

Evaluating Russian wild ryegrass emergence from saline seedbeds using the Gompertz function

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Steppuhn, H., Wang, H. and Gan, Y. 1998. Evaluating Russian wild ryegrass emergence from saline seedbeds using the Gompertz function. *Can. Agric. Eng.* **40**:241-247. Although Russian wild ryegrass (*Psathyrostachys juncea*) is recommended for saline lands, adequate plant stands can be difficult to establish. 'Swift' and 'Tetracan' are two varieties specifically bred for easy establishment. Plants from each variety were tested for their inherent ability to emerge and survive in saline seedbeds maintained at solution electrical conductivities of 2, 10, 20, 30, 40, and 50 dS/m. Canada's Salt Tolerance Testing Facility provided the necessary controls for the tests. By applying the Gompertz function in a non-linear regression fit to the test results, three equation parameters, four derived indices, and a related variable could be evaluated in comparing the two wildrye varieties. The best statistically discriminating indices for between 'Swift' and 'Tetracan' were the rate of emergence and survival at the Gompertz inflection, the asymptotic maximum attained in each test (E_{max}), the time to reach $0.99E_{max}$, the emergence occurring at the Gompertz inflection point, the Gompertz shape parameter, and the Gompertz time constant. They indicated that 'Tetracan' plants emerging from very severely, severely, and moderately saline seedbeds showed better salinity tolerance than 'Swift' wildrye plants.

Même si l'élyme de Russie (*Psathyrostachys juncea*) est recommandée pour la réhabilitation des sols salins, l'établissement d'un peuplement suffisant peut en être difficile. Les variétés d'élyme 'Swift' et 'Tetracan' ont été spécifiquement sélectionnées pour leur facilité d'établissement. Des plants des deux variétés furent testés pour connaître leur capacité à lever et survivre dans des lits de semence salins où la conductivité électrique de la solution du sol était maintenue à 2, 10, 20, 30, 40 et 50 dS/m. Des échantillons de contrôle furent obtenus du laboratoire canadien sur la tolérance au sel. En utilisant la fonction de Gompertz pour l'ajustement non-linéaire des données de test, il fut possible, grâce à la comparaison des deux variétés, de déterminer trois paramètres d'équation, quatre indices dérivés et une variable associée. Les meilleurs indices statistiques qui permirent de distinguer 'Swift' de 'Tetracan' étaient le taux de levée et de survie au point d'inflexion de la fonction de Gompertz, le maximum asymptotique atteint lors de chacun des tests (E_{max}), le temps nécessaire pour atteindre $0.99 E_{max}$, la levée se produisant au point d'inflexion de Gompertz, le paramètre de forme de Gompertz et la constante de temps de Gompertz. Ils indiquèrent que les plants de 'Tetracan' qui poussaient dans des lits de semence où les conditions de salinité étaient extrêmes, très élevées et modérées résistaient mieux à la salinité que la variété 'Swift'.

INTRODUCTION

Farmers, ranchers, and land managers interested in pastures for livestock or in vegetative cover for reclamation or for wildlife often wish to grow perennial forages on saline lands. Often, they also strive to abate root-zone salinization at the same time.

Russian wild ryegrass

Russian wild ryegrass (*Psathyrostachys juncea*) is a nutritious, perennial pasture forage grown across the semiarid prairies. Sometimes growers of this crop report difficulty with plant establishment (Heinrichs and Lawrence 1956; Lawrence and Heinrichs 1977; Tremblay 1997). Difficulties in establishing shallow-seeded forage plants in general can be further exacerbated in saline soils.

Initially, the poor establishment of Russian wild ryegrass (RWR) was related to seeding too deeply (Lawrence 1963; Kilcher and Lawrence 1970). Efforts to solve this depth problem led to better depth controls on seed drills (Dyck and Bowes 1982) and to a varietal breeding program selecting for better emergence from deeper seeding depths (Lawrence 1963). The latter effort resulted in the release of the RWR varieties 'Swift' (Lawrence 1979) and 'Tetracan' (Lawrence et al. 1990).

'Tetracan', a tetraploid cultivar, differs from 'Swift', a diploid cultivar, in possessing two copies of each chromosome pair, making 'Tetracan' a double-diploid. 'Tetracan' plants exhibit larger seed-size, bigger seedheads, and wider leaves than those of 'Swift' (Lawrence et al. 1990). Compared to 'Swift', 'Tetracan' seedlings also have fewer, larger tillers and longer root length (Jefferson 1993). However, above-ground biomass produced by plants of the two varieties in field trials are equivalent (Lawrence et al. 1990).

Salt tolerance

S-114, a test cultivar of RWR was included among twelve grasses evaluated for salinity tolerance in field trials near Saskatoon, SK (Forsberg 1953). This RWR representative rated third best and showed "good growth" while growing in soil whose electrical conductivity of saturated soil paste extracts (EC_e) averaged 3.5 and 9.5 dS/m for the 0-150 and 150-300 mm depth layers, respectively. In a later study, Rauser and Crowle (1963) concluded that RWR seeds rated behind tall wheatgrass (*Thinopyrum ponticum*) but better than slender wheatgrass (*Agropyron trachycaulum*) in germination and emergence from saline seedbeds. This ranking for germination was confirmed by Acharya et al. (1992). At high levels of salinity, RWR (cv. 'Sawki') compared favorably with Altai wild ryegrass (*Leymus angustus*) in emergence and herbage production (McElgunn and Lawrence 1973). Although these studies established RWR as a candidate pasture forage for saline soils, specific varieties of the species have not been compared.

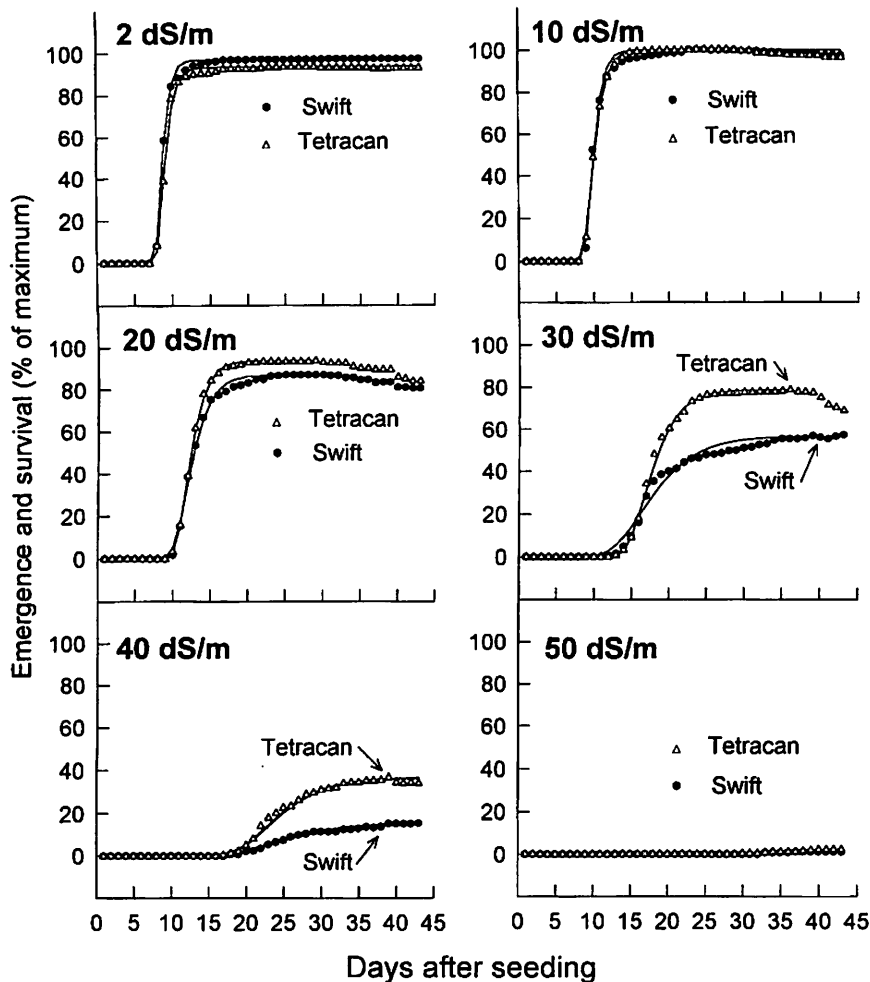


Fig. 1. Percentage of 'Swift' and 'Tetracan' Russian wild ryegrass plants emerging and surviving with time in seedbeds salinized with solutions at the electrical conductivities indicated. Data are plotted from counts, expressed as percent of the best total for the variety at 10 dS/m. Fitted curves are the Gompertz function.

The first step in identifying specific salt-tolerant varieties of RWR, or any other forage species, requires defining acceptable methods and standards for evaluating emergence, establishment, and maturation. The Food and Agriculture Organization of the United Nations outlined the criteria necessary to conduct salt tolerance testing for crop yields (Ayers and Westcot 1985). Ries and Svejcar (1991) suggested that the number of leaves and tillers per grass seedling can indicate plant establishment. They measured four leaves and one tiller among established crested wheatgrass (*Agropyron desertorum*) plants and six leaves and two tillers among established blue grama (*Bouteloua gracilis*) representatives. In their test, these numbers were achieved 21 days after initial emergence. However, the basis for comparing grass emergence under saline conditions has not been well defined. The objective of this study was to apply the Gompertz function to crop emergence and early survival among perennial forages growing in saline seedbeds, as exemplified by 'Swift' and 'Tetracan' RWR varieties and to identify suitable indices for these comparisons.

Gompertz function and indices

According to Lapp and Skoropad (1976), actuaries used a form of an equation proposed by Gompertz (1825) for many years to predict human mortality (King 1902). In various forms, the same equation has been applied in botany to model germination (Tipton 1984), emergence (Gan et al. 1992), and growth (Baker et al. 1975).

The form of the Gompertz equation evaluated in this manuscript follows the original:

$$E = E_{\max} \exp[-b \exp(-kt)] \quad (1)$$

where:

- t = time from seeding (d),
- E = cumulative emergence and survival in percent of the best experimental total at any specific salinity level at time t (%),
- E_{\max} = asymptotic maximum E, taken as the maximum cumulative emergence and survival at each specified salinity level in percent of the best experimental total (%),
- b = empirical shape parameter determined by regression, and
- k = time constant (d^{-1}).

If, under each set of environmental conditions, RWR plants emerge from seeds in infinitely small numbers proportional to their maximum emergence within equal, infinitely small intervals of time, the plants will emerge in a manner described by the Gompertz function. Although this is a reasonable assumption, the application of this equation is empirical. At this time, no

biological evidence exists on which to base selecting this, or any other equation, as a process analog.

Application of the Gompertz function to evaluate plant emergence also leads to four additional Gompertz-derived indices:

- R_i = maximum rate of plant emergence and survival which occurs at the inflection point of the function (%/d);
- t_i = time from seeding to the inflection point of the function (d);
- t_{\max} = time from seeding to reach $0.99E_{\max}$ (d);
- E_i = emergence accumulated by time t_i (%).

With respect to Eq. 1, these indices are defined as:

$$R_i = (kE_{\max})/e \quad (2)$$

$$t_i = (\ln b)/k \quad (3)$$

$$t_{\max} = (4.6 + \ln b)/k \quad (4)$$

$$E_i = E_{\max}/e \quad (5)$$

Table I. Statistical summary of non-linear regression fits of the Gompertz function to daily emergence and survival of 'Swift' and 'Tetracan' Russian wild ryegrass sown in seedbeds maintained at the specified electrical conductivities.

Electrical conductivity ⁺ (dS/m)	Regression N ⁺⁺	Mean of the residuals [#] (%)	Standard error of the residuals (%)	Confidence limits at p=0.01 (±%)
'Swift'				
2	430	-0.510	0.0192	0.049
10	398	-0.772	0.0766	0.197
20	346	-1.518	0.1083	0.279
30	406	-1.007	0.0960	0.247
40	420	0.046	0.0113	0.029
'Tetracan'				
2	409	-0.333	0.0345	0.089
10	386	-0.194	0.0299	0.077
20	346	-0.151	0.0437	0.112
30	342	-0.586	0.0658	0.170
40	410	-0.353	0.0241	0.062

⁺ electrical conductivity of seedbed test solutions

⁺⁺ Regression number (N) equals the number of days that the emergence was counted times the replication (10).

[#] Residuals are the differences between the simulated and actual daily counts.

with *e* indicating the base of the natural logarithm. Although not dependent on the Gompertz function, the lag time from seeding to the initial emergence defines another index, t_{lag} [d].

TESTING PROCEDURES

Testing was conducted at Canada's Salt Tolerance Testing Laboratory (Steppuhn et al. 1996). Nine-litre cylindrical pots filled with pure silica (mean particle sizes from 0.1 to 1.0 mm in nominal diameter) formed seedbeds for 60 seeds per pot. The seedbeds were irrigated four times daily with a modified, half-strength Hoagland's nutrient solution consisting of 2.0 mM Ca(NO₃)₂, 2.5 mM KNO₃, 0.17 mM KH₂PO₄, 1.0 mM MgSO₄, 0.05 mM chelated Fe, 0.5 mM NH₄NO₃, 0.05 mM KCl, 0.023 mM H₃BO₄, plus trace elements including Mn, Zn, Cu, Si, and Mo. The selected solutions were salinized by adding NaCl and CaCl₂ (1:1 by mass) resulting in pH values of 7.5-7.9. Solution electrical conductivities (EC_{sol}) of 2, 10, 20, 30, 40, and 50 dS/m relate to equivalent electrical conductivity of saturated soil paste extracts (EC_e) by the approximate relationship: EC_e ≈ 0.5EC_{sol} (Ayers and Westcot 1985). These test solutions represent the upper values for root-zone salinity classed respectively as none, slight, moderate, severe, very severe, and extremely severe. Each irrigation continued for twelve minutes until the sand was completely saturated after which the solutions drained into 612-litre reservoirs for the next irrigation. Water lost by evapotranspiration was replenished

weekly or when necessary to maintain the concentrations of salts in solution. The electrical conductivity (EC_{sol}) of each solution was checked initially and weekly.

The test was conducted with an appropriate course for day/night time sequences mimicking an April 15 seeding at 50° north latitude adjusted by 15 minute increments. Day/night temperatures were set at 18/16°C and maintained within one or two degrees of these setpoints.

All seedlots were pretested for germination in a standard germinator and none were used whose seeds germinated below 90%. All nutrients and salts were prepared and added to the irrigated solutions prior to seeding.

Two irrigations preceded seeding in order to firm the seedbed. A template guided placement of each seed into a known position within each seedbed. This allowed assessment of emergence and survival associated with each seed on a daily basis. Any protrusion of the plant above the sand surface counted it as emerged. Records

were kept on paper copies of the seeding template. This procedure resulted in daily counts per pot of the number of newly emerged plants and their survival with time.

The experiment utilized 60 pots laid out in groups of six forming ten replicate blocks each containing one pot salinized to one of the six salt levels and randomized within each block. Thirty seeds each of 'Swift' and 'Tetracan' Russian wild ryegrass were planted 12 mm deep in either the west or east half of each pot following a random choice. The daily emergence counts were fitted to the non-linear Gompertz function (Eq. 1) using the NLIN regression program of SAS with the Marquardt option (Statistical Analysis Systems Institute 1990).

In time, the number of emerged and surviving plants in each test reached a peak or plateau. Counts were continued along the plateau or peak until the number for each salinity level or variety in any replicate pot began to decline. Thus, the number of counting days varied for each salinity level and RWR variety. Also, the total possible emergence per test, reflecting seed viability, was assumed to equal the most emergence counted at any salinity level for each variety. This occurred at 10 dS/m in both varieties.

The regression fit of the Gompertz function was evaluated by comparing differences in simulated and actual percentages as residuals, standard error of the residuals, and resulting

Table II. Parameter values derived from non-linear regression fits of the Gompertz function applied to daily emergence and survival of ‘Swift’ and ‘Tetracan’ Russian wild ryegrass sown in seedbeds maintained at the specified electrical conductivity.

Parameter and Seedbed salinity (dS/m)	Mean (standard deviation*)		Absolute difference between means
	‘Swift’	‘Tetracan’	
E_{max} (%)			
2	97.1 (2.03)	93.4 (1.59)	3.7
10	100.0**	100.0**	0.0
20	89.2 (2.95)	93.8 (3.35)	4.6
30	59.5 (5.63)	79.3 (3.54)	19.8*
40	16.5 (2.34)	36.3 (4.20)	19.8**
50 [#]	--	--	--
b			
2	164909 (52425)	70024 (29196)	94885
10	25406 (11611)	7790.8 (1836.1)	17615
20	490.2 (124.1)	4474.9 (1068.8)	3984.7**
30	25.3 (3.2)	908.7 (193.7)	883.4**
40	51.8 (8.9)	323.3 (65.2)	271.5**
50	--	--	--
k (d ⁻¹)			
2	1.402 (0.036)	1.263 (0.046)	0.139
10	1.043 (0.046)	0.919 (0.023)	0.124
20	0.523 (0.020)	0.712 (0.020)	0.189**
30	0.192 (0.007)	0.409 (0.012)	0.217**
40	0.162 (0.007)	0.262 (0.009)	0.100**
50	--	--	--

* based on 10 replicates

** taken as 100% for seedlot maxima based on 27.9 emerged plants for ‘Swift’ and 25.6 for ‘Tetracan’ out of 30 sown seeds per replicate

[#] emergence too low for regression

** statistically significant at p=0.01, t-test and confidence limits

confidence limits. The fits also resulted in equation parameters (E_{max} , b, and k) which were subsequently compared between the RWR varieties using confidence limits and unpaired t-tests. Significance was inferred at the p=0.05 error probability. The derived indices were similarly compared.

RESULTS and DISCUSSIONS

The number of ‘Swift’ and ‘Tetracan’ Russian wild ryegrass plants emerging and surviving each day in different saline seedbeds satisfactorily followed the Gompertz function when the total (maximum) number were known (Fig. 1). At 2 and 10 dS/m, both ‘Swift’ and ‘Tetracan’ plants emerged within 10 days of seeding, entered a period characterized by very rapid emergence rates, and leveled to plateaus totaling, on average, 90% or more of the number of viable seeds planted. As salinity increased, the lag period to initial emergence (t_{lag}) increased, the emergence rate (R_i) decreased, and the total emergence (E_{max}) declined. At 50 dS/m, the emergence was too few to relate by the Gompertz equation. The residual standard errors for simulated and actual emergence resulted in mean confidence limits of $\pm 0.3\%$ or less for either RWR variety at each salinity level (50 dS/m excluded) (Table I). This implies average fits for the Gompertz function within 0.6% or less.

Application of the Gompertz function to the daily emergence and survival data involve three empirical parameters: E_{max} , b, and k. We determined each E_{max} from the data set and calculated b and k by regression to evaluate according to each RWR variety (Table II). Comparisons with these parameters indicated that the greater E_{max} measured for ‘Tetracan’ was significant (with p=0.01) at 40 and 30 dS/m but not at 20 dS/m. However, both b and k for the two varieties were significantly different at each of the three salinities (20, 30, and 40 dS/m). Thus, the Gompertz parameters, used as indices, confirmed the observation in Fig. 1, i.e. that ‘Tetracan’ plants emerged better than the ‘Swift’ plants when seedbed salinity ranged from moderate to very severe. Significant differences in the Gompertz parameters were not detected between the varieties in the non-or- slightly saline environments.

Three of the indices compared pertained to time from seeding: t_{lag} (lag time to initial emergence), t_i (time to the Gompertz inflection point), and t_{max} (time to 0.99 E_{max}). Only t_{max} differed significantly between test varieties and only at 30 and 40 dS/m (Table III). Differences between ‘Swift’ and ‘Tetracan’ for t_i or t_{lag} were not significant at any level of salinity. Nevertheless, the inference does not follow that comparisons among other varieties or crops will also fail to show differences using these indices.

Table III. Gompertz indices⁺ of time for 'Swift' and 'Tetracan' Russian wild ryegrass emergence and survival compared at the specified electrical conductivity.

Index and Seedbed salinity (dS/m)	Mean (standard error)		Absolute difference between means
	'Swift'	'Tetracan'	
t_{lag} (d)			
2	8.2 (0.13)	8.3 (0.15)	0.1
10	9.4 (0.16)	9.1 (0.10)	0.3
20	10.8 (0.25)	10.6 (0.22)	0.2
30	14.3 (0.37)	14.7 (0.45)	0.4
40	21.0 (0.76)	19.3 (0.42)	1.7
50	34.3 (1.33)	34.8 (1.66)	0.5
t_i (d)			
2	8.6 (0.13)	8.8 (0.17)	0.2
10	9.7 (0.21)	9.7 (0.15)	0.0
20	11.9 (0.23)	11.8 (0.21)	0.1
30	16.8 (0.37)	16.6 (0.47)	0.2
40	24.4 (0.78)	22.1 (0.75)	2.3
50	--	--	--
t_{max} (d)			
2	11.9 (1.73)	12.5 (1.33)	0.6
10	14.1 (1.33)	14.8 (1.06)	0.7
20	20.7 (2.54)	18.3 (0.70)	2.4
30	40.8 (1.88)	27.9 (1.56)	12.9**
40	52.9 (2.32)	39.6 (1.43)	13.3**
50	--	--	--

⁺ Indices

t_{lag} = lag time from seeding to initial emergence

t_i = time from seeding to the Gompertz inflection point

t_{max} = time from seeding to the Gompertz point where 99% of the total emergence had occurred

** statistically significant at $p=0.01$, confidence limits of actual data

Comparisons between 'Swift' and 'Tetracan' for R_i (rate of emergence and survival at the Gompertz inflection point) concluded with significant differences at each of the five salinity levels (Table IV). However, closer inspection showed that only at the moderate, severe, and very severe salinity levels had 'Tetracan' plants emerged faster than the 'Swift' plants. At lower EC_{soil} levels, emergence rate seemed to favor 'Swift' over 'Tetracan'. This implies that although growers can expect better emergence with 'Tetracan' compared to 'Swift' for seeds sown

in moderately and severely saline seedbeds, the opposite may be true in non-to-slightly saline seedbeds.

Comparisons between 'Swift' and 'Tetracan' for E_i (emergence at inflection) resulted in significant differences at 30 and 40 dS/m only (Table IV). Differences under the lower levels of salinity did not prove significant. The E_i index led to the same conclusions as E_{max} . For both E_i and E_{max} , the differences between varieties were greater relative to the total E -values at 40 dS/m than at 30 dS/m (Fig. 1). Consequently, the statistical probabilities for confidence error (for both E_i and E_{max}) were greater for the 40 dS/m than the 30 dS/m data.

CONCLUSIONS

The Gompertz function provided a good empirical analog for the emergence and early survival of 'Swift' and 'Tetracan' Russian wild ryegrass plants sown in saline seedbeds. Sufficient numbers emerged from the 2, 10, 20, 30, and 40 dS/m substrates to apply the function and compare its indices. Confidence limits on the standard error of the residuals between the simulated and actual emergence were within $\pm 0.3\%$ among all salinity levels.

Eight indices were evaluated to compare differences between 'Swift' and 'Tetracan' emergence across a full range of seedbed salinities:

b, k discriminated satisfactorily between varieties but are empirical;

t_i did not discriminate well, likely, because the two varieties do not differ genetically with respect to time;

t_{lag} failed to index any difference at any salinity level; R_i showed the differences inherent between 'Swift' and 'Tetracan' without salinity as well as with it and proved to be the most discriminating index between these Russian wild ryegrass varieties;

E_{max} was a good index but required a companion indicator related to time;

t_{max} proved to be a reasonable discriminating index for time;

E_i discriminated between 'Swift' and 'Tetracan' as well as E_{max} .

Of the eight indices compared, the three which most closely verified statistically the visual differences in the emergence and early survival of 'Swift' and 'Tetracan' RWR plants evident in Fig. 1 were b, k, and R_i . Similar results may have resulted from applying other empirical functions. However, as Tipton (1984) emphasized, the Gompertz equation showed acceptable suitability reflecting its flexibility and general applicability.

On the basis of the above indices, we concluded that the emergence and early survival of 'Tetracan' RWR from moderately to very severely saline seedbeds was better than that of 'Swift' RWR. Furthermore, this conclusion was reached following FAO standard salinity tolerance testing procedures (Ayers and Westcot 1985). No scientific reasons or restrictions exist which suggest that the genetic performance obtained in this study cannot be attained in the field.

Table IV. Gompertz indices* pertaining to rate of daily emergence and survival of 'Swift' and 'Tetracan' Russian wild ryegrass sown in seedbeds maintained at the specified electrical conductivity.

Index and Seedbed salinity (dS/m)	Mean (standard error)		Absolute difference between means
	'Swift'	'Tetracan'	
R_i (%/d)			
2	50.1 (1.05)	43.4 (0.74)	6.7**
10	38.2 (0.84)	33.8 (0.84)	4.4*
20	17.2 (0.57)	24.6 (0.88)	7.4**
30	4.2 (0.40)	11.9 (0.53)	7.7**
40	1.0 (0.14)	3.5 (0.40)	2.5**
50	--	--	--
E_i (%)			
2	35.7 (0.75)	34.3 (0.58)	1.4
10	36.6 (0.81)	36.8 (0.91)	0.2
20	32.8 (1.08)	34.5 (1.23)	1.7
30	21.9 (2.07)	29.2 (1.30)	7.3*
40	6.1 (0.86)	13.4 (1.55)	7.3**
50	--	--	--

* Indices

R_i = rate of emergence and survival at Gompertz inflection point

E_i = percentage emergence and survival at Gompertz inflection point

* difference statistically significant at $p=0.05$

** difference statistically significant at $p=0.01$

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