

A Simulation Model for the Study of the Territorial Behavior of Subterranean Termites

Wonju Jeon¹ · Sang-Hee Lee^{1†}

흰개미 테리토리행동 연구를 위한 시물레이션 모델

전원주 · 이상희

ABSTRACT

Subterranean termites forage by constructing tunnel networks in soil and encounter food resources during tunnel excavation. Some species of termites can travel up to 150 m underground. They often travel to the surface to find wood cellulose to feed their colony, which in turn causes extensive damage to wooden architecture, such as timber-frame houses. This type of damage has been constantly increasing along with global warming because higher temperatures provide an ecological niche for termites. The damage is closely related to termite territory size and distribution. Recently, as a way to research termite control, the necessity of a mathematical model to simulate termite territory formation in relation to damage has increased. So far, however, few studies have been conducted on the development of a model because it is difficult to quantify or characterize the relationship between territorial behavior and field conditions including complicated environmental factors. In the present study, we suggest a simulation model of the territoriality of the Formosan subterranean termites, *Coptotermes formosanus* (Shiraki), and *Reticulitermes flavipes* (Kollar), based on empirical data. The model consists of 2 procedures. One describes tunnel network growth for each colony, and the other represents territoriality based on tunnel-tunnel interactions between different colonies. Using the model, we show changes in territorial competition according to the termination probability of tunnel growth.

Key words : Subterranean termites, Tunnel networks, Territorial competition, Global warming

요약

흰개미는 땅 아래 서식하면서 네트워크형태의 터널 구조물을 만들어 먹이자원을 획득한다. 종에 따라서는 지하 150m 깊이까지 터널을 형성하기도 하고, 목재의 섬유질을 찾기 위해 종종 지표면까지 이동하기도 하는데, 이로 인해 목재로 지어진 건축물 특히 가옥에 엄청난 피해를 끼친다. 지구 온난화에 의한 온도상승으로 흰개미가 활동하기에 적합한 고온 지역이 넓어지며 이와 같은 피해는 꾸준히 증가하고 있다. 이 피해규모는 흰개미 테리토리영역의 크기 및 그 분포와 밀접한 관련을 가지고 있다. 흰개미 본 연구에서는 흰개미 두 종(*Coptotermes formosanus* (Shiraki) 와 *Reticulitermes flavipes* (Kollar))에 대한 테리토리행동을 시물레이션 할 수 있는 실험치 기반의 모델을 제안하였다. 모델은 콜로니별로 형성하는 터널네트워크의 성장부분과, 서로 다른 콜로니 사이의 터널교차를 고려한 영역성 부분, 이렇게 두 부분으로 구성된다. 본 모델을 이용하여 터널 성장확률에 따라 테리토리간 경쟁이 어떻게 변하는지에 대한 간단한 결과를 보여 주었다.

주요어 : 지하 흰개미, 터널 네트워크, 테리토리 경쟁, 지구 온난화

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¹ 국가수리과학연구소 융복합수리과학부 가상생태계팀

주 저 자 : 전원주

교신저자 : 이상희

E-mail; sunchaos@nims.re.kr

1. Introduction

Recent climatic extremes due to global warming, such as unseasonably high temperatures, have led to speculation that ecosystem disturbances are ubiquitous from local to global scales^[1]. Climate change strongly affects ecosystem

stability and resilience^[2]. For this reason, many researchers have attempted to understand the effects in terms of system adaptability and variation at the ecosystem level^[3]. Climatic changes also affect community and population dynamics within the ecosystem. Besides the effect at the population and community levels, climate change may further affect animal behavior at the individual level. There have been several studies showing behavioral and physiological changes due to temperature increase (e.g., favorable effects of a slight temperature increase on insect pest development)^[4]. So far, however, such studies mainly focused on terrestrial and aquatic systems, including total assemblages of plants and animals, but not on subterranean animals, because of the technical difficulties in observing animal behaviors and environmental factors in underground conditions. Understanding the effects of climate change on the subterranean ecosystem is indeed important because the terrestrial ecosystem is directly connected to the subterranean ecosystem^[5, 6], and would be critical in maintaining sustainability both in natural (e.g., underground nests of animals) and human (e.g., house safety) systems. According to an Intergovernmental Panel on Climate Change (IPCC) report^[7], subterranean termites are the second largest natural source of methane gas, which accelerates global warming. Termites destroy forest and wooden architecture by constructing a tunnel network underground. The amount of damage has constantly increased worldwide along with global warming because the warmer temperatures provide a niche for termites.

As regarding the termite damage, it is extremely important to understand the territorial behavior of termites because the territory size and habitat quality affect the composition of the above-ground ecosystem^[8, 9]. So far, however, few studies have been carried out to understand termite ecosystems in relation to the damage they cause because it is difficult to directly research termite tunneling activities and their ecological impacts. The degree of damage is closely related to termite territory formation through competition. In our previous studies^[10-12], we have suggested a lattice model to simulate the growth of termite territories in a landscape; further, we used this model to explore the territory size distribution at the steady state. Our lattice model was able to explain the

territory size distribution of mangrove termites on the Atlantic coast of Panama, which had been reported by Adams and Levings^[13]. In the model, territorial competition was mathematically described as “boundary–boundary bordering”. However, this competition type is not suitable for the territoriality of subterranean termites because a foraging territory of subterranean termite compete with another territories through tunnel–tunnel encountering. This difference in the type of competition is because mangrove termites move from trees to trees via pathways provided by the prop roots of fallen trees, whereas subterranean termites construct their foraging tunnels with tree-like branching patterns.

In the present study, we developed a new model for termite territorial behavior based on empirical data obtained from studies on 2 subterranean termites, *Coptotermes formosanus* (Shiraki) and *Reticulitermes flavipes* (Kollar) in consideration of the tunnel-tunnel encountering. The developed model was applied to predict the territorial competition between colonies by varying the termination probability for the primary tunnel.

2. Simulation Model Description

Tunnel patterns of foraging termites were simulated in a continuous two-dimensional area. The simulated tunnels were classified into primary and secondary tunnels—those originating from the nest were classified as primary, while those branching from the primary tunnel were classified as secondary^[14]. Tertiary and quaternary tunnels were excluded because they were rarely formed during the test period^[15]. In this study, the simulated tunnel patterns were constructed for 2 species, *C.formosanus* and *R. flavipes*. For all tunneling activities, the model presented in this study is based on probabilistic decisions. A territory was defined as the polygon completely covering a tunnel network pattern. The main procedure of the model consists of 2 procedures. One describes tunnel network growth and the other represents territoriality based on tunnel-tunnel interactions (see Apend.).

In the model, 8 variables are used to simulate the tunnel network pattern. The variables are: (1) number of primary tunnels, (2) linear length of primary tunnel segments, (3)

Table 1. The values (mean ± SD) of the variables used to generate tunnel network patterns in this simulation model

Parameters	<i>C. formosanus</i>	<i>R. flavipes</i>
N_0	6.78 ± 1.01	11.6 ± 0.69
L (cm)	1.03 ± 0.04	0.87 ± 0.02
T_{angle} (deg)	19.69 ± 0.68	22.72 ± 0.36
B_{angle} (deg)	51.14 ± 2.83	60.55 ± 1.87
P_{branch} (%)	10.52 ± 0.97	19.42 ± 3.46
P_{term1} (%)	18.68 ± 1.33	14.73 ± 1.88
P_{term2} (%)	41.17 ± 3.94	45.55 ± 5.01
P_{inter} (%)	50.0 ± 16.69	42.71 ± 6.15

turning angle of each linear segment of the primary tunnel, (4) branching angles of secondary tunnels, (5) probability of branching per linear segment of a primary tunnel, (6) termination probability for primary tunnels, (7) termination probability for secondary tunnels, and (8) probability of continuing through an intersection of 2 tunnels.

The values of the variables mentioned above were obtained from Su et al.^[15] (see Table 1). A single termite tunnel pattern is generated by the addition of linear segments with lengths and turning angles obtained from the appropriate empirical distributions. The values of the variables determine whether a tunnel terminates, branches, or extends beyond any intersecting tunnels.

In order to simulate territorial competition, the following additional 7 variables were used (Table 1): (1) system size, (2) number of colonies, (3) blocking probability, (4) number of iteration, (5) colony location, (6) species selection, and (7) landscape type.

As a process to appropriately visualize the territoriality dynamics, we added 3 variables in the simulation model: (1) tunnel color selection, (2) system size visibility, and (3) simulation speed.

In this model, the values of the variables mentioned above are inputted in the graphical user interface (GUI) windows shown in Fig. 1.

2.1 Explanation of the variables for constructing tunnel patterns

Number of primary tunnels (N_0)

Primary tunnels are defined as the tunnels originating from the nest.

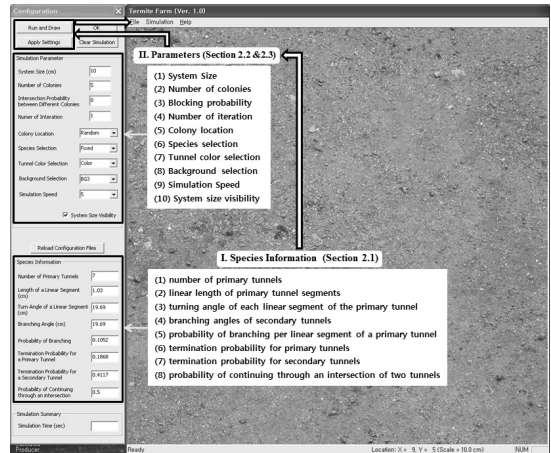


Fig. 1. Simulation software for termite territory dynamics based on tunnel network patterns

Length of a linear segment (L)

The present simulation is executed in discrete time steps ($t = 0, 1, 2, \dots$). For each time step, the tunnel is advanced by adding a linear segment of length L starting from the endpoint of the previous segment.

Branching probability (P_{branch})

After advancing a tunnel, a probability is generated by a random process. When the value of the probability is larger than the branching probability initially given, a new tunnel begins advancing at the end position with a branching angle B_{angle} .

Turning angle of the linear segment of a tunnel (T_{angle})

After excavation of a segment of length L , termites change the direction of tunneling by a certain angle from the segment excavated at the previous time step. This angle is called the turning angle of a linear segment. The orientation of the turning angle, either clockwise or counter-clockwise, is determined by a coin-tossing rule.

Branching angle of secondary tunnels (B_{angle})

A secondary tunnel branching from the primary tunnel has a specific angle from the primary tunnel. The direction of orientation can be either clockwise or counter-clockwise.

Termination probability for the primary tunnel (P_{term1})

Continuation of primary tunnel construction is determined by comparing a random number to the termination probability for primary tunnels. If the random number is greater than the termination probability, then tunnel excavation goes on, if not, it stops. This probability is an important tunneling factor influencing the total number of tunnels and the size of the termite territory.

Termination probability for secondary tunnels (P_{term2})

Similar to the termination probability for primary tunnels, this termination probability determines continuation of secondary tunnel construction. When the advance of all primary and secondary tunnels stops, the simulation finishes.

Probability of continuing through an intersection of 2 tunnels (P_{inter})

Due to the turning angle of primary tunnels and the branching angle of secondary tunnels, newly constructed tunnels can encounter existing ones. In that case, continuation of tunnel excavation is determined by the intersection probability. If a random number is less than the intersection probability, then intersection between 2 tunnels is permitted, and the new tunnel stops not at the intersection point, but at the endpoint of a linear segment.

2.2 Explanation of the variables for simulating territorial competition**System Size (L_{sys})**

L_{sys} is the length of one side of the square where the territory seeds were distributed initially. Simulated tunnels can exceed the boundary of the system.

Number of territories (N)

To consider the situation that multiple territories compete with each other, an arbitrary number of territories is chosen initially.

Blocking probability between tunnels of different colonies (P_{block})

The blocking probability describes the likelihood that an advancing tunnel stops when it encounters another tunnel; higher values of the probability indicate that it is

easier for a tunnel to stop advancing.

Number of repetitions (N_{rep})

For statistical analysis, repeated simulations are required under the same simulation conditions. This variable determines the number of repetitions.

Location of the territorial seeds (Loc)

The location of each territorial seed can be determined either by users clicking on the background picture or by providing X-Y coordinates as a text file.

Species selection

This variable provides information on how many species will be considered in the simulation model.

Landscape type

The present model provides 2 types of landscapes, a random landscape or a fractal landscape. Fractal landscapes are created by the neutral landscape model^[16].

2.3 Explanation of the variables for the visualization**System size visibility (Vis)**

When this variable has a value of 1, the system size is illustrated in the background figure by a white rectangle. When the value is 0, system size does not appear on the background figure.

Tunnel color selection

This variable is for visual purposes. The tunnel color for each colony can be distinguished by different red, green, and blue (RGB) colors, or gray scales.

Simulation Speed

The present model provides a movie showing the temporal variations of tunnel growth. This variable controls the speed of the movie.

3. Simulation Procedures and Results**3.1 Simulation procedure**

At the beginning of the simulation run, N (=10, 20, ...,

100) territory seeds are randomly distributed in the given $L_{\text{sys}} \times L_{\text{sys}}$ sized square area. Non-dimensional time (t) starts from $t=1$ and finishes at $t=t_{\text{max}}$. Inside the time-loop, there are two sub-loops about n (the colony number) and m (the tunnel number). For each pair of (n, m) , the primary and secondary tunnels can be generated by the addition of linear segments with length and turning angles drawn from the appropriate empirical distributions. For the construction of primary and secondary tunnels, the random values should be less than the termination probabilities P_{term1} and P_{term2} . When the primary tunnel is made, the branching probability (P_{branch}) determines the secondary tunnel generated from the primary tunnel.

To describe the territorial competition, we introduced an additional variable, the blocking probability (P_{block}), which describes the degree of how well an advancing

tunnel stops when it encounters another tunnel. Higher values of P_{block} indicate that it is easier for a tunnel to stop advancing. The probability variables such as P_{term1} , P_{term2} , P_{branch} and P_{block} determine whether a tunnel terminates, branches, or penetrates through the existing tunnels. Simulation is stopped at the steady state after a sufficiently long simulation time step. The state means that the growth of all colonies is stopped by the termination probability of primary and branching tunnels or by blocking probability. Territories grown from the seeds can exceed the given area. This rule was adopted to consider many field cases in which termite territories are distributed without any physical or chemical barriers as boundaries in open space. In this study, the simulation results were statistically averaged over 200 runs. The simulation procedure is summarized by a flow-chart in the Fig. 2.

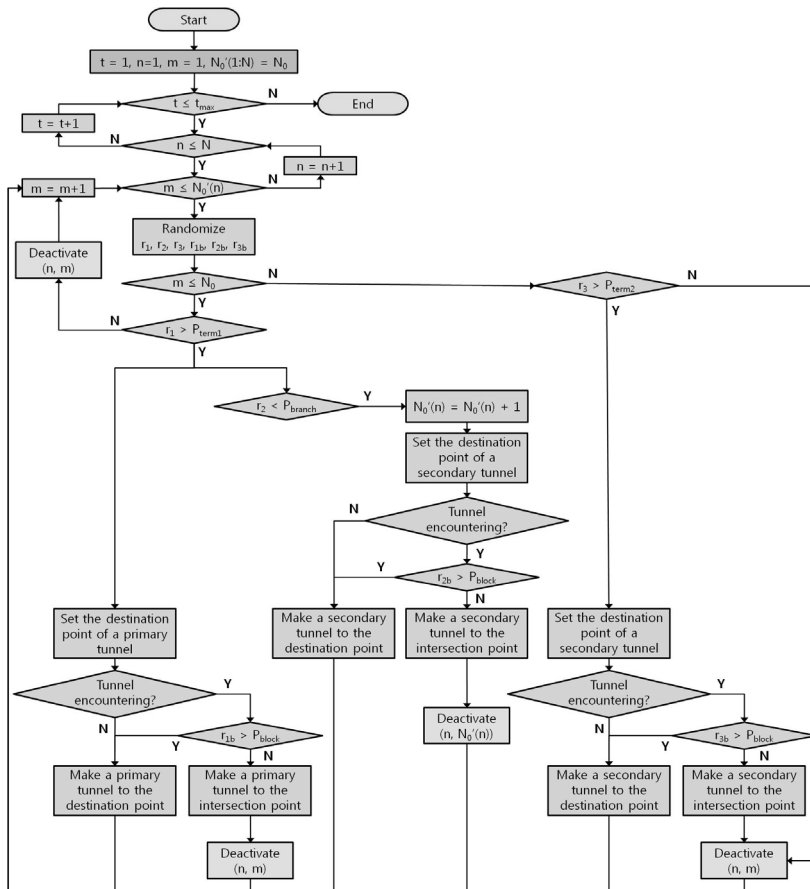


Fig. 2. Flow-chart of the simulation procedure in termites territory model

3.2 Results and analysis

Fig. 3 shows a simulated tunnel network pattern for *C.formosanus* and *R.flavipes* termites. From the tunnel pattern, a territory was formed by drawing a convex polygon covering the entire tunnel pattern.

Fig. 4 shows territorial competition among 20 territories. The upper figures show the tunnel network patterns for the 2 species. Different colors were used to discern each colony. The lower figures show the territory distribution corresponding to the upper tunnel patterns. Fig. 5 shows a simulated tunnel network of *C. formosanus* and the corresponding data file containing the X-coordinates of all nodes. This file can be obtained by clicking the “File” button and then choosing “Save Results” in the GUI of the model. X- and Y-coordinates of all nodes in the tunnel

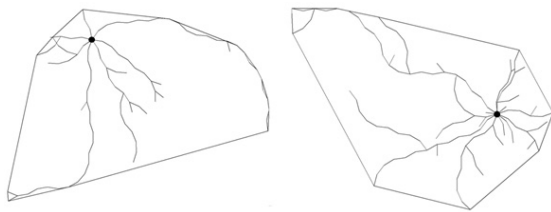


Fig. 3. Tunnel networks (black lines) and territory borders (blue lines) of single-colony termites for *Coptotermes formosanus* (left) and *Reticulitermes flavipes* (right). The black circle represents the nest of each colony.

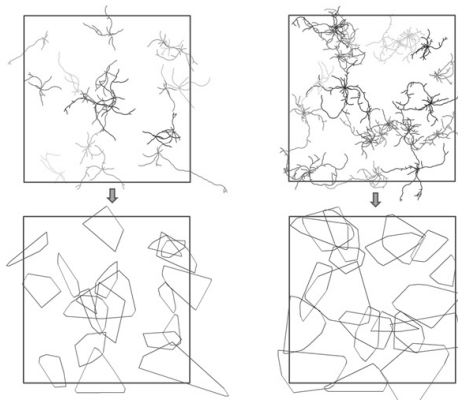


Fig. 4. Twenty termite tunnel networks (top) and their territories (bottom) for *Coptotermes formosanus* (left) and *Reticulitermes flavipes* (right). Different colors indicate the different colonies, and the system size is expressed by a gray rectangle

network are saved in X1.txt and Y1.txt, respectively. For a single colony, the network is expressed by a single matrix when the simulation is finished.

The rows indicate discrete time steps. In the first row, the X-coordinate of the nest is written from the first column to the N_0 th column where N_0 is the number of primary tunnels starting from the nest. In the second row, the X-coordinate of the endpoint after one-step of excavation is written. The next location at the next time step is written in the third row, and so on, until tunnel excavation is terminated. The columns indicate the number of primary and secondary tunnels. From the first column to the N_0 th column, each X-coordinate of each primary tunnel is written from the nest position to the terminated position. When termites make a secondary tunnel from a node of a primary tunnel, an additional column is created, and the starting node of the secondary tunnel is written in the same row of the primary tunnel to identify its branched location.

In Fig. 5, branching occurred twice as shown in the tunnel network. One was from the 2nd primary tunnel at the third time step and the other was from the 5th primary tunnel at the fourth time step. Two branching nodes are marked by colored rectangles.

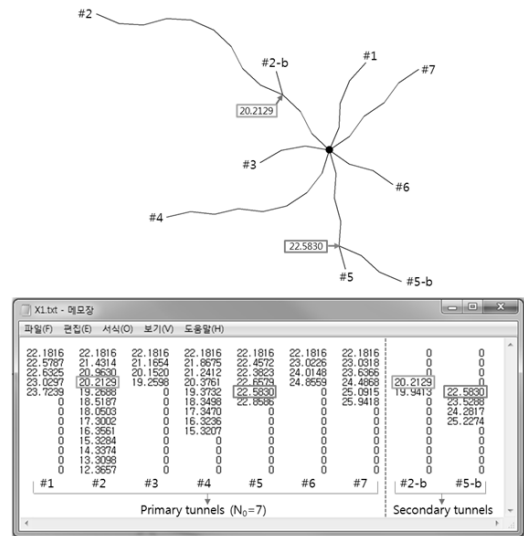


Fig. 5. Simulated tunnel network (top) and X-coordinates of location data for primary and secondary tunnels (bottom). The black circle represents the nest of the colony

the starting node of the secondary tunnel and the branching node of the primary tunnel. Using this file, users can identify the branching location, time, and the primary tunnel of every secondary tunnel.

Fig. 6 shows the simulated tunnel networks, their territories, and block matrices expressing the tunnel networks. Each block matrix has all locations of primary and secondary tunnels of each colony.

In order to understand the effects of the degree of interaction on the territory size distribution, we investigated the territory size distribution for different levels of P_{block} at the steady state that was reached after a sufficiently long simulation time. At the steady state, territory size distribution does not change according to time.

In order to capture the differences between the degrees of interaction of *C.formosanus* and *R.flavipes*, we introduced the following interference coefficient γ .

$$\gamma = \frac{\sum_{n=1}^N (A_n^{P_{block}=0} - A_n^{P_{block}})}{\sum_{n=1}^N A_n^{P_{block}=0}}$$

where N and n are the total number of territories, and the number assigned to each territory in descending order of size, respectively. $A_n^{P_{block}}$ represents the n^{th} territory size for the P_{block} value. By calculating the differences between the territory size for $P_{block} = 0$ and the territory size for $P_{block} \neq 0$, the effect of P_{block} on the territory size distribution could

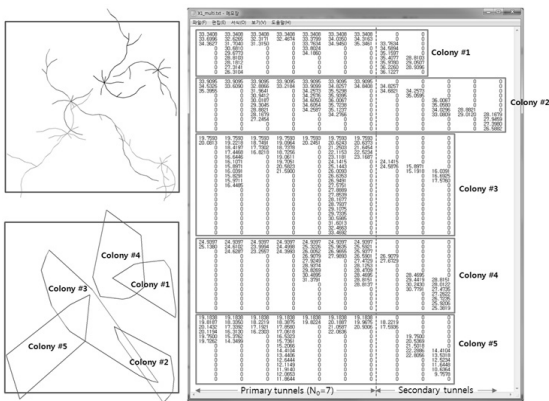
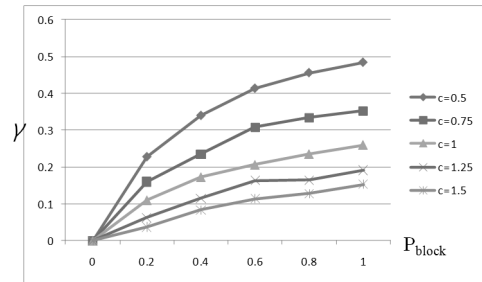


Fig. 6. Simulated tunnel networks (top left) and territories (bottom left) and the location data of all nodes for each colony (right) in case of multi-colony termites

be easily quantified. The denominator was introduced to normalize the γ value.

By using the present simulation model and calculating the γ value as a quantitative measure of territorial competition, we investigated the effect of P_{term1} and P_{term2} on territorial competition. The γ values against P_{block} were plotted where P_{term1} and P_{term2} are changed in a domain (Fig. 7). The number of territories was fixed at 20 and the blocking probability, P_{block} , between tunnels from the different colonies ranged from 0.0 to 1.0 by increments of 0.2. The domain of the values of P_{term1} and P_{term2} was determined by multiplying by a value c : 0.5, 0.75, 1.0, 1.25, and 1.5. Changes in the values of P_{term1} and P_{term2} can be understood by the situation that in heterogeneous landscape, many local regions hostile to tunneling in a heterogeneous landscape are likely to increase or decrease P_{term1} and P_{term2} value. In the simulation, we assumed that P_{term1} and P_{term2} are altered with same ratio, c . In Fig. 7, the interference coefficient, γ , increased when c decreased because the territory size increased when c decreased. For lower values of c , termites may have more chance to find

(a) *C. formosanus*



(b) *R. flavipes*

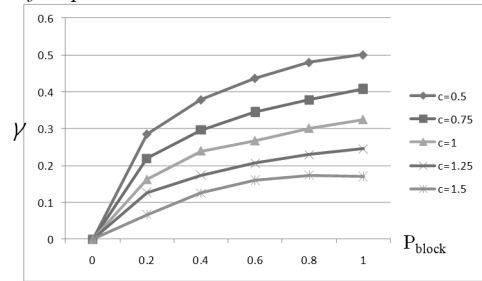


Fig. 7. Interference coefficients of multi-colony termites against blocking probability, P_{block} , for (a) *Coptotermes formosanus* and (b) *Reticulitermes flavipes*

the randomly distributed food resources whereas the degree of territorial competition increases. On the other hand, for higher value of c , the food finding probability may be decreased as the degree of territorial competition decreases. When considering the simulation results, we can indirectly conjecture that the ecological reason that termites choose $c=1$ is probably related to 2 factors; one is the foraging efficiency for tunnel pattern itself in geometrical aspect^[17] and the other is competition efficiency in territoriality for occupying space. Further analyzing the relationship between the 2 factors would be interesting, however, we remain the work for the future study in order to avoid our focus entangled.

4. Conclusions

In the present study, we suggested a simulation model to mimic termite territoriality based on tunnel network patterns. A territory was defined as a polygon covering an entire tunnel pattern.

We were unable to provide sufficient evidence for the validity of the simulation results because of a lack of field data, and because the present model did not consider the effects of other biotic and abiotic factors on termite tunnel networks. Nevertheless, this study is valuable in that the proposed termite territory model makes it possible to predict the territory size distributions resulting from territorial competition. Further, the γ function can serve as a useful tool to characterize termite territory formation and dynamics. We believe that this simulation model can be effectively used to not only understand the termite's territorial behavior, but also the termite's tunneling strategy to increase foraging efficiency. Although more field data are required to confirm the simulation results, these studies are valuable in that the simulation results provided a possible explanation for many characteristics of termite foraging behavior, and provided a baseline for future empirical work on the territorial behavior of subterranean termites.

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전 원 주 (wjeon@nims.re.kr)

2006 KAIST 항공우주공학과 박사
 2006~2010 한국과학기술원 기계기술연구소 박사후 연구원
 2011~현재 국가수리과학연구소 위촉연구원

관심분야 : 생물행동 및 생태계요소 모델링, 파동이론 및 생물음향, 응용복소함수 및 특수함수론



이 상 희 (sunchaos@nims.re.kr)

2005 부산대학교 물리학과 박사
 2008 국가수리과학연구소 가상생태계 모델 개발 팀장
 2009~현재 한국수리생물학회 운영위원
 2010~현재 국가수리과학연구소 융복합수리과학연구부 부장

관심분야 : 생물행동 모델링, 생태계 모델링, 최적화 이론, 비선형동역학