

Effects of cadmium toxicity on sesame seed germination explained by various nonlinear growth models

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Received 1 September 2019 – Accepted 1 October 2020

Abstract – This experiment was conducted to evaluate the effects of cadmium toxicity on the seed germination properties of sesame cultivars (Halil, Nazok Shakhei, Oltan, and Yellow White) using non-linear growth models. Seeds were germinated in petri dishes (90 mm diameter), with a double layered of filter paper soaked in distilled water as control treatment or cadmium (CdSO₄) solutions in concentrations of 0, 100, 200, 400, 600, 800 and 1000 ppm. Each treatment was replicated four times and included 50 seeds in each petri dishes. Hyperbolic growth models for the description of seed germination data were compared to Richards, Weibull, Logistic and Gompertz models. Our results revealed that all studied cultivars were germinated at the cadmium-polluted germination medium to a maximum of 200 ppm without reduction in germination fraction, while seed germination rate was decreased at this concentration compared to 0 and 100 ppm. Increasing cadmium concentration resulted in the germination fraction reduction from 1 to 0.4 at the 400 ppm. The recommended hyperbolic growth model was type III or (H3) as it provided the best model with the lowest Corrected Akaike Information Criterion for cv. Halil (AICc = -14.6) and cv. Nazok Shakhei, (AICc = -14.2).

Keywords: Germination / growth model / heavy metal / pollution / sesame

Résumé – Les effets de la toxicité du cadmium sur la germination de graines de sésame expliqués par divers modèles de croissance non linéaire. Cette expérience a été menée pour évaluer les effets de la toxicité du cadmium sur la cinétique de germination de graines issues de différents cultivars de sésame (Halil, Nazok Shakhei, Oltan et Yellow White), en comparant des modèles de croissance non linéaire. Les graines ont germé dans des boîtes de Pétri (90 mm de diamètre), entre deux couches de papier filtre imbibées d'eau distillée (contrôle) ou dans des solutions de cadmium (CdSO₄) à des concentrations de 0, 100, 200, 400, 600, 800 et 1000 ppm. Chaque traitement a été répété quatre fois et comprenait 50 graines par boîte. Les cinétiques de croissances ont été modélisées avec modèles de croissance hyperbolastique, dont l'ajustement a été comparé aux modèles sigmoïdes classiques (Richards, Weibull, Logistic et Gompertz). Nos résultats ont révélé que tous les cultivars étudiés ont germé, sans réduction du taux de germination, jusqu'à une concentration de de 100 ppm. Au-delà, le taux de germination était réduit. À la concentration de 400 ppm, le taux de germination est passé de 1 à 0,4. Le modèle de croissance hyperbolastique recommandé était de type III ou (H3), car il présentait un critère d'information d'Akaike (AIC) corrigé le plus bas pour les cultivars Halil (AICc = -14,6) et Nazok Shakhei, (AICc = -14,2).

Mots clés : Germination / modèle de croissance / métal lourd / pollution / sésame

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1 Introduction

Industrialization and human activities caused serious environmental pollution by heavy metals. This not only causes direct hazardous effects to both human and ecosystems, but has also influenced food safety and security in agriculture lands (Das *et al.*, 1997; Benavides *et al.*, 2005). Cadmium is a heavy metal that does not have any known nutritious function for plants (Hanc *et al.*, 2009; Gallego *et al.*, 2012). However, due to the increase of mine production, industrial activities and urbanization, its concentrations in the environment has increased drastically. Cadmium is considered a highly significant pollutant due to its high toxicity and large water solubility (Benavides *et al.*, 2005). It has been accepted that cadmium can interfere with water uptake and reduce root growth and development of plants (DalCorso *et al.*, 2008). Exploring the interaction of cadmium and seed germination is important for the safety of crop production. It is also worth to study the risks of good and uniform seed germination in the soils with various levels of cadmium contaminations.

Modeling biological data conveniently summarizes information into small sets of parameters that can be interpreted biologically. Growth models are mainly empirical and they rely on physiological or biochemical mechanisms (Eby *et al.*, 2017). Generally, growth models are expressed as the rate function of an independent variable over time. It is very important to consider that each growth function must be biologically meaningful. The benefits of nonlinear regression analysis in seed biology is due to their interpretability, parsimony and prediction possibility for biologically related phenomena, especially outside the range of actual experimental data (Archontoulis and Miguez, 2015). Many nonlinear growth models have been successfully applied in biological science. Gompertz, Richards, Weibull, Logistic and Hill are the most applied nonlinear functions to describe cumulative seed germination (Dumur *et al.*, 1990; Shafii *et al.*, 1991; Tjørve and Tjørve, 2017). The number of parameters in each model varies from three to five depending on the mathematical bases of the model construction method, to provide the best curve fit for experimental data. In the logistic model, the period to reach the maximum growth rate is equal to the inflection point, thus, this model is symmetric around the maximum growth rate. In contrast, Richards and Gompertz models have different durations for short and fast growth rates and they are considered asymmetric models (Shafii *et al.*, 1991). Recent reports suggested that hyperbolic nonlinear growth models in some cases provide a better fit for complex growth patterns in biological studies, over more traditional models such as generalized Gompertz or logistic functions (Tabatabai *et al.*, 2005; Ahmadi and Golian, 2008; Eby *et al.*, 2017; Barrera *et al.*, 2018). Hyperbolic models were introduced by Tabatabai *et al.* to study tumor and stem cells growth rates (Tabatabai *et al.*, 2005). The term *Hyperbolic* for this type of nonlinear models comes from the model function equation showing that these models are a function of the inverse hyperbolic sine (Ahmadi and Golian, 2008). Hyperbolic growth models are classified into three types: H1, H2 and H3, according to their function. Hyperbolic growth models are developed to provide higher accuracy and more flexibility,

compared to other growth models such as Gompertz, Weibull, and others (Eby *et al.*, 2017).

The purpose of our study was to evaluate the possible application of Hyperbolic models to fit empirical data obtained from an experiment exploring the influence of various concentrations of heavy metals on sesame genotypes.

2 Material and methods

Seeds of sesame (*Sesame indicum* L.) cultivars were obtained from the oil seed division at the Seed and Plant Improvement Institute in Karaj, Iran in 2018. Seeds of five sesame cultivars (Halil, Nazok Shakhei, Oltan, and Yellow White) were used in this experiment, and generally followed the ISTA rules for standard seed germination test (ISTA, 2017). The seeds were germinated in petri dishes (90 mm diameter), with a double layered of filter paper soaked in distilled water as control treatment or cadmium (CdSO₄) solutions in concentrations of 0, 100, 200, 400, 600, 800 and 1000 ppm. Each treatment was replicated four times and included 50 seeds in each petri dishes. Seeds were subjected to standard seed germination tests using top of paper method and at alternate temperature regime (20/30 °C) under dark conditions (ISTA, 2013). The number of germinated seeds were recorded every 12 h until day six after test initiation. Germination test was ended when seed germination was reached to the maximum and no seeds have germinated for three subsequent counts.

2.1 Statistical analyses

Two-way ANOVA with Tukey's *post-hoc* analysis (Seal *et al.*, 2018) was used to analyze the effects of cultivar, concentrations of cadmium, and their interaction on seed germination and the germination index of sesame. Analysis of variance and comparison of means were conducted using the Minitab® 18 statistical software. The Software SigmaPlot (SigmaPlot 14, Systat Software, Inc.) was used for non-linear regression analyses and model fit on seed germination data.

Seed germination index was calculated according to (Fenner and Edwards, 1991). In this study various nonlinear growth models were applied on the cumulative seed germination data, in order to make an appropriate comparison between hyperbolic models and other models generally applied in seed biology. The applied hyperbolic models have been previously explained using three different models of H1 to H3, and are presented in equations (1) to (3) below (Tabatabai *et al.*, 2005; Ahmadi and Golian, 2008; Eby *et al.*, 2017). The hyperbolic growth rate of type I (H1) (Tabatabai *et al.*, 2005) is:

$$P(t) = \frac{Y_{max}}{1 + \alpha \exp[-Y_{max}\beta t - \theta \operatorname{arcsinh}(t)]}, \quad (1)$$

Where:

$$\alpha = \frac{Y_{max} - P_0}{P_0} \exp[Y_{max}\beta t_0 + \theta \operatorname{arcsinh}(t_0)],$$

Where $P(t)$ is the number of germinated seeds at time t , the constant Y_{max} is the parameter representing carrying capacity, and β and θ are constants. It is worth noting that both β and θ are parameters that describe growth (germination) rate. The $\text{arcsinh}(t)$ is the inverse hyperbolic sine function of t .

The hyperbolic growth rate of type II (H2) (Tabatabai *et al.*, 2005) is:

$$P(t) = \frac{Y_{max}}{1 + \alpha \text{arcsinh}[\exp(-Y_{max}\beta t^\gamma)]},$$

$$\alpha = \frac{Y_{max} - P_0}{P_0 \text{arcsinh}[\exp(-Y_{max}\beta t_0^\gamma)]}. \quad (2)$$

With the initial condition $P(t_0) = P_0$; and Y_{max} , β , and γ as parameters. The growth rate is determined using β (intrinsic growth rate) and γ (allometric constant).

The hyperbolic growth rate of type III (H3) (Tabatabai *et al.*, 2005) is:

$$P(t) = Y_{max} - \alpha \exp[-\beta t^\gamma - \text{arcsinh}(\theta t)],$$

$$\alpha = (Y_{max} - P_0) \exp[\beta t_0^\gamma + \text{arcsinh}(\theta t_0)]. \quad (3)$$

With the initial condition $P(t_0) = P_0$; and Y_{max} , β (by the time prescribed for the, final count), γ (allometric constant) and the distance from symmetric sigmoidal growth is determined by the value of $|\theta|$.

In hyperbolic models H1, H2 and H3 the parameter Y_{max} will represent the maximum fraction of germination percentage, while the parameter β will represent the rate of increase of seed germination with respect to time. In H1 the additional parameter θ helps determine variation in the intrinsic rate. In H2 the additional parameter γ is an allometric parameter that also provides departure from logistic symmetry by rescaling, and the effective rate is determined by both β and γ . Finally, the parameter γ in H3 is an allometric parameter as in H2, while θ is a shape parameter, and its role is comparable to the role in H1 and H2; and β , γ , and θ collectively determine the effective growth rate.

A three parameter logistic function is fitted on our experimental data using equation (4) (Verhulst, 1838; Tanveer *et al.*, 2017; Soler-Guilhen *et al.*, 2020). An additional parameter, d , has the effect of shifting the graph vertically (the lower asymptote), and it turns the three-parameter logistic to a four-parameter logistic function (Eq. (5)).

$$Y = Y_{max}[1 + \exp(L - Kt)] - 1, \quad (4)$$

$$Y = d + Y_{max}[1 + \exp(L - Kt)] - 1. \quad (5)$$

Y is the cumulative percentage of germination at time t , Y_{max} is the maximum rate of seed germination (the upper asymptote), K is the increasing rate of germination, L is time scale constant, and d is the lower asymptote.

Gompertz is a sigmoid model which has been widely used to curve fitting of growth data. The three- and four-parameter Gompertz functions were fitted on data using the following

equations (Gompertz, 1825; Tjørve and Tjørve, 2017):

$$Y = Y_{max}[\exp(-\exp(L - Kt))], \quad (6)$$

$$Y = d + Y_{max}[\exp(-\exp(L - Kt))]. \quad (7)$$

Richards' function is a modified to a four-parameter sigmoid function having an especial shape parameter to provide a flexible curve fitting our experimental data. This model was fitted to our experimental data using equation (8) (Richards, 1959).

$$Y = Y_{max}[1 - \exp(-K(t - L))] / (1 - c). \quad (8)$$

Y is the cumulative percentage of germination at time t , Y_{max} is the maximum rate of seed germination (the upper asymptote), K is the increasing rate of germination, L is time scale constant, and c is the shape parameter to provide a flexible curve fitting our experimental data.

Weibull function has also been successfully applied in seed germination studies by many researchers. This model not only have biologically interpretable parameters, but also have unique properties when the exponential distribution is not well explained for experimental data due to the limitations of randomization (Shafii *et al.*, 1991). A Weibull model was fitted to our experimental data using the following equation (Weibull, 1951):

$$Y = Y_{max}[1 - \exp(-K(t - L)^c)]. \quad (9)$$

These models were applied to a cumulative fraction dataset of sesame cultivars seed germination, using nonlinear regression to estimate the parameters for each model. The statistical calculations for the determination coefficient (R^2) was used to assess the accuracy of each model. However, it should be noted that R^2 may not always represent the most appropriate metric because it does not account for the number of parameters in the model (Archontoulis and Miguez, 2015). To increase the precision of the model selection criterion, the Corrected Akaike Information Criterion (AICc) was calculated for all applied models. Data with a probability index resulted in a lower AICc and better fit to the data (Bullied *et al.*, 2012).

$$R^2 = 1 - \frac{(\text{residual sum of squares})}{\text{Total sum of squares}}, \quad (10)$$

$$AIC = n \ln\left(\frac{\text{residual sum of squares}}{n}\right) + 2k, \quad (11)$$

$$AICc = n \ln\left(\frac{\text{residual sum of squares}}{n}\right) + 2k + \left(\frac{2k(k + 1)}{n - k - 1}\right), \quad (12)$$

Where n is the number of observations, and k is the number of model parameters (Burnham and Anderson, 2002).

Table 1. The analysis of variance and comparison of means for seed germination traits of sesame cultivars exposed to various levels of cadmium concentrations.

Cultivar	Cadmium (ppm)	Seed germination (%)	Germination Index
Means that do not share a letter are significantly different			
Halil	0	99 ^a	1073 ^a
	100	98 ^a	1025 ^a
	200	93 ^{ab}	920 ^{ab}
	400	43 ^c	405 ^d
	600	12 ^{ef}	93 ^{fgh}
	800	2 ^f	13 ^h
	1000	0 ^f	0 ^h
Nazok Shakhei	0	93 ^{ab}	999 ^a
	100	92 ^{ab}	947 ^{ab}
	200	81 ^b	740 ^c
	400	27 ^{cde}	190 ^{ef}
	600	3 ^f	18 ^h
	800	1 ^f	6 ^h
	1000	0 ^f	0 ^h
Oltan	0	96 ^{ab}	1016 ^a
	100	95 ^{ab}	971 ^a
	200	81 ^b	690 ^c
	400	31 ^{cd}	257 ^{de}
	600	21 ^{de}	172 ^{efg}
	800	3 ^f	21 ^{gh}
	1000	0 ^f	0 ^h
Yellow White	0	95 ^{ab}	1003 ^a
	100	93 ^{ab}	929 ^{ab}
	200	86 ^{ab}	794 ^{cb}
	400	27 ^{cde}	268 ^{de}
	600	11 ^{ef}	117 ^{efgh}
	800	0 ^f	0 ^h
	1000	0 ^f	0 ^h
Source	DF	MS: Seed Germination	MS: Germination rate
Cultivar	3	260.7 ^{**}	39 442 ^{**}
Cadmium	6	31 554.6 ^{**}	3 351 260 ^{**}
Cultivar × Cadmium	18	62.4 [*]	10 090 ^{**}
Error	84	34.2	3166 ^{**}
Total	111		

*Significant ($P \leq 0.05$); **Significant ($P \leq 0.01$).

3 Results and discussion

Seed germination of all sesame cultivars declined as the cadmium concentration increased. Our results revealed that sesame seeds are tolerated to 200 ppm of cadmium. However, the germination rate declined as the cadmium contamination increased. At cadmium concentrations over 400 ppm, there was a drastic reduction of final seed germination for all the sesame cultivars (Tab. 1). Among all studied cultivars, cv. Halil exhibited the highest tolerance to cadmium toxicity up to 400 ppm, at which seed germination was 43%, 27%, 31% and 27% for cv. Halil, cv. Nazok Shakhei, Oltan and Yellow wWhite respectively (Tab. 1). The fastest seed germination was observed when there was no cadmium pollution for cv. Halil.

However, at a cadmium concentration of 600 ppm, the fastest seed germination was observed in cv. Oltan (Tab. 1). The germination index for the control treatment was 1003 for cv. Yellow White. However, the index was reduced to 117 by increasing the cadmium concentration up to 600 ppm. Similar findings regarding the reduction of seed germination due to heavy metals toxicity have been previously reported with (Akpofure, 2012; Asgher *et al.*, 2015; Fattahi *et al.*, 2019). It has been shown that cadmium pollution may increase seeds' indigenous abscisic acid levels and inhibit seed germination (Munzuroğlu *et al.*, 2008). Cadmium toxicity can damage normal seed respiration during imbibition (Deswal and Laura, 2018). It has also been shown that antioxidants and amylase enzyme functionality is reduced when cadmium concentrations

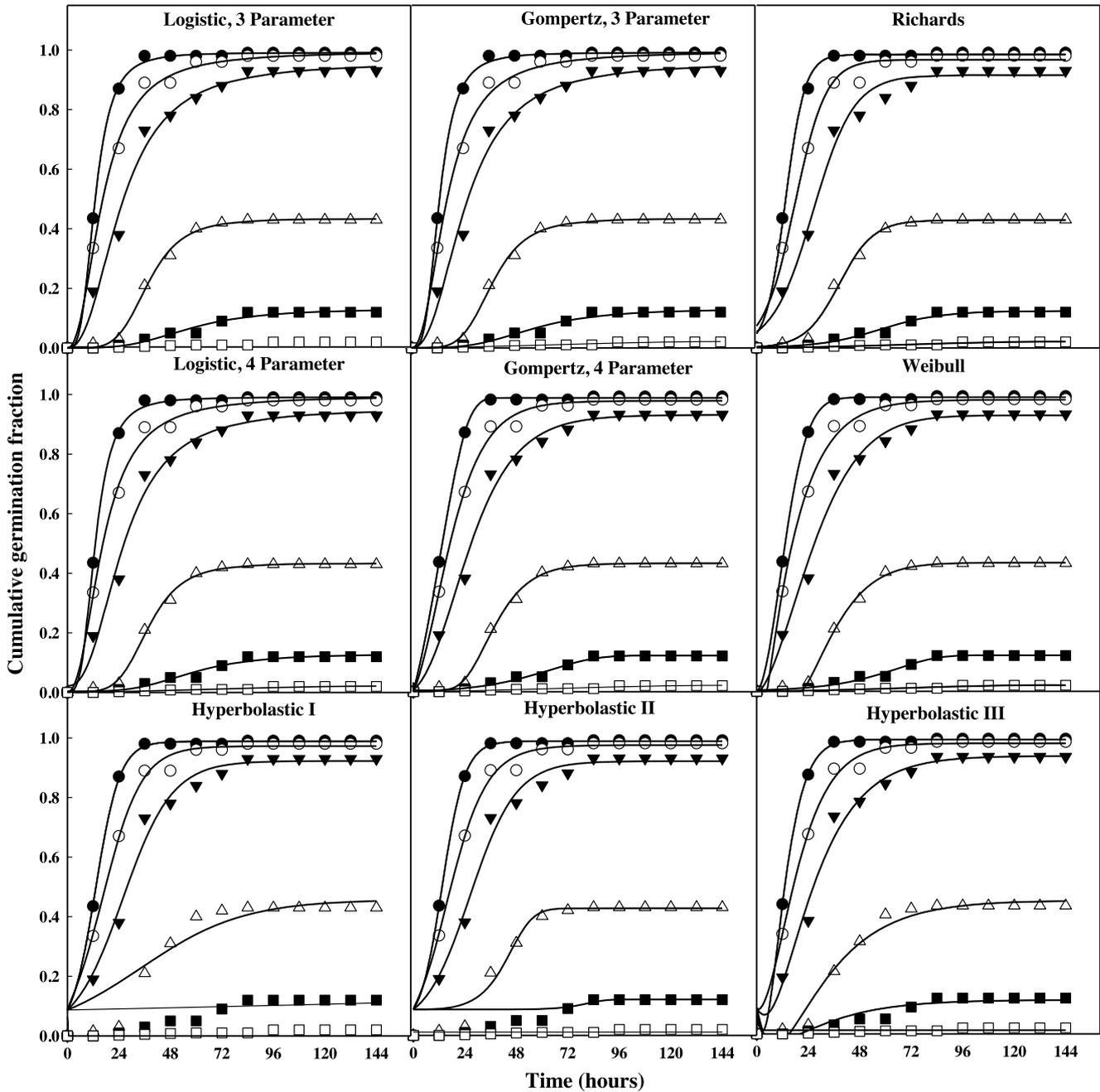


Fig. 1. Non-linear regression models for describe cumulative germination function cv. Halil under cadmium stress. Symbols ●: 0 ppm; ○: 100 ppm; ▼: 200 ppm; △: 400 ppm; ■: 600 ppm and □: 800 ppm.

increase in the seed environment, causing a decrease in the seed germination rate index (Afzal *et al.*, 2019; Chugh and Sawhney, 1996; Zhang *et al.*, 2009).

In our case, cumulative germination fraction of cv. Halil was reduced from 1 to 0.4 at a 400 ppm cadmium concentration and to lower than 0.2 at 600 ppm. The seed germination pattern of cv. Halil was well fitted by the sigmoid models while hyperbolic functions were capable of describing the data with reasonable fit at cadmium concentrations of 200 ppm (Fig. 1). For instance, the estimated AICc of three-parameter logistic for cv. Halil at cadmium concentrations of 100, 200, 400 ppm were -23.1, -16.1, and -29.0 respectively, which were the lowest

estimated AICc among other studied models. Hyperbolic models I, II and III poorly fit the germination data above 200 ppm cadmium concentration. In cv. Oltan for instance, the estimated AICc were 12.8, -13.8 and -16.4 for hyperbolic models I, II and III; while the AICc of Gompertz 3p was estimated at -21.1, showing better fit compared to the hyperbolic models.

In cv. Yellow White, the estimated AICc at cadmium concentrations of 200 ppm was -18.8, -15.1, -16.0, -15.6, -8.2, -15.8, -13.7, -14.1 and -10.9 for three-parameter logistic, four-parameter logistic, three-parameter Gompertz, four-parameter Gompertz, Richards, Weibull and hyperbolic I through III respectively (Tab. 2).

Table 2. Nonlinear regressions to describe Cumulative seed germination fraction of sesame (*Sesamum indicum* L.) cultivars under cadmium contaminations. AICc is represented of the best model fit.

Genotypes	Models types	Cadmium (ppm)						
		0	100	200	400	600	800	
Halil	Logistic,3P	-32.9	-23.1	-16.1	-29.0	-30.6	-47.3	
	Logistic,4P	-29.1	-19.3	-12.1	-25.2	-26.8	-43.5	
	Gompertz, 3P	-39.1	-23.6	-16.9	-30.0	-33.9	-47.5	
	Gompertz, 4P	-33.0	-17.7	-13.0	-26.2	-26.8	-43.6	
	Richards	-18.8	-12.1	-11.1	-22.0	-28.2	-43.6	
	Weibull	-35.3	-19.8	-12.6	-28.2	-30.1	-44.0	
	Hyperbolastic I	-18.2	-16.2	-13.3	-7.80	-10.5	-19.5	
	Hyperbolastic II	-18.4	-16.4	-13.5	-12.8	-11.3	-31.2	
	Hyperbolastic III	-14.6	-12.8	-9.80	-10.3	-12.8	-14.3	
	Logistic,3P	-22.4	-19.8	-14.9	-19.8	-25.0	-52.1	
Oltan	Logistic,4P	-18.7	-16.0	-11.3	-16.3	-22.0	-48.7	
	Gompertz, 3P	-18.5	-15.1	-16.0	-21.1	-25.3	-51.0	
	Gompertz, 4P	-18.7	-16.8	-13.2	-17.3	-21.7	-47.4	
	Richards	-9.3	-7.0	-10.8	-18.2	-23.9	-51.4	
	Weibull	-20.2	-17.3	-13.4	-19.5	-27.5	-56.3	
	Hyperbolastic I	-15.5	-14.7	-15.1	-12.8	-9.3	-19.5	
	Hyperbolastic II	-16.5	-15.7	-16.1	-13.8	-10.3	-20.5	
	Hyperbolastic III	16.8	-15.4	-14.4	-16.4	-15.1	-17.3	
	Logistic,3P	-28.1	-14.0	-15.9	-20.6	-50.9	-65.3	
	Logistic,4P	-24.3	-10.2	-12.2	-17.8	-48.1	-61.6	
Nazok	Gompertz, 3P	-29.4	-14.8	-16.5	-20.2	-50.8	-63.2	
	Gompertz, 4P	-26.2	-12.6	-13.3	-17.3	-48.1	-59.5	
	Richards	-16.9	-8.4	-9.8	-18.5	-47.5	-62.9	
	Weibull	-27.5	-12.9	-13.4	-21.0	-51.2	-68.7	
	Hyperbolastic I	-18.0	-14.0	-12.9	-7.2	-18.0	-21.9	
	Hyperbolastic II	-18.0	-13.7	-13.0	-7.6	-24.6	-24.6	
	Hyperbolastic III	-14.2	-11.0	-10.1	-11.6	-14.7	-13.3	
	Logistic,3P	-28.5	-19.2	-18.8	-26.1	-47.4	-	
	Logistic,4P	-24.7	-15.5	-15.1	-22.6	-43.6	-	
	Gompertz, 3P	-19.5	-14.3	-16.0	-25.3	-39.1	-	
Shakhei	Gompertz, 4P	-19.6	-14.5	-15.6	-23.9	-18.8	-	
	Richards	-10.1	-6.7	-8.2	-19.6	-30.1	-	
	Weibull	-26.8	-15.9	-15.8	-23.9	-44.5	-	
	Hyperbolastic I	-15.6	-13.3	-13.7	-17.2	-17.3	-	
	Hyperbolastic II	-16.2	-8.9	-14.1	-17.9	-17.6	-	
	Hyperbolastic III	-12.3	-10.3	-10.9	-14.1	-13.9	-	
	Yellow white	Logistic,3P	-28.5	-19.2	-18.8	-26.1	-47.4	-
		Logistic,4P	-24.7	-15.5	-15.1	-22.6	-43.6	-
		Gompertz, 3P	-19.5	-14.3	-16.0	-25.3	-39.1	-
		Gompertz, 4P	-19.6	-14.5	-15.6	-23.9	-18.8	-
Richards		-10.1	-6.7	-8.2	-19.6	-30.1	-	
Weibull		-26.8	-15.9	-15.8	-23.9	-44.5	-	
Hyperbolastic I		-15.6	-13.3	-13.7	-17.2	-17.3	-	
Hyperbolastic II		-16.2	-8.9	-14.1	-17.9	-17.6	-	
Hyperbolastic III		-12.3	-10.3	-10.9	-14.1	-13.9	-	

The cv. Nazok Shakhei was sensitive to cadmium toxicity and it did not germinate at the 800 ppm concentration. The seed germination fraction reduced from 1 to 0.2 at the 400 ppm concentration. Hyperbolastic type III was the only hyperbolic function that provided a good fit for the cadmium concentrations of 0 to 400 ppm (Fig. 2). The seed germination rate was considerably reduced at the 200 ppm cadmium concentration, while seeds could still germinate at the 800 ppm cadmium concentration. Our results show that without cadmium contaminations, the best fit for the hyperbolastic models were obtained from hyperbolastic II for cv. Halil (AICc = -18.4), hyperbolastic III for cv. Oltan (AICc = -16.5), hyperbolastic I for cv. Nazok Shakhei (AICc = -16.5) and hyperbolastic II for

cv. Yellow White (AICc = -16.2). Increase in the cadmium concentration from 200 to 400 ppm caused drastical reduction of the seed germination potential in all investigated cultivars. In cv. Hali and cv. Yellow White, the best model fit for all cadmium concentrations above 100 ppm were obtained from the three-parameter logistic function.

Hyperbolastic curves fitted for the seed germination data of cv. Oltan did not satisfactorily cover data points at high cadmium concentrations (600 to 800 ppm) (Fig. 3). For instance, AICc values of Hyperbolastic I and II were -9.3 and -10.3 at the 600 ppm cadmium concentrations, while the AICc values for Weibull and Logistic 3p at the same cadmium concentration were -27.5 and -25 respectively (Tab. 2).

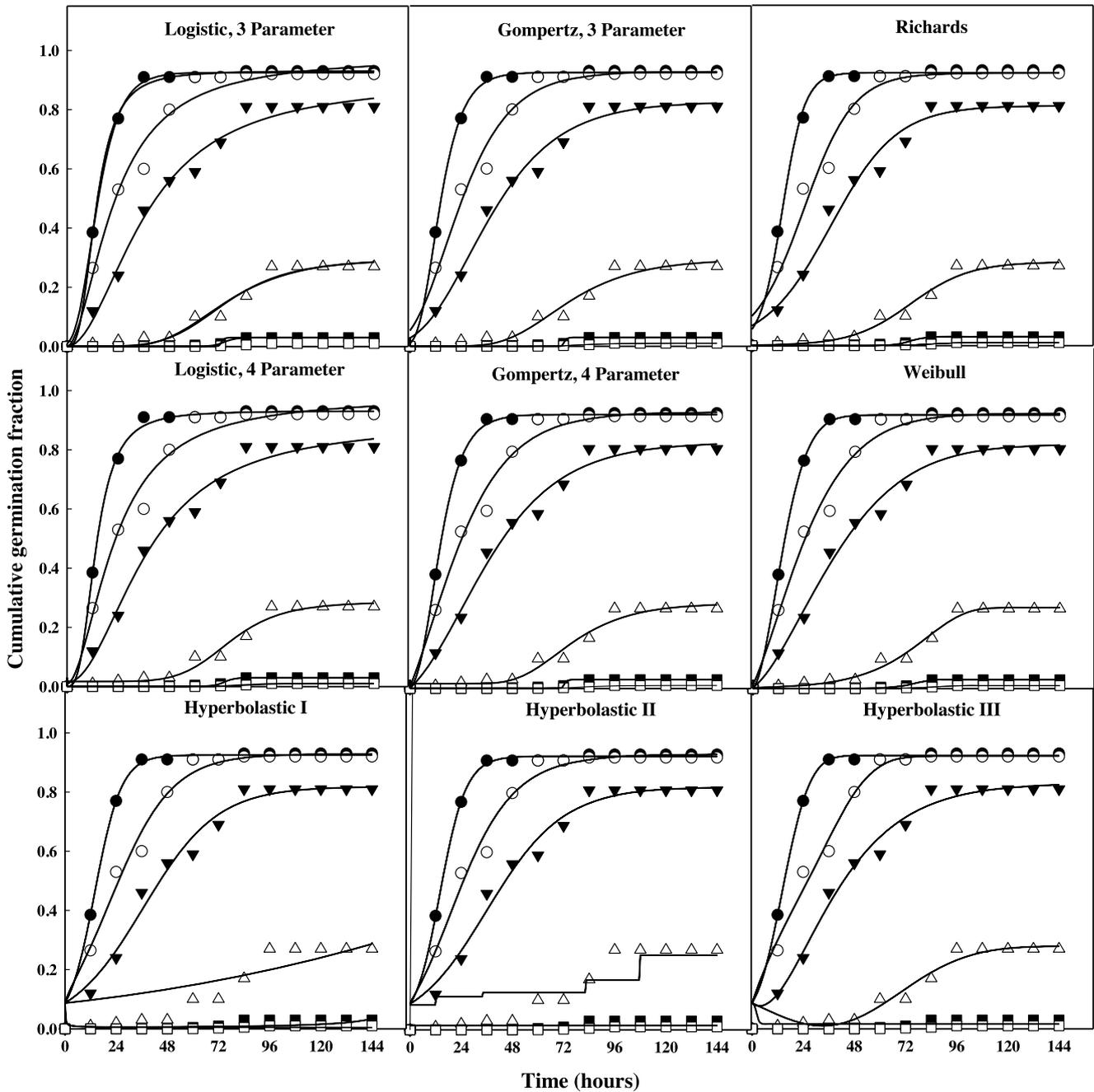


Fig. 2. Non-linear regression models for describe cumulative germination function cv. Nazok Shakhei under cadmium stress. Symbols ●: 0 ppm; ○: 100 ppm; ▼: 200 ppm; Δ: 400 ppm; ■: 600 ppm and □: 800 ppm.

Since cv. Yellow White did germinate or survive at the 800 ppm cadmium concentration, it is considered the most sensitive cultivar to cadmium toxicity among the studied sesame cultivars. There was no seed germination at the 800 ppm cadmium concentration for cv. Yellow White. The total seed germination fraction declined from 1 at no cadmium treatment to approximately 0.15 at the 600 ppm cadmium concentration (Fig. 4).

Application of mathematical and empirical models allowed us to describe the seed germination patterns of sesame cultivars without the common limitations of single-value germination indices. For instance, in the studied sigmoid models, the

outcome is either binary or dichotomous. The binary outcome in our study is either germinated (survived) or non-germinated seeds. The probability of seed germination as our outcome of interest is investigated under various levels of cadmium toxicity. Using natural logarithm (ln), the odd ratio of seed germination (probability/1-probability) was used to model the probability of seed germination at various levels of cadmium toxicity. In sigmoid models, every unit increase in the x variable (cadmium concentrations) doesn't have the same decrease in the probability of seed germination. Thus, there isn't a consistent slope or changes in probability of seed germination versus increases of cadmium concentrations,

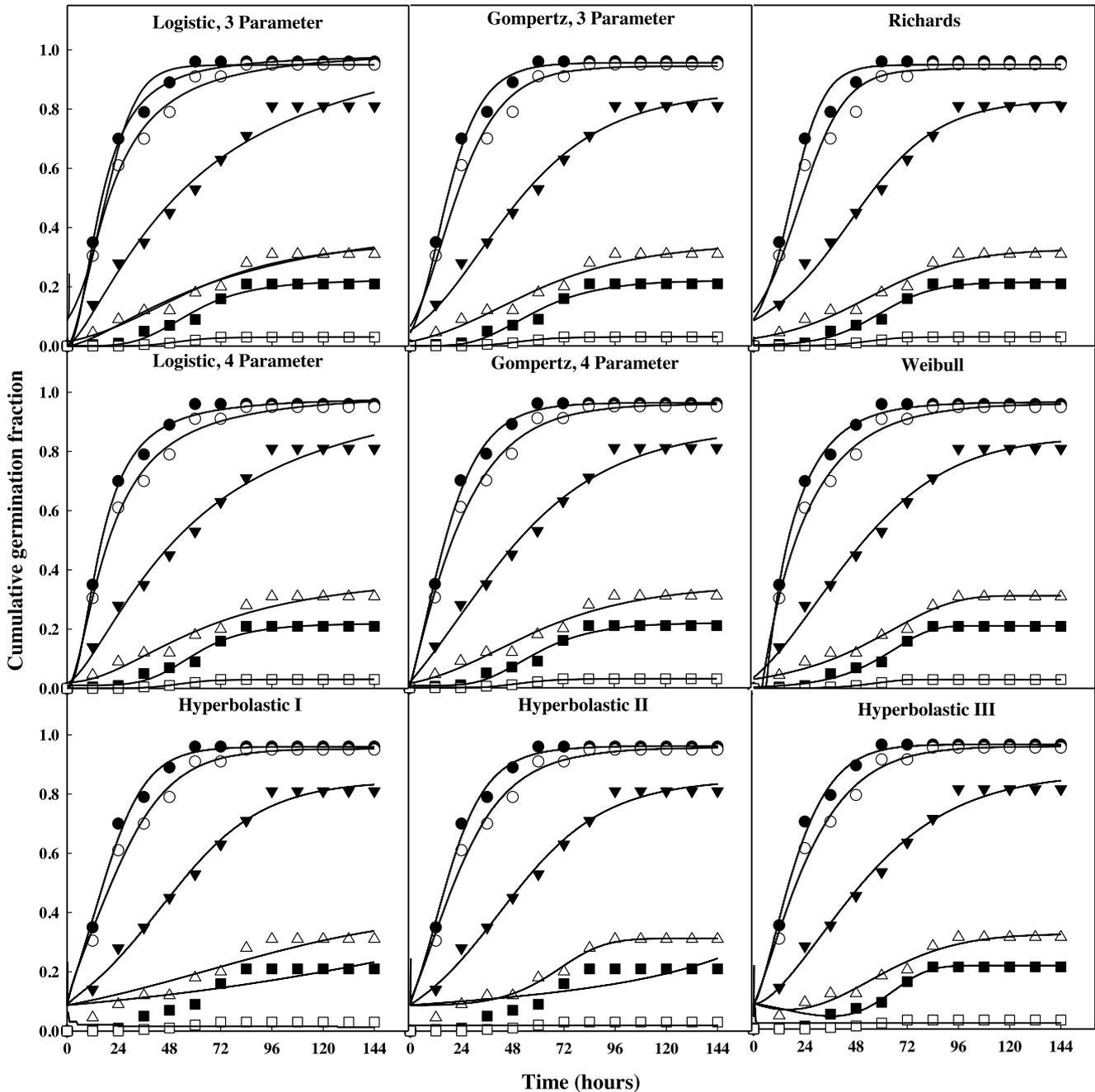


Fig. 3. Non-linear regression models for describe cumulative germination function cv. Oltan under cadmium stress. Symbols ●: 0 ppm; ○: 100 ppm; ▼: 200 ppm; △: 400 ppm; ■: 600 ppm and □: 800 ppm.

instead the slope varies at different points across the cadmium concentrations. To interpret the relationship between seed germination and cadmium concentration, logic transformation is applied in our logistic regression analysis. This allows us to fit a line with a constant slope. In fact, this slope shows how the log-odds of seed germination change with each increase in cadmium concentration. In other words, it tells us that for every 100 ppm increase in cadmium concentration, the log-odds of seed germination decreased by the value of the estimated slope. The critical point of the sigmoid models as their important parameter, also shows us that the amount of cadmium concentrations inhibits completion of seed germination by half

of its maximum potential. The maximum seed germination potential for each of the studied sesame cultivars under various levels of cadmium concentrations (carrying capacity) is also estimated as a parameter of Ymax in the applied mathematical models.

Fitted models provided a great result for describing the time course of seed germination. The predicted seed germination values, and our models' goodness of fit and residuals are presented in [Table 2](#). The best model fit among studied empirical models was varied in each genotype under no stress conditions. The lowest AICc value – which is the best goodness of fit – was found for the Weibull model of the cv. Halil seed germination

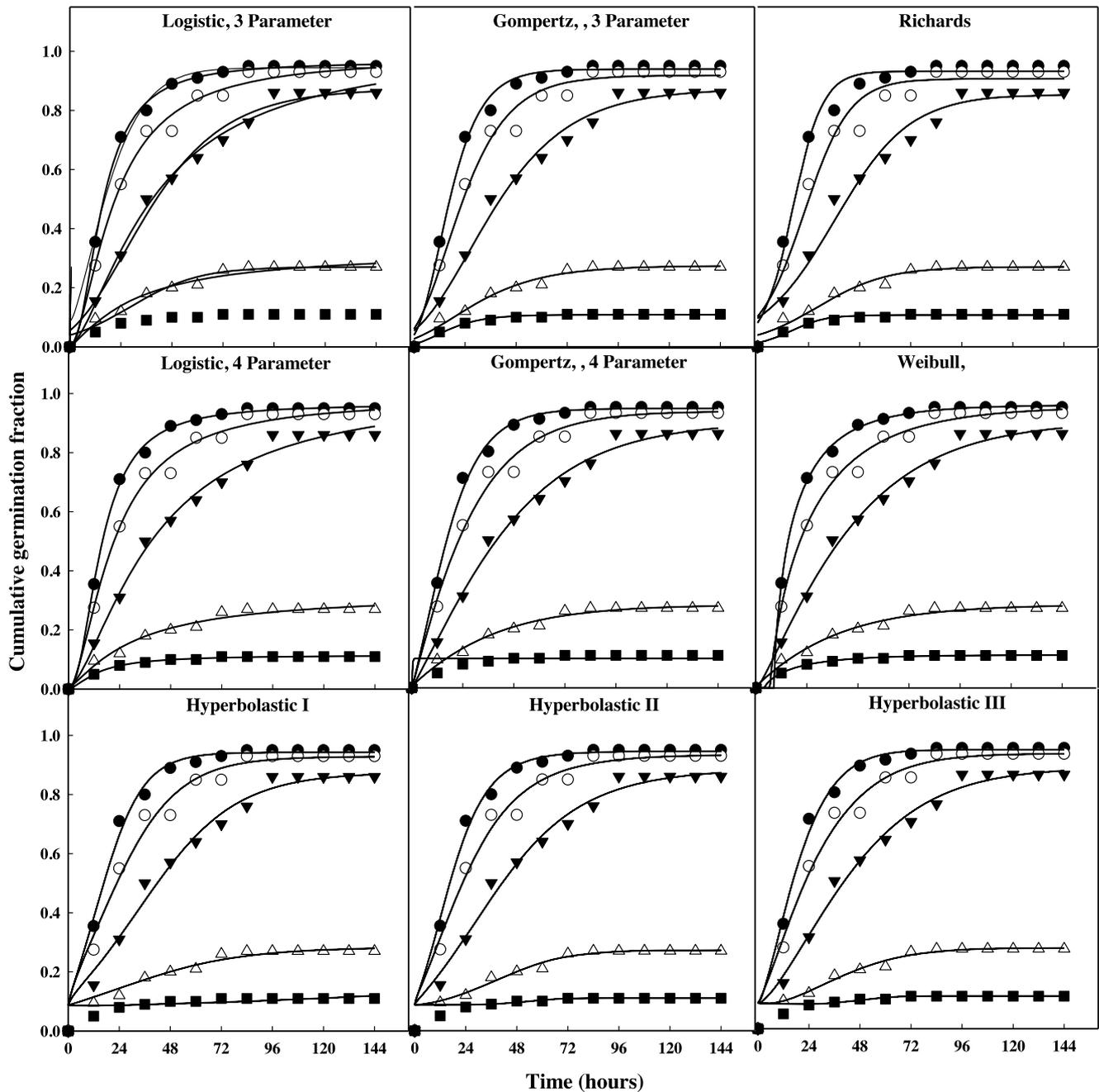


Fig. 4. Non-linear regression models for describe cumulative germination function cv. Yellow white under cadmium stress. Symbols ●: 0 ppm; ○: 100 ppm; ▼: 200 ppm; △: 400 ppm and ■: 600 ppm.

($AICc = -35.3$), However, in the case of Oltan ($AICc = -22.4$) and YellowWhite ($AICc = -28.5$), the three-parameter Logistic model performs better. The three-parameter Gompertz ($AICc = -29.4$) provide the best fit for Nazok Shakhei. Increase in cadmium concentrations, significantly influenced the best model fit for each individual genotype except for Yellow White. The three-parameter logistic model was always the best fitted model to describe germination of Yellow White (Tab. 2). At concentrations of 600 ppm cadmium, the best data fit of seed germination for Oltan and Nazok Shakhei was obtained from the Weibull model with $AICc$ of -27.5 and -51.2 respectively. Estimated parameters of all studied growth models are presented

in Table 3. It is clear that hyperbolic growth models are well suited to describe seed germination data; however, when data get close to the lower limits of germination fraction, the goodness of fit is drastically decreased for all studied cultivars. This was evident at cadmium concentrations above 400 ppm. Tabatabai *et al.* (2005) developed Hyperbolic models to resolve this issue. These models have mobile inflection points, which provide them with special properties to fit the biological data. Of all the sigmoidal models tested, the Richards has the least flexibility and in general has the poorest fit to the data. Our results suggest that hyperbolic models perform well in modeling time-course seed germination, compared with competing

Table 3. Estimated germination parameter of Oltan using Weibull and Hyperbolic models.

Cadmium (ppm)	Weibull			Hyperbolic I			Hyperbolic II			Hyperbolic III		
	k	d	L	β	θ	β	β	θ	β	θ	β	θ
0	14.6 ± 3.2	0.90 ± 0.19	15.6 ± 0.5	0.085 ± 0.02	6.4 × 10 ⁻¹ ± 0.23	0.36 ± 0.10	0.70 ± 0.09	2.0 × 10 ⁻² ± 2.0 × 10 ⁻³	-0.026 ± 2.33	1.31 ± 1.1		
100	22.1 ± 4.5	0.94 ± 0.22	18.8 ± 0.9	0.058 ± 0.01	7.7 × 10 ⁻¹ ± 0.18	0.40 ± 0.10	0.72 ± 0.08	2.5 × 10 ⁻² ± 1.7 × 10 ⁻²	-0.026 ± 0.34	1.17 ± 1.3		
200	66.9 ± 10.5	1.71 ± 0.45	43.2 ± 2.5	0.049 ± 0.01	1.5 × 10 ⁻¹ ± 0.15	0.11 ± 0.04	0.85 ± 0.11	9.2 × 10 ⁻² ± 1.1 × 10 ⁻²	-0.026 ± 0.25	1.24 ± 2.4		
400	16.8 ± 2.2	5.78 ± 0.76	54.4 ± 3.2	0.048 ± 0.04	1.3 × 10 ⁻¹ ± 0.19	0.00 ± 0.00	2.74 ± 0.97	4.0 × 10 ⁻⁴ ± 2.3 × 10 ⁻²	-0.026 ± 0.04	1.93 ± 1.3		
600	5.4 ± 5.3	3.13 ± 0.31	59.9 ± 5.6	0.008 ± 0.15	1.2 × 10 ⁻¹ ± 0.35	-0.05 ± 0.9	0.83 ± 4.80	4.8 × 10 ⁻⁹ ± 2.7 × 10 ⁻⁸	-0.026 ± 0.02	4.57 ± 3.3		
800	1.9 ± 0.8	1.66 ± 0.73	54.3 ± 0.7	-0.014 ± 0.0	1.6 × 10 ⁻¹⁶ ± 0.00	-0.09 ± 0.0	0.48 ± 0.00	-	-0.026 ± 0.00	5.04 ± 0.0		

Table 4. Estimated germination parameter of Yellow white using Weibull and Hyperbolic models.

Cadmium (ppm)	Weibull			Hyperbolic I			Hyperbolic II			Hyperbolic III		
	k	d	L	β	θ	β	β	θ	β	θ	β	θ
0	10.4 ± 1.3	0.69 ± 0.08	14.7 ± 0.3	0.093 ± 0.02	6.16 × 10 ⁻¹ ± 0.25	0.37 ± 0.10	0.70 ± 0.09	2.0 × 10 ⁻² ± 1.17 × 10 ⁻²	-0.026 ± 3.07	1.32 ± 4.6		
100	20.8 ± 3.5	0.79 ± 0.19	19.7 ± 1.0	0.057 ± 0.01	7.29 × 10 ⁻¹ ± 0.21	0.39 ± 0.11	0.73 ± 0.09	2.4 × 10 ⁻² ± 1.82 × 10 ⁻²	-0.026 ± 0.35	1.17 ± 1.4		
200	46.7 ± 6.1	1.17 ± 0.29	34.8 ± 1.9	0.049 ± 0.01	3.64 × 10 ⁻¹ ± 0.18	0.20 ± 0.07	0.72 ± 0.10	1.2 × 10 ⁻² ± 1.40 × 10 ⁻²	-0.026 ± 0.29	1.22 ± 2.2		
400	37.5 ± 4.3	1.05 ± 0.18	25.6 ± 2.3	0.025 ± 0.07	6.04 × 10 ⁻¹ ± 0.28	0.03 ± 0.06	1.39 ± 0.53	3.7 × 10 ⁻³ ± 14.6 × 10 ⁻²¹	-0.026 ± 0.22	1.54 ± 2.8		
600	15.5 ± 4.3	0.77 ± 0.19	13.7 ± 0.6	-0.028 ± 0.01	5.72 × 10 ⁻¹¹ ± 0.00	0.00 ± 0.00	3.96 ± 4.10	2.7 × 10 ⁻⁶ ± 2.0 × 10 ⁻⁴	-0.026 ± 0.20	3.30 ± 4.0		
800	-	-	-	-	-	-	-	-	-	-		

Table 5. Estimated germination parameter of Nazok Shakhei using Weibull and Hyperbolic models.

Cadmium (ppm)	Weibull		Hyperbolic I		Hyperbolic II		Hyperbolic III			
	k	d	L	β	θ	β	θ	β	θ	arcsinh(t)
0	17.6±2.1	1.80±0.22	13.9±0.2	0.175±0.01	9.0 × 10 ⁻¹² ±0.08	0.20±0.07	0.97±0.12	8.0 × 10 ⁻⁴ ±7.2 × 10 ⁻⁴	0.034±0.16	2.36±2.7
100	30.9±3.9	1.38±3.86	22.2±1.3	0.071±0.01	4.5 × 10 ⁻¹¹ ±0.22	0.25±0.09	0.75±0.10	4.6 × 10 ⁻⁶ ±2.1 × 10 ⁻⁵	0.058±0.02	2.21±1.2
200	46.9±7.4	1.55±0.35	35.4±1.8	0.071±0.01	2.8 × 10 ⁻¹¹ ±0.18	0.30±0.05	0.93±0.14	2.5 × 10 ⁻² ±6.0 × 10 ⁻³	-0.076±0.12	1.11±0.5
400	34.6±0.5	1.90±0.00	75.0±2.3	0.010±0.12	1.5 × 10 ⁻¹¹ ±0.42	0.30±0.00	0.90±0.00	8.8 × 10 ⁻² ±4.4 × 10 ⁻⁵	-0.138±0.02	2.73±1.1
600	10.7±4.5	1.67±0.32	74.5±1.0	-0.091±0.0	1.7 × 10 ⁻¹⁴ ±0.00	0.18±0.00	0.13±0.0	3.8±3.2 × 10 ⁻²	-0.232±0.00	3.47±2.8
800	8.4±1.7	1.05±0.67	83.5±2.5	-0.016±0.0	1.9 × 10 ⁻¹⁵ ±0.00	0.18±0.00	0.13±0.0	0.10±0.0	-0.326±0.00	3.46±0.0

Table 6. Estimated germination parameter of Halil using Weibull and Hyperbolic models.

Cadmium (ppm)	Weibull		Hyperbolic I		Hyperbolic II		Hyperbolic III			
	k	d	L	β	θ	β	θ	β	θ	arcsinh(t)
0	16.4±1.6	1.92±0.18	13.2±0.1	0.180±0.05	1.15 × 10 ⁻¹⁰ ±0.36	0.18±0.057	1.01±0.11	4.8 × 10 ⁻² ±3.3 × 10 ⁻²	-0.23±1.60	1.31±1.9
100	16.2±3.7	1.09±0.25	16.3±0.6	0.111±0.02	3.02 × 10 ⁻¹¹ ±0.25	0.25±0.073	0.82±0.09	4.8 × 10 ⁻² ±1.2 × 10 ⁻²	-0.12±0.30	1.15±0.6
200	31.1±8.8	1.58±0.53	25.2±1.4	0.095±0.02	2.43 × 10 ⁻¹¹ ±0.26	0.10±0.049	1.01±0.14	4.8 × 10 ⁻² ±8.6 × 10 ⁻²	-0.14±0.20	1.06±0.4
400	21.4±1.8	1.39±0.17	37.1±0.6	0.092±0.06	2.26 × 10 ⁻¹¹ ±0.38	0.10±0.00	3.03±1.30	4.8 × 10 ⁻² ±9.5 × 10 ⁻²	-0.29±0.37	1.01±0.5
600	10.6±1.3	5.65±0.68	58.9±2.8	0.002±1.31	1.14 × 10 ⁻¹¹ ±0.41	0.09±0.00	1.67±2.00	4.8 × 10 ⁻² ±2.4 × 10 ⁻²	-6.42±6.75	1.00±1.2
800	2.4±0.6	7.86±0.22	67.6±5.8	0.003±0.00	1.00 × 10 ⁻⁴ ±0.00	0.02±0.00	0.93±0.00	4.8 × 10 ⁻² ±0.00	0.00±0.00	3.65±0.0

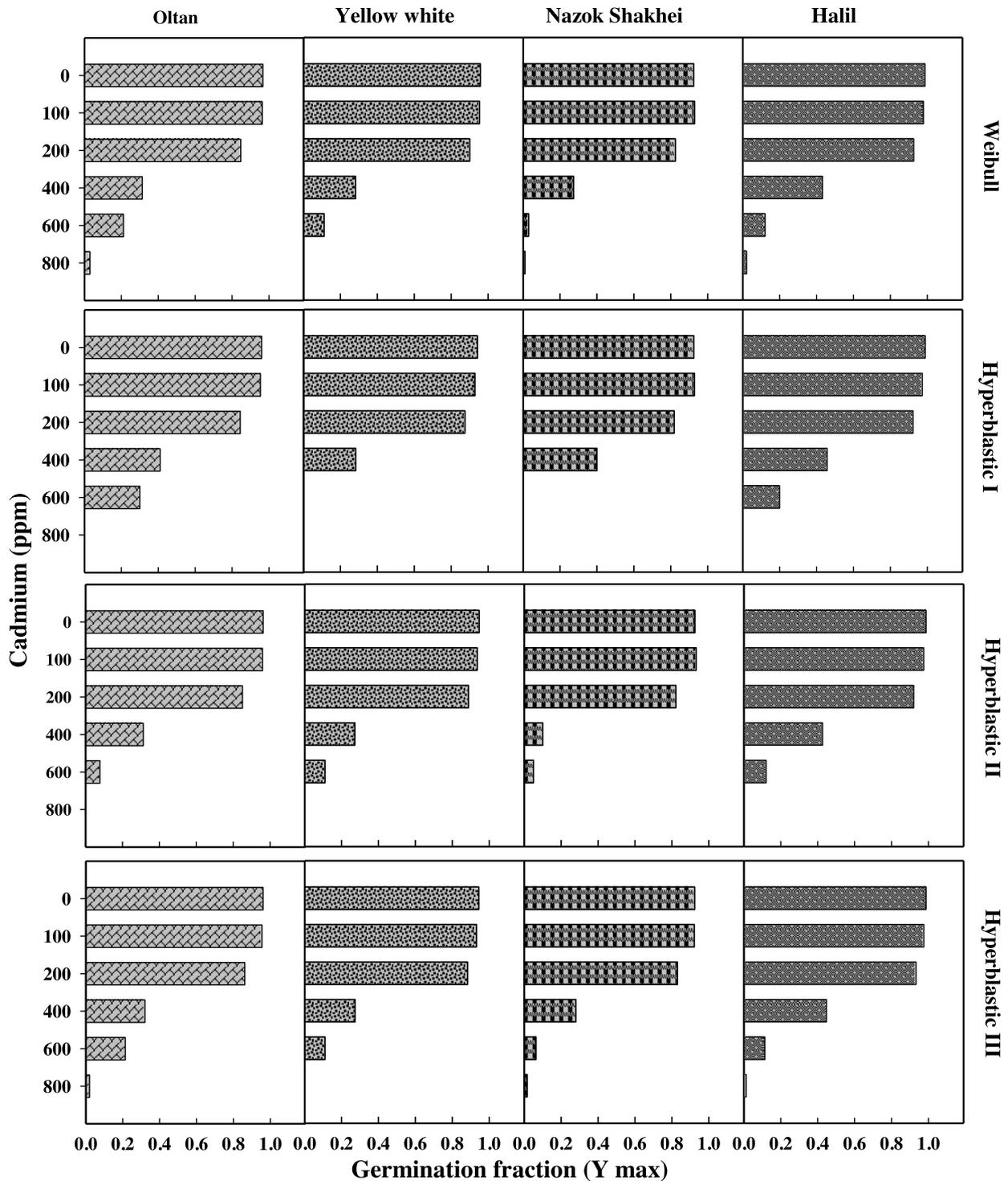


Fig. 5. Predicted germination fractions of sesame cultivars by Hyperplastics and Weibull function models under cadmium stress.

Gompertz, Richards, Weibull, and other commonly used models as shown in Table 2.

Our study results suggest that the shape flexibility of the investigated hyperbolic models I to III leads to a good fit, and thus, these models could be considered when describing seed germination data. For our dataset, we observed that the Weibull function gave a reasonable representation of the data, followed closely by the hyperbolic models type-I to type-III.

Estimated parameters for the rate of seed germination in the Weibull function (k) declined as the concentration of cadmium exceeded 400 ppm for all cultivars. In addition, due to an increase in cadmium toxicity, there was a higher lag time for germination to be completed (Tabs. 3–6). The reasons for the lower values for R^2 and high values for AICc at the 800 ppm cadmium concentrations, appear to be due to high toxicity and rapid mortality rate in seeds that can be observed within the

data. The estimated Y_{max} using hyperbolastic type III was very similar to the Weibull function. Results are in agreement with Tabatabai *et al.* (2011) regarding the similarity of hyperbolastic models to other growth models such as Logistic, Weibull and Gompertz. We suggest that the hyperbolastic growth model type-II (H2) is more flexible to fit the data than the other model types (H1 and H2), with the lowest AICc value in most of the cadmium concentrations (Tab. 2). As germination reduces when cadmium toxicity increases, the goodness of model fit also decreases. Our findings show that in many cases the best fitting model was not hyperbolastic growth models type-I (H1), type-II (H2), or type-III (H3), although they provided reasonable goodness of fit. It is also important to note that the Richards model provided less accuracy than all other models. The goodness of fit by hyperbolastic models can be attributed to their flexibility in shape. The cumulative seed germination time course of sesame genotypes was successfully fitted using nonlinear regression models including hyperbolastic growth models (Figs. 1–4). Therefore, we recommend that hyperbolastic growth models type-I (H1), type-II (H2), and type-III (H3), be considered among the available nonlinear models in seed biology. Results of model outputs predicting seed germination fraction using Weibull and hyperbolastic models are presented in (Fig. 5).

4 Conclusion

As germination reduces when cadmium toxicity increases, the goodness of model fit also decreases. Increasing cadmium concentration resulted in the germination fraction reduction from 1 to 0.4 at the 400 ppm. The recommended hyperbolastic growth model was type III or (H3) as it provided the best model with the lowest Corrected Akaike Information Criterion for *cv.* Halil (AICc = -14.6) and *cv.* Nazok Shakhei, (AICc = -14.2).

Acknowledgments. Authors wish to thank Iranian Ministry of Science, Research and technology financial supports (Grant #42/1/226405).

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Cite this article as: Parmoon G, Moosavi SA, Poshtdar A, Siadat SA. 2020. Effects of cadmium toxicity on sesame seed germination explained by various nonlinear growth models. *OCL* 27: 57.