ARTICLE

Germination of *Cenchrus ciliaris*, *Pennisetum divisum*, and *Panicum turgidum* is seasonally dependent

Arvind Bhatt, Willian Batista-Silva, David J. Gallacher, and Marcelo F. Pompelli

Abstract: Knowledge of optimal conditions for germination facilitates more efficient practices, such as fodder production and restoration. We assessed seeds of three grass species harvested in winter and summer 2018. Germination ability was assessed under two night/day temperature regimes (15 °C/20 °C, 20 °C/30 °C) and two photoperiod regimes (0, 12 h light per day). Winter-maturing seeds had a slightly lower mass and reduced germination. Temperature and light requirements for optimal germination were dependent on species and harvest-time. Summer-maturing seeds of all three species had higher germination rates regardless of germination temperature. Interactions among treatment temperatures and species were 0.7- to 5.4-times higher than the control, as shown by heatmaps. Therefore, attention to these factors will improve the efficiency of seedling establishment for rehabilitation work.

Key words: germination speed, grasses, halophyte, mean germination time, synchrony.

Résumé : La connaissance des conditions optimales de germination facilite la mise en œuvre de pratiques plus efficaces telles que la production et la restauration des fourrages. Les auteurs ont évalué les semences de trois espèces de graminées, récoltées à l'hiver et à l'été 2018. La capacité de germination a été évaluée sous deux régimes de température (15 °C/20 °C et 20 °C/30 °C) et deux régimes de photopériode (0 et 12 heures de lumière par jour). Les graines arrivant à maturité à l'hiver avaient une masse légèrement plus faible et une germination réduite. Les exigences de température et de lumière pour une germination optimale étaient dépendantes de l'espèce et de la période de récolte. Les graines des trois espèces arrivant à maturité à l'été avaient des taux de germination plus élevés, quelle que soit la température de germination. Les interactions entre les températures de traitement et les espèces étaient de 0,7 à 5,4 fois supérieures à celles du témoin, comme le montrent les cartes thermiques. Ainsi, l'attention portée à ces facteurs permettra d'améliorer l'efficacité d'établissement des semis pour des travaux de réhabilitation. [Traduit par la Rédaction]

Mots-clés : vitesse de germination, graminées, halophyte, temps de germination moyen, synchronie.

Introduction

Successful reproduction is essential for a plant species population to persist. Germination is under strong genetic control and environmental influence (Chiang et al. 2009; Kendall and Penfield 2012; Huang et al. 2016). Environmental cues such as temperature and rainfall strongly influence plant phenology, including the timing of seed production and dispersal (Baskin and Baskin 2014). Photoperiod during seed formation and development frequently influences seed dormancy, but direction (i.e., positive, negative, or neutral) and extent or depth of dormancy are species specific (McCarty 1995;

Gutterman 2000; Ellis 2019; Jo et al. 2019). Variation of the maternal environment during the growing season can influence seed provisioning, thus affecting dormancy and germination (Galloway 2002; Baskin and Baskin 2014). The influence of maternal conditions that is not apparent in seed morphology might still affect seed viability, particularly after long-term storage (Luzuriaga et al. 2006).

Grasses are ecologically important to arid systems as a primary ungulate feed source and for soil stabilization (van Oudtshoorn 2002). *Cenchrus ciliaris* L., *Panicum turgidum* Forssk., and *Pennisetum divisum* (Forssk. ex J.F.Gmel.) Henrard are perennial grasses distributed widely throughout

A. Bhatt. Kuwait Institute for Scientific Research, P.O. Box 24885, Safat, Kuwait; Lushan Botanical Garden, Chinese Academy of Science, Jiujiang, China.
W. Batista-Silva. Departamento de Biologia Vegetal, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil.
D.J. Gallacher. School of Life and Environmental Sciences, The University of Sydney, Narrabri NSW 2390 Australia.
M.F. Pompelli. Laboratório de Ecofisiologia Vegetal, Departamento de Botânica, Centro de Biociências, P.O. Box 50670901, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil.

Corresponding authors: Arvind Bhatt (email: drbhatt79@gmail.com); Marcelo F. Pompelli (email: mfpompelli@gmail.com).

the Arabian desert (Batanouny 2002). They are preferred by camel and sheep herders for their flocks because of their relatively high nutritional qualities (Assaeed 1997; Khan et al. 2009; Marshall et al. 2012) and have potential for rangeland rehabilitation, soil erosion control, and urban landscaping (Bolo et al. 2019). Germination studies of these species have focused on the influences of temperature, light, salinity, harvesting date, and plant growth regulating hormones (El-Keblawy 2004; Al-Khateeb 2006; El-Keblawy et al. 2011, 2014; Bhatt et al. 2018; Bhatt and Santo 2018). These studies have prioritized measurement of germination percentage and, in some cases, time to first germination; the latter of which excludes the behavior of most seeds in a sample (Bewley et al. 2013). This approach can miss some important details of the strategies used by xeric species in unfavorable environments.

Several different ways to describe seed germination and its dormancy-breaking mechanisms have been offered (Cardina and Sparrow 1997; Baskin and Baskin 1998, 2004; Bradbeer 1998; Penfield and King 2009; Bhatt and Pérez-García 2016; Elgabra et al. 2019). The time taken to complete germination is most often measured by mean germination time (MGT). MGT was proposed in 1875 by Haberlandt (Haberlandt 1875) but became commonly used much later (Laboriau and Pacheco 1978; Labouriau and Valadares 1983). Variation in germination timing can be measured by synchrony (SYN), uncertainty (UNC), or other measures such as MGT, standard deviation, or confidence intervals (Laboriau and Pacheco 1978; Labouriau and Valadares 1983). Synchrony measures the number of different days in which a batch of seeds complete germination, regardless of whether days are contiguous, whereas uncertainty (UNC) is an adaptation from the Shannon Index measuring dispersion (Laboriau and Pacheco 1978). Measures of the variation in germination timing are most useful for industrial seed production but can also assist ecologists to predict or interpret recruitment patterns (Bewley et al. 2013). Completion of germination frequencies over time tend to deviate from normality, thus justifying the use of non-parametric tests (Ranal and Santana 2006).

Heatmaps are a useful tool for visualizing physiological responses in a matrix where individual values are represented as colors. Previous greyscale heatmaps were known as shading matrices (Wilkinson and Friendly 2009), but were less appealing before color and high-resolution greyscale became commonplace. Sneath (1957) displayed results of a cluster analysis by permuting the rows and columns of a heatmap to place similar values near each other, and Loua (1973) used heatmaps to visualize social statistics across the districts of Paris. In seed science, heatmaps have helped researchers understand the function of some candidate genes encoding proteins influencing the germination process (relative mRNA expression), embryo responses to different stresses, and the relationship between maternal plant and fruit and seed development (Cleary et al.

2019; Ferreira et al. 2019; Geshnizjani et al. 2019; Jiang et al. 2019; Mérai et al. 2019; Na et al. 2019; Weidong et al. 2019; Ye et al. 2019b; Zamora-Briseño et al. 2019). Heatmaps have recently been used to express the modifications that occurs in embryos or seedlings during germination (Mérai et al. 2019; Ponnaiah et al. 2019; Tong et al. 2019; Han et al. 2020). However, the authors of this study are unaware of any scientific study using heatmaps to help understand the parameters involved in seed germination.

Improved understanding of the germination patterns for *C. ciliaris*, *P. divisum*, and *P. turgidum*, across seasons, may enable better seedling establishment during rehabilitation work in extreme environments such as deserts. We expect germination parameters to vary among species, and seasons. To test this, we examined (*i*) whether seeds produced in different seasons exhibit different germination patterns, and (*ii*) whether the light and temperature requirements for germination are affected by the season in which the seed was collected.

Materials and methods

Seed collections and climate description

Freshly matured seeds of *C. ciliaris*, *P. divisum*, and *P. turgidum* were harvested from cultivated plots at the Kuwait Institute for Scientific Research (KISR), Sulaibia, Kuwait (29°9′39″N; 47°41′24″E). Plots were >95% monocultural stands of the target species. Harvesting was conducted in December 2017 (winter) and May 2018 (summer). Seeds were collected from 35–40 maternal plants per species and season, selected from a plot transect. Seed caryopses were separated and the seeds cleaned using a hand-made rubber thresher. Each species' seed mass was determined from three 100-seed replicates in accordance with the International Seed Testing Association (Allen and Alvarez 2019). Germination experiments commenced within 10 days of harvest. Climatological data was collected from an on-site weather station at KISR, Sulaibia. Rainfall events occurred prior to both the December 2017 and May 2018 collection dates (Fig. 1).

Germination

Germination was assessed for eight treatments, of two harvest times (summer and winter), two night/day temperature regimes (15/20, 20/30 °C), and two light regimes (0 and 12 h light per day). Four 25-seed replicates were used for each treatment. The seeds were placed in 9-cm tight-fitting Petri dishes containing one disc of Whatman N° 1 filter paper moistened with 10 mL distilled water. Darkness was achieved by wrapping the Petri dishes in aluminum foil. Germination was defined as the protrusion of a radicle by ≥2 mm through the external integument, as proposed by International Seed Testing Association (Allen and Alvarez 2019). Germinated seeds under light-exposed conditions were evaluated daily for 26 consecutive days and removed from Petri dishes, whereas seeds under dark conditions were checked at the end of the 26th day.

Fig. 1. Monthly rainfall (A), maximum and minimum air temperature (B), and maximum and minimum relative humidity during 2017 in Sulaibiya, Kuwait.
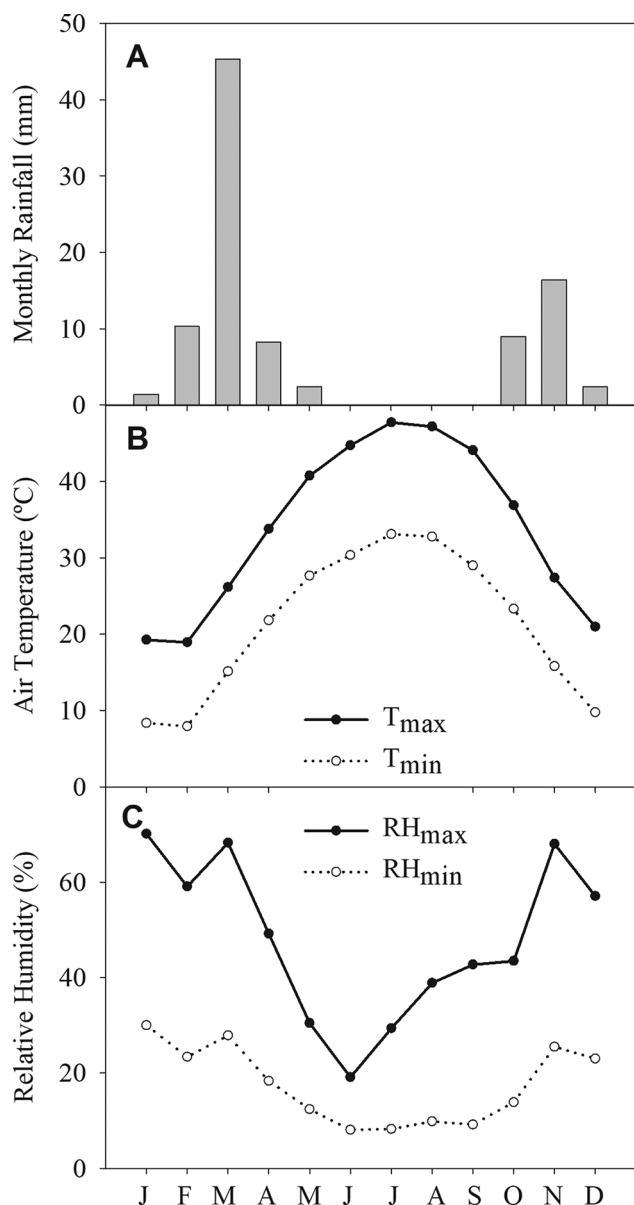
Data were arranged in a matrix of treatments and replicates in rows, and daily, non-accumulated germination in columns. Eight germination parameters were computed (Table 1) using R version 1.4.2 for Windows (Lozano-Isla et al. 2019).

Statistical analyses

Germination parameters, as listed and described in Table 1, were calculated using R version 1.4.2 (Lozano-Isla et al. 2019). Statistical analyses were conducted using Sigmaplot 14.0 (Systat Software, Inc., San José, California, USA). Pairwise comparisons of germination parameters were conducted using Pearson correlation analysis. Color standardization for heatmaps was obtained by expressing values as a ratio of the value obtained for seeds har-

vested in December and germinated in the 20/30 °C temperature regime.

Results

Seed mass

Summer-maturing seeds were heavier than winter-maturing seeds for all species, although the difference was not significant for *P. divisum* (Table 2). Seed mass positively correlated with germination capacity. This correlation was far stronger in the winter-maturing than in the summer-maturing seeds (Table 3).

Collection time and incubation temperature

Winter-maturing seeds exhibited a higher GRP for all treatments, which were statistically significant for all except *P. divisum* at the lower temperature regime. The difference was most pronounced in *P. turgidum*, which showed a 4-fold difference between seed collected in summer and winter (Fig. 2C). Higher GRP was associated with a shorter MGT in *P. divisum* ($r = -0.777$; $P = 0.0004$) and *P. turgidum* ($r = -0.758$; $P = 0.029$), but was not significant in *C. ciliaris* ($r = -0.444$; $P = 0.085$). An inverse relationship between MGT and GRP was significant in *P. divisum* ($r = -0.777$; $P = 0.0004$), and *P. turgidum* ($r = -0.758$; $P = 0.029$), but not significant in *C. ciliaris* ($r = -0.444$; $P = 0.085$). Summer-maturing seeds had a 1.7-fold higher MGT than winter-maturing seeds, regardless of incubation temperature (Fig. 2).

Synchrony (SYN) and UNC showed a strong negative correlation in *C. ciliaris* and *P. divisum*. Summer-maturing *P. divisum* seeds showed much greater SYN (Fig. 2H) but season had no clear impact in *C. ciliaris*, and SYN was not clearly influenced by incubation temperature (Figs. 2G–2I). For example, in *P. turgidum*, where germination was temporally distributed, SYN was not possible to measure but UNC among treatments was higher than other species. The UNC of summer-maturing *P. turgidum* seeds was 5- and 8-fold higher than winter-maturing seeds, compared with seeds germinated in 20/30 °C and 15/20 °C (Figs. 2J–2L). The mean SYN of summer-maturing *P. divisum* seeds was 4.5-fold higher than winter-maturing seeds (Fig. 2H), while UNC decreased 50% in summer-maturing seeds when compared with winter-maturing seeds (Fig. 2K). Winter-maturing *C. ciliaris* seeds were not significantly different for SYN and UNC when comparing collection time or even under different incubation temperatures. However, summer-maturing seeds germinated in 15/20 °C showed increased SYN (59%; Fig. 2G) and decreased UNC (12%; Fig. 2J).

Light

Photoblastic response was different in all of the species studied (Fig. 3). Photoblasticity was positive in *C. ciliaris* ($p = 0.002$), negative in *P. turgidum* ($p = 0.015$), and neutral in *P. divisum* ($p = 0.568$). *Cenchrus ciliaris* seeds were 1.5 times more likely to germinate if exposed to light. Germination in *P. turgidum* was more likely when ex-

Table 1. Germination variable descriptions and formulae.

Variables	Abbreviation	Unit	Summary	Formula (Ranal and Santana 2006)
Measures of germination volume				
Germinated seed number	GSN	Count	Sum of germinated seeds	$= \sum_{n=1}^{k} n_i$
Germination percentage	GNP	Percent	Percentage of germinated seeds	$= 100\dfrac{GSN}{N}$
Measures of germination time				
Mean germination time	MGT	Days	Average number of days it takes for a seed to germinate	$= \sum_{n=1}^{k} \dfrac{n_i i}{n_i}$
Mean germination rate	MGR	Days^{-1}	Average immediacy of germination, where the maximum value of 1 is achieved if all seeds germinate within the first day.	$= \dfrac{1}{MGT}$
Measures of the spread of germination time				
Synchrony	SYN	No units	Extent to which seeds germinate on the same day, where 0 = no overlap and 1 = complete overlap	$= \dfrac{\sum_{i=1}^{k} \frac{n_i(n_i-1)}{2}}{N}$
Uncertainty	UNC	Bits (number of binary occurrences)	Extent to which germination is dispersed over multiple days, where 0 = complete overlap and 1 = no overlap. Adapted from the Shannon Index.	$= -\sum_{i=1}^{k} \dfrac{n_i}{GSN} \log_2 \dfrac{n_i}{GSN}$
Germination standard deviation	SDG	Days	Standard deviation of MGT	$= \sqrt{\dfrac{\left[\sum_{i=1}^{k} n_i(t_i-t)^{-2}\right]}{\sum_{i=1}^{k} n_i-1}}$
Germination coefficient of variation	CVG	Percent	Coefficient of variation for MGT	$= 100\dfrac{SDG}{MGT}$

Note: The variable n_i represents the number of seeds from a batch of size N that germinated on day i, where i varies from 0 (day of moisture imbibition) to k (day of experiment termination).

Table 2. Seed mass [mean ± SE, g·(100 seeds)$^{-1}$] calculated from three 100-seed replicates.

Species	Month of seed harvest		P
	Dec. 2017	May 2018	
Cenchrus ciliaris	0.11 ± 0.01	0.14 ± 0.01	0.0064
Pennisetum divisum	0.27 ± 0.01	0.28 ± 0.01	0.1682
Panicum tugidum	0.22 ± 0.01	0.23 ± 0.01	0.0325

Note: P values indicate the significance of season on seed mass for each species, calculated using Student's t test.

posed to both darkness and a warmer incubation temperature, indicating a preference for seed burial and later-season germination.

Germination rate over time

Summer-maturing seeds of all species showed a higher germination percentage than winter-maturing seeds (Fig. 4). Germination of *C. ciliaris* continued for 10 days in all treatments except for winter-maturing seeds germinated in the cooler temperature regime, which required 14 days (Fig. 4A). Germination of *P. divisum* continued for 5 days after sowing in summer-maturing seeds and 12 days in winter-maturing seeds (Fig. 4B). An intermediate pattern was exhibited by *P. turgidum*, with summer- and winter-maturing seeds reaching maximum germination on the 9th and 10th day, respectively (Fig. 4C).

The rate of germination of the summer-maturing seeds germinated in 20/30 °C, increased 5.3-fold in *P. turgidum* and 1.3-fold in *C. ciliaris* (Fig. 5). A 1.1-fold increase in MGT was observed in *C. ciliaris*, while *P. divisum* exhibited a 45% decrease. Summer-maturing seeds, germinated at 20/30 °C increased 1.1-fold in *C. ciliaris* and 4.7-fold in *P. turgidum*. The UNC of *P. divisum* decreased 58%. Germination variance shows a similar pattern to UNC. While VGT decreased 66% in *C. ciliaris* and 83% in *P. divisum*, VGT increased 5.5-fold in *P. turgidum*. All comparisons were made between summer-maturing seeds germinated at 20/30 °C, and winter-maturing seeds germinated at 20/30 °C (Fig. 5).

Discussion

Plant survival and growth is strongly influenced by local stress factors. The timing of seed maturity and germination is important for population survival (Baskin and Baskin 2014; Lu et al. 2014). Seeds of the three studied species showed considerable differences across seasons of maturity, morphology (seed mass), and physiology (germination parameters). Winter-matured seeds were slightly smaller than summer-matured seeds. Many studies have explored how the maternal environment affects seed mass (Halpern 2005; Hoyle et al. 2008; Pompelli et al. 2010; Bhatt et al. 2018; Li et al. 2019). For example, seed mass of *Lupinus perennis* varied 1.2-fold to 4.5-fold, with the range of masses span-

Table 3. Correlation between seed mass and time of seed maturation.

Species	Winter-matured seeds		Summer-matured seeds	
	Correlation (*r*)	Significance (*P*)	Correlation (*r*)	Significance (*P*)
Cenchrus ciliaris	0.635	0.041	0.543	0.123
Pennisetum divisum	0.858	0.046	0.102	0.115
Panicum turgidum	0.977	0.004	0.981	0.022

Note: *N* = 3.

Fig. 2. Percent germination (A–C), mean germination time (MGT; D–F), synchrony (G–I), and uncertainty (J–L) of *Cenchrus ciliaris* (A, D, G, J), *Pennisetum divisum* (B, E, H, K), and *Panicum turgidum* (C, F, I, L) collected in December 2017 (black columns) and May 2018 (gray columns) and germinated under two temperature regimes. Upper-case letters denote significant differences between season of seed collection in each temperature regime, and lower-case letters denote significant differences between incubation temperatures within each season. All values presented are the mean ± SE; α = 0.01.
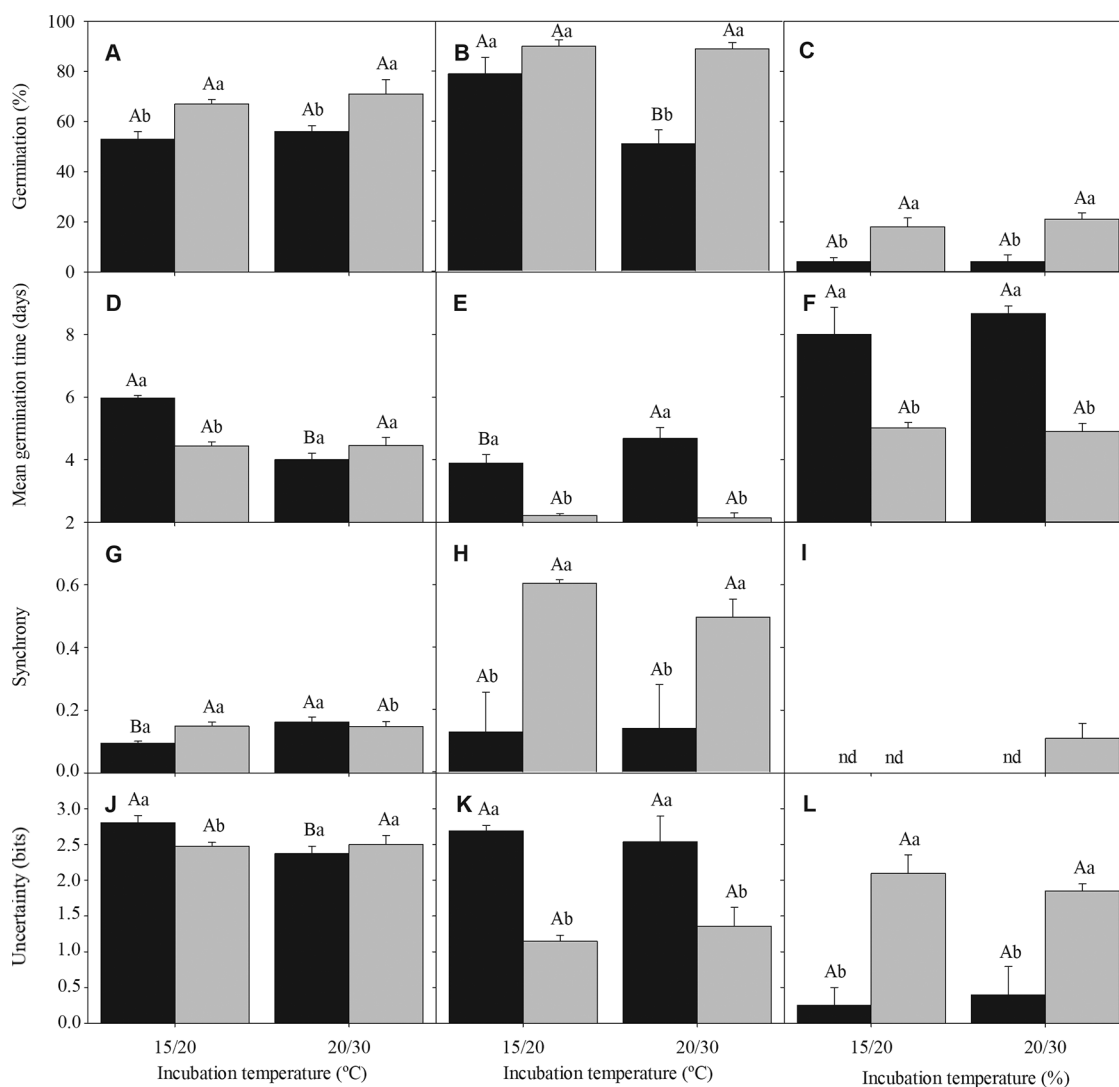

ning 4–27 mg and the coefficient of variation ranging from 0.06–0.26 (Halpern 2005). Spring-matured *Potentilla tanacetifolia* seeds were 12.4% lighter than summer-maturing seeds (Li et al. 2019). *Plantago lanceolata* seeds that matured in direct sunlight were longer than those maturing in shade, although neither light intensity nor light quality alone affected seed length (Van Hinsberg 1998).

Germination of all the studied species differed significantly between the two observed seasons. This variation in germination could be due to the variation in maternal environment during seed development and maturation. In previous studies, maternal exposure to temperature regimes, photoperiod, light intensity/quality, soil moisture, and mineral availability were all factors in determining seed dormancy and germination (Baskin and

Fig. 3. Germination percentage of *Cenchrus ciliaris* (A), *Pennisetum divisum* (B), and *Panicum turgidum* (C), under two temperature regimes germinated in light (black columns) and dark (gray columns). Upper case letters denote significant differences between photoperiods in each temperature regime, and lower case letters denote significant differences between incubation temperatures within each photoperiod. All values presented are the mean ± SE; α = 0.01.
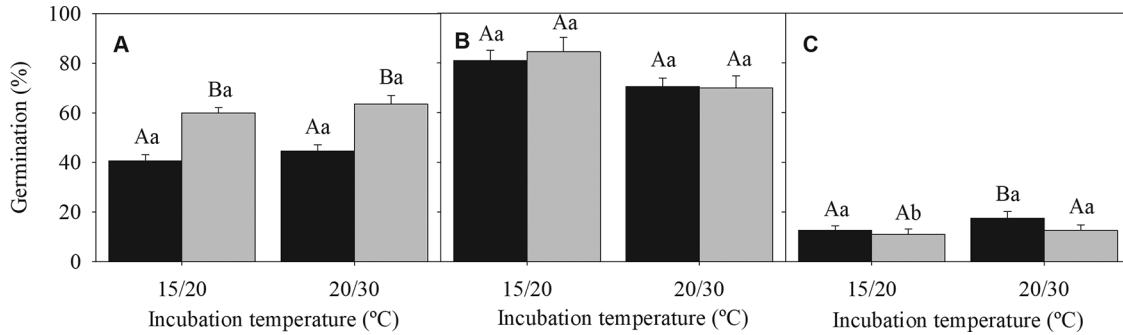
Fig. 4. Cumulative germination rate (%, mean of four replicates) of *Cenchrus ciliaris* (A), *Pennisetum divisum* (B), and *Panicum turgidum* (C) collected in two seasons and germinated under two temperature regimes.
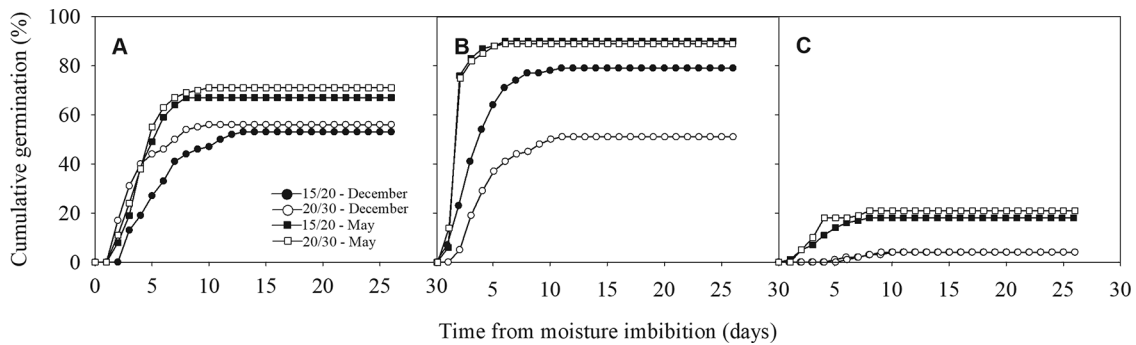
Fig. 5. Heatmap showing the effect of incubation temperature and seed harvesting time on germination parameters in *Cenchrus ciliaris*, *Pennisetum divisum*, and *Panicum turgidum* seeds. Bars directed to the left indicate an decrease, and to the right an increase, for seeds collected in December and germinated under a 20/30 °C temperature regime. For the statistical analyses, see the Supplementary data, Table S1[1].
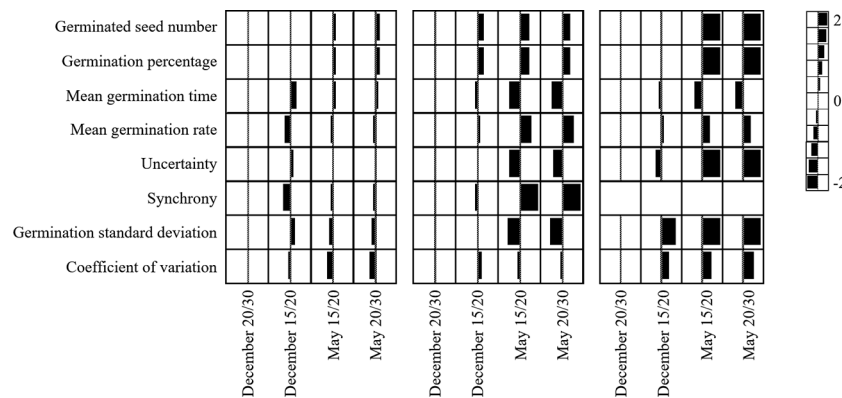
Baskin 1998; Qaderi et al. 2003; El-Keblawy and Al-Rawai 2006; Donohue et al. 2008; El-Keblawy et al. 2009). However, it is hard to predict which factors contribute to seed dormancy and germination among seasons (Bewley et al. 2013).

Seed dormancy is a common phenomenon in plants that allows them to survive adverse environmental conditions. In general, extent of dormancy was greater when seeds were matured at lower temperature regimes and shorter photoperiods (El-Keblawy et al. 2019; Elgabra et al. 2019; Ye et al. 2019a). This observation is supported by the present study, because winter-maturing seeds of all three species exhibited lower germination percentages than summer-maturing seeds. High temperature regimes during seed maturation can induce gibberellic

acid and reduce abscisic acid levels, which can act together to increase the mRNA levels for α-amylases and hydrolytic enzymes and thus increase germination potential (Kendall et al. 2011; Savaedi et al. 2019). These findings are similar to previous findings that desert seeds maturing at warm temperature regimes exhibit lower dormancy (Huang et al. 2016; Bhatt et al. 2018). Variation in photoperiod might also affect dormancy in these species, because day length varies with season. At the study site, daylight varies from approximately 12.5 h in March to May, to 10.8 h in October to December. Similar results have been observed in other species such as *Aegilops ovata* (Datta et al. 1972), *Carrichtera annua* (Zaady et al. 1997), and *Polypogon monspeliensis* (Gutterman 2000). These results indicate that environmental and maternal conditions during seed development and maturation have a critical role in determining the dormancy status of seeds. Seed maturation environment has been reported to have a significant effect on the dormancy status of seeds (Baskin and Baskin 2014). Dormancy level varied among species, with highest dormancy in *P. turgidum* and lowest in *P. divisum* irrespective of season. Previous studies also reported that *P. turgidum* has a higher degree of innate dormancy than *C. ciliaris* or *P. divisum*. These species have physiological dormancy requiring one month to two years of dry storage to overcome dormancy, depending on species (El-Keblawy 2004, 2013; Parihar and Pathak 2006; Bhatt and Santo 2018).

The present study demonstrates that optimum temperature regimes for germination vary significantly among the studied species and collection times. Seeds of *P. divisum* presented a higher germination percentage than the other studied species. Summer-maturing *P. divisum* seeds showed a germination percentage near 100%, whereas winter-maturing seeds showed germination rates of about 80% and 50% in seed incubated at 15/20 °C or 20/30 °C, respectively. *Cenchrus ciliaris* showed a similar pattern to *P. divisum*, with summer-maturing seeds germinating more than winter-maturing seeds. Incubation temperature regimes affected seed germination. The germination rate of summer-maturing *C. ciliaris* seeds incubated at 15/20 °C or 20/30 °C was 1.3-fold higher than the winter-maturing seeds germinated at the same temperature regime. The results for *P. divisum* and *C. ciliaris* demonstrate that seeds could germinate at any time when moisture conditions are favorable for their germination and seedling establishment. *Panicum turgidum* showed the lowest rate of seed germination of all the studied species, and the incubation temperature regimes did not show any significant effect on seed germination. Previous studies on temperature regimes during germination of *P. turgidum* showed results that corroborate those presented in this study, reporting that *P. turgidum* germinated equally well in a wide range of temperature regimes (Al-Khateeb 2006; Bhatt and Santo 2018). These results are in accordance with previous studies, where local climate of seed provenance has been found to be an important factor and responsible for changing the germination sensitivity to germination temperature regimes (El-Keblawy et al. 2016, 2017). However, winter-maturing *P. divisum* seeds showed significantly higher germination at lower temperature regimes, but summer-maturing seeds showed no difference in germination percentage among the tested temperature regimes. The lower temperature regimes for germination of winter-maturing seeds may be an ecological advantage because they may complete germination more readily after maturation to take advantage of the better conditions for seedling survival (Omar et al. 2007).

In the present study, *P. divisum* seeds germinated equally well in light and dark treatments irrespective of collection season. Sand burial is common in deserts, thus a neutral photoblasticity increases the chances of germination in the natural environment (Lai et al. 2016; Ye et al. 2019a). However, the germination percentages of *C. ciliaris* seeds under both incubation temperature regimes expressed positive photoblasticity, while results for *P. turgidum* were mixed but small. Rehabilitation work therefore requires precautions to minimize the burial of *C. ciliaris* seeds. The interseason variation in seed mass, dormancy, and germination might be associated with differences in maternal environment. Prediction of this factor would enable batch-specific seed management.

The results from this study contrast those of another desert halophyte *Brachypodium hybridum* (Elgabra et al. 2019). The final germination percentage of *B. hybridum* was significantly greater at 15/25 °C and 20/30 °C than at 25/35 °C and in light rather than in darkness. Seeds that reached maturity at 15/25 °C attained greater germination rates than those that reached maturity at 20/30 °C. Lower germination percentage of winter-harvested seeds of all the studied species could be attributed to lower water availability, because these seeds faced more severe temperatures during their formation and maturation, which might hasten the natural dehydration process of seed by changing integument structure and enhancing its permeability (Clua and Gimenez 2004).

Conclusions

This study has demonstrated the use of heatmaps to visualize the influence of treatments on seed germination parameters. Germination analysis, however accurate, can often give rise to double interpretation, which is easily identified by heatmaps. The adoption of this technique in seed technology and ecophysiology could provide a powerful tool to seed researchers.

Acknowledgements

References

Al-Khateeb, S.A. 2006. Effect of salinity and temperature on germination, growth and ion relations of *Panicum turgidum* Forssk. Bioresour. Technol. **97**(2): 292–298. doi:10.1016/j.biortech.2005.02.041.

Allen, E., and Alvarez, S. 2019. International rules for seed testing 2019. The International Seed Testing Association, Zürichstr, Bassersdorf, Switzerland.

Assaeed, A.M. 1997. Estimation of biomass and utilization of three perennial range grasses in Saudi Arabia. J. Arid Environ. **36**(1): 103–111. doi:10.1006/jare.1996.0200.

Baskin, C.C., and Baskin, J.M. 1998. Seeds: ecology, biogeography and evolution of dormancy and germination. Academic Press, San Diego, Calif.

Baskin, C.C., and Baskin, J.M. 2014. Seeds: ecology, biogeography and evolution of dormancy and germination. 2nd ed. Elsevier, San Diego, Calif.

Baskin, J.M., and Baskin, C.C. 2004. A classification system for seed dormancy. Seed Sci. Res. **14**(1): 1–16. doi:10.1079/SSR2003150.

Batanouny, K.H. 2002. Biodiversity strategy and rangelands in the Arab world. *In* National biodiversity planning in the Arab world. *Edited by* R. Hamzah, M.N. Alaa El-Din, and S.A. Mohammed. Arabian Gulf University Publication, Bahrain. pp. 121–142.

Bewley, J.D., Bradford, K.J., Hilhorst, H.W.M., and Nonogaki, H. 2013. Seeds: physiology of development, germination and dormancy. 3rd ed. Springer-Verlag, New York.

Bhatt, A., and Pérez-García, F. 2016. Seed dormancy of *Ochradenus baccatus* (*Resedaceae*), a shrubby species from Arabian Desert regions. Rev. Biol. Trop. **64**(3): 965–974. doi:10.15517/rbt.v64i3.19824. PMID:29461763.

Bhatt, A., and Santo, A. 2018. Different ecological strategies during the seed germination phase of nine grasses inhabiting the hyper-arid Arabian Desert. Plant Species Biol. **33**(4): 305–311. doi:10.1111/1442-1984.12220.

Bhatt, A., Phondani, P.C., and Pompelli, M.F. 2018. Seed maturation time influences the germination requirements of perennial grasses in desert climate of Arabian Gulf. Saudi J. Biol. Sci. **25**(8): 1562–1567. doi:10.1016/j.sjbs.2016.02.004. PMID:30581318.

Bolo, P.O., Sommer, R., Kihara, J., Kinyua, M., Nyawira, S., and Notenbaert, A. 2019. Rangeland degradation: causes, consequences, monitoring techniques and remedies. Working Paper. CIAT Publication No. 478. International Center for Tropical Agriculture (CIAT), Nairobi, Kenya.

Bradbeer, J.W. 1998. Seed dormancy and germination. Chapman and Hall, New York.

Cardina, J., and Sparrow, D.H. 1997. Temporal changes in velvetleaf (*Abutilon theophrasti*) seed dormancy. Weed Sci. **45**(1): 61–66. doi:10.1017/S0043174500092481.

Chiang, G.C., Barua, D., Kramer, E.M., Amasino, R.M., and Donohue, K. 2009. Major flowering time gene, FLOWERING LOCUS C, regulates seed germination in *Arabidopsis thaliana*. Proc. Natl. Acad. Sci. U.S.A. **106**(28): 11661–11666. doi:10.1073/pnas.0901367106. PMID:19564609.

Cleary, M., Oskay, F., Doğmuş, F., Lehtjärvi, A., Woodward, S., and Vettraino, A.M. 2019. Cryptic risks to forest biosecurity associated with the global movement of commercial seed. Forests, **10**(5): 459. doi:10.3390/f10050459.

Clua, A.A., and Gimenez, D.O. 2004. Environmental factors during seed development of narrow-leaved bird's-foot-trefoil (*Lotus tenuis*) influences subsequent dormancy and germination. Grass Forage Sci. **58**(4): 333–338. doi:10.1046/j.1365-2494.2003.00385.x.

Datta, S.C., Gutterman, Y., and Evenari, M. 1972. The influence of the origin of the mother plant on yield and germination of their caryopses in *Aegilops ovata*. Planta, **105**(2): 155–164. doi:10.1007/BF00385574. PMID:24477754.

Donohue, K., Heschel, M.S., Butler, C.M., Barua, D., Sharrock, R.A., Whitelam, G.C., and Chiang, G.C.K. 2008. Diversification of phytochrome contributions to germination as a function of seed-maturation environment. New Phytol. **177**(2): 367–379. doi:10.1111/j.1469-8137.2007.02281.x. PMID:18028293.

Elgabra, M., El-Keblawy, A., Mosa, K.A., and Soliman, S. 2019. Factors controlling seed dormancy and germination response of *Brachypodium hybridum* growing in the hot arid mountains of the Arabian Desert. Botany, **97**(7): 371–379. doi:10.1139/cjb-2018-0207.

El-Keblawy, A. 2004. Salinity effects on seed germination of the common desert range grass, *Panicum turgidum*. Seed Sci. Technol. **32**(3): 873–878. doi:10.15258/sst.2004.32.3.24.

El-Keblawy, A. 2013. Impacts of dormancy-regulating chemicals on innate and salinity-induced dormancy of four forage grasses native to Arabian deserts. Grass Forage Sci. **68**(2): 288–296. doi:10.1111/j.1365-2494.2012.00901.x.

El-Keblawy, A., and Al-Rawai, A. 2006. Effects of seed maturation time and dry storage on light and temperature requirements during germination in invasive *Prosopis juliflora*. Flora, **201**: 135–143. doi:10.1016/j.flora.2005.04.009.

El-Keblawy, A., Al-Sodany, Y.M., and Al-Hadad, F.A. 2009. Effects of time of seed maturation on dormancy and germination requirements of *Sporobolus spicatus* (Vahl) Kunth, a native desert grass of the United Arab Emirates. Grassl. Sci. **55**(1): 11–17. doi:10.1111/j.1744-697X.2009.00131.x.

El-Keblawy, A., Al-Ansari, F., and Al-Shamsi, N. 2011. Effects of temperature and light on salinity tolerance during germination in two desert glycophytic grasses, *Lasiurus scindicus* and *Panicum turgidum*. Grass Forage Sci. **66**(2): 173–182. doi:10.1111/j.1365-2494.2010.00773.x.

El-Keblawy, A., Bhatt, A., and Gairola, S. 2014. Perianth colour affects germination behaviour in wind-pollinated *Salsola rubescens* in Arabian Deserts. Botany, **92**(1): 69–75. doi:10.1139/cjb-2013-0183.

El-Keblawy, A., Gairola, S., and Bhatt, A. 2016. Maternal salinity environment affects salt tolerance during germination in *Anabasis setifera*: a facultative desert halophyte. J. Arid Land, **8**(2): 254–263. doi:10.1007/s40333-015-0023-2.

El-Keblawy, A., Gairola, S., Bhatt, A., and Mahmoud, T. 2017. Effects of maternal salinity on salt tolerance during germination of *Suaedaa egyptiaca*: a facultative halophyte in the Arab Gulf desert. Plant Species Biol. **32**(1): 45–53. doi:10.1111/1442-1984.12127.

El-Keblawy, A., Soliman, S., Al-Khoury, R., Ghauri, A., Al Rammah, H., Hussain, S.E., et al. 2019. Effect of maturation conditions on light and temperature requirements during seed germination of *Citrullus colocynthis* from the Arabian Desert. Plant Biol. **21**(2): 292–299. doi:10.1111/plb.12923. PMID:30311346.

Ellis, R.H. 2019. Temporal patterns of seed quality development, decline, and timing of maximum quality during seed development and maturation. Seed Sci. Res. **29**(2): 135–142. doi:10.1017/S0960258519000102.

Ferreira, M.D.G., Castro, J.A., Silva, R.J.S., and Micheli, F. 2019. HVA22 from citrus: a small gene family whose some members are involved in plant response to abiotic stress. Plant Physiol. Biochem. **142**: 395–404. doi:10.1016/j.plaphy.2019.08.003. PMID:31408843.

Galloway, L.F. 2002. The effect of maternal phenology on offspring characters in the herbaceous plant *Campanula americana*. J. Ecol. **90**(5): 851–858. doi:10.1046/j.1365-2745.2002.00714.x.

Geshnizjani, N., Khorami, S.S., Willems, L.A.J., Snoek, B.L., Hilhorst, H.W.M., and Ligterink, W. 2019. The interaction between genotype and maternal nutritional environments affects tomato seed and seedling quality. J. Exp. Bot. **70**(10): 2905–2918. doi:10.1093/jxb/erz101. PMID:30828721.

Gutterman, Y. 2000. Maternal effects on seeds during development. *In* Seeds: the ecology of regeneration in plant communities. *Edited by* M. Fenner. CAB International, Wallingford, UK. pp. 59–84.

Haberlandt, F. 1875. Die untere und obere Temperaturgrenze fiir die Keimung einigicer Kulturpflanzeni warmere Klimate. Haberlandt's wiss. prakt. Unters. auf dem Gebiete des Pflanzenbaues, **1**: 117–122.

Halpern, S.L. 2005. Sources and consequences of seed size variation in *Lupinus perennis* (Fabaceae): adaptive and non-adaptive hypotheses. Am. J. Bot. **92**(2): 205–213. doi:10.3732/ajb.92.2.205. PMID:21652397.

Han, Z., Wang, B., Tian, L., Wang, S., Zhang, J., Guio, S., et al. 2020. Comprehensive dynamic transcriptome analysis at two seed germination stages in maize (*Zea mays* L.). Physiol. Planta. **168**(1): 205–217. doi:10.1111/ppl.12944. PMID:30767243.

Hoyle, G.L., Steadman, K., Daws, M.I., and Adkins, S. 2008. Pre- and post-harvest influences on seed dormancy status of an Australian Goodeniaceae species, *Goodenia fascicularis*. Ann. Bot. **102**(1): 93–101. doi:10.1093/aob/mcn062. PMID:18430743.

Huang, Z., Liu, S., Bradford, K.J., Huxman, T.E., and Venable, D.L. 2016. The contribution of germination functional traits to population dynamics of a desert plant community. Ecology, **97**(1): 250–261. doi:10.1890/15-0744.1. PMID:27008793.

Jiang, J., Zhu, S., Yuan, Y., Wang, Y., Zeng, L., Batley, J., and Wang, Y.-P. 2019. Transcriptomic comparison between developing seeds of yellow- and black-seeded *Brassica napus* reveals that genes influence seed quality. BMC Plant Biol. **19**: 209. doi:10.1186/s12870-019-1821-z.

Jo, L., Pelletier, J.M., and Harada, J.J. 2019. Central role of the LEAFY COTYLEDON1 transcription factor in seed development. J. Integr. Plant Biol. **61**(5): 564–580. doi:10.1111/jipb.12806. PMID:30916433.

Kendall, S., and Penfield, S. 2012. Maternal and zygotic temperature signalling in the control of seed dormancy and germination. Seed Sci. Res. **22**(S1): S23–S29. doi:10.1017/S0960258511000390.

Kendall, S.L., Hellwege, A., Marriot, P., Whalley, C., Graham, I.A., and Penfield, S. 2011. Induction of dormancy in *Arabidopsis* summer annuals requires parallel regulation of DOG1 and hormone metabolism by low temperature and CBF transcription factors. Plant Cell, **23**(7): 2568–2580. doi:10.1105/tpc.111.087643. PMID:21803937.

Khan, M.A., Ansari, R., Ali, H., Gul, B., and Nielsen, B.L. 2009. *Panicum turgidum*, a potentially sustainable cattle feed alternative to maize for saline areas. Agric. Ecol. Environ. **129**(4): 542–546. doi:10.1016/j.agee.2008.10.014.

Laboriau, L.G., and Pacheco, A.A. 1978. On the frequency of isothermal germination in seeds of *Dolichos biflorus* L. Plant Cell Physiol. **19**(3): 507–512. doi:10.1093/oxfordjournals.pcp.a075620.

Labouriau, L.G., and Valadares, M.E.B. 1983. The germination of seeds. OEA, Washington, D.C.

Lai, L., Chen, L., Jiang, L., Zhou, J., Zheng, Y., and Shimizu, H. 2016. Seed germination of seven desert plants and implications for vegetation restoration. AoB Plants, **8**: plw031. doi:10.1093/aobpla/plw031. PMID:27179541.

Li, Y., Hou, L., Song, B., Wan, S., Sun, X., and Li, L. 2019. Seasonal distribution of increased precipitation in maternal environments influences offspring performance of *Potentilla tanacetifolia* in a temperate steppe ecosystem. J. Plant Ecol. (U.K.), **12**(4): 742–750. doi:10.1093/jpe/rtz011.

Loua, T. 1973. Atlas statistique de la population de Paris. J. Dejey, Paris, France.

Lozano-Isla, F., Alfaro, O.B., and Pompelli, M.F. 2019. GerminaR: an R package for germination analysis with the interactive web application 'GerminaQuant for R'. Ecol. Res. **34**: 339–346. doi:10.1111/1440-1703.1275.

Lu, J.J., Tan, D.Y., Baskin, J.M., and Baskin, C.C. 2014. Germination season and watering regime, but not seed morph, affect life history traits in a cold desert diaspore-heteromorphic annual. PLoS ONE, **9**(7): e102018. doi:10.1371/journal.pone.0102018. PMID:25013967.

Luzuriaga, A.L., Escudero, A., and Pérez-García, F. 2006. Environmental maternal effects on seed morphology and germination in *Sinapis arvensis* (*Cruciferae*). Weed Res. **46**(2): 163–174. doi:10.1111/j.1365-3180.2006.00496.x.

Marshall, V.M., Lewis, M.M., and Ostendorf, L.B. 2012. Buffel grass (*Cenchrus ciliaris*) as an invader and threat to biodiversity in arid environments: a review. J. Arid Environ. **78**(1): 1–12. doi:10.1016/j.jaridenv.2011.11.005.

McCarty, D.R. 1995. Genetic control and integration of maturation and germination pathways in seed development. Annu. Rev. Plant Physiol. Plant Mol. Biol. **46**(1): 71–93. doi:10.1146/annurev.pp.46.060195.000443.

Mérai, Z., Graeber, K., Wilhelmsson, P., Ullrich, K.K., Arshad, W., Grosche, C., et al. 2019. *Aethionema arabicum*: a novel model plant to study the light control of seed germination. J. Exp. Bot. **70**(12): 3313–3328. doi:10.1093/jxb/erz146. PMID:30949700.

Na, G., Mu, X., Grabowski, P., Schmutz, J., and Lu, C. 2019. Enhancing microRNA167A expression in seed decreases the α-linolenic acid content and increases seed size in *Camelina sativa*. Plant J. **98**(2): 346–358. doi:10.1111/tpj.14223. PMID:30604453.

Omar, S.A.S., Al-Mutawa, Y., and Zaman, S. 2007. Vegetation of Kuwait. Kuwait Institute for Scientific Research, Kuwait.

Parihar, S.S., and Pathak, P.S. 2006. Flowering phenology and seed biology of selected tropical perennial grasses. Trop. Ecol. **47**(1): 81–88.

Penfield, S., and King, J. 2009. Towards a systems biology approach to understanding seed dormancy and germination. Proc. R Soc. B Biol. Sci. **276**(1673): 3561–3569. doi:10.1098/rspb.2009.0592. PMID:19605392.

Pompelli, M.F., Ferreira, D.T.R.G., Cavalcante, P.P.G.S., Salvador, T.L., Hsie, B.S., and Endres, L. 2010. Environmental influence on the physico-chemical and physiological properties of *Jatropha curcas* L. seeds. Aust. J. Bot. **58**(6): 421–427. doi:10.1071/BT10102.

Ponnaiah, M., Gilard, F., Gakière, B., El-Maarouf-Bouteau, H., and Bailly, C. 2019. Regulatory actors and alternative routes for *Arabidopsis* seed germination are revealed using a pathway-based analysis of transcriptomic datasets. Plant J. **99**(1): 163–175. doi:10.1111/tpj.14311. PMID:30868664.

Qaderi, M.M., Cavers, P.B., and Bernards, M.A. 2003. Pre- and post-dispersal factors regulate germination patterns and structural characteristics of Scotch thistle (*Onopordum acanthium*) cypselas. New Phytol. **159**(1): 263–278. doi:10.1046/j.1469-8137.2003.00777.x.

Ranal, M.A., and Santana, D.G.D. 2006. How and why to measure the germination process?. Braz. J. Bot. **29**(1): 1–11.

Savaedi, Z., Parmoon, G., Moosavi, S.A., and Bakhshande, A. 2019. The role of light and gibberellic acid on cardinal temperatures and thermal time required for germination of Charnushka (*Nigella sativa*) seed. Ind. Crop Prod. **132**: 140–149. doi:10.1016/j.indcrop.2019.02.025.

Sneath, P. 1957. The application of computers to taxonomy. J. Gen. Microbiol. **17**: 201–226. doi:10.1099/00221287-17-1-201. PMID:13475686.

Tong, J., He, R., Tang, X., Li, M., and Yi, T. 2019. RNA-sequencing analysis reveals critical roles of hormone metabolism and signaling transduction in seed germination of *Andrographis paniculata*. J. Plant Growth Regul. **38**(1): 273–282. doi:10.1007/s00344-018-9839-2.

Van Hinsberg, A. 1998. Maternal and ambient environmental effects of light on germination in *Plantago lanceolata*: correlated responses to selection on leaf length. Funct. Ecol. **12**(5): 825–833. doi:10.1046/j.1365-2435.1998.00251.x.

van Oudtshoorn, F. 2002. Guide to grasses of southern Africa. Briza Publications, Pretoria, South Africa.

Weidong, W., Tong, G., Jiangfei, C., Jiankun, Y., Huiyu, H., and Youben, Y. 2019. The late embryogenesis abundant gene family in tea plant (*Camellia sinensis*): genome-wide charac-

terization and expression analysis in response to cold and dehydration stress. Plant Physiol. Biochem. **135**: 277–286. doi:10.1016/j.plaphy.2018.12.009. PMID:30593000.

Wilkinson, L., and Friendly, M. 2009. The history of the cluster heat map. Am. Stat. **63**(2): 179–184. doi:10.1198/tas.2009.0033.

Ye, X., Li, L., Baskin, C.C., Baskin, J.M., Du, J., and Huang, Z. 2019*a*. Sand burial helps regulate timing of seed germination of a dominant herb in an inland dune ecosystem with a semi-arid temperate climate. Sci. Total Environ. **680**: 44–50. doi:10.1016/j.scitotenv.2019.05.087. PMID:31100667.

Ye, X., Wang, H., Cao, X.L., Jin, X., Cui, F., Bu, Y., et al. 2019*b*. Transcriptome profiling of *Puccinellia tenuiflora* during seed germination under a long-term saline-alkali stress. BMC Genomics, **20**: 589. doi:10.1186/s12864-019-5860-5. PMID:31315555.

Zaady, E., Gutterman, Y., and Boeken, B. 1997. The germination of mucilaginous seeds of *Plantago coronopus*, *Reboudia pinnata*, and *Carrichtera annua* on cyanobacterial soil crust from the Negev Desert. Plant Soil, **190**(2): 247–252. doi:10.1023/A:1004269031844.

Zamora-Briseño, J.A., Pereira-Santana, A., Reyes-Hernández, S.J., Castaño, E., and Rodríguez-Zapata, L.C. 2019. Global dynamics in protein disorder during maize seed development. Genes, **10**(7): 502. doi:10.3390/genes10070502. PMID:31262071.