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Drought tolerance classification of common oilseed species using seed germination assay

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Abstract

Drought stress delays the onset of germination, reduces germination rate and percentage and reduces normal seedling emergence which may limit plant growth and crop yield.This study quantified the germination responses of 10 industrial and edible oilseed crops (*Brassica alba, B. carinata, B. juncea, B. napus, B. rapa, Camelina sativa, Crambe abyssincia, Thlaspi arvense, Arachis hypogea* and *Glycine max*) at different levels of osmotic potential (OP) to determine the effect of OP on germination time course, maximum seed germination (MSG), time to 50% seed germination (T_{50}), and germination rate (GR). Maximum germination varied with different levels of OP. MSG and GR decreased with decreasing OP and the time required for the onset of germination increased with decreasing OP. Averaged across species, there were 10, 22, 38 and 62 hours delay in onset of germination when OP was gradually decreased from 0 MPa (control) to -0.2 MPa, -0.4 MPa, -0.6 MPa and -0.8 MPa respectively. The time to 50% germination increased across species and germination rate decreased linearly with decreasing OP. The average time to reach 50% of MSG increased 10, 42, 70 and 142 % with decreasing OP and GR decreased by 8, 27, 39 and 58% when OP changed from 0 MPa to -0.2, -0.4.-0.6 and -0.8 MPa respectively. Based on the T_{50} drought tolerance index and GR index, *juncea*, *carinata* and *pennycress* were more drought tolerant, canola and *rapa* were considered as intermediate drought tolerant and other species (soybean, peanut, a*lba*, *camelina* and *crambe*) were drought susceptible. The effect of OP on onset of germination, time to 50% germination, MSG and GR arose from the inhibitory effect of OP reduction on the overall process of germination when OP decreased from 0 MPa.The species-specific functions can be used to model germination under variable moisture stress conditions.

Keywords: *Drought tolerance, germination rate, Oilseed crops, polyethylene glycol, maximum seed germination*

Introduction

Biofuels are an alternative renewable source of energy capable of reducing net greenhouse gas emissions (Nelson *et al*., 2014) while alleviating current and future world energy and economic crisis (Alagumalai, 2014). Greater than 80% of global energy consumption is from fossil fuels, of which 58% is used in the transportation sector as liquid transportation fuels (Escobar *et al*., 2009). Currently, biofuels account for 3.5% of the world's fuel usage for road transportation, which is forecasted to increase to 25% by 2050 (ENMC, 2016) (ENMC, 2016).Plant sourced fuels provide a renewable and sustainable alternative to fossil fuels (Singh, 2010). Corn and soybean are the most common crops used for ethanol and biodiesel production in the US while rapeseed (canola) is the dominant biodiesel feedstock in Europe (Extension, 2014). In Europe, 66% of total biodiesel was produced from canola while soybean and palm oil accounted for 13 and 12% respectively (Junginger *et al*., 2014). To meet the demands for biofuels, emerging novel alternative oilseed feedstocks are currently being developed including *carinata*, mustard, pennycress, *camelina, rapa* and *juncea* (Zanetti *et al*., 2013).

For the commercial success of emerging second and third generation advanced biofuel feedstocks, high rates of germination, emergence and stand establishment are required for high yields. Seed germination under suboptimal conditions is key in determining emergence, establishment and subsequent yield and productivity. Many internal (seed viability maturation, dormancy, and genotype etc.) and external factors (water, oxygen, temperature, light etc.) have an effect on seed germination (Durr *et al*., 2016; Wang *et al.*, 2016). Among the external environmental factors, temperature and drought stress determines the periodicity of germination (Torabi*et al*., 2016) and even the distribution of species (Seepaul, 2012, Shelef *et al.*, 2016). Osmotic stress have an effect on germination and development of the crops depending on the severity of the stress (Panuccio *et al*., 2014). Germination may be delayed when water stress < -0.4 MPa or reduced by up to 30% when water stress< -0.6 MPa (Patanè *et al*., 2013).

Germination studies can be used to establish an adaptive range of a given species to drought stress as well as influence of stress on germination properties which could be useful in making decisions regarding planting in sub-optimum conditions. Germinating seeds in polyethylene glycol (PEG) solution has been successfully used as a proxy for drought conditions (Hardegree and Emmerich, 1990) to determine the effect of osmotic potential on seed germination responses of different plant species.

Among the abiotic stresses, drought is the major yield limiting factor of crops globally. Novel alternative oilseed feedstocks are currently being developed for suboptimal conditions (Zanetti *et al*., 2013). There is limited information on the germination properties of oilseed species in response to osmotic stress. The objective of this study was to identifythe effect of OP on oilseed germination properties and a proxy for drought tolerance by measuring a) maximum seed germination b) time to 50% seed germination, and c) germination rate.

Materials and Methods

Experimental setup

This controlled environment study was conducted in germination chambers at University of Florida North Florida Research and Education Center (NFREC), Quincy, FL from 28 May to 20th June 2016. Treatments were species and osmotic potential (OP). Species and OP were combined in a 7×10 factorial experiment, with each treatment combination replicated 6 times in a completely randomized design with 100 seeds per replicate. Ten oilseed species (Table 1) were germinated in Petri dishes containing different osmotic potential solutions ranging from 0 MPa to -1.2 MPa with -0.2 MPa increments.

The required aqueous solution of different levels of OP were prepared by calculating the requisite amount of Polyethylene Glycol 8000 (PEG) according to (Michel, 1983) (Equation 1).

Ψ=1.29 (PEG) 2T-140(PEG)2-4.0 (PEG)……..(Equation 1)

where, Ψ is OP (bars), PEG is amount of PEG (ml) and T is temperature at 25°C. The following PEG concentrations i.e. 118.9, 175, 218.2, 254.6, 286.7, and 315.7 g/L based on the equation were poured in a 1-liter volumetric flask and mixed with deionized water to make up the required solutions. Deionized water was used for the 0 MPa (control) treatment.

All seeds used in this study were grown during the 2015 growing season at NFREC Quincy, Florida and stored at 5°C. Seeds were surface sterilized with 1% bleach solution for five minutes and uniformly distributed on two layers of Whatman No. 1 filter paper in a 9 cm Petri dish (small seeds) or 15 cm Petri dish (peanut and soybean), moistened with a similar volume of deionized water (for control) or PEG solution for each level of OP.

The Petri dishes were kept at 25±0.6°C constant temperature in an incubator under dark conditions. Petri dishes were grouped by OP and placed in a 14 × 18" plastic seed tray. The number of germinated seeds in each dish was counted and removed every 6 hours until four consecutive constant germination counts were observed. Seeds with radicle length of at least 2mm were considered germinated. The seeds were moistened every 24 hours with the respective PEG solution and the filter paper was changed every 72 hours to prevent accumulation of PEG. Petri dishes and non-germinated seeds were removed after two weeks (small seeds) or three weeks (large seeds) after the first seed germination of each respective species. The position of each OP seed tray was changed every 6 hours to reduce the effect of temperature variability in the germination chamber.

Table 1. Scientific and common names, and 1000-seed weight (g) of oilseed species evaluated.

Scientific name	Common name	Family	1000-seed weight (g)
Brassica alba	Alba/Mustard yellow	Brassicaceae	4.62
Brassica carinata	Carinata/Ethiopian mustard	Brassicaceae	3.88
Brassica juncea	Indian mustard, Chinese mustard, brown mustard, leaf mustard	Brassicaceae	2.53
Brassica napus	Rape or canola	Brassicaceae	3.62
Brassica rapa	Field mustard/rape mustard	Brassicaceae	2.98
Camelina sativa	Camelina	Brassicaceae	0.57
Crambe abyssinica	Crambe	Brassicaceae	5.17
Thlaspi arvense	Pennycress	Brassicaceae	0.79
Arachis hypogaea	Peanut	Fabaceae	700.68
Glycine max	Soybean	Fabaceae	133.71

Curve fitting procedure

A four-parameter sigmoidal growth function (Equation 2 and Figure 1) was fitted to the cumulative seed germination data from each respective treatment by using SigmaPlot vers. 13 (Systat Software, Inc).

$$Y = y_0 + \alpha/\{1+\exp(-(x-x0)/b)\} \quad \text{(Equation 2)}$$

From the family of sigmoidal curves, MSG percentage (á) at time t, the shape and steepness of the response function (b), % of median germination time (T_{50}) and minimum germination value (y_0) were estimated. Maximum seed germination (MSG %) was calculated using the following formula:

$$\text{MSG \%} = \frac{\text{Total number of germinated seeds}}{\text{Total no. of seeds}} \times 100 \quad \text{(Equation 3)}$$

Similarly, time to 50% germination was calculated based on Coolbear *et al*. (1984) andmodified by Farooq *et al*. (2005) using the following formula:

Where, N is the final number of germination and ni and nj are the cumulative number of seeds germinated by adjacent counts at times ti and tj, respectively when ni< N / 2 <nj.

Similarly, germination rate (rate of development) was calculated as the reciprocal of the time to 50% seed germination using the following formula:

$$\text{Germination rate (GR)} = \frac{1}{T50} \quad \text{(Equation 5)}$$

Drought Tolerance Classification

All species were classified for drought tolerance using seed germination parameters based on their relative index's values of T_{50} and GR. The MSG was not used as a drought tolerance indicator as MSG capacity is related to the genetic potential of the seeds. Relative indices for $T_{50}$was calculated by dividing T_{50} at -0.2, -0.4, -0.6 and -0.8 MPa by T_{50} at 0 MPa for each species. Following the summation of individual indices, species with a greater T_{50} cumulative index means more time was taken to achieve T_{50}, therefore, these species were considered drought susceptible. Species were classified as drought tolerant (minimum T_{50} I + 1standard deviation (SD), intermediately drought tolerant (minimum T_{50} I + 2 SD) and drought susceptible (minimum T_{50} I + 3 SD) using T_{50} cumulative index. On the contrary, species with a greater germination rate cumulative index were considered drought tolerant. Species were classified as drought tolerant (minimum GRI + 3 SD), intermediately drought tolerant (minimum GRI + 2 SD) and drought susceptible (minimum GRI + 1 SD) using GR cumulative index.

Data Analysis

The germination parameters (MSG, T_{50} and GR) were modelled using polynomial functions for all 10 species. The linear and quadratic regression functions were determined for all three germination parameters separately. Based on the coefficient of determination (r^2 value) obtained from both regression functions, the linear regression function for all three parameters were chosen to explore the relationship of each parameter with respect to time. The quadratic regression functions were ignored as it did not substantially improve the explanation of the response as compared to linear response function. Similarly, the value of MSG, T_{50} and GR from all replications and all levels of treatments were analyzed using PROC MIXED in SAS (SAS Institute) to determine the effect of OP on these three parameters. Analysis of variance was used to test whether differences existed for MSG, T50, and GR for the main effects of species and OP and their interactions.

Results and Discussion

Cumulative seed germination

The germination time course data in response to OP was fitted with a 4-parameter sigmoidal function, only 6 species are presented for clarity (Fig.1). Germination did not occur at the extreme osmotic potentials tested (from -1.2 to -2.0 MPa). Germination of all species was completed by day 7 although the study was continued for 21 days. Camelina, soybean and peanuts did not germinate at -0.8 MPa while camelina did not germinate at -0.4 MPa. Cumulative germination of camelina and pennycress at 0MPa was less than 60%. All PEG treated seeds showed significantly lower final cumulative germination than the control similar to findings by Seepaul *et al*. (2011). Cumulative germination decreased with increasing OP among all species, however, species such as carinata, canola and crambe that germinate at high OP (-0.8 MPa or greater) can be considered drought tolerant based on their germination properties.

In carinata, canola and crambe MSG decreased by almost 14% compared to the control when OP increased to -0.2 MPa. Similarly, MSG in alba and pennycress decreased 21% and 30%, respectively, when OP changed from 0 MPa to -0.2 MPa. Rapa, juncea, peanut and soybean were highly sensitive to OP with a 40 to 44% decrease in MSG when OP increased to -0.2 MPa. In camelina MSG decreased by 60% when OP increased from 0 to -0.2 MPa. These results showthat small changes in OP inhibit germination capacity of the seedsacross the species tested. All species except carinata, canola and crambewere significantly influenced by small changes in OP.

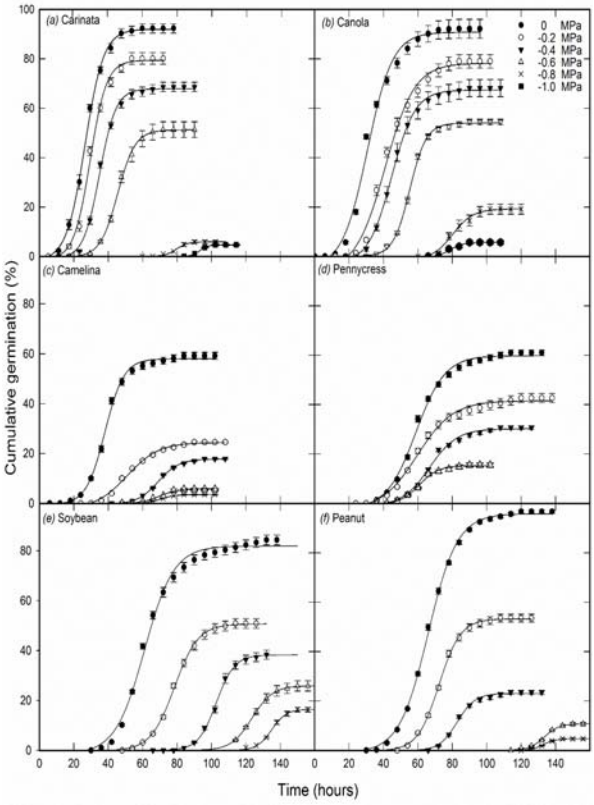

Figure 1. Cumulative germination time course (mean ± SE, n=6) of carinata, canola, camelina, pennycress, soybean and peanut at different osmotic potentials (0 to -1.0 MPa). Different symbols indicate the osmotic potential with their cumulative germination percentage data and lines represents the times in hours fitted using the four-parameter sigmoidal function

Table 2. Onset of germination, time to reach maximum seed germination and delay in onset of germination with respect to MPa varied among species

Species	Onset of germination	Time to reach MSG	Time from onset to final	Delay in onset of germination with respect to 0 MPa (hr)			
	(hr)	(hr)	MSG (hr)	0 to -0.2	0 to -0.4	0 to -0.6	0 to -0.8
Alba	18	96	78	6	18	30	60
Camelina	18	84	66	18	36	42	48
Canola	12	78	66	12	18	24	60
Carinata	12	60	48	6	12	18	60
Crambe	12	54	42	6	12	18	60
Juncea	30	102	72	6	12	30	42
Pennycress	30	108	78	0	12	18	30
Rapa	18	102	84	12	18	42	84
Peanut	36	120	84	18	36	90	96
Soybean	36	132	96	18	48	66	84
Average	22	94	71	10	22	38	62

Increasing OP increased the time required for onset of germination across all species. Carinata, canola and crambe required the shortest time (~12 hours) for onset of germination whereas alba, rapa and camelina were intermediate (~18 hours) while the other species required >30 hours for onset of germination under control conditions (Table 2). Peanut and soybean required 36 hours for onset of germination. This onset of germination time as well as time to reach maximum final germination across each species was affected by OP.

Under control conditions (MPa), carinata and crambe required approximately 60 hours to reach MSG, while canola, camelina, juncea, alba and pennycress required 66 to 78 hours to reach MSG. Rapa, juncea, peanutand soybean required >100 hours to reach MSG under control conditions. Averaged across species, there was a 10, 22, 38 and 62 hours delay for onset of germination when OP increased from 0 MPa to -0.2 MPa,-0.4 MPa, -0.6 MPa and -0.8 MPa, respectively (Table 2). The duration of the delayed onset of germination with decreasing OP varies with species and may be due to their genetic makeup, seed size, and stored energy.

Seeds must imbibe water to activate enzymes leading to resource mobilization for radical and plumule development. Any factor that limits the imbibition rate may also limit the rate of germination. For example, osmotic stress decreases á-amylase and á-glucosidase activity leading to decreased germination (Muscolo *et al*. (2014). Species or cultivars of species that germinate at >-0.6 MPa osmotic potential should have the ability to germinate and establish in areas where cultivars or species that require high moisture levels cannot (Oberbauer and Miller, 1982). Drought tolerance may be process specific; hence drought tolerance during seed germination may not confer tolerance at later stages of development.

Maximum seed germination

Maximum seed germination varied with a species × OP interaction (P<0.0001) partly due to the steep slope of the peanut MSG response to OP relative to the other species. The linear regression model was tested to describe the response of MSG to OP (Fig. 2) and linear equation constant and regression coefficient for MSG of all species are presented in Table 3. MSG was influenced by the concentration of PEG induced osmotic stress, decreasing gradually with increasing PEG concentration (increasing OP). MSG of carinata and canola showed a similar response to OP (P = 0.567) at 0 MPa. MSG of all species decreased when OP decreased from 0 MPa (Table 5). MSG of soybean, peanut and camelina had a 41-54% decline when OP changed from 0 MPa to -0.2 MPa while that of pennycress, rapa and alba declined by 19 to 34%. Carinata, canolaand crambeis more tolerant to relatively small changes in OP from 0 MPa to -0.2 MPa. MSG decreased by 25 to 73%, 41 to 90% and 82 to 100% across species when OP changed from 0 to -0.4, -0.6 and -0.8 MPa, respectively. Carinata, canola, alba and crambe were more tolerant to reduced OP with a MSG reduction ranging between 41 to 49%. The MSG of the other species were >70% when OP changed from 0 MPa to -0.6 MPa. The difference in slopes of the MSG response (Fig. 2) across species indicated the sensitivity to the level of osmotic stress. In carinata and canola, the MSG remained around 50% with -0.4 MPa (Fig. 2). These results are similar to diverse switchgrass ecotypes linear decrease with increasing OP (Seepaul *et al*., 2011).

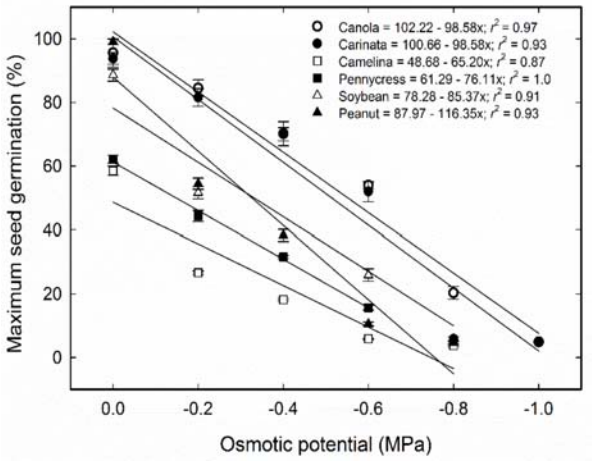

Figure 2. Effect of different osmotic potential on maximum seed germination (mean ± SE, n=6) of oilseed species. Symbols represents the maximum seed germination values of species and lines are fitted using linear equations

Median germination and rate

Median germination (T_{50}) and germination rate (GR) responses varied with a species × OP interaction (P< 0.0001). The slope of the GR response line showed that pennycress and camelina were almost zero as opposed to the positive slope of the other species contributing to the interaction effect. Only 6 species are presented in Fig.3 for clarity. Across all species, T_{50} increased linearly while GR decreased linearly with increasing OP (Figure 3). Crambe reached 50% germination within 26 hours followed by canola (31 hr) and carinata (33 hr) under control conditions. Alba, camelina and rapa required 36, 38 and 39 hours respectively to reach 50% germination while juncea, pennycress, soybean and peanut required 52 to 66 hours to achieve 50% of MSG.

Table 3. Maximum seed germination, time to 50% germination and germination rate with linear equation constants and regression coefficients (r^2) for ten different oilseed species in response to osmotic potential (0 to -1.2 MPa).

Species	Parameters	Coefficients		r^2
		a	b	
		Maximum seed germination (%)		
Alba	74.59±1.77	75.56	-74.71	0.96
Camelina	58.53±1.45	48.68	-65.2	0.87
Canola	95.60±4.44	102.22	-94.62	0.97
Carinata	93.85±1.79	100.66	-98.58	0.93
Crambe	93.78±1.60	100.13	-97.42	0.93
Juncea	47.30±1.50	43.91	-66.65	0.94
Pennycress	62.18±1.24	61.29	-76.11	1.0
Rapa	57.55±1.74	52.86	-67.36	0.95
Peanut	99.12±0.015	87.97	-116.35	0.93
Soybean	88.65±0.017	78.28	-85.37	0.91
		Time to 50% germination (hours?)		
Alba	36.10±0.27	32.69	59.99	0.96
Camelina	38.14±0.25	43.08	41.35	0.82
Canola	30.74±0.56	24.57	58.84	0.93
Carinata	33.04±0.56	22.35	56.83	0.83
Crambe	25.70±0.58	20.82	57.03	0.88
Juncea	52.19±1.68	45.98	33.11	0.62
Pennycress	52.84±0.30	52.49	13.99	0.79
Rapa	38.68±0.92	29.31	81.01	0.87
Peanut	65.53±0.27	62.13	98	0.92
Soybean	59.87±0.14	60.72	98.03	0.99
		Germination rate		
Alba	0.028	-0.02	0.03	0.96
Camelina	0.026	0.02	-0.01	0.78
Canola	0.033	-0.02	0.03	0.93
Carinata	0.030	0.03	-0.02	0.87
Crambe	0.039	-0.03	0.04	0.96
Juncea	0.019	0.02	-0.01	0.56
Pennycress	0.019	0.02	0	0.8
Rapa	0.026	0.03	-0.02	0.97
Peanut	0.015	0.015	0.011	0.91
Soybean	0.017	0.016	-0.012	0.92

The average T_{50} increased by 10, 42, 70 and 142% with increasing OP from 0 MPa to -0.2, -0.4, -0.6 and -0.8 MPa, respectively across the species. T_{50} for carinata, canola, juncea, pennycress from 0 and -0.2 MPa were similar, however, the response was different when OP increased further (Table4). Across species, GR decreased by 8, 27, 39 and 58% when OP changed from 0 MPa to -0.2, -0.4.-0.6 and -0.8 MPa respectively (Table 4).

Higher positive slopes for T_{50} and higher negative slopes for GR with increasing level of OP indicates the sensitivity of the PEG induced drought stress across species. The response to decreasing OP varied among the species, however, the slope of T_{50} and GR in camelina and pennycress seemed to be less responsive to increasing OP. This response conferred intermediate drought tolerance during germination while the remainder of the species were highly responsive to increasing OP. OP delayed the T_{50} and reduced the GR because of the reduction of water potential with increasing PEG concentration which may have impeded water absorption and inhibit germination metabolic process due to decreased imbibition (Jamil *et al.*, 2006). PEG induced drought stress has a negative relationship with germination and T_{50} similar to previous findings (Khodarahmpour, 2011).

Table 4. Maximum seed germination, time to 50% germination and germination rate percent change with reference to 0 MPa control as a function of osmotic potential.

Species	% change in MSG				% Change in T_{50}				% Change in GR			
	0 to -0.2	0 to -0.4	0 to -0.6	0 to -0.8	0 to -0.2	0 to -0.4	0 to -0.6	0 to -0.8	0 to -0.2	0 to -0.4	0 to -0.6	0 to -0.8
Alba	-19	-38	-49	-92	17	58	71	138	-15	-37	-41	-58
Camelina	-54	-69	-90	-94	34	81	83	84	-25	-45	-45	-46
Canola	-12	-27	-44	-79	1	46	80	164	-1	-32	-44	-62
Carinata	-13	-25	-45	-94	-9	7	39	140	10	-7	-28	-58
Crambe	-14	-28	-41	-92	22	47	83	209	-18	-32	-45	-68
Juncea	-41	-73	-84	-	-13	5	36	-	15	-5	-27	-
Pennycress	-29	-49	-75	-	1	15	13	-	-1	-13	-12	-
Rapa	-34	-65	-82	-93	11	27	88	171	-10	-22	-47	-63
Peanut	-45	-61	-89	-95	10	57	104	103	-9	-36	-51	-51
Soybean	-42	-57	-71	-82	31	72	106	126	-23	-42	-52	-56
Average	-30	-49	-67	-90	10	42	70	142	-8	-27	-39	-58

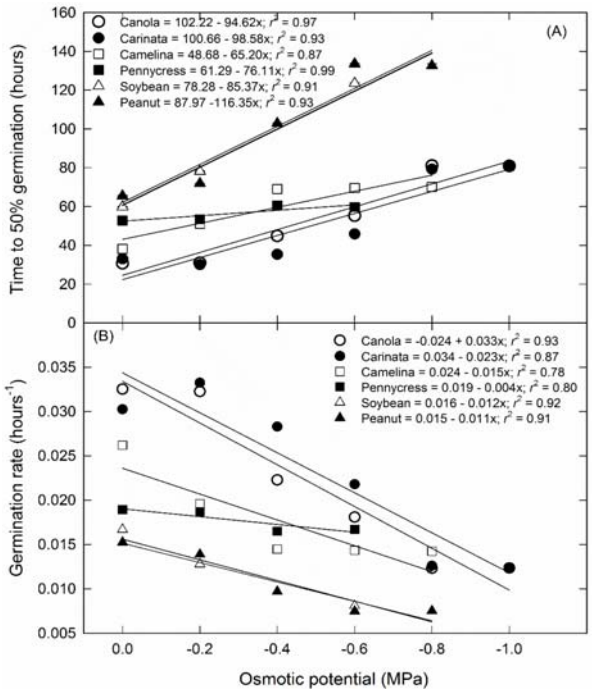

Figure 3. Effect of osmotic potential on (A) time to 50% germination and (B) germination rate of oilseed crops. Symbols represents the time to 50% germination and germination rates, and lines are fitted linear equations.

Drought tolerance classification

Classification of species using 1 standard deviation into drought tolerance categories differed between T_{50} and GRI (Table 5). However, there was no discontinuity where species skipped a classification. Based on the T_{50} relative index, pennycress and juncea were drought tolerant, carinata was intermediately drought tolerant while the remaining species were considered drought susceptible. Similarly, germination rate relative index (GRI) classified juncea and carinata as drought tolerant while canola, rapa and pennycress were classified as intermediately drought tolerant. Greater the cumulative germination rate index, the greater potential to resist the PEG induced stress, therefore, the greater capacity for drought tolerance.

Species selection based on the identification of their drought tolerance capacities is very crucial for high yields. Based on the two screening techniques (T_{50} and GR index) used to determine the drought tolerance of species at germination stage, we identified species differences for drought stress tolerance at the seed germination stage. Species which have a higher final germination, shortest time to 50% germination and higher germination rates with increasing OP were more drought stress tolerant.

Conclusion

This study compared drought tolerance of oilseed crops with biofuel potential using PEGto simulate drought stress on seed germination traits (germination time course, maximum seed germination, time to 50% seed germination, and germination rate). The germination time course, MSG, T_{50} and GR varied with OP across species. Higher MSG, GR and lower T_{50} were observed in control (0 MPa) treatments. Based on the two screening criteria used to determine drought tolerance, juncea, carinata and pennycress were more drought tolerant, canola and rapa were moderately drought tolerant while other species were susceptible to PEG-induced drought stress during seed

Table 5. Classification of species for drought tolerance based on a time to 50% germination and germination rate relative index

Drought susceptible	Intermediate	Drought tolerant
Drought tolerance classification based on T50*		
(7.47 - 9.04)	(5.88 - 7.46)	(4.29 - 5.87)
Canola, Alba, Camelina, Crambe, Rapa, Peanut, Soybean	Carinata	Pennycress, Juncea
Drought tolerance classification based on GR index		
(3.27- 3.54)	(3.55 - 3.80)	(3.81 - 4.06)
Alba, Camelina, Crambe, Peanut, Soybean	Canola, Rapa, Pennycress	Juncea, Carinata

*Cumulative response indices were classified into tolerance groups using 1 standard deviation

germination stage. Drought tolerance during seed germination may not confer tolerance at later stages of development. Classifying species using T_{50} and GR drought tolerance index may be useful in breeding programs to rapidly screen for drought tolerance using seed germination assay. This dataset can also aid in farm operations by informing the choice of species planted in moisture stressed conditions. However, factors other than germination which may affect the growth and yield of the species.

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