

Research Paper

Enhanced germination performance of dormant seeds of *Eragrostis tef* in the presence of light

Germinación mejorada de semillas de Eragrostis tef con latencia en presencia de luz

ISKENDER TIRYAKI AND SAKIR ANIL KAPLAN

Çanakkale Onsekiz Mart University, Çanakkale, Turkey. www.comu.edu.tr

Abstract

Lack of germination or low germination due to seed dormancy prevents successful crop establishment in several important plants. To determine the presence of innate seed dormancy and effects of stress-related plant hormones on germination performance of Teff (*Eragrostis tef*) seeds, we primed seeds in 1% KNO₃ for 24 hours in dark conditions at 21 ± 0.5 °C along with varying concentrations of chemicals known to influence seed germination, including: acetyl salicylic acid (ASA); methyl jasmonate (JA-Me); gibberellic acid (GA₃); and indole acetic acid (IAA). Primed seeds were incubated either in constant light (210 µM/m²/s) or in darkness at 21 ± 0.5 °C. The results indicated that priming significantly improved final germination percentage (FGP) in both light (92.5%) and dark (89.4%) conditions compared with untreated seeds. The inclusion of plant hormones in the priming media generally had limited effects, except for 10 µM ASA (94.5%) and 100 µM GA₃ (92.5%). ASA generally provided faster seed germination than seeds primed in 1% KNO₃ only, while the other plant hormones had no effect on the time required for 50% of FGP in the dark. Priming had no significant effect on time span of germination in either light or dark incubation conditions. The results demonstrate that *E. tef* has light-inducible seed germination and about half of freshly harvested seeds can be dormant, which can be eliminated to some extent by priming seeds in 1% KNO₃.

Keywords: Dormancy, hormone, photoblastism, priming, Teff.

Resumen

La ausencia de germinación o la germinación baja debido a la latencia (dormancia) de las semillas puede impedir el establecimiento exitoso de cultivos importantes. Para determinar la presencia de latencia endógena y los efectos de hormonas vegetales en la germinación de semillas de Teff (*Eragrostis tef*), muestras de estas fueron remojadas en KNO₃ al 1% durante 24 horas en condiciones de oscuridad a 21 ± 0.5 °C aplicando concentraciones variables de cuatro hormonas vegetales que influyen en la germinación de las semillas: ácido acetilsalicílico (ASA); jasmonato de metilo (JA-Me); ácido giberélico (GA₃); y ácido indolacético (IAA). Las semillas tratadas fueron incubadas a luz constante (210 µM/m²/s) o en la oscuridad a 21 ± 0.5 °C. Los resultados indicaron que el acondicionamiento mejoró significativamente el porcentaje de germinación final (FGP), tanto en condiciones de luz (92.5%) como de oscuridad (89.4%), en comparación con las semillas no tratadas. La inclusión de hormonas vegetales generalmente tuvo solo efectos limitados, a excepción de 10 µM de ASA (94.5%) y 100 µM de GA₃ (92.5%). El ASA generalmente proporcionó una germinación de semillas más rápida que cuando se trataron solo con KNO₃ al 1%, mientras que las otras hormonas no tuvieron efecto en el tiempo requerido para el 50% de germinación final en condiciones de oscuridad. El acondicionamiento no tuvo un efecto significativo sobre el período de tiempo para la germinación en condiciones de incubación a luz ni en la oscuridad. Los resultados demuestran que (1) la germinación de semillas de *E. tef* es inducida por la luz y (2) que aproximadamente la mitad de semillas recién cosechadas

Correspondence: Iskender Tiryaki, Çanakkale Onsekiz Mart University, Faculty of Agriculture, Department of Agricultural Biotechnology, 17100 Çanakkale, Turkey.
E-mail: itiryaki@comu.edu.tr

pueden estar en estado de latencia la cual podrá eliminarse, hasta cierto punto, mediante acondicionamiento de las semillas en KNO_3 al 1%.

Palabras clave: Fotoblastismo, hormonas, latencia, osmoacondicionamiento, Teff.

Introduction

Teff (*Eragrostis tef*), also known as lovegrass or annual bunch grass, is an ancient gluten-free cereal crop mostly adapted to environments with warm seasons (Spaenij-Dekking et al. 2005; Assefa et al. 2015). Teff originated in Ethiopia (Ketema 1993; Girma et al. 2014), and has been introduced to regions and countries with a range of climates, including the USA, India, Africa, Western Europe and Australia (Ketema 1997; Girma et al. 2014) owing to its importance for supplying good quality proteins for human use and for animal feeding as a forage or silage crop (Hagos and Melaku 2009; Zhu 2018).

Teff seeds are the world's smallest cereal grain, with an average 1,000-seed weight of 0.3–0.4 g (Kreitschitz et al. 2009). The market value of Teff seed is determined mainly by seed color, which varies from white to dark brown (Ketema 1993). An often temporary state of physiological seed dormancy means many cereal seeds either do not germinate or have low germination percentage (Khan et al. 2017), which prevents a successful start to the season and uniform stand establishment in several important plant species including *Lolium rigidum* (Steadman et al. 2003), *Elymus elymoides* (Meyer et al. 2000) and *Bromus tectorum* (Bauer et al. 1998). Some research into Teff seed has been conducted including hydrothermal time modelling (van Delden 2011), plus grain structure and properties of caryopses of Teff seeds (Kreitschitz et al. 2009). However, there is still a lack of information about the severity of innate seed dormancy, and the effects of stress-related plant hormones and light on germination performance of Teff seed.

Seed priming, or osmoconditioning, which is influenced by several factors such as temperature, water potential and duration, is a relatively common method for treating seed to initiate seed germination. Priming is done prior to the emergence of the primary root during later seed imbibition (Pill 1995), thereby enhancing germination under conditions marginal for establishment. Osmotica used in priming include polyethylene glycol (PEG), sodium or potassium salts (e.g. K_3PO_4 , KH_2PO_4 , MgSO_4 , NaCl), which control water uptake of seeds during seed imbibition and can provide a higher germination percentage and rate than unprimed vegetable and grass seeds (Frett and Pill 1995). Previous reports indicated that dormancy in freshly harvested seeds of *Amaranthus cruentus* (Tiryaki et al. 2005), *Poa pratensis* (Tiryaki et al. 2006) and *Phacelia*

tanacetifolia (Tiryaki and Keles 2012) could be eliminated, to some extent, by priming in the presence of stress-related plant hormones like methyl jasmonate (JA-Me), 1-amino-cyclopropane-1-carboxylic acid (ACC) and 6-benzyl-amino-purine (BAP) (Tiryaki and Buyukcingil 2009).

The objectives of this study were to determine the presence and severity of innate seed dormancy of *Eragrostis tef* seeds, and to reveal the effects of stress-related plant hormones on germination performance of the seeds when incubated with and without light.

Materials and Methods

Material

Eragrostis tef (accession PI 197210) seeds used in the experiments were harvested by hand from plants grown under field conditions on 12 October 2017, in Canakkale, Turkey. Harvested seeds came from a single lot and were immediately used for germination experiments at Canakkale Onsekiz Mart University, Canakkale.

Methods

Pre-experimental trials indicated the best priming medium and duration of priming were 1% KNO_3 for 24 hours (Tiryaki unpublished data). A single layer of seeds (0.3 g) was placed on double layers of filter paper and 3 mL of 1% KNO_3 was applied plus various concentrations of the following primers: acetyl salicylic acid (ASA – 1, 5, 10 and 15 μM), methyl jasmonate (JA-Me – 0.3, 0.6, 0.9 and 1.2 μM), gibberellic acid (GA_3 – 50, 100, 150 and 200 μM) and indole-3-acetic acid (IAA – 0.5, 1.0, 1.5 and 2.0 μM) for 24 h at $21 \pm 0.5^\circ\text{C}$ in darkness. Prior to the germination test, the priming solution was removed from the primed seeds by washing with tap water for 1 minute and then placing seeds on paper towels for 2 h under room conditions. Surface-dried and primed seeds were then used for the germination experiments. Seeds treated with 1% KNO_3 only, seeds treated with distilled water (dH_2O) only (hydropriming) and non-primed seeds were used as controls.

Germination experiments were conducted in a growth chamber held at $21 \pm 0.5^\circ\text{C}$ either in constant light (210 $\mu\text{mol}/\text{m}^2/\text{s}$ for 24 h/d) or darkness. A completely randomized block design with 4 replications of 50 seeds was arranged as a factorial. Replicates of each treatment

were placed either in different shelves of the same growth chamber or were arranged in different positions in light-sealed boxes in light and dark experiments, respectively, and were randomized after each count. Seeds, which showed a radicle exceeding 2 mm in length emerged from the testa, were counted as germinated and were removed daily from the petri dishes for 7 days in light and 12 days in dark germination experiments. The final germination percentage (FGP) was determined and its angular transformation ($\arcsin\sqrt{\text{FGP}}$) was used to provide a normal distribution for data analysis. Germination rate (estimated as days to 50% of FGP) and the span of germination (time from 10% to 90% of FGP) were calculated from the total number of seeds germinated using a method used successfully on sugarbeet seeds (Murray et al. 1993).

SAS statistical software was used to analyze the data (SAS 1997) and Fisher's least significant difference (LSD) test was applied, if the F test was significant at $P < 0.05$.

Results

Effects of priming media and plant hormones in darkness

Approximately half of the Teff seeds were considered dormant shortly after harvesting when incubated in the absence of light. Priming seeds in 1% KNO_3 for 24 h at 21

$\pm 0.5^\circ\text{C}$ in the dark significantly improved germination percentage over that of untreated control seeds (89.4 vs. 56.5%, respectively; Figure 1). The results also revealed that hydropriming significantly reduced FGP and gave the lowest FGP (40.5%) in comparison with untreated control seeds.

The inclusion of plant hormones in the priming medium generally had little effect on FGP with values ranging from 79.5 to 94.5% (Figure 1).

Priming in the presence of hormones generally had little effect on the speed of germination of seeds, while seeds primed in dH_2O had the slowest ($G_{50} = 3.76$ days; $P < 0.05$) seed germination (Table 1).

Effects of priming media and plant hormones in light

In general, seeds germinated in light had higher FGP than seeds germinated in the dark (Figure 1). In light, priming seeds in 1% KNO_3 significantly improved FGP compared with untreated control seeds (92.5 vs. 72.5%; Figure 1). Adding 150 μM GA_3 and 1 μM ASA to the priming medium (Figure 1) improved FGP to 99 and 98.5%, respectively, while adding the other plant hormones provided intermediate results. Hydroprimed seeds had significantly higher FGP (82.5%) than untreated control seeds (72.5%), which was in complete contrast to the results obtained in darkness (Figure 1).

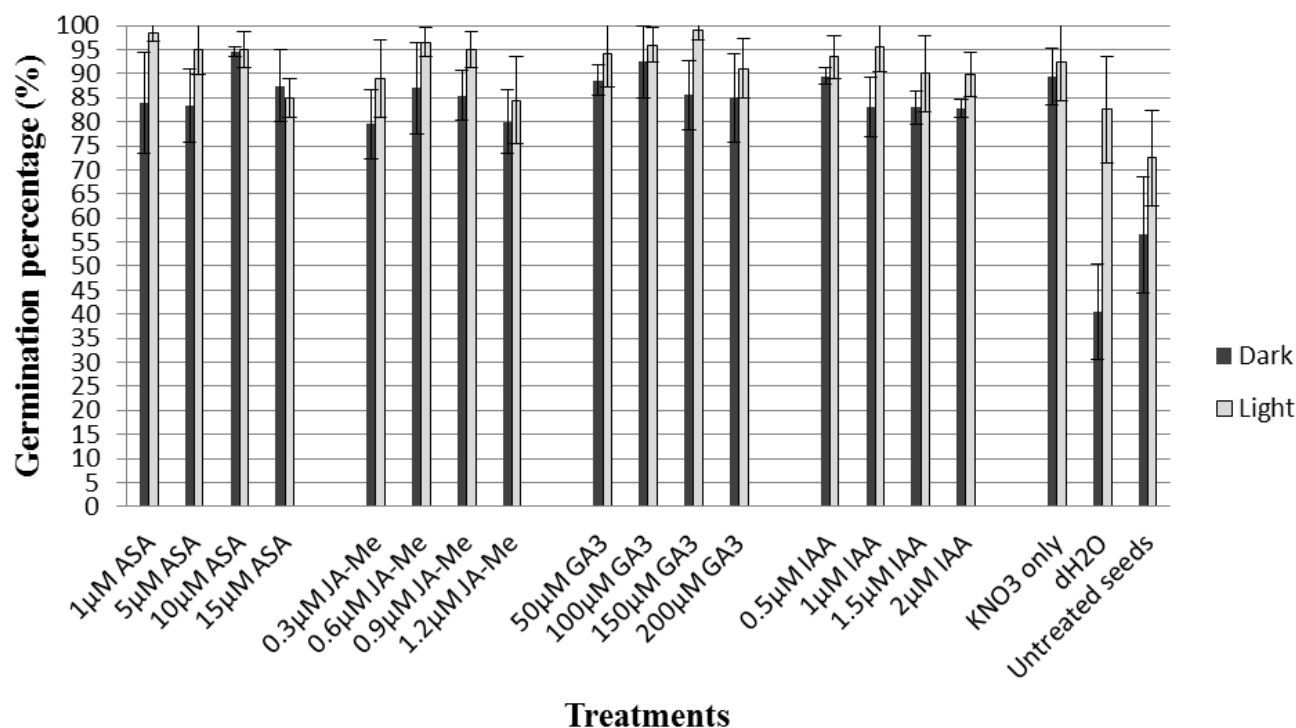


Figure 1. The final germination percentage (FGP) of Teff seeds primed in 1% KNO_3 supplemented with various concentrations of different plant hormones for 24 h at 21 °C and germinated under light or dark conditions at 21 °C. Bar indicates SD ($n = 4$).

Table 1. The angular transformation [FGP] of final germination percentage (FGP), speed (G_{50}) and span (G_{10-90}) of Teff seed germination incubated in dark or light at 21 °C following priming for 24 hours at 21 °C in 1% KNO_3 combined with different plant hormones at various concentrations.

Treatment ¹	FGP [FGP]	G_{50} (days)	G_{10-90} (days)	FGP [FGP]	G_{50} (days)	G_{10-90} (days)
	Dark			Light		
Acetyl salicylic acid						
1	[66.9]ab ²	2.13c	4.91	[85.0]ab	1.69b	2.38
5	[66.5]ab	2.70bc	6.29	[79.3]a-c	1.84b	2.53
10	[76.4]a	2.18c	6.78	[77.7]a-c	1.68b	2.46
15	[69.9]ab	2.08c	5.96	[67.3]cd	1.79b	3.00
Methyl jasmonate						
0.3	[63.3]b	2.91bc	6.29	[73.8]a-c	1.88b	3.03
0.6	[71.6]ab	2.44bc	6.26	[79.7]a-c	1.52b	2.36
0.9	[67.8]ab	2.47bc	5.19	[77.7]a-c	1.53b	2.32
1.2	[63.7]b	2.76bc	5.11	[67.4]cd	1.78b	2.62
Giberellic acid						
50	[70.4]ab	2.27bc	5.65	[77.1]a-c	1.75b	2.55
100	[76.6]a	3.10ab	4.95	[80.3]a-c	1.56b	2.44
150	[68.3]ab	2.44bc	5.06	[87.1]a	1.71b	3.11
200	[68.0]ab	2.88bc	5.27	[73.4]a-c	1.79b	2.74
Indole acetic acid						
0.5	[71.2]ab	2.55bc	7.46	[77.1]a-c	1.55b	2.26
1.0	[65.9]ab	2.80bc	5.47	[80.0]a-c	1.86b	2.54
1.5	[65.7]b	2.80bc	7.39	[75.2]a-c	1.86b	2.88
2.0	[65.5]b	2.35bc	5.32	[71.8]b-d	1.54b	2.15
Controls						
1% KNO_3 only	[71.6]ab	2.54bc	5.68	[76.5]a-c	1.89b	2.40
dH ₂ O	[39.4]d	3.76a	7.36	[69.6]cd	2.65a	3.37
Untreated seed	[48.8]c	2.50bc	6.80	[58.6]d	2.43a	2.47

¹ KNO_3 + related plant hormone at given concentrations (μM).

²Values within columns followed by different letters differ ($P < 0.05$).

Seeds primed in 1% KNO_3 had significantly enhanced germination rate ($G_{50} = 1.89$ days) compared with untreated control seeds ($G_{50} = 2.43$ days) (Table 1), while there was no further improvement from inclusion of plant hormones (Table 1). Hydroprimed ($G_{50} = 2.65$ days) and untreated ($G_{50} = 2.43$ days) control seeds had the slowest germination speeds (Table 1). There were no significant differences between primed and control seeds for span of germination (G_{10-90}) in either light or dark germination conditions (Table 1).

Discussion

One of the most important prerequisites for a successful plant stand is even, fast and successful seed germination. This can depend on external factors such as light, temperature and water supply to the seed as well as endogenous seed factors including ripeness (seed maturity), hormone levels and other forms of dormancy (van Delden 2011). Of those, seed dormancy can delay and spread seed germination over time, and is a characteristic of several plant

species (Schonbeck and Egley 1981; Gu et al. 2003). Several methods are used to reduce or overcome seed dormancy, and these can vary among species (Steadman et al. 2003; Nee et al. 2017). Priming seeds in an appropriate osmoticum improves germination and seedling emergence of several plant species (Tiryaki and Keles 2012), and a positive photoblastism, light-inducible seed germination, was recently reported for *Eragrostis ciliaris* (Khan et al. 2017). Although existence of slight embryo dormancy was previously mentioned in fresh seeds of *Eragrostis abyssinica* [synonym of *E. tef* (Zuccagni) Trotter] (Katayama and Nakagama 1972; van Delden 2011), this study has demonstrated that *E. tef* has light-inducible seed germination and half of freshly harvested seed can be dormant. In addition, the study revealed that untreated control seeds had higher FGP (72.5%) in the presence of light than untreated control seeds germinated in darkness (56.5%). Priming of dormant seeds in 1% KNO_3 for 24 h at 21 ± 0.5 °C significantly improved FGP and provided faster seed germination in the presence of light (Figure 1), while the same priming treatment had no effect on the span of

germination in both light and dark conditions (Table 1). In addition, hydropriming appeared to decrease FGP (40.5%) in darkness in comparison with untreated control seeds (56.5%), whereas hydroprimed seeds had a higher FGP (82.5%) than untreated control seeds (72.5%) in the light (Figure 1). These results suggest that hydropriming of Teff seed could be considered if planting alone or in a mixture with other grasses as a seeding material for temporary nurse grass or erosion control.

Light is one of the most important regulatory factors of seed germination for many plant species including reed canary grass ([Lindig-Cisneros and Zedler 2001](#)), weedy rice ([Lee et al. 2010](#)), *Arabidopsis* ([Auge et al. 2018](#)), lettuce ([Sawada et al. 2008](#)), tomato ([Auge et al. 2009](#)) and phacelia ([Tiriyaki and Keles 2012](#)). Positively photoblastic species often have small and dormant seeds ([Flores et al. 2011](#)). Previous reports indicated that seed dormancy was influenced by the nitrate concentrations in both soil and seed ([Matakiadis et al. 2009](#); [Huang et al. 2018](#)) and phytochrome plays a very significant role in this action ([Footitt et al. 2013](#)). However, this may not be the case in Teff seeds since seeds primed in KNO_3 gave about the same FGPs with (92.5%) and without (89.4%) light during incubation (Figure 1). It may be that use of KNO_3 as a priming agent with Teff seeds enhances seed germination by balancing endogenous nitrate content or by accelerating the decrease in abscisic acid (ABA) level prior to the completion of germination triggered by the production of N-related signals ([Footitt et al. 2013](#)).

It is well known that the level of physiological seed dormancy is influenced by ABA and GA (giberellic acid) homeostasis during seed maturation ([Seo et al. 2009](#)). Although the exact dormancy-release mechanisms of the hormones are still unknown for many plant species ([Nakabayashi et al. 2012](#)), recent new molecular approaches partially shed light on these mechanisms ([Shen et al. 2018](#); [Auge et al. 2018](#)). In general, inclusion of plant hormones with priming solution used in this study did not provide any further improvement on FGP under both light and no light conditions except for ASA and GA_3 at certain concentrations. A high concentration of ASA (10 μM), which had FGP of 94.5%, appeared to be more effective under no light conditions, while the lower concentration of ASA (1 μM) provided a better improvement in FGP under light conditions (98.5%) (Figure 1). In contrast, a higher GA_3 concentration (150 μM) gave a higher FGP (99.0%) in the light than the seeds primed in the presence of 100 μM GA_3 (92.5%) under no light conditions. The differences are relatively small, but indicate germination and dormancy-release processes of Teff seeds may be influenced by ASA and GA homeostasis with light playing an important role in this regulation. A similar regulation of

ASA and GA was previously shown for lettuce ([Sawada et al. 2008](#)) and pepper seeds ([Korkmaz 2005](#)).

Recent advances in genetic and biochemical studies have revealed that GA metabolism of seeds is controlled by light-response ([Varbanova et al. 2007](#); [Footitt et al. 2017](#)). Involvement of light and GA in seed germination was also previously shown in *Arabidopsis* at the molecular level ([Ogawa et al. 2003](#)). Those authors suggested that increased levels of GA in germinated seeds were controlled mainly by both transcriptional activation and repression of GA biosynthetic as well as GA catabolic genes ([Ogawa et al. 2003](#)). However, this is not the case for Teff seeds, since exogenous application of ASA and GA_3 produced similar additional increments in FGP under both light and no light conditions (Table 1).

Jasmonic acid (JA) or methylated jasmonic acid (JA-Me) affects several biological activities in plants, including plant growth and development, as well as responses to biotic and abiotic stresses ([Tiriyaki and Staswick 2002](#)). Previous reports indicated that exogenous applications of JA or JA-Me stimulate germination of dormant seeds in various plant species ([Berestetzky et al. 1991](#); [Ranjan and Lewak 1992](#)), while non-dormant seed germination was inhibited in some other plant species ([Corbineau et al. 1988](#); [Daletskaya and Sembdner 1989](#)).

In this study we found that JA-Me neither stimulated nor inhibited the germination percentage of dormant *E. tef* seeds when primed with KNO_3 . This may indicate that JA-Me has no, or only a limited, function in the germination processes of Teff seed. It is well known that JA-Me and IAA have signaling cross talk to control or to regulate several important plant growth parameters, including response to light ([Westfall et al. 2016](#); [Kučko et al. 2017](#); [Sherp et al. 2018](#)). Regulatory involvement of these two plant hormones in seed germination was previously shown in wheat ([Xu et al. 2016](#)), pepper ([Korkmaz 2005](#)), Kentucky bluegrass ([Tiriyaki et al. 2006](#)) and *Arabidopsis* ([Shu et al. 2016](#)). Altogether the results of this study suggested that JA-Me and IAA neither regulate Teff seed germination nor are involved in N-related signals with ABA ([Footitt et al. 2013](#); [Jacobsen et al. 2013](#)), further physiological or molecular studies are needed to confirm these results.

In conclusion, this study indicates that Teff has light-inducible seed germination and a substantial proportion of freshly harvested *E. tef* seeds can be dormant. This can be overcome to some extent by priming seeds in 1% KNO_3 . The results also revealed that including ASA and GA_3 in priming media may play a role in enhancing the Teff germination process. These findings have possible implications for treatment of seed following harvesting and prior to sowing.

References

(Note of the editors: All hyperlinks were verified 11 April 2019.)

- Assefa K; Cannarozzi G; Girma D; Kamies R; Chanyalew S; Plaza-Wuthrich S; Bloesch R; Rindisbacher A; Rafudeen S; Tadele Z. 2015. Genetic diversity in tef [*Eragrostis tef* (Zucc.) Trotter]. *Frontiers in Plant Science* 6:177. doi: [10.3389/fpls.2015.00177](https://doi.org/10.3389/fpls.2015.00177)
- Auge GA; Perelman S; Crocco CD; Sanchez RA; Botto JF. 2009. Gene expression analysis of light-modulated germination in tomato seeds. *New Phytologist* 183:301–314. doi: [10.1111/j.1469-8137.2009.02867.x](https://doi.org/10.1111/j.1469-8137.2009.02867.x)
- Auge GA; Blair LK; Karediya A; Donohue K. 2018. The autonomous flowering-time pathway pleiotropically regulates seed germination in *Arabidopsis thaliana*. *Annals of Botany* 121:183–191. doi: [10.1093/aob/mcx132](https://doi.org/10.1093/aob/mcx132)
- Bauer MC; Meyer SE; Allen PS. 1998. A simulation model to predict seed dormancy loss in the field for *Bromus tectorum* L. *Journal of Experimental Botany* 49:1235–1244. doi: [10.1093/jxb/49.324.1235](https://doi.org/10.1093/jxb/49.324.1235)
- Berestetzky V; Dathe W; Daletskaya T; Musatenko L; Sembdner G. 1991. Jasmonic acid in seed dormancy of *Acer tataricum*. *Biochemie und Physiologie der Pflanzen* 187:13–19. doi: [10.1016/S0015-3796\(11\)80178-2](https://doi.org/10.1016/S0015-3796(11)80178-2)
- Corbineau F; Rudnicki RM; Come D. 1988. The effect of methyl jasmonate on sunflower (*Helianthus annuus* L.) seed germination and seedling development. *Plant Growth Regulation* 7:157–169. doi: [10.1007/BF00028238](https://doi.org/10.1007/BF00028238)
- Daletskaya T; Sembdner G. 1989. Effect of jasmonic acid on germination of non-dormant and dormant seeds. *Fiziologiya Rastenii* 36:1118–1123.
- Flores J; Jurado E; Chapa-Vargas L; Ceroni-Stuva A; Dávila-Aranda P; Galíndez G; Gurvich D; León-Lobos P; Ordóñez C; Ortega-Baes P; Ramírez-Bullón N; Sandoval A; Seal CE; Ullian T; Pritchard HW. 2011. Seeds photoblastism and its relationship with some plant traits in 136 cacti taxa. *Environmental and Experimental Botany* 71:79–88. doi: [10.1016/j.envexpbot.2010.10.025](https://doi.org/10.1016/j.envexpbot.2010.10.025)
- Footitt S; Huang Z; Clay HA; Mead A; Finch-Savage WE. 2013. Temperature, light and nitrate sensing coordinate *Arabidopsis* seed dormancy cycling, resulting in winter and summer annual phenotypes. *The Plant Journal* 74:1003–1015. doi: [10.1111/tpj.12186](https://doi.org/10.1111/tpj.12186)
- Footitt S; Olcer-Footitt H; Hambidge AJ; Finch-Savage WE. 2017. A laboratory simulation of *Arabidopsis* seed dormancy cycling provides new insight into its regulation by clock genes and the dormancy-related genes *DOG1*, *MFT*, *CIPK23* and *PHYA*. *Plant, Cell & Environment* 40:1474–1486. doi: [10.1111/pce.12940](https://doi.org/10.1111/pce.12940)
- Frett JJ; Pill WG. 1995. Improved seed performance of four fescue species with priming. *Journal of Turfgrass Management* 1:13–31. doi: [10.1300/J099v01n03_02](https://doi.org/10.1300/J099v01n03_02)
- Girma D; Assefa K; Chanyalew S; Cannarozzi G; Kuhlemeier C; Tadele Z. 2014. The origins and progress of genomics research on Tef (*Eragrostis tef*). *Plant Biotechnology Journal* 12:534–540. doi: [10.1111/pbi.12199](https://doi.org/10.1111/pbi.12199)
- Gu XY; Chen ZX; Foley ME. 2003. Inheritance of seed dormancy in weedy rice. *Crop Science* 43:835–843. doi: [10.2135/cropsci2003.8350](https://doi.org/10.2135/cropsci2003.8350)
- Hagos T; Melaku S. 2009. Feed intake, digestibility, body weight and carcass parameters of Afar rams fed tef (*Eragrostis tef*) straw supplemented with graded levels of concentrate mix. *Tropical Animal Health and Production* 41:599–606. doi: [10.1007/s11250-008-9230-6](https://doi.org/10.1007/s11250-008-9230-6)
- Huang Z; Footitt S; Tang A; Finch-Savage WE. 2018. Predicted global warming scenarios impact on the mother plant to alter seed dormancy and germination behaviour in *Arabidopsis*. *Plant, Cell & Environment* 41:187–197. doi: [10.1111/pce.13082](https://doi.org/10.1111/pce.13082)
- Jacobsen JV; Barrero JM; Hughes T; Julkowska M; Taylor JM; Xu Q; Gubler F. 2013. Roles for blue light, jasmonate and nitric oxide in the regulation of dormancy and germination in wheat grain (*Triticum aestivum* L.). *Planta* 238:121–138. doi: [10.1007/s00425-013-1878-0](https://doi.org/10.1007/s00425-013-1878-0)
- Katayama TC; Nakagama A. 1972. Studies on the germination behaviour of Tef seeds (*Eragrostis abyssinica* Schrad.) with the emphasis on storage condition. *Japanese Journal of Tropical Agriculture* 16:97–105. doi: [10.11248/jsta1957.16.97](https://doi.org/10.11248/jsta1957.16.97)
- Ketema S. 1993. Tef (*Eragrostis tef*): Breeding, agronomy, genetic resources, utilization, and role in Ethiopian agriculture. Ethiopian Institute of Agricultural Research (EIAR), Addis Ababa, Ethiopia. hdl.handle.net/123456789/2177
- Ketema S. 1997. Tef. *Eragrostis tef* (Zucc.) Trotter. Promoting the conservation and use of underutilized and neglected crops No. 12. Institute of Plant Genetics and Crop Plant Research (IPK) and International Plant Genetic Resources Institute (IGPRI), Gatersleben, Germany and Rome, Italy. bit.ly/2wNzDEp
- Khan MA; Shaikh F; Zehra A; Ahmed MZ; Bilquees G; Ansari R. 2017. Role of chemicals in alleviating salinity and light related seed dormancy in sub-tropical grasses. *Flora* 233:150–155. doi: [10.1016/j.flora.2017.06.001](https://doi.org/10.1016/j.flora.2017.06.001)
- Korkmaz A. 2005. Inclusion of acetyl salicylic acid and methyl jasmonate into the priming solution improves low-temperature germination and emergence of sweet pepper. *HortScience* 40:197–200. doi: [10.21273/HORTSCI.40.1.197](https://doi.org/10.21273/HORTSCI.40.1.197)
- Kreitschitz A; Tadele Z; Gola EM. 2009. Slime cells on the surface of *Eragrostis* seeds maintain a level of moisture around the grain to enhance germination. *Seed Science Research* 19:27–35. doi: [10.1017/S0960258508186287](https://doi.org/10.1017/S0960258508186287)
- Kučko A; Czeszewska-Rosiak G; Wolska M; Glazińska P; Kopcewicz J; Wilmowicz E. 2017. Auxin increases the *InJMT* expression and the level of JAMe-inhibitor of flower induction in *Ipomoea nil*. *Acta Societatis Botanicorum Poloniae* 86:3518. doi: [10.5586/asbp.3518](https://doi.org/10.5586/asbp.3518)
- Lee HS; Aim SN; Sasaki K; Chung NJ; Choi KS; Sato T. 2010. Identification of molecular markers for photoblastism in weedy rice. *Korean Journal of Breeding Science* 42:144–150. bit.ly/2F2d0k5
- Lindig-Cisneros R; Zedler J. 2001. Effect of light on seed germination in *Phalaris arundinacea* L. (reed canary grass). *Plant Ecology* 155:75–78. doi: [10.1023/A:1013224514980](https://doi.org/10.1023/A:1013224514980)

- Matakiadis T; Alboresi A; Jikumaru Y; Tatematsu K; Pichon O; Renou JP; Kamiya Y; Nambara E; Truong HN. 2009. The *Arabidopsis* abscisic acid catabolic gene *CYP707A2* plays a key role in nitrate control of seed dormancy. *Plant Physiology* 149:949–960. doi: [10.1104/pp.108.126938](https://doi.org/10.1104/pp.108.126938)
- Meyer SE; Debaene-Gill SB; Allen PS. 2000. Using hydrothermal time concepts to model seed germination response to temperature, dormancy loss, and priming effects in *Elymus elymoides*. *Seed Science Research* 10:213–223. doi: [10.1017/S0960258500000246](https://doi.org/10.1017/S0960258500000246)
- Murray G; Swensen JB; Gallian JJ. 1993. Emergence of sugar beet seedlings at low soil temperature following seed soaking and priming. *HortScience* 28:31–32. doi: [10.21273/HORTSCI.28.1.31](https://doi.org/10.21273/HORTSCI.28.1.31)
- Nakabayashi K; Bartsch M; Xiang Y; Miatton E; Pellengahr S; Yano R; Seo M; Soppe WJJ. 2012. The time required for dormancy release in *Arabidopsis* is determined by Delay of Germination1 protein levels in freshly harvested seeds. *The Plant Cell* 24:2826–2838. doi: [10.1105/tpc.112.100214](https://doi.org/10.1105/tpc.112.100214)
- Nee G; Xiang Y; Soppe WJJ. 2017. The release of dormancy, a wake-up call for seeds to germinate. *Current Opinion in Plant Biology* 35:8–14. doi: [10.1016/j.pbi.2016.09.002](https://doi.org/10.1016/j.pbi.2016.09.002)
- Ogawa M; Hanada A; Yamauchi Y; Kuwahara A; Kamiya Y; Yamaguchi S. 2003. Gibberellin biosynthesis and response during *Arabidopsis* seed germination. *The Plant Cell* 15:1591–1604. doi: [10.1105/tpc.011650](https://doi.org/10.1105/tpc.011650)
- Pill WG. 1995. Low water potential and pre-sowing germination treatments to improve seed quality. In: Gough RE, ed. *Seed quality: Basic mechanisms and agricultural implications*. CRC Press, Boca Raton, FL, USA. p. 319–359. [bit.ly/2MOctZw](https://doi.org/10.1016/j.pbi.2016.09.002)
- Ranjan R; Lewak S. 1992. Jasmonic acid promotes germination and lipase activity in non-stratified apple embryos. *Physiologia Plantarum* 86:335–339. doi: [10.1034/j.1399-3054.1992.860222.x](https://doi.org/10.1034/j.1399-3054.1992.860222.x)
- SAS. 1997. User software: Changes and enhancements through release. Version 6.12. SAS Institute Inc., Cary, NC, USA.
- Sawada Y; Aoki M; Nakaminami K; Mitsuhashi W; Tatematsu K; Kushihiro T; Koshihara T; Kamiya Y; Inoue Y; Nambara E; Toyomasu T. 2008. Phytochrome- and gibberellin-mediated regulation of abscisic acid metabolism during germination of photoblastic lettuce seeds. *Plant Physiology* 146:1386–1396. doi: [10.1104/pp.107.115162](https://doi.org/10.1104/pp.107.115162)
- Schonbeck MW; Egley GH. 1981. Changes in sensitivity of *Amaranthus retroflexus* L. seeds to ethylene during preincubation. II. Effects of alternating temperature and burial in soil. *Plant, Cell & Environment* 4:237–242. doi: [10.1111/1365-3040.ep11611005](https://doi.org/10.1111/1365-3040.ep11611005)
- Seo M; Nambara E; Choi G; Yamaguchi S. 2009. Interaction of light and hormone signals in germinating seeds. *Plant Molecular Biology* 69:463–472. doi: [10.1007/s11103-008-9429-y](https://doi.org/10.1007/s11103-008-9429-y)
- Shen W; Yao X; Ye T; Ma S; Liu X; Yin X; Wu Y. 2018. *Arabidopsis* aspartic protease ASPG1 affects seed dormancy, seed longevity and seed germination. *Plant & Cell Physiology* 59:1415–431. doi: [10.1093/pcp/pcy070](https://doi.org/10.1093/pcp/pcy070)
- Sherp AM; Westfall CS; Alvarez S; Jez JM. 2018. *Arabidopsis thaliana* GH3.15 acyl acid amido synthetase has a highly specific substrate preference for the auxin precursor indole-3-butyric acid. *Journal of Biological Chemistry* 293:4277–4288. doi: [10.1074/jbc.RA118.002006](https://doi.org/10.1074/jbc.RA118.002006)
- Shu K; Liu XD; Xie Q; He ZH. 2016. Two faces of one seed: Hormonal regulation of dormancy and germination. *Molecular Plant* 9:34–45. doi: [10.1016/j.molp.2015.08.010](https://doi.org/10.1016/j.molp.2015.08.010)
- Spaenij-Dekking L; Kooy-Winkelaar Y; Koning F. 2005. The Ethiopian cereal Tef in celiac disease. *The New England Journal of Medicine* 353:1748–1749. doi: [10.1056/NEJMc051492](https://doi.org/10.1056/NEJMc051492)
- Steadman KJ; Bignell GP; Ellery AJ. 2003. Field assessment of thermal after-ripening time for dormancy release prediction in *Lolium rigidum* seeds. *Weed Research* 43:458–465. doi: [10.1046/j.0043-1737.2003.00363.x](https://doi.org/10.1046/j.0043-1737.2003.00363.x)
- Tiriyaki I. 2006. Priming and storage of amaranth seeds: Effects of plant growth regulators on germination performance at low temperature. *Seed Science and Technology* 34:169–179. doi: [10.15258/sst.2006.34.1.18](https://doi.org/10.15258/sst.2006.34.1.18)
- Tiriyaki I; Staswick PE. 2002. An *Arabidopsis* mutant defective in jasmonate response is allelic to the auxin-signaling mutant *axr1*. *Plant Physiology* 130:887–894. doi: [10.1104/pp.005272](https://doi.org/10.1104/pp.005272)
- Tiriyaki I; Korkmaz A; Nas MN; Ozbay N. 2005. Priming combined with plant growth regulators promotes germination and emergence of dormant *Amaranthus cruentus* L. seeds. *Seed Science and Technology* 33:571–579. doi: [10.15258/sst.2005.33.3.05](https://doi.org/10.15258/sst.2005.33.3.05)
- Tiriyaki I; Ozbay N; Nas MN; Korkmaz A. 2006. Inclusion of benzyladenine into priming solution promotes germination of Kentucky bluegrass (*Poa pratensis* L.) seeds. *Cuban Journal of Agricultural Science* 40:229–234.
- Tiriyaki I; Buyukcingil Y. 2009. Seed priming combined with plant hormones: Influence on germination and seedling emergence of sorghum at low temperature. *Seed Science and Technology* 37:303–315. doi: [10.15258/sst.2009.37.2.05](https://doi.org/10.15258/sst.2009.37.2.05)
- Tiriyaki I; Keles H. 2012. Reversal of the inhibitory effect of light and high temperature on germination of *Phacelia tanacetifolia* seeds by melatonin. *Journal of Pineal Research* 52:332–339. doi: [10.1111/j.1600-079X.2011.00947.x](https://doi.org/10.1111/j.1600-079X.2011.00947.x)
- van Delden SH. 2011. On seed physiology, biomechanics and plant phenology in *Eragrostis tef*. Ph.D. Thesis. Wageningen University, Wageningen, The Netherlands. edepot.wur.nl/169451
- Varbanova M; Yamaguchi S; Yang Y; McKelvey K; Hanada A; Borochoy R; Yu F; Jikumaru Y; Ross J; Cortes D; Ma CJ; Noel JP; Mander L; Shulaev V; Kamiya Y; Rodermel S; Weiss D; Pichersky E. 2007. Methylation of gibberellins by *Arabidopsis* GAMT1 and GAMT2. *The Plant Cell* 19:32–45. doi: [10.1105/tpc.106.044602](https://doi.org/10.1105/tpc.106.044602)
- Westfall CS; Sherp AM; Zubieta C; Alvarez S; Schraft E; Marcellin R; Ramirez L; Jez JM. 2016. *Arabidopsis thaliana* GH3.5 acyl acid amido synthetase mediates metabolic crosstalk in auxin and salicylic acid homeostasis.

- Proceedings of the National Academy of Sciences of the United States of America 113:13917–13922. doi: [10.1073/pnas.1612635113](https://doi.org/10.1073/pnas.1612635113)
- Xu Q; Truong TT; Barrero JM; Jacobsen JV; Hocart CH; Gubler F. 2016. A role for jasmonates in the release of dormancy by cold stratification in wheat. *Journal of Experimental Botany* 67:3497–3508. doi: [10.1093/jxb/erw172](https://doi.org/10.1093/jxb/erw172)
- Zhu F. 2018. Chemical composition and food uses of teff (*Eragrostis tef*). *Food Chemistry* 239:402–415. doi: [10.1016/j.foodchem.2017.06.101](https://doi.org/10.1016/j.foodchem.2017.06.101)

(Received for publication 11 November 2018; accepted 12 January 2019; published 30 June 2019)

© 2019



Tropical Grasslands-Forrajes Tropicales is an open-access journal published by *International Center for Tropical Agriculture (CIAT)*. This work is licensed under the Creative Commons Attribution 4.0 International (CC BY 4.0) license. To view a copy of this license, visit <https://creativecommons.org/licenses/by/4.0/>.