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Evaluation of Three Growth Curve Models for Germination Data Analysis

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Abstract. **Polynomial, monomolecular, logistic, and Gompertz growth curves were evaluated for their suitability as mathematical models for germination data. Germination of hulled or leached creosote bush [*Larrea tridentata* (DC.) Cov.] mericarps were used in the evaluation. The Gompertz model gave the best fit. Germination curves and germination rate curves gave similar patterns of response to results obtained by other methods, which suggests the Gompertz model may have application in germination data analysis. Hulling improved germination over leaching intact mericarps. Nine hours was the optimum leaching duration for intact mericarps.**

Seed germination is a continuing process beginning with water imbibition and culminating in radicle or hypocotyl emergence. This process is influenced by a multitude of factors, both environmental and genetic. The effect of specific factors usually is presented in a germination curve relating the cumulative percentage of germination of a seed sample to time. Typically, this curve is S-shaped, indicating that germination rate is not constant but varies with time. The relevant values from the curves are final percentages of germination, germination rate, and variability in germination rate. Several authors have attempted to express a single rate of germination (2, 12, 13). This effort is hampered not only by the variable germination rate, but also because the frequency distribution of germination times often is skewed. Nichols and Heydecker (12) calculated time to 50% of the ultimate number germinating by quartiles and the mean time to germination for the ultimate number germinating by moments. They concluded both methods were suitable, and while the method of moments was more accurate in determining skewness, suggested the use of quartiles based on ease of calculation. Orchard (13) compared 5 methods for estimating mean and variance of time to germination, including the methods of quartiles and moments. He found significant differences in accuracy among methods and, given adequate frequency of germination counts, concluded the method of moments is preferred based on accuracy and ease of calculation.

Using the method of moments, one must assimilate the final percentage of germination, the mean and variance of time to germination, and both the degree and direction of skewness in order to interpret the germination curve and the germination rate curve adequately. Actually, these values do not describe the germination rate curve but merely represent it, based on the mean time to germination. Tucker and Wright (19) suggested the time to 50% germination could be determined by fitting a linear regression line to the germination curve, but this procedure is not valid if the frequency distribution of germination times is skewed. Goodchild and Walker (5) used orthogonal polynomial regressions to describe germination curves which overcome the problem of skewed data, but provide limited information about the germination rate. Seeking to avoid these limitations, this study was initiated to explore the use of growth models to describe germination data by nonlinear regression.

Three common asymptotic growth models for evaluation were chosen: 1) the monomolecular, where $Y = a[1 - b \exp(-kt)]$; 2) the logistic, where $Y = a[1 + b \exp(-kt)]^{-1}$; and 3) the Gompertz, where $Y = a \exp[-b \exp(-kt)]$. These models are discussed by Draper and Smith (4). In each model, Y is the predicted cumulative percentage of germination, t is time, and a is the asymptote or theoretical maximum value for Y. The constants b and k will have different values for the different curves (4). The monomolecular curve rises to the asymptote at a decreasing rate; there is no inflection point. The logistic curve is sigmoid and symmetrical about the inflection point, a limitation in fitting germination data (8, 10). The Gompertz curve is sigmoid and asymmetrical about the inflection point.

To test the curves an investigation of the effects of leaching and hulling on creosote bush fruit was made. The creosote bush is an evergreen shrub that dominates much of the deserts in the arid southwestern United States and northern Mexico (9). The fruit is a mericarp consisting of a single seed enclosed in an indehiscent pericarp. There is conflicting evidence as to whether the pericarp contains a germination inhibitor that may be removed either by leaching with water or by hulling (1, 6, 7). These reports suggested that leaching mericarps for various times might provide a series of germination curves ranging from a slow germination rate with a low final percentage of germination, to a moderate rate with moderate final percentage of germination. Hulled mericarps might provide a rapid germination rate and high final percentage of germination. Such a series of curves would be useful in testing the growth models.

Materials and Methods

Creosote bush mericarps were harvested in the Fall 1981 from native shrubs growing on a deep, sandy soil in the vicinity of El Paso, Texas. The mericarps were stored at room termperature for about a year to satisfy potential after-ripening requirements (20). Some of the mericarps were hulled in a Burr Clover Huller (Forsberg's Inc., Thief River Falls, Minn.) and cleaned with screens and a forced-air seed blower (Mater Machine Works Inc., Corvallis, Ore.). Visual examination revealed no apparent damage due to hulling; unhulled mericarps were placed in aerated, deionized water for 0, 3, 6, 9, and 12 hr prior to sowing. All mericarps were leached in the same 10-liter volume of water, and the water was changed every 3 hr. The treated mericarps were placed between layers of Kimpack germination paper in a

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Table 1. Total and residual sum of squares from fitting various nonlinear regression models to the germination data.

Treatment	Total sum of squares	Residual sum of squares[z]			
		Polynomial	Monomolecular	Logistic	Gompertz
Hulled	7441.2	541.6	187.3	24.9	9.3
Leached					
0 hr	296.6	6.3	6.2	14.5	9.3
3 hr	613.9	10.0	11.1	16.7	8.5
6 hr	1250.3	24.1	29.2	21.2	9.4
9 hr	2469.5	34.4	49.4	14.5	2.3
12 hr	1234.7	21.1	29.0	13.7	7.1

[z]All models have 3 parameters.

dark seed germinator (Cleland International Model 500TLR, Rogers, Minn.) maintained at a constant 23°C.

The experimental design was completely randomized with 4 replications per treatment and 100 seeds per replication for hulled mericarps. A cutting test indicated the intact mericarps were 48% filled, so 209 mericarps were used per replication for the leaching test. Germination counts were made daily for 11 days, and germination was defined as the appearance of a radicle as long as the mericarp. The mean cumulative percentage of germination was calculated for each treatment by days and fitted to the nonlinear regression models by the multivariate secant (don't use derivatives-DUD) option of the nonlinear regression (NLIN) procedure in statistical analysis system (SAS) (16). In addition to the models already described, the data were fitted to a 2nd degree orthogonal polynomial.

Results

The Gompertz model resulted in the lowest residual sum of squares for all treatments except 0 hr leaching (Table 1). Germination in this treatment was slow, resulting in an almost linear germination curve (Fig. 1). The Gompertz model germination rate is given by $GR = kY \log_e(a\ Y^{-1})$, calculated for the range of Y values. The maximum germination rate occurs where the rate of change in the germination rate is 0, i.e., at the time of inflection of the curve, $t_i = (\log_e b)k^{-1}$ and its value is $GR_{max.} = (ka)e^{-1}$. Inflection time and maximum germination rate are given in Table 2, and the germination rate curves are depicted in Fig. 2. The peak in germination rate occurred earlier and became more narrow with increasing leaching duration up to 9 hr, indicating that germination rate and uniformity increase with leaching. Germination rate of the hulled mericarps was more uniform and rapid than for intact mericarps. The maximum germination rate of hulled mericarps was reached almost a full

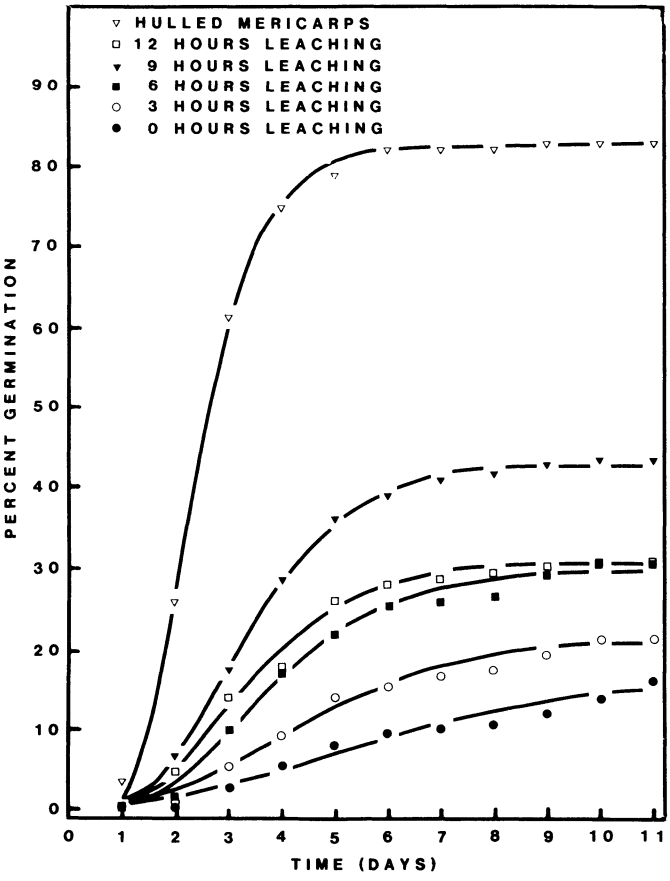

Fig. 1. Effect of hulling and leaching duration (intact mericarps only) on the germination of creosote bush mericarps. Curves of data fitted to the Gompertz growth model. Parameter estimates are given in Table 2.

Table 2. Parameter estimates, standard errors, inflection times, and maximum germination rates from fitting data to the Gompertz growth model.

Treatment	Parameter estimates (SE)			Inflection time (days)	Maximum germination rate
	a	b	k		
Hulled	82.37 (+0.43)	14.02 (+1.73)	1.26 (+0.05)	2.09	38.32
Leached					
0 hr	16.84 (+2.12)	4.84 (+1.36)	0.33 (+0.08)	4.79	2.04
3 hr	21.33 (+0.89)	6.38 (+1.57)	0.50 (+0.07)	3.73	3.90
6 hr	29.58 (+0.64)	8.59 (+1.90)	0.67 (+0.07)	3.20	7.30
9 hr	43.04 (+0.28)	8.52 (+0.65)	0.75 (+0.02)	2.84	11.92
12 hr	30.48 (+0.50)	8.12 (+1.51)	0.74 (+0.06)	2.82	8.32

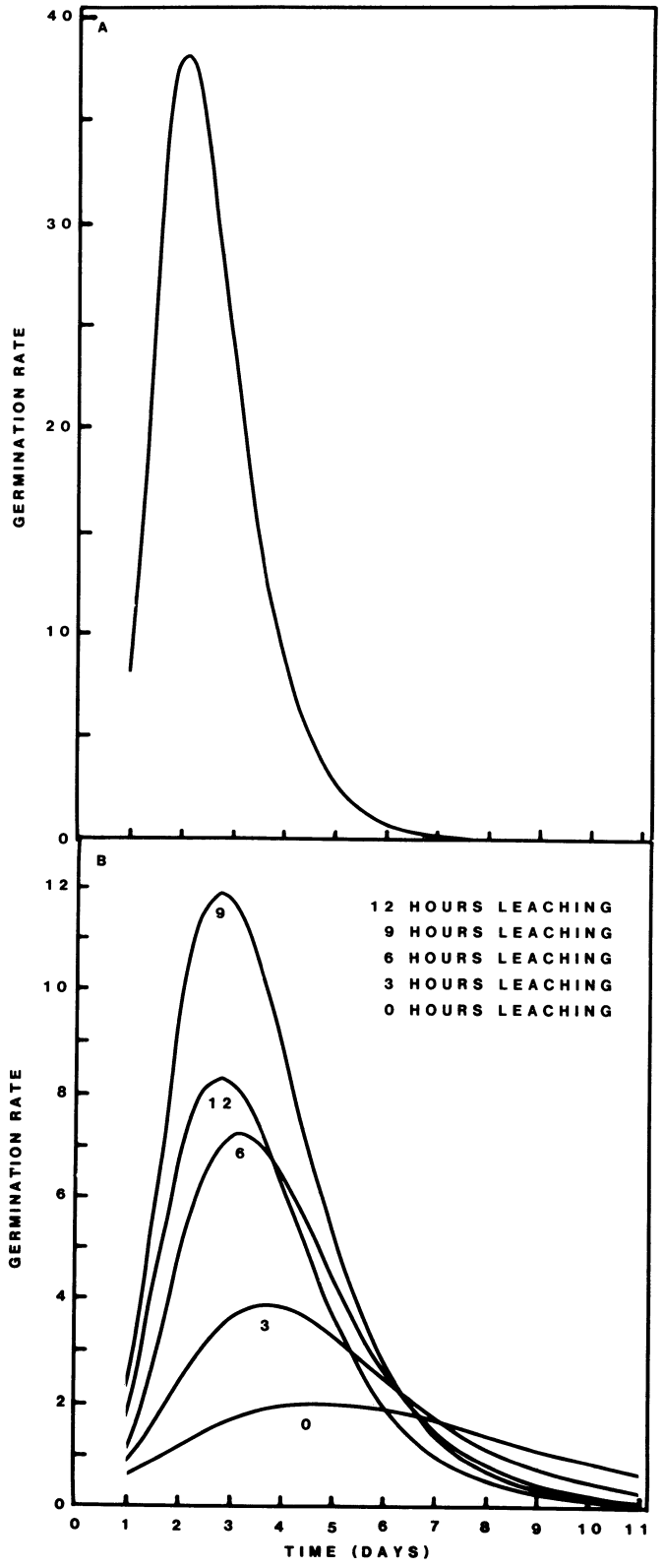

Fig. 2. Effect of hulling (**A**) and leaching duration (intact mericarps) (**B**) on germination rate of creosote bush mericarps. Germination rate curves of data fitted to the Gompertz growth model.

day before the best intact mericarps, and was over 3 times the rate of the latter.

Inflection time of the intact mericarps was related to hours leaching by a 2nd-degree polynomial, indicating no advantage in increasing leaching duration from 9 to 12 hr (Fig. 3). Final

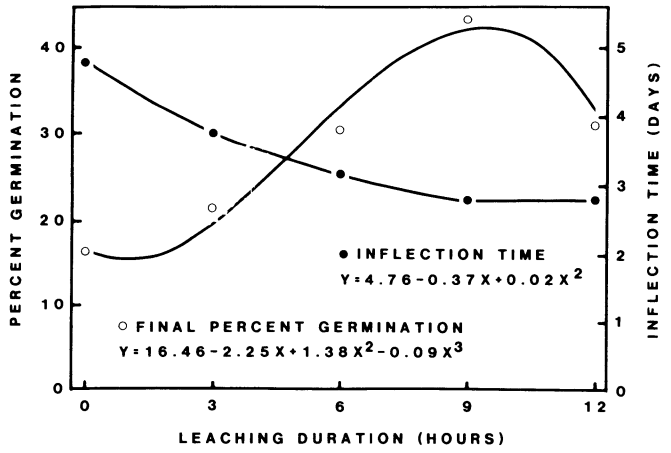

Fig. 3. Effect of leaching duration on final percentage of germination and inflection time of intact creosote bush mericarps.

percentage of germination of the intact mericarps was related to hours leaching by a 3rd-degree polynomial, indicating a detrimental effect of increasing leaching duration from 9 to 12 hr (Fig. 3). Maximum germination rate for these treatments was not significantly related to leaching duration at less than a 4th-degree polynomial.

The germination rate curves in Fig. 2 reveal a similar pattern as analysis of the data by the method of moments (Table 3). The time to 50% germination in Table 3 was calculated from the Gompertz models for comparative purposes. The relationship between treatments is the same whether analyzed by the Gompertz model or the method of moments.

Discussion

The data indicate the Gompertz growth model gave the best fit of several nonlinear regression models, and merits consideration as a useful model for germination data. This model provides a better fit than a 2nd-degree polynomial except for slow, low final percentage of germination cases. It has the advantage of allowing estimation of a germination rate curve, maximum germination rate, and time of maximum germination rate (inflection time). The polynomial is particularly inappropriate for rapid, high percentage of germination cases and for asymptotic curves in general. The Gompertz model gives comparable results to the method of moments, but is easier to present and interpret. Only 2 graphs are required to describe data adequately, the germination curve and germination rate curve. Lapp and Sko-

Table 3. Mean, variance, and skewness of germination time determined by the method of moments and time to 50% germination from the Gompertz growth model.

Treatment	Time to 50% germination[y]	Time of germination[z]		
		Mean	Variance	Skewness
Hulled	2.4	3.1	1.4	1.3
Leached				
0 hr	5.4	6.5	8.0	0.3
3 hr	4.4	5.4	5.7	0.6
6 hr	3.7	4.8	4.6	1.0
9 hr	3.3	4.2	3.4	1.2
12 hr	3.3	4.2	3.4	1.3

[z]Calculated by the method of moments (9).
[y]Time to 50% of the ultimate number germinating as calculated from the Gompertz growth model.

ropad (8) used the Gompertz model to describe fungal spore germination, but did not calculate germination rate. Their approximation method of fitting the Gompertz is laborious (17). Probit analysis, suggested by Moore and Roos (10), also is mathmatically complex, requiring a mainframe computer.

The DUD option of the NLIN procedure for nonlinear regression in SAS provides an easy method for fitting germination data to the Gompertz growth model, in that partial derivatives for the parameters are not required, only initial parameter estimates (16). The procedure also can be found as the PAR program of the BMPD-77, P-Series (3). Initial estimates can be provided as follows (adapted from 4). Select 2 observations: 1) t_j = last day counted where Y_j = final percentage of germination, and 2) t_i = first day where Y_i is greater than 0. The initial estimate for a is $a_0 = Y_j + 0.1$. The initial estimate for k is $k_0 = [\log_e (Y_j' Y_i'^{-1})] (t_i - t_j)^{-1}$, where $Y_j' = \log_e (Y_j a_0^{-1})$ and $Y_i' = \log_e (Y_i a_0^{-1})$. The initial estimate for b is $b_0 = -Y_i' [\exp(-k_0 t_i)]^{-1}$, where Y_i' is as above.

If SAS or BMPD-77 is not available, the Gompertz model can be solved by the approximation method of Stevens (18) and Patterson (14, 15) or the maximum likelihood method of Nelder (11) on a microcomputer or even a programmable calculator. Neither method will reduce the residual sum of squares as much as the DUD method of SAS, and the efficiency of either former method in reducing residual sum of squares relative to the latter will depend upon the data. A Microsoft BASIC program for fitting the Gompertz model by Nelder's method is available from the author.

The results indicate that hulling creosote bush mericarps increases both final percentage of germination and the maximum germination rate, and reduces both germination variability and time to maximum germination rate (inflection time) over non-hulled, leached mericarps. Leaching in aerated, deionized water for 9 hr gave optimum results for intact mericarps within the confines of this test. The results suggest the pericarp contains germination inhibitors of low solubility in water. Prolonged soaking might lead to reassimilation of the inhibitors or activation of other inhibitors to prevent germination in water-soaked soils.

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