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Effect of Seed Position on Parental Plant of *Kroenleinia grusonii* (Hildm.) Lodé. and *Echinocactus platyacanthus* Link & Otto on Seed Germination at High Temperatures

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ABSTRACT

The position in which seeds develop on the parental plant can have effects on their physical and physiological characteristics. The current global temperature increase may affect these characteristics. The hypothesis was that seeds at the apex of the crown of *Kroenleinia grusonii* (Hildm.) Lodé. and *Echinocactus platyacanthus* Link & Otto plants differ in size, viability, dormancy and germination, at six temperatures, from 20°C to 45°C, from those at the periphery of the crown. Our evaluations included the seed dimensions, mass, viability, and vigor, and seed imbibition and germination at constant temperatures. The seeds at the apex of the crown of *K. grusonii* plants were longer, heavier, and had more vigor and also significantly higher germination regardless of temperature than those from the periphery. Seeds at the apex of the crown of *E. platyacanthus* plants were less heavy and wide, but longer than those of the periphery. Seed dormancy, greater than 80%, in both species was eliminated by mechanical scarification. Diversity in physical and physiological characteristics of a seed cohort likely increases dispersal success and survival in the natural climate, accommodating to some extent the distribution of plant species with temperature changes due to global warming.

1 | Introduction

The Cactaceae taxa include *Kroenleinia grusonii* (Hildm.) Lodé. and *Echinocactus platyacanthus* Link & Otto (Vargas-Luna et al. 2018). Both species are native and endemic to Mexico; *K. grusonii* is distributed from State of Tamaulipas to the State of Hidalgo, while *E. platyacanthus* is found from the southern Chihuahuan desert regions to the Tehuacán-Cuicatlán Valley in Puebla and Oaxaca (South central Mexican plateau) (Jiménez-Sierra and Eguiarte 2010; Vargas-Luna et al. 2018). Both species have been harvested and used since ancient times. They are important ecologically and economically; they serve as ornamental plants, and as food for humans and livestock (de la Torre-Hernández et al. 2020; del Castillo and Trujillo 1991;

Jiménez-Sierra and Eguiarte 2010; Ruiz 2012). *K. grusonii* is in the category of endangered species and *E. platyacanthus* is subject to special protection in the Mexican Standard NOM-059 (Norma Mexicana NOM-059-SEMARNAT-2010, n.d.). Both species are listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix II, which includes species not necessarily threatened with extinction but could become so, unless their trade becomes strictly managed (CITES 2022). In addition, *K. grusonii* is listed as critically endangered by The International Union for Conservation of Nature's Red List of Threatened Species (Hernández-Oria et al. 2007). The effect of anthropogenic factors that affect both species' survival, such as their natural habitat destruction, land use changes, and excessive plant extraction for their

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commercialization, are increased by their demographic factors, such as low growth rates, seed germination, and seedling survival in the field (Hernández-Oria et al. 2007; Martorell et al. 2015). At the same time, droughts and temperatures are globally increasing as a result of climate change and *Kroenleinia* and *Echinocactus*, as well as many other genera, may be disfavored by such changes (Aragón-Gastélum et al. 2021; Ramírez-Tobías et al. 2012).

Plants of *K. grusonii* and *E. platyacanthus* have flowers distributed at the apex and periphery of the crown (Bravo-Hollis and Sánchez-Mejorada 1978). Both species produce flowers and fruits asynchronously during several months in a year, exposing the seeds to long periods of changing environmental conditions (Díaz-Hernández et al. 2008; Pavón and Briones 2001; Trujillo-Argueta and del Castillo 2013; Vázquez 2017) which may affect their quality. There are few studies on seed germination of *K. grusonii*; Osuna-Ávila et al. (2025) found only three studies, between 1994 and 2022, related to this species. However, *E. platyacanthus* has been more extensively studied. Osuna-Ávila et al. (2025) evaluated seed germination of *K. grusonii* in relation to seed size. They evaluated intact seeds (control), mechanically scarified seeds and seeds scarified with acid (sulfuric and hydrochloric); at 25°C and at a 16:8 h photoperiod. Germination of intact seeds reached 38%, 66% with mechanical scarification and between 6% and 42% after acid scarification. Manzo Rodríguez et al. (2022) evaluated viability and germination of seeds of *E. platyacanthus* and *K. grusonii* with the aim of planning seed conservation under unfavorable environments; evaluations included seeds scarified with concentrated acid, in different substrates and germinated on Murashige and Skoog medium, at 27°C under constant light. In this study seed germination of *E. platyacanthus* was between 10 and 94% and 6% and 64% in *K. grusonii*. Hernández Aguilar (2007) evaluated the effect of light (white, red, far red and darkness) and temperature (between 15°C and 35°C) on the seed germination of *E. platyacanthus*; the seeds were collected from the “aerial seed bank” (fruits in the crown of the plants) from three regions of Mexico. In that study, seeds from Metztlán, Hidalgo, germinated between 3% and 66% at 20°C to 35°C under three light conditions and in darkness, while seeds from Tehuacán, Puebla, germinated up to 43% under the same light and temperature conditions. These studies highlighted the variability on the seed germination response of intact and scarified seeds of both species from different regions under different environmental conditions including darkness, continuous light, or light/darkness, and constant temperature or thermoperiod.

Although photoblastism, viability, dormancy, and germination (at 25°C) of seeds from these species have been documented (Contreras-Quiroz et al. 2016; Gómez-Serrano et al. 2021; López-Escamilla et al. 2016; Manzo Rodríguez et al. 2022; Osuna-Ávila et al. 2025; Padrón 2012; Rojas-Aréchiga and Batis 2001; Rojas-Aréchiga et al. 2013; Rosas-López and Collazo-Ortega 2004) before the present investigation, there was no information related to the effect of seed position on the parental plant of *K. grusonii* and *Echinocactus* spp. on its physical or physiological quality.

Most cacti seeds have morphological, physiological, and biochemical adaptations to germinate under adverse conditions (Mihalte et al. 2011), one of which is dormancy. Seeds

continually adjust their dormancy by sensing a variety of environmental cues. Slow seasonal change is reflected by temperature and allows for temporal detection for seed germination. This alters seed sensitivity to environmental signals, including light, temperature, and soil moisture, and temperature detection indicates whether conditions are suitable for germination and thus triggers the dormancy release (Nakabayashi and Leubner-Metzger 2021). Seed dormancy is a common adaptation in plants from arid and semi-arid environments (Flores et al. 2008). Environmental temperature regulates timing and speed of seed germination (Rojas-Aréchiga et al. 1998). Assuming that with climate change global temperatures will increase (Aragón-Gastélum et al. 2021; Ramírez-Tobías et al. 2012), its effects in the soil may affect the viability and seed germination in seed banks (Pérez-Sánchez et al. 2011). Thus, climate change threatens the sustainability of livestock production systems. In this context, cacti may be a resource to improve productivity and sustainability (Padrón 2012) because of their ability to tolerate high temperatures (Barrios et al. 2020). Overall, the environmental conditions during fruiting and seed growth impact seed quality, and in this regard extreme temperatures and both, high and low moisture availability, negatively affect vigor and seed viability (Elizalde et al. 2017).

The objective of this research was to evaluate the effect of the seed position within the crown of the plants of *E. platyacanthus* and *K. grusonii* on their physical quality, imbibition and germination response to different temperatures. The hypothesis was that *K. grusonii* and *E. platyacanthus* seeds differ in their physical and physiological characteristics, such as size, viability, dormancy, and response to the germination environment, such as temperature, according to their position on the plant crown.

2 | Materials and Methods

2.1 | Seed Collection

Seeds were obtained from ripe fruits of *Kroenleinia grusonii* and *Echinocactus platyacanthus* classified as apical (34 and 18, respectively) and peripheral (47 and 37, respectively) on the plant crown. The fruits were harvested as follows: an imaginary circle or ellipse, depending on the shape of the plant's crown, was drawn on the crown, with radii equidistant from the center; the apical fruits corresponded exclusively to those in the center of the circle, and the peripheral fruits corresponded to those on the outside of the circle (Figure 1) (Vargas-Luna et al. 2018). The fruits of both species were harvested in 2020, from 10 plants growing in an experimental area, with occasional irrigation and natural thermoperiod, at the Institute for Research in Desert Areas of the Autonomous University of San Luis Potosí, México. Experiments were undertaken during the 6 months after fruits were collected. Fruits were kept in paper bags at laboratory temperature (20°C ± 2°C) during evaluations in 2020–2021 and the seeds were extracted from the fruits during the evaluations.

2.2 | Experimental Design

The study of the physical characteristics of the seeds was conducted with a completely randomized experimental design with

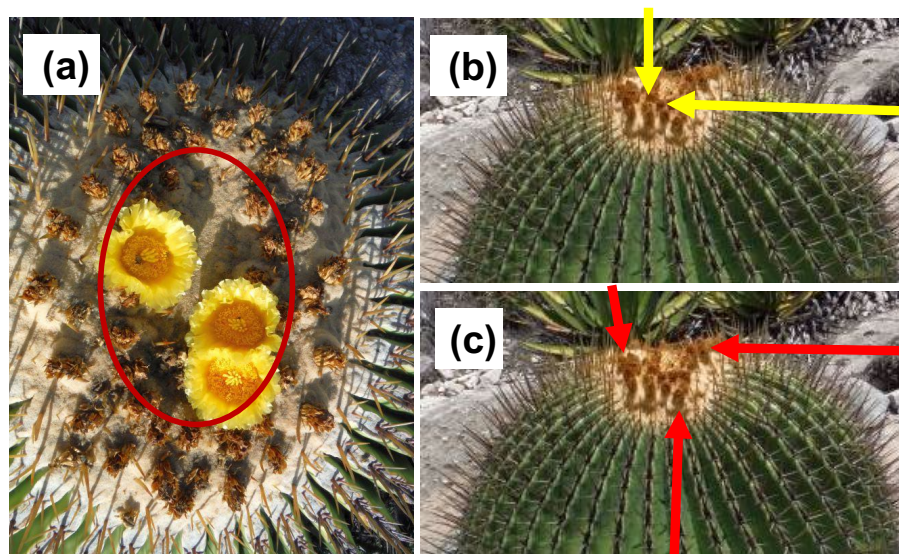


FIGURE 1 | Plants of *Echinocactus platyacanthus* Link & Otto (a) Flowers and fruits on the crown of the plant, (b) ripe-dry fruits on the crown of the plant, the yellow arrows indicate the fruits at the apex of the crown and (c) ripe-dry fruits on the crown of the plant, the red arrows indicate the fruits at the periphery of the crown. The red ellipse (a) represents an imaginary line on the crown; the apical fruits corresponded exclusively to those inside the circle, and the peripheral ones were those outside the circle.

two treatments per species (fruit position on the plants crown). Similarly, the study of seed imbibition and seed germination of each species was conducted with a completely randomized experimental design with twelve treatments generated by the combination of two fruit position on the plants crown (apex and periphery) and six temperatures (20°C, 25°C, 30°C, 35°C, 40°C, and 45°C per species).

2.3 | Seed Dimension and Seed Mass Assessment

The width (mm), length (mm), and area (mm²) of 1000 seeds were assessed with the ImageJ software for digital and printed image analyses (<https://imagej.softonic.com/>). The seed mass was determined on an analytical balance (Scientech SA 120, USA). Two hundred and twenty *K. grusonii* seeds groups of ten (experimental unit) were weighed in because the analytical balance did not record the weight of a single seed. Nine hundred and fifty seeds of *E. platyacanthus* were weighed individually. Treatment differences in seed width, length, area, and mass were analyzed with the Student's *t*-test.

2.4 | Viability Assessment

The viability of the seminal embryos was evaluated following directions by the International Seed Testing Association (ISTA 2010), which involved staining the tissues with 2, 3, and 5 triphenyl tetrazolium chloride (tetrazolium). This evaluation included four groups of 25 seeds (experimental unit) of the apical fruits and 25 of the peripheral ones from each species. The embryo classification, according to their coloration (ISTA 2010; Maldonado-Peralta et al. 2016; Manzo Rodríguez et al. 2022), was: (1) alive with high viability (total staining and intense red color), (2) alive with low viability (partially stained or pale red coloration), and (3) non-viable. embryos (colorless). The proportion of viable embryos was the sum of

classes 1 and 2 dividing by the total seed number. Values were expressed as a percentage. Seed viability was analyzed using a contingency table.

2.5 | Imbibition and Germination Assessment

The intact (non-scarified) seeds were placed in Petri dishes with a filter paper support, moistened with distilled water, and kept in controlled environment chambers (Seedburo ATTGPT-B, USA), set at constant 20°C, 25°C, 30°C, 35°C, 40°C, or 45°C in darkness. The initial seed mass (mg) of each experimental unit was recorded before placing the seeds in Petri dishes, and moistening them, subsequently the evaluations of seed mass were made every 3 h for 36 h. Because the analytical balance did not record the weight of a single *K. grusonii* seed, this species imbibition was evaluated in six experimental units, with 10 groups of 10 seeds each; while 10 seeds for each experimental unit of *E. platyacanthus* were evaluated. The imbibition was expressed as a percentage of weight gained by the seeds, due to water absorption, compared to their initial weight (ISTA 2010). Differences in maximum seed imbibition at each temperature for both species were analyzed with the Student's *t*-test.

Germination was evaluated following the ISTA method (ISTA 2010). Ten intact-dry (non-scarified and non-soaked) seeds per replicate were placed in a Petri dish with a filter paper support, moistened with distilled water, and kept in controlled environmental chambers (Seedburo ATTGPT-B, USA), at constant 20°C, 25°C, 30°C, 35°C, 40°C, or 45°C and in darkness (ISTA 2010). Six replicates were evaluated per treatment. The germinated seeds were counted every 24 h, for 45 days, to derive total or maximum accumulated germination (%) and the daily germination rate. To complete seed characterization, the germination of scarified seeds, by abrading the testa with sandpaper, was assessed at 25°C (Hernández Aguilar 2007). According to the ISTA rules (2010), a seed was

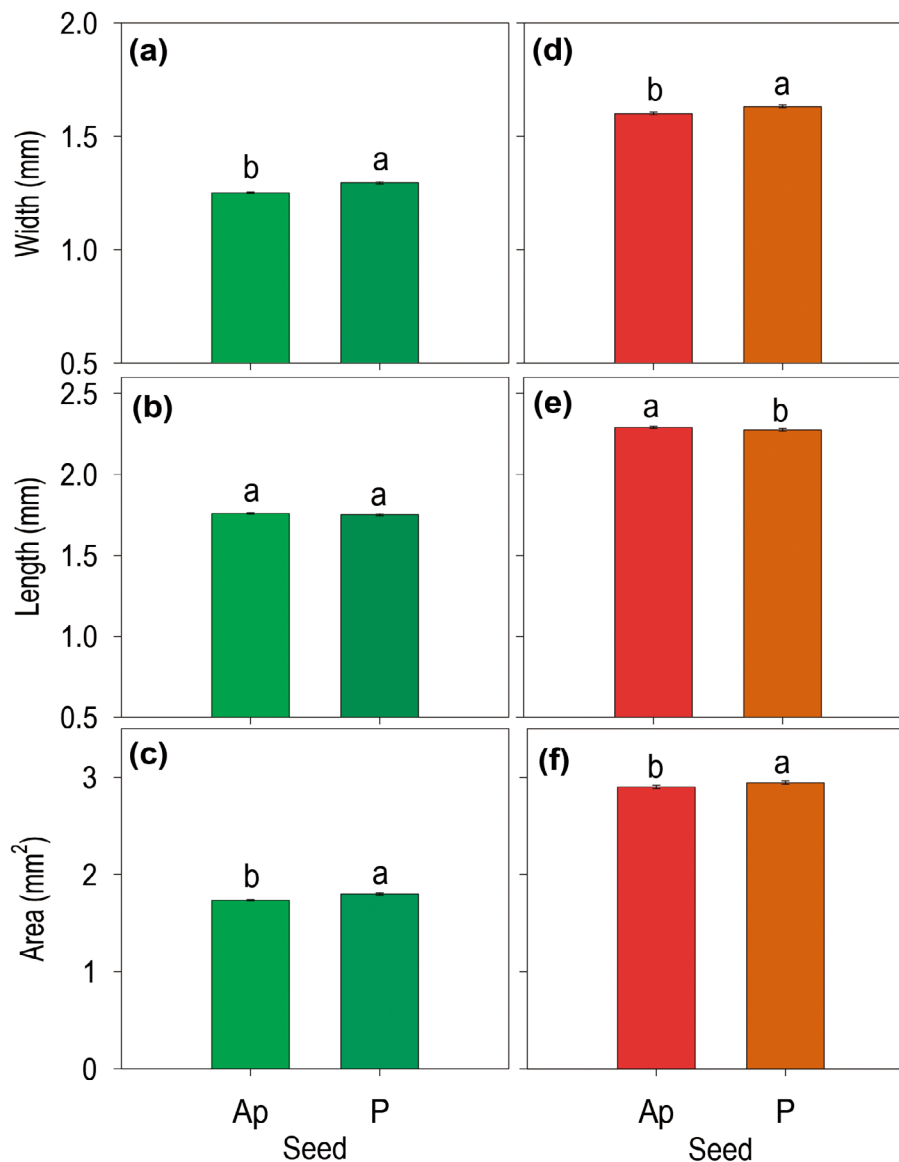


FIGURE 2 | Width, length, and area ($\pm$ standard error) of the seeds from the apex (Ap) or from the periphery (P) of the crown of *Kroenleinia grusonii* (Hildm.) Lodé. (a–c) plants and *Echinocactus platyacanthus* Link & Otto (d–f) plants; $n = 1000$. Different letters over the bars indicate a significant difference among seeds for each species studied according to the Student's t -test.

considered germinated when the length of its emerged root was 5 mm or more (ISTA 2010). Differences in maximum seed germination at each temperature and species were analyzed with the t -Student test.

2.6 | Data Analysis

The data were analyzed using the frequency distribution for seed mass, imbibition and germination curves. The equations with the best fit, and the relevant parameters of each, were obtained with the SigmaPlot 11.0 software (free version: <https://sigmaplot.software.informer.com/11.0/>). A t -test was used to examine the effects of the seed position on the plant crown on seed physical characteristics, imbibition and germination. Data for total imbibition and total germination were transformed to the $\log_{10}$ prior to statistical analyses. Figures show untransformed data. The assumptions of normality

using the Shapiro–Wilk test were verified automatically by the SigmaPlot software; when this assumption failed, the Mann–Whitney rank sum test was used for comparisons also using the SigmaPlot software.

3 | Results

3.1 | Physical Characteristics of the Seeds and Viability

3.1.1 | *Kroenleinia Grusonii*

The average size of the *K. grusonii* seeds differed depending on their position on the plant crown. Although the lengths, the seeds from periphery were wider and had a greater area compared to those from apex (Figure 2a–c; Table 1). Also, the seeds of the apex were heavier (by 20%) than those from the periphery

TABLE 1 | Values of t and p , and degree of freedom (d.f.) of the t -test used to examine the effects of the seed position (apex or periphery) on the plant crown on seed physical characteristics, imbibition and germination under 20°C to 45°C. Data of total imbibition and total germination were transformed to the $\log_{10}$ prior to statistical analyses.

Response variable	<i>Kroenleinia grusonii</i>			<i>Echinocactus platyacanthus</i>		
	d.f.	t	p	d.f.	t	p
Seed						
Width	998	840700.500	<0.001	998	924989.000	<0.001
Length	998	1004323.000	=0.767	998	963390.500	<0.001
Area	998	893290.500	<0.001	998	946974.000	<0.001
Mass	218	64600.000	<0.001	948	834242.500	<0.001
Imbibition at						
20°C	10	4.529	<0.001	10	−4.521	<0.001
25°C	10	3.401	=0.003	10	0.252	=0.806
30°C	10	−3.401	=0.003	10	1.181	=0.265
35°C	10	94.000	=0.427	10	0.101	=0.922
40°C	10	77.500	=0.348	10	3.590	=0.005
45°C	10	−2.474	=0.024	10	5.002	<0.001
Germination at						
20°C	10	4.235	0.002	10	5.250	<0.001
25°C	10	−1.660	=0.128	10	0.099	=0.923
30°C	10	51.500	=0.041	10	1.337	=0.211
35°C	10	1.434	=0.182	10	129.500	0.049
40°C	10	2.439	=0.035	—	—	—
45°C	10	6.437	<0.001	10	48.000	=0.074

(Figure 3a; Table 1). The relative frequency of the seed mass distribution showed a rightward bias in both *K. grusonii* seed groups, with a relative abundance around 1 mg and 0.85 mg in the apical and peripheral seeds (Figure 3b,c). No significant differences were observed in the viability and vigor between crown plant position for the *K. grusonii* plants. On average they had close to 95% viability and 86% vigor (Table 2).

3.1.2 | *Echinocactus platyacanthus*

Seed sizes were different depending on the seed position on the plant crown of *E. platyacanthus*. Those from the periphery were wider, heavier (17%) with greater planar area compared to those from the apex; in contrast, the latter were longer (Table 1; Figures 2d–f and 3d). The relative distribution frequency of the seed mass from the apex showed irregular alternating high and low values, there were even intervals with no record, and four maxima. In contrast, the distribution of the mass of the seeds from the periphery exhibited a high number of values around the central value (leptokurtic distribution) (Figure 3e,f). Embryos viability was similar between the seeds at the apex and those at the periphery of the plant crown. The similarity was also recorded in the percentage of embryos with high and low viability (Table 2).

3.2 | Effects of Temperature on the Seed Imbibition and Germination

3.2.1 | *Kroenleinia Grusonii*

The cumulative imbibition of the seeds of both treatments increased exponentially ($y = a*(1 - \exp(-b*x))$) in the first 30–36 h, regardless of the temperature during imbibition. However, seeds from the apex imbibed less water at 20°C to 30°C compared to those from the periphery. Also, the greatest statistically significant differences were between both seed treatments with these temperatures. The maximum imbibition of the apical seeds remained relatively constant, between 61% and 71%, at 20°C to 35°C; however, at 40°C and 45°C it decreased to 53% and 47%. The highest imbibition of the peripheral seeds was 90% at 20°C compared to the other temperatures, and decreased at higher temperatures. At 25°C–35°C the maximum imbibition reached 80% and was lower (54%) at 40°C and 45°C (Figure 4; Table 1).

The cumulative germination, between 20°C and 45°C of both seed treatments showed a sigmoid trend ($y = a/(1 + \exp(-(x-x_0)/b))$) with the exception of the apical seeds at 20°C for which the best-fit trend was cubic polynomial ($y = y_0 + ax + bx^2 + cx^3$). Depending on seed position and the temperature of seed germination, seeds showed differences in initial germination, total

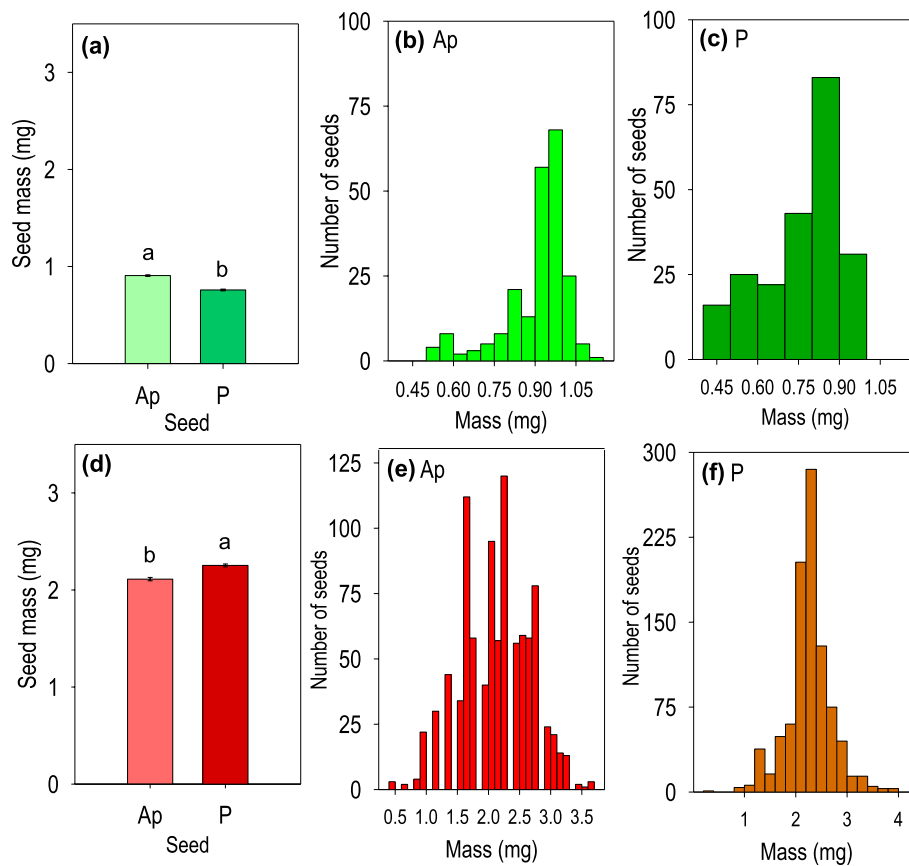


FIGURE 3 | Average seed mass ($\pm$ standard error) and frequency distribution of seed mass from the apex (Ap) or periphery (P) of the crown plants. (a–c) *Kroenleinia grusonii* (Hildm.) Lodé and (d–f) *Echinocactus platyacanthus* Link & Otto. Different letters over the bars indicates a significant difference among seeds by species according to the Student's *t*-test; $n = 250$.

TABLE 2 | Viability of seed embryos of *Kroenleinia grusonii* (Hildm.) Lodé. and *E. platyacanthus* Link & Otto.

Species	Seeds ^a	Viability (%)	High viability (%)	Low viability (%)
<i>Kroenleinia grusonii</i>	Apical	96	84	12
	Peripheral	92	88	4
<i>Echinocactus platyacanthus</i>	Apical	96	80	16
	Peripheral	96	80	16

^aThe embryos corresponded to the apical or the peripheral seeds on the crown of the plants; $n = 25$.

germination, cumulative germination rate, and mean daily germination (Figure 5; Table 1).

The initial seed germination of that from the apex of *K. grusonii* was faster regardless of the temperature, compared to the peripheral seeds. An exception occurred at 30°C, the temperature at which the peripheral seeds began germination 3 days earlier than those of the apex. With the temperature increase, the time to start the apical seed germination decreased from 19 to 4 days at 20°C and 35°C, respectively. At 40°C and 45°C the trend was not maintained (Figure 5e,f).

The germination onset of peripheral seeds, foremost, decreased with the increase in temperature. In these seeds, the time to initiate germination varied between 4 and 36 days. The longest germination onset corresponded to the lower temperatures, 20°C

and 25°C; although, at higher temperatures (40°C and 45°C) germination was also partially delayed (by 10 and 16 days), compared to that at 30°C. In other words, at 30°C the peripheral seeds started germination in half the time compared to apical seeds (Figure 5a–f).

The total apical seed germination varied between 18% and 98% and that of the periphery varied between 7% and 86%. The seeds of the apex showed higher total germination, regardless of the temperature, compared to those from the periphery; the exception was at 25°C, a temperature at which germination was similar for both seed position (Figure 5b; Table 2). In addition, those seeds exhibited total germination in a shorter time than that of the periphery in most temperatures, again except at 25°C, where peripheral seeds had maximum germination 5 days earlier. The seed germination differences between seed

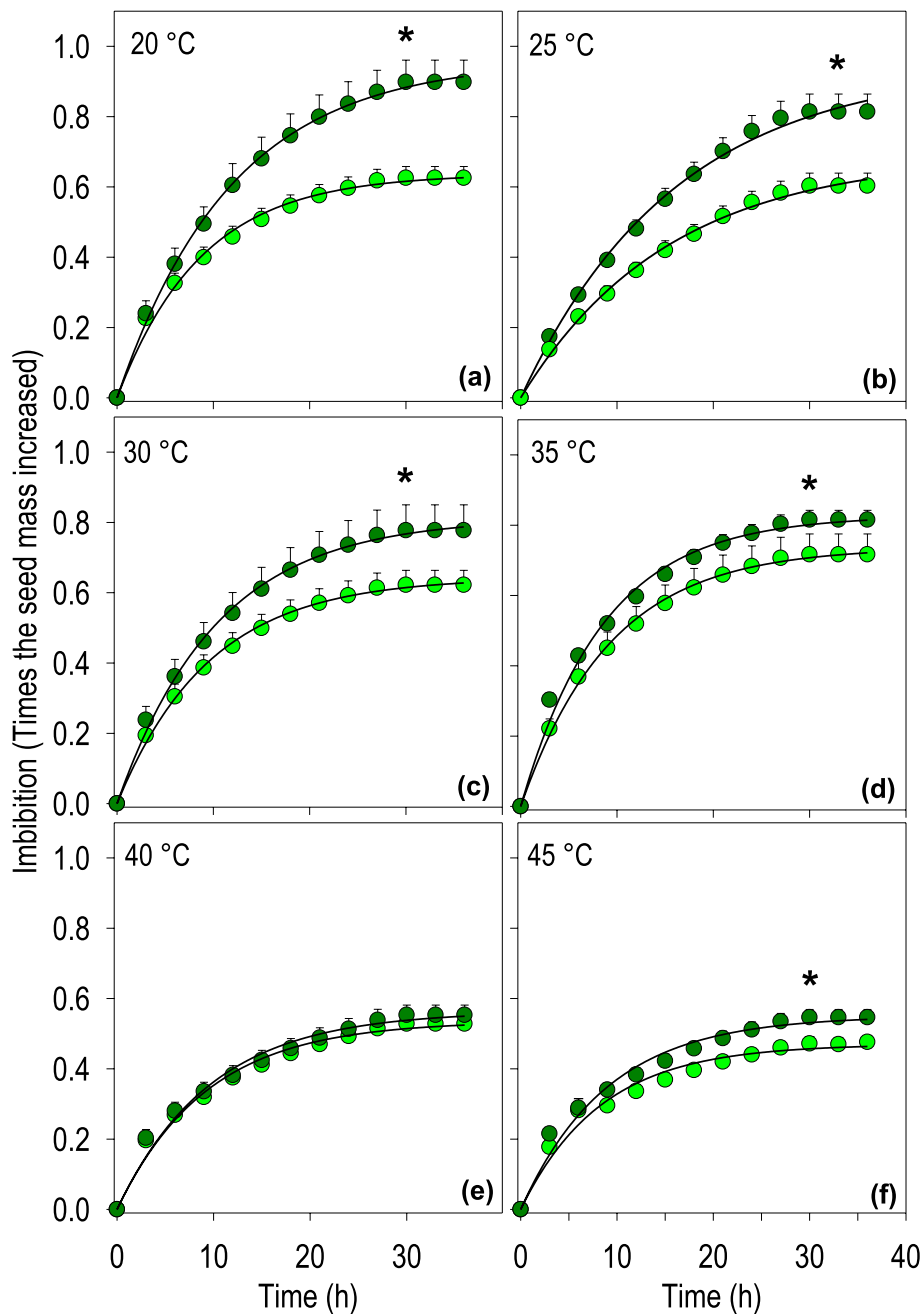


FIGURE 4 | Cumulative imbibition (+ standard error) of the seeds from the apex (light-green circles) or the periphery (dark-green) of the crown of *Kroenleinia grusonii* (Hildm.) Lodé. plants, at constant temperature (20°C to 45°C) and in darkness; $n=6$. The asterisk over the maximum imbibition indicates significant differences among seed positions at each temperature ($p \leq 0.05$).

position are incorporated by the values of the average daily germination and the accumulated germination rate. For the apical seeds, the minimum and maximum values of the average daily germination were 0.57 and 2.18 seeds per day each, at 20°C and 30°C. In contrast, in the peripheral seeds, germination dropped to 0.17 and 1.91 seeds per day, at the same temperatures. Since the minimum and maximum total germination values did not coincide with the average daily germination, the minimum, and maximum cumulative germination rates were obtained with temperatures different from those of total germination. In the apical seeds, the minimum and maximum cumulative germination rate (29.97 and 91.25 seeds per day) occurred at 20°C and 35°C respectively, and in the

peripheral seeds (10.29 and 78.18 seeds per day) at 30°C and 45°C, respectively (Figure 5a–f). Germination of apical scarified seeds was higher (81.38%) than in that at the peripheral scarified seeds (72.31% at 25°C the only temperature tested for scarified seed) (Figure 5b; Table 1).

3.2.2 | *Echinocactus platyacanthus*

The cumulative imbibition of the seeds of both seed treatments exponentially increased ($y = a*(1 - \exp(-b*x))$) within the first 30–36 h, regardless of the temperature during imbibition. At 25°C–35°C, the differences in maximum imbibition, after

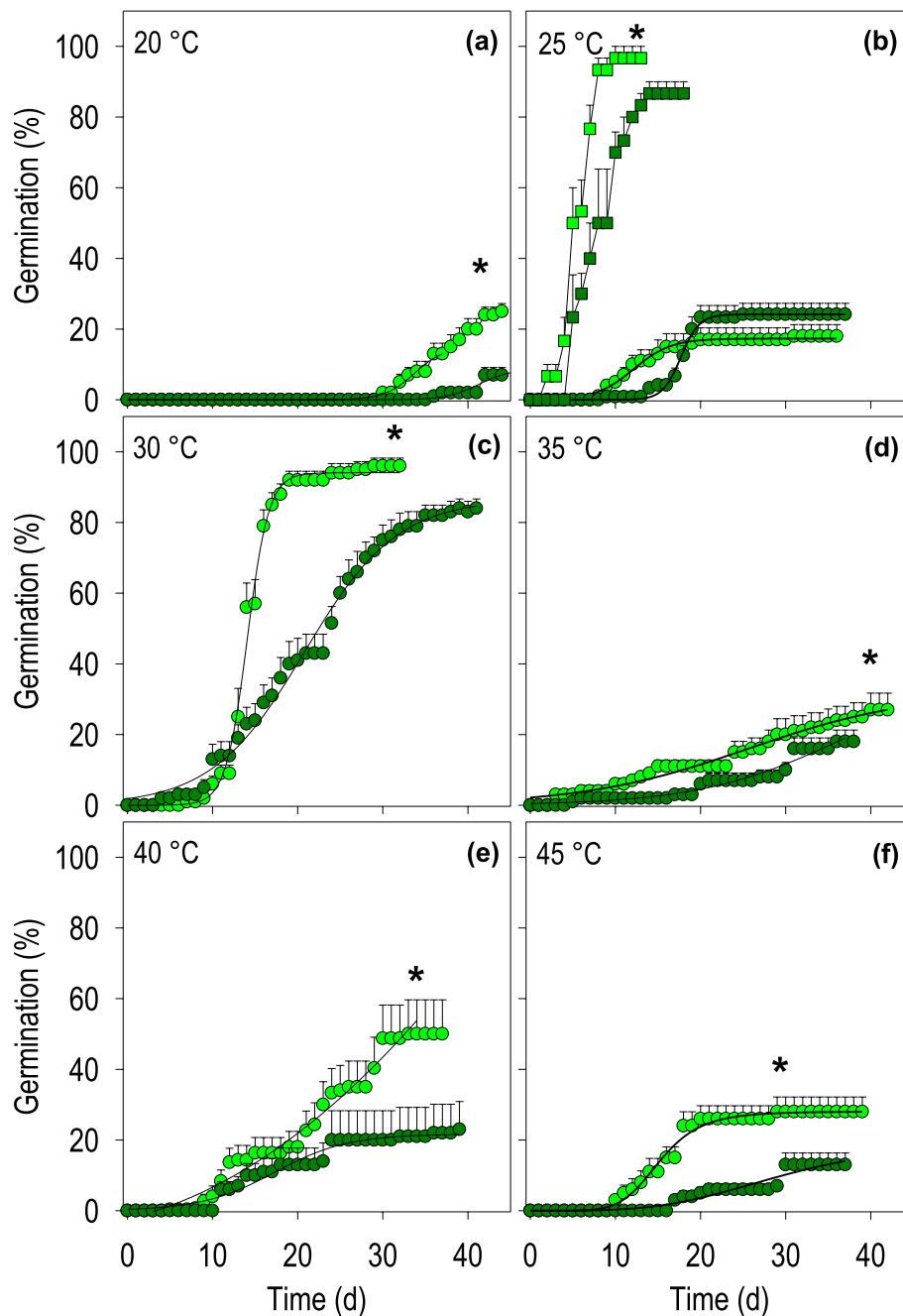


FIGURE 5 | Cumulative germination (+ standard error) of the seeds from the apex (light green symbols) or the periphery (dark green symbols) of the crown of *Kroenleinia grusonii* (Hildm.) Lodé. plants, at constant temperature (20°C to 45°C) and in darkness; circles: Intact seeds and squares: Mechanically scarified seeds; $n = 6$. The asterisk over the maximum germination indicates significant differences among seed positions at each temperature ($p \leq 0.05$).

36 h, were not significant; however, at the outermost temperatures (20°C, 40°C, and 45°C) the difference in the maximum imbibition was significant between seed treatments (Table 1). Temperature increases also significantly increased seed maximum imbibition, on average 1.20 times the original mass of the seeds at 20°C, 1.80 at 25°C and 30°C, and 2.22% to 2.80% at 40°C and 45°C. The exception in this tendency was the maximum imbibition at 35°C, with a maximum of 1.50. In contrast, in the peripheral seeds the maximum imbibition decreased as the temperature increased. Their values were from 1.86 times the original mass of the seeds at 20°C and 24°C to 1.36 at 45°C (Figure 6).

The cumulative seed germination, between 20°C and 45°C showed different tendencies between seed position. Although, cumulative germination on apex and the periphery seeds at 20°C, 25°C, and 35°C showed a sigmoid tendency, at 35°C and 45°C only the seeds of the apex showed the same tendency. In contrast, the only instance in which cumulative germination described a linear trend was that of seeds from the periphery at 30°C. For variants of seeds there was no germination at 40°C nor for those of the periphery at 45°C. It was noteworthy that at any temperature, between 20°C and 45°C, none of the non-scarified seeds in these 12 treatments achieved germination above 30%. (Figure 7).

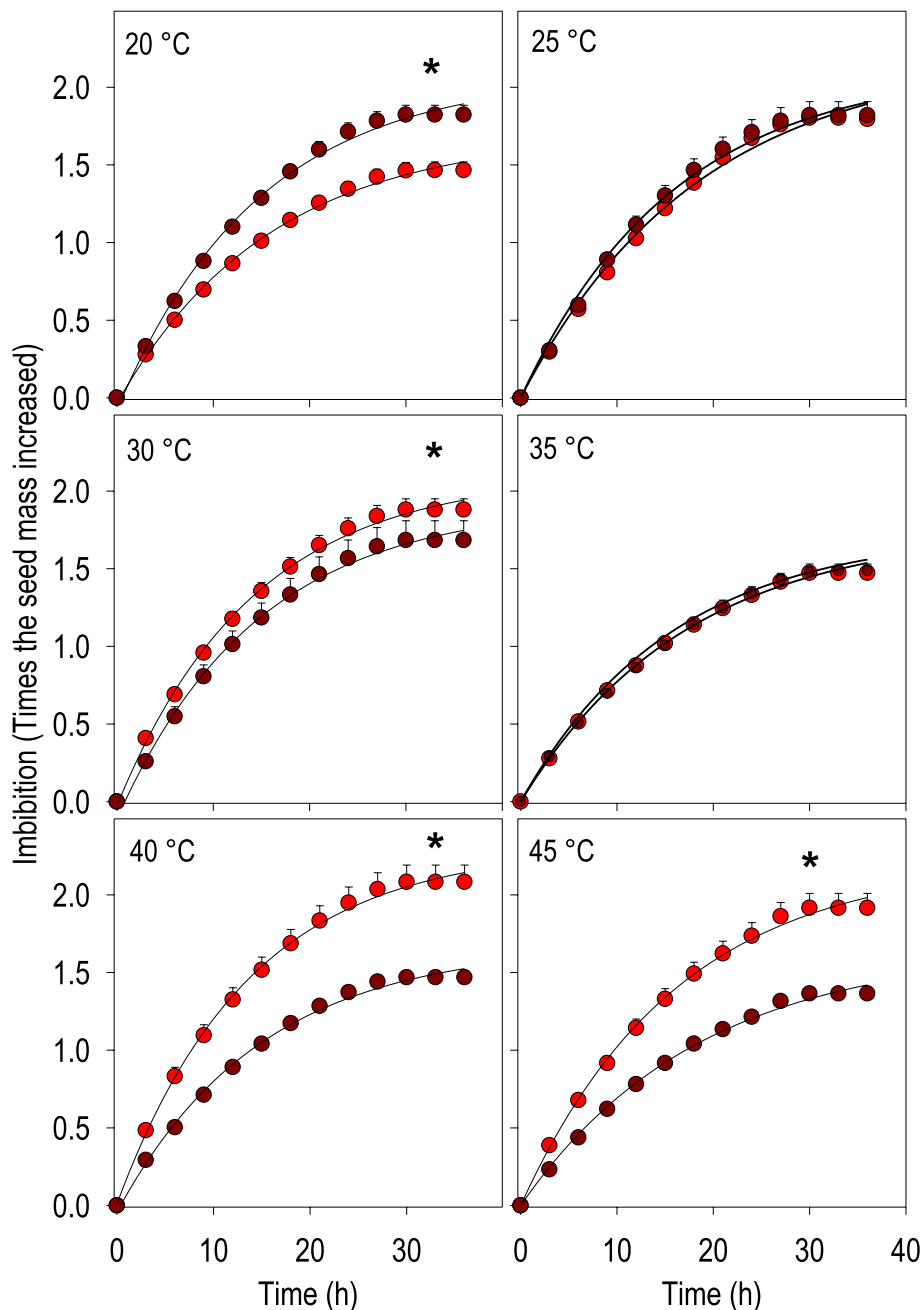


FIGURE 6 | Cumulative imbibition (+ standard error) of the seeds from the apex (light-red circles) or the periphery (dark-red) of the crown of *Echinocactus platyacanthus* Link & Otto plants, at constant temperature (20°C to 45°C) and in darkness; $n = 6$. The asterisk over the maximum imbibition indicates significant differences among seed positions at each temperature ($p \leq 0.05$).

In the apex seeds, the total germination varied between 0, at 40°C and 45°C, and 24% at 35°C. In contrast, for the seeds of the periphery, the total germination varied between 0%, at 40°C, and 17%, at 20°C and 25°C. Both seeds from both positions had accelerated germination onset at 25°C, 30°C, and 35°C, from 33 days to 7–8 days. Total germination and the time for its expression varied between seed position and between the evaluated temperatures. The time in which these maximum values occurred was between 32 and 45 days (Figure 7a–f). The average daily seed germination of both seed position of this species, was ≤ 0.59 seeds per day. The values of the cumulative germination rate at temperatures which germination varied from 20.95 seeds per day, in the apex seeds at 20°C, to 96.32 seeds of the periphery

per day at the same temperature. Quantifying the germination of scarified and intact seeds at 25°C showed that there were no differences between both seed positions, which was on average 81.38% (Figure 7b; Table 1).

4 | Discussion

4.1 | *Kroenleinia Grusonii*

Seeds at the periphery had significantly greater width and area and weighed less compared to those at the apex. Likewise, among the peripheral seeds the most frequent were heavier

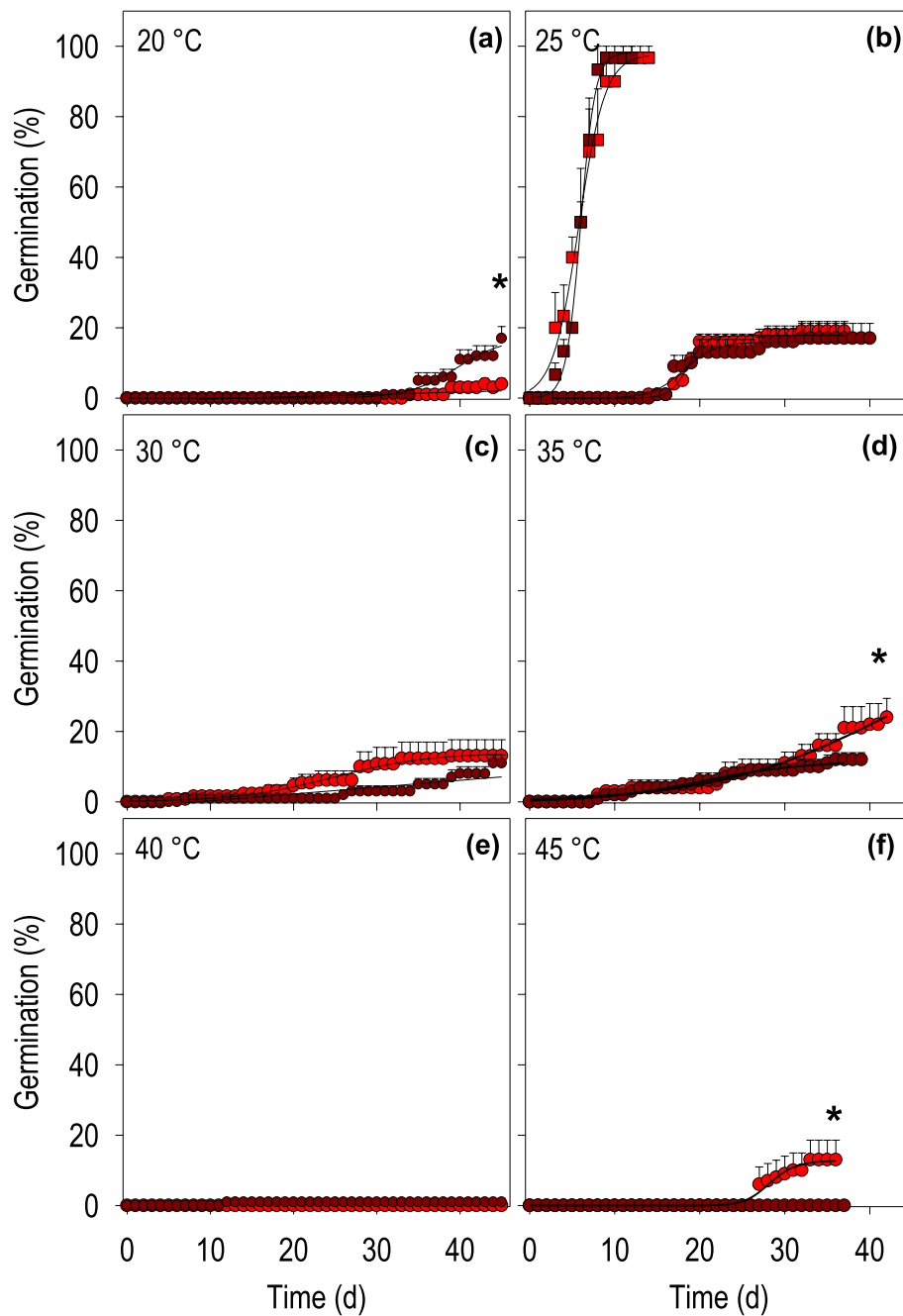


FIGURE 7 | Cumulative germination (+ standard error) of the seeds from the apex (light red symbols) or the periphery (dark red symbols) of the crown of *Echinocactus platyacanthus* Link & Otto plants, at constant temperature (20°C to 45°C) and in darkness; circles: Intact seeds and squares: Mechanically scarified seeds; $n = 6$. The asterisk over the maximum germination indicates significant differences among seed positions at each temperature ($p \leq 0.05$).

than those at the apex. These contrasts allow us to explain the differences in seed imbibition and germination. Differences in the dimensions and mass of the seeds result from intrinsic and extrinsic factors acting on plants, and their interaction (Smith et al. 2018). This is due to reproductive asynchrony and its relationship with the allocation of resources to the seeds; particularly during seed growth and development, in which a plant may be vulnerable to stress affecting their reproductive development (Kranner et al. 2010). Flower and fruit development asynchrony in *Kroenleinia* and *Echinocactus* species is well documented; so, during the reproductive stage, the same plant can simultaneously show buds, flowers, and fruits (Pavón and Briones 2001)

for several months (Díaz-Hernández et al. 2008; Pavón and Briones 2001; Trujillo-Argueta and del Castillo 2013). In this regard, the course of flowering as modified by abiotic and biotic factors that affect the development of flowers, fruits, and seeds (Trujillo-Argueta and del Castillo 2013). However, the seeds evaluated in this study were mature, with their characteristic black testa color according to Ruiz-Pérez et al. (2021). The seed viability of *K. grusonii* of the apical and peripheral seeds was close to 100% and their viability was greater than 80%, suggesting that germination is possible under favorable environmental conditions (Elizalde et al. 2017; Monroy-Vázquez et al. 2017). The viability results were about 4% higher than those obtained

by Manzo Rodríguez et al. (2022) in seeds of the same species stored for 3 years, without identifying their area of collection. The differences in viability and vigor of the orthodox seeds, such as that of *K. grusonii*, within and between collections are related to habitat, harvest conditions and time and storage conditions (Pérez-Sánchez et al. 2011). In the present research, regardless of the time that the seeds remained in the fruits before the evaluations, the viability of the apical and peripheral seeds remained at 97% and 90% respectively.

The description of seed imbibition is important because it allows one to know the minimum amount of water that the seeds need for seedling emergence (El-Maarouf-Bouteau 2022). Maximum imbibition of apical and peripheral seeds of *K. grusonii* varied among temperatures. In this regard, peripheral seeds imbibed from 10 to 30% more water compared to those of the apex, the greatest differences were observed at 20°C–25°C and the least at 40°C–45°C. Regardless of the seed position and temperature, the seeds took 30 h for maximum imbibition. In addition, the cumulative imbibition over time of the twelve treatments showed the same cubic polynomial trend. This indicates that the process of imbibition is similar regardless of seed position in the plant crown, but its extent is determined by temperature during imbibition. Both imbibition curves superimposed at 40°C but not at 45°C. This may be due to the heterogeneity of the seeds in the fruits. Interestingly, statistically significant differences were determined in the onset of germination, germination percentage and mainly in the speed and rate of germination at 30°C under three photoperiod lengths between and within both *K. grusonii* seed position (unpublished results from our own group).

Germination onset, total germination, and germination rate partially differed between treatments. At 30°C and 35°C both treatments accelerated the germination onset compared to the other temperatures; at 30°C peripheral seeds decreased it from 32 to 4 days, while the apical seeds decreased it from 29 to 2 day compared to 20°C. Despite the similarity in vigor and viability of the apical and peripheral seeds, at 30°C apical seeds showed highest total germination (almost 100%) compared to the peripheral seeds (86%). A similar difference was observed in scarified seeds germinated at 25°C. However, the seeds from the apex at 30°C to 45°C seemed to be more vigorous compared to those from the periphery. According to the latter, the optimal germination temperature for intact (not scarified) seeds of *K. grusonii* is 30°C.

The results suggest that the reproductive asynchrony and the length of reproductive interval that extends for several months affect the seed quality at the apex of the crown in *K. grusonii* plants in a manner different to those at the periphery. These effects include physical and physiological characteristics, such as seed size, mass and response to temperature of imbibition and germination. The maximum imbibition at 40°C–45°C was (50%) the lowest compared to the other temperatures, which seems an advantage for *K. grusonii* seed germination in its natural dry environments. The optimal temperature for germination of intact apical and peripheral seeds was 30°C; however, the differences in final germination were statistically significant, with nearly 100% and just over 80% germination, respectively. Furthermore, peripheral seeds took 15 days longer to reach total germination compared to apical seeds.

4.2 | *Echinocactus platyacanthus*

Seeds at the apex of the crown of *E. platyacanthus* plants were significantly different in width, area, and length with respect to those at the periphery of the plant crown. The latter showed a 2% greater area and 1.5% greater width and little more than 6% greater mass compared to those from the apex. The differences in mass between the apical and peripheral seeds were evidenced by their class frequency histograms. On average, the mass of the seeds at the apex was similar to that of six collections of the *E. platyacanthus* plants from arid and semi-arid zones of Queretaro, Oaxaca, and San Luis Potosí, México (Vázquez 2017).

The phases of the reproductive cycle of *E. platyacanthus* plants overlap, as these last for months, and the reproductive structures are exposed to environmental seasonal variability. In this regard, the plants of *E. platyacanthus* of five arid and semi-arid zones in Queretaro, Oaxaca, and San Luis Potosí, México, continued blooming throughout spring, from April to July, while those in the Coyoteras region, Querétaro, México, kept flowering and fruiting from April to December; additionally, in the six sites, fruits with seeds were present throughout the year (Vázquez 2017). The fruiting intensity was also asynchronous and varied during the year, during June to September was more abundant, except for Tempequistle, Querétaro, where the fruits produced more fruits from June to December (Vázquez 2017). The reproductive asynchrony of *E. platyacanthus* was also documented by Díaz-Hernández et al. (2008), Pavón and Briones (2001), and Trujillo-Argueta and del Castillo (2013). Therefore, the plant resources invested in buds, flowers, fruits, and seeds at the plant's apex may differ from the resources assigned to those of the periphery. Seed exposure, due to phenological asynchrony, to environmental variation may modify their physical and physiological characteristics (León and Domínguez-Cadena 1991).

The physiological quality evaluation of *E. platyacanthus* seeds included the vigor, viability, and germination. Because all seeds were 96% viable and 80% vigorous, the seeds were of good quality, and expected to germinate in optimal conditions (Elizalde et al. 2017; Monroy-Vázquez et al. 2017). The seed viability in this research was 11.5% higher than that stored for three years, coming from an unidentified collection site, by Manzo Rodríguez et al. (2022) and was close to the 100% in the seeds collected in the Chihuahuan Desert by Aragón-Gastélum et al. (2018). These results indicate that *E. platyacanthus* seed exhibit maximum viability regardless of the moment and place of development in the plant crown, the area of recollection site, or the storage time, even if it is for a few years.

The seeds imbibition, between 20°C to 45°C, at the apex and the periphery of the crown of *E. platyacanthus* plants exponentially increased during the first 30–36 h. Regardless of the temperature, the apical and peripheral seeds of this species exhibited maximum imbibition around 30 h. However, the values of maximum imbibition differed significantly between apical and peripheral seeds depending on temperature. Only at 20°C did the seeds from the periphery imbibe more than the apical ones. At 25°C and 35°C the imbibition of apical seeds did not differ significantly from peripheral ones, and at 40°C and 45°C, the apical seeds imbibed up to 42% more water than those of the periphery, the opposite of what occurred at 20°C. Depending

on the temperature, seeds of this species imbibed water equivalent to twice its mass. However, in our maximum imbibition assessment, the seeds took longer compared to the seeds in Petri dishes with agar as a moisture source, collected in the Chihuahuan Desert, and stored for 5 months in a laboratory (Contreras-Quiroz et al. 2016). Differences in seed water uptake during imbibition may be due to differences in testa permeability, to environmental factors during seed development and to seed shape and initial seed moisture (Taylor et al. 1992; Vertucci 1989).

The apical and peripheral intact seeds of *E. platyacanthus* responded differently to the germination temperature. None of twelve treatments exceeded 25% final germination. Only at 20°C did seeds from the periphery of the plant crown show higher germination than those from the apical position. At 25°C and 30°C the differences in total germination were not statistically significant between the seeds position. At 35°C and 45°C the apical seeds had greater total germination than peripheral ones; however, no seed germinated at 40°C. Since the evaluated seed viability was optimal (96%), and scarified seeds reached near 100% of total germination, the germination percentages of intact seeds are attributed to seed dormancy. Comparison of these results with those reported by other authors is difficult due to differences in seed germination conditions. However, the total germination of intact seeds at 25°C in this study was similar to that of seeds germinated on salt-free Murashige-Skoog medium at 27°C and constant light (Manzo Rodríguez et al. 2022). But in contrast, the total germination at 30°C in the present study was one quarter of the total seed germination at 30°C:16°C day:night temperature, and 12:12 h photoperiod of the seeds collected in the South of the Chihuahuan Desert (Contreras-Quiroz et al. 2016). Seeds collected in six arid and semi-arid zones of Queretaro, Oaxaca, and San Luis Potosí, Mexico showed maximum germination of 22 to 100% after 30 days with a light:dark photoperiod of 12 h, and a thermoperiod of 25°C:5°C day:night (Ruiz-Pérez et al. 2021). In addition, the seeds of the same species scarified for 1 or 2 min with concentrated sulfuric acid did not germinate at 27°C and constant light on agar, salt-free MS medium, or on a water-moistened substrate; however, total germination increased from 13% to 30% and up to 95% when scarified seeds were germinated on MS medium with 50 and 100% salts (Manzo Rodríguez et al. 2022). Outstanding statistically significant differences were observed due to the effect of photoperiod length between seeds from the apex and those from the periphery of the crown of *E. platyacanthus* in germination at 30°C; for example, intact seeds from the apex initiated germination after 20–25 days depending on the photoperiod length, and their total germination was less than 30%; in contrast, seeds from the periphery initiated germination in 4–8 days under different photoperiods, and their total germination (40%) did not differ significantly due to the number of daylight hours during germination (unpublished results from our own group).

Differences in quality of seeds at the apex of the crown in *E. platyacanthus* plants compared to those at the periphery seem to be effects of reproductive asynchrony and the length of reproductive interval that extends for several months. Some of these differences were width, length, area, and seminal mass. Although vigor, viability, and dormancy are similar between seeds produced at the apex and the periphery of the crown, the

optimal imbibition for germination varies between them and is modified by temperature during germination. These characteristics seem relevant to the permanence of this species in the face of fluctuations generated by climate change. Seed maximum imbibition of this species can be between 1.5 times and twice the weight of the seeds; optimum germination temperature for intact seeds is between 25°C and 35°C, but it differs between apical and peripheral seeds, and is however less than 35%.

5 | Conclusions

On average, seeds at the crown apex of *K. grusonii* plants are wider, heavier, and more vigorous than those at the periphery. In addition to the differences in physical characteristics, other differences between the apical and peripheral seeds in the crown of this species were evident. The differences in imbibition and germination between the two seeds were not due to differences in their viability, since after mechanical scarification seed dormancy of apical seeds was almost totally removed during germination at 25°C, and to a lesser extent, with the same temperature, in the seeds of the periphery. The inverse relationships between seed imbibition and temperature and the ability of *K. grusonii* to maintain certain levels of germination at 45°C are characteristics that will allow it to cope with predicted climate change, with increased ambient temperature and low moisture availability due to scarce and erratic rainfall.

Differences in various characteristics between the seeds at the apex and the periphery of *E. platyacanthus* plant crown were demonstrated. On average, the seeds at the apex of the crown of *E. platyacanthus* plants are longer and have less mass compared to those at the periphery, however, both have the same vigor, viability, and dormancy. Seed position or mass has no effect on their imbibition between 25°C and 35°C. Contrary to that, the apical seeds, which have less mass compared to those peripheral seeds, have higher imbibition at 40°C and 45°C. Seed dormancy in this species is greater than 90% (similar in the apical and peripheral seeds); this characteristic is eliminated by mechanical scarification.

This heterogeneity in the physical and physiological characteristics of seeds from the apex and periphery of the crown of both cacti species was currently unknown. Knowledge of these characteristics is necessary for decision-making bodies regarding these endangered cacti; among them, generating reforestation programs, protecting the diversity of species, strengthening the ecosystems of these cacti, even generating programs for multiplying both cacti for their commercialization and stopping the predation by illegal extraction of plants. The physical and physiological differences between seeds from the apex and periphery of the crown of both species cacti indicate the existence of a pattern of seed production in the plant and, with it, a pattern of resource allocation toward reproductive structures in the crown.

Author Contributions

C.A.Z. carried out the experiment and wrote the original draft with support from C.T., D.P., and L.P. C.B.P.-V. conceived and planned the experiments and supervised the findings of this study. H.V. processed the

experimental data. All authors discussed the results and contributed to the final manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

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