

# Do fires affects growth, seed production and germination of the globose cactus *Gymnocalycium monvillei*?

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## ABSTRACT

The habitats of many cactus species are being subjected to increasing fire frequencies. Globose cacti have a high survival to fire; however, little is known about other characteristics, such as their post-fire growth or reproductive responses. The objective of this work was to evaluate the short-term effects of fire on growth and reproductive characteristics of the globose cactus *Gymnocalycium monvillei*. The study was carried out in a population located in the Sierras Chicas de Córdoba, Argentina, which was partially affected by a fire in 2017. Sixty individuals were selected, 30 of them had been burned and 30 had not been burned (controls). Growth was measured; fruits were collected and seed mass and seed production per fruit were measured. In addition, germination experiments were performed to estimate final germination percentage and mean germination time. The results show that the studied species did not suffer post-fire effects on growth or the measured reproductive variables. Fire also had no effect on seed quality, since neither final germination percentage nor mean germination time showed significant differences between burned and unburned individuals. It can be concluded that *Gymnocalycium monvillei* is a fire-tolerant species. Although more studies are needed (i.e. regarding to fire intensity and frequency), globose cactus species seem particularly tolerant to fire group.

## 1. Introduction

The family Cactaceae is endemic to the Americas, where it is distributed from Canada to southern Argentina (Bravo-Hollis, 1978; Gibson and Nobel, 1986; Ortega-Baes and Godínez-Alvarez, 2006). It is an important family because of both the ecological roles of its species (e.g. where cacti are dominant they manage ecosystem processes) and the different benefits to humans (e.g. food production, ornamental plants, cultural benefits; Nobel, 2002). In the Sierras de Córdoba, there is a high diversity of cacti, with about 31 native species (Giorgis et al., 2011). Cactaceae is the fifth largest family in number of species in the Sierras de Córdoba, of which 13 belong to the genus *Gymnocalycium* (Gurvich et al., 2006; Giorgis et al., 2011). *Gymnocalycium monvillei* is a globose cactus endemic to the mountains of Córdoba and San Luis Provinces (Argentina), and has a very wide altitudinal distribution (Gurvich et al., 2014; Bauk et al., 2015).

Fire is one of the most important factors that affect vegetation dynamics, modifying different aspects that range from the physiognomy and floristic composition to the recycling of materials from terrestrial ecosystems (Bond and Keeley, 2005; Bowman et al., 2009; Keeley, 2012;

Giorgis et al., 2013; Kowaljow et al., 2019). Climate change, in combination with changes in land use, are increasing the frequency and intensity of fires on the planet, even in biomes where fire was an almost non-existent factor, such as humid tropical forests (Kasischke et al., 1995; Westerling et al., 2006).

In ecosystems that have evolved with fire, as in Mediterranean ecosystems or some tropical savannas, species may present adaptations to fire and even be favored by fire presence, for example through increased growth and production of flowers and seeds (Wallace, 1966; Abbott and Loneragan, 1983; Lamont and Runciman, 1993; Whelan, 1995). In species of ecosystems that have not evolved with fires, this agent can cause tissue damage (Spurr and Barnes, 1980), with the consequent negative effects on the subsequent development of individuals.

Most cactus species inhabit regions where fires are now a common disturbance, despite lacking a long fire history (Kowaljow et al., 2019; Roca et al., 2021). Cactus species with globose life forms have been found to be more fire tolerant than columnar life forms (Thomas, 2006). In a study conducted in Arizona, mortality of cactus and succulent species was less than 25% within 14 months after burning (Thomas and Goodson, 1992). In addition, globose cacti of central Argentina were

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found to have a high survival rate after fires, of about 80%, reflecting that they would be well adapted to resist this disturbance (Zupichiatti et al., 2022). Although in globose cacti a high fire survival rate has been reported (Thomas, 2006; Zupichiatti et al., 2022), little is known about the medium and long-term effect of fire on both growth and sexual reproduction (Eugenio and Lloret, 2004; Fulé and Laughlin, 2007). This information is particularly relevant, since cacti tend to have low growth rates and generally long life cycles (Gibson and Nobel, 1986).

Various studies have shown that reproductive variables, such as seed number and mass, and germination characteristics affect the establishment, growth and survival of plants (Bowers and Pierson, 2001; Baloch et al., 2001). A higher number of seeds translates into a higher fitness (Westoby et al., 1992; Leishman et al., 2000). Seed mass has been considered an important factor in the regenerative biology of plants (Bu et al., 2007), since it is related to the dispersal capacity (smaller seeds disperse over longer distances), as well as to the chances of establishment (larger seeds produce more vigorous seedlings) (Harper, 1977; Daws et al., 2007). These functional trade-offs, which have been studied mainly between species, can also operate at the intraspecific level. Numerous studies have shown that intraspecific seed mass can vary (Hendrix, 1984). Larger seeds have been associated with individuals/populations living in less disturbed habitats (Werner and Platt, 1976). Germination percentage is a good indicator of seed quality and has direct effects on species fitness (Long et al., 2015). A higher germination speed may be an advantage, since it would facilitate establishment after fires (Enright and Kintrup, 2001). To date, a few studies have analyzed regenerative aspects of cacti after fires. Two years after a prescribed fire in New Mexico, no effect on the frequency of flowering or on the number of flowers and fruits were observed in the globose cactus *Echinocereus kuenzleri* (May, 2006).

The aim of this study was to analyze the short-term effects of fire on the growth and reproductive characteristics of *Gymnocalycium monvillei*. The hypothesis of this study is that fire negatively affects tissues, which in turn will affect post-fire growth and resource allocation for reproduction.

## 2. Materials and methods

### 2.1. Study area and species

The study was carried out in the Sierras Chicas, particularly in a site on Provincial Route E 66, 14.5 km away from the town of La Cumbre, Córdoba province, Argentina ( $30^{\circ} 57' 25'' \text{S}$   $64^{\circ} 25' 22'' \text{W}$ , Fig. 1). The site is located at about 1600 m a.s.l.; the climate is sub-humid. Rainfall is

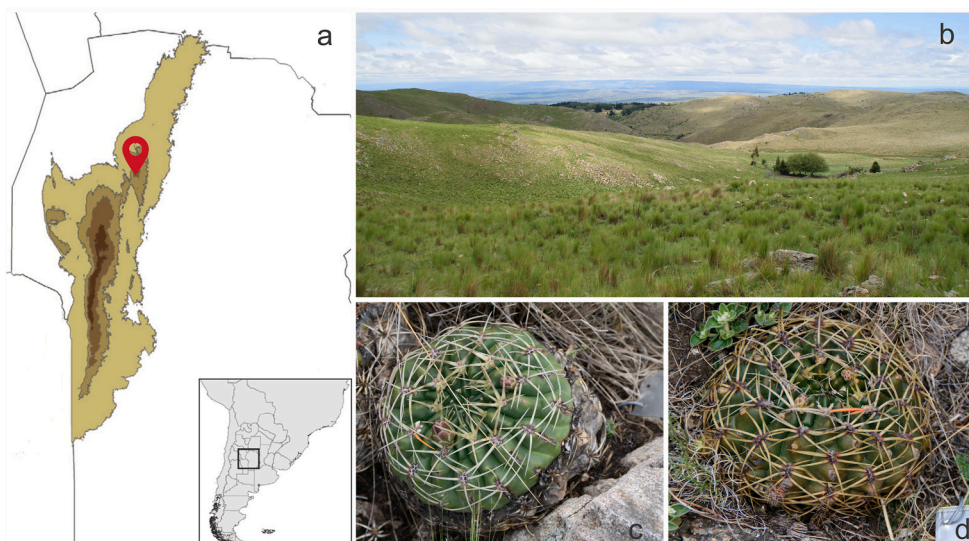
concentrated during the warm season (approximately 85%), between October and March, with an annual average of about 800 mm (Capitanelli, 1979). The average annual temperature is  $13.9^{\circ}\text{C}$ . Maximum daily temperatures during the warm season, when germination and establishment occur, vary between  $23$  and  $28^{\circ}\text{C}$ . The vegetation of the study area corresponds to the Stipeas and Festuceas grasslands (Unit 8 of Oyarzabal et al., 2018), characterized by a mosaic of shrublands, grasslands and rocky outcrops (Gurvich et al., 2014); vegetation is subject to cattle grazing and exposed to recurrent fires (Gavier and Bucher, 2004).

The study species was *Gymnocalycium monvillei* (Lem.) Britton and Rose, an endemic species of the central Argentine Mountains. The study population was located in an area that was partly affected by a fire in September 2017. This species was selected because it is common and abundant in a great part of the Sierras de Córdoba (Gurvich et al., 2014); therefore, it is a good model to study the effect of fire on globose cacti. Wildfires are common in the area, with a return interval of about 13 years (Kowaljow et al., 2019). These wildfires occurred mainly in late winter-early spring, when humidity reaches the lowest values and high temperatures increase (Argañaraz et al., 2015, 2020). Although fires can be caused by natural causes, such as lightning strikes, most of them are man-made both accidentally and intentionally (Argañaraz et al., 2015). Their intensity depends on the biomass load. Particularly in the rocky outcrops the fires are of medium or low intensity due to the low biomass load. The extent of the fires is highly variable, from a few hectares to thousands, depending on the characteristics of the environment (i.e. topography, fuel loads), the weather, and the response of the firefighters.

### 2.2. Growth and reproductive measurements

To evaluate growth after the fire that occurred in 2017, measurements of total diameter (cm) of 60 individuals from the same population, 30 that had been burned and 30 that had not been burned (controls), were taken one year after the fire, starting in September 2018. Individuals were randomly selected. Sexually mature individuals with flower buds were selected and a wide range of sizes were included. The individuals were georeferenced, using a GPS, and marked with a metal tag. Plant diameter was measured again at the end of the growing season, in April of the following year (2019). These two measurements were used to calculate growth between the two dates, expressed as percentage.

Ripe fruits (between 1 and 2 per individual) were collected from burned and unburned individuals between December (2018) and



**Fig. 1.** a Location of the study area ( $30^{\circ} 57' 25.4'' \text{S}$   $64^{\circ} 25' 22.5'' \text{W}$ ) in Argentina. b Photograph of the site where the *Gymnocalycium monvillei* population is found (darker colors indicates increasing altitudes, 300–1000, 1000–1500, 1500–2000, 2000–2300 m a.s.l.). c Specimen of *G. monvillei* affected by fire (note the fire scars). d Specimen of *G. monvillei* not affected by fire (control). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

January (2019). The height and width of these fruits were measured with a caliper; then the seeds they contained were separated and cleaned. Seeds were air-dried and then stored in paper bags at room temperature in the dark, until the beginning of the experiments, which were performed five months after collection. Seed germination of this species is higher during the first year and then decreases with time (Gurvich et al., 2021). On the other hand, we measured width and height of all the fruits to estimate the total production of seeds per plant (see below).

Seed mass was recorded using an analytical balance. Due to the small size of the seeds, 5 groups of 10 seeds each were weighed per fruit to reduce the error. Subsequently, an average of the recorded weight values was obtained. In addition, for each fruit, the number of seeds present was estimated by dividing the total mass of seeds in the fruit by the average mass of a single seed.

Regressions were performed between the size of the fruits and the number of seeds (of the collected fruits). From these regressions, the total production of seeds produced by each plant was estimated by multiplying the number of fruits of each plant by the number of seeds estimated based on the mass of the fruit.

For the germination experiments, the seeds of each individual were placed in Petri dishes (20 seeds per dish, three dishes per individual) on filter paper and incubated in germination chambers under controlled conditions of light and temperature, with a photoperiod of 12 h at 25 °C. These conditions are considered to be optimal for the germination of *G. monvillei* (Gurvich et al., 2008). Seeds that appeared healthy were used, with those that were not fully developed or that showed evidence of fungal or insect damage being discarded. The seeds were kept moist, by watering with distilled water when necessary. Seed germination was recorded for a period of 31 days (Gurvich et al., 2008). Germination was checked every other day, and the germination criterion was the emergence of 2 mm of the radicle (International Seed Testing Association, 1985). We also calculated mean germination time (MGT), i.e. the number of days in which 50% of the seeds germinate. The MGT was calculated only in those replicates that had germination percentages  $\geq 20\%$  (Gurvich et al., 2017), with the following formula:

$$\text{MGT} = \sum n_i t_i / \sum n_i$$

In which:  $n_i$  is the number of newly germinated seeds in time  $i$  and  $t_i$  is the period elapsed since the beginning of the germination test, expressed in number of days (Ellis and Roberts, 1978).

### 2.3. Data analyses

To evaluate whether there are significant differences between growth and reproductive variables of burned and unburned individuals (control), a Student's t-test was used for independent samples, for growth percentage and total number of seeds. We also run one way ANOVA to analyzed seed mass and MGT, and generalized linear models to evaluated germination. Statistical analyses were performed using InfoStat v. 2018 (Di Rienzo et al., 2018) and R software in version 4.0.2 (R Core Team, 2020).

### 3. Results

Growth of individuals, evaluated as the difference between the second and the first measurements of diameter and expressed in percentage, varied between 0% and 27.82% in burned individuals, and between 0% and 17.02% in unburned individuals. Seven burned specimens and nine unburned showed no growth. Growth (%) was not significantly different between treatments ( $p = 0.4309$ , Fig. 2).

Average seed mass varied between 0.250 and 0.480 mg in burned individuals and between 0.243 and 0.468 mg in unburned individuals. The average mass was 0.34 mg for burned cactus seeds and 0.33 mg for controls (Fig. 3a). Seed mass did not show significant differences between burned and unburned individuals ( $p = 0.4559$ ).

Total seed production per plant varied between 0 and 12,044 in burned individuals and between 0 and 7862 seeds in unburned individuals. Five individuals (three burned and two unburned) did not produce fruits. These individuals presented flower buds, but did not develop into fruits. Although a trend of higher seed production is observed in burned individuals (Fig. 3b), total seed production did not differ significantly between treatments ( $p = 0.5940$ ).

Because of the overdispersion of germination data, we run a quasi-binomial model. Final germination percentage did not show significant differences between burned and unburned individuals ( $p = 0.7550$ ) (Fig. 4a). For mean germination time we run a one way ANOVA, which also did not differ significantly between burned and unburned cacti ( $p = 0.757$ ), varying between 6 and 13 days in the former, and between 7 and 16 days in the latter. The average MGT value was 9.24 days for burned individuals and 9.42 days for unburned individuals. (Fig. 4b).

### 4. Discussion

Contrary to our expectations, fire did not have a negative, or positive, effect on growth or on the reproductive variables of *Gymnocalycium*

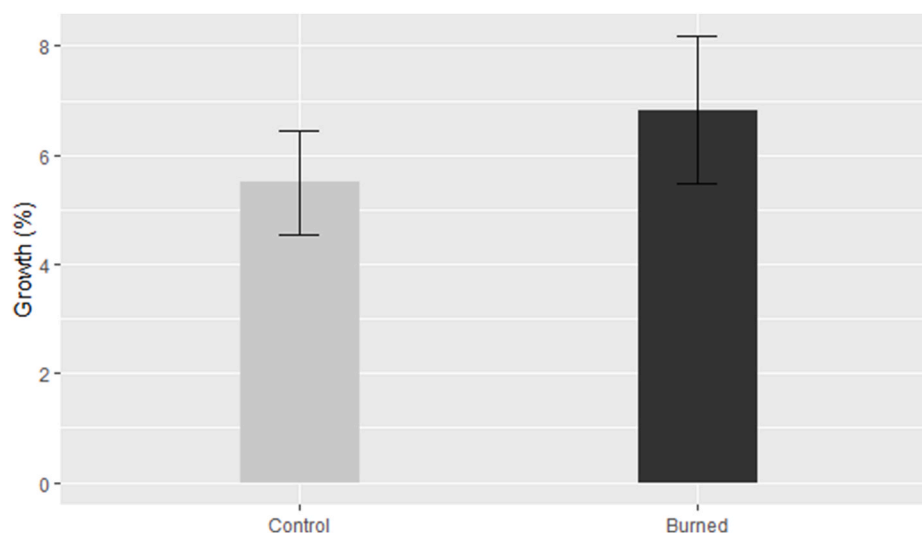
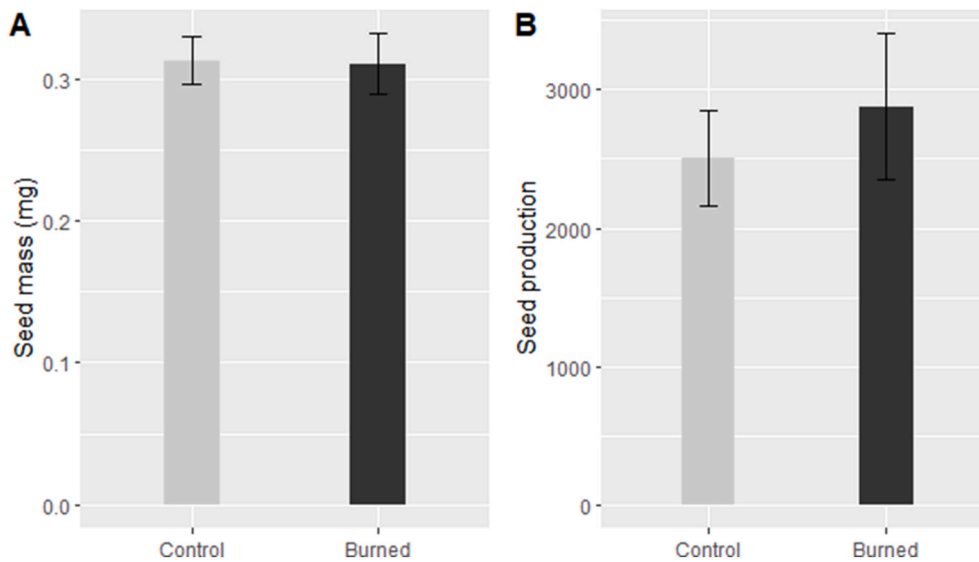
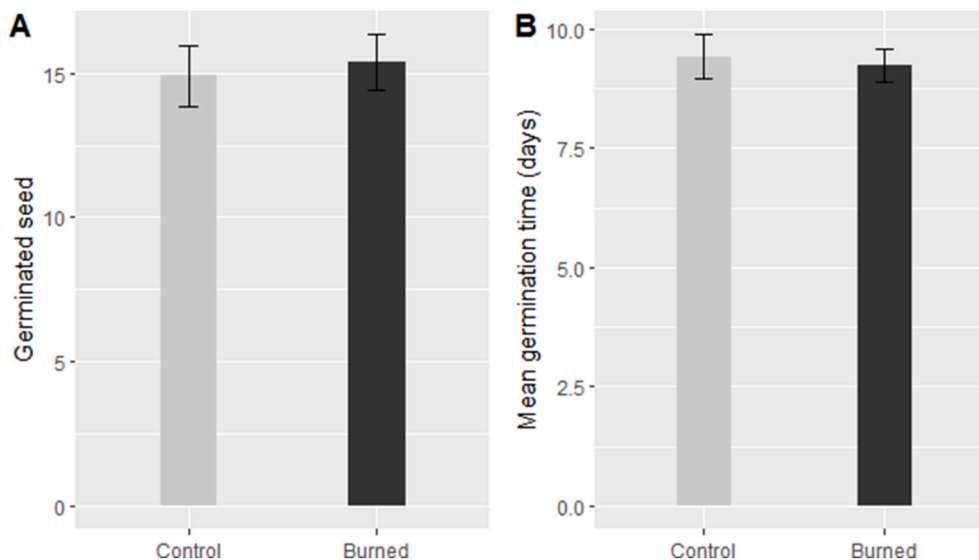


Fig. 2. Growth, expressed as %, (mean  $\pm$  S.E.) in unburned (control) and burned individuals of *Gymnocalycium monvillei* control (T test,  $p = 0.4309$ ).



**Fig. 3.** a Seed mass, mg (mean  $\pm$  S.E.) and b total number of seeds per plant (mean  $\pm$  S.E.) in unburned (control) and burned individuals of *Gymnocalycium monvillei*. (ANOVA,  $p = 0.927$  and T test  $p = 0.5940$ ).



**Fig. 4.** a Germination percentage (mean  $\pm$  S.E.) and b mean germination time (mean  $\pm$  S.E.) in unburned (control) and burned individuals of *Gymnocalycium monvillei* (GLM,  $p = 0.7550$  and ANOVA,  $p = 0.757$ ).

*monvillei*. Post-fire growth did not differ significantly between burned and unburned individuals. This result may be attributed to the protection of the apical meristem from heat provided by a fold at the apex and a thick bark bearing spines (Thomas, 1991). Initial diameter was not correlated with growth either in burned or unburned individuals (data not shown); by contrast, Zupichiatti et al. (2022) reported that growth in two globose cactus species, *Gymnocalycium mostii* and *Parodia submammulosa*, depends on their size before the fire event. However, the same study did not find a relationship between previous size and post-fire growth for other species, *Echinopsis aurea* and *G. bruchii*. These controversial results suggest that the relationship between post-fire growth and size of individuals depends on the particular characteristics of the species.

Seed mass as well as total seed production did not differ significantly between burned and unburned individuals. These results are consistent with those reported by May (2006), who found that fire had no effect on the reproductive traits of the globose cactus *Echinocereus kuenzleri* of New Mexico, USA.

Fire did not increase or accelerate germination, since neither final germination percentage nor mean germination time showed significant differences between burned and unburned individuals. This result shows that fire had no effect on seed quality. To our knowledge, no other studies have analyzed similar aspects. These results indicate that, even in the short term, burned plants have the same reproductive capacity as unburned ones. This would indicate that the species could recover quickly from the loss of individuals caused by fire.

The studied species did not suffer post-fire effects both in terms of growth and in the measured reproductive variables. So far, only globose cacti had been found to have high fire survivability among cacti (Thomas, 2006; Zupichiatti et al., 2022). Indeed, cacti can survive burning through several mechanisms. They can avoid fire, or at least high fire intensities, since they occupy fire shelters, such as rock outcrops (Gurvich et al., 2014). In addition, due to their epidermal characteristics and the surface area to volume ratio, which give them high thermal inertia, they can resist heat pulses and thus protect their phloem and cambium (Thomas, 1991). Similarly, a cactus can produce new



lateral shoots from meristems in the remaining unaffected parts of the body or from roots after fire, in response to injury or death (Roller and Halvorson, 1997).

Many cactus and succulent species occur in habitats prone to recurrent fires (Thomas, 1991; Reemts and Ferrato, 2020); therefore, their response to fire is of great interest. In addition, 30% of the species in the family are at some risk of extinction, with fire being one of the risk factors (Goettsch et al., 2015). Although *G. monvillei* was found to tolerate this disturbance well, further studies should include other cactus species and address still unexplored aspects, such as post-fire establishment or fire frequency and intensity, which could affect population dynamics. Furthermore, the existing records (e.g. Zupichiatti et al., 2022) suggest that different cactus species, even globose cacti, could have different responses to fires.

## CRediT authorship contribution statement

**M.A. Lorenzati:** Methodology, Data curation. **N.L. Aliscioni:** Methodology, Formal analysis. **F.L. Barroso:** Methodology, Data curation. **D.E. Gurvich:** Conceptualization, writing, Software, Investigation, Supervision.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## References

- Abbott, I., Loneragan, O., 1983. Influence of fire on growth rate, mortality, and butt damage in Mediterranean forest of Western Australia. *For. Ecol. Manag.* 6, 139–153. [https://doi.org/10.1016/0378-1127\(83\)90018-X](https://doi.org/10.1016/0378-1127(83)90018-X).
- Argañaraz, J.P., Pizarro, G.G., Zak, M., Bellis, L.M., 2015. Fire regime, climate, and vegetation in the Sierras de Córdoba Argentina. *Fire Ecology* 11, 55–73. <https://doi.org/10.4996/fireecology.1101055>.
- Argañaraz, J.P., Cingolani, A.M., Bellis, L.M., Giorgis, M.A., 2020. Fire incidence along an elevation gradient in the mountains of central Argentina. *Ecol. Austral* 30, 268–281. <https://doi.org/10.25260/EA.20.30.2.0.1054>.
- Baloch, H.A., Di Tommaso, A., Watson, A.K., 2001. Intrapopulation variation in *Abutilon theophrasti* seed mass and its relationship to seed germinability. *Seed Sci. Res.* 11, 335–343. <https://doi.org/10.1079/SSR200190>.
- Bauk, K., Pérez-Sánchez, R., Zeballos, S.R., Las Peñas, M.L., Flores, J., Gurvich, D.E., 2015. Are seed mass and seedling size and shape related to altitude? Evidence in *Gymnocalycium monvillei* (Cactaceae). *Botany* 93, 529–533. <https://doi.org/10.1139/cjb-2015-0026>.
- Bond, W.J., Keeley, J.E., 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends Ecol. Evol.* 20, 387–394. <https://doi.org/10.1016/j.tree.2005.04.025>.
- Bowers, J.E., Pierson, E.A., 2001. Implications of seed size for seedling survival in *Carnegiea gigantea* and *Ferocactus wislizeni* (Cactaceae). *SW. Nat.* 46, 272–281. <https://doi.org/10.2307/3672423>.
- Bowman, D.M.J.S., Balch, J.K., et al., 2009. Fire in the earth system. *Science* 324, 481–484. <https://doi.org/10.1126/science.1163886>.
- Bravo-Hollis, H., 1978. Las cactáceas de México, vol. 1. Universidad Nacional Autónoma de México, México City.
- Bu, H., Chen, X., Xu, X., Liu, K., Jia, P., Du, G., 2007. Seed mass and germination in an alpine meadow on the eastern Tsinghai–Tibet plateau. *Plant Ecol.* 191, 127–149. <https://doi.org/10.1007/s11258-006-9221-5>.
- Daws, M.I., Ballard, C., Mullins, C.E., Garwood, N.C., Murray, B., Pearson, T.R., Burslem, D.F., 2007. Allometric relationships between seed mass and seedling characteristics reveal trade-offs for neotropical gap-dependent species. *Oecologia* 154, 445–454. <https://doi.org/10.1007/s00442-007-0848-2>.
- Di Rienzo, J.A., Casanoves, F., Balzarini, M.G., Gonzalez, L., Tablada, M., Robledo, C.W., 2018. InfoStat. Software Estadístico, Universidad Nacional de Córdoba, Córdoba. <http://www.infostat.com.ar>.
- Ellis, R.H., Roberts, E.H., 1978. Towards a Rational Basis for Testing Seed Quality. State University Press, Pennsylvania.
- Enright, N.J., Kintrup, A., 2001. Effects of smoke, heat and charred wood on the germination of dormant soil-stored seeds from a *Eucalyptus baxteri* heathy-woodland in Victoria, SE Australia. *Austral Ecol.* 26, 132–141. <https://doi.org/10.1046/j.1442-9993.2001.01096.x>.
- Eugenio, M., Lloret, F., 2004. Fire recurrence effects on the structure and composition of Mediterranean *Pinus halepensis* communities in Catalonia (northeast Iberian Peninsula). *Ecoscience* 11, 446–454. <https://doi.org/10.1080/11956860.2004.11682854>.
- Fulé, P.Z., Laughlin, D.C., 2007. Wildland fire effects on forest structure over an altitudinal gradient, Grand Canyon National Park, USA. *J. Appl. Ecol.* 44, 136–146. <https://doi.org/10.1111/j.1365-2664.2006.01254.x>.
- Gavier, G.I., Bucher, E.H., 2004. Deforestación de las Sierras Chicas de Córdoba (Argentina) en el período 1970–1997. Academia nacional de ciencias, Córdoba.
- Gibson, A.C., Nobel, P.S., 1986. The Cactus Primer. Harvard University Press, Cambridge.
- Giorgis, M.A., Cingolani, A.M., Cabido, M.R., 2013. El efecto del fuego y las características topográficas sobre la vegetación y las propiedades del suelo en la zona de transición entre bosques y pastizales de las sierras de Córdoba, Argentina. *Bol. Soc. Argent. Bot.* 48, 3–4. <https://doi.org/10.31055/1851.2372.v48.n3.4.7555>.
- Giorgis, M.A., Cingolani, A.M., Chiarini, F., Chiapella, J., Barboza, G., Ariza Espinar, L., Morero, R., Gurvich, D.E., Tecco, P.A., Subils, R., Cabido, M., 2011. Composición florística del Bosque Chaqueño Serrano de la provincia de Córdoba, Argentina. *Kurtziana* 36, 9–43.
- Goettsch, B., Hilton-Taylor, C., et al., 2015. High proportion of cactus species threatened with extinction. *Nature Plants* 1, 1–7. <https://doi.org/10.1038/nplants.2015.142>.
- Gurvich, D.E., Demaio, P., Giorgis, M.A., 2006. The diverse globose cactus community of Argentina's Sierras Chicas Ecology and conservation. *Cactus Succulent J.* 78, 224–231. <https://doi.org/10.2985/0007-9367>.
- Gurvich, D.E., Funes, G., Giorgis, M.A., Demaio, P., 2008. Germination characteristics of four Argentinean endemic *Gymnocalycium* (Cactaceae) species with different flowering phenologies. *Nat. Area J.* 28, 104–108. <https://doi.org/10.3375/0885-8608>.
- Gurvich, D.E., Pérez-Sánchez, R., Bauk, K., Jurado, E., Ferrero, M.C., Funes, G., Flores, J., 2017. Combined effect of water potential and temperature on seed germination and seedling development of cacti from a mesic Argentine ecosystem. *Flora* 227, 18–24. <https://doi.org/10.1016/j.flora.2016.12.003>.
- Gurvich, D.E., Zeballos, S.R., Demaio, P.H., 2014. Diversity and composition of cactus species along an altitudinal gradient in the Sierras del Norte Mountains (Córdoba, Argentina). *South Afr. J. Bot.* 93, 142–147. <https://doi.org/10.1016/j.sajb.2014.03.018>.
- Gurvich, D.E., Lorenzati, M.A., Sosa Pivatto, M., Bauk, K., Barroso, F.L., 2021. Effects of long term seed storage on germination of 13 cacti species from Central Argentina. *J. Arid Environ.* 185, 104382. <https://doi.org/10.1016/j.jaridenv.2020.104382>.
- Harper, J.L., 1977. *Population Biology of Plants*. Academic Press, London.
- Hendrix, S.D., 1984. Variation in seed weight and its effects on germination in *Pastinaca sativa* L. (Umbelliferae). *Am. J. Bot.* 71, 795–802. <https://doi.org/10.1002/j.1537-2197.1984.tb14144.x>.
- International Seed Testing Association, 1985. International rules for seed testing. *Seed Sci. Technol.* 13, 299–513. Rules 1985.
- Kasischke, E.S., Christensen Jr., N.L., Stocks, B.J., 1995. Fire, global warming, and the carbon balance of boreal forests. *Ecol. Appl.* 5, 437–451. <https://doi.org/10.2307/1942034>.
- Keeley, J.E., 2012. Fire in Mediterranean climate ecosystems—a comparative overview. *Israel Journal of Ecology and Evolution* 58, 123–135. <https://doi.org/10.1560/IJEE.58.2.3.123>.
- Kowalijew, E., Morales, M.S., Whitworth-Hulse, J.I., Zeballos, S.R., Giorgis, M.A., Rodríguez Catón, M., Gurvich, D.E., 2019. A 55-year-old natural experiment gives evidence of the effects of changes in fire frequency on ecosystem properties in a seasonal subtropical dry forest. *Land Degrad. Dev.* 30, 266–277. <https://doi.org/10.1002/ldr.3219>.
- Lamont, B.B., Runciman, H.V., 1993. Fire may stimulate flowering, branching, seed production and seedling establishment in two kangaroo paws (Haemodorraceae). *J. Appl. Ecol.* 30, 256–264. <https://doi.org/10.2307/2404627>.
- Leishman, M.R., Wright, I.J., Moles, A.T., Westoby, M., 2000. The evolutionary ecology of seed size. In: Fenner, M. (Ed.), *Seeds: the Ecology of Regeneration in Plant Communities*. CABI Publishing, Wallingford, pp. 31–57.
- Long, R.L., Gorecki, M.J., Renton, M., Scott, J.K., Colville, L., Goggin, D.E., Commander, L.E., Westcott, D.A., Cherry, H., Finch-Savage, W.E., 2015. The ecophysiology of seed persistence: a mechanistic view of the journey to germination or demise. *Biol. Rev.* 90, 31–59. <https://doi.org/10.1111/brv.12095>.
- May, B.C., 2006. The Effects of Fire on the Hedgehog Cactus of Kuenzler. Doctoral dissertation, Texas Tech University. <http://hdl.handle.net/2346/16808>.
- Nobel, P.S., 2002. *Cacti: Biology and Uses*. University of California Press, Los Angeles.
- Ortega-Baes, P., Godínez-Alvarez, H., 2006. Global diversity and conservation priorities in the Cactaceae. *Biodivers. Conserv.* 15, 817–827. <https://doi.org/10.1007/s10531-004-1461-x>.
- Oyarzabal, M., Clavijo, J., Oakley, L., Biganzoli, F., Tognetti, P., Barberis, I., Maturo, H. M., Aragón, R., Campanello, P.I., Prado, D., León, R.J.C., Oesterheld, M., 2018. Unidades de vegetación de la Argentina. *Ecol. Austral* 28, 40–63. <https://doi.org/10.25260/EA.18.28.1.0.399>.

- R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for statistical computing, Vienna. Available from URL: <http://www.Rproject.org/>.
- Reemts, C.M., Ferrato, J.R., 2020. Prescribed fires cause minimal damage to a threatened cactus (Tobusch fishhook cactus, *Sclerocactus brevihamatus* ssp. *tobuschii*, Texas, USA). *J. Arid Environ.* 185, 104380. <https://doi.org/10.1016/j.jaridenv.2020.104380>.
- Roca, J., Jaureguiberry, P., Gurvich, D.E., 2021. Does fires affects seed germination in cacti species? An experimental assessment. *Austral Ecol.* 46, 818–832. <https://doi.org/10.1111/aec.13027>.
- Roller, P.S., Halvorson, W.L., 1997. Fire and Pima pineapple cactus (*Coryphantha scheeri* Kuntze var. *robustispina* Schott) in southern Arizona. In: *Proceedings of Fire Effects on Rare and Endangered Species and Habitats Conference*. Coeur d'Alene, Idaho, pp. 267–274.
- Spurr, S.H., Barnes, B.V., 1980. *Ecología Forestal*. AGT Editor. México.
- Thomas, P.A., 1991. Response of succulents to fire: a review. *Int. J. Wildland Fire* 1, 11–22. <https://doi.org/10.1071/WF9910011>.
- Thomas, P.A., 2006. Mortality over 16 years of cacti in a burnt desert grassland. *Plant Ecol.* 183, 9–17. <https://doi.org/10.1007/s11258-005-9001-7>.
- Thomas, P.A., Goodson, P., 1992. Conservation of succulents in desert grasslands managed by fire. *Biol. Conserv.* 60, 91–100. [https://doi.org/10.1016/0006-3207\(92\)91159-P](https://doi.org/10.1016/0006-3207(92)91159-P).
- Wallace, W.R., 1966. Fire in the jarrah forest environment. *J. Roy. Soc. West Aust.* 49, 33–44.
- Werner, P.A., Platt, W.J., 1976. Ecological relationships of co-occurring goldenrods (*Solidago*: compositae). *Am. Nat.* 110, 959–971. <https://doi.org/10.1086/283120>.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313, 940–943. <https://doi.org/10.1126/science.1128834>.
- Westoby, M., Jurado, E., Leishman, M., 1992. Comparative evolutionary ecology of seed size. *Trends Ecol. Evol.* 7, 368–372. [https://doi.org/10.1016/0169-5347\(92\)90006-W](https://doi.org/10.1016/0169-5347(92)90006-W).
- Whelan, R.J., 1995. *The Ecology of Fire*. Cambridge university press, Cambridge.
- Zupichiatti, V., Zeballos, S.R., Whitworth Hulse, J.I., Gurvich, D.E., 2022. Survival and growth of cactus species after a wildfire in central Argentina: differences among species and the effects of microenvironmental characteristics. *Austral Ecol.* <https://doi.org/10.1111/aec.13102> (in press).