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ORIGINAL PAPER

The importance of the minimal number of workers required in the dispersal of *Reticulitermes santonensis* Feytaud, 1924 by budding

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ABSTRACT

In Europe, there are 6 species of subterranean termites *Reticulitermes* Holmgren, 1913. The 10°C isotherm is the northernmost limit for the genus *Reticulitermes*. The dispersal of *Reticulitermes* species is mainly due to artificial distribution in particular the transport of goods by rail and ships. In recent years, *R. santonensis* Feytaud, 1924 has been possibly considered synonymous with *R. flavipes* (Kollar, 1937) in the United States of America. *R. flavipes* has been present in Hamburg, Germany since 1930. Subterranean termites of the genus *Reticulitermes* can be invasive pests and they tend to persist in cities outside the 10°C isotherm. *R. santonensis*, in particular, is a budding dispersal species with worker groups of *R. santonensis* wandering far from the colony which may be accidentally be taken with the soil in plant containers. An experiment was carried out to answer the following question: how many individuals must there be in a group of *R. santonensis* workers to survive for the budding process to give rise to a new colony?

The modified ASTM D 3345-08 (2017) procedure was used to perform the experiment. Groups of 3, 5, 10, 15 and 20 workers were cultured in laboratory glass vessels for 10 months with *Pinus sylvestris* L. sapwood. Five groups of workers in separate laboratory glass vessels were used for 1 variant of the experiment. Laboratory glass vessels with a volume of 450 ml were used. In each vessel 2 blocks of *P. sylvestris* sapwood were placed at the bottom with block dimensions of 15×15×35 mm. One block of undecayed wood and one block of brown rot wood were placed in each glass vessel. The wood was covered with 200g of sand that had been moistened.

Groups of 3 and 5 workers died in the first 2 weeks. Groups of 10 workers died in 4-5 weeks leaving no next generation. Only budding groups of 15 and 20 workers have a chance of surviving, reproducing and establishing a new colony. A new generation was observed at very different times. Most often it was about 5-6 months from the beginning of the experiment. *R. santonensis* poses a real threat of expansion by budding from with the production of greenhouse plants.

KEY WORDS

invasive organisms, soil organisms, subterranean termites

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Introduction

Subterranean termites are important soil organisms and one of the most significant agents of wood degradation in structures. They can travel relatively long distances and eat wood that is far from the colony. In Europe, they are represented by the genus *Reticulitermes*. *R. lucifugus* Rossi is present in many places on the Mediterranean coast, Moldova and even Ukraine (Rui, 1956; Becker, 1970, 1974; Serment and Tourteaux, 1991; Vieau, 1999). The taxonomy of the genus *Reticulitermes* is still in the process of being defined with many changes until the present (Clément *et al*., 2001). For example, *R. grassei* Clément was previously considered a subspecies of *R. lucifugus* (Clément *et al*., 2001), and *R. santonensis* (Feytaud) is likely to be synonymous with *R. flavipes* (Kollar) (Laine, 2002). Phylogenetic analysis showed a genetic relationship between *R. flavipes* from the United States and *R. santonensis* from France (Jenkins *et al*., 2001; Laine, 2002; Austin *et al*., 2005; Dronnet *et al*., 2005), and a new species, *R. urbis* Bagnčres & Clément, has been recently identified in Italy (Ferrari *et al*., 2011).

Termite expansion is slow in temperate regions of the world. However, the spread of *Reticulitermes* species is thought to be mainly due to artificial distribution and particularly through the movement of freight via railways and ships (Fougerousse and Perlade, 1975; Sellenschlo, 1988; Serment and Tourteaux, 1991; Vieau, 1991, 1993; Laine, 2002).

At the end of the 18th century the presence of termites in the southwest of France was officially recognised (Feytaud, 1911; Fougerousse and Perlade, 1975; Serment and Tourteaux, 1991; Vieau, 1991). From the 1830s to 1850s, there were many accounts of damage by termites in South-Western France (Feytaud, 1911, 1924; Thompson, 1917; Vieau, 1991). One of the first observations of termites in Paris was by Lesne (1923) in 1922 (Fougerousse and Perlade, 1975). Several well-established infestations, which were identified as being *R. lucifugus* and *R. santonensis* (now thought to have been *R. santonensis)*, were discovered in the 1940s and 1960s in Paris (de Feytaud, 1955; Jacquiot, 1955; Fougerousse and Perlade, 1975). *R. lucifugus* was found south of the Gironde River (between 46° and 47° N) (Clément, 1978). In recent decades there has been a marked expansion of termite distribution towards the northeast (Serment and Tourteaux, 1991). *R. lucifugus* has moved much further north than its distribution at the turn of the last century (Feytaud, 1912; Vieau, 1999). *R. lucifugus* was introduced to Basel (Switzerland) through infested potatoes imported from Naples (Italy) (Ghesini *et al*., 2020).

R. santonensis has been gradually spreading northwards since the first reports of damage. In the 1950s, termites thought to have been *R. santonensis* were said to have spread up to the town of Nantes (47°15' N) in northwest France (Jacquiot, 1955; Vieau, 1991; Laine, 2002). More recently, only *R. santonensis* was thought to be present in Nantes, whereas Bordeaux is thought to have both species (Vieau, 1993). During the 1950s, the distribution boundary between the two species was the Gironde (Jacquiot, 1955), a river that lies just to the north of Bordeaux. In the 1970s, *R. santonensis* was found to be 50 km towards the country interior from the Charente Maritime coast (central-western France) and was also found as far north as Rouen (49°30' N) and Normandy (Fougerousse and Perlade, 1975; Clément, 1977). *R. santonensis* is now also found in and around Bordeaux (Vieau, 1999). The lack of swarming and thus of physogastric queens in *R. santonensis* has been said to be a sign that this species is in the process of establishing itself and therefore an introduced species (Vieau, 1993, 1999).

In 1994, an accidental introduction of *R. grassei* to Devon (UK) was discovered. A new subterranean termite infestation was found in 2018 in the winter garden of a house on Zürich's lake (northeastern Switzerland) which was also *R. grassei*. Termites were probably introduced through olive and palm trees that were planted on the affected property and in a neighboring one (Ghesini *et al*., 2020).

R. flavipes has been present in Hamburg, Germany since 1930 (Weidner, 1952, 1954, 1978; Becker, 1970; Sellenschlo, 1988), although this has been recently said to be *R. santonensis* (Clément *et al*., 2001). *R. flavipes* has also been found in Mannheim (Wichmann, 1957; Becker, 1970), in Austria as early as 1837 (Becker, 1970) and later also in Romania.

Human influence on the dispersal of termites was thought to be particularly important for *R. santonensis* which is considered to be mainly an urban termite (Laine, 2002). There is a concern that due to global warming *R. santonensis* may potentially move from cities to the surrounding forest areas. This species can spread, for example, with potted plants. A small number of pseudergates and workers is enough, which together with the settled soil, to be placed in containers with plants for their spread. The question remains as to how many individuals must be in such a container for a new colony of *R. santonensis* to form? The aim of this research is to provide an answer to this question.

Materials and methods

The modified ASTM D 3345-08 (2017) procedure was used to perform the experiment. Blocks of *Pinus sylvestris* L. made of sapwood without decay caused by fungi and sapwood with brown rot at the level of about 15-20% were used for the study. The dry wood density of Scots pine sapwood was 0.53 g/cm^3. The moisture content at the start was 6% ±1%. The dimensions of the blocks were 15×15×35 mm. One block of undecayed wood and one block of brown rot wood were placed in each glass vessel.

Each pair of blocks were placed individually on the bottom of a glass vessel and sprinkled with 200 g of river sand which was sieved, washed and thermally sterilized. The volume of the glass vessel was 450 ml. The amount of water used to moisten the sand in the testing container was then reduced by 7% from the saturation point of the sand.

Different numbers of workers of the subterranean termite *R. santonensis* were used in different variants of the experiment. The number of termites in the variants were as follows: 3, 5, 10, 15 and 20 individuals. Each variant of the experiment contained 5 repetitions (glass vessels).

The glass vessels with wood blocks and termites were placed in an incubator at 27°C for 10 months. The water content of the testing glass vessels was checked and replenished weekly as needed. Weekly checks were made for the condition of termites that were visible through the bottom of laboratory glass near the wood blocks. The presence of live termites from the start group placed initially in laboratory glassware was recorded. The appearance of eggs or young larvae that were a new generation was also noted. The experiment period was from October 8th, 2021 to the end of July 2022.

Results

The bottom of the glass vessel with live start group termites and juvenile larvae is shown in Fig. 1. This is typical of the variant repetitions where a new generation of termites has appeared.

In the experiment variant with 15 workers, a new generation was found in two glasses on 03.03.2022 and 28.07.2022. In the experiment variant with 20 workers, a new generation was found in four glasses on 17.03.2022, 17.03.2022, 31.04.2022 and 25.04.2022.

The experimental results obtained are shown in Fig. 2 indicating the presence of live termites from the start group and young larvae.

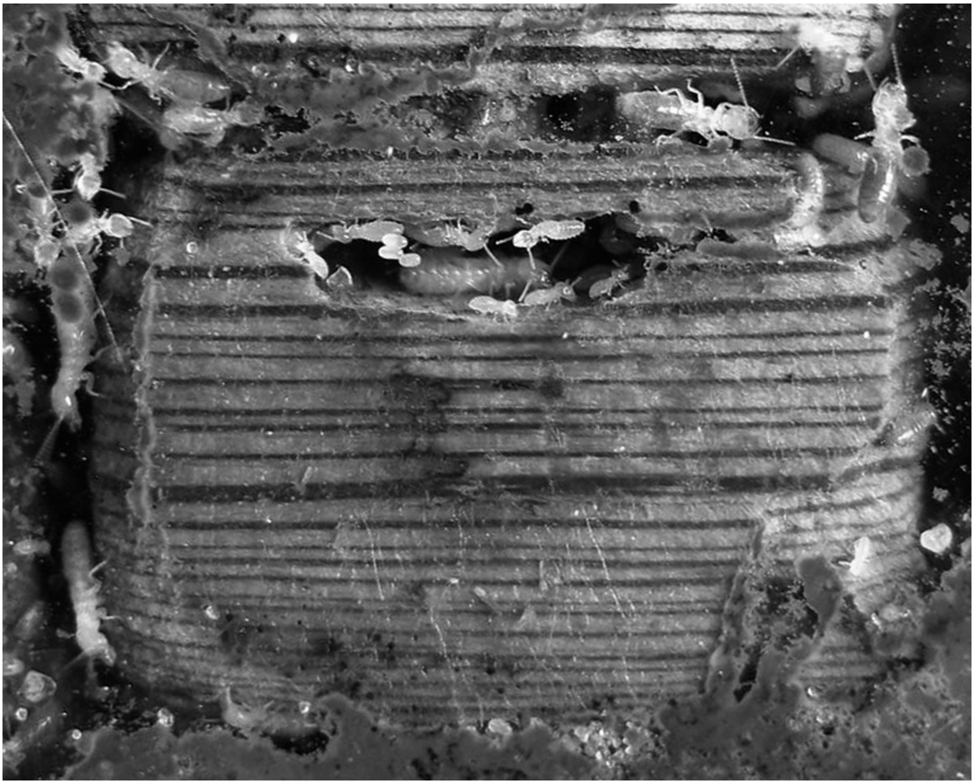

Fig. 1.
View of the bottom of the glass vessel in the variant with a starting group of 20 termites (repetition II): the presence of live termites of the starting group and young larvae

In variants where there were 3 and 5 individuals in the start group, all termites died within 2 weeks. In the variant with 10 individuals in the start group, all termites also died but after a longer period of 4-5 weeks.

In the variant with 15 individuals in all repetitions, termites from the start group survived 10 months of the experiment. After some time, the presence of young larvae was found in 2 glass vessels. In the variant with 20 individuals in all repetitions, termites from the start group survived for 10 months. Only one container had no individuals of a new generation.

Discussion

New termite colonies are formed in nature, as a rule, through alates. Workers are the first caste to develop when a new colony is founded by alates with their developmental time lasting approximately one year with them then living for several years (Laine, 2002). However, new colonies can also arise through the formation of neotenics in a group of pseudergates and workers that have been separated from the old parent colony. The process of forming new colonies by the formation of neotenics within a group of individuals that has been separated from the colony is commonly termed 'budding' (Perez, 1907; Harris and Sands, 1965; Plateaux and Clément, 1984; Serment and Tourteaux, 1991; Laine, 2002). The extent to which budding occurs in nature is uncertain, although this is commonly observed in the field in France (Vieau, 1999) and is true for *R. santonensis*.

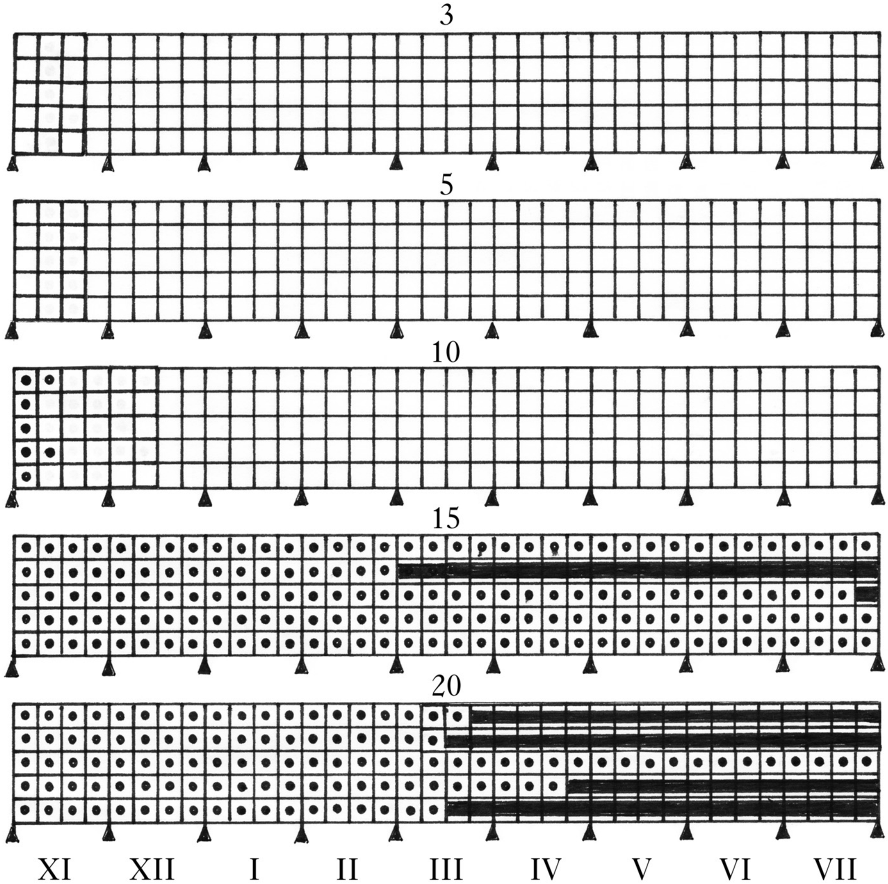

Fig. 2.
Experimental results: • presence of live termites of the starting group, – presence of a new generation

'Budding' is of particular importance for the spread of termites beyond their current range. This applies particularly to their transfer by humans along with horticultural production. This is how termites appeared in Austria as early as 1837 (Becker, 1970). They appeared there in orangeries and greenhouses from imported exotic plants where the soil in the pots probably contained clusters of termites. If *R. santonensis* is indeed synonymous with *R. flavipes*, then the species may have appeared in France in the 18th century in this way as well. For this reason, the issue of the numbers of pseudergats and workers required in the start groups for the budding process to occur is very important.

The size of the start group for 'budding' is also of great importance in experiments in the laboratory glass vessels. The group must be large enough that the termites not only have a chance to survive, but also cause visible damage to the test material or control blocks quickly enough. The smallest groups of termites used in standard tests were in East Germany with 100 workers (Schultze-Dewitz, 1958; Schultze-Dewitz and Unger, 1972). ASTM D 3345-08 (2017) is the standard method for laboratory evaluation of wood and other cellulosic materials for resistance to subterranean termites. This method requires the proportion of weight 1 ±0.05 g of termites includes 90% of workers. Based on the measurement of the weight of 100 workers and pseudergats of *R. santonensis*, it can be estimated that the weight of 1 g corresponds up to 400 individuals. The EN 117:2013-04 standard (PKN, 2023) recommends the use of 250 workers for a test in one laboratory glass vessel. Additionally, this standard recommends the following: 'to each group made up in this way add a number soldiers corresponding to the proportion found in the colony from which the workers were taken: add a corresponding proportion of nymphs (1% to 5%).' The number of termites used in this method's laboratory tests is several times higher than the results obtained in my research.

In *Reticulitermes* spp. all castes are made up of individuals of both sexes (Perez, 1907; Snyder, 1926; Laine, 2002). Workers can live for several years (Laine, 2002). Since any instar can eventually develop into either a primary or secondary reproductive termite, means that a viable colony could form from any group of individuals (Noirot, 1990; Laine, 2002). According to our experience, however, this is not an arbitrarily quantifiable group of individuals as it must have least a dozen workers and pseudergats. A group of 20 individuals clearly increases the probability of survival and reproduction.

The young worker instars are difficult to differentiate from the larvae as mentioned by Laine (2002). The definition of what constitutes workers is a further problem. There are outstanding questions of whether they should be termed pseudergates or whether there should be an additional terminology to differentiate between pseudergates and true workers. Termite workers are not necessarily at their final instar stage and are, therefore, able to retain the capacity to become either a soldier or a supplementary reproductive individual with no wing buds (ergatoid) (Noirot, 1985, 1988). Reproductive neotenics can develop from nymphs or workers. The development of neotenics is said to take place from between 6 weeks to 4 months after a group of termites have separated from the main colony (Thorne, 1998; Laine, 2002). At the same time, female neotenics lay eggs at a lower rate than true queens (Laine, 2002). Egg laying starts approximately 4 to 8 weeks after the formation of a neotenic has occurred (Laine, 2002). Thus, based on this information, the time for the emergence of a new generation ranges from 10 to 24 weeks. In our experiment, the presence of eggs and young larvae was found at the earliest after 9-10 weeks, which confirms this information.

Workers in natural conditions can live for several years (Laine, 2002). In cases where there were only a few to ten workers in budding groups, the termites died very quickly in our experiment (Fig. 2). The size of the budding group is, therefore, important not only for the formation of neotenics and reproduction but also for the survival of the start group in a very small colony.

Light in 1934 gave the 10°C isotherm as the northernmost limit for the genus *Reticulitermes* (Laine, 2002). In Laine's experiments (2002), *R. santonensis* survived for 6 months at 10°C as *R. santonensis* can reproduce at 15°C (Laine, 2002). Overall observations of the impact of climate change on phytophagous insects suggest that the role of thermophilic species has now increased. Higher temperatures caused by global warming would be very significant for populations of *Reticulitermes* species that are at the edge of their range. Also, the soil is likely to act as a buffer to air temperature, so termites may be able to escape cold winter air temperatures by tunneling to greater depths.

Reticulitermes species are able to install in the environment of Central European cities, where climatic factors cease to play a key role. Global warming may also mean that termites that are accidentally introduced may become lingering in areas previously considered too cold (Jacquiot, 1956; Laine, 2002). The higher risk seems to come from *R. santonensis*, as evidenced by our research along with the research of others. Budding groups of termites with only about

15-20 workers can be a new trend. Cities, therefore, can become places from which *Reticulitermes* termites will spread to neighboring forest areas. As the 21st century progresses, forests are likely to undergo dramatic changes in composition and overall growth and development. Future climate shifts have the potential to forever alter the species composition of forests around the world (Lawson and Michler, 2014). Therefore, in Central Europe conditions may be created that will enable termites to enter our forests from small budding groups from cities.

Conclusions

The following conclusions can be drawn from the results:

- Only budding groups of 15 or more workers have a chance of surviving, reproducing and establishing a new colony.
- Starting with a budding group of at least 20 workers, the chances increase greatly for establishing a new colony. *R. santonensis* is a termite species that can easily be introduced and spread from the production of greenhouse plants.

Conflicts of interest

The author declares no conflicts of interest.

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STRESZCZENIE

Znaczenie liczby robotników w rozprzestrzenianiu się *Reticulitermes santonensis* Feytaud, 1924 poprzez odkłady

Termity są ważnymi organizmami glebowymi i jednymi z najważniejszych czynników degradacji drewna w konstrukcjach. Izotermę 10°C uważa się za północną granicę dla rodzaju *Reticulitermes*. W Europie wyróżniono dotąd *R. lucifugus* Rossi, *R. santonensis* (Feytaud), *R. flavipes* (Kollar), *R. grassei* Clément, *R. urbis* Bagnčres & Clément i *R. clypaeus* Lash. Taksonomia rodzaju *Reticulitermes* jest wciąż w trakcie definiowania i dokonano w niej wielu zmian. Stanowisko systematyczne *R. santonensis* jest niejasne: do niedawna uchodził on za odmianę *R. lucifugus* lub hybrydę tego gatunku i *R. flavipes*. Ostatnio stwierdzono związek genetyczny między *R. flavipes* ze Stanów Zjednoczonych i *R. santonensis* z Francji. Zachodzi obawa, że termity z rodzaju *Reticulitermes* mogą się przystosowywać i znajdować miejsce rozwoju poza dotychczasową granicą występowania w miastach, jak ma to np. miejsce w Hamburgu od lat 30. XX w. W warunkach ocieplenia klimatu potencjalnie mogą z czasem przenosić się z miast na otaczające tereny leśne. Dotyczy to szczególnie *R. santonensis*, który jest uważany za termita głównie miejskiego. Gatunek ten nie wykazuje tendencji do rójki. Może jednak rozprzestrzeniać się np. z produkcją roślinną poprzez odkłady, określane również jako tzw. pączkowanie (angl. budding), jeśli pewna liczba robotników wraz z zasiedloną glebą trafi do donic lub pojemników z roślinami. Robotnicy są najliczniejszą kastą w kolonii. Celem przeprowadzonych badań było dostarczenie odpowiedzi na pytanie: jaka jest minimalna liczba osobników, żeby grupa mogła przeżyć i założyć nową kolonię *R. santonensis*.

Globalne ocieplenie może oznaczać, że termity, które zostały przypadkowo zawleczone, mogą utrzymać się na obszarach uważanych wcześniej za zbyt zimne. Większe ryzyko wydaje się pochodzić właśnie od tego gatunku. Stwierdzono przeżycie *R. santonensis* w hodowli laboratoryjnej w temperaturach tak niskich jak 10°C przez okres 6 miesięcy, a rozmnażanie w temperaturze 15°C. Zatem gatunek ten mógłby potencjalnie przetrwać zimę np. w Wielkiej Brytanii i rozmnażać się. Jak funkcjonowałby w klimatycznych warunkach Polski, zakładając ocieplenie klimatu?

W ramach badań umieszczono po 3, 5, 10, 15 i 20 robotników w zlewkach szklanych o pojemności 450 ml z klockami z bielu *Pinus sylvesstris* L. i hodowano w temperaturze 27°C przez 10 miesięcy. Każdy wariant doświadczenia zawierał 5 powtórzeń (zlewek szklanych). W każdym naczyniu znajdowały się po 2 klocki o wymiarach 15×15×35 mm (jeden z rozkładem brunatnym 5-20% i jeden bez rozkładu) przykryte 200 g nawilżonego piasku. Wykorzystując tendencję do gromadzenia się termitów na dnie naczynia przy drewnie, obserwowano termity co tydzień przez dno naczyń (ryc. 1), odnotowując obecność żywych osobników starego pokolenia i ewentualnie nowe pokolenie (jaja i larwy). Stwierdzono, że jedynie grupy „pączkowania" o liczebności od 15 robotników wzwyż mają szanse na przeżycie, rozmnożenie i założenie nowej kolonii (ryc. 2). Szanse te bardzo wzrastają przy liczebności grupy od 20 robotników. Grupy te wielokrotnie przewyższają liczebność grup termitów używanych w doświadczeniach laboratoryjnych. Wydaje się, że szczególne zagrożenie w rozprzestrzenianiu się tego gatunku stwarza szklarniowa produkcja roślin.