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A stochastic analysis of seed germination

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Abstract. Seed germination under constant temperature is modeled stochastically. It is assumed that a potentially germinable seed passes a series of transition or active states before it germinates. The present stochastic model provides detailed information about the phenomenon under consideration, for example, the mean and the variance of the number of germinated seeds as functions of time, and, therefore, is a generalization of the germination model appeared in the literature. The shape of germination curve is found to be affected by the number of transition states.

Key words: Seed germination; Stochastic analysis.

Introduction

Modeling seed germination is of major importance in practice for obvious reason. To this end, a great deal of work has been devoted to investigating the phenomenon. Unfortunately, it is found that previous effort in this area is either focus mainly on the experimental aspect or lack of sound theoretical ground. In a study of the effect of temperature on germination rate, Goloff and Bazzaz (1975) have derived a linear relation between the logarithm of the number of germinable seeds and time. It should be pointed out that, more often than not, functional dependence of the number of germinated seeds on time which does not follow this relation is often observed in a typical germination experiment. By arbitrarily assuming the probability of germination as a function of time, Bould and Abrol (1981) are able to predict germination curve of various shapes. The approach adopted can be classified as semi -empirical since it is difficult to assign physical meaning to the assumed functions. Thornley (1977) has proposed an interesting way of portraying seed germination. It is assumed that seed germination occurs in a stagewise procedure. The waiting time of germination is found to have a gamma distribution provided that the rate constant between successive stages is constant. It should be noted that seed germination is a complicated bioprocess which involves series of bioreactions. Furthermore, the sample size of a typical seed germination experiment is often small, and thus, its random nature can be significant. It appears that the phenomenon can best be modeled by a stochastic representation.

Modeling

We assume that seed germination occurs in the following manner:

1st or initial state	→	2nd transition state	→	3rd transition state	→ ⋯ →	nth or germinated state

That is, starting with the germination experiment, a seed is assumed to be in state 1. A seed in state n corresponds to that it is germinated. Let the random variable N(t) represents the status of a seed at time t, a specific value of N(t) is represented by i, $i=1,2,\cdots,n$. Denote $p_i(t)$ as the probability that $N(t)=i$. The follow-

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ing conditions are assumed:

1) $Pr[N(t+\Delta t)=i+1 \text{ given } N(t)=i] = \lambda_i\Delta + o(\Delta t)$
2) $Pr[N(t+\Delta t)=i+j \text{ given } N(t)=i] = o(\Delta t),\ j \geqq 2$
3) $Pr[N(t+\Delta t)=i \text{ given } N(t)=i] = 1 - \lambda_i\Delta t + o(\Delta t)$

where $(t,t+\Delta t)$ is an infinitesimal but finite time interval and the function $o(\Delta t)$ satisfies the condition

$$\lim_{\Delta t\to 0} \frac{o(\Delta t)}{\Delta t} = 0$$

Condition 1) indicates that a certain probability is associated with the transition from a state to the next higher state during an extremely small time interval; 2) states that the probability of two or more transitions in this time interval is of order $o(\Delta t)$; 3) is the statement of probability conservation. Under these conditions, it can be shown that $p_i(t)$ satisfies the following set of differential equations:

$$\frac{dp_i(t)}{dt} = \lambda_{i-1}p_{i-1}(t) - \lambda_i p_i(t),\ i=2,3,\cdots,n-1 \quad (1)$$

$$\frac{dp_1(t)}{dt} = -\lambda_1 p_1(t) \quad (2)$$

and

$$\frac{dp_n(t)}{dt} = \lambda_{n-1}p_{n-1}(t) \quad (3)$$

Equations (1) through (3) describe the probability distribution of the status of a seed. The solution of these equations subject to the initial condition

$$p_i(0) = \begin{cases} 1 & i=1 \\ 0 & i\neq 1 \end{cases} \quad (4)$$

takes the following form

$$p_1(t) = e^{-\lambda_1 t} \quad (5)$$

$$p_i(t) = \sum_{k=1}^{i} \left[\frac{\prod_{m=1}^{i-1}\lambda_m}{\prod_{m=1, m\neq k}^{i}(\lambda_m-\lambda_k)}\right] e^{-\lambda_k t},\ i=2,3,\cdots,n-1 \quad (6)$$

$$p_n(t) = 1 - \sum_{i=1}^{n-1} p_i(t) \quad (7)$$

Suppose that seeds behave independently during germination, it is clear that the number distribution of the seeds in each state is multinomial (see, e.g., Rogatgi, 1976) with the mean or expected value

$$E[M_i(t)] = M_0 p_i(t),\ i=1,2,\cdots,n \quad (8)$$

and the variance

$$Var[M_i(t)] = M_0 p_i(t)\ [1-p_i(t)]\ ,\ i=1,2,\cdots,n \quad (9)$$

where M_0 denotes the total number of germinable seeds initially present in the system and $M_i(t)$ is the number of seeds in state i at time t. Higher moments of $M_i(t)$ can also be obtained in a straightforward manner. Thus, the mean number of germinated seeds and the corresponding variance can be evaluated by letting $i=n$ in equations (8) and (9), respectively.

If the transition intensity between successive states is constant, i.e.,

$$\lambda_1 = \lambda_2 = \cdots = \lambda_{n-1} = \lambda \quad (10)$$

it can be shown, by induction, that the solution to equations (1) through (3) takes the following form

$$p_1(t) = e^{-\lambda t} \quad (11)$$

$$p_i(t) = \frac{e^{-\lambda t}(\lambda t)^{i-1}}{(i-1)!},\ i=1,2,\cdots,n-1 \quad (12)$$

$$p_n(t) = 1 - \sum_{i=0}^{n-1} p_i(t) \quad (13)$$

The dynamic behavior of seed germination, as predicted by the present stochastic model, is examined through numerical simulations. For illustration, only the results for the case where the transition intensity between successive states is constant are presented. Figure 1 shows the mean number of germinated seeds as a function of time for various values of the number of transition states. The corresponding variances are illustrated in Fig. 2.

Discussion

As can be seen from Fig. 1, the present stochastic model yields an inflection point when there exists at least one transition state, i.e., the germination curve is of S or sigmoid shape when $n \geqq 3$. Germination curve of sigmoid shape is often observed in a typical germination experiment (see, e.g., Hsu *et al.,* 1984; Gummerson, 1986). Figure 2 reveals that the variance of the number of germinated seeds increases with time, achieves a maximum value, and then vanishes in each case, meaning that the measurement made in the intermediate times may suffer a greater variation than those made in the initial or final stages. In practice, the number of

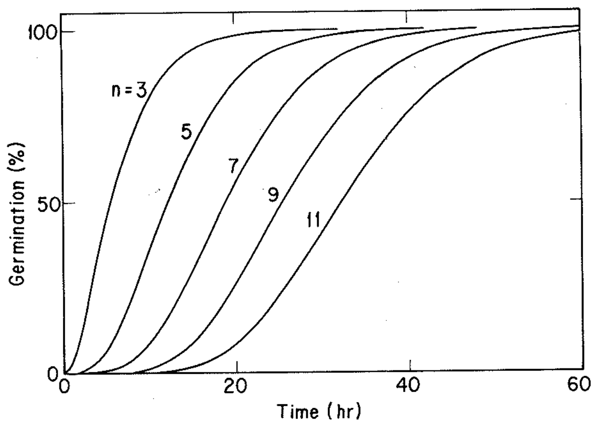

Fig. 1. Mean number of germinated seeds as a function of n ($n \geqq 3$) for the case $\lambda = 0.5$/hr, $M_0 = 100$.

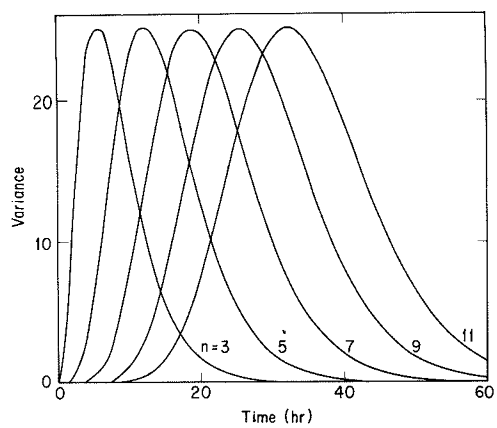

Fig. 2. Transient behavior of the variances corresponding to the case of Fig. 1.

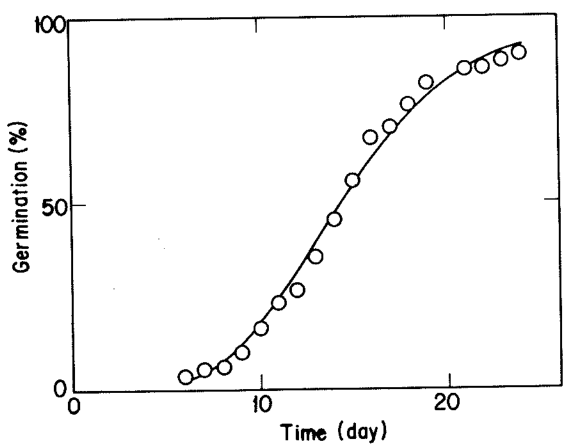

Fig. 3. The experimental data of Bould and Abrol (1981, Fig. 6) and the fitted result by the present stochastic model with $n=8$, $\lambda = 0.5396$/hr, and $M_0 = 98$.

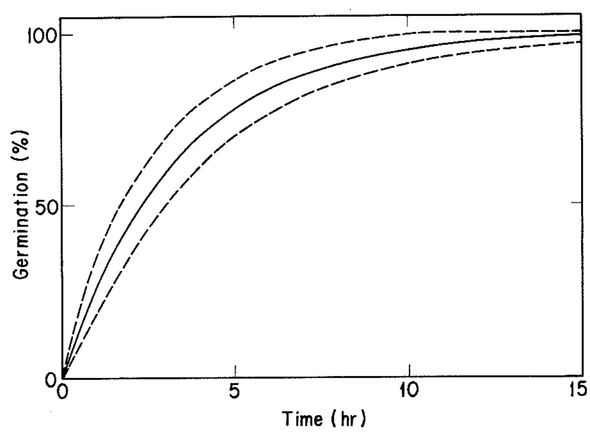

Fig. 4. Transient behavior of the mean number of germinated seeds and an approximate 95% confidence band for the case $\lambda_1 = 0.5$/hr, $M_0 = 100$, and $n = 2$.

transition states can be estimated by fitting the experimental data to one of the germination curves in Fig. 1. Figure 3 illustrates the experimental data reported by Bould and Abrol (1981) along with the predicted results evaluated by the present model.

In the case when $n=2$, i.e., seeds reach the germinated state without going through transition states, equations (5) through (7) become, respectively,

$$p_1(t) = \exp(-\lambda_1 t) \tag{14}$$

and

$$p_2(t) = 1 - \exp(-\lambda_1 t) \tag{15}$$

Under this condition, the mean number of germinated seeds and the corresponding variance are, respectively,

$$E[M_2] = M_0[1 - \exp(-\lambda_1 t)] \tag{16}$$

and

$$\mathrm{Var}[M_2] = M_0 \exp(-\lambda_1 t)\ [1 - \exp(-\lambda_1 t)] \tag{17}$$

By referring to equation (16), the mean number of germinable seeds, $E[M_1(t)]$, is

$$\begin{aligned} E[M_1] &= M_0 - E[M_1(t)] \\ &= M_0 \exp(-\lambda_1 t) \end{aligned} \tag{18}$$

Equation (18) describes a linear relation between the logarithm of the number of germinable seeds with time. Thus, the mean of the present stochastic model reduces to that of Goloff and Bazzaz (1975). The simulated results for this case are pictured in Fig. 4. A 95% (approximate) confidence band as calculated by $E[M_2(t)] \pm 1.96\mathrm{Var}[M_2(t)]^{1/2}$ is also shown in this figure.

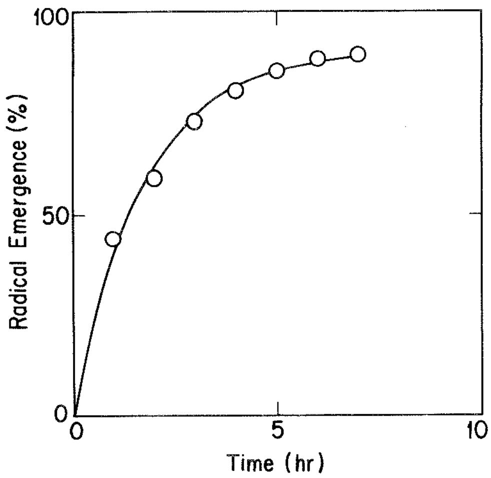

Fig. 5. The experimental data of Bould and Abrol (1981, Fig. 5) and the fitted result by the present stochastic model with n=2, $\lambda_1=0.5825$/hr, and $M_0=90$.

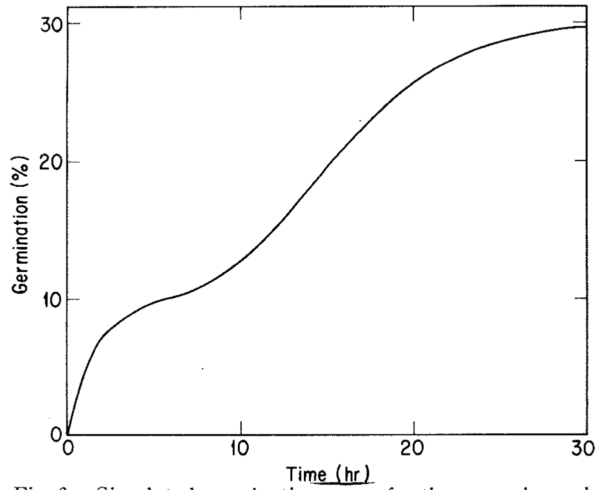

Fig. 6. Simulated germination curve for the case when sub-groups exist.

Figure 5 illustrates the experimental data of Bould and Abrol (1981) as well as the predicted value by the present model.

If sub-groups exist among seeds, i.e., seeds of different germination behavior present simultaneously, then the total number of germinated seeds at time t, $N_T(t)$, can be evaluated by the following expression:

$$N_T(t) = \sum_{p=1}^{r} N_{pT}(t) \tag{19}$$

where $N_{pT}(t)$ denotes the number of germinated seeds in sub-group p, and r represents the number of sub-groups. Figure 6 shows the example where there are two sub-groups in the system. One sub-group has 20 seeds initially with n=8, and $\lambda=0.5$/hr; the other sub-group has 10 seeds initially with n=2, and $\lambda_1=0.6$/hr. The qualitative behavior of the curve shown in Fig. 6 is quite similar to that observed experimentally by Bould and Abrol (1981, Fig. 7), indicating the possibility of the existing of sub-groups in their experiment.

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以隨機程序模型模擬種子發芽

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本文以隨機程序模型模擬種子在恆溫下之發芽行為。吾人假設種子由發芽前到發芽須經歷一連串之過渡階段。所推導之動態模型對發芽的動態行為提供了詳盡之訊息，例如平均發芽數隨時間之變化與其變異數隨時間之變化等等。因此，所得結果推廣了文獻中之發芽模型。數值模擬之結果顯示，發芽曲線之形狀受到過渡階段個數之影響。