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LIFE SCIENCE AND BIOMEDICINE
NOVEL-RESULT

Evaluation of seed morphology, seedling genetic variation, and components for seed storage of Agave landraces of commercial interest

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Abstract
Sexual propagation of Agave plants is an incipient cultivation method, these plants withstand drought and adverse growing conditions; therefore, research on Agave's diversity, seed processing, and storage could support its cultivation on marginal lands. The aim of this work was to evaluate seed morphology, germination, and seedling genetic diversity of six seed origins (species × provenance) of Agave plants collected in five provenances from Mexico. Seed longevity was evaluated in two seed origins after a 10-year storage period. Seed morphology and seedling genetic variation results demonstrated intra- and interspecific variation within *Agave salmiana* and with the other seed origins, respectively. After a 10-year storage period seed germination of two *A. salmiana* seed origins remained relatively stable, storage conditions, and seed variables of this work can serve as reference parameters for future analyses. To the best authors' knowledge, this is the first report of Agave's seed longevity evaluation after a 10-year storage period.

Key words: *Agave americana*; *Agave mapisaga*; *Agave salmiana*; seed longevity; 10-year storage

Introduction

The "maguey pulquero" term identifies some *Agave* species used for sap extraction to produce a fermented beverage called "pulque", producers of the Central region from the Trans Mexican Volcanic Belt have recognized diverse landraces of *Agave mapisaga* Trel. and *Agave salmiana* Otto ex Salm-Dyck, based on morphological traits and uses (Mora-Lopez et al., 2011). The analysis of molecular markers through randomly amplified polymorphic DNA (RAPDs) can help to elucidate the effect of anthropogenic or environmental factors on Agave's genetic variation (Alfaro et al., 2007; Gil-Vega et al., 2001).

The current and forecasted climatic events have led to revisiting the importance of the *Agave* genus, as these plants are able to withstand drought and adverse growing conditions (Corbin et al., 2015; García-Moya et al., 2011). Asexual reproduction is the traditional propagation method; therefore, seed collection and sexual propagation are still incipient practices of maguey pulquero production and diverse aspects related to seed processing and preservation have been little explored (Aragon-Gastellum et al., 2018; Huerta-Lovera et al., 2018). To this date, little is known about seed morphology, and some works have studied seed germination of maguey pulquero plants (Ramírez-Tobías et al., 2012, 2014), and viability of *Agave striata* seeds under contrasting conditions (Aragon-Gastellum et al., 2018); those aspects

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are important to consider for improving the understanding of sexual propagation, and Agave seed preservation.

The aim of this work was to evaluate the seed morphology, germination, and seedling genetic variation of six seed origins (species × provenance) of *Agave americana*, *A. mapisaga*, and *A. salmiana* collected at five provenances from Hidalgo State, Mexico; the seed morphological variables evaluated were relative weight, area, roundness, length, and width. Germination was evaluated for an 8-day period. Seedling genetic variation was evaluated using random polymorphic DNA (RAPDs) markers. Seed longevity after a 10-year storage period (117 months) was evaluated with maximum germination in two seed origins of *A. salmiana.* The hypothesis was that anthropogenic and environmental factors of the provenances might influence on the responses evaluated.

Materials and methods

The information of this section is available at DOI: https://doi.org/10.17504/protocols.io.6qpvr6j12vmk/v1.

Results and discussion

Seed relative weight, morphometric variation, and germination

Seeds of *A. americana* from Sauz Xathe provenance (AmerSauz) exhibited the maximum relative weight and had the highest values ($\alpha \leq 0.05$) in all the morphometric variables, except for roundness; seed length appeared as a distinctive feature of AmerSauz, while roundness was uniformly higher in all the *A. salmiana* seed origins relative to *A. mapisaga* and *A. americana* (Table 1). Multivariate analysis of the seed morphology results demonstrated divergence of *A. americana* respect to *A. salmiana* and *A. mapisaga* according to Andrews curves (Figure 1).

AmerSauz germination of 89% was inferior relative to the rest of the seed origins (range from 93 to 100%; Table 1). AmerSauz seed capsules were brown color at the collection time, indicative of a dry capsule and the actual moment of flowering stalk maturation was unknown. The variable time that the seeds remained under the abiotic elements might influence on seed's relative moisture content possibly affecting embryo viability, or enabling dormancy induction; as consequence, reducing germination regardless of its highest relative seed weight (McDonald, 2007; Peña-Valdivia et al., 2006). In contrast, capsules of the rest of the seed origins were green yellowish, the green color was indicative of physiological activity of the capsules' outer tissue and the yellow color exhibited chlorophyll denaturation part of the aging process; thus, the capsules of these seed origins had a similar maturation time and less affectation by the abiotic elements.

Table 1. Relative weight (RW), morphometric evaluation, and initial maximum germination (Max. Germ.) of seeds collected in 2012.

Seed origin	RW (mg)	Area	Roundness (cm)	Length	Width	Max. Germ. (%)
SalmMet	9.5d	0.2920d	1.2479a	0.7517b	0.5320de	93
SalmMetβ	9.4d	0.3046cd	1.2485a	0.7688b	0.5433d	97
SalmTlajo	10.2c	0.2800d	1.2383a	0.7323b	0.5211e	98
SalmTlax	12.3b	0.3818b	1.2150a	0.8255b	0.6286b	99
MapsMet	12.5b	0.3400bc	1.1213b	0.7822b	0.5813c	100
AmerSauz	13.4a	0.5614a	1.1446b	1.0025a	0.7439a	89
MSD	0.8	0.0426	0.0553	0.1108	0.0147	

Note. Mean values with different letters within columns are statistically different according to Tukey's test ($\alpha \leq 0.05$). Seed origin = species × provenance, described in Section 2.
Abbreviations: MSD, minimum significant difference; RW, relative weight.

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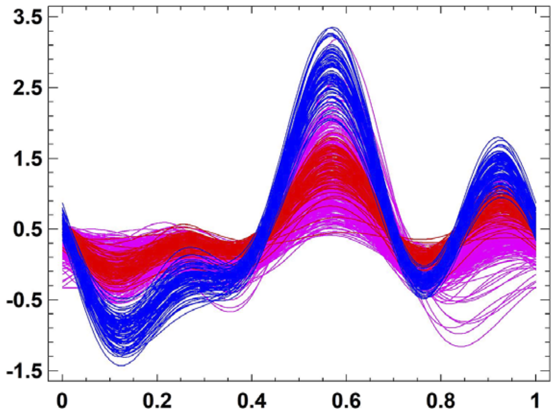

Figure 1. Andrews curves constructed with seed morphometric variables evaluated from *A. americana* (blue), *A. mapisaga* (red), and *A. salmiana* (purple) seed origins.

Within *A. salmiana* seed origins the seeds from Tlaxiaca provenance (SalmTlax), had the highest relative weight, greatest area, and width, which were proportional with high germination of 99%, exhibiting intraspecific variation given by anthropogenic and/or environmental factors. Seed origin of *A. mapisaga* from Metepec (MapsMet) showed a greater germination of 100%, which was proportional to higher weight, similar to SalmTlax (Table 1). These results indicated that higher relative seed weight was proportional to elevated germination (Penfield, 2017); also, pinpointed the importance of capsule maturation stage for seed harvest, which is an anthropogenic factor that should be considered to standardize Agave seed processing and storage.

Seedlings genetic variation

Seedling DNA amplification exhibited 70 fragments which 57 (81.42%) were polymorphic. Asexual propagation, used traditionally, can reduce genetic variation by 8% for *A. salmiana* and *A. mapisaga* populations (Alfaro et al., 2007), and by 10% for *Agave tequilana* plantations (Abraham et al., 2009), which can lead to genetic erosion (Gil-Vega et al., 2001).

The dendrogram (Figure 2) shows AmerSauz isolated from the rest of the seed origins, which is consistent with the differences observed in the seed morphometric results (Table 1 and Figure 1). These results exhibited the interspecific variation of AmerSauz with respect to the plants from the Salmianae section (Gentry, 1982); given by geographic isolation of Sauz Xathe provenance located in the Meztitlan Canyon (INEGI, 1997), reducing its distribution and interaction with other Agave species. Also, the anthropogenic influence can accentuate AmerSauz characters, subjected to less domestication that induce smaller plants with less sap production, compared to *A. salmiana* and *A. mapisaga* landraces that have been intensively selected for those purposes (Mora-Lopez et al., 2011; Trejo et al., 2020).

SalmMet and MapMet were paired in the closest cluster, as both came from the same plantation with similar inflorescence maturation which inferred that hybridization might occur. SalmTlajo and SalmTlax were paired, as both might share genetic traits as a consequence of similar environmental factors, which provenances are in the northern convergent plateau between Mexico City, for Tlajomulco in the northeast toward Tulancingo Valley, and for Tlaxiaca in the northwest toward Actopan Valley, both provenances are communicated by a natural corridor that passes through Pachuca city possessing xerophytic vegetation with sub-humid to semi-arid conditions; contrasting to SalmMetβ located in mild conditions of Tulancingo Valley (INEGI, 1992; Jimenez-Torres et al., 2021).

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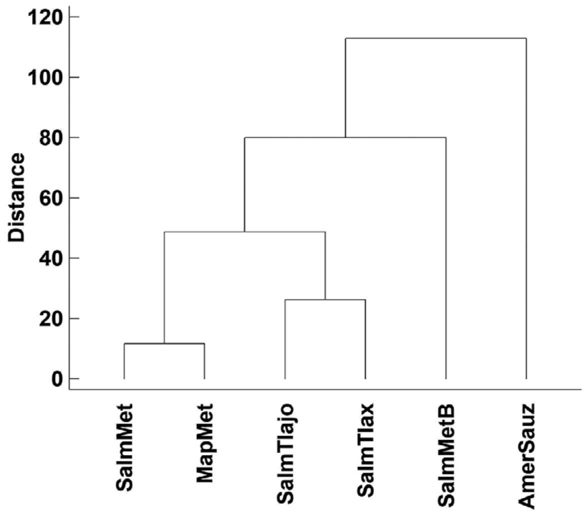

Figure 2. Dendrogram constructed according to the binary matrix of DNA bands amplified from seedlings of Agave seed origins (species × provenance) using Ward's method (city block distance).

Germination after a 10-year storage period

After a 117-month storage period (≈ 10-year storage period), when the lids were removed from the glass jars it was broken a vacuum seal making a characteristic sound while releasing the lid, although these containers were only airtight sealed not vacuum sealed, which indicated that seed respiration during storage consumed the oxygen present into the jar generating a vacuum by itself. The maximum germination for *A. salmiana* seeds from Metepec (SalmMetβ) and Tlaxiaca (SalmTlax) after a 10-year storage period was 96 and 95%; respectively (Table 2), with a germination reduction of 1 and 4% compared to the initial germination observed at 2012 (Table 1).

Seeds of *A. salmiana* collected in September 2017 from Tlajomulco provenance (SalmTlajo17) after a 55-month storage period, exhibited no statistical differences in maximum germination results with respect to the other seed origins, regardless of a longer storage period of SalmMetβ and SalmTlax (Table 2). These results pinpointed the importance of the capsules' maturation stage for seed preservation, as SalmTlajo17 capsules were brown color fully mature, having similar germination results as AmerSauz (Table 1).

After a 10-year storage period, no statistical differences were observed between SalmMetβ and SalmTlax in seed moisture content, relative weight, and dry weight (Table 2). SalmTlajo17 exhibited significant differences for all the variables evaluated (except maximum germination) respect SalmTlax (Table 2).

Table 2. Evaluation of maximum germination (Max. Germ.), SM content, RW, and DW of seeds after 55-month (SalmTlajo17) and 10-year storage period (SalmTlax and SalmMetβ).

Seed origin	Max. Germ. (%)	SM (%)	RW (mg)	DW (mg)
SalmTlax	95a	5.25b	9.83a	9.31a
SalmMetβ	96a	5.5ab	9.54ab	9.02ab
SalmTlajo17	90a	6.5a	9.31b	8.7b
MSD	11.08	1.09	0.47	0.41

Note. Mean values with different letters within columns are statistically different according to Tukey's test ($\alpha \leq 0.05$). Seed origin = species × provenance, described in Section 2.
Abbreviations: DW, dry weight; MSD, minimum significant difference; RW, relative weight; SM, seed moisture.

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These values demonstrated that *A. salmiana* seeds can withstand desiccation and long storage periods (>5 years), such as orthodox seeds, which maintained relatively adequate germination under the given storage conditions. Seed moisture content, storage temperature, and oxygen exposition are key factors that must be considered when working with species without known adequate storage parameters (Bewley et al., 2013; De Vitis et al., 2020).

The results obtained in this work can be used as reference parameters to determine the optimum Agave's seed moisture content threshold for adequate storage conditions. In this work, the storage temperature was not controlled nor recorded, but according to normal climatic data of the nearest weather station (Zempoala, Hidalgo) from the storage facility, the storage temperature did not surpass the range of 24–26°C during the warmer season of March–April, and the rest of the year was below that temperature range (CONAGUA, 2021). Oxygen exposition was controlled by airtight containers, the seeds consumed the air that remained in the glass jar and generated a vacuum seal.

Conclusion

Seed morphology and seedling genetic variation were useful to elucidate the interspecific differences of the seed origins evaluated; also, the intraspecific variation observed within *A. salmiana* seed origins. Greater germination was proportional to higher relative seed weight within seed origins with similar capsule maturity at the moment of seed collection time. Airtight sealed glass jars and temperate room temperature were adequate conditions for seed storage as little germination reduction was observed after a 10-year storage for SalmMetβ and SalmTlax. These results helped to elucidate the anthropogenic and environmental factors that influenced divergences and similarities of the variable responses evaluated.

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Data availability statement. The data that support the findings of this study are available on request from the corresponding author. Materials and methods used in this study are available at doi: https://doi.org/10.17504/protocols.io.6qpvr6j12vmk/v1.

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Conflict of interest. The authors have no conflicts of interest to declare.

Authorship contributions. J.J.-M. conceived the study, Z.M.-G. performed the laboratory experiments and wrote the article, J.A.J.-T. complemented the study and wrote the article.

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Peer Reviews

Reviewing editor: Dr. Bodil Jørgensen

University of Copenhagen, Department of Plant and Environmental Sciences, Thorvaldsensvej 40, Frederiksberg C, Denmark, 1871

This article has been accepted because it is deemed to be scientifically sound, has the correct controls, has appropriate methodology and is statistically valid, and met required revisions.

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Review 1: Evaluation of seed morphology, seedling genetic variation, and components for seed storage of Agave landraces of commercial interest

Reviewer: Dr. Laura TrejoDra.

Instituto de Biología UNAM, Laboratorio Regional de Biodiversidad y Cultivo de Tejidos Vegetales, Ex-Fabrica San Manuel de Morcom s/n, Santa Cruz Tlaxcala, Tlaxcala, Mexico, 90640

Date of review: 15 August 2022

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Conflict of interest statement. Reviewer declares none

Comment

Comments to the Author: After reviewing the work, it is suggested to strengthen the writing by attending to the following observations.

- The summary could improve if a justification of the work and the methods is included, also if the results and conclusions are deepened.

Methods

- Describe what farming systems and what is the intensity of farming from which the seeds come.
- Define and explain how the roundness of the seed was measured.
- In the analyzes of genetic diversity, how many individuals were analyzed by place of origin?
- Differentiate and explain the statistical analyzes of each of the experiments.
- Line 84. In agaves?
- Explain the main differences between harvesting green fruits and ripe brown fruits. Since it is understood that the green fruits used in this work could be harvested 3 to 4 months before being ripe.
- It is suggested to represent through graphs and multivariate statistical analysis the differences between the morphological characteristics of the seeds.
- Present data on genetic diversity by species and by population or origin place.
- Lines 165-167. Explain the factors mentioned throughout the writing and not only in a general way.
- The discussion needs to be compared with a greater number of works that exist on topics related to Agave.

Score Card

Presentation

3.0 /5

Is the article written in clear and proper English? (30%)	4/5
Is the data presented in the most useful manner? (40%)	3/5
Does the paper cite relevant and related articles appropriately? (30%)	2/5

Context

3.5 /5

Does the title suitably represent the article? (25%)	5/5
Does the abstract correctly embody the content of the article? (25%)	2/5
Does the introduction give appropriate context? (25%)	3/5
Is the objective of the experiment clearly defined? (25%)	4/5

Analysis

2.0 /5

Does the discussion adequately interpret the results presented? (40%)	2/5
Is the conclusion consistent with the results and discussion? (40%)	2/5
Are the limitations of the experiment as well as the contributions of the experiment clearly outlined? (20%)	2/5

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Review 2: Evaluation of seed morphology, seedling genetic variation, and components for seed storage of Agave landraces of commercial interest

Reviewer: Dr. Bodil Jørgensen

University of Copenhagen, Department of Plant and Environmental Sciences, Thorvaldsensvej 40, Frederiksberg C, Denmark, 1871

Date of review: 30 August 2022

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Conflict of interest statement. None

Comment

Comments to the Author: Methods

Germination as in 2.2 – should this refer to 2.1?

In one of the lines – 2000 milibar – "l" missing (millibar)

DNA purity measured by spectrophotometer – Please describe how this is done, OD etc.

Update the table with geographical information with references to all names used in the text. If you do not know the area it is very difficult to relate to the names used in the full text as these are not the same as used in the table. Consider showing a map to help the reader.

As it is now the result part is difficult to read as the names used is not mentioned for the areas in the table.

The results (table and figure) relate to the areas where the seed where collected. It is missing what the story to be told is for the different species collected – please elaborate.

Illustrations of the seeds stages and perhaps combined with how it is measured will be a help.

Table 1; the table text does not specify whether these results are from collecting time or later.

Include a table with comparison start and after storage.

Score Card

Presentation

3.0 /5

Is the article written in clear and proper English? (30%)	3/5
Is the data presented in the most useful manner? (40%)	3/5
Does the paper cite relevant and related articles appropriately? (30%)	3/5

Context

3.0 /5

Does the title suitably represent the article? (25%)	3/5
Does the abstract correctly embody the content of the article? (25%)	3/5
Does the introduction give appropriate context? (25%)	3/5
Is the objective of the experiment clearly defined? (25%)	3/5

Analysis

3.0 /5

Does the discussion adequately interpret the results presented? (40%)	3/5
Is the conclusion consistent with the results and discussion? (40%)	3/5
Are the limitations of the experiment as well as the contributions of the experiment clearly outlined? (20%)	3/5

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