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Propagation of keystone-woody species as a first step in restoration of an overgrazed seasonal dry forest

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Abstract

In degraded forest ecosystems, reintroduction of keystone-woody species is an important step for restoration because it provides regeneration niches. However, lack of information on how to propagate species restricts the use of native species; specially in tropical dry forests where seed germination is seasonal and is synchronized with the onset of the wet season. We evaluated the dormancy-breaking and germination requirements of nine keystone-woody species from Dry Chaco Forest. Most fresh viable seeds of the keystone species are nondormant, but viability decreases during dry-cold storage restricting the use of some species. Seeds of three keystone species germinated to higher percentages in light than darkness and those of five species germinated equally well in light and darkness; seeds of *Castela coccinea* germinated to higher percentages in darkness than in light. Alternating vs. constant temperatures had no effect on germination in seven species. Seeds of *Anisocapparis speciosa* and *Cynophalla retusa* were nondormant and remained viable for only 1 month during cold-dry storage; and 62–95% of the seeds of the other seven species were nondormant. Dormancy-break was studied in five of the seven species; seeds of four species had physiological dormancy and one had physical dormancy. Dormancy-breaking was promoted by environmental conditions in the habitat, i.e. warm stratification, after seed dispersal. *Castela coccinea*, *Achatocarpus praecox*, *Mimosa detinens*, and *Capparicordis tweedieana* are the most suitable keystone species for the restoration of overgrazed areas in the Dry Chaco Forest because their seeds germinate to a high percentage and retain viability during dry storage at low temperatures. Seeds of *Mimosa detinens* and *Capparicordis tweedieana* required mechanical scarification and 6-weeks of warm stratification, respectively, for dormancy-break.

Keywords Germination · Nurse plants · Seed dispersion · Seed dormancy · Seed storage

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Introduction

In extremely degraded forest or shrubland ecosystems, reintroduction of keystone-woody species can be an important step for restoration (Aronson et al. 1993; Khurana and Singh 2001; Elliott et al. 2002; Brooker et al. 2008; Pérez et al. 2019). Keystone species are species critical to ecosystem function and structure, and when established they accelerate secondary succession by providing regeneration niches for other species (Rey-Benayas et al. 2008; McDonald et al. 2016; Navarro-Cano et al. 2019). Nurse plant species are highly desirable as keystone species because they can facilitate the establishment, survival, and growth of seedlings (Bertness and Callaway 1994; Flores and Jurado 2003; Padilla and Pugnaire 2006; Gómez-Aparicio 2009), so they are recommended for restoration programs. In semiarid lands, many studies have shown that seedling survival of herbs, trees, and shrubs is higher under the shade of shrubs than in open spaces (Lieberman and Li 1992; Ray and Brown 1995; Breshears et al. 1998; Holl 2002; Castro et al. 2004; Gómez-Aparicio et al. 2004; Barchuk et al. 2008; Gómez-Aparicio 2009). Furthermore, keystone species attract animals that disperse seeds, since these species provide bird-perching structures and animal refugees (Callaway 1995; Holl 2002; Flores and Jurado 2003; Tálamo et al. 2015b). Choosing mid-successional shrub species as keystone species is highly desirable because they can become established in the harsh environmental conditions of degraded places and grow faster than late-successional species (Padilla-Ruiz et al. 2004; Padilla et al. 2009; Martínez-Carretero and Dalmasso 2015; Waiboonya and Elliott 2020). However, before a potentially good shrub-nurse plant species can be used as a keystone species in restoration programs we must be able to propagate it. Unfortunately, for many ecosystems information on how to germinate the seeds of native species that would be good nurse plants and keystone species is not available (Elliott et al. 2003; Meli et al. 2014).

In tropical dry forests, seed germination is restricted to periods with favorable soil moisture conditions and temperatures (Khurana and Singh 2001); thus, seedlings have time to grow and develop a good root system before the onset of the dry season (Garwood 1983; Khurana and Singh 2001; Jurado and Flores 2005; Baskin and Baskin 2014; Waiboonya and Elliott 2020). Plant species have developed two strategies to synchronize seed germination with the occurrence of the favorable wet season: (1) dispersing non-dormant seeds at the beginning of the rainy season and (2) delaying germination until the next rainy season via seed dormancy (Lieberman and Li 1992; van Schaik et al. 1993). Both strategies have been reported to occur simultaneously among the species in different seasonal tropical forests such as those on Barro Colorado Island in Panamá (Garwood 1983), in Pinkwae in Ghana (Lieberman and Li 1992), the canal watershed in Panamá (Sautu et al. 2006), central Brazil (Salazar et al. 2011), and the Cerrado of Brazil (Ramos et al. 2017; Escobar et al. 2018). Thus, it is likely that these strategies are present in other seasonal tropical forests that have not been studied, such as Dry Chaco Forest. Therefore, we hypothesized that seeds maturing at the beginning of the rainy season would be nondormant, and those maturing at the end of the rainy season would be dormant. To test this hypothesis, we tested fresh seeds of each species to determine if they were dormant or nondormant at the moment of seed dispersal.

In shrubs of dry tropical forests (tropical deciduous forest sensu Baskin and Baskin 2014) about 80% of the species have dormant seeds with physical dormancy followed by physiological dormancy in importance; while morphophysiological dormancy is not common (Baskin and Baskin 2014). If dormant seeds are dispersed when environmental conditions are not favorable for germination (i.e. too cold and/or dry), the environmental

conditions during this unfavorable period for seedling growth may promote the breaking of dormancy. For example, physiological dormancy (PD) can be broken during the dry season in tropical regions, and seeds germinate as soon as it rains (Baskin and Baskin 2014, Baskin and Baskin 2022). However, some seeds with PD of various species from dry tropical forests in Brazil required 47 to 113 days for initiation of germination on a moist substrate (Zamith and Scarano 2004); while seeds of *Adina cordifolia* in India germinated over a 7-week period (Beniwal and Singh 1989). In species with physical dormancy (PY), i.e. a water-impermeable seed/fruit coat, a period of warm dry weather can make the seeds sensitive to dormancy-breaking conditions (e.g. wet soil) that follow the time when seeds became sensitive (e.g. Gama-Arachchige et al. 2012). That is, the breaking of PY is a two-step process, and the first step can occur when it is too dry in the habitat for germination and seedling establishment to occur; the second step occurs after the rainy season begins. Thus, we hypothesized that dormancy-break would be promoted by the environmental conditions that occur after the seeds are dispersed. To test this hypothesis, we determined the dormancy-breaking requirements of dormant seeds and compared them to environmental factors in the habitat following seed dispersal.

After dormancy is broken, the germination at the beginning of the favorable (wet) season gives seedlings the maximum period of time for establishment and growth before the onset of the dry season (Khurana and Singh 2001; Jurado and Flores 2005; Baskin and Baskin 2014); therefore, the climate conditions during that time would enhance germination if we germinate seeds in controlled conditions. In tropical dry forests, the optimum temperature for germination of seeds of 60 species of shrubs was 26.9 ± 0.2 °C, but data for germination in light vs. dark were available for only six species, which germinated equally well in light and dark (Baskin and Baskin 2014). Understanding the requirements for dormancy-break and germination is the first step to facilitate seedling propagation in nurseries for restoration activities.

Seed storage is often an important part of a restoration program in which plants are propagated from seeds (De Vitis et al. 2020); and several studies pointed out the necessity of storing seeds, for example for seeds of *Carex* spp. from meadow wetlands in United States (Budelsky and Galatowitsch 1999), seeds of trees from a tropical dry forest in Mexico (Cervantes et al. 2014), and seeds of *Mimosa foliolosa* from a seasonal grassland in Brazil (Silveira et al. 2014). Storage in cool dry conditions, e.g. at 4–5 °C in a refrigerator may be a convenient way for restoration workers to store small seed lots (Baskin and Baskin 2014). Since seeds of many tropical dry forest tree species lose viability during dry cold storage or even at room temperatures (Khurana and Singh 2001), it is important to know how long seeds will remain viable during dry storage.

Large areas of dry tropical forests have been destroyed and need to be restored (Hansen et al. 2013). In South America, Dry Chaco Forest occupies 1,100,000 Km² in Argentina, Bolivia, Brazil, and Paraguay (Kuemmerle et al. 2017), while the majority is in Argentina (600,000 Km²) (Morello and Rodriguez 2009). Rapid loss of Dry Chaco Forest is occurring in northwestern Argentina. From 1992 to 1999, annual loss of this type of forest in Argentina was 5% (Boletta et al. 2006), but between 1972 and 2007 deforestation reached 43% (Gasparri and Grau 2009). Agricultural expansion, mainly for soybean cultivation, has changed this area into crop fields, resulting in fragmentation of the forest into small remnants (Zak et al. 2004; Gasparri and Grau 2009). In 2004, the conversion of Argentinean Dry Chaco Forest into agricultural land was 91,000 km² (Morello and Rodriguez 2009). In the forest remnants, extensive grazing is practiced transforming these areas into patches of highly degraded secondary forest. Natural regeneration of woody species is decreased because livestock diminish propagule sources (due to selective grazing), reduce

the emergence of seedlings (due to trampling), and decrease regeneration niches (due to soil compaction, erosion, and loss of soil nutrients) (Abril and Bucher 1999; Czeglédi and Radácsi 2005; Macchi and Grau 2012; Mazzini et al. 2018). Reintroduction of keystone-nurse-woody species could be a suitable restoration technique for Dry Chaco Forest because facilitation is an important mechanism for the establishment of some species (Páez and Marco 2000; Barchuk et al. 2008). Further, the use of thorny shrubs as keystone species would enhance their ability to serve as a refuge for the establishment of seedlings (Tálamo et al. 2015a). However, if we want to propagate keystone-woody species to restore overgrazed sites knowledge of seed dormancy-breaking and germination requirements is a key first step. The objective of our research was to determine the dormancy-breaking and germination requirements of nine shrub species from Dry Chaco Forest that potentially could perform as keystone-nurse-woody species. Specifically, we determined the (1) kind/class of dormancy, (2) effective treatments to break dormancy, (3) light and temperature requirements for germination of nondormant seeds and (4) the retention of seed viability during dry storage at 4 °C.

Methodology

Study species

Nine native shrubs species of Dry Chaco Forest were selected (Table 1). They could be suitable keystone species for the restoration of overgrazed sites since they have a conspicuous evergreen canopy, functional characteristics for grazing deterrence (thorns or chemical compounds), and fruits that attract native seed-dispersing animals.

Seed collection

Fruits were obtained from Copo National Park in Santiago del Estero, Argentina (25° 39′ 11″ to 26° 10′ 37″ S and 61° 42′ 46″ to 62° 12′ 55″ W). Vegetation in the park corresponds to Dry Chaco Forest, semi-deciduous thorn forest (Bucher 1982), or dry tropical forest (Walter and Burnett 1971). The climate is semiarid and seasonal (Bucher 1982). The warm-rainy season (favorable period for seed germination) occurs between October and March; during which time the mean temperature is 25.6 °C, and the daily mean maximum and minimum temperatures are 32.4 °C during the day and 19.2 °C during the night. During the wet season, precipitation is 649.35 mm. The cold-dry season (unfavorable period for seed germination) occurs between April to September; during which time the mean temperature is 18.1 °C, and the daily mean maximum and minimum temperatures are 25.0 °C during the day and 11.6 °C during the night. During the dry season, precipitation is only 208.7 mm, and the water balance is negative resulting in soil moisture deficit (average of the last 15 years of the closest climate stations located in Sáenz Peña, Castelli, and Pampa del Infierno in Argentina) (INTA 2020).

Ripe fruits were collected from a minimum of 20 adult plants of each species between 2016 and 2018. Seeds were removed from the dry fruits and berries, and the exocarp and mesocarp were removed from drupes, leaving the embryo enclosed by the endocarp. Seeds from berries and drupes (with the exocarp and mesocarp removed) were washed with tap water and dried at room temperature for 3 days. All seeds and drupes (hereafter drupes

Table 1 Description of the keystone-woody species from Dry Chaco Forest

Family/species	Embryo morphology[a]	Kind of fruit[c]	Protection from grazing[c]	Fruit dispersion	Distribution[d]
Simaroubaceae					
Castela coccinea	Spatulate fully developed embryo	Fleshy—drupe	Thorny	November	North east of Argentina, Paraguay
Achatocarpaceae					
Achatocarpus praecox	Peripheral embryo with starchy perisperm in the middle	Fleshy—drupe	Thorny	January	North east of Argentina, Paraguay
Cannabaceae					
Celtis pallida	Investing embryo and folded cotyledons	Fleshy—drupe	Thorny	January	North east of Argentina, Uruguay, Brazil
Capparaceae					
Anisocapparis speciosa	Embryo globose with asymmetrical cotyledons. The root apex shows as a small protuberance[b]	Fleshy—berry	Conspicuous canopy	December	North east of Argentina, Paraguay
Capparicordis tweedieana	Folded embryo. Cotyledons asymmetrically folded one over the other	Fleshy—berry	Pubescence leaves and branches, dense branching pattern	December	North east of Argentina, Paraguay, Brazil
Capparis salicifolia	Folded embryo. Cotyledons asymmetrically folded one over the other	Fleshy—berry	Pubescence leaves and branches, dense branching pattern	December	North east of Argentina, Paraguay
Atamisquea emarginata	Folded embryo. Cotyledons asymmetrically folded one over the other	Fleshy—berry	Pubescence leaves and branches, dense branching pattern	February	North east of Argentina, Paraguay
Cynophalla retusa	Embryo straight with asymmetrical cotyledons covering the axis except the root tip[b]	Dry—siliques	Conspicuous canopy	February	North east of Argentina, Paraguay
Leguminosae					
Mimosa detinens	Spatulate fully developed embryo	Dry—legume	Thorny	March	North east of Argentina, Paraguay

[a]Classification sensu Baskin and Baskin (2014)

[b]Franceschini and Tressens (2004)

[c]Franceschini and Tressens (2004), Peña-Chocarro et al. (2006), Abraham De Noir and Bravo (2014), Oscar-Palacio and Roger (2016)

[d]Instituto de Botánica Darwinion (2022)

are referred to as seeds) were stored dry in closed plastic containers at 4 °C until used in experiments.

Germination test of fresh seeds

Four replicates of 25 freshly-harvested (3 to 7 days after collection) seeds of *Castela coccinea*, *Capparicordis tweedieana*, *Capparis salicifolia*, *Anisocapparis speciosa*, *Achatocarpus praecox*, *Celtis pallida*, *Cynophalla retusa*, *Atamisquea emarginata*, and *Mimosa detinens* were incubated at 27 °C in light and in darkness for 30 days following a randomized design. Seeds were placed in Petri dishes on filter paper moistened with distilled water. Seeds incubated in light were exposed to a 12 h daily photoperiod, while those incubated in darkness were covered with two layers of aluminum foil and placed in a black plastic bag. Germination in light was recorded at 2-day intervals (germination criterion was radicle emergence > 2 mm), while dark germination was recorded only at the end of the test. Non-germinated seeds were checked for viability using the cut test, and seeds with a white firm embryo were recorded as viable and those with a soft grey embryo as nonviable. Differences between treatments were tested using a t-test.

Seeds of *A. speciosa* and *C. retusa* (Capparaceae) were covered with fungi after 1 month of dry storage at 4 °C. Thus, due to their low viability we could not performed any additional experiments with seeds of these two species.

To determine the mechanism that controls seed germination, we compared the maximum percentage of germination and percentage of non-germinated viable seeds (i.e. dormant seeds) of each species with the month(s) of seed dispersal, using regression analyses.

Effect of constant versus alternating temperature on germination

We used seeds that had been stored dry at 4 °C for a period of time equal to that of the time between seed dispersal and the beginning of the following favorable wet period for seed germination: *C. coccinea,* 46 weeks; *C. tweedieana*, 44 weeks; *C. salicifolia,* 37 weeks; *A. emarginata,* 37 weeks; *A. praecox*, 34 weeks; *C. pallida*, 36 weeks; and *M. detinens*, 36 weeks. Seeds of all species were incubated in light (12 h daily photoperiod), except *C. coccinea*, at a constant temperature of 27 °C and at an alternating temperature regime of 35/20 °C. Seeds of *C. coccinea* were incubated in darkness because their germination percentage is higher in darkness than in light. Four replicates of 25 seeds were sown on the surface of white quartz sand moistened with distilled water in Petri dishes, and then we followed the procedure described for the germination test of fresh seeds. To determinate the effect on temperature on seed germination and to avoid any effect due to seed storage, we compared these results with the maximum germination obtained in the germination test of fresh seeds (seeds collected the same year). However, results for *C. coccinea* were compared with germination of fresh seeds and of stored seeds for 31 months, which were collected the previous year and tested following the procedure described for the germination test of fresh seeds.

To determine the effect of dry storage at 4 °C on retention of seed viability, we compared the viability of fresh and stored seeds of *C. coccinea*, *C. tweedieana*, *C. salicifolia*, *A. praecox*, *C. pallida*, *A. emarginata*, and *M. detinens*. Viable seeds were the germinated plus the non-germinated viable seeds.

Differences between treatments were tested using a one-way ANOVA. Variance homogeneity was tested using the Levenne test, and contrast between pairs of treatments was made using a Tukey test. When heteroscedasticity existed, we used a Kruskal–Wallis test.

Kind of dormancy and treatments to break dormancy

Baskin and Baskin (2004) defined five kinds (classes) of seed dormancy: morphological dormancy (MD), physical dormancy (PY), physiological dormancy (PD), morphophysiological dormancy (MPD), and combinational (PY+PD). From results of the germination test of fresh seeds, we determined that 23–39% of the fresh seeds of *A. emarginata*, *C. salicifolia*, *C. tweedieana*, *C. pallida*, and *M. detinens* was dormant; the other portion was non-dormant (see below). We determined the class of dormancy for the portion of dormant seeds of each species and tested different methods to break it.

Morphological dormancy

The embryo is differentiated (i.e. it has organs) but underdeveloped (small in comparison to the length of the seed), and it must growth inside the seed before germinates occurs (Baskin and Baskin 2014). To check for the presence of an underdeveloped embryo, three seeds of each species were cut opened, and embryo and seed length were measured. None of the five species had an underdeveloped embryo (See information about embryo morphology in Table 1).

Physical dormancy

Physical dormancy (PY) is caused by presence of a layer of water-impermeable palisade cells in the seed or fruit coat, while the embryo is fully developed and ready to germinate (Baskin and Baskin 2014). To determinate if seeds of *C. tweedieana*, *C. salicifolia*, *C. pallida*, *A. emarginata*, and *M. detinens* have PY, they were tested for imbibition of water. Twenty-five nontreated (intact-fresh) and manually scarified (cut individually with a razor blade) seeds were placed on filter paper moistened with distilled water. Seeds were weighed (to the nearest 0.0001 g) individually at time 0, and after 2 h, 4 h, 6 h, 8 h, 10 h, 12 h, 24 h, and 48 h. Each seed was removed from the Petri dish, blotted dry, and then weighed. Percentage increase in mass was calculated for each weighing time for each seed. Based on percentage of water imbibition, we decided if the seeds had a water-impermeable seed coat or not.

Fresh seeds of *M. detinens* collected in 2018 had PY, and they were given various treatments known to break PY: mechanical scarification (cutting a small hole at the cotyledon end of the seed with a razor blade), wet heat (dipping seeds in boiling water for 5 s, 15 s, and 5 min), wet (soaking in water for 24 h), soaking in concentrated sulfuric acid (for 5 min, 30 min, and 30 min). After performing the treatments, the seeds were tested for germination following the procedure for the germination test of fresh seeds. Differences between treatments were tested using a t-test to compare two treatments and a one-way ANOVA to compare more than two treatments. For ANOVA, variance homogeneity was tested using the Levenne test, and contrast between pairs of treatments was made using a Tukey test.

Physiological dormancy

Physiological dormancy (PD) is caused by a germination inhibiting mechanism in the embryo. Fresh seeds have a fully developed embryo, imbibe water but fail to germinate within 4 weeks (Baskin and Baskin 2014). Some seeds of *C. pallida*, *C. tweedieana*, *A. emarginata,* and *C. salicifolia* had PD.

Fresh seeds of *Celtis pallida* collected in 2017 and 2018 were given a GA_3-treatment (0 ppm, 26 ppm, 260 ppm, or 2600 ppm of GA_3), cold stratification (seeds placed in wet sand at 4 °C for 0, 3, 6, 9 and 12 weeks), and warm stratification (seeds placed in wet sand at 30 °C for 0, 3, 6, 9 and 12 weeks). Then, seeds were incubated at 27 °C for 30 days following the procedure for the germination test of fresh seeds.

Fresh seeds of *Capparicordis tweedieana*, *C. salicifolia*, and *A. emarginata* collected in 2017 and 2018 were given a GA_3-treatment, cold stratification, warm stratification, and allowed to after-ripen at room temperature in paper bags for 0, 3, 6, 9 and 12 weeks. Then, seeds were incubated at 27 °C for 30 days following the procedure for the germination test of fresh seeds.

Differences between treatments were tested using one-way ANOVA; except when we analyzed the results for GA_3 when we used a two-way ANOVA (factors GA_3 + seed scarification). For ANOVA, variance homogeneity was tested using the Levenne test, and contrast between pairs of treatments was made using a Tukey test. When heteroscedasticity existed, we used a Kruskal–Wallis test.

Morphophysiological dormancy

Seeds have an underdeveloped embryo that also has PD. Seeds will not germinate until the PD has been broken and the embryo has grown inside the seed. Embryo growth may occur at the same time PD is being broken or after PD has been broken, depending on the species (Baskin and Baskin 2014). None of the five species had MPD.

Combinational dormancy

Seeds have a water-impermeable seed or fruit coat, and the embryo is fully developed but has PD. Depending on the species, PD may be broken before or after PY is broken (Baskin and Baskin 2014). None of the five species had PY + PD.

Data analyses

All tests were performed at a 5% of significance level. We used the statistical software INFOSTAT and R programming environment (R Core Team 2018) to create the figures.

Results

Germination test of fresh seeds

Based on number of viable seeds, maximum germination of *A. speciosa*, *C. retusa*, *A. praecox*, *C. coccinea*, *A. emarginata, C. salicifolia*, *C. tweedieana*, *C. pallida*, and *M. detinens* was 100.0%, 100%, 94.5%, 90.3%, 77.1%, 70.1%, 69.5%, 67.3%, and 62.1%, respectively

(Fig. 1). Thus, all seeds of *A. speciosa* and *C. retusa* were nondormant, and 62 to 95% of the seeds of the other seven species were nondormant.

Incubating seeds of *C. coccinea* in darkness increased germination by 29% compared to that of seeds in light, while incubating seeds of *C. retusa*, *C. pallida*, and *C. salicifolia* in light increased germination by 26%, 18%, and 17%, respectively, compared to that in darkness. Seeds *of A. speciosa*, *C. tweedieana*, *A. praecox*, *A. emarginata*, and *M. detinens*, were indifferent to light vs. dark (Fig. 1). After incubation in light, there were no non-germinated viable seeds of *C. retusa* and *A. speciosa* (Online Resource 1). Performance of the non-germinated seeds for each species is presented in Online Resource 1.

When we compared the highest germination percentage and the percentage of non-germinated viable seeds (Fig. 1 and Onlince Resource 1) of species that dispersed seeds at different times during the rainy season (Table 1), the relationship was not linear nor significant ($b = -2.89$, $p = 0.5361$), and in the intermediate months (December, January, and
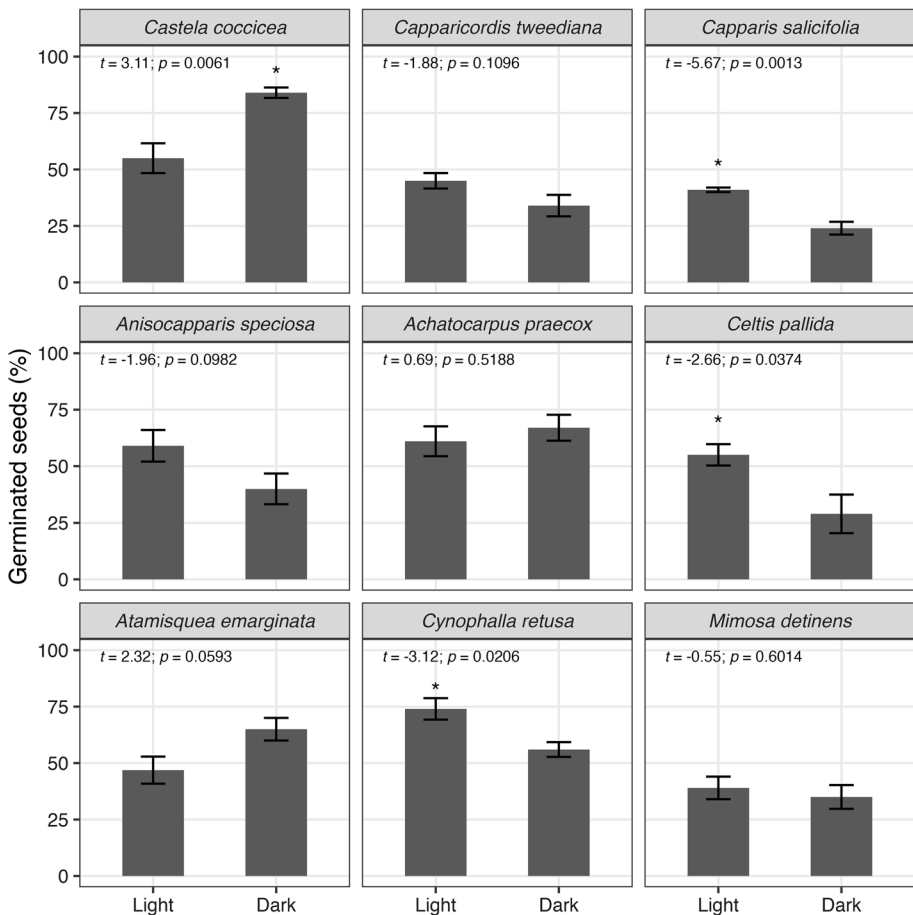
Fig. 1 Germination of fresh seeds of keystone-woody species from Dry Chaco Forest. Percentage of seed germination (mean ± standard error). Seeds incubated at 27 °C in light (12 h of daily photoperiod) or in darkness for 30 days. Results of t-test (*t*-values, *p*-values). * indicates the significantly best treatment at a *p*-value < 0.05
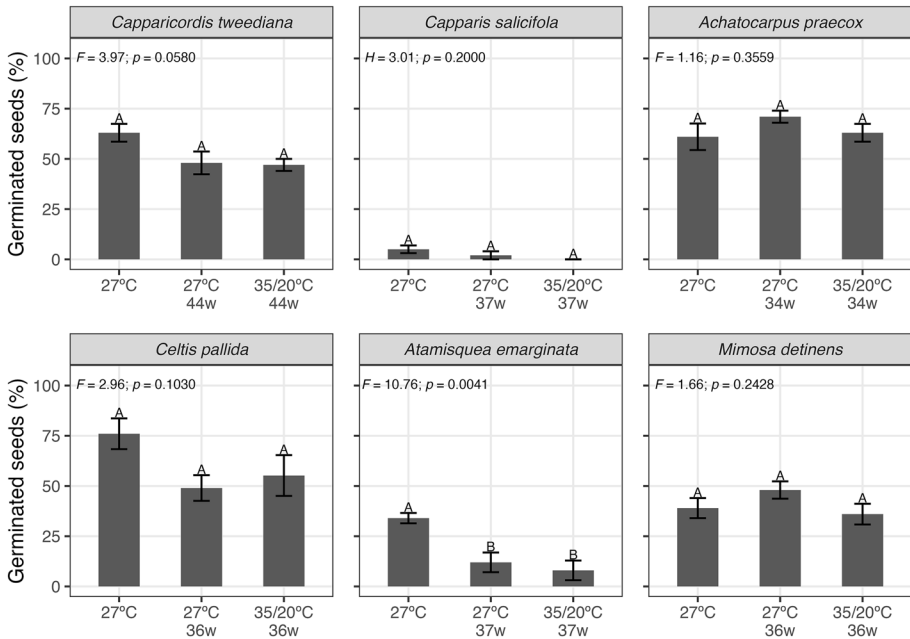
Fig. 2 Effect of constant vs. alternating temperature on germination of keystone-woody species from Dry Chaco Forest. Percentage of seed germination (mean ± standard error). Fresh seeds and stored seeds (dry at 4 °C) incubated at 27 °C or 35/20 °C in light (12 h of daily photoperiod) for 30 days. Results of ANOVA or Kruskal–Wallis (*F*-values or *H-values*, *p-values*). Different letters indicate significant differences at a *p*-value < 0.05 according to Tukey or Kruskal–Wallis test. w = weeks

February) the relationship was positive. The percentage of viable seeds increased slightly towards the end of the rainy season, although the relationship was not linear nor significant ($b = 1.73$, $p = 0.5792$).

Effect of constant versus alternating temperature on germination

The alternating temperature regime (35/20 °C) did not increase the germination percentage of cool-dry-stored seeds of *C. tweedieana*, *C. salicifolia*, *A. praecox*, *C. pallida*, or *M. detinens* compared to constant temperature (27 °C) or compared to germination of fresh seeds at 27 °C. Fresh seeds of *A. emarginata* germinated to a higher percentage at 27 °C than those stored for 37 weeks and tested at 27 °C or 35/20 °C (Fig. 2). Performance of the non-germinated seeds for each species is presented in Online Resource 1.

Germination percentage of fresh seeds of *C. coccinea* tested in darkness at 27 °C did not differ from that of seeds dry-stored at 4 °C for 46 weeks and tested in light or darkness at 27 °C or 35/20 °C or from that of seeds dry-stored at 4 °C for 31 months and tested in light at 27 °C (Fig. 3). Performance of the non-germinated seeds is presented in Online Resource 1.

Dry storage at 4 °C promoted the retention of seed viability of *C. coccinea*, *C. tweedieana*, *C. pallida*, and *A. praecox*. However, dry storage at 4 °C decreased the percentage
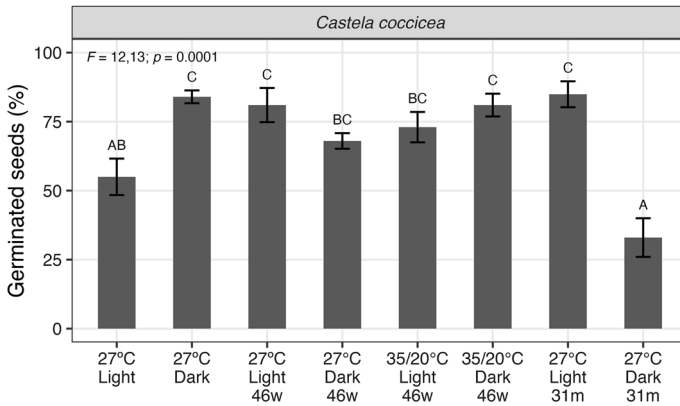
Fig. 3 Effect of constant vs. alternating temperature on germination of *Castela coccinea*. Percentage of seed germination (mean ± standard error). Fresh seeds and stored seeds incubated at 27 °C or 35/20 °C in light (12 h of daily photoperiod) or darkness for 30 days. Result of ANOVA test (*F*-values, *p*-values). Different letters indicate significant differences at a *p*-value < 0.05 according to Tukey test. w = weeks, m = months

of viable seeds by 43% for *C. salicifolia* and 39.5% for *A. emarginata* and increased the percentage of viable seeds for *M. detinens* by 18% (Fig. 4).

Kind of dormancy and treatments to break dormancy

Physical dormancy

Scarified and intact seeds of *M. detinens* had an increase in mass of 90% and 39% respectively. Mass increase for scarified and nonscarified seeds of *C. tweedieana*, *C. salicifolia*, *C. pallida*, and *A. emarginata* was similar and varied between 30–50% (Fig. 5).

Mechanical scarification, soaking in concentrated sulfuric acid (regardless of soaking time), and soaking in water for 24 h (wet treatment) improved germination of *M. detinens* by 54% ($t = -10.09$, $p = 0.0001$), 39.6% ($F = 34.70$, $p < 0.0001$), and 14% ($t = -2.50$, $p = 0.0465$), respectively. The best treatment was mechanical scarification, which resulted in $73.0 \pm 3.4\%$ germination. Wet heat treatment did not improve germination ($F = 1.09$, $p = 0.3902$) (Online Resource 2).

Physiological dormancy

The effect of GA$_3$ on germination of *C. pallida* seeds depended on scarification ($F_{GA3*esc} = 6.41$, $p = 0.0024$). If seeds were manually scarified, the germination percentage was low, and GA$_3$ did not promote germination. In contrast, if seeds were not manually scarified germination percentage decreased at the highest GA$_3$ concentration tested. Neither cold stratification nor warm stratification improved germination ($F = 7.39$, $p = 0.0252$; $F = 7.20$, $p = 0.0019$; respectively) (Online Resource 3).

The effect of GA$_3$ on germination of *C. tweediana* seeds depended on scarification ($F_{GA3*esc} = 8.86$, $p = 0.0004$). If seeds were manually scarified, the germination percentage
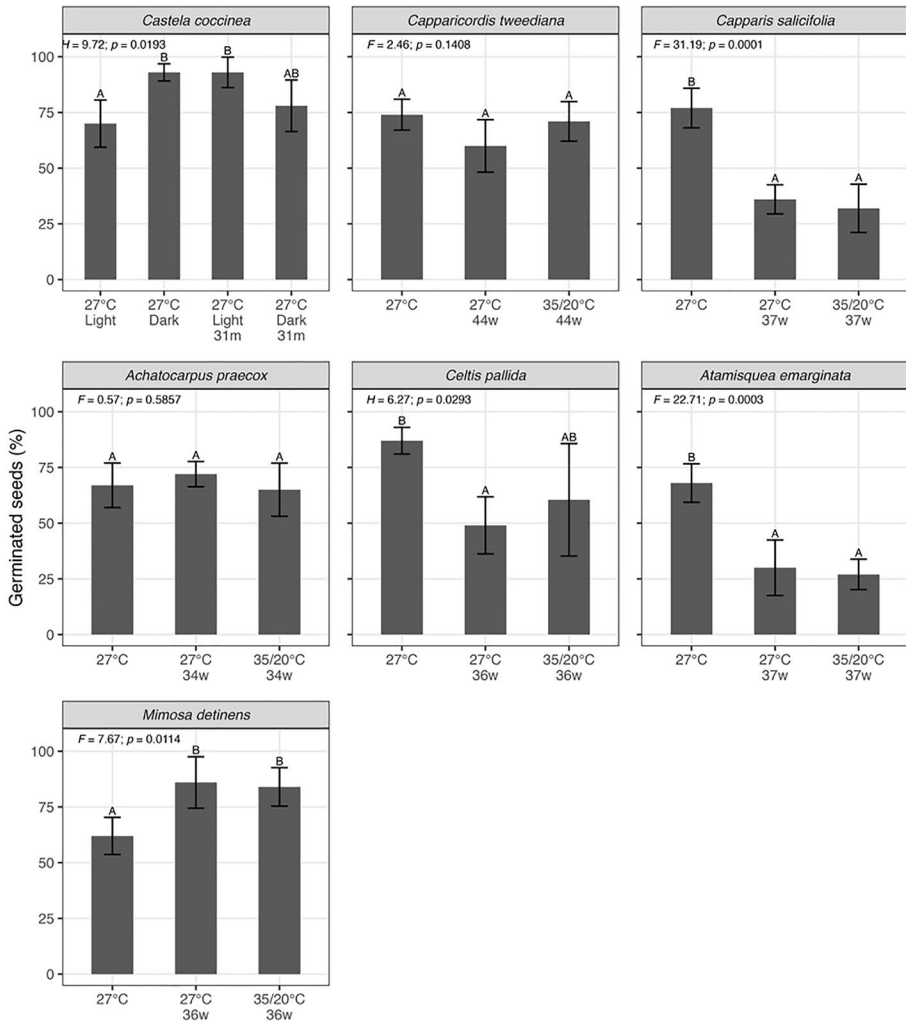
Fig. 4 Effect of dry storage at 4 °C on retention of seed viability of keystone-woody species from Dry Chaco Forest. Percentage of viable seeds of fresh seeds and stored seeds. Results of ANOVA or Kruskal–Wallis (*F*-values or *H*-values, *p*-values). Different letters indicate significant differences at a *p*-value < 0.05 according to Tukey or Kruskal–Wallis test. w = weeks, m = months

decreased with increased GA_3 concentration. In contrast, if seeds were not manually scarified the germination was similar to that of control seeds. Six weeks of warm stratification improved germination by 18.0% ($H = 13.04$, $p = 0.0106$), which was the best PD dormancy-breaking treatment resulting in $81.0 \pm 1.7\%$ germination. Three weeks of cold stratification did not have an effect on germination, and an increase in time of cold stratification decreased germination ($F = 12.89$, $p = 0.0001$). Afterripening decreased germination ($F = 2.70$, $p = 0.0712$) (Online Resource 4).

Three weeks of warm stratification of *C. salicifolia* seeds improved germination by 7.0% ($F = 4.81$, $p = 0.0107$), resulting in $12.0 \pm 1.6\%$ germination. Neither GA_3 (including
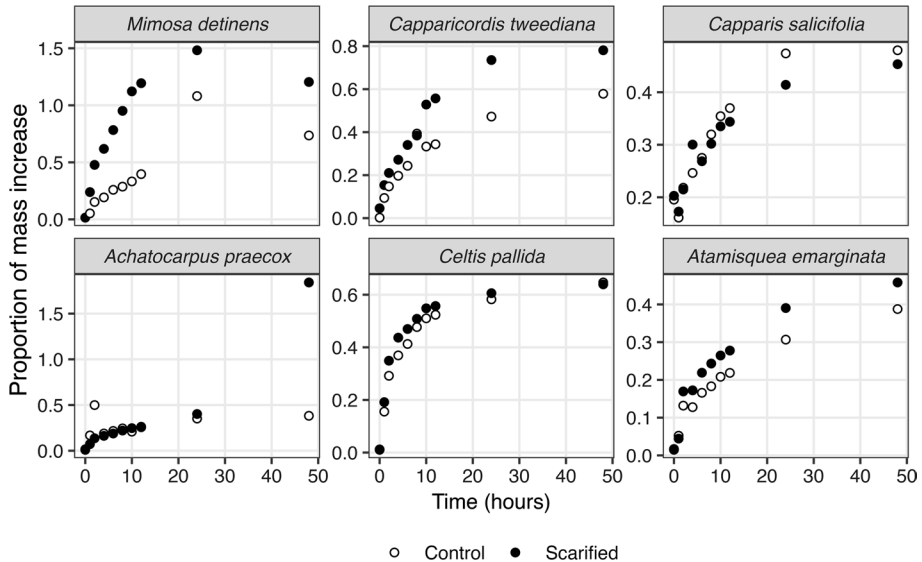
Fig. 5 Imbibition test of keystone-woody species from Dry Chaco Forest. Proportion of mass increase for intact (control) and manually-scarified seeds for 48 h

scarification treatment), cold stratification, nor afterripening improved germination ($H = 7.31$, $p = 0.1066$; $H = 13.35$, $p = 0.0050$; $F = 71.24$, $p < 0.0001$; respectively). While there was little change in number of viable seeds (compared to control) following treatment of non-scarified seeds with GA_3, cold stratification, and afterripening at room temperature, only $1.0 \pm 1.0\%$ of the seeds receiving warm stratification were viable after 12 weeks (Online Resource 5).

Nine weeks of warm stratification of *A. emarginata* seeds improved germination by 7.0% ($F = 34.71$, $p < 0.0001$), resulting in $41.3 \pm 0.4\%$ germination; but a longer time of warm stratification diminished germination. Neither GA_3 (including scarification treatment), cold stratification, nor afterripening ($H = 11.34$, $p = 0.1182$; $F = 1.28$, $p = 0.3247$; $F = 2.22$, $p = 0.1156$; respectively) improved germination (Online Resource 6).

Discussion

Our hypothesis that seeds maturing at the beginning of the rainy season will be nondormant and those maturing at the end of the rainy season will be dormant was not supported by our data. A high percentage (62–100%) of fresh viable seeds of all nine species was nondormant, regardless of when they were dispersed. Thus, a significant portion of the seed crop of the nine species can germinate (under good conditions) as soon as they are dispersed. However, for seven species, 6–39% of the seeds was dormant. Having some seeds that can germinate right away and other seeds that are dormant seems like a good strategy for survival in Dry Chaco Forest, which has a strong seasonality (Bianchi and Yáñez 1992). Perhaps, having dormancy and nondormant seeds at the time of dispersal is a bet hedging strategy for Chaco keystone species, but this needs to be tested experimentally to determine if a decrease in arithmetic mean fitness (i.e. seed dormancy) reduced variance

in fitness and increases geometric mean fitness of the population. Nonetheless, the dormant portion of the seed cohort of the seven species can form at least a short-term soil seed bank that helps ensure persistence of the species in the Dry Chaco Forest. A similar strategy has been found in the arid zone of eastern Australia, where the germination response of eight species was studied. Fresh seeds of six species germinated rapidly in response to rainfall and those of two species had PD. Also, non-dormant seeds of many of these species had long viability, which helps to explain how they persisted in the soil seed bank (Duncan et al. 2019).

Although many seeds of *C. tweediana*, *C. salicifolia*, *C. pallida*, and *A. emaraginata* were nondormant, some seeds of each species had PD. Also, some seeds of *M. detinens* were nondormant and others had PY. In general, dormancy-break in seeds with PD supports our second hypothesis that dormancy-break is promoted by the environmental conditions in the habitat after the seeds are dispersed. Further, warm-wet conditions are optimal for dormancy-break of the relatively small fraction of the seed population of *C. tweediana*, *C. salicifolia*, and *A. emarginata* that has PD but not seeds of *C. pallida*. However, these conditions may not occur until the subsequent rainy period, in which case we suggest that seeds remain in the soil seed bank for several months before dormancy is broken. Similarly, in a tropical seasonal rain forest in Panama, the seeds dispersed at the end of the rainy season or during the dry season will not germinate until the following wet season (Garwood 1983; Sautu et al. 2006). In a seasonal grassland in Brazil, *Mimosa foliolosa* seeds are dispersed in the middle of the dry season and after storage in room dry conditions the germination increased probably due to seed coat softening (Silveira et al. 2014).

About 33% of the seeds of *Celtis pallida* had PD, but it was not broken by treatment with GA_3, manual scarification, cold stratification, or warm stratification, suggesting that the seeds might have intermediate or deep PD. If the seeds have deep PD, the excised embryo will not grow or produce only a dwarf plant (Nikolaeva 1969), and many months of warm stratification may be required for dormancy break (Baskin et al. 2005). If the seeds have intermediate PD, warm followed by cold stratification may be effective for dormancy-break (Nikolaeva 1969). It is interesting to note that germination of *C. pallida* seeds was increased by exposing seeds to 3 days of wet heat at 30 °C followed by 2 weeks of cold stratification (Fulbright et al. 1986). Clearly more research is needed on the portion of the seed crop of *C. pallida* that has PD.

A relatively short period of warm stratification broke the dormancy in *C. tweedieana* seeds; thus, we concluded that they have nondeep PD (sensu Nikolaeva 1969; Baskin and Baskin 2014). The best dormancy-breaking treatment was 6 weeks of warm stratification, which reflects the conditions in the field when seeds of this species are dispersed at the beginning of the warm wet season. Cold and dry conditions were suitable for seed storage of this species. However, cold stratification did not increase germination and increased the percentage of dead seeds. Therefore, probably after dispersal, the seeds that did not germinate during the favorable season enter the soil seed bank where the cold dry conditions during the non-favorable season for germination maintain dormancy. During the subsequent favorable period, the temperature increases, and the rainy period produces a warm stratification that breaks dormancy allowing for germination. Dry storage at room temperatures did not increase germination of *C. tweedieana* seeds and lead to an increase in percentage of dead seeds; thus, storing seeds at room temperature is not recommended.

About 30% of seeds of *C. salicifolia* and 23% of seeds of *Atamisquea emarginata* were dormant and possibly possess deep PD because neither GA_3, cold scarification, nor manually scarification promoted germination, and they did not afteripen (Nikolaeva 1969; Baskin and Baskin 2014). To be sure that seeds of these species have deep PD we should

perform the treatments mentioned previously for *C. pallida* seeds. Warm stratification increased the germination of *A. emarginata* and *C. salicifolia* but to only 7.0% in both species. Furthermore, after 3-weeks of warm stratification the seeds of *C. salicifolia* died. Thus, more research is needed to determine the dormancy-breaking requirements for seeds of these two species, including extended periods of cold or warm stratification. For example, the germination of *Capparis ovata* was enhanced up to 46.6% after 60 days of cold stratification (Olmez et al. 2004). In contrast, the tropical montane species *Leptecophylla tameiameiae* required extended periods (162 days) of warm stratification to germinate (Baskin et al. 2005). The results of the afterripening experiment (i.e. dormancy-break during dry storage) demonstrate that we can store the seeds of *A. emarginata* and *C. salicifolia* dry at room temperature for 12-weeks without loss of viability.

Manual scarification was the most effective treatment to break PY of *Mimosa detinens* seeds than acid scarification; however, acid scarification could be useful to treat large numbers of seeds for sapling production in restoration programs. All soaking times tested were equally effective, thus we recommend 5 min of soaking in acid to save operation efforts.

Many fresh seeds of all species can germinate to high percentages. Further, seeds germinated better in light or equally well in light and dark (except for *C. coccinea*), and there was no effect of incubation at alternating vs. constant temperatures on germination in seven species. Germination of 17 woody species from Dry Chaco Forest in Argentina (including *Celtis ehrenbergiana*) was indifferent to light conditions and their germination was only promoted by the temperatures that occur during the warm-wet period (favorable season) (Funes et al. 2009). Thus, based on our results and the available information for Chaco species, we suggest that planting seeds on-site as soon as they mature via direct sowing in open spaces in the overgrazed places (with the exception of *C. coccinea* whose seeds will need to be covered by soil or litter) potentially is a good strategy for reintroduction of keystone-nurse-woody species to the open spaces in Dry Chaco Forest. However, the ability of seeds to germinate in the field has not been tested as there might be other factors, such as predation, that decreased their germination success, and thus seeds with only a short period of viability may need to be sown in a nursery. Based on light and temperature requirements, a similar recommendation was made for *Guaiacum sanctum* seeds. Since temperature mainly regulates seed germination of this species, it potentially can be introduced to open and partially-open sites to restore degraded areas of dry forests in Nicaragua (González-Rivas et al. 2009).

Seeds of some trees species from tropical dry forests lose viability during dry cold storage and even at room temperatures (Khurana and Singh 2001), so it is important to determinate proper seed storage procedures for each species. Although we did not study seed storage specifically, we could use our data to suggest some guidelines. Dry storage of seeds of *C. coccinea*, *C. tweedieana*, *A. praecox*, *C. pallida*, and *M. detinens* at 4 °C from time of dispersal until the following favorable season for germination is useful to retain seed viability. However, fresh seeds of *C. retusa*, *A. speciosa*, *C. salicifolia*, or *A. emarginata* should be sown immediately after collection. More research is needed to determine long term storage of these species. For example, seeds of *Mimosa foliolosa* retained viability during 3 years of dry storage at room temperature (Silveira et al. 2014).

Conclusions

Seeds of the nine keystone-nurse-woody species germinated to a high percentage and can be used for restoration purposes if they are fresh. We suggest planting seeds of the nine species in a nursery (or possibly on-site) as soon as they mature. Most fresh viable seeds are nondormant, but viability decreases during dry-cold storage restricting the use of some species. *C. coccinea*, *A. praecox*, *M. detinens*, and *C. tweedieana* are the most suitable keystone species for the restoration of overgrazed areas in the Dry Chaco Forest because their seeds germinate to a high percentage and retain viability during dry storage at low temperatures. Seeds of *M. detinens* and *C. tweedieana* require mechanical scarification and 6-weeks of warm stratification, respectively, for dormancy-breaking. *Cynophalla retusa* and *A. speciosa* have nondormant seeds that remain viable for only 1 month. *Celtis pallida* remained viable during cold-dry storage, but the degree of physiological dormancy increased. *Atamisquea emarginata* and *C. salicifolia* are not recommended as keystone species unless the seeds can be sown immediately after harvesting; most fresh viable seeds are nondormant, but viability decreases during dry-cold storage. Finally, the variation in dormancy and germination found in the Chaco species included in our study emphasizes the importance of conducting detailed studies on dormancy-breaking and germination requirements of species that are deemed to be of high value in forest restoration efforts.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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