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# Post-burning regeneration of the Chaco seasonally dry forest: germination response of dominant species to experimental heat shock

Pedro Jaureguiberry · Sandra Díaz

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**Abstract** Plant species of the Chaco seasonally dry forest of central Argentina have presumably been under a low evolutionary pressure to develop specialized fire-response traits, such as heat-stimulated germination. Nevertheless, other historical factors such as seasonal drought and/or endozoochorous dispersal could have led some species to develop heat-tolerant seeds. Therefore, heat-tolerant germination should be more common than heat-stimulated or heat-sensitive germination. To test this, we exposed seeds of 26 dominant species from the Chaco region to a broad range of experimental heat treatments and incubated them for 30 days at 25 °C and 12 h photoperiod. We then scored the percent germination and classified them as heat-stimulated, heat-tolerant or heat-sensitive based on their germination following heat treatments relative to control. Seventeen species showed heat-tolerant germination, including all native graminoids. Seven species showed heat-stimulated germination, under the less-intense heat treatments. Only two species showed heat-sensitive germination. Endozoochory had no influence on germination responses. We suggest that, unlike Mediterranean-climate ecosystems, fire was not a major evolutionary force in the development of Chaco forests, and our results provide

greater understanding of the potential response of Chaco plant communities in the face of increasingly frequent fires.

**Keywords** Exaptation · Fire adaptations · Fire history · Plant regeneration strategies · Seed dormancy and germination

## Introduction

Seed germination is a key process in the life cycles of sexually reproducing plants. Germination can occur under a great variety of environmental conditions because species maximize establishment and survival of new sexually produced individuals in different abiotic and biotic contexts (Bewley and Black 1994; Baskin and Baskin 1998a).

Fire has an important influence on the distribution, composition and evolution of the vegetation cover, especially in fire-prone regions such as Mediterranean-climate ecosystems (Trabaud 1980; Whelan 1995; Keeley 1995; Bond and van Wilgen 1996). Consequently, many plant species have evolved seed germination strategies that optimise plant survival after fire, such as the stimulation of germination by smoke, charred wood and high temperatures associated with fire (Keeley et al. 1985; Keeley and Fotheringham 1998). The latter has been the most studied factor, especially in Mediterranean ecosystems (Keeley 1987; Keeley and Bond 1997; Keeley and Baer-Keeley 1999; Hanley and Lamont 2000; Hanley et al. 2001; Luna et al. 2007; Ne'eman et al. 2009), where some species can tolerate temperatures above 120 °C, or increase germination following the heat shock produced by fire (Keeley 1991; Herranz et al. 1998; Valbuena and Vera 2002; Luna et al. 2007). Other strategies, such as the physical dormancy of seeds (sensu Baskin and Baskin 1998a), due to the impermeability of the seed coat,

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P. Jaureguiberry (✉) · S. Díaz  
Instituto Multidisciplinario de Biología Vegetal (CONICET-UNC) and FCEFyN, Universidad Nacional de Córdoba, Casilla de Correo 495, CP 5000 Córdoba, Argentina  
e-mail: pedro\_jaureguiberry@hotmail.com; pedrojaureguiberry@efn.uncor.edu

are also common in these ecosystems. Fire can break seed dormancy by scarifying the seed coat and allowing water and gas exchange (Thanos and Georghiou 1988).

In regions where fire is not as frequent and/or intense as in Mediterranean ecosystems, such as in the South American Chaco, there is very limited knowledge of the effect of heat shock on seed dormancy and germination. Studies have mostly focused on variation of ambient temperatures, ranging from 5 to 35 °C (e.g., Funes and Venier 2006; Funes et al. 2009; Zalazar et al. 2009; Venier 2011).

Given the large influence of climate on plant recruitment mainly through temperature and water supply (Adler and Hill Ris Lambers 2008), climatic alterations and other environmental changes (e.g., land use) predicted for the near future (IPCC 2013) are expected to affect recruitment, through the increase of mean air and soil temperature (Ooi et al. 2012, 2014), and also plant population dynamics in different regions of the world (Arft et al. 1999; Diemer 2002; Fitch et al. 2007; Walck and Dixon 2009; Baeten et al. 2010) including the Chaco forests (Hoekstra et al. 2005; Grau et al. 2008). In addition, increasingly frequent fires due to the expansion of human populations and agricultural lands challenge the adaptive capacity of wild plants to regenerate after fire (Keeley and Fotheringham 2003). Therefore, studies of germination responses to fire are greatly needed for predicting vegetation dynamics under different global change scenarios, and could help elucidate aspects of plant evolution in relation to fire. This question has been widely studied in Mediterranean-climate ecosystems, where correspondences between historical fire regime, regeneration strategy (i.e. resprouting or seeding) and germination in response to heat have been reported for many species (Keeley 1991; Keeley and Bond 1997; Lloret et al. 2005; Luna et al. 2007; Paula and Pausas 2008; Ne'eman et al. 2009).

In this context, it is generally accepted that resprouting ability is an ancestral trait acquired by many lineages in response to different aboveground disturbances, which is widespread both in fire-prone and non-fire-prone ecosystems (Wells 1969; Bellingham et al. 1994; Lloret et al. 1999; Pausas and Verdú 2005). Therefore, resprouting after fire is a less specialized trait; whereas post-fire seed traits, such as the stimulation of seed germination by heat shock, are considered specialised post-fire traits that appeared later in evolution (Wells 1969; Pausas and Verdú 2005; Paula and Pausas 2008).

Several studies report high resprouting capacity of Chacoan species (Tálamo and Caziani 2003; Gurvich et al. 2005; Jaureguiberry 2012; Bravo et al. 2014), and, particularly, Torres et al. (2013) showed that resprouting is more important than seedling recruitment for regeneration after fire in the Chaco Serrano forest, which has some species in common with our study area. This supports the idea that resprouting is one of the main strategies of Chaco species for recovering

after fire and other disturbances. However, studies of recruitment from seeds in the Chaco are scarce, hindering the assessment of regeneration strategies after disturbance. For example, Barchuk et al. (1998) reported significant seedling recruitment of *Aspidosperma quebracho-blanco* in protected areas of the western Chaco, and little recruitment in areas with extensive grazing and uncontrolled logging. Casillo et al. (2012) reported considerable recruitment of graminoids after a fire treatment in a Chaco savanna, whereas forbs were not affected by fire and woody species responded negatively.

Although the Chaco region has been historically subjected to some burning, at least as a result of aboriginal fire (Morello and Saravia Toledo 1959), and also possibly due to occasional lightning during the wet, warm season, there is no record-based evidence of recurring fire having been a strong natural selection pressure over evolutionary time. Therefore, considering both the fire history in the region and the widespread post-fire resprouting ability, it is reasonable to expect that plant species in the Chaco have been subjected to little evolutionary pressure for traits that enhance germination after fire (Paula and Pausas 2008).

However, fire tolerance of seeds of Chaco species could have evolved as a consequence of the evolutionary pressure exerted by other factors, a phenomenon called “exaptation” (Gould and Vrba 1982). Specifically, the presence of hard seed coats, a trait of adaptive value in endozoochorous species dispersed by ungulates (Malo and Suárez 1998), or subjected to seasonal desiccation (Baskin et al. 2000)—both common in the Chaco region—could be an exaptation conferring the seeds a high tolerance to heat. Consequently, heat-tolerant germination rather than heat-stimulated or heat-sensitive germination should be more common.

Here, we test the hypothesis that Western Chacoan species have been subjected to low evolutionary pressure to acquire traits that enhance germination after fire, and other factors with long history in the system could have promoted heat tolerance. To do this, we subjected seeds of the dominant forest species to different experimental heat shock treatments (i.e. different temperature and time of exposure). By comparing the percentages of germination after the heat treatments with those under the control treatments, we aimed to characterize the germination response of the selected species in terms of their sensitivity to heat. This allowed us determine the frequency of each germination response (i.e. heat-sensitive, -tolerant or -stimulated).

## Materials and methods

### Study area

The study was carried out in an area located in western Córdoba Province, central Argentina (31°17'–31°55'S,

65°12'–65°32'W). Phytogeographically, this corresponds to the Western Chaco (Cabrera 1976), which is characterized by highly seasonal semi-deciduous xerophytic forest. Mean annual precipitation is 450 mm, concentrated in the spring–summer months (October–March). Minimum and maximum mean annual temperatures are 10.7 °C (July) and 26.1 °C (January), respectively. In the dry season (April–October), the water balance is negative, resulting in soil moisture deficit (Cabido et al. 1992, 1994). The forest canopy is c. 12 m high and discontinuous, dominated by *Aspidosperma quebracho-blanco* and *Prosopis flexuosa*. The shrub layer (4 m high) is thorny, dense and usually continuous, dominated by *Larrea divaricata*, *Mimozyanthus carinatus* and *Acacia gilliesii*. A lower and discontinuous layer of grasses and herbs is dominated by *Trichloris crinita*, *Gouinia paraguayensis*, *Setaria* spp. and *Pappophorum* spp. (Cabido et al. 1993).

#### Plant species selection and seed collection

On the basis of previous surveys (Cabido et al. 1992, Díaz et al. 1998; Conti and Díaz 2013), we selected a total of 26 species that dominated the canopy and understorey of the forest in the study area. They included 11 taxonomic families and different growth forms (8 trees, 10 shrubs, 7 perennial grasses and 1 perennial forb; Table 1). All the species in this study are able to resprout after fire (Jaureguiberry 2012).

With the exception of the exotic graminoid *Cenchrus ciliaris*, all the selected species are native to the Chaco region (Flora del Cono Sur 2014). Some of them have a wide distribution and can be found both in the western semiarid Chaco subregion (i.e. our study area) as well as in the eastern subhumid Chaco subregion, namely the tree species *A. quebracho-blanco*, *Celtis ehrenbergiana*, *Castela coccinea* and *Geoffroea decorticans*, the shrubs *Acacia aroma*, *A. caven*, *A. praecox*, *Aloysis gratissima* and *Moya spinosa*, and the graminoids *Aristida mendocina*, *G. paraguayensis*, *Setaria pampeana*, *Pappophorum vaginatum* and *Trichloris* spp. Other species are more restricted to the semiarid subregion, such as the tree species *Cercidium praecox*, *Prosopis chilensis*, *P. flexuosa* and *P. torquata*, the shrubs *Acacia gilliesii*, *Condalia microphylla*, *L. divaricata*, *M. carinatus* and *Tricomaria usillo*, the forb *Justicia squarrosa*, and the graminoids *C. ciliaris* and *Neobouteloua lophostachya* (Flora del Cono Sur 2014).

Most fire events across all the Chaco region are anthropogenic and are mainly associated with the use of fire as a tool to open agricultural land and to prevent accidental fires (Morello and Saravia Toledo 1959; Morello 1970; PPMF 2007; PNMF 2012). Therefore, it is reasonable to assume that all the species studied have been under a similar selective pressure in terms of fire history.

Seeds were collected from at least 10 healthy-looking, sexually mature, randomly selected individuals of each species, following the sampling protocols of Pérez Harguindeguy et al. (2013), and were then stored in paper bags until the experiments. In some cases, it was necessary to keep the seeds in a freezer (−6 °C) to prevent predation by insects. Post-dispersal units were used for the experiment; therefore, before the experiment seeds were cleaned by removing fruit tissues that would normally be lost in dispersal. In some cases, the “seed” that was incubated included fruit tissues (e.g., endocarp in drupes).

#### Experimental procedures

The treatments levels used were: control (no heating), 70 °C for 1 h, and 100, 120 and 180 °C for 5 min in a Marne® NEO-LINE digital controlled oven, except *T. usillo*, subjected only to control and 70 °C treatments, and *Castela coccinea*, not subjected to the 100 °C treatment due to the limited number of seeds available. We selected these treatments to represent a range of conditions potentially encountered by seeds in the soil at open sites or during fire and within the range of temperatures shown in prior studies to stimulate germination in some species (Keeley 1987; Bóo et al. 1996; Hanley et al. 2001; Luna et al. 2007; Ne'eman et al. 2009; Casillo et al. 2012; Bravo et al. 2014). In a pilot test, we evaluated the response of seeds of three of the selected species (*Prosopis flexuosa*, *Acacia caven* and *Condalia microphylla*) to extreme temperatures of 250, 350 and 450 °C during 3 min in an Indef Model 331 laboratory oven. None of them survived; therefore these temperatures were not included in the subsequent experiment.

After the heat treatments, we placed seeds on filter paper (65 g m<sup>−2</sup>) within polystyrene dishes, and incubated them in germination chambers at a constant temperature of 25 °C, with a 12/12 h daily photoperiod. Each dish contained 30 seeds of trees and shrubs and 50 seeds of smaller-seeded grasses and forbs. We used three replicates per treatment per species. At the beginning of the experiment, we added 2.5 ml of distilled water per dish with a broad-spectrum fungicide to prevent fungal infection. Seeds were subsequently kept moist by adding distilled water when necessary. The number of germinated seeds was recorded every 2–4 days for 30 days. Germination percentage was defined on the basis of the number of germinated seeds (emerged radicle) per replicate.

Considering previous studies reporting or suggesting the presence of physical dormancy in six of the studied species (Campos et al. 2008; Funes and Venier 2006; Funes et al. 2009; Venier 2011; Venier et al. 2012), the remaining ungerminated seeds of *Acacia aroma*, *Acacia caven*, *Cercidium praecox*, *Prosopis chilensis*, *Prosopis flexuosa* and *Prosopis torquata* were scarified using an 80-grit sandpaper

**Table 1** Characteristics of plant species in this study and classification of germination responses to heat: *H* heat-sensitive, *T* heat-tolerant and *S* heat-stimulated

Plant species	Family	Growth form	Fruit type	Physical dormancy	Endozoochory	Treatment with highest germination	Germination response
<i>Acacia aroma</i> Gillies ex Hook. and Arn.	Fabaceae	Shrub	Loment	Yes <sup>a</sup>	Yes <sup>a,f</sup>	Control and 70 °C	T
<i>Acacia caven</i> (Molina) Molina	Fabaceae	Shrub	Indehiscent legume	Yes <sup>a</sup>	Yes <sup>b,c</sup>	70 °C	T
<i>Acacia gilliesii</i> Steud.	Fabaceae	Shrub	Legume	No <sup>a</sup>	No <sup>?</sup>	<b>100 °C</b>	S
<i>Acacia praecox</i> Griseb.	Fabaceae	Shrub	Legume	No <sup>a</sup>	No <sup>?</sup>	100 °C	T
<i>Aloysia gratissima</i> (Gillies and Hook.) Tronc.	Verbenaceae	Shrub	Capsule	No	No	100 °C	T
<i>Aristida mendocina</i> Phil.	Poaceae	Grass	Caryopsis	No	No	Control	T
<i>Aspidosperma quebracho-blanco</i> Schtdl.	Apocynaceae	Tree	Capsule	No	No	70 °C	T
<i>Castela coccinea</i> Griseb.	Simaroubaceae	Tree	Drupe	No	Yes <sup>a,g</sup>	<b>Control</b>	H
<i>Celtis ehrenbergiana</i> (Klotzsch) Liebm.	Celtidaceae	Tree	Drupe	No	Yes <sup>a,f</sup>	<b>70 °C</b>	S
<i>Cenchrus ciliaris</i> L.	Poaceae	Grass	Caryopsis	No	No	<b>70 °C</b>	S
<i>Cercidium praecox</i> (Ruiz and Pav.) Burkart and Carter	Fabaceae	Tree	Indehiscent legume	Yes	Yes <sup>?i</sup>	<b>120 °C</b>	S
<i>Condalia microphylla</i> Cav.	Rhamnaceae	Shrub	Drupe	No	Yes <sup>a,g</sup>	70 °C	T
<i>Geoffroea decorticans</i> (Gillies ex Hook. and Arn.) Burkart	Fabaceae	Tree	Drupe	No	Yes <sup>a</sup>	70 °C	T
<i>Gouinia paraguayensis</i> (Kuntze) Parodi	Poaceae	Grass	Caryopsis	No	No	70 °C	T
<i>Justicia squarrosa</i> Griseb.	Acanthaceae	Forb	Capsule	No	No	120 °C	T
<i>Larrea divaricata</i> Cav.	Zygophyllaceae	Shrub	Capsule	No	No	Control	T
<i>Mimozyanthus carinatus</i> (Griseb.) Burkart	Fabaceae	Shrub	Legume	No	Yes <sup>?i</sup>	120 °C	T
<i>Moya spinosa</i> Griseb	Celastraceae	Shrub	Capsule	No	Yes <sup>?a</sup>	<b>70 °C</b>	S
<i>Neobouteloua lophostachya</i> (Griseb.) S.Gould	Poaceae	Grass	Caryopsis	No	No	100 °C	T
<i>Pappophorum vaginatum</i> Buckley	Poaceae	Grass	Caryopsis	No	No	70 °C	T
<i>Prosopis chilensis</i> (Molina) Stuntz.	Fabaceae	Tree	Indehiscent legume	Yes <sup>b</sup>	Yes <sup>h</sup>	70 °C	T
<i>Prosopis flexuosa</i> DC	Fabaceae	Tree	Indehiscent legume	Yes <sup>b</sup>	Yes <sup>d,h</sup>	<b>120 °C</b>	S
<i>Prosopis torquata</i> (Cav. ex Lag.) DC	Fabaceae	Tree	Indehiscent legume	Yes <sup>b</sup>	Yes <sup>e,h</sup>	Control and 180 °C	T
<i>Setaria pampeana</i> Parodi ex Nicora.	Poaceae	Grass	Caryopsis	No	No	Control and 70 °C	T
<i>Trichloris</i> spp. ( <i>crinita</i> + <i>pluriflora</i> ) (Lag.) Parodi; E. Fourn.	Poaceae	Grass	Caryopsis	No	No	<b>70 °C</b>	S
<i>Tricomaria usillo</i> Hook. and Arn.	Malpighiaceae	Shrub	Caryopsis	No	No	<b>Control</b>	H

Nomenclature follows Zuloaga et al. (1994), Zuloaga and Morrone (1996, 1999) and updates (<http://www2.darwin.edu.ar/Proyectos/FloraArgentina/FA.asp>). Fruit type follows Flora Argentina (<http://www.floraargentina.edu.ar/>)

References on *Physical dormancy*: <sup>a</sup> Venier et al. (2012), <sup>b</sup> Campos et al. (2008)

References on *Endozoochory*: <sup>a</sup> De Noir et al. (2002), <sup>b</sup> Gutiérrez and Armesto (1981), <sup>c</sup> Fuentes et al. (1986), <sup>d</sup> Campos and Ojeda (1997), <sup>e</sup> Núñez and Bozzolo (2006), <sup>f</sup> Varela and Bucher (2006), <sup>g</sup> Serbent et al. (2011), <sup>h</sup> Campos et al. (2008), <sup>i</sup> Morello and Saravia Toledo (1959)

In the column *Endozoochory*, species for which the presence (*Yes?*) or absence (*No?*) of endozoochory is uncertain were considered as “yes” or “no” in the statistical analyses. See details in the text. In the column *Treatment with highest germination* bold type indicates significant differences with other treatments

(or a razor blade in smaller seeds) and incubated for 10 additional days. By comparing the germination of dormant seeds after heat treatments alone with the germination after mechanical scarification, we were able to determine the ability of heat shock treatments to break dormancy. To assess germination responses (see below) of seeds with documented or presumed physical dormancy, we considered the germination percentages obtained before mechanical scarification (i.e. those after heat treatment alone).

On the basis of Luna et al. (2007) and Paula and Pausas (2008), we defined three types of germination response in the face of heat shocks:

- (a) Heat-sensitive: germination after all the heat treatments significantly lower than the control treatment.
- (b) Heat-tolerant: germination after at least one of the heat treatments as high as, but not higher than, the control treatment.
- (c) Heat-stimulated: germination after at least one of the heat treatments significantly higher than the control treatment.

#### Data analysis

All statistical analyses were performed using InfoStat v.2013p (Di Rienzo et al. 2013, Grupo InfoStat, Facultad de Ciencias Agropecuarias, Universidad Nacional de Córdoba, Argentina). To determine differences in germination among species and treatments within each species, we analyzed data through a generalized linear model (Bates et al. 2014), which included species, heat treatment and their interaction as fixed factors, assuming a binomial distribution of the error.

To test the influence of the different heat treatments and the presence/absence of endozoochory on germination, we used a generalized linear mixed model (Bates et al. 2014). The model included endozoochory, heat treatment and their interaction as fixed factors, and species as random factor. The model was fit using a binomial distribution of the error. Presumed but uncertain presence or absence of endozoochory in some species (referred to as “yes?” or “no?” in Table 1) were considered as “yes” and “no”, respectively, in statistical analyses. The analyses were repeated considering the opposite options, and results did not differ from those reported here.

In all cases, means were compared with the a posteriori DGC test (Di Rienzo, Guzmán, Casanoves pair-wise comparison procedure; Di Rienzo et al. 2002). The model selection was based on the Akaike criterion (1972). The adjustment of the models was made using the software InfoStat (Di Rienzo et al. 2013) which uses *lme4* library (Bates et al. 2014) of the R-package (R Development Core Team 2008).

Given the small proportion of seeds that germinated after the 180 °C treatment, we excluded it from the

statistical analyses. Nevertheless, results of this treatment are included in tables and figures and discussed in the text.

## Results

### Germination of species under different heat shock treatments

The percentages of germination recorded under control conditions and after different heat treatments were highly variable between species (Table S1; Fig. S1). Six species showed germination percentages below 20 % after all treatments: *Aspidosperma quebracho-blanco*, *Aloysia gratissima*, *Larrea divaricata*, *Condalia microphylla*, *Geoffroea decorticans* and *Setaria pampeana*. In the three latter germination was <10 %.

Only four out of the 26 species were able to germinate after the 180 °C treatment (Table S1; Fig. S1), from which only *Prosopis flexuosa* showed a considerable germination percentage (29 %), whereas *Cenchrus ciliaris*, *Neobouteloua lophostachya* and *Prosopis torquata* showed very low germination compared to other treatments (12.7, 4.0 and 1.1 %, respectively). *Acacia caven* and *A. aroma* were among the species with the highest germination percentages after all treatments (excluding 180 °C), ranging from 84.4 to 98.9 %. Other species with high germination percentages were *A. praecox* (71.1–94.4 %), *A. gilliesii* (60.0–88.9 %), *C. ciliaris* (71.3–91.3 %) and *Aristida mendocina* (63.3–76 %).

### Characterization of species by germination response categories

Most species (17 out of 26) showed heat-tolerant germination (Fig. 1; Table 1), whereas seven species were stimulated by heat shock treatments: *A. gilliesii*, *Celtis ehrenbergiana*, *C. ciliaris*, *Cercidium praecox*, *Moya spinosa*, *P. flexuosa* and *Trichloris* spp. Four of these species had their maximum germination after the 70 °C treatment, one after the 100 °C treatment and *P. flexuosa* and *C. praecox* after the 120 °C treatment (Table 1). Apart from these two latter species, only two other species had maximum germination at 120 °C (although not significantly different from the control), *Justicia squarrosa* and *Mimozyanthus carinatus* (33.3 and 61.1 %, respectively; Table S1). On the other hand, *Castela coccinea* and *Tricomaria usillo* were the only species that fell into the heat-sensitive category. Nevertheless, both of them showed low germination percentages in all treatments (Table S1; Fig. S1).

Endozoochory had a significant effect on germination responses only in the 100 °C treatment, for which germination of endozoochorous species was lower than non-endozoochorous ones (Fig. 2).

## Effects of heat shock and mechanical scarification on the physical dormancy of seeds

Heat shock alone was effective in breaking physical seed dormancy only in two out of the six species with dormant seeds in this study, namely *C. praecox* and *P. flexuosa* (Fig. 1; species *d* and *f*, respectively). In both cases, the 120 °C treatment produced a significant increase in germination. *Acacia caven* showed a slight increase in germination at 70, 100 and 120 °C with respect to control, although this increase was not significant (Fig. 1; species *i*). *A. aroma* and *P. torquata* did not increase their germination in response to heat treatment alone (Fig. 1; species *h* and *w*).

With the exceptions of *P. flexuosa* and *P. torquata*, mechanical scarification promoted seed germination considerably in four of the six scarified species (Table S1; AS column). The strongest scarification effects were recorded in *A. aroma* and *A. caven*. Other species significantly stimulated by scarification were *C. praecox* and *P. chilensis*, although both of them showed considerable germination under the control treatment before scarification (14.5 and 36.7 %, respectively; Table S1).

## Discussion

### Germination responses to heat treatments and mechanical scarification

Percentages of germination were highly variable. For example, germination of *A. caven* and *A. aroma* (both with dormant seeds) after mechanical scarification, and of *A. gilliesii* (non-dormant seeds) agree with previous studies of their germination requirements (Funes and Venier 2006; Venier et al. 2012). *Prosopis chilensis* and *P. flexuosa* have also been reported as having coat-imposed seed dormancy (Cony and Trione 1996), although only *P. chilensis* responded significantly to scarification in the present study.

The low germination percentages recorded in some other woody species are also consistent with previous studies. For example, *Geoffroea decorticans* and *Condalia microphylla* showed percentages of germination similar to those reported in control treatments (at 30/20 °C light/dark) by Renison et al. (2010). Campos et al. (2008) reported very low percentages of germination of *Prosopis torquata* and *P. flexuosa* in control treatments. This could be due to overall low seed viability or to specific germination requirements. For example, Renison et al. (2010) reported a significant increase of germination of *G. decorticans* after the passage of seeds through the digestive tract of frugivorous bird *Rhea americana*, while Campos et al. (2008) reported a similar pattern for *Prosopis* species after endozoochoral dispersion by mammals. Other plant species

may present physiological mechanisms which inhibit germination (“physiological dormancy”; sensu Baskin and Baskin 2004), which require previous treatments that were not relevant to the main goal of this study, such as thermal stratification (cold or warm) or treatments with gibberellic acid (Baskin and Baskin 2004; Figueroa and Jaksic 2004).

Although some Fabaceae species were stored at cold temperatures before the experiments, and this may affect germination, the fact that temperatures several degrees below zero are not unusual in the study area, together with the very low water content of seeds (which decreases the probability of damage) and the similar germination percentages reported in other studies with seeds of some of the same species but stored at room temperature (e.g., Funes and Venier 2006; Funes et al. 2009; Venier et al. 2012), suggest that cold storage had little or no effect on the germination of these species.

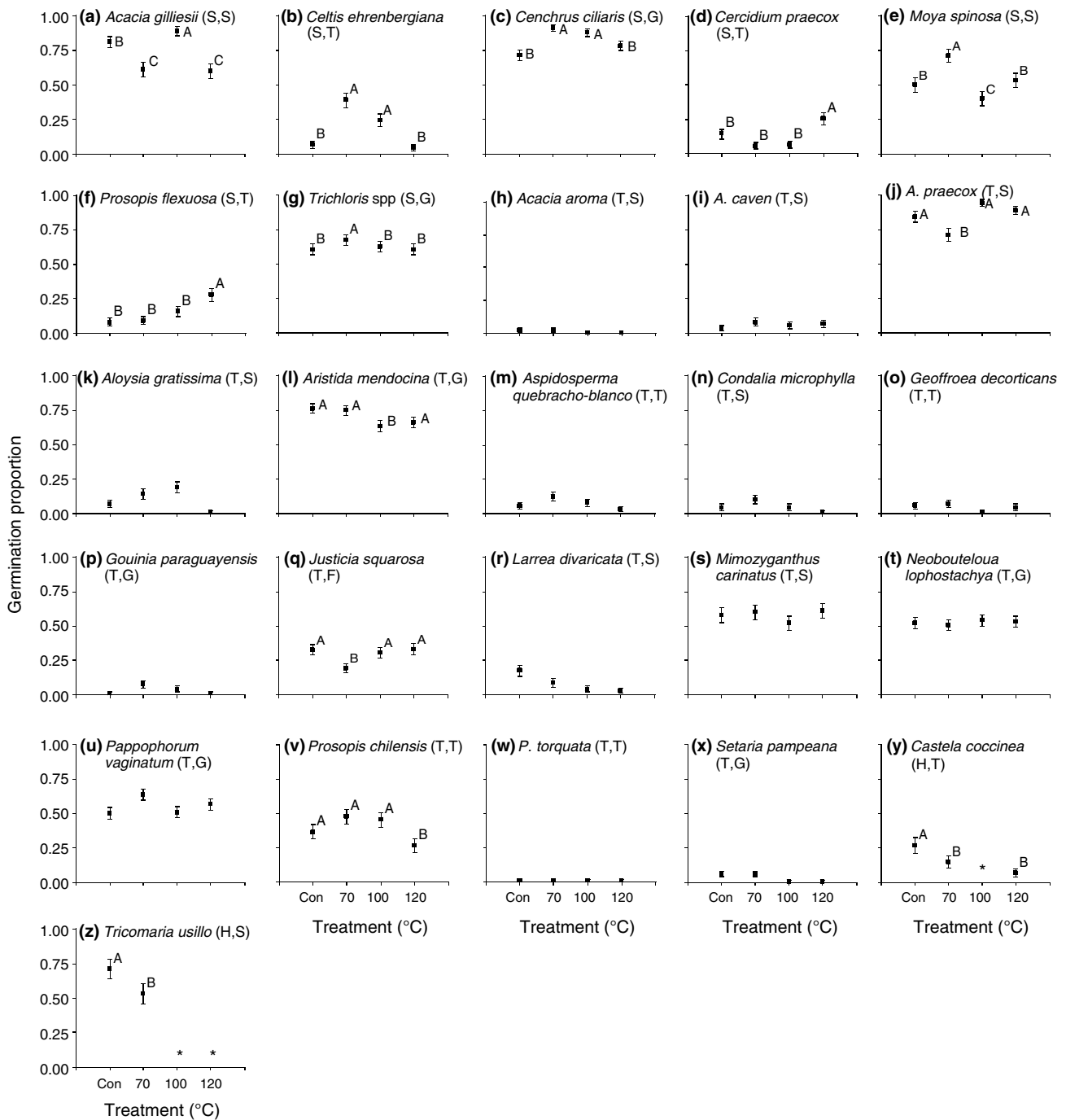
Among the graminoids, *Setaria pampeana* and *Gouinia paraguayensis* showed very low germination percentages under all treatments. This could be due to the presence of physiological dormancy, which is common in the Poaceae (Baskin and Baskin 1998b). Evidence indicates that grass seeds usually have weak physiological dormancy that can be broken during dry storage at room temperature (Nikolaeva 1969, 1977). This could explain the high percentage of germination of graminoids that are known to have non-deep physiological dormancy such as *C. ciliaris* (Baskin and Baskin 1998b), while the low germination of *S. pampeana* and *G. paraguayensis* could presumably be due to either a deeper level of physiological dormancy, which cannot be broken by dry storage alone, or to low seed viability.

Most of the native graminoids showed heat-tolerant germination. *Trichloris* spp was the only native heat-stimulated species, although it was under the less intense treatment of 70 °C, while the exotic species *C. ciliaris* not only showed heat-stimulated germination but also that it was able to germinate after the 180 °C treatment. This is consistent with other studies reporting high fire tolerance in this species. For example, Butler and Fairfax (2003) reported that positive interaction with fire accelerates invasion of this graminoid in *Acacia* shrublands in northeastern Australia. A similar process has been reported in northern Mexico (Alejandro Castellanos, personal communication)

### Heat-tolerant germination and evolutionary history of fire

Our results showed that the seeds of most of species are able to tolerate heat shocks up to 120 °C, but only four survived 180 °C, with few germinated seeds. Most of the species classified as heat-stimulated increased their germination in the 70 °C treatment, which can be considered a moderate or low temperature for a fire. Similar



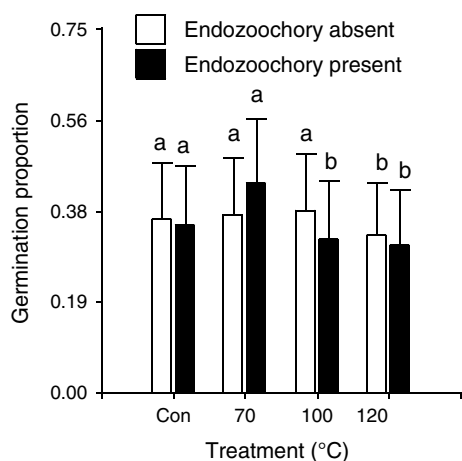


**Fig. 1** Germination proportion (mean + SE;  $n = 3$ ) of 26 species following heat treatments. Values with different capital letters within each species indicate significant differences (DGC test;  $\alpha = 0.05$ ). Responses to heat treatments were used to determine germination

categories: *S* heat-stimulated; *T* heat-tolerant and *H* heat-sensitive. *Castela coccinea* and *Tricomaria usillo* were not subjected to all treatments because of lack of seeds. Growth forms are indicated in parentheses: *T* tree; *S* shrub; *F* forb; *G* grainoid

temperatures may be reached in summer in the absence of fire in open sites with high sunshine exposure, such as bare soil patches generated by overgrazing and erosion, or in burned soils after fire (Auld and Bradstock 1996; Pugnaire and Lozano 1997; Keeley and Fotheringham 2000).

This suggests that heat stimulation in these species does not necessarily need to be linked to fire. That is to say that both heat-stimulated and heat-tolerant species seem to have a high resistance to heat, but they do not depend on it to germinate (Ooi et al. 2014). Our results also suggest that,



**Fig. 2** Germination proportion (mean + SE;  $n = 14$  for endozoochory absent;  $n = 12$  for endozoochory present) following different heat treatments for seeds with and without endozoochory. Different letters indicate significant differences in germination response across all treatments (DGC test;  $\alpha = 0.05$ )

although a high germination response could be expected after a low intensity fire in some species, in the presence of high intensity fires, with temperature at soil surface can exceed 600 °C (Bóo et al. 1996)—and therefore temperature at 2 cm deep can reach 200 °C (Bradstock and Auld 1995)—germination can be severely reduced. In this context, the soil insolation capacity, together with the characteristics of the seeds that determine how deep they can bury in soil, play a fundamental role in determining the temperatures at which seeds will be exposed during a fire event. Further studies relating these two factors may help elucidate seed survival probabilities after a fire event.

Most Chaco species that showed high germination at temperatures higher than 70 °C also showed high germination in the control (e.g., several graminoid species; Table S1). This, together with the fact that heat shock alone was able to break seed dormancy only in two of the six dormant-seeded species, supports the hypothesis that species have been under low selective pressure over evolutionary time to develop fire-dependent germination, at least in comparison with other regions of the world. However, many species were tolerant to heat shock, which is the first requirement to recruit after a fire. Consequently, we cannot rule out the possibility of increased post-fire recruitment induced by other fire cues such as smoke, charred wood and/or nitrates. This has been widely studied in species of Mediterranean-climate regions, some of which are capable of germinating only after being exposed to one or more fire-related cues (Keeley 1987; Thanos and Rundel 1995; Keeley and Bond 1997; Keeley and Fotheringham 1998, 2000). Moreover, in the two species in which heat shock was able to break seed dormancy (i.e. *Cercidium praecox*

and *Prosopis chilensis*), subsequent mechanical scarification produced further increase in germination. This indicates that a significant number of seeds did not respond to heat shock alone.

The high tolerance to heat shock observed in most species suggests that they could have developed exaptations as a consequence of factors other than fire. Among these factors, there is the presence of fruit-eating animals (Traveset 1998; Malo and Suárez 1998). It is reasonable to assume that some species could have developed exaptations to fire as a result of the long history of herbivory by vertebrates in the Chaco region (Bucher 1987; Díaz et al. 1999, 2007). Endozoochory is common in Chacoan species, including several considered in this study, and the traits which originally confer them the capacity to tolerate or take advantage of frugivory could indirectly enhance heat shock tolerance. This appears to be the case of the endozoochorous *Celtis ehrenbergiana* and *Prosopis flexuosa*, which were stimulated by heat shock. However, statistical analyses considering all the species only showed a significant influence of endozoochory on germination after the 100 °C treatment, and this result was inconsistent with our hypothesis (i.e. that endozoochorous species would show higher germination). We suggest that high tolerance to heat shock among the studied species could be associated with other factors.

Considering the marked seasonal drought typical of the Chaco region, water stress is one of the most probable factors explaining the thick seed coats of some species, as has been suggested for several families including Fabaceae (Noodén et al. 1985; Baskin et al. 2000). Drought stress during seed development influences seed coat characteristics and germination (Clua et al. 2006). Genetic and/or environmental factors such as soil moisture content (Barton 1965), relative humidity (Harrington 1949; Quinlivan 1971), temperature alternation (Wurzberger and Koller 1976), daily average temperature or thermo-period (von Abrams and Hands 1956) and photoperiodic regime (Koller 1962; Evenari et al. 1966; Karssen 1970; Gutterman and Evenari 1972; Gutterman and Heydecker 1973; Kigel et al. 1977, 1979) during seed development and maturation have been reported to affect seed production and hard-seededness. Therefore, although only few species in this study have hard coats, others may have developed seed coats with characteristics that allow them to tolerate heat and that are induced by drought stress and associated factors.

## Conclusions

We show that seed germination of the vast majority of the species studied tolerate low and medium temperature heat-shock treatments, suggesting that they are able to survive moderate intensity fires. Only a few species showed sensitive

or stimulated germination by heat shock, and the latter mostly by relatively low temperatures. These results support the hypothesis that fire has been a weak evolutionary force in Chaco forests as compared to Mediterranean-climate ecosystems. We propose that the heat-shock tolerance observed in the seeds of the majority of species is possibly an exaptation to fire, originated in response to other selective factors.

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