rubber (0.048, 0.048, 0.034, 0.028, and 0.026 mg/termite per day, respectively), but no significant difference was observed between these two groups, except for hinoki sapwood and spruce sapwood (Tukey's test: $P < 0.05$). Sugi heartwood was much less consumed by *I. minor* (0.001 mg/termite per day on average), but no significant difference was observed with the 13-specimen group (Tukey's test: $P < 0.05$) (Fig. 8C).

Discussion

Survival rates

Our previous study using no-choice feeding tests with flat-surface wood blocks of jabon (*Anthocephalus chinensis*) (without consideration of whether the sample was from sapwood or heartwood) showed a relatively high survival rate (68.67%) of workers of a dry-wood termite, *Cryptotermes cynocephalus* (Light) after 10 weeks.[16] In the present study, no-choice feeding tests with a hole in the center of the rubber wood specimen gave a higher mean survival rate of 73.3% against *Incisitermes minor* after 3 months (Figs. 4 and 5). This may indicate the advantage of using holed wood specimens in wood-feeding experiments for dry-wood termites. As shown in Figs. 4 and 5, in no-choice feeding tests, the highest mean survival rates of *I. minor* after 3 months were generally obtained in sapwood specimens rather than in heartwood specimens; for example, the survival rates observed were 75.0% and 56.67% in the buna sapwood and heartwood specimens, respectively. These results were very consistent with those of Smythe and Carter,[5] who tested the responses of *Coptotermes formosanus*, *Reticulitermes flavipes*, and *Reticulitermes virginicus* against 11 wood species; white oak (heartwood), black walnut (heartwood), black cherry (heartwood), western larch (heartwood), slash pine (sapwood), ponderosa pine (heartwood), loblolly pine (sapwood), Douglas fir (heartwood), redwood (heartwood), sugar maple (not differentiated), and bald cypress (heartwood), showing low survivals in heartwood samples. They assumed that the toxicity of the heartwood was probably linked to the presence of single or multiple extractives.[5] Furthermore, Morales-Ramos and Rojas,[14] who worked on *C. formosanus*, stated that negative food preference in termites might be mediated by the presence of noxious compounds, such as wood extractives, in the food source.

The choice feeding tests employed in this study revealed that the survival rates of *I. minor* after 3 months were generally higher than in the no-choice feeding tests, resulting in 77.50%, 75.60%, and 83.40% for the sapwood and heartwood choice feeding test, and the combined choice feeding tests, respectively (Fig. 7). These results clearly indicated that the choice feeding test method in the present study could give a better resolution of the wood preference with higher survival rates of test insects. The reason why the termites in the choice feeding tests showed higher survival rates than those in the no-choice feeding tests might be partly explained by the fact that the termites were fed on more than one wood species, and that they could choose the preferred wood species for their survivorship. In addition, the volume of nesting sites in the choice feeding tests was larger than that in the no-choice feeding tests, so that the termites move about as they do in their natural environments. Morales-Ramos and Rojas[14] stated that the choice feeding test was a more appropriate method to determine termite wood preference than the no-choice test, because in the latter, the termites were forced to feed on whatever resources were available for survivorship.

Mass loss

As shown in Table 3, the only highly resistant species was western red cedar in the heartwood no-choice feeding tests. We assume that chemical deterrents in the western red cedar heartwood acted against *I. minor*. Scheffrahn[18] has stated that the resistance of wood to termite attack is mainly determined by the presence of chemicals in the lignocellulosic tissue. This might be related to the fact that the presence of insect feeding deterrents has been reported in the foliage of western red cedar,[19] and that wood extractives of western red cedar have been shown to be significantly toxic to eastern subterranean termites.[14]

It is interesting to note that the heartwood of western red cedar was reported to have a higher wood preference than the Douglas fir heartwood,[7] in contrast to the results of this study. However, similar results to our investigation were obtained by Rust and Reierson,[3] who found that the heartwood of Douglas fir was more preferred by *I. minor* than that of western red cedar. Su and Tamashiro[6] also showed similar results to our study when workers of *C. formosanus* were fed on western red cedar, showing a lower

Table 6. Comparison of resistance levels in all feeding test methods

Wood species	No-choice feeding tests		Choice feeding tests		Combined choice feeding tests	
	Sapwood	Heartwood	Sapwood	Heartwood	Sapwood	Heartwood
Spruce	NR	NR	NR	S	NR	NR
Hinoki	NR	MR	NR	MR	NR	MR
Western hemlock	NR	NR	MR	NR	MR	MR
Akamatsu	S	MR	MR	R	NR	R
Rubber[a]	NR	NR	MR	MR	MR	MR
Douglas fir	MR	NR	MR	MR	R	R
Western red cedar	NR	HR	MR	R	MR	R
Sugi	MR	NR	MR	R	MR	R
Karamatsu	R	MR	R	MR	R	R
Buna	MR	MR	R	R	R	R

[a] No consideration was made whether it was from sapwood or heartwood

wood consumption than for Douglas fir and western hemlock. The heartwood of western red cedar showed relatively high natural resistance against *I. minor* in this study, while sapwood was ranked as nonresistant or moderately resistant. These results were also consistent with a study by Ohmura et al.,[20] who reported a lower mass loss of western red cedar heartwood than sugi sapwood against *C. formosanus*.

A comparison of the resistance levels of all wood species against *I. minor* in the choice and no-choice feeding tests is summarized in Table 6. The ranking of the wood preference by *I. minor*, which was determined from the total mean wood mass losses of both the choice and no-choice feeding tests including sapwood and heartwood, was as follows: spruce > hinoki > western hemlock > akamatsu > rubber > Douglas fir > western red cedar > sugi > karamatsu > buna. The present investigation revealed that spruce was particularly favorable for *I. minor*. However, buna had the lowest preference by the termites (Table 6). In the no-choice feeding tests in both sapwood and heartwood, buna was classified as a moderately resistant species. This result was similar to the classification by Imamura,[21] who noted that buna heartwood was classified as moderately resistant to *C. formosanus* by no-choice feeding tests.

The total comparison of all heartwood samples in the no-choice feeding tests are shown in Table 6. Regarding Table 7, it is likely that the antitermite performance of the timbers strongly depends on the habitation of termites such as subterranean and dry-wood termites. When the specimens were set up in the sapwood and heartwood choice feeding tests and combined choice feeding tests, buna was classified as a resistant species. This might be because in the choice feeding tests the termites were fed on more than one wood species, so that consequently they could choose the other preferred wood species for their survivorship, as described above.

Wood consumption

Observation of the wood consumption rates in this study revealed that akamatsu showed the highest consumption rate in the sapwood no-choice feeding tests, while in the heartwood no-choice feeding tests, western hemlock was the most consumed wood species by *I. minor* (Fig. 6). The termites consumed spruce wood at the significantly highest rate among the ten wood species in all choice feeding tests (each sapwood and heartwood test or the combined test) (Fig. 8). Generally, as the wood consumption rate increased, wood mass losses also increased in this study. It is naturally believed that high wood mass loss is due to high wood consumption by termites.

Table 7. Comparison of resistance levels in heartwood no-choice feeding tests

Wood species	Level of resistance	
	Literature[a]	Present study[b]
Karamatsu	MR	MR
Sugi	MR	NR
Douglas fir	S	NR
Buna	MR	MR
Western red cedar	S	HR
Hinoki	MR	MR
Rubber	–	NR
Western hemlock	S	NR
Spruce	–	NR
Akamatsu	S	MR

[a] Study by Imamura,[21] exposure to *Coptotermes formosanus*
[b] Exposure to *Incisitermes minor*

Wood utilization

Karamatsu sapwood showed a minus value of wood utilization (Table 4). Before the tests, the termites were kept in a termite culturing room and placed in closed plastic containers with small blocks of Douglas fir as their food sources. It is possible that the termites excreted more Douglas fir-originated pellets (after set up) than the mass losses of karamatsu, which was the least attacked wood species. In this study, the highest wood consumption was generally followed by the highest wood utilization (Fig. 6, Table 4). A similar result was reported by Cabrera and Rust,[17] who found that the highest wood consumption rate by *I. minor* was followed by the highest wood utilization after 6 weeks.

It is worth mentioning that in this study, the choice feeding test with a hole in the center of the specimen was found to be a good method for investigating the wood preferences of dry-wood termites. As the next step, it is necessary to investigate environmental condition preferences such as optimum temperature and relative humidity to achieve total understanding of the feeding activity of the invasive dry-wood termite, *I. minor*.

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