

Article

Recruitment of Dry Tropical Woody Species After Fire: Germination Phase and Seedling Establishment

Amalia Valeria Ibañez Moro ^{1,2,*} , Fabian Borghetti ³ , Leonardo Galetto ⁴ , Juan Manuel Cellini ⁵ 
and Sandra Josefa Bravo ¹ 

- ¹ Complejo Edificio Jardín Botánico, Facultad de Ciencias Forestales, Universidad Nacional de Santiago del Estero, Avenida Belgrano (S) 1912, Santiago del Estero 4200, Argentina; sjbravo@unse.edu.ar
 - ² Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Complejo Edificio Jardín Botánico, Facultad de Ciencias Forestales, Universidad Nacional de Santiago del Estero, Avenida Belgrano (S) 1912, Santiago del Estero 4200, Argentina
 - ³ Departamento de Botánica, Universidade de Brasília, Campus Darcy Ribeiro, Brasília CEP 70910-900, DF, Brazil; borghetti.fabian@gmail.com
 - ⁴ Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Instituto Multidisciplinario de Biología Vegetal, Universidad Nacional de Córdoba, Casilla de Correo 495, Córdoba 5000, Argentina; leo@imbiv.unc.edu.ar
 - ⁵ Laboratorio de Investigaciones en Maderas (LIMAD), Universidad Nacional de La Plata (UNLP), La Plata 1900, Buenos Aires, Argentina; jmc@agro.unlp.edu.ar
- * Correspondence: ibanezmoro@unse.edu.ar

Abstract

The objective of this study was to evaluate the effect of fire on the recruitment of six woody species sown at two soil depths. The study area was the western Argentine Chaco region, South America. The selected species were *Aspidosperma quebracho-blanco* Schlecht, *Schinopsis lorentzii* (Griseb.) Engl., *Sarcomphalus mistol* (Griseb.) Hauenschild, *Neltuma nigra* (Griseb.) Hieron, *Senegalia gilliesii* (Steud.) Seigler & Ebinger, and *Vachellia aroma* (Gillies ex Hook. & Arn.) Seigler & Ebinger. Seedling emergence was monitored following experimental burns (EB) in 2017 and 2019 under similar environmental conditions. In 2017, seeds were placed on the litter layer in 2 × 2 m plots; in 2019, seeds were buried at 2 cm depth in 2.5 × 10 m plots. Field emergence was recorded, and viability of non-germinated seeds was tested in the lab. Recruitment was also assessed two years post-EB 2017 in 20 plots (2 × 5 m) under burnt and control conditions. No emergence occurred from seeds on the litter layer, but *S. lorentzii* and *N. nigra* germinated in the laboratory (<7%, significant difference, $p < 0.0001$). All species with buried seeds germinated in the field, with significant differences among species and compared to controls ($p < 0.0027$). Field recruitment revealed regeneration of *A. quebracho-blanco*, *N. nigra*, and *S. gilliesii* in the burnt area, with variations in seedling size and density.

Keywords: seed viability; recruitment; experimental burns; woody species; dry forest



Academic Editor: Giorgos Mallinis

Received: 2 June 2025

Revised: 25 August 2025

Accepted: 26 August 2025

Published: 31 August 2025

Citation: Ibañez Moro, A.V.; Borghetti, F.; Galetto, L.; Cellini, J.M.; Bravo, S.J. Recruitment of Dry Tropical Woody Species After Fire: Germination Phase and Seedling Establishment. *Forests* **2025**, *16*, 1390. <https://doi.org/10.3390/f16091390>

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1. Introduction

The dry tropical and subtropical forests are the world's most threatened natural areas by anthropogenic perturbations and climate change [1]. Fire frequency is increasing across different continents, driven by persistent droughts, heat waves, and deforestation, with alarming changes in forest structure, biodiversity, and provision of ecosystem services [2,3]. The persistence of these valuable ecosystems requires integrative research that explores

seed biology and the effects of fire on seed germination and recruitment of plant species to address conservation and sustainable management strategies [4,5].

Fire can induce seed mortality through heat shock [6] but also may promote germination by breaking physical dormancy [7] or through the release of compounds from burnt biomass, such as ash and smoke [8]. Plants develop different adaptive strategies to establish and maintain populations in fire-disturbed environments, such as thick bark to resist the heat shock on tissues and organs, soil seed bank (SSB) formation to recruit after fire, and delayed germination to reduce germination failure under adverse conditions [9]. Seed recruitment is a key ecological process to maintain genetic diversity, vegetation structure, and population resilience in native species [10]. The post-disturbance recruitment also depends on seed functional traits such as size, mass, dormancy, seed bank persistence, and tolerance of seedlings to growth in altered environments [5,11].

The soil seed bank (SSB) represents reservoirs of viable seeds for recruitment of new individuals [12,13], under natural conditions or after disturbance. The seed-to-seedling transition represents a highly selective bottleneck in the life cycle of native plant species. This feature is exacerbated in semiarid fire-prone environments due to high temperatures, water deficit, changes in irradiance levels, and increased predation or seed removal [14]. Plant species from arid and semiarid environments have seeds with morphophysiological traits such as physical dormancy and protective structures (e.g., hard seed coats, woody endocarps), which are adaptations to selective pressures such as predation, fire, drought, and seasonality [15–17]. These functional traits also enhance fire resistance through mechanisms such as insulation provided by indehiscent fruits [18] or thicker seed coats, which regulate physiological tolerance to environmental changes caused by fire [19].

Fire is a key factor in the plant communities' dynamics from semiarid, arid, and temperate environments because of the pulses of fuel accumulation and desiccation [20], and its action can alter the SSB by direct combustion of their components. In addition to natural factors, land use patterns may also affect SSB formation and its persistence in changing environmental sceneries [21,22]. Like other biomes of the world, the Chaco region is experiencing climatic and land use changes, with increasing fires with extreme behavior [3]. Previous studies under laboratory conditions have shown that seeds of native woody species from the Chaco region differ in thermal shock responses under controlled conditions. For example, seeds of some species are considered heat-tolerant when thermal shock does not significantly affect the germination, and this behavior has been attributed to protective fruit structures or their hard seed coats, while others are categorized as sensitive to heat shock [16]. However, studies with post-fire recruitment evaluation under natural conditions are still scarce in the semiarid Chaco forests.

Experimental burns have been broadly used to understand the role of fire in plant regeneration, since this methodology allows for evaluating the short- to medium-term recruitment after this disturbance. These research lines have been conducted mainly in fire-adapted ecosystems, such as Mediterranean systems [23], and in fire-sensitive ecosystems, such as Brazil's Cerrado [17,24], with remarkable differences among biomasses and species.

According to previous studies [25,26], post-fire regeneration of native species in the Central Chaco, Argentina, seems to depend mainly on sprouting strategies, since there is low similarity between the standing vegetation and SSB composition [27]. This trend has also been observed in other semiarid regions [13,28,29], suggesting that woody species differ markedly in their ability to form SSBs and to persist after fire. A previous study [11] assessed the aptitude of six native woody species from the Chaco region to form transient SSBs in native forest, suggesting that seed size and shape may influence burial capacity and protect seeds against heat shock. This aptitude could be critical in SSB persistence, and for recruitment under increasing fire frequency or intensity. Additionally, another study [22]

found that combinations of different land management practices could affect the soil seed density of the most representative woody species. Such information is crucial for species conservation, restoration of burned areas, and development of sustainable forest management plans. However, despite increasing interest in fire ecology, detailed studies on seed germination and survival after fire in semi-arid tropical forests, such as the Chaco, remain notably scarce [13,29]. This knowledge gap could limit our understanding of recruitment mechanisms in ecosystems increasingly affected by natural and anthropogenic fires.

This study evaluated the post-fire germination and field recruitment of six forest species after experimental burns. All these species form transient SSBs in areas disturbed by fires and mechanical vegetation removal methods, and the SSB sizes have been evaluated in previous studies [11]. We considered the following hypotheses: (a) Species have seeds with different burial aptitudes, mainly determined by the seed mass and dispersal unit shape, which influence the maintenance of seed viability after fire and recruitment probabilities in burnt areas [29–31]. (b) Forest disturbances such as fire, logging, and roller chopping create unfavorable environments for recruitment due to causing more severe abiotic and biotic conditions [32]. We predicted that fire-tolerant species with seed traits that allow them to be buried in the soil would have greater recruitment in fire-disturbed forests, whereas fire-sensitive species with seed traits that prevent soil burial would face recruitment limitations [11].

2. Materials and Methods

2.1. Study Area

The study area was located in the Western Chaco, Argentina (28°03' S, 64°15' W), (Figure 1). The region presents a semiarid seasonal climate, defined as monsoonal [33], with cold and dry winters. Daily temperatures vary from −15 to −10 °C and 38 to 40 °C in spring and summer, respectively [33]. The annual precipitation is 574 mm, concentrated in the wet season from October to March [34]. The dry season extends from April to September. The fire season matches the dry season, accompanied by hot winds from the north and northeast, which promote the occurrence of fires [33]. More severe fires occur at the end of the dry season, coinciding with the increase in spring temperatures and the prolonged accumulation and drying of fuels [33]. Fire has been used in the Chaco region since pre-Columbian times to improve the quality of pastures for livestock, control the invasion of woody in cattle-raising areas, and reduce or control the shrub layer in silvopastoral systems [33]. The typical vegetation of the semiarid Chaco region is a seasonal xerophytic forest, which is generally characterized by three strata. The open canopy is dominated by *Aspidosperma quebracho-blanco* Schlecht and *Schinopsis lorentzii* (Griseb.) Engl. The intermediate tree layer includes *Sarcomphalus mistol* (Griseb.) Hauenschild and *Neltuma nigra* (Griseb.) Hieron, while the lower stratum is mainly composed of thorny shrubs and subshrubs such as *Vachellia aroma* (Gillies ex Hook. & Arn.) Seigler & Ebinger, *Senegalia gilliesii* (Steud.) Seigler & Ebinger, *Condalia microphylla* Cav., *Castela coccinea* Griseb., *Monteverdia spinosa* (Griseb.) Biral, *Celtis ehrenbergiana* (Klotzsch) Liebm., and *Ximenia americana* L., along with several non-thorny species such as *Atamisquea emarginata* Miers ex Hook. & Arn. and *Justicia* spp. [18]. The soil is classified as Entic Haplustoll, with a texture composed of 43% sand (2000–53 µm), 49% silt (53–2 µm), and 8% clay (<2 µm) [35].

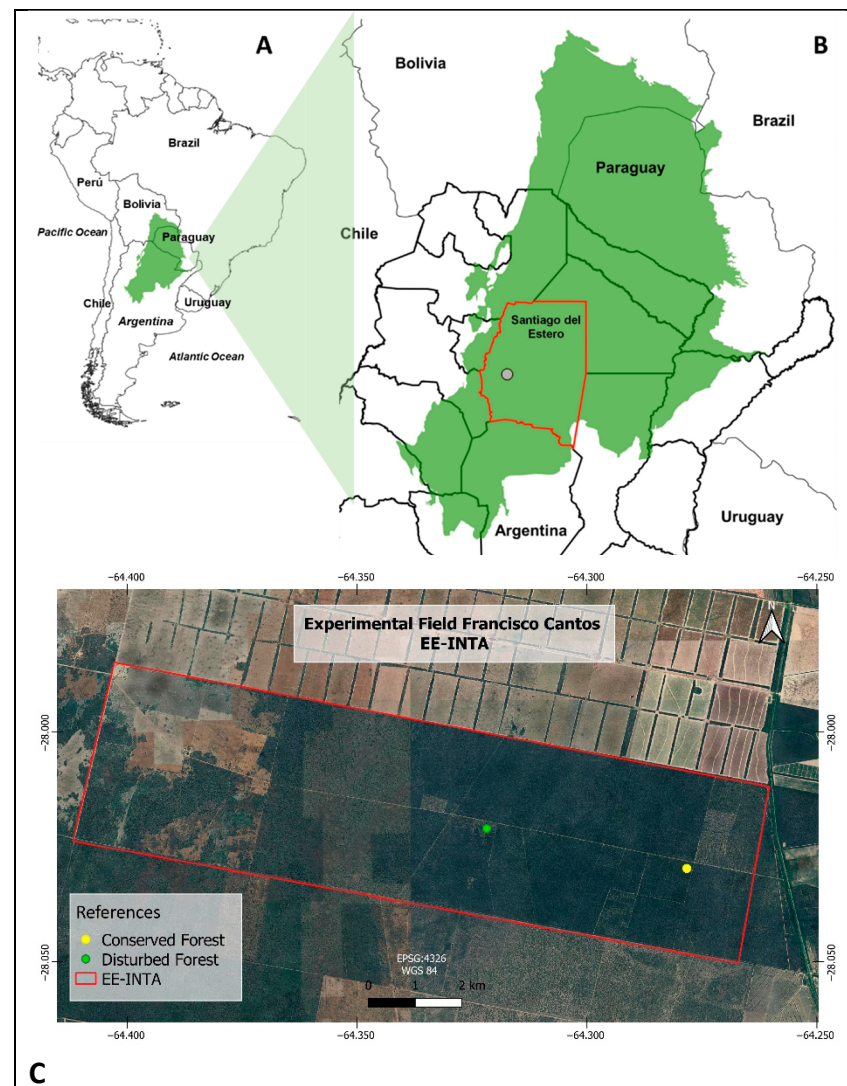


Figure 1. (A) The Chaco biogeographic region is shown in green. (B) The province of Santiago del Estero, situated within the Chaco region, is indicated by a red outline. (C) The research area and sampling location are at the Francisco Cantos Experimental Station, part of the National Institute of Agricultural Technology (INTA).

2.2. Sampling Sites

To analyze the germination capability of seeds from six woody species under natural conditions, we selected two sampling sites located within the Campo Experimental Francisco Cantos ($28^{\circ}03' S$, $64^{\circ}15' W$), belonging to the Instituto Nacional de Tecnología Agropecuaria (INTA), situated 28 km from the capital city of the province of Santiago del Estero. Within the experimental ranch, two forest sites with different land use histories were identified using satellite images, references, and field surveys [11]. The sampling sites were identified as follows: (a) disturbed forest—subjected to uncontrolled fires and mechanical treatments for partial reductions in the shrub layer (DF); (b) conserved forest (CF)—representing a reference condition, with very limited human intervention in the past four decades [36]. The distance between the two sites was approximately 4.4 km. For the experimental burns, the forest site with fire and rolling (DF) was selected because of the permits required to conduct these experiments in natural environments.

2.3. Species Selected and Seed Collection

Six woody species were selected for this study: *A. quebracho-blanco*, *S. lorentzii*, *S. mistol*, *N. nigra*, *S. gilliesii*, and *V. aroma*. These represent different forest strata of native forests in the Western Chaco [37] and show a significant variability in seed traits [11,38]. Fruits and seeds were collected in the CF area from at least ten individuals of each selected species [39,40] during the reproductive seasons of 2017 and 2019. Selection criteria to collect seeds from individual plants included mature individuals with a healthy appearance and no signs of pathogen attack [16]. The fruit collection was adjusted to the phenology calendar of each selected species [41]. The material was stored for between 1 and 7 months in paper bags under controlled conditions [18], free of impurities, and refrigerated at $12^{\circ} \pm 2^{\circ} \text{C}$ to prevent insect attacks [16] until the start of the experiments.

2.4. Seed Water Content (Cw) and Viability

The seed water content and viability were assessed prior to the trials. To determine the seed water content (Cw), two independent samples of 60 seeds for each species were weighed on a digital scale with a precision of $\pm 0.001 \text{ g}$. Then, the samples were placed in a drying oven ($103 \pm 3^{\circ} \text{C}$) for 24 h, after which the samples were allowed to cool and were weighed again [42]. The water content was calculated using Equation (1). The results obtained are expressed as percentages of moisture [6,43].

$$Cw = [(Mf - Md) (Mf)^{-1}] \times 100 \quad (1)$$

where Mf is the fresh mass (fresh weight) and Md is the dry mass (dry weight) of the seeds.

The initial viability of the seed lots for each selected species was evaluated using the tetrazolium (TZ) test [42]. Four replicates of 25 seeds per species were tested. Previously, seeds were hydrated in distilled water for 24 h at 30°C , then immersed in a 1% tetrazolium (TZ) solution and incubated in darkness at 30°C for an additional 24 h [24,42]. After incubation, each seed was bisected with a scalpel to expose the embryo and assess the staining pattern. Embryos that stained red or pink were classified as viable, while unstained embryos were considered non-viable, based on topographic staining patterns [44,45].

2.5. Characterization of Experimental Burn

In October 2017 and 2019, two experiments using experimental burns (EBs) were conducted at the DF site under similar environmental conditions, during the fire season in the Chaco region, following local prescribed burning guidelines for this area [34]. The burns took place at the end of the dry season, when high temperatures and prolonged drought promote fuel accumulation and desiccation, and the fine fuel moisture content is typically low ($<30\%$) [33]. The first one was in 2017, when six $2 \text{ m} \times 2 \text{ m}$ plots (one for each species) were randomly established, and seeds were located in metallic mesh cells at litter level; the second one was in 2019, when a $2.5 \text{ m} \times 10 \text{ m}$ plot was delimited and excavated at 2 cm depth to metallic boxes containing soil and seeds of the studied species (4 replicates of each one), which were then covered with soil. Control replicates for each species were set in nearby unburned plots at the DF site to compare the effects of the burns. Before the EB, the fine fuel load for igniting and spreading surface fires was assessed. In plots with insufficient fuel load, an additional load of this fuel was added to each experimental plot to achieve $\cong 4000 \text{ kg/ha}$, considered the minimum required to ignite and sustain fire [34,46]. In both experiments, fire ignition was carried out with a drip torch, following strict regional protocols [33].

Before each EB, seeds of selected species were either disposed over the leaf litter (2017) or buried at a 2 cm soil depth (2019). In 2017, four replicates of 25 seeds or fruits (referred to as propagules) of each species were placed in 20 cells made of fine metal and distributed

over the leaf litter lightly covered with mulch. These meshes prevented seed loss due to runoff and predation after the burns. For *N. nigra*, both isolated seeds and segments with endocarp were tested, whereas for *S. mistol* and *S. lorentzii*, endocarps and samaras were tested, respectively. For *A. quebracho-blanco*, closed capsules were used to assess heat-induced fruit opening and seed release. In 2019, EB was conducted to evaluate its effects on buried propagules. Four replicates of 25 propagules of each species were placed in heat-resistant trays, buried 2 cm deep, and covered with 2 cm of soil. *A. quebracho-blanco* was not included due to its inability to be buried under natural conditions. Unburned controls were set up for each species in plots similar to the burned ones.

The meteorological conditions during EB dates were monitored every 30 min (air temperature (°C), air relative humidity (%), wind speed (Km h⁻¹), and wind direction for fire control) [34]. The variable used to characterize fire behavior [46] during the burns were:

Fire intensity (I): Defined as the energy released during the burn, estimated using flame length with the Formula (2) [47]:

$$I \text{ (kWm}^{-1}\text{)} = 259.83 \times LL^{2.174} \quad (2)$$

where LL is the average flame length, visually estimated by two independent observers; greater LL indicates higher fire intensity [46].

Residence time (II): Recorded as the time for the fire to traverse the entire plot (tt, minutes) and until the fuels were fully burned (tf, minutes); longer residence times correlate with more severe effects on vegetation and soil [48].

2.6. Experimental Evaluation of Fire Effects on Seed Germination at Two Soil Depths

Post-experimental burn (EB) evaluations were carried out in two phases, in both burned and unburned (controls) plots. In 2017, the first phase involved monitoring seedling emergence in the field every two weeks for nine months. After this period, ungerminated hard propagules were extracted from grids and transported to the lab for germination tests (second evaluation phase). In 2019, the evaluation period was extended for 12 months after EB, and the remaining propagules were extracted and transported to the lab for germination tests. Before this, the propagules were manually scarified and placed in Petri dishes on moistened filter paper for germination. These sequential analyses allowed us to determine the number of ungerminated but viable seeds. To accurately identify the emerging seedlings, preliminary trials were conducted for their identification, and references were consulted whenever necessary [49]. The purpose of this post-burn scarification treatment was to confirm whether the seeds were still viable. The Petri dishes were placed in germination chambers at 30 °C with a 12/12 h light cycle. Samples were evaluated every two days for 15 days [50].

2.7. Field Assessment Recruitment

Two years after the 2017 EB, the field recruitment of the six selected woody species was again evaluated within both the DF and CF plots as the controls, using 20 plots of 2 × 5 m randomly selected in each sampling site. Only the seedlings originated from propagules (without resprouting at the base of the plant), with a base diameter (BD) > 1 mm and a height < 50 cm, were identified and measured. These size thresholds correspond to established regeneration according to studies for the Chaco region [49,51]. These data allowed us to obtain the average seedling diameter, the average seedling height, and the density of seedlings per hectare.

To assess the possible effects of tree occupation on species regeneration, the total and species-specific basal area (BA) density (m²·ha⁻¹) (K = 3) values were estimated for the CF

and DF forests using Bitterlich's angular count method [52]. This method is considered precise and unbiased across a range of spatial patterns and diameter distributions [53].

2.8. Data Analysis

The initial viability of the seeds from both years was compared through a one-way ANOVA with Tukey's post hoc tests. Differences were considered significant at $p < 0.05$. Data about germination percentages (seedling emergence) in the field were analyzed considering four treatments: propagules placed on the leaf litter and exposed to fire (PL-F), propagules placed on the leaf litter without fire (control) (PL-C), propagules buried in the soil and exposed to fire (PI-F), and propagules buried in the soil without fire (control) (PI-C). General linear models (GLM) were used to assess post-fire germination percentages between species, under different treatments, with fire as the main fixed factor. Since zeros were not excessive, a standard GLM was adopted instead of zero-inflated models. This model was considered for heterogeneity of variances, and the model selection was based on Akaike's information criterion (AIC). The intraspecific differences under the different treatments were assessed using the Kruskal–Wallis non-parametric test, due to the presence of zero germination, which makes using a general linear model difficult. Two models were performed, one for the seed germination percentage (seedling emergence) based on evaluation under field conditions (G1: germination one), and another for the germination percentage of seeds extracted from field samples with mechanical scarification applied under laboratory conditions (G2: germination two). In both models, the germination percentage of seeds was evaluated based on fire treatments and controls (PL-F, PL-C, PI-F, and PI-C).

Field recruitment data of the studied species in CF and DF were collected two years after the 2017 experimental burn (EB) (the relative abundance of the native woody species, basal area of trees per treatment, basal area of standing trees, height and density of seedlings, and proportion of each species based on total number of seedlings) were analyzed using a one-way ANOVA with Tukey's post hoc tests. Differences were considered significant at $p < 0.05$. Statistical analyses were performed using InfoStat v.2017 [54].

3. Results

3.1. Seed Water Content and Viability

The seed water content (Cw) and seed viability values for the six species under study are shown in Table 1. The seed water contents varied from 5.8% in *S. lorentzii* to 11.2% in *S. gilliesii*. Only *S. mistol* and *N. nigra* showed significant differences in the seed viability percentages among years ($p = 0.0047$ and 0.0036 , respectively). The percentages of seed viability for *V. aroma* and *N. nigra* were the highest among the studied species, but interannual variability in seed viability was significant only for *N. nigra* and *S. mistol*, without a clear tendency among years (Table 1).

3.2. Experimental Burns

The experimental burns (EB) conducted in 2017 and 2019 were of medium intensity, with average flame lengths (mean $\pm$ SD) of 1.51 ± 0.30 m and 1.6 m, respectively (Table 2). The meteorological conditions during the burns and data about fire behavior are shown in Table 2. The average fire duration across the experimental plots was 78 ± 32 s.

After 2017 EB, we did not observe seedling emergence for any of the studied species, neither in the fire treatments (PL-F) nor in the controls (PL-C) (Phase 1) (Figure 2a). Seed losses were primarily due to both carbonization and post-fire seed predation. Seeds damaged by carbonization ranged from 28% for *V. aroma* to 100% for *A. quebracho-blanco*, and seeds damaged by predation ranged from 13% for *S. mistol* to 34% for *N. nigra* with

endocarp (Appendix A). The results of germination in phase 2 are shown in Table 3 (PL-F; PL-C).

Table 1. Average seed water content (Cw; mean $\pm$ SD, 2017) and seed viability (mean $\pm$ SD) values of six native woody species from the semi-arid Chaco of Argentina, corresponding to different harvest years. Different letters indicate significant differences among means (Tukey test; $\alpha = 0.05$).

Species	Cw (%)	Viability (%)	
		2017	2019
<i>Aspidosperma quebracho-blanco</i>	6.3 $\pm$ 0.4	21.0 $\pm$ 9.4	-
<i>Schinopsis lorentzii</i>	5.8 $\pm$ 5.3	33.0 $\pm$ 12.3 a	44.0 $\pm$ 8.6 a
<i>Sarcomphalus mistol</i>	9.5 $\pm$ 0.1	28.0 $\pm$ 3.2 a	64.0 $\pm$ 8.6 b
<i>Neltuma nigra</i>	7.4 $\pm$ 2.8	86.2 $\pm$ 4.0 b	74.0 $\pm$ 20.7 a
<i>Senegalia gilliesii</i>	11.2 $\pm$ 0.1	37.0 $\pm$ 14 a	49.0 $\pm$ 15.7 a
<i>Vachellia aroma</i>	8.5 $\pm$ 0.3	80.0 $\pm$ 3.2 a	89.0 $\pm$ 5.0 a

Table 2. Meteorological conditions and flame lengths were recorded during the experimental burns conducted in the 2017 and 2019 fire seasons in the semi-arid Chaco region of Argentina.

Year of the Burns	Date and Hour of Burns	Air Temperature (°C)	Air Relative Humidity (%)	Wind Speed (Km h ⁻¹)	Wind Direction	Mean Flame Length (m)	Intensity (kW m ⁻¹)
2017	10 October (between 8:15 and 10:35)	19.5–27	51–69	2–4.5	east-northwest	1.51 $\pm$ 0.30	612.32 $\pm$ 336.19
2019	14 November (between 9:30 and 11:50)	32	40	4.5	east-northwest	1.6	721.88

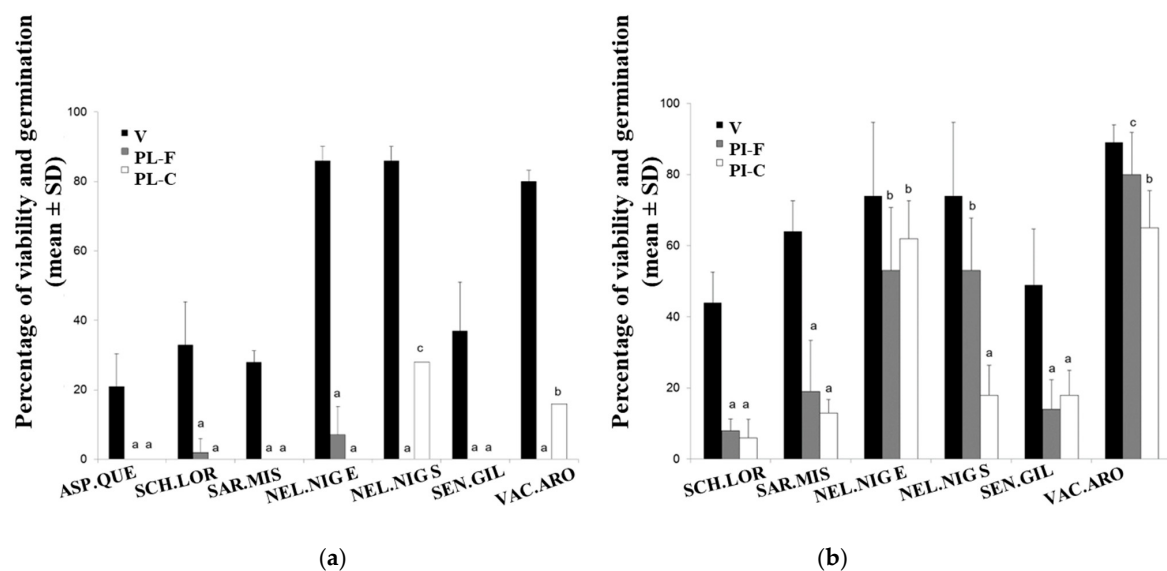


Figure 2. Percentage of viability (V) and accumulated germination (mean $\pm$ SD) of seeds from six woody species native to the semi-arid Chaco of Argentina, subjected to experimental burning treatments: (a) experimental burn 2017, with propagules placed over the litter exposed to fire (PL-F) and their respective controls in unburnt plots (PL-C); (b) experimental burn 2019, with propagules buried in the soil and exposed to fire (PI-F) and their respective controls (PI-C). APS.QUE: *Aspidosperma quebracho-blanco*; SCH.LOR: *Schinopsis lorentzii*; SAR.MIS: *Sarcomphalus mistol*; NEL.NIG E (with endocarp): *Neltuma nigra* with endocarp; NEL.NIG S (seed): *N. nigra* with seed; SEN.GIL: *Senegalia gilliesii*; VAC.ARO: *Vachellia aroma*. Different letters indicate significant differences among treatments within each species, as determined by a general linear model (GLM), followed by Fisher's LSD test ($\alpha = 0.05$).

Table 3. Germination percentages ($\pm$ standard deviation) under lab conditions of the seeds germinated under field conditions after EBs in 2017 and 2019. Seeds were scarified (G2 phase) to check viability by germination under lab conditions. An analysis was performed using the Kruskal–Wallis test ($\alpha = 0.05$).

Species	Average Germination Percentage (G2) ($\pm$ SD)							
	2017				2019			
	PL-F		PL-C		PI-F		PI-C	
		n		n		n		n
<i>Aspidosperma quebracho- blanco</i>	0 $\pm$ 0	0	0 $\pm$ 0	0	-	-	-	-
<i>Schinopsis lorentzii</i>	0.50 $\pm$ 1.00	2	0 $\pm$ 0	0	0 $\pm$ 0	0	0 $\pm$ 0	0
<i>Sarcomphalus mistol</i>	0 $\pm$ 0	0	0 $\pm$ 0	0	0 $\pm$ 0	0	0 $\pm$ 0	0
<i>Neltuma nigra</i> with endocarp	1.75 $\pm$ 2.06	7	0 $\pm$ 0	0	10.50 $\pm$ 10.13	42	9.00 $\pm$ 2.94	36
<i>Neltuma nigra</i> seed	0 $\pm$ 0	0	7 $\pm$ 0	7	2.00 $\pm$ 0.82	8	3.50 $\pm$ 1.29	14
<i>Senegalia gilliesii</i>	0 $\pm$ 0	0	0 $\pm$ 0	0	0 $\pm$ 0		0 $\pm$ 0	
<i>Vachellia aroma</i>	0 $\pm$ 0	0	4.00 $\pm$ 0.00	4	14.75 $\pm$ 3.20	59	11.25 $\pm$ 3.40	45

The accumulated post-fire germination percentages (considering both field germination and laboratory germination) varied significantly ($p < 0.001$) among species in the EB of 2017. Only two species with seeds protected by fruit structures and disposed on leaf litter showed post-fire germination—*S. lorentzii* and *N. nigra*—and only two species germinated under control conditions showed the same in phase 2—*N. nigra* and *V. aroma*. In all cases, the germination percentages were low considering the average viability of the seed lots, and delayed germination (approximately nine months after EB) was observed in *S. lorentzii* and *N. nigra*. Significant differences in germination percentages were observed for in *N. nigra* and *V. aroma* compared to controls ($p < 0.0001$; $p = 0.0082$; respectively) (Figure 2a).

During the EB of 2019, the temperatures above ground ranged between 115 °C and 320 °C, while the temperatures at 2 cm depth in the soil varied between 27 °C and 67 °C. The mulch was consumed superficially. In this EB, there was recruitment in the field for five species (phase 1). Only *N. nigra* and *V. aroma* showed germination in phase 2 (Table 3). For the accumulated germination as a percentage for each species under the different treatments, PI-F and PI-C showed significant differences ($p = 0.0027$) (Figure 2b). *A. quebracho-blanco* was not included in this trial, considering their seeds are not prone to be buried and always remain over the fallen litter (Figure 2b). *V. aroma*, *N. nigra*, *S. lorentzii*, and *S. mistol* showed higher accumulated germination in the burnt plot than control plots but differences were significant only in the two first species (80 and 53%, respectively) ($p = 0.0249$ and $p = 0.0002$). *Neltuma nigra* seeds included in endocarps and *S. gilliesii* showed the opposite tendency, with higher germination in the control plot than in the burnt plots (62 and 18%, respectively), but the differences were not significant. *S. lorentzii* and *S. mistol* presented the lowest germination percentages (<20%), with almost one-third of the average seed viability percentages determined in their seed plots.

The germination percentages of phase 1 after the EB of 2019 showed the responses for the propagules to fire under field conditions; higher germination percentages were observed for *N. nigra* and *V. aroma* in burnt plots than in control plots, although significant differences were found only for the first species. However, seeds of *N. nigra* within the endocarp showed higher germination in the control plot (Figure 3).

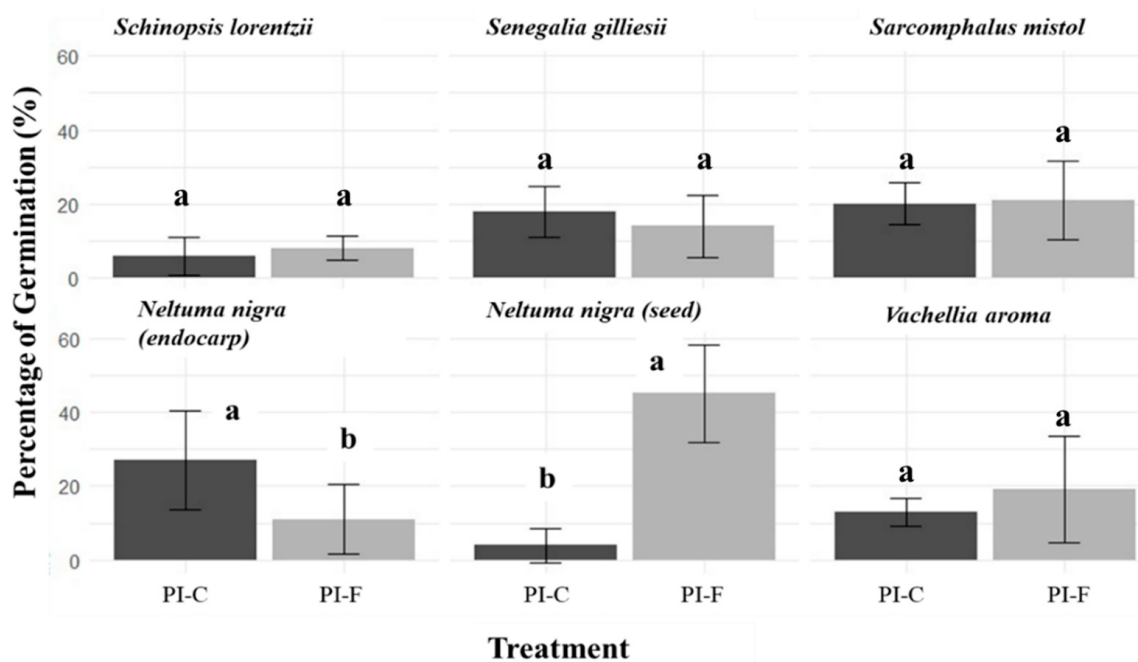


Figure 3. Germination percentages of seeds from five native species of Chaco region forests, Argentina. The values correspond to phase 1 of field germination after EB 2019 with buried seeds. Ref.: PI-F: propagules incorporated into soil and exposed to fire; PI-C: propagules incorporated into soil without experimental burns. Different letters indicate significant differences among means according to the Kruskal–Wallis test ($\alpha = 0.05$).

The results of germination in phase 2 corresponding to 2017 and 2019 EBs are shown in Table 3, indicating that *S. lorentzii* (2017), *N. nigra* (2017 and 2019), and *V. aroma* (2019) remained ungerminated yet viable for nine and twelve months, respectively, after fires in the burnt plots. The mechanical scarification stimulated germination in *N. nigra* ($10.50 \pm 10.13\%$) and *V. aroma* ($14.75 \pm 3.20\%$). In PI-C, seeds of *N. nigra* with endocarp and *V. aroma* exhibited lower germination than in PI-F, whereas seeds of *N. nigra* with the endocarp removed showed a higher germination percentage in PI-C (Table 3).

3.3. Field Recruitment Two Years After an Experimental Burn

Two years after the EB of 2017, a total of 346 seedlings of ten native woody species of the Chaco region forest, belonging to eight botanical families, were recorded in the field: 223 in CF and 123 in DF (Table 4). Only four of the six species selected for this study were registered in these field surveys: *A. quebracho-blanco*, *S. gilliesii*, *S. lorentzii*, and *N. nigra* (Figure 4). The first two species were recorded in both forest types, while the third was found only in CF, and the last one only in DF (Table 4). There was no recruitment of *S. mistol* or *V. aroma* in either forest type. Other native woody species recorded both CF and DF, namely *Atamisquea emarginata*, *Condalia microphylla*, *Schinus fasciculatus*, and *Celtis ehrenbergiana*, whereas *Monteverdia spinosa* and *Ximenia americana* were recorded only in CF (Table 4). The relative abundance levels of seedlings varied among forest types, with *S. gilliesii* and *A. quebracho-blanco* exhibiting the highest values in the DF forest. Regeneration in the disturbed forest was dominated by *A. quebracho-blanco* seedlings.

Table 4. Relative abundance of seedlings of woody species in the semi-arid Chaco forests with different disturbance regimes, namely the conserved forest (CF) and forest with fire and rolling (DF). Ref: (*): study species; (**): recorded species common to both sites; (-): absences.

Species	Family	Relative Abundance %	
		CF	DF
<i>Senegalia gilliesii</i> *,**	Fabaceae	34	4
<i>Atamisquea emarginata</i> **	Capparaceae	9	5
<i>Condalia microphylla</i> **	Rhamnaceae	2	10
<i>Monteverdia spinosa</i>	Celastraceae	13	-
<i>Schinus fasciculatus</i> **	Anacardiaceae	4	6
<i>Celtis ehrenbergiana</i> **	Cannabaceae	9	6
<i>Aspidosperma quebracho-blanco</i> *,**	Apocynaceae	26	63
<i>Neltuma nigra</i> *	Fabaceae	-	6
<i>Ximenia americana</i>	Olacaceae	1	-
<i>Schinopsis lorentzii</i> *	Anacardiaceae	2	-



Figure 4. Recruitment seedlings: (A) *Senegalia gilliesii*; (B) *Aspidosperma quebracho-blanco*.

3.4. Tree Canopy in Forest and Regeneration

The CF and DF did not show statistically significant differences in total basal area (m^2/ha^1) (Appendix B). The mature individuals of canopy species, *A. quebracho-blanco* and *S. lorentzii*, and intermediate forest stratum species, *S. mistol* and *N. nigra*, were present in both forest types, with no significant differences in the basal areas among types of forests. Other characteristic species of the Chaco forests, such as *Opuntia* sp. and *Parkinsonia praecox*, were found only in CF (Appendix B).

Height (H), average basal diameter (ABD), and seedling density (SD) values of *A. quebracho-blanco* differed significantly between forest types, with a higher, lower-sized seedling density in the DF than in the CF forest. *S. gilliesii* seedlings were recorded in both forest types (CF and DF), with a higher seedling density in the CF ($p = 0.0064$) (Table 5) (Figure 3). On other hand, *S. lorentzii* seedlings were absent in the DF, but *N. nigra* seedlings were only present in this forest type, with a high seedling density (Table 5). Other studied species did not show significant differences in these seedling variables (Table 5).

Table 5. Height, diameter at the base, and density of seedlings of native woody species from Chaco forests, under different treatments. CF: conserved forest (without recent disturbances, considered as control); DF: disturbed forest with rolling chopping and experimental burns; H: seedling height (cm); ABD: average basal diameter of seedlings (mm); SD: seedling density (individuals/ha). Average values $\pm$ standard error. Different letters indicate significant differences among means (Tukey test; $\alpha = 0.05$). Fisher's F-statistic values and corresponding error probability (p) are indicated. Dots (.) indicate missing data or measurements not available.

Species		Treatment		F	p
		CF (n = 20)	DF (n = 20)		
<i>Aspidosperma quebracho-blanco</i>	H	9.9 $\pm$ 1.2 b	5.6 $\pm$ 0.9 a	7.07	0.0012
	ABD	2.4 $\pm$ 0.2 b	1.7 $\pm$ 0.1 a	7.6	0.0094
	SD	1351 $\pm$ 243 a	6899 $\pm$ 1565 b	12.2	0.0012
<i>Schinopsis lorentzii</i>	H	3.8 $\pm$ 1.6	.	.	.
	ABD	0.7 $\pm$ 0.2	.	.	.
	SD	83 $\pm$ 33	.	.	.
<i>Neltuma nigra</i>	H	.	3.7 $\pm$ 1.5	.	.
	ABD	.	0.4 $\pm$ 0.2	.	.
	SD	.	735 $\pm$ 302	.	.
<i>Senegalia gilliesii</i>	H	23.3 $\pm$ 3.0 a	21.0 $\pm$ 10.4 a	0.12	0.7375
	ABD	4.3 $\pm$ 0.3 a	4.5 $\pm$ 2.1 a	0.03	0.8668
	SD	1715 $\pm$ 366 b	473 $\pm$ 255 a	8.33	0.0064
Total	H	6.89 $\pm$ 0.99 b	3.30 $\pm$ 0.99 a	5.73	0.0178
	ABD	1.41 $\pm$ 0.18 b	0.74 $\pm$ 0.21 a	5.96	0.0157
	SD	787.50 $\pm$ 264.4 a	2027.28 $\pm$ 264.4 b	10.99	0.0010

4. Discussion

Our results represent a significant improvement in understanding of the germination behavior and post-fire recruitment of native woody species in the semi-arid Chaco of Argentina. The relative position of propagules in the substrate (soil or litter) significantly influenced both seed viability and seedling emergence. Two years after the EB, recruitment of some studied species was still observed in the field. The results suggest that morphological traits of dispersal units, their burial potential in the soil, and seed quality could regulate the sexual regeneration in burned areas.

The absence of recruitment after the EB of 2017 for all studied species with propagules placed over the litter indicated their low tolerance to the high temperatures generated during a fire, and also the potential effects of seed predation and pathogen attacks on their recruitment potential. Despite flame lengths recorded during the EBs of 2017 suggesting fires of intermediate intensity [46], carbonization of seeds and fruits was observed in the litter. The maintenance of viability observed later under lab conditions (phase 2) for a low number of ungerminated seeds of *S. lorentzii* and *N. nigra* could be considered negligible. Except for *N. nigra* and *V. aroma*, the absence of viability observed among the ungerminated seeds of most studied species in the controls also suggests that the impacts of low seed quality or drastic desiccation in litter on the potential recruitment of these species (Table 3). These species exhibited significant differences in seed viability between the 2017 and 2019 harvests, consistent with results reported by [55] for native woody species from the Argentine Chaco region. These authors attribute these differences to particular environmental conditions such as desiccant winds or abnormal rains or temperatures during reproductive phases. The lack of viable seeds for *A. quebracho-blanco*, *S. mistol*, and *S. gilliesii* in phase 2 of the 2017 EB could indicate additive effects of low initial viability of their seed lots, and unfavorable environmental conditions in post-fire environments (e.g., wide thermal amplitudes and high radiation levels, soil desiccation) could affect seed

viability under field conditions [5]. On the other hand, the low germination percentage (<7%) observed for propagules of *S. lorentzii* and *N. nigra* over the litter in phase 2 could be attributed to their protective pericarps or hard seed coats. Both traits have been related to physical dormancy, which may likely enhance tolerance to dehydration during flame exposure or seedling establishment [24]. A previous study [18] established physical dormancy in these species attributed to ligneous fruit walls and hard seed coats, respectively, by experiments with thermal shock in the laboratory. The absence of germination in *A. quebracho-blanco*, *S. lorentzii*, *S. mistol*, and *N. nigra* endocarps in control plots suggests that recruitment of these species under field conditions may be limited by the harder physical conditions [10]. The interannual variation in seed viability observed could be attributed to climate variability and plague or pathogen incidence during the reproductive phases. In addition to thermal tolerance, studies have shown that fire-induced changes in abiotic and biotic factors affect recruitment in burned areas due to biomass loss and predation [5,56]. Environmental factors post-disturbance, such as high desiccation risk [57], low water availability for imbibition [58], and increased predation rates [50], may limit recruitment.

The recruitment percentages observed for most of the studied species after the 2019 EB indicate that the soil protected the propagules from the high temperatures reached during the fire [24]. Temperatures recorded in the soil during combustion, as recorded in our study, were markedly lower than temperatures registered at the litter level; these findings aligned with results obtained in other studies, such as in the Brazilian Cerrado [17,59], suggesting that burial could help the maintenance of seed viability in areas subjected to fire. Heat tolerance thresholds for plant tissues typically sit around 60 °C but depend on the tissue type, hydration level, genetics, and duration of heat exposure [34]. Seeds of several woody species do not tolerate temperatures exceeding 100 °C, as was observed in lab heat shock tests [16,60]. Species with lower heat tolerance experience higher seed mortality and reduced seed bank viability post-fire [61]. The high accumulated germination percentages in *N. nigra* and *V. aroma* in burned plots suggest some level of germination stimulation within the recorded temperature range, since they were significantly higher compared to their respective controls (Figure 2b). This germinative behavior observed in the field after EBs exhibits some differences compared to propagule responses to heat shock in the laboratory. Based on their responses to different experimental heat shock temperatures, Ref. [18] assigned the category “sensitive” to *N. nigra* and “tolerant” to *V. aroma*. However, in our study, both species showed a positive response to fire when seeds were buried in soil.

Seed distribution within the soil profile is related to seed traits influencing burial potential [11]. Species with larger seeds or softer seed coats are more susceptible to fire due to limited burial [14]. According to [11], species such as *A. quebracho-blanco*, *S. lorentzii*, and *S. gilliessi* have shape indexes that can limit their burial, making them more sensitive to heat shocks in fire-prone areas. Conversely, some Fabaceae species such as *N. nigra* and *V. aroma* have the potential to be buried in the soil, increasing their potential for fire tolerance. Results obtained in this study corroborate the important role of seed burial for the fire tolerance of seeds and fruits. Our results support the hypothesis that propagule distribution within soil profiles significantly influences post-fire seedling survival and establishment.

Field Recruitment Two Years After an Experimental Burn

Recruitment studies of woody species in forests with different disturbance histories are mandatory for designing forest management plans [62]. In our study, the recruitment observed for four of the six species analyzed in the CF and DF reflects the challenges of seed-based establishment in semi-arid environments [29]. Basal area values observed in the species selected for this study were twice as high as those reported for recovering forests [37]. However, recruitment patterns varied according to disturbance history. This

variation could be attributed to biomass removal due to roller chopping and accidental fires (DF), as well as the recent impact of the 2017 EB [63].

S. lorentzii, the canopy tree species of greatest conservation interest, showed no natural seed regeneration in the DF, suggesting specific germination requirements and seed sensitivity to disturbances. The woody pericarp arrests seed imbibition [18], which may cause require high moisture levels for germination and successful recruitment [5,36]. The exclusion of disturbances has been identified as a key factor for its regeneration [64,65], which is in line with its low frequency of occurrence in the study area and the size of its SSB in the CF [11].

In contrast, *A. quebracho-blanco* was the only species of the canopy that showed seed-based regeneration in the DF. This species exhibited a higher density of seedlings in the DF, although smaller in size (H and ABD). Its seeds can germinate under very low moisture levels, and this process may be facilitated by the potential moisture retention provided by the litter [29]. Efficient dispersal from surrounding areas and rapid response to low-intensity fires [3] may explain its predominance in open sites with recurrent disturbances. However, previous studies reported higher recruitment in protected areas compared to disturbed areas [21,66]. On the other hand, Ref. [66] reported a rapid positive population response of *A. quebracho-blanco* to low-intensity fires, provided it is accompanied by grazing exclusion.

The absence of recruitment for *S. mistol* and *V. aroma* in both forest types could be due to the irregular distribution of their propagules in the SSB, short-term seed viability loss [67], and physical dormancy [68,69]. Additionally, the sensitivity of *S. mistol* to heat shock [17] may explain its absence in the DF. The lack of dispersers and seed predation could be additional factors limiting recruitment in these species [70].

The lack of recruitment of *V. aroma* does not align with what was expected. This species has the largest SSB size among the studied species, together with *N. nigra*, and its seeds exhibit a considerable tolerance to heat shock [11,18], especially when its propagules are buried. These results support previous findings that highlight the dissimilarity between the species composition of standing vegetation and that of the SSB [27,29]. Therefore, the availability of propagules is not the only bottleneck for the recruitment of native species.

The recruitment of *N. nigra* exclusively in DF highlights its behavior as a pioneer species and its ability to colonize disturbed environments, which is similar to other pioneer species of Fabaceae [71,72]. The high predation rates (>30%) observed within *N. nigra* seeds suggest that propagule predation (such as observed after EB 2017) may have prevented recruitment in CF, despite the presence of adult individuals in both forest types [50,63]. While *N. nigra* and *V. aroma* propagules have shown relative tolerance to heat shock (80–110 °C), recruitment levels were lower than expected [18]. The smaller SSB size in the DF than CF [12] suggests that their recruitment is hindered by several constraints, likely influenced by unfavorable environmental conditions following disturbances.

The presence of *S. gilliesii* seedlings in both forest types aligns with previous findings on SSBs [11], which confirmed the presence of propagules of this species in both sites. The similar seedling structures (height and diameter) in both forest types suggest seedling establishment likely occurred during the same period, with higher recruitment success in the CF. *S. gilliesii* is dominant in undisturbed sites and regenerates successfully under such conditions [58]. However, the seedling density in the DF seems to indicate high tolerance to post-disturbance conditions, as this species can regenerate under varying light conditions and low soil moisture levels, thereby favoring germination even in more stressful environments [58].

The results obtained in the field recruitment experiments post-EB with seeds in different soil depths seem to indicate the combined effect of interannual seed viability and fire resistance, since all species showed higher viability in the seed plots collected in 2019, but

the differences were significant only in two of the species studied. Both the seed viability and the recruitment observed after the 2019 EB support the hypothesis regarding the effect of burial capacity on the maintenance of seed viability, since all species recruited differentially after fire. The increase in average germination observed in *N. nigra*, *V. aroma*, and *S. mistol* in 2019 burnt plots suggests a stimulation by heat shock, despite the temperature range in the soil not exceeding 100 °C, and the differences were significant only in the first two species.

Half of the studied species showed no recruitment in the DF, suggesting that environmental and biological factors influence their seed-based regeneration. When the propagules do not have the aptitude to bury in the soil, their availability from adjacent, undisturbed sites and the presence of dispersers become crucial for the recruitment of these woody species in Chaco forests [29,58,63]. Both dominant tree species from these forests depend on this strategy to recolonize burnt areas, highlighting the demand for conservation areas with mature trees to ensure the seed-based regeneration. Other studied species exhibited aptitude to bury into the soil and to recruit in forests disturbed by fires and roller chopping, allowing for the recovery of biomass, protecting soil from erosion, and promoting nutrient cycling with restrictions related to the physical changes generated by disturbances.

Our results allowed us to generate recommendations for the native forest management plans, which should consider the importance of soil structure conservation as a reservoir of native species seeds. The litter has a significant role in seed storage [22], but in this soil fractions are exposed to high mortality during fires, becoming highly susceptible. The canopy species, *S. lorentzii* and *A. quebracho-blanco*, do not have the aptitude to burrow in the soil; therefore, they are dependent on mature trees as seed sources to recruit in fire-disturbed areas. The intermediate forest stratum species, such as *N. nigra*, *S. mistol*, and *V. aroma*, have a relative aptitude to incorporate into the soil [11], providing them the opportunity to germinate after fires. *N. nigra* and *V. aroma* showed higher germination rates after fires when propagules were buried. However, the seedlings' establishment seems to be another bottleneck in seed regeneration, demonstrated by only four of the studied species recruiting in disturbed forests. *A. quebracho-blanco* is the only forest canopy species that recruits in disturbed forest, probably from seed rain after fires. On the other hand, *V. aroma* showed the highest germination rate after EB, but it was absent in the forest disturbed by roller chopping and fires, suggesting particular environmental requirements for the growth and establishment of seedlings. The monitoring of environmental conditions over time in disturbed forests and the knowledge of the physical and biological requirements of species for seedling growth are indispensable for the conservation of the Chaco region's native forests. This represents an important knowledge gap that could contribute to a better interpretation of different forest degradation patterns. This understanding will contribute to the restoration activities, since the studied species revealed differences in their regeneration potential in disturbed forests. More studies including high numbers of native forest species, their responses to other fire severities, and the monitoring of environmental changes in burnt forest areas are desirable to assess the issues analyzed in this work. In particular, integrating post-fire climatic monitoring, such as for rainfall and soil temperature, could clarify additional constraints on seedling recruitment and survival.

5. Conclusions

The results of our study indicate different post-fire recruitment patterns among the selected native woody species. The distribution of propagules within the soil profile (soil or litter) was a key factor for seed survival and successful field recruitment after medium- to low-intensity wildfire events (EBs). Seeds located in the litter can be lethally affected by fire. However, when incorporated into the soil, their chances of recruitment increased

due to insulation from surface temperatures. Species such as *A. quebracho-blanco*, whose seeds cannot burrow, seem to depend on the seed rain that allows them to recruit in burnt or disturbed areas. The higher the viability and heat shock tolerance of propagules, the greater their recruitment potential, as demonstrated in *N. nigra*. The field recruitment rates two years after the EB differed among the studied species, indicating that the species with the highest seedling establishment success were *A. quebracho-blanco*, *N. nigra*, and *S. gilliesii*. These species exhibit higher tolerance for germination and seedling establishment under the environmental conditions of the disturbed forests. The absence of *S. lorentzii* recruitment in disturbed forests affected by rolling and fire highlights the need for differentiated forest management strategies to facilitate the sexual regeneration of this valuable canopy species. Our results will contribute to forest land management and restoration activities in the Chaco region's native forests, as demonstrated by the differential susceptibility of the studied species to fires affecting seed viability. These results also highlight the need to monitor environmental changes generated by this disturbance that can limit the growth and establishment of seedlings, affecting the natural regeneration dynamic.

Author Contributions: A.V.I.M.: Conceptualization, investigation, methodology, formal analysis, writing—original draft, writing—review and editing. F.B.: Methodology, investigation, formal analysis, writing—review and editing, visualization. L.G.: Methodology, investigation, formal analysis, writing—review and editing, visualization. J.M.C.: Investigation, formal analysis, data curation. S.J.B.: Conceptualization, investigation, methodology, writing—original draft, writing—review and editing, visualization. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Secretaría de Ciencia y Técnica, Universidad Nacional de Santiago del Estero, under the project Estudios ecológicos en bancos de semillas de especies leñosas nativas del Chaco y su relación con disturbios antrópicos (2016–2020), code: 23/B133. Additionally, A.V.I.M. acknowledges the fellowship granted by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), and F.B. acknowledges funding from Fundação de Apoio à Pesquisa do Distrito Federal (FAPDF, Projeto 00193.00001818/2023-98) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, projeto 407132/2023-6).

Data Availability Statement: Data will be made available on request.

Acknowledgments: We express our gratitude to the Facultad de Cs. Forestales (FCF) at Universidad Nacional de Santiago del Estero (UNSE), the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), and the authorities and field staff of the INTA Experimental Station in Santiago del Estero Province for their valuable support. We also appreciate the assistance of the field personnel and our colleagues from the Chair of General Botany and the Forest Species Germplasm Bank (BAGEFOR), FCF, and UNSE, for their collaboration during both fieldwork and laboratory activities, as well as Dante Loto, who provided important comments on this manuscript.

Conflicts of 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.

Appendix A

Table A1. Post-fire seed fates of six native woody species from Chaco forests. Percentages of carbonized and predated seeds (mean $\pm$ SD, $n = 100$).

Species	Carbonized Seeds (%)	Predated Seeds (%)
<i>Aspidosperma quebracho-blanco</i>	100 $\pm$ 0	0 $\pm$ 0
<i>Schinopsis lorentzii</i>	33.0 $\pm$ 27.3	25.0 $\pm$ 6.8
<i>Sarcomphalus mistol</i>	56.0 $\pm$ 30.4	13.0 $\pm$ 17.7

Table A1. Cont.

Species	Carbonized Seeds (%)	Predated Seeds (%)
<i>Neltuma nigra</i> with endocarp	32.0 ± 26.0	34.0 ± 13.2
<i>Neltuma nigra</i> seed	59.0 ± 6.8	30.0 ± 20.0
<i>Vachellia aroma</i>	28.0 ± 24.8	32.0 ± 11.3
<i>Senegalia gilliessi</i>	45.0 ± 34.0	26.0 ± 36.5

Appendix B

Table A2. Species compositions in Chaco forests with different land uses: conserved forest (CF) and forest disturbed by rolling chopping and experimental burns (DF). Average values ± standard error of basal area (m²/ha^{−1}). Fisher's F-statistic values and corresponding error probability (*p*) are indicated.

Species	Basal Area		f	p
	CF	DF		
<i>Aspidosperma quebracho-blanco</i>	5.89 ± 0.93	4.62 ± 0.58	1.34	0.2549
<i>Schinopsis lorentzii</i>	3.18 ± 0.76	2.55 ± 0.63	0.41	0.52
<i>Neltuma nigra</i>	0.47 ± 0.26	1.11 ± 0.53	1.16	0.28
<i>Sarcomphalus mistol</i>	2.71 ± 1.04	2.07 ± 0.81	0.23	0.63
<i>Opuntia</i> sp.	0.31 ± 0.21	0	2.11	0.15
<i>Parkinsonia praecox</i>	0.15 ± 0.15	0	1	0.32
total	12.75 ± 1.24	10.36 ± 1.26	1.82	0.1859

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