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# Seed germination and emergence of *Eragrostis tenuifolia* (A. Rich.) Hochst. ex Steud. in response to environmental factors

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**Abstract:** *Eragrostis tenuifolia* is a weed species that is gaining ground in Brazil. This weed occurs in pastures, grasslands, crop fields, and roadsides. The objective of this study was to examine the effects of different environmental factors on *E. tenuifolia* seed germination and seedling emergence. The optimum constant temperature for germination was around 35–30°C. It was also found that 85% of seeds germinated under a 30/20°C alternate temperature regime. Light appears to have a positive effect on seed germination. No seedlings emerged when seeds were buried 3 cm or deeper. The results suggested that *E. tenuifolia* has the potential to spread into pastures and in no-tillage crop systems in Brazil. Measures such as the use of cover crops and/or soil cultivation can be used to limit germination and seedling emergence, respectively.

Key words: burial depth, Eragrostis tenuifolia, irradiance, temperature, weed biology, weed ecology, weed establishment

#### Introduction

Elastic grass [*Eragrostis tenuifolia* (A. Rich.) Hochst. ex Steud.] belongs to the Poaceae family and the Chloridoideae subfamily. It is one of around 400 described species of the *Eragrostis* genus (Clayton *et al.* 2006). Up to 35 taxa from this total can be found in different Brazilian regions, usually presenting preference for open locations with direct sunlight and well-drained soils (Boechat and Longhi-Wagner 2000). The seed germination of the *Eragrostis* species in dry habitats is eased due to a slime layer of cells on the surface of the seed that allows for rapid water uptake (Kreitschitz *et al.* 2009).

*Eragrostis tenuifolia* was introduced to Brazil and other countries, from its origins in Indochina, Southern Asia, Madagascar, and tropical Africa (Jung *et al.* 2008). This species has increased its frequency in Brazil in recent years, and is now registered in several states (Guglieri-Caporal *et al.* 2011).

Eragrostis tenuifolia is a perennial and caespitose plant, attaining a height of up to 70 cm. The narrow leaves were a characteristic used to give the species its name (from the Latin tenuis: thin and delicate, and folia: leaf). The leaves have a width of from 1 to 3 mm. The plant has a panicle type complex inflorescence, similar to the vast majority of species of the same genus. The seeds are fruits of the caryopsis type, oblong and compressed laterally, with

the embryo arranged laterally. The seeds are about 1 mm long (Clayton *et al.* 2006).

The species has the C4 type photosynthetic mechanism (Watson *et al.* 1985) and the chromosomal number 2n = 40 (Tateoka 1965). *Eragrostis tenuifolia* morphology resembles that of African lovegrass (*Eragrostis plana* Ness) (Guglieri-Caporal *et al.* 2011), Indian lovegrass [*Eragrostis pilosa* (L.) P. Beauv.], weeping lovegrass [*Eragrostis curvula* (Schrad.) Nees], and *Eragrostis pilosiuscula* Ohwi (Jung *et al.* 2008). It is considered ruderal because of the environmental characteristics where its populations usually occur (Guglieri-Caporal *et al.* 2011).

*Eragrostis tenuifolia* is an autogamous species in the East Africa region, which when combined with other grasses, form areas of natural grassland that are used by farmers for animal feeding. In these places, it is considered one of the dominant plant species, maintaining up to 20% ground cover in medium to high grazing pressures (Taddese *et al.* 2002). Moreover, it has a high resistance to trampling (Sun and Liddle 1993).

According to the United States Department of Agriculture (USDA), *E. tenuifolia* has economic importance as a forage and as a weed (USDA 2015). Due to its characteristics, the species infest agroecosystems, margins of roads and railways, as well as urban areas, similar to other species of the same genus (Guglieri-Caporal



et al. 2011). It is believed that this is a difficult species to be controlled with the use of selective herbicides on pastures composed mainly of grasses. It may also be the host of the maize streak virus (MSV), which infects corn and other cultivated Poaceae. The virus is transmitted by a leafhopper (Hemiptera: Cicadellidae) (Njuguna et al. 1997).

Germination is one of the most critical stages for weeds during the processes of invasion and establishment. The invasiveness rate of a seed-propagated plant is believed to be closely related to its seed's respective germinative power (Knapp 1996). Therefore, a successful establishment depends on the ability of a seed-propagated plant to germinate under a wide range of soil and climatic conditions. In general, the critical factors in the germination process are: temperature, light, pH, soil moisture, depth in the soil, soil texture, seed weight, and concentration of plant hormones (Koger *et al.* 2004; Chauhan *et al.* 2006; Miransari and Smith 2014; Sladonja *et al.* 2014).

The presence of weed species from the *Eragrostis* gender has become increasingly common in pastures, natural grasslands, crop fields, and roadsides in Brazil. Because of its similarity to other *Eragrostis*, it is suspected that *E. tenuifolia* tends to show control issues, similar to *E. plana* (Goulart *et al.* 2009).

To date, there is a lack of information available about the species' biology, including the germination and emergence processes. One of the few studies that included this species in a number of germination tests, failed to produce consistent results (Teketay 1998). The understanding of the species' biology is essential information, both to estimate the potential for expansion of the invaded area and to establish management and control strategies (Bhowmik 1997; Bryson and Carter 2004). The objective of this study was to determine the effects of temperature, radiation, and burial depth on *E. tenuifolia* seed germination and seedling emergence.

## **Materials and Methods**

# Seed collection and preparation

Eragrostis tenuifolia seeds were collected from 100 individuals in April 2013 in an infested annual cropland situated in Mariópolis, Paraná, Brazil (26.33014° S 52.666734° W). After collection, seeds were bulked, sun-dried, cleaned, packed in white paper envelopes, and stored in a refrigerator at a temperature of 10±2°C until they were used 12 months later in the experiments. No treatment for overcoming seed dormancy was performed before use. The seed moisture content was 10%, obtained by the oven method at 105°C for 24 h (Brasil 2009). Two plants were also sampled for the production of a voucher specimen that was deposited in the herbarium of the Universidade Tecnológica Federal do Paraná. Laboratory experiments were conducted in BOD incubators at the facilities of the Universidade Federal da Fronteira Sul. The experiments were initiated in April 2014.

#### Effect of continuous temperatures on seed germination

Eragrostis tenuifolia germination was evaluated at different continuous temperatures by placing 50 seeds evenly in a Gerbox (11 × 11 cm). The boxes were prepared with two layers of blotting paper which were moistened with a distilled water ratio of 1 : 2 (w/w). The Gerboxes were then incubated in BOD-type chambers at continuous temperatures ranging from 15 to 40°C under 12 h light/dark cycles. Moisture was kept constant by a daily supplementation of the evaporated water loss. There were daily evaluations from the time of the first root protrusion for registering the number of normal seedlings until the time of stabilization, which occurred on the 15th day after the beginning of the experiment. The speed of the germination index was calculated according to the Maguire's equation to estimate seedling vigor (Maguire 1962) (equation 1):

$$SGI = (N_1/T_1) + (N_2/T_2) + ... + (N_n/T_n)$$
 [1]

where: SGI – the speed of germination index, N – the number of germinated seeds in the interval of the first, second, and last count, and T – the time in days, of the first, second, and last count.

A regression test was performed using germination as a function of time to determine the best curve to represent the observed data. The maximum germination point on the regression curve and the temperature that resulted in the highest germination speed index, were considered for the determination of the temperatures that would be tested in the alternating-temperatures experiment.

#### Effect of alternating temperatures on seed germination

The effect of alternating temperatures on *E. tenuifolia* seed germination was evaluated using the same materials and methods described for the previous experiment. The difference was that germination was determined by incubating seeds under alternating day/night temperatures (30/20°C) in light/dark (12 h/12 h) conditions. The cumulative germination data were adjusted to fit the Weibull growth model (Weibull 1951) (equation 2):

$$Y = Y_M - (Y_M - Y_0) \exp \{-1 [(kX) ^g]\}$$
 [2]

where: Y – the germination,  $Y_M$  – the maximum germination value,  $Y_0$  – the minimum germination value, k – the value of 1/X at the average of  $Y_0$  and  $Y_M$ , X – the time in days, and g – the initial value to be fit.

# Effect of light on seed germination

The photoblasticity of the *E. tenuifolia* seeds was evaluated with the same materials and methods described in the previous experiments. Alternating temperatures (30/20°C) were used since it provided the highest germination percentages in the previously conducted experiments. The seeds were stored in a refrigerator at 10±2°C in a lightproof container for 90 days before being used. Later, they were placed in Gerboxes in a room with green lighting to prevent phytochrome activation, then they



were incubated under alternating day/night temperatures (30/20°C) in light/dark (12 h/12 h) conditions. For germination in the continuous dark, the Gerboxes were wrapped in two layers of aluminum foil to simulate complete dark. Normal seedlings, abnormal seedlings, quiescent seeds, and dead seeds were counted on the seventh day after sowing.

#### Effect of seed burial depth on seedling emergence

This bioassay was performed to determine the emergence behavior of seedlings at different depths. Fifty seeds of E. tenuifolia were sown in pots (311 ml) filled with substrate. The substrate was made from a mixture of two parts soil (Eutroferric Red Latosol) and one part sand. The soil was autoclaved for 24 h, dried, crushed, and then passed through a 2-mm sieve before being used. Sowing depths used in the study were 0 (sown on the surface), 1, 2, 3, and 4 cm. Pots were watered to field capacity and kept moist with daily replenishment of the water lost by evaporation. The pots were then incubated in BODtype chambers under alternating day/night temperatures (30/20°C) in light/dark (12 h/12 h) conditions. Seedlings were considered emerged when there was a visible cotyledon on the soil surface. The emerged seedlings visible above the soil surface were counted up to 28 days after sowing. The speed of the germination index was adapted to calculate the speed of the emergence index, trading the number of germinated seeds by the number of emerged seedlings. The cumulative emergence data for 0, 1, and 2 cm depths were adjusted to fit the non-linear models.

#### Statistical analyses

All experiments were conducted in a completely randomised design with four replications. After ANOVA, the means were separated using Fisher's LSD test (p < 0.01). Otherwise, regression analysis was used where appropriate.

## **Results and Discussion**

#### Effect of continuous temperatures on seed germination

The germination of *E. tenuifolia* seeds was significantly different under the evaluated constant temperatures (Table 1). For instance, the lowest percentage of germination was observed at 15°C, which differed significantly

from all other temperatures. On the other hand, the highest percentage of germination was observed at 35°C, which did not differ from 30°C. The highest number of quiescent seeds was observed at the temperatures of 15 to 20°C. In contrast, it was between 30 and 35°C that *E. tenuifolia* showed a lower percentage of non-germinated seeds (Fig. 1).

The highest speed of the germination index was recorded at temperatures of 30 and 35°C, reaching 20.2 and 15.8 respectively. However, the lowest rate was recorded at 15°C, reaching 0.3. A higher percentage of quiescent seeds was also observed at these lower temperatures. The germination speed index and the percentage of quiescent seeds showed an inversely proportional significant correlation (-0.86) using the Pearson correlation test (p < 0.01) (data not shown). There were no significant differences between the continuous temperatures evaluated for the mortality and abnormal seedling variables, on the 15th day after sowing.

A regression analysis was performed using the germination percentage as a function of the different temperatures in order to determine the model that better represents this relationship. The quadratic model was the one that adjusted best to the observed data (Fig. 2).

After defining the equation model using a regression analysis, the values for maximum germination were calculated ( $X = -b_1/2b_2$ ;  $Y = -133.8 + 12.00X - 0.1864X^2$ ). The model can predict the maximum germination (59.33%) at a constant temperature of 32.19°C while the highest speed of the germination index was obtained at 30°C. That being so, the latter was chosen as the diurnal temperature, in the experiment testing the effect of alternating temperatures on seed germination.

## Effect of alternating temperatures on seed germination

The 30/20°C cycles allowed for higher germination than did those observed in the continuous temperature bioassay. Furthermore, the 30/20°C cycles also previously allowed for the highest germination percentages for feather lovegrass (*E. tenella*) (Chauhan 2013).

In addition, a regression analysis was performed to adjust the cumulative percentage of germination versus time, using the cumulative distribution of Weibull model (Weibull 1951). This is a widely used model in the representation of accumulated germination over time (Bridges *et al.* 1989) (Fig. 3).

**Table 1.** Influence of temperatures on germination percentage, quiescent seeds, mortality, abnormal seedling, and the speed of germination index (SGI) of *Eragrostis tenuifolia* seeds on the 15th day after sowing (DAS)

Temperature	Germination <sup>a</sup>	Quiescenta	Mortality	Abnormal seedling	SGIª
[°C]	[%]				SGI"
15	7.0±1.3 d	83.5±3.4 a	6.5±2.1	3.0±1.9	0.3±0.1 d
20	28.0±6.5 c	69.0±6.6 a	2.5±1.5	0.5±0.5	3.4±0.7 cd
25	48.0±5.3 b	49.5±5.6 b	2.5±1.3	$0.0\pm0.0$	11.2±1.8 b
30	56.0±4.3 ab	41.5±4.1 bc	2.5±1.0	$0.0\pm0.0$	20.2±1.9 a
35	67.0±3.7 a	30.0±2.9 c	2.5±1.0	0.5±0.5	15.8±0.8 ab
40	43.0±4.4 bc	50.0±3.3 b	5.5±1.0	1.5±1.0	6.3±0.6 c

 $<sup>^{</sup>a}$ values (the mean $\pm$ SE) followed by different letters are significantly different according Fisher's LSD test (p < 0.01)

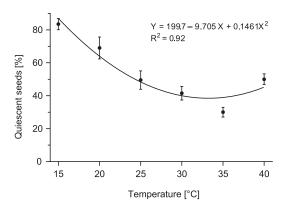


Fig. 1. Quiescent percentage of *Eragrostis tenuifolia* seeds in response to different constant temperatures on the 15th day after sowing. Data points are the overall treatment means with the standard errors reflecting variability among replications. The curve represents a second order polynomial model, where Y represents quiescent seeds (%) at a temperature (°C) X

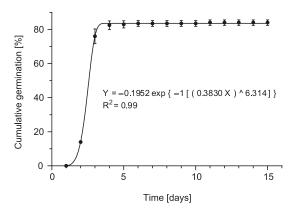
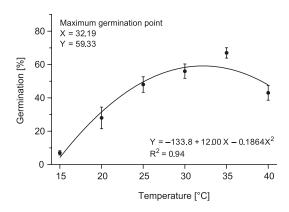


Fig. 3. Cumulative germination percentage of *Eragrostis tenuifolia* seeds at alternating temperatures (30/20°C) until the 15th day after sowing. Data points are the overall treatment means with the standard errors reflecting variability among replications. The curve represents the Weibull non-linear model, where *Y* represents cumulative germination (%) at a certain time (days) *X* 

The temperature variation allowed a fast approach to the stationary phase, with the seeds reaching 85% of germination in the first days after sowing. Hence, this may indicate the necessity of alternating temperature as a stimulus for the germination of *E. tenuifolia* seeds, since at constant temperatures, the maximum germination was 18% lower.

The data concerning the germination percentage as a function of time, showed a normal distribution and was used to build a Gaussian curve. This non-linear model illustrated that nearly 100% of the germinated seeds performed the germination process between the first and fifth day after sowing (Fig. 4).

The percentage of viable seeds that did not germinate with alternating temperature was only 15.5%. This value is almost half of the 30.0% registered in the best treatment with continuous temperature (data of the non-germinat-



**Fig. 2.** Germination percentage of *Eragrostis tenuifolia* seeds in response to different constant temperatures on the 15th day after sowing. Data points are the overall treatment means with the standard errors reflecting variability among replications. The curve represents a second order polynomial model, where *Y* represents germination (%) at a temperature (°C) *X* 

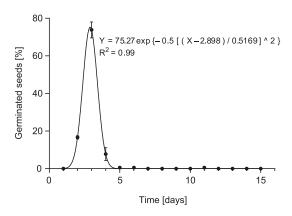


Fig. 4. Distribution percentage of germinated seeds of *Eragrostis tenuifolia* at alternating temperatures (30/20°C) until the 15th day after sowing. Data points are the overall treatment means with the standard errors reflecting variability among replications. The curve represents a Gaussian non-linear model, where Y represents germinated seeds (%) at a certain time (days) X

ed seeds in the bioassay with alternating temperatures not shown). Several factors could explain these results. For example, a part of the increase in the percentage of germinating seeds in alternating temperatures, could be due to the dormancy reduction. This behavior has already been observed in previous studies with other weed species (Benech-Arnold *et al.* 2000).

It is also possible that something similar occurred to what was observed with the seeds of annual ryegrass [Lolium rigidum (Gaud.)]; another species of Poaceae. In that case, an adaptive trace allowed the seeds to relate the oscillation of temperature with the depth at which they were buried. Hence, this would be extremely important for small seeds that have difficulty in germinating at greater depths, where temperatures tend to fluctuate less than they do near the soil surface (Ellery et al. 2003).



Table 2. Influence of light exposure on the seed germination percentage of Eragrostis tenuifolia on the 7th day after sowing (DAS)

Light exposure	Germination*	Quiescent*	Mortality	Abnormal seedlings
		[%	6]	
Light	76.9±2.5	17.1±2.9	4.0±1.8	2.0±1.4
Dark	32.7±1.6	63.8±2.0	2.0±0.0	1.5±0.5

<sup>\*</sup>values (the mean±SE) between treatments are significantly different according F test (p < 0.01)

It can also be assumed that the fluctuation in temperature presents an effect on the hormonal balance and in other physiological processes of the seeds. Therefore, the genes involved in the metabolism of abscisic acid, sugars, and the circadian clock are expressed in leafy spurge (*Euphorbia esula* L.) due to the alternating temperature and are considered key signals in the seed germination process (Foley *et al.* 2010).

The hormonal balance of gibberellic acid (GA) and abscisic acid (ABA) is probably the determining factor of germination. Gibberellic acid positively regulates the germination and ABA negatively regulates it by suppressing the expression of proteins involved in the germination process (Quatrano 1986; Kucera *et al.* 2005; Yamaguchi 2008). The latter may adjust the level of endogenous GA changing routes of biosynthesis and degradation (Seo *et al.* 2006). The hormonal mechanism of action on germination under alternating temperatures, though, is still not fully understood and requires further studies.

Lower temperatures also tend to increase the sensitivity to GA, reducing the dormancy of the seeds of several species (Karssen and Laçka 1986). Thus, it is possible that in alternating temperatures, the lower temperature helps to increase the GA sensitivity and decrease the level and sensitivity of ABA. In contrast, the higher temperature induces an increase in the permeability of the seed coat. For this reason, both could positively influence germination (Baskin and Baskin 2001).

## Effect of light on seed germination

In the bioassay conducted to determine the occurrence of photoblasty, dark conditions showed significantly lower levels of germination than did the light treatment (Table 2). These results suggest the occurrence of positive photoblasty since the light-receiving seeds showed a germination percentage that was 2.35 times greater than did those that remained in the dark. Despite the fact that dependence on light for germination is a specific feature, it was already verified for feather lovegrass (*E. tenella*), a related species of *E. tenuifolia* (Chauhan 2013).

This provides the basis to place *E. tenuifolia* as part of the majority of non-domesticated plants with small seeds and few reserves, which are mostly positively photoblastic (Hartmann and Nezadal 1990; Majerowicz and Peres 2008). Being small seeds, they do not have abundant reserves to sustain prolonged periods of seedling growth in the dark. This means that they require light for germination.

A protein pigment called phytochrome regulates the photoblasty. This pigment has two interconvertible forms: one form that absorbs red and blue light and another that

absorbs far-red light (Borthwick *et al.* 1952). When red and/or blue light is absorbed, there is a photoconversion of the phytochrome form Fv (inactive) to Pfr (active), inducing metabolic responses and the development of the plant. On the other hand, the reversal of Pfr to Fv is also stimulated by the far-red wavelength and the dark (Nagy and Schäfer 2002).

The germination percentage of the *E. tenuifolia* seeds was lower in this bioassay (76.9%) when compared to the one with alternating temperatures (85.5%). This may have happened because in the first condition, the seeds were stored in the dark for a period of 90 days before use, perhaps triggering dormancy mechanisms. The influence of the irradiance on the germination of *E. tenuifolia* should be explored in greater depth in future studies.

#### Effect of seed burial depth on seedling emergence

The highest percentage of seedling emergence was 73.5% when seeds had been sown on the soil surface (0 cm). This percentage of emergence was 35.5 and 66.2% higher than that observed at sowing depths of 1 and 2 cm, respectively (data not shown). Moreover, there was no seedling emergence at burial depths of 3 and 4 cm during the 28 days of observation.

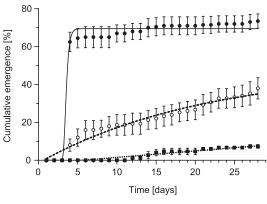
The emergence velocity index was also higher for seeds that had been sown on the soil surface, reaching a value of 8.3. The emergence speed indices to depths of 1 and 2 cm were 2.4 and 0.2, respectively (data not shown). To illustrate this, the differences observed between the tested sowing depths can also be perceived in the cumulative germination curves obtained by regression analysis (Fig. 5).

The increase in seeding depth induced an emergence-decrease, confirming the results from previous experiments with other weed species, especially those with reduced seed size (Benvenuti *et al.* 2001). After regression analysis, it was possible to predict that the burial depth of approximately 0.9 cm, would cause a 50% reduction in seedling emergence when compared to 0 cm (Fig. 6).

The results can also explain why studies on the management of other species belonging to this genus, recommend soil disturbance as a control tool. Since the seeds tend to be buried with plowing, there will be a lower rate of emergence. For *E. tenuifolia*, if the seed is 3 cm or deeper, it is very unlikely that it will give rise to a new plant.

The low emergence rate observed with increasing depths suggests that photoblasty, and daily temperature fluctuations as well as the small size of the seeds are all involved. The more distance from the soil surface, the lower the amount of radiation (at a wavelength of red and blue) that is able to activate the phytochrome and

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- 0 cm, Y = 69.4953 exp{ -exp[-(X -3.4264)/0.2597]}, R<sup>2</sup> = 0.98
- ---- 1 cm, Y = 0.02564 + 1.907 X 0.02303 X<sup>2</sup>, R<sup>2</sup> = 0.95
- •••••• 2 cm, Y =  $-1.062 + 0.1836 \times + 0.005340 \times^2$ , R<sup>2</sup> = 0.93

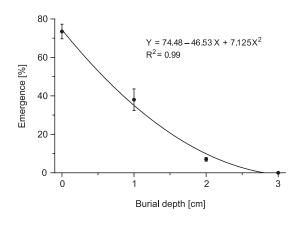
**Fig. 5.** Cumulative emergence percentage of *Eragrostis tenuifolia* seedlings at alternating temperatures (30/20°C) in different sowing depths (0, 1, and 2 cm) until the 28th day after sowing. Data points are the overall treatment means with the standard errors reflecting variability among replications. The curves represent: (0 cm) an Gompertz 3 parameter non-linear model; (1 cm) and (2 cm) a second order polynomial model; where *Y* represents cumulative emergence (%) at a certain time (days) *X* 

stimulate the germination process in seeds of photoblastic positive species. This seems to be the case for *E. tenuifolia*. Furthermore, small seeds tend to have fewer reserves than do larger seeds, limiting the horizontal distance that seedlings can travel before reaching the soil surface and starting the process of photosynthesis.

In summary, the temperature had an effect on *E. tenui*folia germination, with the lowest germination rates observed at a constant temperature of 15°C (7%) and the highest rates between 25 and 35°C (with the last temperature presenting 67%). The effect of daily thermal fluctuation (20/30°C) induced germination to reach 85%; a value 18% higher than was found in the best treatment under constant temperature (35°C). In addition, seeds of E. tenuifolia present typical patterns similar to positive photoblastic seeds. Taking into account that the soil surface is more exposed to daily thermal fluctuations and to the incidence of solar radiation, seeds placed at the surface of the soil will have faster and higher rates of germination. Agronomic management aimed at inhibiting the germination and emergence of *E. tenuifolia* must focus on the avoidance exposure to triggers of the germination process. Such practices can include the use of cover crops and/or plowing.

## **Conclusions**

In conclusion, the present study suggests that *E. tenuifolia* seeds germinate best at alternate temperatures of about 30/20°C and in the presence of light. Seedling emergence occurs only when the germinated seeds are near the soil surface, not emerging from depths equal or higher than 3 cm.



**Fig. 6.** Emergence percentage of *Eragrostis tenuifolia* seedlings at alternating temperatures (30/20°C), and different sowing depths on the 28th day after sowing. Data points are the overall treatment means with the standard errors reflecting variability among replications. The curve represents a second order polynomial model, where *Y* represents emergence (%) at a sowing depth (cm) *X* 

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# References

Baskin C.C., Baskin J.M. 2001. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press, San Diego, USA, 666 pp.

Benech-Arnold R.L., Sánchez R.A., Forcella F., Kruk B.C., Ghersa C.M. 2000. Environmental control of dormancy in weed seed banks in soil. Field Crops Research 67 (2): 105–122.

Benvenuti S., Macchia M., Miele S. 2001. Quantitative analysis of emergence of seedlings from buried weed seeds with increasing soil depth. Weed Science 49 (4): 528–535.

Bhowmik P.C. 1997. Weed biology: importance to weed management. Weed Science 45 (3): 349–356.

Boechat S.C., Longhi-Wagner H.M. 2000. Padrões de distribuição geográfica dos táxons brasileiros de Eragrostis (Poaceae, Chloridoideae). [Patterns of geographic distribution of the Brazilian taxa of Eragrostis (Poaceae, Chloridoideae)]. Revista Brasileira de Botânica 23 (2): 177–194. (in Portuguese)

Borthwick H.A., Hendricks S.B., Parker M.W., Toole E.H., Toole V.K. 1952. A reversible photoreaction controlling seed germination. Proceedings of the National Academy of Sciences USA 38 (8): 662–666.

Brasil. 2009. Regras Para Análises de Sementes. [Brazilian Rules for the Analysis of Seeds]. Brasília: Ministério da Agricultura, Pecuária e Abastecimento [Ministry of Agriculture, Livestock and Supply], 395 pp.

Bridges D.C., Wu H.-I., Sharpe P.J.H., Chandler J.M. 1989. Modeling distributions of crop and weed seed germination time. Weed Science 37 (5): 724–729.



- Bryson C.T., Carter R. 2004. Biology of pathways for invasive weeds. Weed Technology 18 (Special Issue 1): 1216–1220.
- Chauhan B.S. 2013. Seed germination ecology of feather lovegrass [*Eragrostis tenella* (L.) Beauv. Ex Roemer & J.A. Schultes]. PLoS One 8 (11): e79398.
- Chauhan B.S., Gill G., Preston C. 2006. Influence of environmental factors on seed germination and seedling emergence of rigid ryegrass (*Lolium rigidum*). Weed Science 54 (6): 1004–1012.
- Clayton W.D., Vorontsova M.S., Harman K.T., Williamson H. 2006. GrassBase The Online World Grass Flora. Available on: http://www.kew.org/data/grasses-db.html. [Accessed: June 15, 2015]
- Ellery A.J., Gallagher R.S., Dudley S.V. 2003. Dormancy and germination ecology of annual ryegrass (*Lolium rigidum* Gaud.). p. 389–396. In: "The Biology of Seeds: Recent Research Advances" (G. Nicolás, K.J. Bradford, D. Côme, H.W. Pritchard, eds.), Cambridge, CAB International, Wallingford, UK, 496 pp.
- Foley M.E., Anderson J.V., Chao W.S., Doğramaci M., Horvath D.P. 2010. Initial changes in the transcriptome of *Euphorbia esula* seeds induced to germinate with a combination of constant and diurnal alternating temperatures. Plant Molecular Biology 73 (1–2): 131–142.
- Goulart I.C.G.R., Merotto Junior A., Perez N.B., Kalsing A. 2009.

  Controle de capim-annoni-2 (*Eragrostis plana*) com herbicidas pré-emergentes em associação com diferentes métodos de manejo do campo nativo. [Control of South African lovegrass (*Eragrostis plana*) in natural pastures using pre emergent herbicides and different vegetation management methods]. Planta Daninha 27 (1): 181–190. (in Portuguese)
- Guglieri-Caporal A., Caporal F.J.M., Valls J.F.M. 2011. *Eragrostis tenuifolia* (A. Rich.) Hochst. ex Steud. (Poaceae) no Mato Grosso do Sul e Mato Grosso, Brasil. [*Eragrostis tenuifolia* (A. Rich.) Hochst. ex Steud. (Poaceae) in Mato Grosso do Sul and Mato Grosso, Brazil]. Revista Brasileira de Biociências 9 (3): 418–420. (in Portuguese)
- Hartmann K.M., Nezadal W. 1990. Photocontrol of weeds without herbicides. Naturwissenschaften 77 (4): 158–163.
- Jung M.J., Veldkamp J.F., Kuoh C.S. 2008. Notes on *Eragrostis wolf* (Poaceae) for the flora of Taiwan. Taiwania 53 (1): 96–102.
- Karssen C.M., Laçka E. 1986. A revision of the hormone balance theory of seed dormancy: studies on gibberellin and/or abscisic acid-deficient mutants of *Arabidopsis thaliana*. p. 315–323. In: "Plant Growth Substances" (M. Bopp, ed.). Springer-Verlag, Berlin, Germany, 422 pp.
- Knapp P.A. 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert. Global Environmental Change 6 (1): 37–52.
- Koger C.H., Reddy K.N., Poston D.H. 2004. Factors affecting seed germination, seedling emergence, and survival of texasweed (*Caperonia palustris*). Weed Science 52 (6): 989–995.
- Kreitschitz A., Tadele Z., Gola E.M. 2009. Slime cells on the surface of *Eragrostis* seeds maintain a level of moisture around the grain to enhance germination. Seed Science Research 19 (01): 27–35.
- Kucera B., Cohn M.A., Leubner-Metzger G. 2005. Plant hormone interactions during seed dormancy release and germination. Seed Science Research 15 (4): 281–307.

- Maguire J.D. 1962. Speed of germination aid in selection and evaluation for seedling emergence and vigor. Crop Science 2 (2): 176.
- Majerowicz N., Peres L.E.P. 2008. Fotomorfogênese em plantas. [Photomorphogenesis in plants]. p. 421–438. In: "Fisiologia Vegetal" ["Plant Physiology"] (G.B. Kerbauy, ed.). 2nd ed., Guanabara Koogan, Rio de Janeiro, 472 pp. (in Portuguese)
- Miransari M., Smith D.L. 2014. Plant hormones and seed germination. Environmental and Experimental Botany 99: 110–121.
- Nagy F., Schäfer E. 2002. Phytochromes control photomorphogenesis by differentially regulated, interacting signaling pathways in higher plants. Annual Review of Plant Biology 53: 329–355.
- Njuguna J.G.M., Gordon D.T., Louie R. 1997. Wild grass hosts of maize streak virus and its Cicadulina leafhopper vectors in Kenya. p. 236–240. In: "Maize Productivity Gains through Research and Technology Dissemination" (J.K. Ransom, A.F.E. Palmer, B.T. Zambezi, Z.O. Mduruma, S.R. Waddington, eds.). Proceedings of the Fifth Eastern and Southern Africa Regional Maize Conference Arusha, Tanzania, 3–7 June 1996, CIMMYT, Addis Abeba, Ethiopia, 244 pp.
- Quatrano RS. 1986. Regulation of gene expression by abscisic acid during angiosperm embryo development. p. 467–477. In: "Oxford Surveys of Plant Molecular and Cell Biology" (B.J. Miflin, ed.), 3rd ed., Oxford University Press, London, UK, 477 pp.
- Seo M., Hanada A., Kuwahara A., Endo A., Okamoto M., *et al.* 2006. Regulation of hormone metabolism in *Arabidopsis* seeds: phytochrome regulation of abscisic acid metabolism and abscisic acid regulation of gibberellin metabolism. The Plant Journal 48 (3): 354–366.
- Sladonja B., Krapac M., Ban D., Užila Z., Dudaš S., Dorčić D. 2014. Effect of soil type on pyrethrum seed germination. Journal of Plant Protection Research 54 (4): 421–425.
- Sun D., Liddle M.J. 1993. Plant morphological characteristics and resistance to simulated trampling. Environmental Management 17 (4): 511–521.
- Taddese G., Mohamed Saleem M.A., Astatke A., Ayaleneh W. 2002. Effect of grazing on plant attributes and hydrological properties in the sloping lands of the East African Highlands. Environmental Management 30 (3): 406–417.
- Tateoka T. 1965. Chromosome numbers of some East African grasses. American Journal of Botany 52 (8): 864–869.
- Teketay D. 1998. The role of light and temperature in the germination of twenty herbaceous species from the highlands of Ethiopia. Flora 193: 411–425.
- USDA. 2015. Germplasm Resources Information Network Online Database. Available on: http://www.ars-grin.gov.4/cgibin/npgs/html/taxon.pl?15323. [Accessed: May 28, 2015]
- Watson L., Clifford H.T., Dallwitz M.J. 1985. The classification of Poaceae: subfamilies and supertribes. Australian Journal of Botany 33 (4): 433.
- Weibull W. 1951. A statistical distribution function of wide aplicability. Journal of Applied Mechanics 8 (1): 293–297.
- Yamaguchi S. 2008. Gibberellin metabolism and its regulation. Annual Review Plant Biology 59: 225–251.