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Effects of Temperature, Relative Humidity and Moisture Content on Seed Longevity of Shrubby Russian Thistle (*Salsola vermiculata* L.)

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Abstract: *Salsola vermiculata* is a highly palatable shrub and widely used in rangeland rehabilitation programs, but has short seed longevity. To identify the most cost effective storage method for *S. vermiculata*, experiments were carried out to test the effects of fruit bracts (wings), temperature regimes, seed moisture and packaging methods on storage life. Seed samples were removed from storage at monthly intervals for testing and towards the end of the experiments samples were transferred from hermetic to ambient storage conditions and tested for germination. Experiment 1 continued for 1,140 days, Experiment 2 for 720 days. For de-winged seed, high moisture content increased seed longevity, suggesting that desiccation susceptibility is one of the causes of limited longevity in this species. Most longevity regression lines of winged seeds had negative intercepts suggesting increase in germination resulting from gradual dormancy-breaking. Drying and packaging alone increased longevity by 7.6 and 3.8 times in Experiments 1 and 2, respectively. Samples kept at lower temperature and lower moisture treatments survived longer under ambient conditions. Increased longevity by drying and vacuum packaging alone can provide simple, cost effective and environmentally friendly options for rangeland rehabilitation programs.

Key words: *Salsola vermiculata* L., seed storage, vacuum packaging, seed longevity, probit analysis.

1. Introduction

Rangeland degradation is taking place at alarming rates in arid Mediterranean rangelands [1-3]. Severe depletion of soil seed banks associated with rangeland degradation limits self-regeneration, thus necessitating reseeding [4]. The seed required for rehabilitation is usually collected from wild plants of the target species growing in less degraded areas of the rangelands. Due to temporal and spatial erratic rainfall distribution in arid rangelands [5, 6], the required quantities of high quality seed can not be harvested every year. To mitigate seed shortage in drought years, to maintain seed stocks for use in range nurseries, and for distribution to local communities, large seed stocks are collected in seasons with an abundant harvest. These stocks are stored under ambient conditions for long periods. In most rangeland rehabilitation programs in West Asia and North Africa, shrub seed stocks are kept in simple storage structures to minimize cost. This makes seed storability under ambient storage conditions critical for rangeland rehabilitation through reseeding.

Rangeland rehabilitation programs in West Asia and North Africa (WANA), including Syria, rely heavily on *Chenopodiaceae* species, especially *Atriplex* spp. and *Salsolavermiculata* L. [7-9]. However, research on the physical and physiological seed quality attributes and propagation methods for shrubs of the arid Mediterranean basin, is limited [10]. Research on saltbush (*Atriplexhalimus* L.) showed significant variation in seed quality amongst seeds

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from different individual shrubs [11]. Three categories of seed with different germination rates could be differentiated.

The shrubby Russian thistle (*Salsola vermiculata* L.) is a major species in the Syrian rangeland flora and rehabilitation programs [12]. It is a native species with high ecological and forage value found distributed throughout the arid, semi-arid, saline and hyper-saline ecosystems of temperate and subtropical regions [13, 14]. It has a high success rate of establishment when self-sown, direct seeded or transplanted. It is easily propagated from seed and produces high quality biomass for feed and good seed yield for direct sowing under a wide range of rangeland conditions in WANA region [15]. However, seed of *S. vermiculata* loses its viability within 6-9 months under ambient storage conditions [16, 17].

Effects of storage time, moisture and temperature on seed longevity have been investigated and reported for many crops and wild plant species. Based on their desiccation tolerance, seeds are classified as orthodox and recalcitrant [18]. The orthodox seeds include a wide range of annual species [19] for which Harrington's Rule of thumb applies [20]. The term recalcitrant refers to those species for which Harrington's Rule does not apply because desiccation results in rapid loss of seed viability.

For *S. vermiculata*, research findings have already shown that by reducing storage temperature, seed longevity is significantly extended [16, 21]. However, the effect of controlling seed moisture on storage has not been properly investigated. Therefore, this study was intended to investigate the combined effects of storage temperature and seed moisture on *S. vermiculata* seed longevity in order to determine the most cost-effective storage conditions for use in arid rangeland rehabilitation.

2. Materials and Methods

2.1 Test Material

Mature seed from Syrian ecotypes of *Salsola vermiculata* L. were collected in October 2002 and 2003 from the ICARDA rangeland nursery site located in North of Syria at 36°01'N, 36°56'E and 284 m above sea level. The seed stocks were cleaned and then subdivided into two parts, and dried to different moisture contents and stored for 1,140 days (38 months) in Experiment 1 and 720 days (24 months) in Experiment 2. One part of the seed stock was dried to low moisture content of 7% and 6.5% in Experiments 1 and 2, respectively, by storing the seed for 6 weeks in a dehumidification room set at 16 °C and 18%-22% relative humidity. The other part was kept at its harvest moisture content level of 10.7% and 9.6% in Experiments 1 and 2. Then the two batches of seed were subdivided into two parts. One part was de-winged using a Westrup-La-h brushing machine (http://westrup.com/Products-Seed-and-Grain/Laboratory-equipment/LA-H) and the other part was left with wings intact in its natural condition. De-winging was done to break dormancy by eliminating the germination inhibitors accumulated in the wings [16]. These different batches were stored in normal paper envelopes in non-vacuum sealed polythene bags or in sealed vacuum packages prepared using a chamber type vacuum packaging machine equipped with air extraction and heat sealing facilities at ICARDA gene bank. The steps described above resulted in eight batches of seed, namely non-dried and dried batches of winged and de-winged seeds in vacuum-sealed or paper packaging in sealed polythene bags.

2.2 Statistical Design and Set-up

In both Experiments 1 and 2, a completely randomized factorial design was carried out with four treatments: seed type (winged vs. de-winged), three combinations of seed moisture content (SMC) and packaging, combined with three storage temperatures and time of storage. The treatment levels were winged or de-winged seeds, high SMC with vacuum packaging, high initial SMC without vacuum packaging and low SMC with vacuum packaging; the storage temperatures were -21, 4 or 24 °C. Low initial SMC could not have been maintained without vacuum packaging, neither high SMC could have been maintained under non vacuum packaging. In both Experiments 1 and 2, there were two replications and samples were removed at regular intervals for testing. In each of the three storage temperatures, 288 seed samples were stored, representing two replications of six treatment combinations and 24 sample withdrawal with 50 seeds per experimental unit. In Experiment 2, extra seed packages were stored for 720 days, then transferred to non-vacuum polyethylene bags, kept at 24 °C and then tested at one month intervals for a period of 4 months to assess the seed longevity after hermetic storage.

In Experiment 1, the sampling interval was one month for the first 18 months and 4 months for the last 20 months. However, the data of the 7th and 8th months for the winged seeds were removed because of incubator breakdown. In Experiment 2, the sampling interval was one month throughout the period.

2.3 Seed Testing Procedures

Each month, a total of 12 envelopes, representing two replicates of the six treatment combinations were drawn from each of the three temperature regimes and tested for germination according to the International Seed Testing Association rules [22]. Petri dishes of 9 cm diameter with two layers of Whatman No. 41 filter paper were used in the germination tests. For each treatment combination, two replicates of 50 seeds were planted and placed in a germination chamber set at 20 ± 2 °C and light (8 h, fluorescent light of 4.22 W/m^2), dark (16 h) regime. The samples were watered every two days for a period of 10 days and germination was then assessed. The Petri dishes were kept in the germination room for up to 20 days after evaluation but no additional germination was observed.

2.4 Statistical Analysis

Analysis of variance was carried out to evaluate the significance of the main treatment effects and the interactions between them. The means and their standard errors were computed using Genstat statistical package [23]. The restricted maximum likelihood (REML) procedure was used to test the significance of main effects and interactions of the treatment factors and to estimate the standard errors of the means. Instead of simple analysis of variance, REML facilitated to model the unbalanced design arising from the fact that seed could not be maintained at low moisture content without vacuum packaging and that zero germination percentages were recorded in the high moisture, paper-packaged seeds.

Regression analysis was applied by plotting germination proportions against time of storage in days to quantify the effects of time on seed longevity. The time in days for seed viability to drop to 50% (known as P50) was estimated from the probit model.

3. Results

3.1 Longevity Trends

The overall analysis of variance showed that all possible three-way interactions were statistically significant ($P < 0.01$). To facilitate interpretation and simplify presentation, the high order interaction table of seed type, moisture and packaging combination, storage temperature and time was disaggregated into winged and de-winged treatments, each of which was then sub-divided into the three temperature regimes under which the seed was maintained during storage.

Mean germination percentages after one month storage of winged and de-winged seed were 51% and 93%, respectively, in Experiment 1, 27% and 96% for Experiment 2 in the same order. This shows a 42% and 69% increase in initial germination as a result of wing removal in Experiment 1 and Experiment 2, respectively.

The trends of change in seed longevity for winged and de-winged seeds separately are presented in six graphs embedded within two figures representing treatments grouped by temperature regime within each experiment (Fig. 1 for winged and Fig. 2 for de-winged seeds). Regardless of the moisture content and packaging, both winged and de-winged seeds maintained their initial germination levels when stored at -21 °C and 4 °C throughout both experiments. However, at 24 °C, the trends showed different rates of decline depending on seed moisture content.

The mean germination proportions (GP) over the entire storage period are presented in Fig. 3 (Experiment 1) and Fig. 4 (Experiment 2). Within each temperature regime, the GP of winged seeds consistently and significantly (P < 0.01) declined between the vacuum and non-vacuum packaged seeds and from low to high MC treatments. For de-winged seeds, GP was the highest (P < 0.01) under the higher compared to the lower MC seeds. When stored at 24 °C, the mean GP for non-vacuum packaged winged was higher compared to winged seeds in vacuum packages in Experiment 1.

3.2 Parameter Estimates for Longevity Curves

3.2.1 Winged and De-winged Seed

Probit analyses results showed that for winged seeds, the slopes were positive at -21 °C and 4 °C. The intercepts expressed in probit units were either negative or very low when positive. The decline in the P50s expressed inseed germinability gradient and slopes of regression with storage period did not follow the opposite direction of change in SMC. For de-winged seeds, all regression line intercepts were positive and higher compared with the winged seeds. The decline in longevity was irregular along the seed moisture gradient under -21 °C and 4 °C for both winged and de-winged seeds and the seed longevity was the highest under low SMC with vacuum packaging followed by seed with high MC with vacuum then the high SMC with no vacuum packaging (Tables 1 and 2). Moreover, for de-winged seeds stored at 4 °C and 24 °C, the regression coefficients, intercepts and correlation coefficients were all significant (P < 0.01).

Results of the probit analyses also showed that in the control (non-vacuum packaging with MC of 10.7% in Exp. 1 or 9.6% in Exp. 2), lowering the storage temperature from 24 °C to 4 °C resulted in an increase of P50 from 156 to 1,651 days in Exp. 1 and from 161

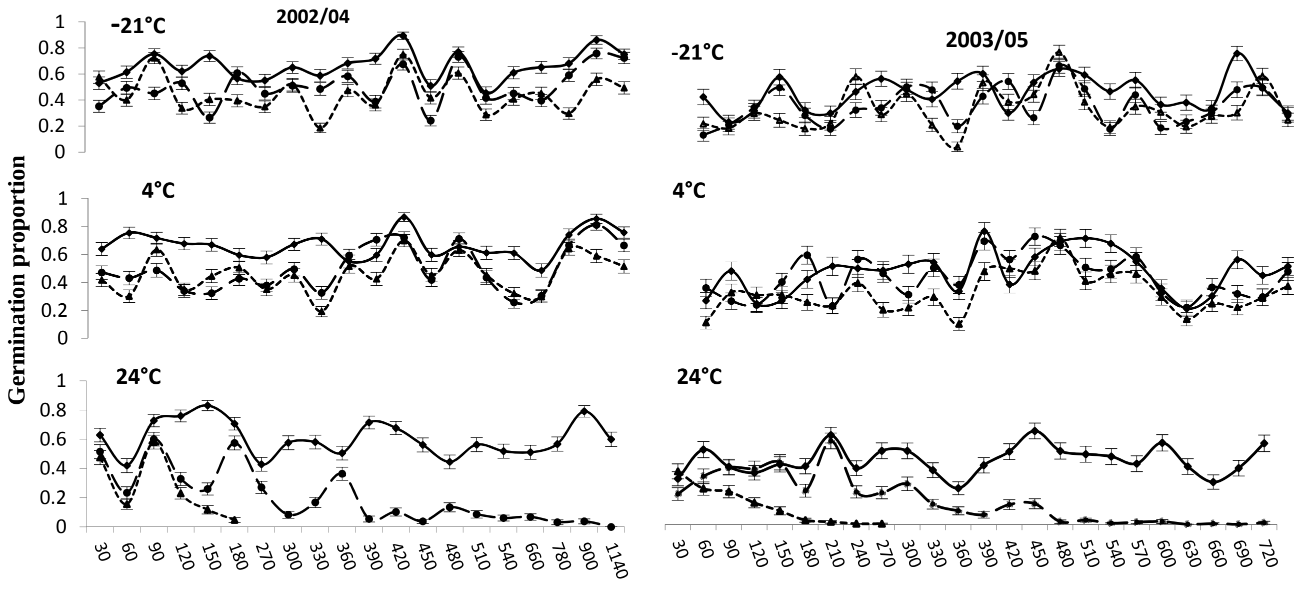

Fig. 1 Proportion of germination of winged seeds of *Salsola vermiculata* L. with a moisture content (MC) of 7% and vacuum packaging (VP) (solid line with diamonds), with MC = 10.7% and VP (dashed line with circles), and with MC = 10.7% and no VP (dotted line with triangles) stored at -21, 4 and 24 °C for 1,140 and 720 days in 2002/04 (left panels) and 2003/05 (right panels), respectively. Note that the scales are not equidistant at the higher end of the x-axes.

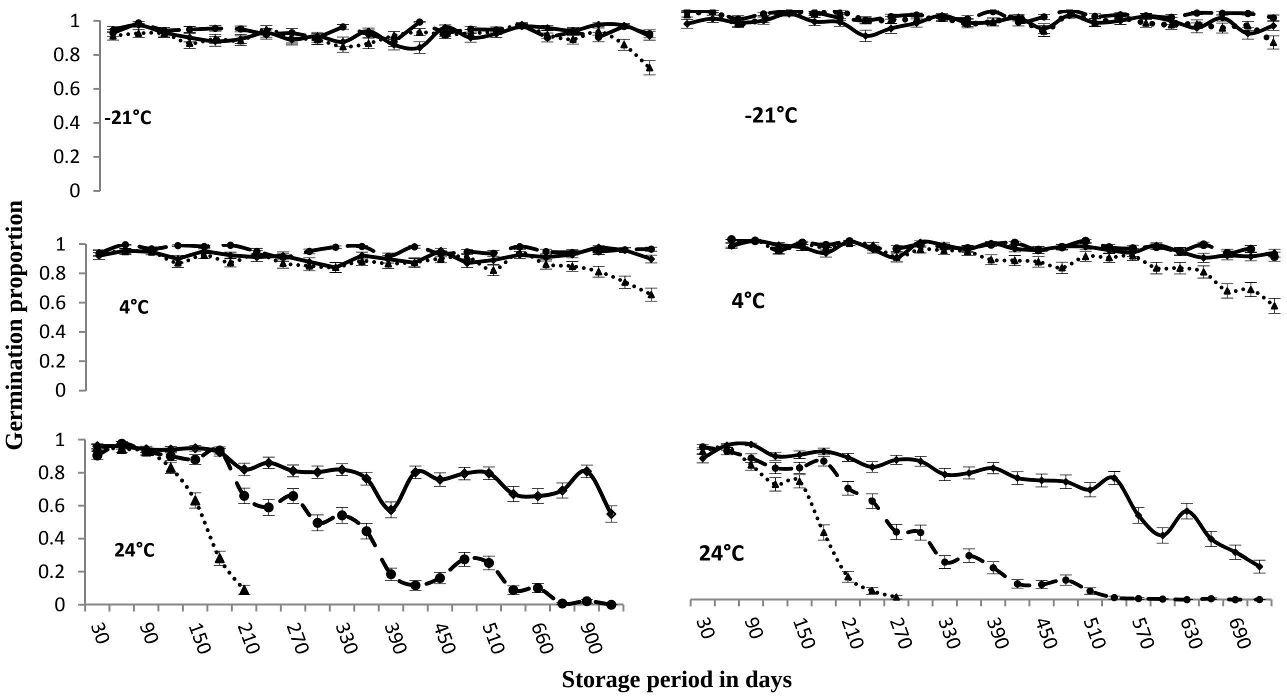

Fig. 2 Proportion of germination of de-winged seeds of *Salsola vermiculata* L. with a moisture content (MC) of 7% and vacuum packaging (VP) (solid line with diamonds), with MC = 10.7% and VP (dashed line with circles), and with MC = 10.7% and no VP (dotted line with triangles) stored at -21, 4 and 24 °C for 1,140 and 720 days in 2002/04 (left panels) and 2003/05 (right panels), respectively. Note that the scales are not equidistant at the higher end of the x-axes.

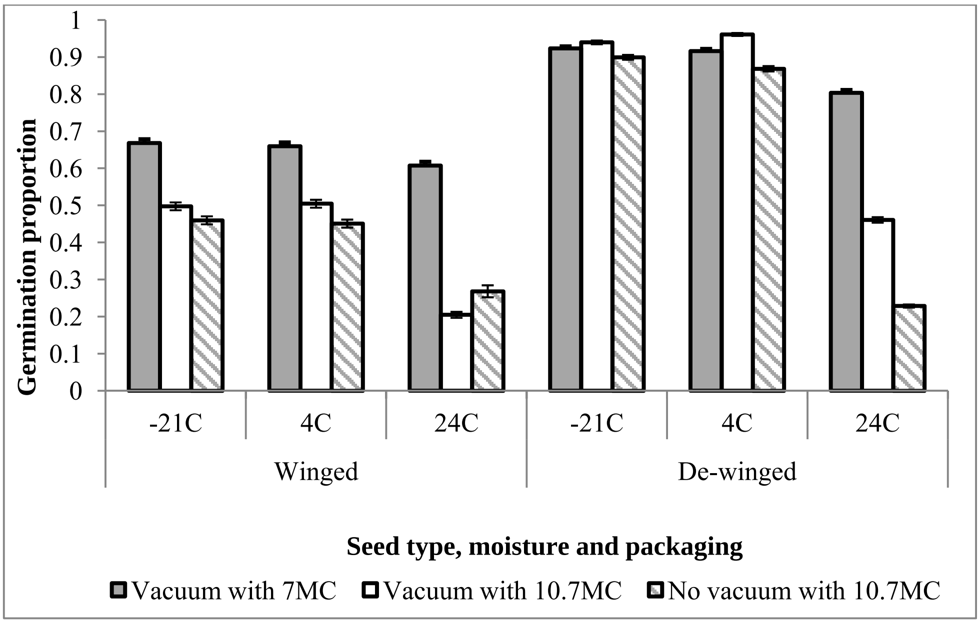

Fig. 3 Mean predicted germination proportions with standard error bars for winged and de-winged seed of *Salsola vermiculata* L. with low (7 MC) and high (10.7 MC) moisture content and vacuum and no-vacuum packaging stored at three temperature regimes for 1,140 days (Experiment 1).

to 929 days in Exp. 2. The increases in P50 in the Experiments 1 and 2, respectively, were 10.6 and 5.6 fold. When stored in vacuum packaging at 24 °C, lowering the MC from 10.7% to 7% in Exp. 1 resulted in an increase of P50 from 322 to 1,179 while MC reduction from 9.6% to 6.5% in Exp. 2 increased the P50 from 274 to 610. The increases in P50 in the Experiments 1 and 2 were in the same order, and of

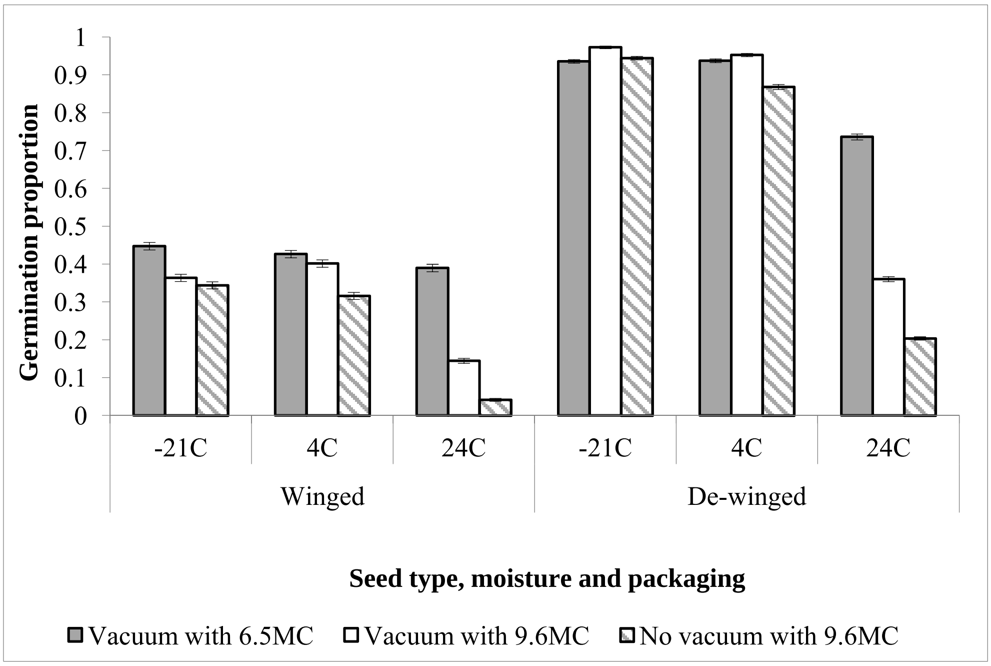

Fig. 4 Mean predicted germination proportions with standard error bars for winged and de-winged seed of *Salsola vermiculata* L. with low (6.5 MC) and high (9.6 MC) moisture content and vacuum and no vacuum packaging stored at three temperature regimes for 720 days (Experiment 2).

Table 1 Parameter estimates for winged seed longevity curves of two seed lots of *Salsola vermiculata* L. under different storage conditions in 2002/04 and 2003/05.

Years	T (°C)	MC%	Packaging	Gradient (1/δ)	P50 (days)	Intercept (probit)	Slope
1	-21	7.0	Vacuum	0.00061	1,665*	0.5 ± 0.1	0.0003 ± 0.0002^{ns}
		10.7	Vacuum	0.00244	410 ±7	-0.2 ± 0.05	0.001 ± 0.0001***
			No vacuum	0.00131	766 ± 774	-0.2 ± 0.05	0.0003 ± 0.0001**
	4	7.0	Vacuum	-0.00108	-930 ± 1464	0.3 ± 0.05	0.0003 ± 0.0001**
		10.7	Vacuum	0.00277	361 ± 62.2	-0.2 ± 0.05	0.0006 ± 0.0001***
			No vacuum	-0.00080	-1,246*	-0.1 ± 0.05	-0.0001 ± 0.0001***
	24	7.0	Vacuum	0.00083	1,203 ± 1,170	0.3 ± 0.05	-0.0003 ± 0.0001***
		10.7	Vacuum	0.08621	11.9 ± 21.6	0.04 ± 0.07	-0.003 ± 0.0002***
			No vacuum	0.02849	35.1 ± 7.9	0.4 ± 0.1	-0.01 ± 0.001***
2	-21	6.5	Vacuum	0.00137	730 ± 236	-0.3 ± 0.05	0.0004 ± 0.0001***
		9.6	Vacuum	0.00068	1,481 ± 1,160	-0.5 ± 0.05	0.0003 ± 0.0001***
			No vacuum	0.00053	1,877 ± 5,365	-0.5 ± 0.06	0.0003 ± 0.0001**
	4	6.5	Vacuum	0.00089	1,120 ± 8,802	-0.3 ± 0.05	0.0003 ± 0.0001**
		9.6	Vacuum	0.00025	4,031*	-0.3 ± 0.05	0.0001 ± 0.0001^{ns}
			No vacuum	0.00061	1,640 ± 776.9	-0.6 ± 0.06	0.0004 ± 0.0001***
	24	6.5	Vacuum	0.00045	2211 ±*	-0.3 ± 0.05	0.0002 ± 0.0001^{ns}
		9.6	Vacuum	-0.02915	-34.3 ± 22.1	-0.1 ± 0.06^{ns}	-0.003 ± 0.0002***
			No vacuum	-0.05244	-19.1 ± 14.9	-0.2 ± 0.1	-0.009 ± 0.001***

The gradient is the inverse of the longevity curve variance (δ) calculated here at P50 in days; ***significant at $P > 0.01$; Letters in front of figures indicate significant differences between treatments; ns: non-significant; *sign for SE shows non converging iteration due to deviation from the standard life curve; T = temperature; MC is moisture content.

Table 2 Parameter estimates for de-winged seed longevity curves of two seed lots of *Salsola vermiculata* L. stored under different storage conditions in 2002/04 and 2003/05.

Years	T (°C)	MC%	Packaging	Gradient (1/δ)	P50 (days)	Intercept (probit)	Slope
1	-21	7	Vacuum	0.00033	3,007 ± 1,065	1.5 ± 0.07	-0.0005 ± 0.0001***
		10.7	Vacuum	0.00011	8,740*	1.6 ± 0.1	-0.0002 ± 0.0002^{ns}
			No vacuum	-0.00007	18,621*	1.4 ± 0.07	-0.0001 ± 0.0002^{ns}
	4	7	Vacuum	0.00011	8747*	1.4 ± 0.07	-0.0002 ± 0.0002^{ns}
		10.7	Vacuum	0.00002	44,069*	1.7 ± 0.09	-0.00004 ± 0.0002^{ns}
			No vacuum	0.00058	1,738 ± 222.5	1.5 ± 0.06	-0.0009 ± 0.0001***
	24	7	Vacuum	0.00096	1,040 ± 66.2	1.4 ± 0.06	-0.001 ± 0.0001***
		10.7	Vacuum	0.00311	322 ± 5.7	1.9 ± 0.08	-0.006 ± 0.0002***
			No vacuum	0.00650	154 ± 2.9	3.2 ± 0.2	-0.02 ± 0.001***
2	-21	6.5	Vacuum	0.00020	5,075*	1.7 ± 0.09	-0.0003 ± 0.0002^{ns}
		9.6	Vacuum	0.00014	7,190*	2.0 ± 0.1	-0.0003 ± 0.0003^{ns}
			No vacuum	0.0004	2,491 ± 2	1.9 ± 0.1	-0.0008 ± 0.0002***
	4	6.5	Vacuum	0.00028	3,562 ± 3,419	1.7 ± 0.1	-0.0005 ± 0.0002***
		9.6	Vacuum	0.00033	3,041 ± 1,616	1.9 ± 0.1	-0.0006 ± 0.0002***
			No vacuum	0.00108	929 ± 43.9	2.0 ± 0.1	-0.002 ± 0.0002***
	24	6.5	Vacuum	0.00164	610 ± 12.5	2.0 ± 0.08	-0.003 ± 0.0002***
		9.6	Vacuum	0.00365	274 ± 4.9	2.0 ± 0.09	-0.007 ± 0.0003***
			No vacuum	0.00620	161 ± 3.4	2.6 ± 0.2	-0.02 ± 0.001***

The gradient is the inverse of the longevity curve variance (δ) calculated here at P50 in days; ***significant at $P > 0.01$; Letters in front of figures indicate significant differences between treatments; ns: non-significant; *sign for SE shows non converging iteration due to deviation from the standard life curve; T = temperature; MC = moisture content.

the magnitude of 3.7 and 2.2 fold, respectively. The increases in P50 resulting from drying and packaging alone were from 156 to 1,179 in Exp. 1 and from 161 to 610 in Exp. 2. These results correspond to 7.6 and 3.8 fold increases in P50 (Fig. 5). When stored at high temperatures and high MC, P50 was consistently higher for vacuum compared to non-vacuum packaged seed but this was only significant in Exp. 2. The P50 values were significantly ($P < 0.01$) higher in Exp. 1 than in Exp. 2. Moreover, all intercepts of the regression lines were positive, and significantly different from zero.

In addition to the trends of change in seed longevity shown in Figs. 1-4, the results of the probit analyses performed on the individual sets of data representing regression of germination proportions against days of storage at 24 °C are presented in Fig. 5. Fig. 5 components showed significant decline in seed viability to zero within a 6, 10 and 23 months period of storage under 24 °C with high MC% with and without vacuum packaging and low MC% with vacuum packaging, respectively.

3.3 Post-hermetic Storage Longevity

In Experiment 2, the seeds transferred from vacuum and non-vacuum packages stored at -21, 4 and 24 °C to ambient conditions showed slopes, intercepts and coefficients of determination for the regression lines which were all significant at $P < 0.01$ (Table 3). Probit analysis on germination proportions with days of storage for seed transferred from hermetic to non-hermetic storage conditions showed that differences in P50 between treatments were significant for winged but not for de-winged seed. For de-winged seeds, differences in P50s were significantly different between vacuum and non-vacuum and among the temperature regimes. For non-vacuum packaging with fixed stable MC, the lower the temperature the higher the P50 became (Table 3).

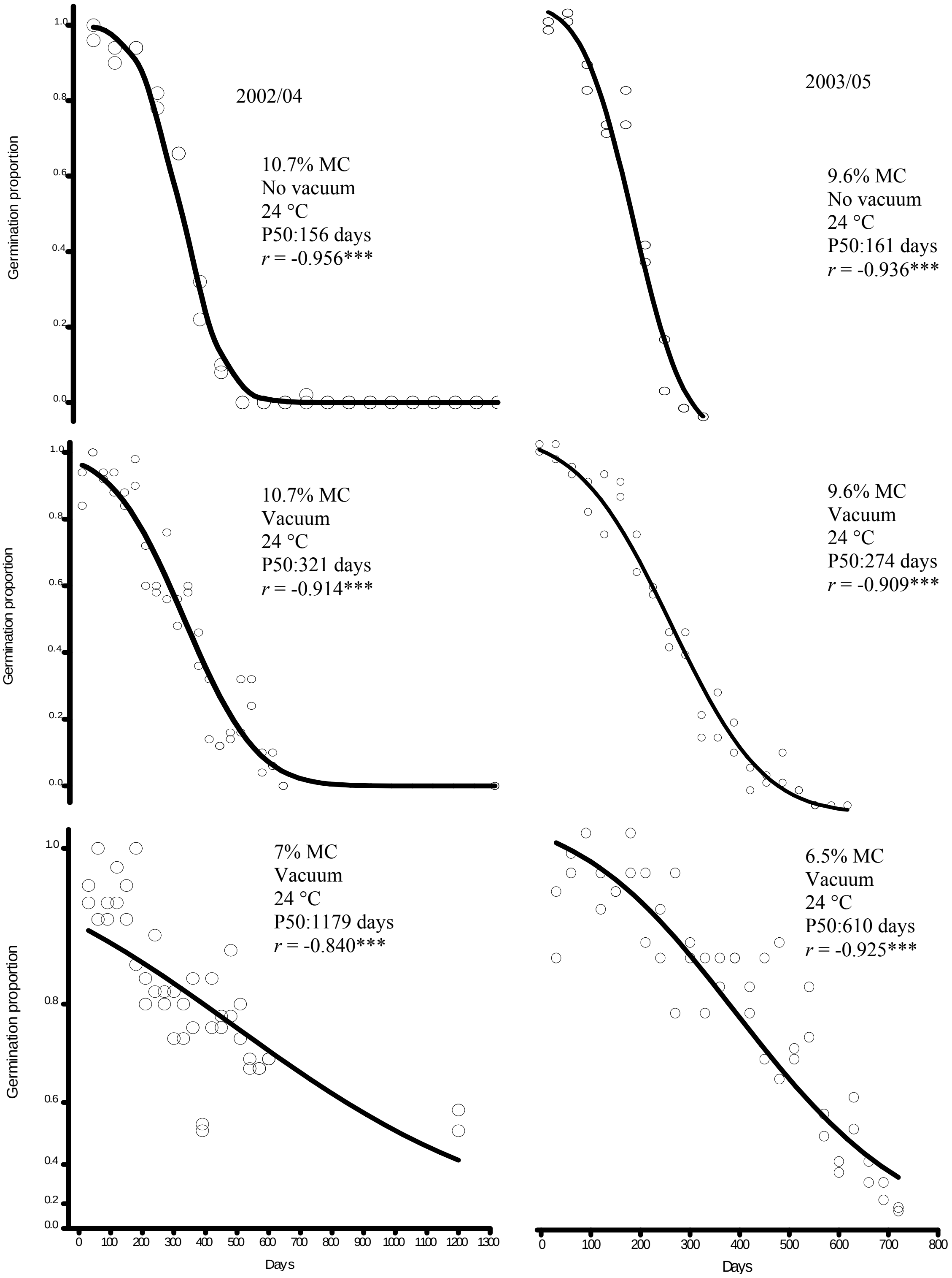

Fig. 5 1:Seed longevity curves for germination proportion with days of storage for *Salsola vermiculata* L. (a1&a2 = 24 °C, without vacuum packaging (WVP) and 10.7% moisture content (MC) for Exp. 1 and 2; b1&2= 24 °C, VP and 10.7%MC for Exp. 1&2; c1&2 = 24 °C, (VP) and 7% MC for Exp. 1&2.

The estimated number of days for a 50% drop in seed germination (P50) was consistently higher for the seed transferred from lower compared to those from higher temperature storage.

Table 3 Parameter estimates for winged and de-winged seed longevity curves of *S. vermiculata* L. transferred to ambient conditions after 720 days of hermetic and non-hermetic storage.

Seed type	T (°C)	MC%	Packaging	Intercept (probit)	Slope (degree)	P50 (days)*
Winged	-21	6.5	Vacuum	-0.1 ± 0.2^{ns}	$-0.01 \pm 0.002^{***}$	-5.6 ± 23.7^{a}
		9.6	Vacuum	-0.3 ± 0.2^{ns}	$-0.01 \pm 0.002^{***}$	-47.7 ± 69.0^{a}
			No vacuum	$-0.7 \pm 0.2^{***}$	$-0.01 \pm 0.003^{***}$	-88.8 ± 95.7^{a}
	4	6.5	Vacuum	-0.2 ± 0.2^{ns}	$-0.01 \pm 0.002^{***}$	-19.5 ± 29.5^{a}
		9.6	Vacuum	0.1 ± 0.2^{ns}	$-0.01 \pm 0.002^{***}$	4.2 ± 13.7^{a}
			No vacuum	$-0.8 \pm 0.2^{***}$	$-0.01 \pm 0.003^{***}$	-96.2 ± 103.1^{a}
	24	6.5	Vacuum	-0.1 ± 0.2^{ns}	$-0.01 \pm 0.003^{***}$	-6.5 ± 16.5^{a}
De-winged	-21	6.5	Vacuum	$1.5 \pm 0.2^{***}$	$-0.02 \pm 0.002^{***}$	71.0 ± 3.4^{a}
		9.6	Vacuum	$1.8 \pm 0.3^{***}$	$-0.03 \pm 0.002^{***}$	71.0 ± 2.9^{a}
			No vacuum	$0.8 \pm 0.2^{***}$	$-0.02 \pm 0.002^{***}$	48.0 ± 5.4^{c}
	4	6.5	Vacuum	$1.3 \pm 0.2^{***}$	$-0.02 \pm 0.002^{****}$	65.0 ± 3.7^{ab}
		9.6	Vacuum	$1.4 \pm 0.2^{***}$	$-0.02 \pm 0.002^{*****}$	59.0 ± 3.2^{b}
			No vacuum	$0.9 \pm 0.2^{***}$	$-0.02 \pm 0.002^{***}$	36.0 ± 4.5^{d}
	24	6.5	Vacuum	$0.1 \pm 0.2^{***}$	$-0.02 \pm 0.003^{***}$	6.0 ± 10.2^{e}

***significant at $P \leq 0.001$; ns: non-significant; *Different letters within seed type indicate significant difference in P50; T = temperature; MC is moisture content.

4. Discussion

4.1 Longevity Trends

Short seed longevity under high temperature and high SMC and extended seed longevity under low temperature and low seed SMC found from the two experiments on both winged and de-winged seeds is consistent with the well-established and widely-reported storage behavior for *S. vermiculata* [13, 16, 21] and for other orthodox seed species [18]. Nonetheless, the previous studies on *Salsola* seed longevity focused on the effect of temperature, whereas, the present study introduced the control of moisture content as a more cost-effective storage approach for rangeland management and rehabilitation.

4.2 Parameter Estimates for Longevity Curves

4.2.1 Winged and De-winged Seeds

The low and negative intercepts and P50 values with high standard errors recorded in the winged seeds are attributable to the confounded effects of simultaneous seed dormancy breaking and natural deterioration in viability due to aging. Loss of dormancy continuously generates new germinable seeds while natural deterioration in seed viability takes place within the seed populations harvested from the wild with high inherent variability clearly expressed in flower and fruit color. The cyclic trend of germination disappeared when fruit bract was removed as shown in the de-winged seed longevity trend graphs.

The large differences in germination percentages between winged and de-winged seeds recorded after one month of storage indicate a high level of dormancy in the winged seeds. The presence of germination inhibitors in *S. vermiculata* wings and their effects on germination have been reported [16]. It seems that the rates of dormancy breaking and natural deterioration among the dormant and non-dormant seeds seem to be canceling out each other and maintaining the overall germination at its initial low level. Nonetheless, the negative intercepts of regressions of the germination proportions against days of storage indicate that the rate at which dormancy breaking is taking place seems to be slightly greater than the rate of deterioration in seed viability. The negative intercepts suggest an increase in seed longevity instead of decline. This increase implies that the regression line will intersect with the x-axis before its zero level. In other words, the model is estimating the number of days required for the seed viability to increase instead of dropping to 50%. Dormancy breaking and deterioration processes have been reported to be controlled by temperature ranging from -10 °C to 70 °C [24]. The experiments were conducted within this range of temperatures.

The higher seed longevity of vacuum packaged seeds with higher MC compared to lower and similar seed moisture content with and without vacuum packing is probably due to desiccation damage in the low MC treatment and higher respiration rate in the non-vacuum packaged seeds (Figs. 3 and 4). Reduced seed longevity under lower moisture content found in this study is not in line with the reported negative logarithmic relationship of seed longevity with moisture content [24]. Upper and lower limits for this negative relationship have been reported [18], although these limits vary among the orthodox species. Beyond the limits, further reduction in seed moisture does not increase or decrease seed longevity. Nevertheless, the moisture and temperature treatments under which change in seed longevity did not match the expected negative relationship falls within the operational boundaries of the negative relationship which is -20 °C to 75 °C [18]. Desiccation below the optimum moisture content greatly increases seed storage deterioration [24]. Low germination in drier compared to more moist seed has been reported in sorghum [25].

The reduced longevity under lower moisture content could also be attributed to interdependence of temperature and moisture effects on longevity or to desiccation damage. It has been found [26] that optimum storage moisture content can not be considered independently of temperature. It seems that the temperature at which longevity was reduced was not optimum for the level of seed moisture content to which the seed was dried. In a study on desiccation-induced damage in orthodox seeds, Leprince et al. [27] concluded that the expression of desiccation damage depends on the drying history and that factors that limit metabolism also reduce the incidence of desiccation injury. The improved seed longevity in the seed with higher moisture content suggests that the short storage life in *S. vermiculata* seed is due to its sensitivity to desiccation. Seed moisture content above 6% is not considered too low for the desert environments in which *S. vermiculata* is widespread and endemic. In addition, the P50 value of 1,651 days predicted for non-vacuum packaged seeds with 10.7% MC stored at 4 °C compared with a predicted P50 value of 1,179 days for vacuum packaged seed with 7% MC stored at 24 °C indicates that *S. vermiculata* seed longevity is more dependent on temperature than moisture. Nevertheless, the actual and the theoretical longevity results from the present study suggest that *S. vermiculata* can be truly classified as an orthodox species. Seeds of some tropical crops show an intermediate category of seed storage behavior [18] and it is not yet clear how many species belong to this category. The findings from the present study suggest that *S. vermiculata* could be a candidate for that intermediate category.

The significantly greater values for P50 in Exp. 1 compared to those in Exp. 2 are probably due to the fact that Exp. 1 continued for longer than Exp. 2. The 7.6 and 3.8 fold increase in P50 achieved in Exps. 1 and 2, respectively through drying and packaging has important practical and cost implications for rangeland rehabilitation. Increases in P50 from 156 to 1,179 in Exp. 1 and from 161 to 610 in Exp. 2 are equivalent to an increase in storage life from less than six months to 3 years in Exp. 1 and to about 2 years in Exp. 2.

4.3 Post-hermetic Storage Longevity

For the seeds which were transferred from vacuum and non-vacuum packages to ambient conditions, the slopes, intercepts and correlation coefficients of determination for the regression lines were all significant at $P < 0.01$ (Table 3). Probit analysis on germination proportion with days of storage for the seed without wings transferred from the vacuum and non-vacuum packaged seeds showed that differences in P50 were not significant between high and low moisture contents within the three storage temperature regimes. For non-vacuum packaging with fixed MC, the lower the storage temperature, the higher the P50 became (Table 3).

The estimated number of days for 50% decline in seed germination (P50) was consistently higher ($P < 0.01$) under high MC and low temperatures compared to low MC and high temperatures. For seed stored at high temperatures and high MC, the P50 was higher for vacuum-packaged seed, but only significantly so in Exp. 2. For the de-winged seeds, the intercepts of the regression lines were all positive and significantly ($P < 0.001$) different from zero, indicating a consistent decline in seed longevity with time.

The slower decline in germination of seed transferred from the lower temperature and moisture content treatment is probably due to the fact that deterioration was minimal in hermetic storage conditions. Seeds continuously deteriorate at a rate that is mainly dependent on moisture content and temperature and, unless germinated, will ultimately die [28]. The most important reasons for Ellis and Roberts to develop an improved equation for predicting longevity was to reflect variations in lot history among crop species and genotypes [29].

5. Conclusions

The improved seed storage in the higher moisture content treatments found in the present study suggests that the short storage life in *S. vermiculata* observed in the field is attributable to sensitivity to desiccation. Special attention should be given to desiccation control in medium and long term storing seed of this species.

The negative intercepts of the regression lines of the winged seeds indicate that seed dormancy resulting from germination inhibitors in the wings increases seed longevity.

The study clearly showed that drying and vacuum packaging alone resulted in a substantial increase in seed longevity. This finding is a significant step towards more cost-effective and environmentally friendly rangeland rehabilitation.

The reduced storage life of seed transferred from vacuum packaging under ambient conditions treatments to non-vacuum packaging needs to be taken into consideration. Such seed should be sown late when the probability of rainfall is high or used in the rangeland nurseries under irrigation.

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