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Mathematical Description of Seedling Emergence of Rice and *Echinochloa* species as Influenced by Soil burial depth

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ABSTRACT : A pot experiment was conducted to investigate the effects of soil burial depth on seedling emergences of rice (*Oryza sativa*) and *Echinochloa* spp. and to model such effects for mathematical prediction of seedling emergences. When the Gompertz curve was fitted at each soil depth, the parameter *C* decreased in a logistic form with increasing soil depth, while the parameter *M* increased in an exponential form and the parameter *B* appeared to be constant. The Gompertz curve was combined by incorporating the logistic model for the parameter *C*, the exponential model for the parameter *M*, and the constant for the parameter *B*. This combined model well described seedling emergence of rice and *Echinochloa* species as influenced by soil burial depth and predicted seedling emergence at a given time after sowing and a soil burial depth. Thus, the combined model can be used to simulate seedling emergence of crop sown in different soil depths and weeds present in various soil depths.

***Keywords*:** *Echinochloa*, emergence, Gompertz curve, modelling, rice (*Oryza sativa*), soil depth

The period between crop and weed emergence is a critical factor that contributes to crop yield losses (Oliver, 1979). Accurate information on dates of weed emergence relative to crop emergence is important in determining potential yield losses, but is difficult to obtain on a practical scale because daily observations are required (Kropff, 1988). Thus, models that could predict plant seedling emergence would be of benefit to agriculture. Such predictions may help to make a decision for early season tillage and herbicide application in crop cultivation. A number of models for predicting plant seedling emergence have been developed (e.g. Cussans *et al.*, 1996). The emergence model is essentially a mathematical description expressed as the time course of cumulative emergence. Cussans *et al.* (1996) used a Gompertz curve (1825) to describe the cumulative distribution of the time to emergence. In plant biology, the Gompertz curve has been used to describe the plant shoot growth (Lapp & Skoropad, 1976), and the seed germination (e.g. Brown & Mayer, 1988). Gompertz curve gives a better description of the emergence data and its parameters are easier for a biological interpretation than Weaver *et al.* (1988)'s model (Vleeshouwers, 1997). Several types of logistic models have also been used for this purpose (King & Oliver, 1994, Myers *et al.*, 2004).

In rice cropping, *Echinochloa* species have long been considered as one of the most troublesome weeds in many temperate and tropical crops (Norris, 1992), and have a wide regional adaptability ranging from north to south (Holm *et al.*, 1977). *Echinochloa* species can emerge more quickly than rice and its low-temperature adaptability is also greater than rice. *Echinochloa* species could emerge even at 11.0°C, while rice could emerge at higher than 12.3°C (Kwon *et al.*, 1996). Moreover, it can also emerge from deeper soil profile than rice. Kim (1993) reported that *Echinochloa* species could emerge from deeper soil profile than 10 cm in a pot test, and this ability was due to its mesocotyl growth. These characteristics thus render *Echinochloa* species as much more competitive than rice.

As seedling emergence is influenced by soil conditions such as soil temperature, soil water content and soil depth, many mathematical approaches have been made to model the effects of soil conditions on the plant seedling emergence. Cussans *et al.* (1996) modelled the changes in the potential maximum seedling emergence of wheat, *Alopecurus myosuroide*, and some broadleaf weeds with increasing soil depth by using an exponential model, and the lag time of seedling emergence with soil depth by using linear and quadratic models. To describe the relationship between the potential maximum seedling emergence of *Bromus tectorum* and *Sorghum halepense*, and soil depth, Prostko *et al.* (1997) used a logistic model. Although these studies mathematically described the effects of soil depth on seedling emergence, no approaches to incorporate such mathematical descriptions into basic emergence models such as the Gompertz curve and the logistic model have been made. Little information is available for the model development for seedling emergences of rice and *Echinochloa* species as influenced by soil burial depth.

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Therefore, this study was conducted to investigate and describe mathematically the effects of soil burial depth on seedling emergence of rice and *Echinochloa* species, and thus to model such effects by incorporating the mathematical description into the seedling emergence model.

MATERIALS AND METHODS

Model development

The emergence model describes mathematically the emergence pattern of seedlings, which is expressed as the time course of cumulative emergence. Although several models have been developed, the simplest and widely used (e.g. Cussans *et al.*, 1996) model is Gompertz curve;

$$Y = C/e^{e^{-B(T-M)}} \tag{1}$$

where Y is the cumulative emergence at days (T) after sowing, C is the maximum emergence, B is the rate of increase of emergence once it is initiated, M is a time lag to reach 50% of the maximum cumulative emergence.

If crop or weed seeds are sown in different soil burial depths, their emergence will be affected, resulting in changes of parameters in eqn 1 with soil depth (i). Therefore, eqn 1 can be rewritten as follows,

$$Y_i = C_i/e^{e^{-B_i(T-M_i)}} \tag{2}$$

As eqn 2 is the most complex model, it requires a large number of parameters for each soil depth. If changes in parameters of eqn 2 with soil depth can be described mathematically using empirical models, these models can be incorporated into eqn 2 to give a simpler model which can describe the time course of cumulative emergence as affected by soil depth.

Prostko *et al.* (1997) applied the Fermi-Dirac distribution function, a kind of logistic function, in order to model plant seedling emergence as affected by soil burial depth. Therefore, if plant seedling emergence decreases logistically with increasing soil depth, eqn 2 can be modified by replacing C_i with the logistic model as follows,

$$Y_i = \left(C_{max}/(1+(i/n)^d)/\left(e^{e^{-B_i(T-M_i)}}\right)\right) \tag{3}$$

where C_{max} is the theoretical maximum emergence at 0 cm soil depth, n is the soil depth to reach 50% of C_{max}, and d is the rate of decrease in seedling emergence.

It is expected that the parameter B may not change with soil depth. If so, eqn 3 can be further modified by replacing B_i with a constant B value as follows,

$$Y_i = \left(C_{max}/(1+(i/n)^d)/\left(e^{e^{-B(T-M_i)}}\right)\right) \tag{4}$$

The deeper the soil depth, the greater the time lag to reach 50% of the maximum cumulative emergence will be. The time lags for the first emergence of rice and *Echinochloa* species also increased with increasing soil depth (Kwon *et al.*, 1996a). It is expected that the increase in the time lag with soil depth may be explained by an exponential model. Therefore, the exponential model can be incorporated into eqn 4 by replacing M_i to give the final model, eqn 5, as follows,

$$Y_i = \left(C_{max}/(1+(i/n)^d)/\left(e^{e^{-B(T-ar^i)}}\right)\right) \tag{5}$$

where a is the time lag to reach 50% of the maximum cumulative emergence at 0 cm soil depth and r is the unknown parameter.

Model development using experimental data

Pot experiment

A pot experiment was conducted at the experimental field station of Seoul National University, Suwon, Korea. Rice (*Oryza sativa* L. cv. Dongjin) and four *Echinochloa* species including *E. utilis*, and *E. crus-galli* vars. *crus-galli*, *oryzicola*, and *praticola* were sown at different soil depth and seeds were covered with different amounts of sandy clay loam soil to adjust the soil depths to be 0.5, 1.5, 2.5, 3.5, 6, 8, and 10 cm on 6 May 1995. The pots were then placed in a side-opened glasshouse to ensure the temperature to follow closely outside conditions and to prevent the pots from rain. The soil water content was maintained to be 30% (w/w) by regular top irrigation. The emerged seedlings were daily recorded until 25 days after sowing. The experiment was consisted of three replicates in a completely randomised design.

Statistical analysis

All measurements were initially subjected to analysis of variance (ANOVA). Non-linear regression was used to fit the Gompertz curve and other models. There was no evidence of lack of fit of the most complex model (eqn 2), so each model in the sequence was compared with its predecessor by calculating the F-value as follows

$$F = \left(\frac{RSS_{j+1}-RSS_j}{df_{j+1}-df_1}\right)/\left(\frac{RSS_a}{df_a}\right) \tag{6}$$

where RSS and df represent the residual sum of square and the degree of freedom, respectively, j+1 represents the reduced model from its predecessor (j) and a represents ANOVA. If the *F*-value was lower than the tabulated *F*-value (5% level) with $(df_{j+1}-df_j, df_a)$ degrees of freedom, the reduced model could be accepted. All statistical analyses were conducted by using Genstat 5 (Genstat 5 Committee, 1997).

RESULTS AND DISCUSSION

Relationships between soil depth and parameters estimated for the Gompertz curve

For each soil depth, non-linear regression analyses were conducted to fit the Gompertz curve (eqn 1) to the emergence data obtained from the pot experiment. Parameters estimated for the Gompertz curve were then plotted against soil depth to explore the relationships between soil depth and the respective parameters (Fig. 1). With increasing soil depth, the parameter *C*, the maximum seedling emergence, decreased significantly, while the parameter *M* increased. Unlikely, the parameter *B* did not change significantly with soil depth (data not shown), assuming that the parameter *B* would be constant regardless of soil depth.

Following Prostko *et al.* (1997) who described decreasing weed emergence with soil burial depth by using the logistic model, the parameter *C* estimated for each soil depth were fitted to the logistic model. The logistic model well described the relationship between the parameter *C* and soil depth. As a result, the parameter C_{max}, the theoretical maximum seedling emergence at 0 cm soil depth, was 98.1, 92.3, 65.0, 51.6 and 62.8% for rice, *E. utilis*, *E. crus-galli* var. *crus-galli*, *oryzicola*, and *praticola*, respectively (Table 1). The parameter *n*, the soil depth to reach 50% of C_{max}, was 4.08, 6.99, 7.1, 6.06, 3.51 cm, and the parameter *d*, the rate of decrease in seedling emergence with soil depth, was 4.9, 11.12, 1.63, 1.4, 1.59 for rice, *E. utilis*, *E. crus-galli* var.

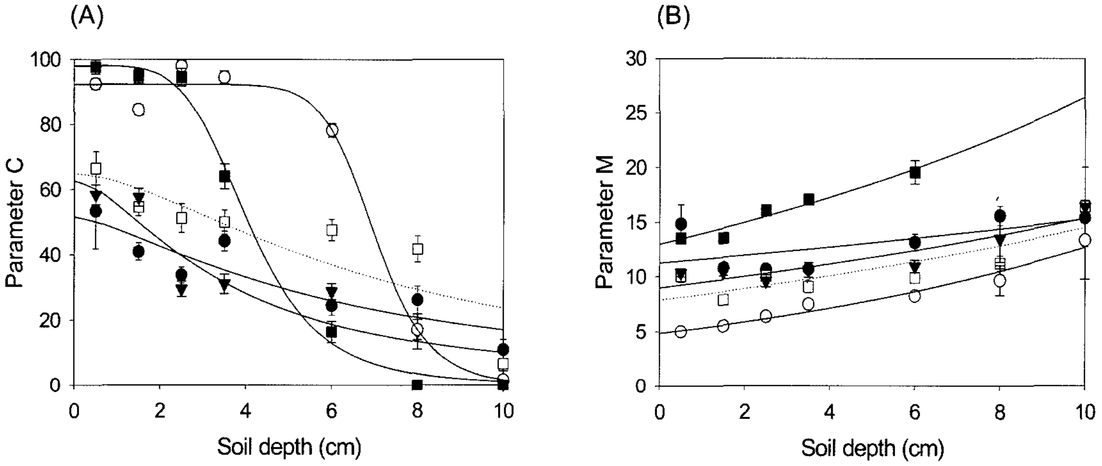

Fig. 1. The relationships between soil burial depth and parameters *C* (A) and *M* (B) of the Gompertz curve. The parameters were estimated using eqn 2 for rice (*O. sativa* cv. Dongjin; ■) and *Echinochloa utilis* (○), *E. crus-galli* vars. *crus-galli* (□), *oryzicola* (●), and *praticola* (▼). The continuous lines are fitted values by using the logistic and the exponential model for the parameters C and M, respectively, and parameter estimates in Table 1.

Table 1. Parameter estimates of the logistic and the exponential model for the parameters *C* and *M* of the Gompertz curve, respectively. The numbers in parentheses are standard errors.

Parameter estimates	Rice (*O. sativa*)	*Echinochloa utilis*	*Echinochloa crus-galli var.*		
			crus-galli	*oryzicola*	*praticola*
For parameter *C*					
C_{max}	98.1 (2.7)	92.3 (2.5)	65.0 (5.2)	51.6 (9.8)	62.8 (13.5)
n	4.08 (0.15)	6.99 (0.18)	7.10 (1.59)	6.06 (2.28)	3.51 (2.84)
d	4.90 (0.61)	11.12 (1.93)	1.63 (0.74)	1.40 (0.80)	1.59 (0.76)
R^2	0.995	0.990	0.858	0.819	0.711
For parameter *M*					
a	13.01 (0.51)	4.86 (0.29)	7.90 (0.93)	11.25 (1.20)	8.99 (0.60)
r	1.073 (0.011)	1.101 (0.009)	1.063 (0.002)	1.031 (0.018)	1.055 (0.011)
R^2	0.941	0.965	0.689	0.372	0.842

crus-galli, *oryzicola*, and *praticola*, respectively. The greater the parameter *n*, the deeper the soil depth to reach 50% of C_{max} is, and the smaller the parameter *d*, the more gentle the slope of decrease in seedling emergence with increasing soil depth. Therefore, our estimations indicate that rice with a smaller *n* and a larger *d* has a shallower soil depth limit for its seedling emergence as compared with *Echinochloa* species. Conversely, *E. crus-galli* vars. *crus-galli* and *oryzicola* with greater *n* and smaller *d* parameters have deeper soil depth limits. Using the parameter estimates, C_{max}, *n* and *d*, the parameter *C* was simulated for every species (Fig. 1A), confirming that the logistic model is suitable to describe the relationship between seedling emergence and soil depth.

The parameter *M*, the lag time to reach 50% of *C*, increased exponentially with soil depth (Fig. 1B), so the exponential model was fitted to the parameter *M* with soil depth and its parameters *a* and *r* were estimated (Table 1). The parameter *a* indicates the parameter *M* at 0 cm soil depth, so the greater the parameter *a*, the longer the time to reach 50% of *C* at 0 cm soil depth is required. Rice had the greatest parameter *a*, 13.01, followed by *E. crus-galli* var. *oryzicola*, *praticola*, *crus-galli*, and *E. utilis*, indicating that rice required the longest time for its seedling emergence but *E. utilis* required the shortest time. The parameter *r* indicates the base for the exponential function of the parameter *M* with soil depth, so the greater the parameter *r*, the greater the exponential rate. *Echinochloa utilis* had the greatest parameter *r*, 1.101, followed by rice, *E. crus-galli* var. *crus-galli*, *praticola* and *oryzicola*, indicating that the increase rate of the time lag for *E. utilis* with soil depth is greatest, while that for *E. crus-galli* var. *oryzicola* is smallest. The relationship between the parameter *M* and soil depth may also be described by other models. For this description, Cussans *et al.* (1996) used a linear model for *Galium aparine* but also a quadratic model for wheat, *A. myosuroides*, and *Stellaria mdedia*.

In overall, our findings clearly demonstrate that rice has the shallowest soil depth limit and the longest time required for its seedling emergence and *E. utilis* emerges most quickly with relatively deep soil depth limit. All the *Echinochloa* species have deeper soil depth limit and faster emergence than rice, clearly demonstrating their weediness in terms of their seedling emergence.

Modelling seedling emergence as affected by soil burial depth

Investigation of each parameter versus soil depth revealed that logistic and exponential models could describe the changes in parameters *C* and *M*, respectively, with increasing soil depth, while the constant describes the parameter *B*, indicating that these models can be incorporated into eqn 2. By replacing C_i with the logistic model, eqn 2 was simplified to eqn 3, which was then further reduced to eqn 4 by replacing B_i with the constant *B*. Finally eqn 4 was then reduced to eqn 5 by replacing M_i with the exponential model.

Lack of fit tests showed that eqn 2 satisfactorily described the time course of cumulative emergence at different soil depths irrespective of plant species (Table 2). When eqn 3 was fitted to seedling emergence data, there was no evidence that eqn 3 fitted less well than eqn 2 for rice and *E. crus-galli* var. *crus-galli*, but for the other species there was evidence that eqn 3 fitted less well than eqn 2. When eqn 4 was fitted, there was no evidence that eqn 4 fitted less well than eqn 3 for all the species except *E. crus-galli* var. *praticola*. Finally when eqn 5 was fitted, there was evidence that eqn 5 fitted less well than eqn 4 for all the species. However, direct comparison of eqn 5 with eqn 2 showed no evidence that eqn 5 fitted less well than eqn 2. These findings thus indicate that the relationships between the parameter *C* and soil depth, and the parameter *M* and soil depth were well described by the logistic model and the exponential model, respectively, with a constant parameter *B*.

Prediction of seeding emergence as affected by soil burial depth

By fitting the final model (eqn 5) to seedling emergence

Table 2. Summary of *F*-values for lack of fit tests and model comparisons by *F*-tests.

Model comparison	Rice (*O. sativa*)	*Echinochloa utilis*	*Echinochloa crus-galli* var.		
			crus-galli	*oryzicola*	*praticola*
Lack of fit (1)	0.559^{NS}	0.154^{NS}	0.114^{NS}	0.197^{NS}	0.122^{NS}
Eqn 3 vs. eqn 2	-2.272^{NS}	5.826***	2.022^{NS}	2.679*	3.550***
Eqn 4 vs. eqn 3	0.252^{NS}	2.274***	1.526^{NS}	1.452^{NS}	5.023***
Eqn 5 vs. eqn 4	15.839 ***	6.484***	2.862*	8.098***	7.186***
Eqn 5 vs. eqn 2	0.656^{NS}	0.753^{NS}	0.745^{NS}	0.761^{NS}	0.742^{NS}

*, **, and *** indicate significance at p=0.05, 0.01 and 0.001, respectively, and NS indicates no-significance at p=0.05.

Table 3. Summary of parameter estimates for the final model, eqn 5. The numbers in parentheses are standard errors.

Plant species	Parameter estimates						R^2
	C_{max}	n	d	B	a	r	
Rice (*Oryza sativa* cv. Dongjinbyeo)	98.97 (2.00)	3.95 (0.12)	4.73 (0.55)	0.697 (0.064)	12.73 (0.15)	1.081 (0.006)	0.938
Echinochloa utilis	92.15 (0.95)	6.97 (0.08)	11.44 (0.82)	1.053 (0.083)	4.93 (0.09)	1.101 (0.005)	0.944
Echinochloa crus-galli							
var. *crus-galli*	53.93 (1.71)	8.69 (0.17)	16.01 (3.06)	0.303 (0.032)	8.35 (0.33)	1.039 (0.009)	0.800
var. *oryzicola*	40.96 (1.98)	8.00 (0.43)	4.00 (0.86)	0.291 (0.039)	10.80 (0.45)	1.029 (0.011)	0.746
var. *praticola*	60.36 (3.03)	3.81 (0.32)	1.72 (0.18)	0.356 (0.044)	10.04 (0.33)	1.018 (0.012)	0.797

data, all parameters for eqn 5 were estimated (Table 3). The parameter C_{max} was 98.97, 92.15, 53.93, 40.96 and 60.36 for rice, *E. utilis*, *E. crus-galli* vars. *crus-galli*, *oryzicola* and *praticola*, respectively. The parameter n, the soil depth to reach 50% of C_{max}, was 3.95, 6.97, 8.69, 8.0, 3.81, and the parameter a, the lag time to reach 50% of C_{max} at 0 cm soil depth, 12.73, 4.93, 8.35, 10.8, 10.04 for rice, *E. utilis*, *E. crus-galli* vars. *crus-galli*, *oryzicola* and *praticola*, respectively. Although the C_{max} was greatest in rice, parameters n and d indicated that the seedling emergence of rice decreases more rapidly with soil depth than *Echinochloa* species, implying that *Echinochloa* species can emerge from deeper soils than rice. Greater parameter B of rice and *E. utilis* than *E. crus-galli* indicates that rice and *E. utilis* can emerge more quickly after their first emergence than *E. crus-galli*. We often observed delayed emergence of weeds in field conditions. Although the first emergence of *E. crus-galli* is faster than rice, the spread of emergence in time is wider in *E. crus-galli*. Greater parameters a and r of rice than *E. crus-galli* also indicate that the lag time of rice to reach a certain emergence is longer than *E. crus-galli* at every soil depth.

Using the final model (eqn 5) and estimated parameters (Table 3), seedling emergences of rice and *Echinochloa* species were predicted in Figs 2 and 3, respectively. The prediction showed that rice started emerging most slowly and its seedling emergence decreased more rapidly with increasing soil depth than *Echinochloa* species (Fig. 2). Among *Echinochloa* species, *E. utilis* started emerging most quickly with the greatest seedling emergence (Fig. 3).

Implication of the combined model

Efforts have been made to investigate and model the effects of soil burial depth on seedling emergence (e.g. Cussans *et al.*, 1996). Prostko *et al.* (1997) described the relationship between seedling emergence and soil burial depth by using the logistic model. However, no model has ever been developed to describe the seedling emergence as a function of both time and soil burial depth simultaneously. Models that predict seedling emergence could help estimate stages of growth and weed interference intensities, which could lead to more effective timing of tillage or herbicide application in crop cultivation (Forcella, 1993). The combined model (eqn 5) developed in our study by combining the Gompertz curve with the logistic and exponential models enabled to predict seedling emergences of rice and *Echinochloa* species for a wide range of soil burial depths in dry direct-seeded rice cultivation. The model can predict the first seedling emergence at a given soil depth and seedling emergences at a given time and a specific soil depth. For example, if seeds are buried at 1 cm soil depth, the first seed-

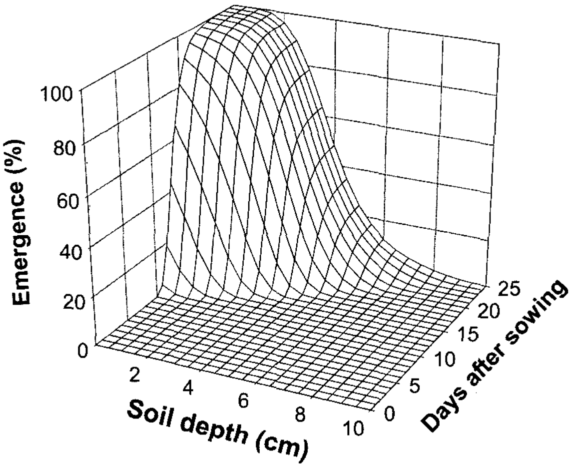

Fig. 2. Simulated seedling emergences of rice (*O. sativa* cv. Dongjin) as influenced by soil burial depth, by using eqn 5 and parameter estimates given in Table 3.

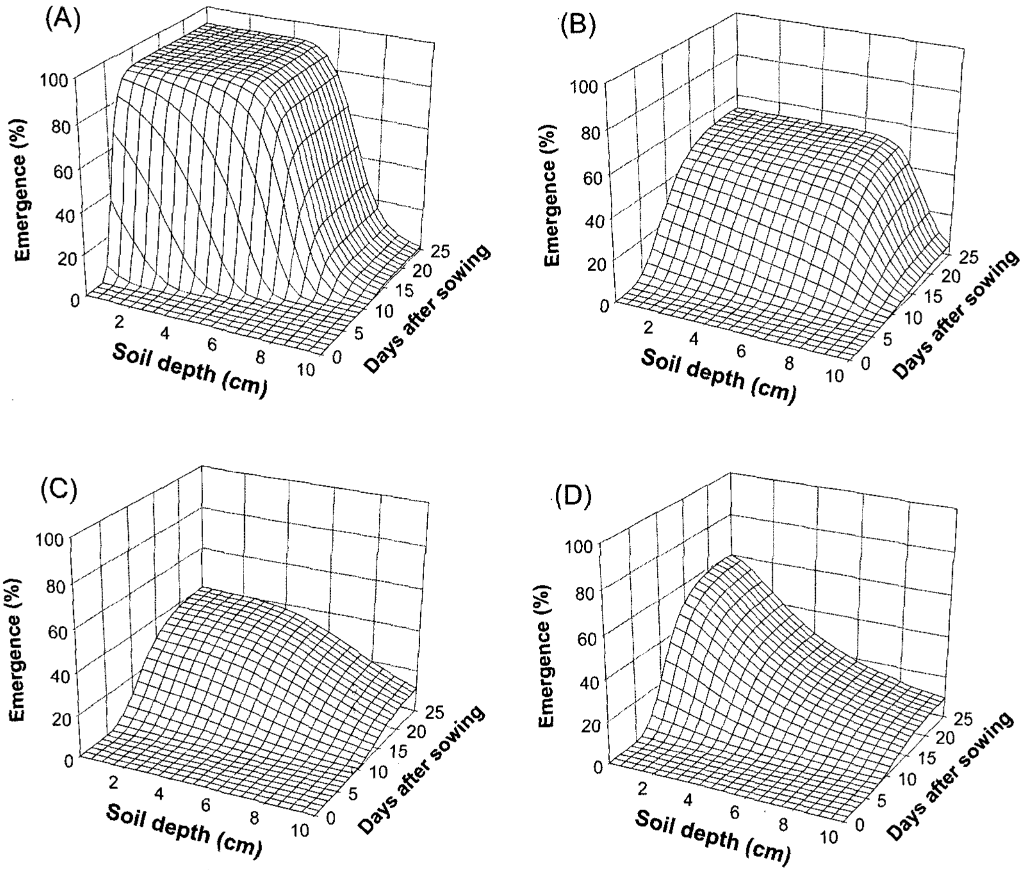

Fig. 3. Simulated seedling emergences of *Echinochloa utilis* (A), *E. crus-galli* vars. *crus-galli* (B), *oryzicola* (C), and *praticola* (D) as influenced by soil burial depth, using eqn 5 and parameter estimates given in Table 3.

ling emergence was predicted to be 4 days after sowing (DAS) for *E. utilis* and *E. crus-galli* var. *crus-galli*, and 6 and 7 DAS for *E. crus-galli* vars. *praticola* and *oryzicola*, respectively, while 12 DAS for rice. The model predicted that at 12 DAS, 92, 37, 19 and 32% of *E. utilis*, *E. crus-galli* vars. *crus-galli*, *oryzicola* and *praticola* buried at 1 cm soil depth would be established when rice starts emerging. These differences of about 5 to 8 days in the first seedling emergence between rice and *Echinochloa* species may give more competitive position to *Echinochloa* species against rice. As the basis of many plant models has been the relationship between temperature and plant growth rate and development, the concept of thermal time or growing degree day has been used in many plant seedling emergence models (Prostko *et al.*, 1998; Ekeleme *et al.*, 2004; Myers *et al.*, 2004). Soil temperature can serve as a good predictor for plant seedling emergence (Forcella *et al.*, 2000). Therefore, instead of time, soil degree days can be used in eqn 5 as an independent variable. This may provide more practical information on seeding emergence of rice and *Echinochloa* species in various geographical regions and seasons. Nonetheless, the model developed in this study can be used to describe seedling emergence of rice and *Echinochloa* species as influenced by soil burial depth. Our approach in model development can also be applied to incorporate other effects such as soil temperature and strength on seedling emergence. As this model was developed using the data generated from pot studies, further works are required for validation and parameter adjustment for practical application in various rice fields.

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