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Suitability of multiple Mediterranean oak species as a food resource for *Reticulitermes grassei* Clément (Isoptera: Rhinotermitidae)

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Abstract

The subterranean termite *Reticulitermes grassei* Clément causes lesions in the trunk of *Quercus suber* L. by constructing feeding galleries, but no information is available regarding other *Quercus* species from the Mediterranean region. This work aimed to study the suitability of the other main oak species of Mediterranean forests as a food resource for *R. grassei*. Two experiments, choice and non-choice feeding, were conducted lasting for 15, 30, and 45 days each. In the non-choice experiment, termites were offered one of the following food types: *Quercus suber*, *Quercus ilex* L., *Quercus faginea* Lam, cork or *Pinus pinea* L., which was considered the control. The choice feeding experiment used all the same food types listed above, supplied simultaneously in the same container. Food selection was examined by analysing the relationships over time between surviving termites and food consumption. The results indicated that *R. grassei* could be considered a generalist species, as it consumed the cork and wood of all oak species, as well as displaying a clear preference for soft wood (pine). Correlation analysis indicated that consumption was not dependent on wood density. Survival of *R. grassei* was influenced by the time of exposure to different oak species, but a high survival rate was maintained over time in the pine treatment (upper 70% in the three experiments). Given these results, it can be concluded that all the oak species are a suitable food source for *R. grassei*.

Keywords: feeding preferences, Isoptera, *Quercus*, *Reticulitermes grassei*, Rhinotermitidae, subterranean termites

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Introduction

Reticulitermes grassei Clément is a subterranean termite native to the Iberian Peninsula and southwest France (Clément *et al.*, 2001). This species occupies the northern, western and southern areas of Spain (Kutnik *et al.*, 2004). *R. grassei* colonizes natural and manmade environments where it is a major pest of wooden urban infrastructure (Gaju *et al.*, 2002; Alcaide, 2010). For this reason, most studies on *R. grassei* have been devoted to exploring methods of managing it in urban environments (Getty *et al.*, 2005; Rojas *et al.*, 2008; Gaju *et al.*, 2010).

Termites are an important element of forest ecosystems because they contribute to natural recycling by eating wood and soil. Decaying wood provides more nutritional benefits to subterranean termites than fresh wood due to the higher availability of nutrients such as nitrogen (Pinzon *et al.*, 2006). Knowledge of the natural foraging ecology of subterranean termites in the family Rhinotermitidae is relatively scarce because their nests are difficult to locate and delimiting their foraging area is complicated (Waller, 1988). However, some information is available on the seasonal feeding behaviour of the genus *Reticulitermes* (Su & Scheffrahn, 1994; Haagsma & Rust, 1995; Haverty *et al.*, 1999) including *R. grassei*. This species has never been considered a pest in Iberian forests but notably its feeding activities create lesions in cork oak (*Quercus*

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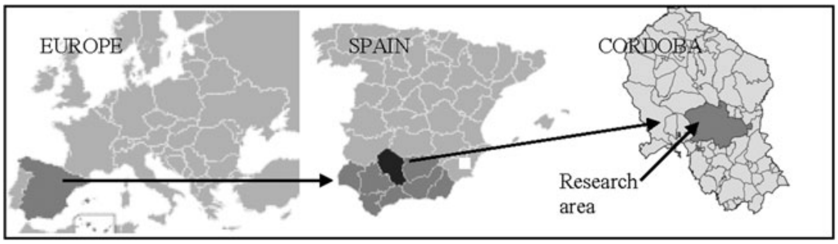

Fig. 1. Location of the research area (source Gallardo *et al.*, 2010).

suber L.) (Gallardo *et al.*, 2010), and its nests and foraging areas are associated with cork oaks (Cárdenas *et al.*, 2012). Consequently, it could be hypothesized that the wood of cork oak, or the cork itself, may be more suitable as food for *R. grassei* than the other vegetal species. In general, it is accepted that the process of termite recruitment to a particular food source may be influenced by the properties of wood (Price, 1984). Specifically, the hardness of the wood are among the main factors influencing the consumption of wood by termites (Peralta *et al.*, 2004), but additional factors such as moisture content and the presence of toxins or fungi may also be involved (Smythe *et al.*, 1971; Carter & Smythe, 1974; Nagnan & Clément, 1990). Understanding food selection by termites requires knowledge of their feeding pattern as well as their detection and attraction behaviour to different food stimuli (Suoja *et al.*, 1999).

The scant information on the feeding preferences of subterranean termites in nature indicates that most of these organisms are generalist consumers (Haverty & Nutting, 1975; Lai *et al.*, 1983), but species with a diet restricted to a few food sources also exist (Waller, 1988).

Studies on feeding preference of some *Reticulitermes* species (*Reticulitermes flavipes* Kollar and *Reticulitermes virginicus* Banks) indicate a clear preference for a particular wood species (southern pines and sugar maple; Smythe & Carter, 1970). *R. grassei* is particularly known to have a strong preference for poplar wood (*Populus* sp.) in comparison with other types of industrial wood (Gaju *et al.*, 1996) suggesting that this species could have a selective feeding preference.

This research aimed to study the suitability of the wood of the main oak species growing in Mediterranean forests (*Q. suber*, *Quercus ilex* L. and *Quercus faginea* Lam.) as well as cork (the bark of the cork oak) as a food resource for *R. grassei* in order to determine whether a preference for wood of cork oak explains the lesions observed on this plant species. Food preference was investigated by analysing the relationships over time between termite survival and food consumption.

Materials and methods

Sampling area

Termites were collected from Los Baldíos (Sierra Morena mountains, southern Iberian Peninsula; fig. 1), where cork oaks showing galleries made by *R. grassei* had been previously observed (Gallardo *et al.*, 2010). In this area there is a Mediterranean mixed forest dominated by *Q. ilex*, *Q. suber* and *Q. faginea*, and also has *Pinus pinea* L. and *Olea europaea* var. *sylvestris* Brot. (Cárdenas *et al.*, 2012). The scrubland in the area is diverse and mostly represented by *Genista* spp., *Cistus salviifolius* L. and *Daphne gnidium* L.

The area sits on the Thermo-Mediterranean and Meso-Mediterranean belts, with broad transitional zones between them (Cárdenas & Bach, 1989). The soils are mainly acidic, with Paleozoic metamorphic rocks, which include quartzite, slate and semi-acidic, intrusive types. The climate is typically Mediterranean with winter rainfall ranging 500–800 mm year, an average annual temperature of 17 °C, relatively warm summers (average 24 °C) and winters with an average temperature ranging between 6 and 10 °C (Gallardo *et al.*, 2010).

Fieldwork

Workers of *R. grassei* were collected from the field between 10 and 14 April 2015, and were found by lifting fallen wood and course woody debris. The termites were transported to the laboratory along with the wood in which they were found.

Laboratory work

To determine the feeding preference of *R. grassei* to the multiple Mediterranean oak species and to the bark of cork oak (cork), we conducted choice and non-choice experiments lasting for 15, 30, and 45 days. The specimens selected for the experiments were workers of at least the third stage (Chouvenc *et al.*, 2011). In the non-choice experiments, termites were offered one of the following food types: *Q. suber* (cork oak), *Q. ilex* (holm oak), *Q. faginea* (gall oak), cork, and the soft wood (*P. pinea*), which was considered to be the control because the wood of pine results the best food for laboratory studies with subterranean termites (Smythe & Carter, 1970; Perkins, 2012; EN 118, 2013). The choice feeding experiment used all the same food types listed above, supplied simultaneously in the same container.

For each individual trial of the non-choice feeding experiment, eight sapwood blocks (approximately $2 \times 2 \times 1$ cm^3 in volume) of each food type were supplied (*Q. suber*, *Q. ilex*, *Q. faginea*, cork and *P. pinea*). Ten individual trials of each food type were performed.

In the individual trials of the choice feeding experiment, ten sapwood blocks of different plant species (two pieces of cork oak, holm oak, gall oak, and pine) and of cork (two pieces) were provided as food. Ten individual trials of this experimental design were also performed.

Small metal tags of different shapes were used to identify the wood species in this experiment. For each trial, 150 workers of the same colony were placed into a container and reared under controlled conditions: a rearing chamber in permanent darkness at a constant temperature of 26 ± 1 °C and 80 ± 5% relative humidity. In total, 180 rearing containers measuring $18 \times 15 \times 7$ cm^3 were used. Following the methods of Gallardo *et al.* (2016) and EN 118 (2013), each container was provided with 60 g of sand, moistened in a

Table 1. Mean survival (%) and Standard Deviation (SD) of the ten individual trials of each non-choice feeding treatment (*Q. suber*, *Q. ilex*, *Q. faginea*, Cork, and *P. pinea*) after 15, 30, and 45 days of exposure.

Days of exposure	Survival (%)				
	Q. suber	*Q. ilex*	*Q. faginea*	Cork	*P. pinea*
15 days					
Mean	76.47	63.60	80.00	54.33	83.20
SD	23.00	25.17	15.50	33.30	14.77
30 days					
Mean	19.47	19.33	40.20	12.00	77.27
SD	17.43	19.27	29.55	9.02	14.89
45 days					
Mean	30.60	33.80	8.73	10.60	70.73
SD	32.45	23.42	13.16	15.23	22.66

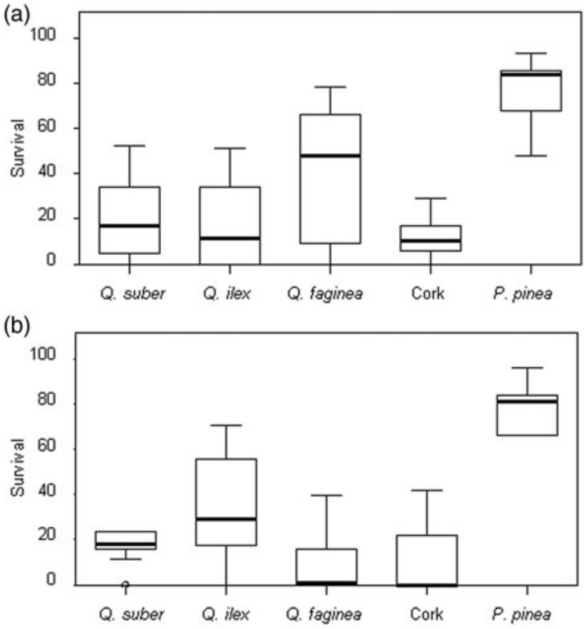

Fig. 2. Termite survival in non-choice feeding experiment for the five food types: (A) after 30 days of exposure, (B) after 45 days of exposure. Vertical bars indicate the minimum and maximum data values. The line in the box indicates the median value of the data. The upper and lower edges of the box indicate the 75th and 25th percentiles, respectively.

proportion of one volume of distilled water to four volumes of sand.

The food types were collected from the same area as the termites and were kiln-dried at 60 °C for 48 h to determine dry weight. This procedure is commonly used to study the wood preferences of termites (Su & La Fage, 1984*a*; Grace & Yamamoto, 1994; Morales-Ramos & Rojas, 2001; EN 118, 2013) because this temperature preserves the properties of the wood (Kačík *et al.*, 2012) and also has the benefit of sterilization (http://www.usgr.com/soil-sterilization).

After each exposure time (15, 30, and 45 days), the pieces of wood were removed, kiln-dried again, and weighed to quantify consumption, and the number of surviving termites were counted to calculate survival.

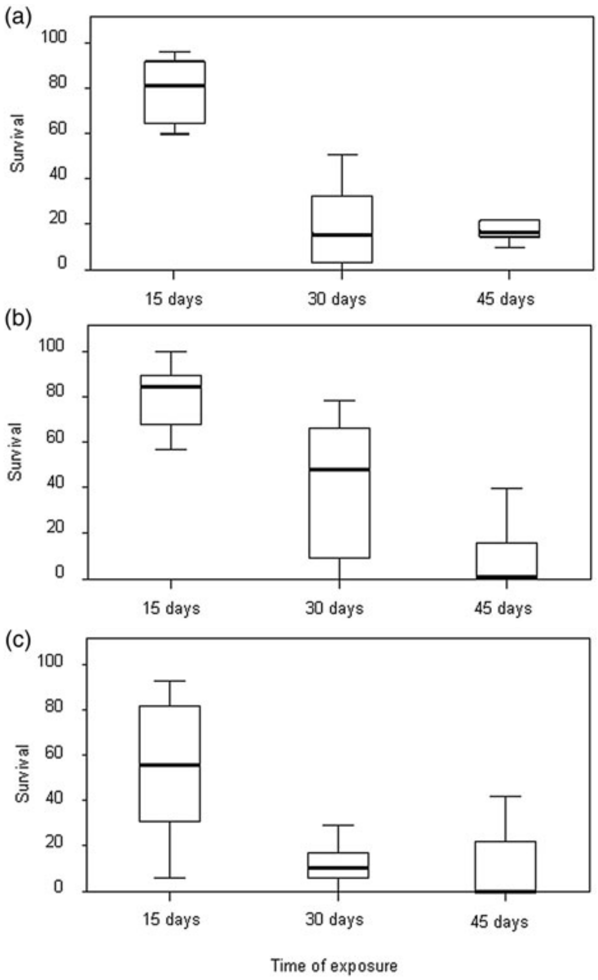

Fig. 3. Termite survival in non-choice feeding experiment after 15, 30, and 45 days of exposure in: (A) *Q. suber*. (B) *Q. faginea*. (C) Cork. Vertical bars indicate the minimum and maximum data values. The line in the box indicates the median value of the data. The upper and lower edges of the box indicate the 75th and 25th percentiles, respectively.

Data analysis

The following parameters were considered:

Survival = percentage of live workers found for each treatment at the end of each experiment.

Consumption = difference between value of initial dry weight of food and value of final dry weight of food in each trial.

Consumption rate = wood weight consumed/surviving termite biomass (Su & La Fage, 1984*b*).

Termite biomass was quantified by individually weighing (with a precision balance) 100 randomly selected workers from the total specimens caught in the field, resulting in an average weight of workers of 0.002 ± 0.0001 g.

An analysis of variance (one-way ANOVA) was used to test for differences in mean survival among food types and different exposure times. The assumptions of normality and homoscedasticity were checked with a Shapiro–Wilk test

Table 2. Comparison of mean survival among the three experimental durations (15, 30, and 45 days) for each non-choice feeding treatment (*Q. suber*, *Q. ilex*, *Q. faginea*, Cork and *P. pinea*).

Statistical values	Non-choice feeding treatments				
	Q. suber	*Q. ilex*	*Q. faginea*	Cork	*P. pinea*
P	0.002*	0.001*	≤0.0001*	0.001*	0.136
F/χ^2	$\chi^2 = 12.58$	$F = 9.84$	$\chi^2 = 19.17$	$\chi^2 = 13.13$	$\chi^2 = 3.98$

F: values of one-way ANOVA test; χ^2: values of non-parametric Kruskal–Wallis test; P: probability, asterisk (*) indicates significance for $\alpha = 0.05$.

and a Levene test, respectively (Zar, 1999). If the data did not satisfy the normality and homoscedasticity criteria, the non-parametric Kruskal–Wallis test was applied instead. In addition, to discern differences in survival *vs.* exposure times and *vs.* food types, the *post-hoc* Tukey–Kramer test or box plots were performed for the ANOVA or the Kruskal–Wallis test, respectively.

The relationship between exposure time and the mean number of surviving termites for each treatment was examined using Pearson's correlation. Because the distribution of termite survival during the study period (15, 30, or 45 days) was not known, a logarithmic transformation of the *y*-axis data was used to obtain a linear regression equation for use as a predictive model.

Because mortality may significantly influence the consumption rate (Su & La Fage, 1984*b*), this parameter was only analysed for the experiments in which the statistical comparison of survival resulted in no significant differences among treatments.

The one-way ANOVA test was also applied to assess differences in total consumption in the non-choice experiments after 15 days; and the differences in total consumption in the choice feeding experiment were tested by the χ^2 test. Because the number of surviving termites varied among treatments, differences in consumption rate were also examined using again one-way ANOVA as statistical procedure. The Pearson's correlation was also applied to assess the relationship between wood density and consumption after 15 days of exposure to each non-choice feeding experiment. Information about wood density was provided by Gutiérrez & Plaza (1967).

The statistical tests were performed using SPSS (SPSS 20.0, 2011).

Results

Survival

Survival versus food type

After 15 days there were no differences in termite survival among treatments (*Q. suber*, *Q. ilex*, *Q. faginea*, cork and *P. pinea*; $P = 0.116$, $\chi^2 = 7.41$) (table 1). However, after 30 and 45 days there were significant differences among food sources ($P = 0$, $\chi^2 = 24.37$; $P = 0$, $\chi^2 = 25.43$, respectively). After 30 days the greatest survival was recorded with *P. pinea*, followed by *Q. faginea*. Survival in *Q. suber*, *Q. ilex* and cork did not surpass 20% (fig. 2a). After 45 days, the greatest survival was recorded again in *P. pinea*, but the lowest rates corresponded to *Q. faginea* and cork (fig. 2b).

Analysis of survival versus exposure time

Termite survival decreased significantly among the three experimental timeframes in each non-choice treatment, except for the *P. pinea* treatment in which high survival was observed in all three times of exposure (tables 1 and 2). Termite survival decreased drastically after 15 days in the *Q. suber*, and cork treatments (fig. 3a, c) and remained at low levels until the end the study. Survival decreased more progressively over time in the *Q. faginea* treatment (fig. 3b).

Table 3. Pearson's correlation coefficient (*r*) and probability values between the survival of each non-choice feeding treatments (*Q. suber*, *Q. ilex*, *Q. faginea*, Cork and *P. pinea*) and the time of exposure.

Correlation values	Non-choice feeding treatments				
	Q. suber	*Q. ilex*	*Q. faginea*	Cork	*P. pinea*
P	0.002*	0.018*	≤0.0001*	≤0.0001*	0.123
r coefficient	−0.55	−0.43	−0.83	−0.62	−0.29

F: values of one-way ANOVA test; χ^2: values of non-parametric Kruskal–Wallis test; P: probability, asterisk (*) indicates significance for $\alpha = 0.05$.

The values of the correlation coefficient between the survival for each type of food and days of exposure are displayed in table 3. Pearson's coefficient was significant and negative for all the treatments except for *P. pinea* ($P = 0.123$, $R = -0.288$). The respective linear equations provided the predictive model of the course of survival within each treatment over time (fig. 4). The regression lines with the highest slopes correspond to cork and *Q. faginea*. In these treatments, 100% mortality would occur after 45–50 days. Conversely and as expected, the lowest slope was observed in *P. pinea* in which termites would remain alive for more than 155 days. The regression lines for *Q. suber* and *Q. ilex* run quite parallel and the last surviving termites would not surpass 55 days.

Consumption

No significant differences were found for consumption among the food types in the non-choice feeding experiment ($P = 0.329$, $F = 1.19$) and in the choice feeding ($P = 0.998$, $\chi^2 = 0.11$) (table 4). Likewise, when consumption rates in the non-choice and choice feeding experiments were compared, no significant differences were found ($P = 0.916$, $F = 0.24$; $P = 0.927$, $\chi^2 = 0.884$, respectively).

There was no relationship between consumption after 15 days and wood density ($P = 0.223$, $R = 0.18$).

Discussion

The survival analysis indicated that an increase in rearing time was associated with a significant decrease in survival, regardless of the type of food, except when pine is supplied. High mortality is typical of this type of bioassay after some

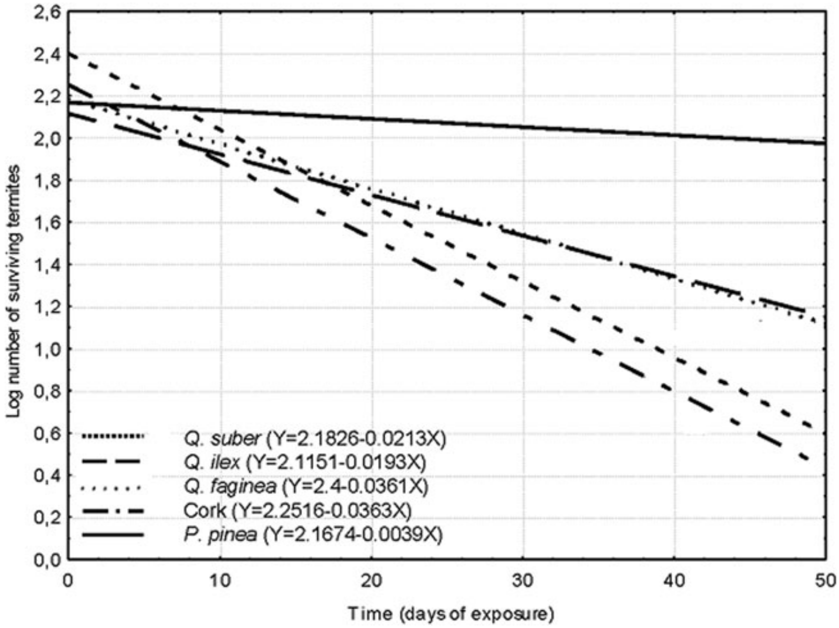

Fig. 4. Linear regressions between log-transformed mean number of surviving termites of each non-choice-feeding treatments (*Q. suber*, *Q. ilex*, *Q. faginea*, Cork, and *P. pinea*) and time of exposure (15, 30, and 45 days).

Table 4. Mean and Standard Deviation (SD) of the consumption (in grams) and consumption rate of the ten individual trials of each non-choice feeding treatments (monospecific diet with *Q. suber*, *Q. ilex*, *Q. faginea*, Cork and *P. pinea*) and of those of choice feeding treatment (mixed diet) for 15 days of exposure.

	Non-choice feeding experiment				
Monospecific diet	*Q. suber*	*Q. ilex*	*Q. faginea*	Cork	*P. pinea*
Consumption					
Mean	0.33	0.28	0.38	0.16	0.37
SD	0.32	0.27	0.30	0.14	0.25
Consumption rate					
Mean	2.43	1.95	1.48	1.72	1.42
SD	4.63	2.60	1.18	2.28	0.87
	Choice feeding experiment				
Mixed diet	*Q. suber*	*Q. ilex*	*Q. faginea*	Cork	*P. pinea*
Consumption					
Mean	0.25	0.13	0.21	0.09	0.35
SD	0.23	0.11	0.20	0.04	0.13
Consumption rate					
Mean	0.91	0.48	0.77	0.33	1.39
SD	0.81	0.41	0.69	0.17	0.61

weeks of exposure (Grace *et al.*, 1989; Grace & Yamamoto, 1994; Arinana *et al.*, 2012) due to the loss of vigour that may be related to age, disease or other intrinsic factors associated with the experimental treatment (Su & La Fage, 1984*a*). In spite of this, a high survival rate was recorded in the control throughout the three times, which validates the experimental design and the affinity of *R. grassei* for soft wood such as *P. pinea*. This finding is in accordance with other species of subterranean termites (e.g. *Heterotermes longiceps* Snyder, *Coptotermes gestroi* Wasmann and *Nasutitermes jaraguae* Holmgren) preferring softwoods (Peralta *et al.*, 2004).

All types of food supplied in the non-choice feeding experiment were palatable to the termites and there were no statistically significant differences among the consumption of different food types in both non-choice and choice feeding experiments. These findings are in accordance with the existence of *Quercus* species classified as 'poorly or not at all resistant' to be eaten by subterranean termites (Reyes *et al.*, 1995).

Similar results were obtained when we compared rate of consumption instead of total consumption in non-choice feeding experiment. However, in the choice–feeding experiment, the consumption rate was higher in pine, which is also in agreement with the preference for soft wood usually attributed to *Reticulitermes* species (Haverty, 1979).

The selective feeding behaviour shown by certain subterranean termites is hypothesized to be primarily a result of the emission by the plants of volatile substances, usually detectable from a distance (Reinhard *et al.*, 1997) that could attract or repel these insects (Scheffrahn, 1991). Volatile compounds emitted include isoprenes and terpenes (Kesselmeier & Staudt, 1999), which perform several functions for the plants, including defence against pathogens and herbivores (Martín *et al.*, 2003; Dudareva *et al.*, 2004; Sánchez-Osorio *et al.*, 2013). Some *Quercus* species, such as *Q. suber*, are strong producers of monoterpenes and triterpenes (Pio *et al.*, 1993; Silva *et al.*, 1999; Lavoir, 2004; Staudt *et al.*, 2004), which would be expected to make them unattractive to termites. However, our field observations and laboratory experiments indicate that *Q. suber* is as palatable as the other wood supplied. Moreover, it is known that as a consequence of the injuries produced during cork extraction, the tree secretes healing substances that are primarily composed of acid resins dissolved in a mixture of terpenes, which act as attractants for other boring insects, such as longhorn beetles (Cogollor, 2002). If these substances are also attractive to termites, the association between termites and cork oaks observed in the field (Gallardo *et al.*, 2010) would be explained. Nevertheless, it has been also indicated that in the same study area the uncorked oaks were not significantly affected by other boring insects, while termites affected nearly 70% of them (Gallardo, 2011). Therefore, the attractant effect of healing substances is not a suitable explanation of the rate of termite presence.

The principal factors affecting wood consumption by termites are the wood species, the hardness or density of the wood, and the moisture content of the wood and soil (Smythe *et al.*, 1971; Carter & Smythe, 1974; Nagnan & Clément, 1990). Notably, there is an inverse relationship between termite consumption and wood density because the hardness of the wood affects the termite's ability to fragment it mechanically with its mandibles (Bultman *et al.*, 1979). Hence termite attack resistance is highly correlated with wood density (Behr *et al.*, 1972; Coulson & Lund, 1973; Bultman *et al.*, 1979; Abreu & Silva, 2000). However, our study did not find a relationship between mean total consumption and wood density for any non-choice feeding treatment, as has also been found prior for *Reticulitermes* sp. (Waller *et al.*, 1990). Likewise, no significant correlations between wood consumption rates and wood densities have been found for other subterranean termite species, despite a clear preference for softwoods (Peralta *et al.*, 2004).

In summary, on the basis of the predictive model obtained for the course of survival of *R. grassei*, it can be concluded that all the wood oak species are equivalent in terms of suitability as food resources.

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