Mathematical models for Isoptera (Insecta) mound growth

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(With 4 figures)

Abstract

In this research we proposed two mathematical models for Isoptera mound growth derived from the Von Bertalanffy growth curve, one appropriated for *Nasutitermes coxipoensis*, and a more general formulation. The mean height and the mean diameter of ten small colonies were measured each month for twelve months, from April, 1995 to April, 1996. Through these data, the monthly volumes were calculated for each of them. Then the growth in height and in volume was estimated and the models proposed.

Keywords: Nasutitermes coxipoensis, Isoptera, Insecta, mound growth.

Modelos matemáticos para crescimento dos ninhos de Isoptera (Insecta)

Resumo

Nessa pesquisa, propusemos dois modelos matemáticos derivados da curva de Von Bertalanffy para o crescimento dos ninhos de Isoptera; um específico para *Nasutitermes coxipoensis*; e outro mais geral. A altura média e o diâmetro médio de dez colônias pequenas foram medidas a cada mês, de abril de 1995 a abril de 1996. Através desses dados, foi calculado o volume mensal de cada colônia. Posteriormente os crescimentos em altura e volume foram estimados e os modelos propostos.

Palavras-chave: Nasutiternes coxipoensis, Isoptera, Insecta, crescimento de ninhos.

1. Introduction

All termites are social insects and live in communities, large or small, within the limits of a nest-system. The nest and associated structures, such as mounds, subterranean galleries and covered runways, comprise a closed system largely isolated from the external environment but allowing for the egress of foraging parties and flight of alates (Lee and Wood, 1971). In this system, within which the micro-climate can be controlled within certain limits, food can be stored, and they obtain some protection from natural enemies (Lee and Wood, 1971; Banerjee, 1975). The nest-system of these insects is not a static structure and is enlarged as the colony grows (Noirot, 1970).

Three recognisable developmental phases exist in termite societies. The first corresponds to a juvenile phase, during which there is just differentiation of the neuter castes. Soon after, the colony passes to the mature or adult phase, period in which the winged reproductives are produced. Finally, a phase of senescence occurs, when there is a decline in the nest population (Noirot, 1969). Collins (1981) deduced that the populations in the nests of *Macrotermes bellicosus* Smeathman 1781 increase exponentially for 4-6 years reaching the maximum number of individuals in its neuter population at the end of this period. Resources are subsequently channelled into the production of winged reproductives and, years later, its population declines and the colony dies.

Considering all three development stages of the Isoptera colonies, recognized by Noirot (1969), one can consider the growth of the colony analogous to that of an organism. Thus, in this study we proposed two mathematical models in order to describe the growth of *Nasutitermes coxipoensis* Holmgren 1910 (Model 1) mounds derived from the Von Bertalanffy (1938) growth curve and a more general formulation (Model 2) for other termite species. Von Bertalanffy developed one of the first models for organic growth, particularly for fishes.

2. Material and Methods

2.1. Study area

Mounds sampled in this study were located in a Cerrado area in the Municipality of Itirapina, São Paulo, Brazil (22° 15' S and 47° 49' W, altitude of 765 m). The word "Cerrado" is a Portuguese term meaning "half-closed" or "dense". In Brazilian terminology it also describes a particular kind of vegetation similar to savannah, although having much broader physiogonomic variation in size and density of trees. That is, the word Cerrado describes a gradient of vegetation comprising "savannah grassland", "low trees and shrub savannah" and "savannah woodland". It is important to point out that the similarities to savannah are only physiogonomic and not floristic. It covers about 2 million km^2, or 25% of the whole Brazilian territory (Ferri, 1976). This supports private farming enterprises where one of the main activities is cattle rearing. Therefore, at times of drought when fire becomes frequent in this locality, the impact of the cattle also becomes more apparent.

The study area is an alluvial plain covered by sandy sediment, with a deep, quartzes' sand soil type (Oliveira and Prado, 1984) and has 12,750 m^2.

Mean annual rainfall is 1,425 mm, with the rainy season extending from October to March, when 84% (1,199 mm) of the precipitation occurs. The most rainy months are December, January and February, with precipitation average values equal to 288, 266 and 262 mm, respectively. The driest months are July and August, with 16 and 19 mm of precipitation, respectively. The mean annual temperature is 19.7 °C, with January and February being the hottest months with respective mean values of 22.2 and 22.3 °C. The coldest months are June and July with respective mean temperatures of 16.4 and 16.2 °C.

2.2. Sampling program

The mean height (n = 3) and the mean diameter (n = 3) of ten previously marked mounds, whose initial volumes varied from 3.88 dm^3 to 19.38 dm^3, were measured each month for twelve months, from April, 1995 to April, 1996, with the aid of two wood stakes approximately 1 metre in length. Considering that the biggest volume found was equal to 192.46 dm^3 (Buschini, 1996), this research was been accomplished with small colonies. During the measurements the stakes were vertically placed on each side of the mound and the diameter measured at this distance. To measure the height, a single stake was placed horizontally on the apex of the mound and, with the aid of the metric tape, the distance between the stake and the soil was measured as closely as possible to the base of the mound.

Although some of the mounds present deformations and considering that they are entirely epigean, it was assumed that they have approximately a spherical calotte shape (Figure 1). Thus, the volume of the mounds was evaluated by the formula: $V = \pi/_6 .h\{3r^2 + h^2\}$ where r = d/2 = radius and h = height of the mound (Gieck, 1979).

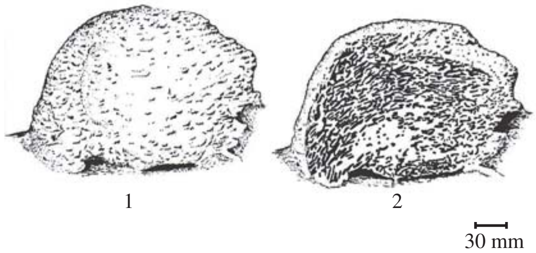

Figure 1. Nests of *Nasutitermes coxipoensis*. 1) External view; and 2) Internal view.

3. Results and Discussion

3.1. Model 1 for Nasutitermes coxipoensis mounds

3.1.1. Growth in height

The growth in height can be expressed by the differential equation:

$$dh_k/_{dt} = k(h_{max} - h_t) \quad (1)$$

where:

h_t = height of the mounds in the instant t; k = constant of growth; h_{max} = maximum height, that is, the maximum height reached by an adult mound.

Let us suppose that in the instant $t = 0 \Rightarrow h_t = 0$

Then,

$$dh/(h_{max} - h_t) = kdt$$

integrating:

$$\int dh/(h_{max} - h_t) = \int kdt$$

$$-\ln(h_{max} - h_t) = kt + c \text{ where c is the integrate constant}$$

$$\text{When } t = 0 \Rightarrow -\ln(h_{max}) = c, \text{ thus}$$

$$-\ln(h_{max} - h_t) = kt - \ln(h_{max})$$

$$\ln(h_{max}) - \ln(h_{max} - h_t) = kt$$

$$\ln\left\{h_{max}/(h_{max} - h_t)\right\} = kt$$

$$h_{max}/(h_{max} - h_t) = e^{kt}$$

$$h_{max} = e^{kt}(h_{max} - h_t)$$

$$e^{-kt}h_{max} = h_{max} - h_t$$

$$h_t = h_{max} - e^{-kt}h_{max}$$

$$h_t = h_{max}(1 - e^{-kt}) \quad (2)$$

The graph of this function is given in Figure 2. Notice that h_{max} is an asymptotic value that needs to be determined together with k, through a non-linear regression.

A more flexible model was proposed by Richards (1959) to describe different patterns of organic growth in which the growth rate, in length, is determined by the differential equation:

$$dD/dT = kD/(1-m)\left[\left(D_{max}/D\right)^{1-m} - 1\right] \quad (3)$$

where D_{max} is the maximum size reached by the organism and k is a growth constant. The solution of this equation is the growth curve defined by:

$$D(t) = D_{max}\left(1 - Ae^{-kt}\right)^{1/(1-m)} \quad (4)$$

If m = 2/3 then we have Von Bertalanffy's model (Brown and Rothery, 1993).

3.1.2. Growth in volume

Considering that the nests of *Nasutitermes coxipoensis* possess the volume of a spherical shape with height h and radius r, we have:

$$V_t = \frac{\pi}{6} h_t \left(3r_t^2 + h_t^2\right) \quad (5)$$

A dispersion diagram of r vs. h of each *N. coxipoensis* mound was drawn. From this graph (Figure 3) we verified that a linear relationship exists, approximately, among them. Then, a model of linear regression $r = \beta_o + \beta_1 h$ was used, and we observed that the slope coefficient of the adjusted straight line is $b_1 = 0.569$.

A test of the hypothesis $\{H_o{:}\beta_1 = 0.5$ and $H_1{:}\beta_1 \neq 0.5\}$ was accomplished and it showed that we should accept the null hypothesis H_o, that is, there is strong evidence that $\beta_1 = 0.5$. Thus, firstly, we suppose that:

$r_t = 2h_t$ then,

$$V_t = \left(\pi/6\right) h_t \left[\left(3.4h_t^2\right) + h_t^2\right]$$

$$V_t = \left(\pi/6\right) h_t 13h_t^2$$

$$V_t = \frac{13\pi}{6} h_t^3 \quad (6)$$

Replacing (2) in (6) then:

$$V_t = \frac{13\pi}{6} . h_{max}^3 \left(1\text{-}e^{-kt}\right)^3$$

considering. $V_{max} = \frac{13\pi}{6} h_{max}^3$

we have:

$$V_t = V_{max}\left(1 - e^{-kt}\right)^3 \quad (7)$$

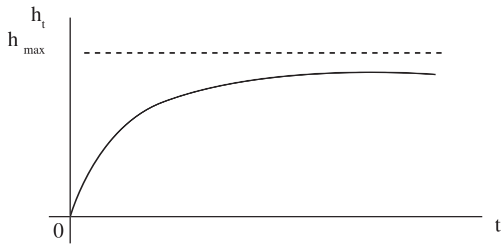

Figure 2. Theoretical growth curve in height (h_t) of the mound as a function of time (t), with h_{max} being an asymptotic height.

Studying the function : $V_t = V_{max}\left(1 - e^{-kt}\right)^3$

$$dV_t/dt = 3V_{max}\left(1 - e^{-kt}\right)^2 ke^{-kt}$$

$$dV_t/dt = 3kV_{max}e^{-kt}\left(1 - e^{-kt}\right)^2 > 0 \text{ for } t > 0,$$

that is, V_t is crescent

$$d^2V_t/dt^2 = 3kV_{max}\begin{Bmatrix} -ke^{-kt}\left(1 - e^{-kt}\right)^2 + \\ e^{-kt}2\left(1 - e^{-kt}\right)ke^{-kt} \end{Bmatrix}$$

$$d^2V_t/dt^2 = 3k^2V_{max}e^{-kt}\left(1 - e^{-kt}\right)\left\{-\left(1 - e^{-kt}\right) + 2e^{-kt}\right\}$$

$$d^2V_t/dt^2 = 3k^2V_{max}e^{-kt}\left(1 - e^{-kt}\right)\left(3e^{-kt} - 1\right)$$

thus, $d^2V_t/dt^t = 0 \Leftrightarrow \left(3e^{-kt} - 1\right) = 0$

$$3e^{-kt} = 1$$

$$3 = e^{kt}$$

$$\ln 3 = kt$$

$$t = \ln 3/k$$

or $\left(1 - e^{-kt}\right) = 0$

$$1 = e^{-kt}$$

$$e^{kt} = 1$$

$$t = 0$$

$$d^2V_t/dt^2 > 0 \Leftrightarrow \left(3e^{-kt} - 1\right) > 0$$

$$3e^{-kt} > 1$$

$$3 > e^{kt}$$

$$\ln 3 > kt$$

$$\ln 3/k > t$$

$$d^2V_t/dt^2 < 0 \Leftrightarrow \left(3e^{-kt} - 1\right) < 0 \quad \Leftrightarrow \quad t > \ln 3/k$$

Thus, in $t = \ln 3/k$ we have one inflexion point;

for $t < \ln 3/k$, V_t has an upward concavity;

for $t > \ln 3/k$, V_t has a downward concavity.

Now, $\lim_{t\to\infty} V_t = \lim_{t\to\infty} V_{max}\left(1 - e^{-kt}\right)^3 =$

$\lim_{t\to\infty} V_{max}\left(1 - 1/e^{kt}\right)^3 = V_{max}1 = V_{max}$

Figure 4 illustrates the behaviour of this function, also asymptotic for V_{max}.

3.2. Model 2 for other termite species

We propose below a more general formulation, without the supposition that $r_t = 2h_t$.

$$\frac{dr_t}{dt} = k_0 \left(r_{max} - r_t\right) \Rightarrow r_t = r_{max}\left(1 - e^{-k_0 t}\right)$$

and,

$$\frac{dh_t}{dt} = k_1 \left(h_{max} - h_t\right) \Rightarrow h_t = h_{max}\left(1 - e^{-k_1 t}\right)$$

thus,

$$V_t = \frac{\pi}{6} h_t \left(3r_t^2 + h_t^2\right)$$

$$V_t = \frac{\pi}{6} h_{max}\left(1 - e^{-k_1 t}\right)\left[3r_{max}^2\left(1 - e^{-k_0 t}\right)^2 + h_{max}^2\left(1 - e^{-k_1 t}\right)^2\right]$$

$$V_t = \frac{\pi}{2} h_{max} r_{max}^2 \left(1 - e^{-k_1 t}\right)\left(1 - e^{-k_0 t}\right)^2 + \frac{\pi}{6} h_{max}^3\left(1 - e^{-k_1 t}\right)^3$$

$$\frac{dV_t}{dt} = \frac{\pi}{2} h_{max} r_{max}^2 \begin{bmatrix} k_1 e^{-k_1 t}\left(1 - e^{-k_0 t}\right)^2 + \\ \left(1 - e^{-k_1 t}\right) 2 \left(1 - e^{-k_0 t}\right) k_0 e^{-k_0 t} \end{bmatrix} +$$

$$+ \frac{\pi}{6} h_{max}^3 3 \left(1 - e^{-k_1 t}\right)^2 k_1 e^{-k_1 t}$$

$$\frac{dV_t}{dt} = \frac{\pi}{2} h_{max} r_{max}^2 \left(1 - e^{-k_0 t}\right) \begin{bmatrix} k_1 e^{-k_1 t}\left(1 - e^{-k_0 t}\right) + \\ 2k_0 e^{-k_0 t}\left(1 - e^{-k_1 t}\right) \end{bmatrix} +$$

$$+ \frac{\pi}{2} h_{max}^3 k_1 e^{-k_1 t}\left(1 - e^{-k_1 t}\right)^2$$

$$\frac{dV_t}{dt} > 0 \quad \text{for} \quad t > 0 \Rightarrow V_t \quad \text{is crescent}$$

$$\lim_{t\to\infty} V_t = \lim_{t\to\infty} \begin{bmatrix} \frac{\pi}{2} h_{max} r_{max}^2 \left(1 - \frac{1}{e^{k_1 t}}\right)\left(1 - \frac{1}{e^{k_0 t}}\right)^2 + \\ \frac{\pi}{6} h_{max}^3 \left(1 - \frac{1}{e^{k_1 t}}\right)^3 \end{bmatrix} =$$

$$= \frac{\pi}{2} h_{max} r_{max}^2 + \frac{\pi}{6} h_{max}^3$$

$$= \frac{\pi}{6} h_{max}\left[3r_{max}^2 + h_{max}^2\right] = V_{max}$$

The graph of Vt will not be sketched here because, as it can be observed, the sign of the second derivate $d^2V/_{dt}{}^2$ depends on the specifications of r_t and h_t, for each species of termites to be studied.

Faced with these models proposed for *N. coxipoensis* in particular, and for other termites species, it can be thought that the juvenile phase would be equivalent to the initial stages of development of the colony with rates of relative growth $\{(w_2\text{-}w_1)/(w_1)\}$ and absolute $\{(w_2\text{-}w_1)/(t_2\text{-}t_1)\}$ height. The mature phase, for its time, would correspond to the inflexion point with a decrease in the growth rates due to a larger reproductive investment (beginning of the production of winged reproductives in termites). And, finally, the older phase would be the stage during which the colonies reach an asymptotic weight (volume). However, other studies will be necessary to test and to discuss the models presented in this study.

This model can be tested simply by measuring height and diameter of the studied species nests. As mentioned above, the V_t graphs have to be sketched for each termite species with their specific values of r_t and h_t. It is important to investigate the relationship between these two variables by initially plotting both variables on the graph and verifying the existence of linearity between them. If $r_t = 2h_t$, the species in question will present the same growth pattern as *N. coxipoensis*, equivalent to that proposed by Von Bertalanffy (1938).

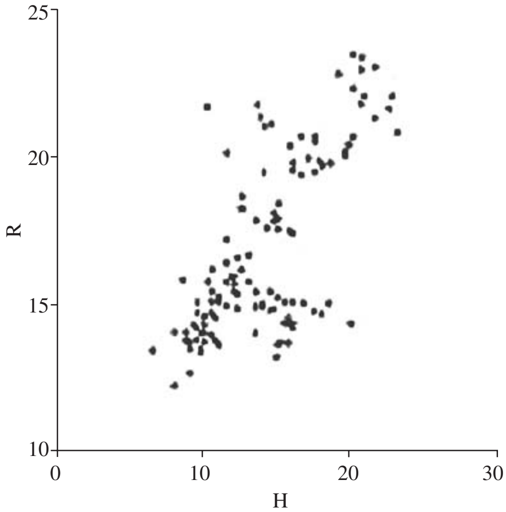

Figure 3. Scatter diagram between the radio (R) and mean height (H) of the mounds.

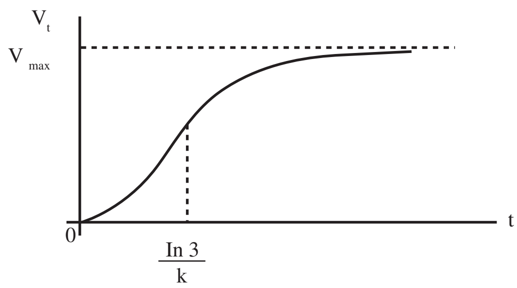

Figure 4. Theoretical growth curve in volume (V_t) of the mound as a function of time (t). V_{max} is the asymptotic volume and ln $3/_k$ is the instant when the inflexion point of the curve occurs.

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