Estimating the Temperature Dependence of Germination Time by Assuming Multiple Rate-Determining Steps

Yoshitaka Hara

(National Agricultural Research Center for Kyushu Okinawa Region, Chikugo 833-0041, Japan)

Abstract: The temperature dependence of the duration of a biological process can be analyzed using the Arrhenius equation. However, germination time does not precisely follow the Arrhenius equation, which is based on the assumption that temperature dependence can be explained by the behavior of one step. In the present study, to analyze germination time precisely, I assumed that temperature dependence could be explained by the behavior of multiple independent steps. According to this assumption, the germination time corresponds to the summed durations of multiple steps, and the duration of each step follows the Arrhenius equation. From these relations, I derived the s-equation, which relates germination time to changes in temperature. This s-equation method was then applied to the germination times of rice seeds at various temperatures. The results were compared to those of the classic breakpoint method, in which different Arrhenius equations are fitted to each temperature range, divided at the breakpoint temperatures. Germination time was correlated more precisely to changes in temperature, and obtained values of activation energies were more stable, with the two-step s-equation method than with the breakpoint method. These results suggest that the two-step s-equation method should be used to relate germination time to changes in temperature and that the temperature dependence of germination time involves two steps.

Key words: Activation energy, Arrhenius equation, Biological process, Breakpoint, Germination time, Rate-determining step, Temperature dependence.

In an elementary reaction, the reaction rate changes with temperature according to the Arrhenius equation (Iwanami’s Dictionary of Physics and Chemistry, 1998). The rate of a chemical reaction also follows the Arrhenius equation, because the overall rate is determined by the rate of the slowest step that follows the Arrhenius equation. This slowest step is called the rate-determining step. The existence of the rate-determining step allows the Arrhenius equation to be applied to some biological processes, even though these processes are more complex than chemical reactions.

Seed germination is an example of a biological process. Owing to the reciprocal relation between time and rate, the Arrhenius equation can be applied to time much as it can be applied to rate. The time from seed sowing to germination, hereafter called the germination time, follows the Arrhenius equation precisely within a limited temperature range and less precisely across the entire temperature range for seed germination (Nishiyama, 1975; Nishiyama, 1978; Hsu et al., 1984; Labouriau and Osborn, 1984; Scott et al., 1984; Washitani and Takenaka, 1984; Hsu et al., 1985; Washitani, 1985; Hageseth and Young, 1994). Conventionally, germination time has been analyzed by using two or more different Arrhenius equations for each temperature range. The temperature range thresholds are called breakpoints, and this method is hereafter referred to as the breakpoint method. However, some previous reports (Labouriau and Osborn, 1984; Washitani and Takenaka, 1984; Washitani, 1985) have indicated that the temperature dependence of germination time changes continuously, which implies that no clear breakpoint temperature exists for the temperature dependence of germination time.

To analyze temperature dependence without using the breakpoint method, Johnson and Thornley (1985) mathematically derived several models that were combinations of several equilibrium reactions that followed the Arrhenius equation. These models provide a conceptual basis for the underlying reaction mechanisms. Their applicability is limited, however, because the values of activation energy that indicate the degree of temperature dependence are difficult to obtain experimentally. As a result, the breakpoint method is still commonly used to analyze the temperature dependence of biological processes.

Germination time is affected by various reactions that depend on temperature; a single rate-determining step may often fail to represent the whole process. In this paper, I propose a new method that yields values of activation energy without using the breakpoint temperatures by assuming multiple rate-determining steps. I also describe the application of this method to germination time.
Materials and Methods

1. Derivation of the s-equation

The rate of a chemical reaction \( (v) \) is described using both the rate constant \( (k) \) and the variable \( (c) \), which reflects the concentrations of reactants related to the rate-determining step, hereafter called the concentration factor (Iwanami's Dictionary of Physics and Chemistry, 1998):

\[
\frac{1}{v} = k'c = k[R_1]^{n_1}[R_2]^{n_2}[R_3]^{n_3} \cdots
\]

(1)

\( [R_1], [R_2], [R_3], \cdots \) are the concentrations of reactants in the rate-determining step. \( O_1, O_2, O_3, \cdots \) are the reaction orders, which depend on the reaction mechanism of the rate-determining step. The rate constant \( (k) \) is described using the Arrhenius equation (Eq. 2) when the absolute temperature \( (T) \) changes.

\[
k = A \exp(-E/R/T)
\]

(2)

where \( E \) is the activation energy, \( A \) is the frequency factor, and \( R \) is the gas constant \( (= 8.31 \text{ J K}^{-1} \text{ mol}^{-1}) \). Equation 2 is transformed into Eq. 3 by taking the logarithm of both sides.

\[
\ln(k) = \ln(A) - E/R/T
\]

(3)

According to Eq. 3, the scatter plot of \( 1/T \) and \( \ln(k) \) should describe a straight line. This plot is generally called the Arrhenius plot. The slope \( (-E/R) \) of the line reflects the activation energy \( (E) \). The intercept \( [\ln(A)] \) reflects the frequency factor \( (A) \).

In a biological process, the rate constant \( (k) \) cannot be calculated. According to Eq. 1, the time \( (t) \) is described by Eq. 4 because it can be defined as the reciprocal of the rate \( (v) \).

\[
t = 1/v = 1/(k'c)
\]

(4)

Equation 5 is obtained from Eq. 3 and Eq. 4:

\[
\ln(1/t) = \ln(Ac) - E/R/T
\]

(5)

The scatter plot of \( 1/T \) and \( \ln(1/t) \) must also describe a straight line if time follows the Arrhenius equation; this can also be called the Arrhenius plot.

Although many reactions occur in a germinating seed, if germination time was to change with changing temperature according to the Arrhenius equation, such temperature dependence could be explained by the behavior of only one step, because the Arrhenius equation can be applied to only one step. However, germination time does not precisely follow an Arrhenius equation, indicating that its temperature dependence cannot be explained by the behavior of only one step. Therefore, I assumed that the temperature dependence of germination time could be explained by the behavior of multiple steps. Assuming that these multiple steps, hereafter also referred to as rate-determining steps, are independent, their durations can be summed to determine germination time.

As each step follows the Arrhenius equation, each time \( (t) \) can be described by Eq. 6, calculated from Eq. 5:

\[
t = \exp(E/R/T)/(Ac)
\]

(6)

The total germination time is determined by summing the times \( (t = t_1 + t_2 + t_3 + \cdots) \) of multiple steps \( (\alpha, \beta, \gamma, \cdots) \) as follows:

\[
t = \exp(E_\alpha/R/T)/(A_\alpha c_\alpha) + \exp(E_\beta/R/T)/(A_\beta c_\beta) + \exp(E_\gamma/R/T)/(A_\gamma c_\gamma) + \cdots
\]

(7)

Hereafter, this equation is referred to as the summation time equation or the s-equation. This equation was used to relate germination time to temperature change assuming multiple steps, in a method called the s-equation method. Because the frequency factor \( (A) \) and the concentration factor \( (c) \) cannot be measured directly, \( Ac \) is hereafter referred to as the apparent frequency factor or the a-factor.

2. Germination time data

Two lots (labeled +N and −N) of rice seeds (Oryza sativa L. cv. Dontokoi) were harvested from different plots of a paddy field in Joetsu, Niigata Prefecture, Japan, in 1997. Nitrogen application to parent plants was 15 g m\(^{-2}\) (Lot +N) or 0 g m\(^{-2}\) (Lot −N). Seeds (2 g) were soaked in water (75 ml) in the dark at eight different constant temperatures between 10˚C and 20˚C. The number of germinating seeds was counted and recorded twice a day. Seeds were considered germinated when either the plumule or the radicle was observed. The water temperature was measured at each seed counting, and the average for the study was used for subsequent calculations. The average standard deviation of the temperature was 0.150˚C.

At each temperature, the Richards function was fitted to the time course of the percentage of seeds that germinated after sowing (Hara, 1999; Hara, 2001). The median time until germination was calculated using the fitted Richards function; this calculation was used as the germination time.

3. Fitting equations to the data

An s-equation (Eq. 7) of one to three steps was fitted to the relationship between temperature and germination time \( (T \text{ vs. } t) \) for each seed lot. Optimal values of the activation energy and the a-factor were calculated for each step using the nonlinear least-squares method conducted by a spreadsheet optimizer (Solver) bundled with Microsoft Excel set up with several options (automatic scaling, non-negative, quadratic estimate, central derivative, and Newton search). The logarithm of germination time was used as a dependent variable, because according to the Arrhenius equation, germination time changes approximately exponentially with temperature. The initial values of activation energy were set at 100 kJ mol\(^{-1}\), a typical value for chemical reactions (Iwanami's Dictionary of Physics and Chemistry, 1998), and were allowed small differences (1 J mol\(^{-1}\)) between multiple steps. The initial a-factor values were set for convenience such that germination time was 1 day at 20˚C, although the differences among the initial
values within a certain range did not affect the optimal parameter values. Two to six \((E\text{ and } A\cdot c\text{ for each of one to three steps})\) parameters were estimated on the basis of 16 measurements per seed lot.

The breakpoint method was applied to the same datasets for comparison with the s-equation method. Each of two Arrhenius equations (Eq. 6) was also fitted to data for each temperature range divided at the breakpoint temperature. Four parameters were fitted for each seed lot (\(E\text{ and } A\cdot c\text{ for each of two equations})\). Because the standard error does not change consistently at a breakpoint, optimal parameter values were obtained by fitting in two stages. First, the breakpoint temperatures were varied at intervals of 0.5°C, and standard errors were estimated for each. Subsequently, all parameters were estimated using Solver and setting initial values that had the lowest standard errors in the previous fitting without fixing the breakpoint temperature.

The coefficient of determination \((R^2)\) of the logarithm of germination time and Akaike’s information criterion (AIC), which is low in a proper model (Suzuki, 1995), were calculated for each fitting to evaluate the goodness of fit.

### Results

#### 1. Germination time data

Germination was almost 100% for both seed lots at all temperatures, indicating that neither temperature nor nitrogen application to the parent plants influenced the final germination percentage. Fitting the Richards function to the time course of germination percentage gave an average standard error of 1.8% in germination percentage. Germination time increased at lower temperatures. Similar to our previous report (Hara and Toriyama, 1998), Lot + N (the parent plants of which received nitrogen) germinated more quickly than Lot − N at all temperatures.

### Table 1. Goodness-of-fit and parameters versus fitting methods.

| Seed lots | Fitting approaches | Standard errors \((\ln(d^{-1}))\) | Coefficients of determination \((R^2)\) | Akaike’s information criterion \((\text{AIC})\) | Numbers of parameters | Activation energies \((E)\) \((\text{kJ mol}^{-1})\) \(^a\) | \(\ln(\text{a-factor})\) \((\ln(d^{-1}))\) \(^a\) | Breakpoints \((^\circ\text{C})\) |
|-----------|--------------------|-------------------------------|-------------------------------|---------------------------------|------------------|---------------------------------|---------------------------------|------------------|
| Lot + N   | Arrhenius equation \(^a\) | 0.1536                        | 0.952                         | −56.1                           | 2                | 132                            | −                  | 53.3             |
|           | Breakpoint \(^b\) | 0.0590                        | 0.995                         | −86.6                           | 4                | 101                            | 260               | 40.5             |
|           | Two-step s-equation | 0.0367                        | 0.997                         | −97.9                           | 4                | 80.4                           | 461               | 31.9             |
|           | Three-step s-equation | 0.0344                        | 0.998                         | −96.0                           | 6                | 23.4                           | 198               | 8.71             |
| Lot − N   | Arrhenius equation \(^a\) | 0.1446                        | 0.958                         | −58.0                           | 2                | 127                            | −                  | 50.8             |
|           | Breakpoint \(^b\) | 0.0668                        | 0.991                         | −78.8                           | 4                | 74.5                           | 178               | 29.3             |
|           | Two-step s-equation | 0.0518                        | 0.995                         | −86.8                           | 4                | 76.2                           | 392               | 30.0             |
|           | Three-step s-equation | 0.0422                        | 0.996                         | −89.4                           | 6                | 8.52                           | 204               | 2.54             |

\(^a\) The Arrhenius equation corresponds to a one-step s-equation; \(^b\) Each of two Arrhenius equations was fitted to each of two temperature ranges divided at the breakpoint temperature; \(^c\) The sum of the numbers of activation energies and \(a\)-factors, except the breakpoints, that can be calculated using the other parameters; \(^d\) Multiple steps were labeled with Greek characters in the order of increasing activation energy.

#### 2. Fitting equations to germination time

The Arrhenius plots \(1/T\text{ vs. } \ln(1/d)\) demonstrated a curvilinear rather than a linear relationship for both seed lots. This result indicates that germination time does not precisely follow the Arrhenius equation.

In the s-equation method, values of three criteria (standard error, coefficient of determination, and AIC) improved when the number of steps increased from one (corresponding to the Arrhenius equation) to two, but the improvement from two to three steps was marginal (Table 1). These findings suggest that the optimal number of steps is two.

When a two-step s-equation was fitted, the standard errors were 0.0367 and 0.0518 ln(d\(^-1\)), and the coefficients of determination were 0.997 and 0.995 (Table 1). These data indicate that germination time precisely follows a two-step s-equation (Fig. 1). Optimal values of the activation energies of two steps were 80.4 and 461 kJ mol\(^-1\) for Lot + N and 76.2 and 392 kJ mol\(^-1\) for Lot − N. Optimal values of the \(a\)-factors were larger for Lot + N than for Lot − N.

In the breakpoint method, the standard error for changes in breakpoint temperature described a broad V-shaped curve for Lot + N and a W-shaped curve for Lot − N (Fig. 2). The optimal breakpoint temperatures were 12.3°C for Lot + N and 15.3°C for Lot − N. The respective standard errors were 0.0590 and 0.0668 ln(d\(^-1\)) (Table 1). Lot − N had another local minimum, with a standard error of 0.0670 ln(d\(^-1\)), at 12.7°C. When the breakpoint was located optimally, the coefficients of determination were 0.995 for Lot + N and 0.991 for Lot − N (Fig. 3). Optimal values of activation energies for the two equations using the breakpoint method were 101 and 260 kJ mol\(^-1\) for Lot + N and 74.5 and 178 kJ mol\(^-1\) for Lot − N (Table 1). Optimal values of \(a\)-factors were larger for Lot + N than for Lot − N.
Discussion

1. Goodness-of-fit versus fitting methods

The s-equation method using a two-step s-equation and the breakpoint method using two Arrhenius equations require the same number of parameters. The coefficients of determination ($R^2$) were slightly greater for the s-equation method (0.997 and 0.995) than for the breakpoint method (0.995 and 0.991).

The standard errors were smaller for the s-equation method (0.0367 and 0.0518) than for the breakpoint method (0.0590 and 0.0668). AIC values, which are low in a proper model, were lower for the s-equation method ($\hat{\psi}$97.9 and $\hat{\psi}$86.8) than for the breakpoint method ($\hat{\psi}$86.6 and $\hat{\psi}$78.8). In addition, the residuals showed some trends for the breakpoint method (Fig. 3) but not for the s-equation method (Fig. 1). These results imply that the relation of germination time to changes in temperature can be more precisely analyzed by the s-equation method than by the breakpoint method.

2. Breakpoints for germination time

The Arrhenius plots for germination time showed curves, especially around the breakpoints (Fig. 3; Nishiyama, 1975; Nishiyama, 1978; Labouriau and Osborn, 1984; Washitani and Takenaka, 1984; Washitani, 1985). These curves imply that breakpoint temperatures may not be clear for germination times. In fact, the standard errors for the breakpoint method were insensitive to changes in breakpoint temperatures from 12˚C to 15 ˚C (Fig. 2). In addition, the residuals showed some trends for the breakpoint method (Fig. 3) but not for the s-equation method (Fig. 1). These results imply that the relation of germination time to changes in temperature can be more precisely analyzed by the s-equation method than by the breakpoint method.
The breakpoint method is commonly used to analyze curved Arrhenius plots (Nishiyama, 1975; Nishiyama, 1978; Hsu et al., 1984; Hsu et al., 1985) because the parameters can be easily estimated by using the linear least-squares method if the breakpoint temperature is known. However, this temperature is difficult to estimate using a personal computer because the residual error of fitting changes discontinuously at the breakpoints. For this reason, the breakpoint method comprised two stages in this study. However, if no breakpoint temperature exists, the nonlinear least-squares method is readily available using a personal computer. Given these considerations, the s-equation method may be preferred for the analysis of curved Arrhenius plots.

Nishiyama (1978) reported varying breakpoint temperatures among germination times (13.5°C — 15.2°C), the majority of plumules or radicles (17.2°C — 17.8°C), oxygen uptake (15°C), and acid phosphatase activity (10.2°C — 12.6°C) in germinating rice seeds. In addition, like the lowest temperature of germination, the breakpoint temperature was not related to the germination time or growth of seedlings at low temperatures (Furter and Venter, 1990). These findings imply that the breakpoint temperature is not an informative parameter in the temperature dependence of germination.

3. Multiple rate-determining steps

In the breakpoint method, an Arrhenius equation is fitted within each limited temperature range under the assumption that the rate of the whole reaction is determined by the slowest step (the rate-determining step) and that other steps can be disregarded. This assumption is applicable to simple objects of chemistry or physics, which contain few steps with different rates. In contrast, biological processes (like germination) involve many steps, some of which may have rates similar to that of the slowest step. Accordingly, multiple steps may affect the time (or rate) of biological processes. The germination time is not dependent on the behavior of only one step; in the s-equation method, the reason for this can be explained using the changes in contribution ratios of multiple steps without the discontinuity of temperature dependence. In addition, the s-equation could be precisely fitted to the relationship between temperature and germination time, suggesting again that multiple steps affect the duration of a biological process.

However, the s-equation method cannot be applied to every process. For example, seeds soaked at high temperatures (over 30°C) did not germinate (Garcia-Huidobro et al., 1982). Nishiyama (1978) reported that the Arrhenius plot of rice germination time had another breakpoint at 30°C. Germination is thought to be delayed because reactions unfavorable to germination occur when the temperature rises. The s-equation method can be applied only to those biological processes in which the same reactions occur at any temperature. If different reactions occur depending on temperature, the superficial fitting (like the breakpoint method) or theoretical models with a temperature optimum to describe the effect of temperature on the contribution ratios of the inactive state of the substance may be required (Johnson and Thornley, 1985; Thornley, 1986; Hageseth, 1993; Hageseth and Cody, 1993; Hageseth and Young, 1994).

However, these theoretical models, which involve time-series data and many parameters, tend to complicate investigations.

4. Interpreting the s-equation

The s-equation is based on the assumption that temperature dependence can be explained by the combination of multiple independent steps. Germination was assumed to involve two steps (Model A in Fig. 4).

![Fig. 4. Two models interpreting the s-equation.](image)

The models are mathematically equivalent because both can be explained by a two-step s-equation (Eq. 9). Model A is the combination of two independent, interchangeable steps (α and β). Model B is an equilibrium that consists of a reversible reaction and a subsequent irreversible reaction, described using an initial substance (S), an intermediate substance (S₁), and a product (P). Activation energies are the same whether the reversible reaction proceeds forward or backward. According to Eq. 9, the two activation energies (Eₐ and Eₜ) are interchangeable within each model.

![Model A](image)

\[
\text{Sowing} \rightarrow \text{Step } \alpha (E_a) + \text{Step } \beta (E_b) \rightarrow \text{Germination}
\]

![Model B](image)

\[
\text{Sowing} \rightarrow \begin{array}{c}
\frac{E_a}{E_a} \rightarrow S_1 \\
E_b \rightarrow P
\end{array} \rightarrow \text{Germination}
\]

Interpreting the s-equation sequence (Eq. 10) explained by Johnson and
The activation energy of a step approximately equals to the difference in energy between two reactants at the reaction rate-determining step. This is evident from the equation:

$$ E = \frac{dP}{dt} \cdot \frac{A_1}{A_2} \cdot \exp \left( \frac{-(E_1 + E_2)}{RT} \right) $$

This correspondence holds true even if the number of steps (or reactions) increases. Thus, the s-equation can also reflect the special case of the reversible reaction sequence, in which the values of activation energies of the reversible reaction are the same whether the reaction proceeds forward or backward (Model B in Fig. 4). Although the reversible reaction sequence consists of a reversible reaction and a subsequent irreversible reaction, the activation energies of the two reactions are exchangeable according to Eq. 9. Accordingly, the s-equation can be interpreted in two different ways: as a combination of multiple independent steps (Model A in Fig. 4) or as the equilibrium of multiple reactions (Model B in Fig. 4). The temperature dependence of germination can also be interpreted in these two ways.

5. Parameters of temperature dependence

The activation energy ($E$) quantifies the sensitivity of the time (or rate) to changes in temperature. Large activation energy values indicate that the time is sensitive to temperature changes; small values indicate that it is insensitive to such changes.

In the breakpoint method, the rate-determining step of a higher-temperature region does not influence the reaction time in the lower-temperature region because the rate-determining step changes at the breakpoint temperature. In the s-equation method, the step that primarily affects the reaction time in the higher-temperature region also influences that in the lower-temperature region because the rate-determining steps do not change at any temperature. Accordingly, the activation energies of the step that primarily affects the reaction time in the lower-temperature region depended on the fitting method (461 and 392 kJ mol$^{-1}$ for the s-equation; 260 and 178 kJ mol$^{-1}$ for the breakpoint method), while the activation energies of the other step that primarily affects the reaction time in the higher-temperature region were relatively similar (80.4 and 76.2 kJ mol$^{-1}$; 101 and 74.5 kJ mol$^{-1}$).

The activation energy of a step approximately corresponds to the energy barrier between the original system and the transition state of the step (Iwamnami’s Dictionary of Physics and Chemistry, 1998). The size of the energy barrier is expected to depend on the reaction mechanism of the step. Because the activation energy of a biological process characterizes its rate-determining step, this value, as well as the temperature constant (Kotowski, 1926), is thought to represent one aspect of the metabolism of germination. Accordingly, the calculation of the precise activation energy is important to characterize this biological process.

In the s-equation method, activation energies of each step (80.4 and 76.2 kJ mol$^{-1}$; 461 and 392 kJ mol$^{-1}$) were similar for both seed lots. These data imply that the application of nitrogen to the parent plants did not significantly affect the temperature dependence of germination. In addition, activation energies may be stable within a given rice variety with identical genes. Accordingly, the temperature dependence of germination of this rice variety is probably characterized by two steps with different activation energies (one ~ 80 kJ mol$^{-1}$ and one ~ 400 kJ mol$^{-1}$).

In the breakpoint method, however, the activation energies calculated for each temperature range (101 and 74.5 kJ mol$^{-1}$; 260 and 178 kJ mol$^{-1}$) tended to differ between the seed lots. In addition, the estimated breakpoint temperatures differed by 3°C between the seed lots, a difference that could affect plant physiology. These differences show the importance of selecting the proper fitting method; different parameter estimates may lead to different conclusions.

The a-factor (A*c) is the other parameter obtained through the fitting process. According to Eq. 5, the a-factor represents the degree to which the component is not influenced by temperature. Theoretically, the frequency factor (A), as well as the activation energy, depends on the reaction mechanism of the rate-determining step (Iwamnami’s Dictionary of Physics and Chemistry, 1998). Accordingly, the frequency factor may also be stable within each step, such that the variance of the a-factor may be caused by the variance of the concentration factor (c), which represents the concentrations of reactants in the rate-determining step. In the present study, applying nitrogen to parent plants increased the a-factor of germination. This result suggests that the effect of nitrogen application on the temperature dependence of germination could be investigated using the a-factor rather than the activation energy (which was hardly affected by nitrogen application). As another example, Giner et al. (1991) incorporated the moisture effect into the pre-exponential factor, which corresponds to the a-factor, in an analysis of loss of wheat seed viability.

Acknowledgments

I would like to thank Dr. K. Toriyama, Dr. K. Kamekawa, Dr. T. Takahashi, Dr. K. Tsuchiya, and Ms. K. Kusa for their valuable suggestions, and Ms. Y. Takeuchi and Ms. H. Hirose for their technical support.

References

Furter, M. and Venter, H.A. 1990. A comparison of parameters for the assessment of relative cold tolerance of germinating kernels of maize. S. Afr. J. Plant Soil. 7 : 207-211.

García-Huidobro, J., Monteith, J.L. and Squire, G.R. 1982. Time, temperature and germination of pearl millet. J. Exp. Bot. 33 :
Hara — Estimating Temperature Dependence of Germination Time by Assuming Multiple Steps

288-296.

Giner, S.A., Lupano, C.E. and Anon, M.C. 1991. A model for estimating loss of wheat seed viability during hot-air drying. *Cereal Chem.* 68 : 77-80.

Hageseth, G.T. 1993. The four-compartment energy level diagram for seed germination. *J. Theor. Biol.* 160 : 73-84.

Hageseth, G.T. and Cody, A.L. 1993. Energy-level model for isothermal seed germination. *J. Exp. Bot.* 44 : 119-125.

Hageseth, G.T. and Young, C.W. 1994. The four-compartment thermodynamic energy-level diagram for isothermal seed germination. *J. Therm. Biol.* 19 : 1-11.

Hara, Y. and Toriyama, K. 1998. Seed nitrogen accelerates the rates of germination, emergence, and establishment of rice plants. *Soil Sci. Plant Nutr.* 44 : 359-366.

Hara, Y. 1999. Calculation of population parameters using Richards function and application of indices of growth and seed vigor to rice plants. *Plant Prod. Sci.* 2 : 129-135.

Hara, Y. 2001. Application of parametrization using the Richards function to nitrogen release from coated urea and growth of rice seeds. *JARQ.* 35 : 155-161.

Hsu, F.H., Nelson, C.J. and Chow, W.S. 1984. A mathematical model to utilize the logistic function in germination and seedling growth. *J. Exp. Bot.* 35 : 1629-1640.

Hsu, F.H., Nelson, C.J. and Matches, A.G. 1985. Temperature effects on germination of perennial warm-season forage grasses. *Crop Sci.* 25 : 215-220.

Iwanami’s Dictionary of Physics and Chemistry. Fifth edition. 1998. Iwanami Shoten, Tokyo. 55, 253, 655, 750-751, 775, 1080-1082, 1142, 1442-1443*.  

Johnson, I.R. and Thornley, J.H. 1985. Temperature dependence of plant and crop processes. *Ann. Bot.* 55 : 1-24.

Kotowski, F. 1926. Temperature relations to germination of vegetable seed. *Am. Soc. Hort. Sci.* 23 : 176-184.

Labouriau, L.G. and Osborn, J.H. 1984. Temperature dependence of the germination of tomato seeds. *J. Therm. Biol.* 9 : 285-294.

Nishiyama, I. 1975. A break on the Arrhenius plot of germination activity in rice seeds. *Plant Cell Physiol.* 16 : 533-536.

Nishiyama, I. 1978. Further evidence for the break on the Arrhenius plot of germination activity in rice seeds. *Jpn. J. Crop Sci.* 47 : 557-562.

Scott, S.J., Jones, R.A. and Williams, W.A. 1984. Review of data analysis methods for seed germination. *Crop Sci.* 24 : 1192-1199.

Suzuki, G. 1995. Guide to Statistics Analysis by Information Criterion (jouhouryou kijun niyoru toukei kaiseki nyuumon). Kodansha Scientific, Tokyo. 127-130**.

Thornley, J.M.H. 1986. A germination model: responses to time and temperature. *J. Theor. Biol.* 123 : 481-492.

Washitani, I. 1985. Germination-rate dependency on temperature of Geranium carolinianum seeds. *J. Exp. Bot.* 36 : 330-337.

Washitani, I. and Takenaka, A. 1984. Germination responses of a non-dominant seed population of *Amaranthus patulus* Bertol. to constant temperatures in the sub-optimal range. *Plant Cell Environ.* 7 : 353-358.

* In Japanese.

** Translated from Japanese by the present author.