379

FOREST
ECOLOGY AND
MANAGEMENT
SCIENCE TO SUSTAIN THE WORLD'S FORESTS

Post-fire resprouting capacity of seasonally dry forest species – Two quantitative indices

Pedro Jaureguiberry*, Aníbal Cuchietti, Lucas D. Gorné, Gustavo A. Bertone, Sandra Díaz

Instituto Multidisciplinario de Biología Vegetal (CONICET-UNC) and FCEFyN, Universidad Nacional de Córdoba, Casilla de Correo 495, CP 5000 Córdoba, Argentina

ARTICLE INFO

ABSTRACT

Qualitative measures of resprouting capacity often fail to capture inter- and intra-species variation, whereas available quantitative methods can be complex and time-consuming, hindering broad-scale comparative studies. Here, we propose two quantitative indices that can be applied in a standard way in different regions. We sampled 1046 plants of 20 dominant species (6 shrubs, 7 trees and 7 tree/shrubs) from the seasonally dry forests of the arid Chaco, central-western Argentina. Sampling was conducted in burned field sites one growing season after fire. For each sampled plant we measured the diameter of the main burned trunk (MTD) and main resprout (MRD), and the number of burned trunks (TN) and resprouts (RN); we then built estimated composite diameters for trunks and resprouts (ECTD and ECRD) and we calculated two alternative Resprouting Capacity Indices: RCI 1 (ECRD/ECTD); and RCI 2 (MRD/MTD). The indices were validated against a measure of Resprouting Vigour (RV) that included detailed measurement of all trunks and resprouts for a subset of sampled plants. In all cases, variables indicative of fire severity were measured and included in the analyses. The RCIs and RV were highly related, both at the species and growth form levels. Fire severity had no significant effect on these relationships, but growth form affected RCI 2. All species were capable of resprouting, showing considerable inter-species variation for the two proposed RCIs. Species rank differed considerably between RCIs and survival-only estimations. RCI 1 was higher in tree/shrubs (i.e. species regarded as trees or shrubs) and trees than in shrubs. All species showed decreasing resprouting capacity with increasing ECTD. Our results support the use of the proposed RCIs as a robust tool to assess resprouting capacity, providing more details than survival-based assessments. Choosing one or the other implies a trade-off between accuracy and simplicity, and may depend on the scale and objective of the study, and resprouting patterns of studied species. Species, growth form and individual plant size are relevant in explaining post-fire resprouting capacity and survival.

1. Introduction

Resprouting is one of the most common plant regeneration strategies, allowing recovery after disturbances such as logging, herbivory and fire, via dormant buds that consume below-ground reserves, even when the entire aerial biomass has been lost (Bond and Midgley, 2001). Being widespread in species from contrasting regions worldwide (Bond and Van Wilgen, 1996; Del Tredici, 2001; Vesk and Westoby, 2004), resprouting capacity is considered an ancestral trait in most plant lineages (Wells, 1969; Bond and Midgley, 2003).

Resprouting capacity can vary widely among different species due to factors acting at different spatial and temporal scales. Key factors at

larger scales are historical disturbance regimes, disturbance type and severity, and environmental characteristics, among others (Kruger et al., 1997; Bellingham and Sparrow, 2000; Del Tredici, 2001; Bond and Midgley, 2001; Bond and Midgley, 2003; Vesk and Westoby, 2004; Pausas and Keeley, 2014). At a smaller scale, growth form (Vesk et al., 2004; Vesk, 2006; Zizka et al., 2014) and individual plant size (Burrows, 1985; Hodgkinson, 1998; Keeley, 2006; Schafer and Just, 2014) are also key to explain plant response to disturbance, mainly because there is a trade-off between reserve storage and the production of new tissues (Bond and Midgley, 2001; Schwilk and Ackerly, 2005; Vesk, 2006). For example, it's been reported that shrubs in semiarid environments tend to produce a greater number of thinner resprouts

than trees, and a greater total volume of resprouts per unit area, so their canopies can rapidly achieve the reproductive size; whereas trees allocate reserves to a smaller number of thicker resprouts to grow tall and escape the flame zone (Hoffmann and Solbrig, 2003; Zizka et al., 2014). However, the interactions between these and other species-specific factors (such as plant functional traits) can be complex, and therefore the physiological responses observed in the field can be difficult to interpret in terms of growth form (Hodgkinson, 1998; Jackson et al., 1999; Hoffmann and Solbrig, 2003; Falster and Westoby, 2005; Gurvich et al., 2005; Vesk, 2006; Casals et al., 2018).

Furthermore, there is evidence that resprouting capacity in woody species, including trees and shrubs, peaks between the first years of life and maturity, and afterwards decreases with age (Burrows, 1985; Hobbs and Mooney, 1985; Bond and Van Wilgen, 1996; Hodgkinson, 1998; Del Tredici, 2001; Hoffmann and Solbrig, 2003; Keeley, 2006; Vesk, 2006; Clarke et al., 2013). In some cases a bimodal peak in resprouting (measured as number of resprouts per plant) has been observed (MacDonald and Powell, 1983).

Resprouting in response to fire has been widely studied (Lloret et al., 1999; Higgins et al., 2000; Pausas et al., 2004), especially in ecosystems with a long evolutionary history of periodic fires, such as Mediterranean-climate ecosystems, where the frequency distribution of post-fire resprouting tends to follow a bimodal pattern (Pausas et al., 2004; Vesk et al., 2004; Pausas and Keeley, 2014). Therefore, in these regions a dichotomous measure of presence/absence of resprouting has proven useful for vegetation prediction and modelling at a large scale (Noble and Slatyer, 1980; Loehle, 2000). However, in other fire-prone regions, such as the Chaco of central-western Argentina, where the evolutionary history of fire may not be as long and intense as in Mediterranean-climate ecosystems, a dichotomous classification of fire response does not satisfactorily explain the inter- and intra-species variations observed in the field (Vesk and Westoby, 2004; Moreira et al., 2012). In these ecosystems, the response to fire may be better described as a continuous gradient, for example, from species with high to species with low resprouting capacity (Bellingham and Sparrow, 2000; Bond and Midgley, 2003; Vesk and Westoby, 2004; Pausas et al., 2016).

Different protocols have been proposed for measuring resprouting capacity, from estimations of post-disturbance survival percentage at the species level (Pérez-Harguindeguy et al., 2013), which is a measure of resprouting capacity based on a qualitative binary classification of resprouting success (i.e. yes/no), to more complex quantitative measures. The former are usually simple and fast but they lack precision for detailed comparative studies, since they often fail to capture the intra- and inter- species variability. The latter generally involve several parameters such as pre-fire and post-fire plant height and basal diameter, and/or number and length of resprouts, in order to estimate canopy volume, plant biomass and/or resprouted biomass, (e.g. Cruz, Pérez, and Moreno, 2003; Fulbright, Dacy, and Drawe, 2011; Gittins, Ghermandi, and Bran, 2011; Gurvich et al., 2005; Moreira et al., 2012; Zizka et al., 2014). Another method of special interest for the present study is that of Neke et al. (2006), who proposed measuring the number and diameter of all trunks (pre-disturbance independent variables) and the number and diameter of all resprouts (post-disturbance dependent variables) to calculate composite diameters (i.e. the diameter of aggregated cross-sectional areas) of both and estimate the resprouting vigour as the composite diameters of resprouts divided by the composite diameters of trunks. All these protocols can be logistically complex and/or time-intensive and therefore impractical in many situations, for example for measuring a large number of species for comparative purposes. Therefore, developing a quantitative measurement of resprouting capacity that captures inter- and intra-specific variations, and is simple enough to be used in different ecosystems and situations, can be very useful for comparative studies in fire ecology.

Here we propose a quantitative resprouting capacity index that considers the diameters of the main trunk and the main resprout (i.e. the thickest ones), and the number of burned trunks and resprouts in

each individual plant, to estimate the respective composite diameters (see Methods). As an even simpler option, we also propose an index that uses only the diameters (i.e. not number) of the main burned trunks and resprouts. The proposed indices account for non-resprouted individuals (i.e. no resprouts recorded during sampling, used as proxy for non-surviving), therefore combining not only a measure of resprouting vigour, but also the survival rate at the individual level, hence better reflecting the resprouting capacity of species in the field. We support the proposed indices with detailed measurements of actual composite diameters (following Neke et al., 2006), and we illustrate their potential by reporting on the resprouting capacity of 20 woody species of three different growth forms (6 shrubs, 7 trees and 7 tree/shrubs) from the dry Chaco region of central Argentina.

Resprouting (rather than recruitment) is the main post-fire regeneration strategy of dominant species in the Chaco (Morello and Saravia Toledo, 1959; Gurvich et al., 2005; Barchuk et al., 2006; Bravo et al., 2014; Torres et al., 2014). Although Chaco forests have been historically subjected to fire for centuries to millennia, due to hunting practices of indigenous peoples (Morello and Saravia Toledo, 1959) and also possibly to natural fires produced by lightning during summer storms, there is no evidence of fire as a strong natural selection pressure over longer evolutionary time. However, fire is a common factor in the region, mainly due to its use as a management tool (Kunst et al., 2000; Kunst et al., 2003; Casillo et al., 2006) and the expansion of population and agriculture (Tálamo and Caziani, 2003; Grau et al., 2005; Boletta et al., 2006; Bravo et al., 2010), which has increased the frequency of fires (Argañaraz et al., 2015a), challenging the adaptive capacity of plants.

On these bases, here we (1) propose two quantitative indices of resprouting capacity with the potential to be applied in a standard way in different regions; (2) assess and compare the resprouting capacity of 20 woody dominant species of the arid Chaco forests; (3) analyse the influence of growth form and trunk diameter (as a proxy for plant size) on the resprouting capacity of woody plants. For completeness, patterns of survival are also explored and discussed in relation to the proposed indices.

2. Materials and methods

2.1. Study area

The study area is located in north-western Córdoba Province, central Argentina (30°20′-32°10′ S, 64°10′-65°38′W). Phytogeographically, this area belongs to the arid Chaco, including also a portion of the Chaco Serrano District (Cabrera, 1976; Morello et al., 1985) (Fig. 1). The vegetation is characterized by highly seasonal semi-deciduous xerophytic forests, with a mean annual precipitation ranging from < 500 mm to > 750 mm, concentrated in the spring-summer months (October-March) lowest mean monthly minimum and highest mean monthly maximum temperatures of 10.7 °C (July) and 26.1 °C (January), respectively (Capitanelli, 1979; Giorgis et al., 2015). The canopy of the lowland forests is discontinuous, dominated by *Aspidosperma quebracho-blanco* and *Prosopis flexuosa*. The shrub layer is thorny, dense and usually continuous, dominated by *Larrea divaricata, Mimozyganthus carinatus* and *Senegalia gilliesii*. A lower and discontinuous layer of grasses and herbs is dominated by *Trichloris crinita, T. pluriflora, Gouinia paraguayensis*, *Setaria* spp. and *Pappophorum* spp. (Cabido et al., 1992). In the mountain areas, the most representative species include *Lithraea molleoides, Zanthoxylum coco, Vachellia caven* and *Jarava pseudoichu* (Giorgis et al., 2011)

Fire season spans from June through December (i.e. early winter through early summer), with highest occurrence of fires in August–September (Miglietta, 1994; Argañaraz et al., 2015a). Fire frequency varies considerably within the study region, mainly depending on climatic variables, human population density and vegetation type (Argañaraz et al., 2015b). The fire return interval for most of the study
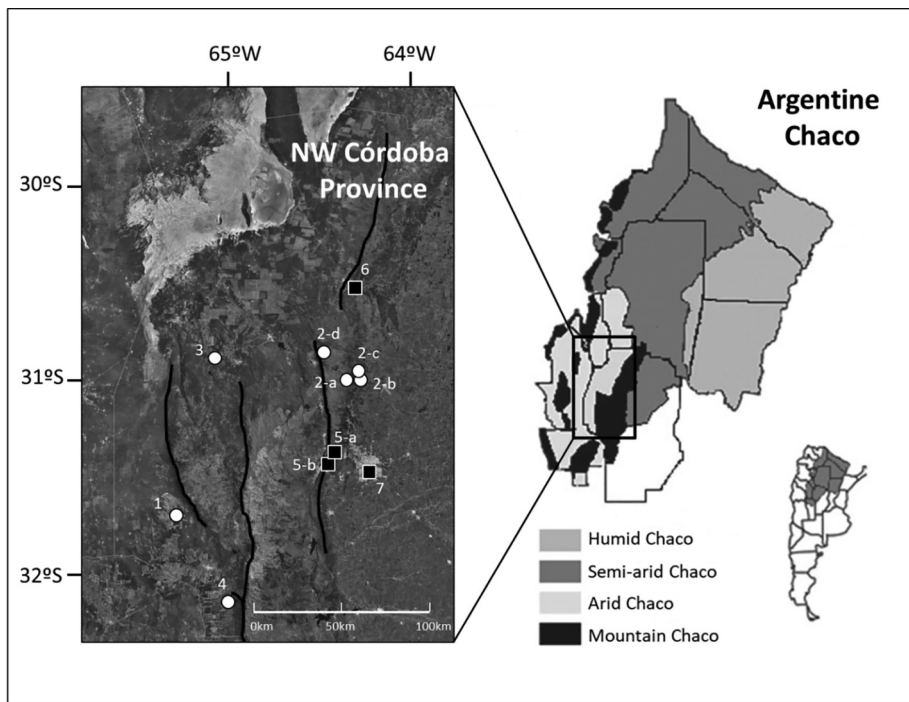
Fig. 1. Location of sampling sites within the study area in NW Córdoba Province, central Argentina. Sampling sites included seven independent fire events (numbered 1 to 7 in the left panel) of different sizes (see Table 2 and main text for details). We sampled 11 sites in total, including more than one site in the most extensive fires (labelled with lowercase letters). Black squares correspond to sampling sites for Data Set 1; white circles correspond to sampling sites for Data set 2. Black lines indicate the main mountain ranges in the study area.

area is 10 years or more, but some areas burn every 5–6 years, and others every 3–4 years (especially grasslands) (Bravo et al., 2010; Argañaraz et al., 2015a).

2.2. Plant species selection

Based on previous surveys (Cabido et al., 1992; Díaz et al., 1998; Conti and Díaz, 2013) we selected a total of 20 woody species dominant in the study area, representing 10 taxonomic families. We classified these species into three growth form types: shrubs (six species), trees (seven species), and tree/shrubs (seven species), with the latter including species whose growth form can be regarded either as tree or shrub (Demaio et al., 2002; Zuloaga et al., 2008) (Table 1). The selected species account for approximately 80% of the woody biomass, therefore their response to fire largely accounts for the response of the entire ecosystem.

2.3. Field measurements

Resprouting capacity was measured in individual plants at sites that have been subjected to accidental fires. A total of seven independent fire events were visited (Fig. 1; Table 2). Five of them had a surface area of 1–300 ha, and were extensively traversed during sampling, covering all, or a large part of the affected area. The remaining two fires were

Table 1
List of species included in this study, with their corresponding taxonomic information and growth form (trees = 7; shrubs = 6; tree/shrubs = 7). Nomenclature follows the Catálogo de las Plantas Vasculares del Cono Sur (Zuloaga et al., 2008) and online updates (http://www.floraargentina.edu.ar/). The last columns indicate if the species were included in one or the two datasets compiled for the study (see details in the main text), and the respective number of individuals sampled for each dataset.

| Species | Family | Growth form | Dataset 1 (N = 192) | | Dataset 2 (N = 854) | |
			Yes/No	n	Yes/No	n
Aloysia gratissima (Gillies & Hook.) Tronc.	Verbenaceae	shrub	Yes	19	Yes	60
Aspidosperma quebracho-blanco Schltdl.	Apocynaceae	tree	Yes	25	Yes	57
Castela coccinea Griseb.	Simaroubaceae	tree/shrub	No	–	Yes	31
Celtis ehrenbergiana (Klotzsch) Liebm.	Celtidaceae	tree/shrub	Yes	16	Yes	64
Cercidium praecox (Ruiz & Pav.) Burkart & Carter	Fabaceae	tree	No	–	Yes	60
Condalia microphylla Cav.	Rhamnaceae	shrub	Yes	19	Yes	62
Geoffroea decorticans (Gillies ex Hook. &Arn.) Burkart	Fabaceae	tree	Yes	19	Yes	56
Jodina rhombifolia (Hook. & Arn.) Reissek	Santalaceae	tree	Yes	2	Yes	14
Larrea divaricata Cav.	Zygophyllaceae	shrub	Yes	8	Yes	35
Lycium sp. Miers	Solanaceae	shrub	No	–	Yes	56
Mimozyganthus carinatus (Griseb.) Burkart	Fabaceae	shrub	No	–	Yes	30
Maytenus spinosa Griseb.	Celastraceae	shrub	Yes	15	Yes	27
Prosopis chilensis (Molina) Stuntz.	Fabaceae	tree	No	–	Yes	14
Prosopis flexuosa DC	Fabaceae	tree	Yes	20	Yes	61
Prosopis torquata (Cav. ex Lag.) DC	Fabaceae	tree/shrub	Yes	5	Yes	35
Senegalia gilliesii Steud.	Fabaceae	tree/shrub	No	–	Yes	35
Senegalia praecox Griseb.	Fabaceae	tree/shrub	Yes	8	Yes	27
Vachellia aroma Gillies ex Hook. & Arn.	Fabaceae	tree/shrub	Yes	10	Yes	51
Vachellia caven (Molina) Molina	Fabaceae	tree/shrub	Yes	26	Yes	60
Ziziphus mistol Griseb.	Rhamnaceae	tree	No	–	Yes	19

Table 2
Relevant information of the fire events visited during the present study. The first column refers to the fire events as presented in Fig. 1.

Fire event	Reference location	Approximate coordinates	Average altitude (m.a.s.l.)	Approximate area of fire (hectares)	Date of fire	Date of sampling
1	El Poniente	31°40′S, 65°23′W	350	250	September 2008	March 2009
2a	Ascochinga	30°56′S, 64°20′W	1000	45,000	September 2008	April 2009
2b	Ascochinga	30°57′S, 64°15′W	690	45,000	September 2008	April 2009
2c	Ascochinga	30°54′S, 64°15′W	760	45,000	September 2008	April 2009
2d	Los Terrones	30°47′S, 64°28′W	1250	45,000	September 2008	June 2009
3	Pichanas	30°50′S, 65°08′W	490	280	≈August 2008	April 2009
4	Luyaba	32°07′S, 65°03′W	670	570*	≈August 2009	June 2010
5a	Casa Bamba	31°20′S, 64°24′W	790	6,000	September 2017	April 2018
5b	Carlos Paz	31°23′S, 64°26′W	750	6,000	September 2017	April 2018
6	Deán Funes	31°27′S, 64°16′W	830	220	September 2017	May 2018
7	Córdoba city	31°26′S, 64°11′W	430	1	August 2017	May 2018

*Only 300 ha occurred in vegetation relevant to the present study.

much larger, covering 6,000 and 45,000 ha (J. Argañaraz, pers. comm.); therefore representative sites for sampling were chosen within them (Fig. 1; Table 2). At each visited site plants were randomly selected and sampled. In an attempt to cover different diameter classes within each species and obtain the fullest possible picture of the response capacity at different plant sizes, a total of 1046 individuals were sampled. The number of individuals sampled for each species was mainly determined by the combination of logistic feasibility and relative abundance of each species in the visited sites.

In all cases, measurements were taken after the growing season following the fire, between March and June (Table 2). These measurements comprised two distinct datasets: one included a detailed measurement of the diameters of each burnt trunk and resprout of each individual plant. This dataset (Dataset 1) comprised a total of 192 individuals belonging to 13 species (4 shrubs; 4 trees and 5 tree/shrubs; Table 1). The other dataset (Dataset 2) included the measurement of the diameter of only the main trunk and main resprout (i.e. the thickest ones), and total number of trunks and resprouts recorded in each individual plant (see details below). This dataset comprised 854 individuals belonging to 20 species (6 shrubs, 7 trees and 7 tree/shrubs; Table 1). The number of sampled individuals per species ranged between 2 and 26 for Dataset 1, and between 14 and 64 for Dataset 2 (Table 1). All diameter measures were recorded and analysed in millimetres.

For Dataset 1 (N = 192; Table 1) the following variables were measured in each plant:

1. Diameter of burned trunks (TD): the diameter of all burned trunks was measured close to the ground with a measuring tape or –in the case of smaller individuals- a manual caliper. Then, following the methodology of Neke et al. (2006), a composite trunk area (CTA) was calculated by adding the area of the measured trunks, as follows:

$$CTA = \sum_{i}^{n} \pi \times (TD_i/2)^2 \qquad (1)$$

And then a composite trunk diameter (CTD) was obtained as:

$$CTD = \sqrt{CTA \times 4/\pi} \qquad (2)$$

2. Diameter of resprouts (RD): the diameter of all resprouts was measured at approximately 5 cm from its base using a manual caliper. Composite resprout area (CRA) and resprout diameter (CRD) were calculated with equations analogous to the previous point.

Following Neke et al. (2006), CTD and CRD were used to calculate the resprouting capacity (hereafter referred to as 'Resprouting Vigour', RV) for each individual, using the following equation:

$$RV = CRD/CTD \qquad (3)$$

Next, using only the diameter of the main burned trunk (MTD) and the number of burned trunks (TN), for each sampled plant we calculated the estimated composite trunk area (ECTA) as follows:

$$ECTA = \pi \times (MTD/2)^2 \times TN \qquad (4)$$

Analogously, the diameter of the main resprout (MRD) (i.e. the thickest ones), and the number of burned resprouts (RN) were used to calculate, for each sampled plant, the estimated composite resprout area (ECRA).

The respective estimated composite trunk diameter (ECTD) and estimated composite resprout diameter (ECRD) were also calculated for each sampled plant as follows:

$$ECTD = \sqrt{ECTA \times 4/\pi} \qquad (5)$$

$$ECRD = \sqrt{ECRA \times 4/\pi} \qquad (6)$$

Afterwards, we calculated a resprouting capacity index (hereafter referred to as RCI 1) as:

$$RCI1 = ECRD/ECTD \qquad (7)$$

Additionally, we calculated an alternative resprouting capacity index (hereafter referred to as RCI 2) considering only MTD and MRD of each sampled individual as:

$$RCI2 = MRD/MTD \qquad (8)$$

For Dataset 2 (N = 854; Table 1), the diameter of the main trunk (MTD) and main resprout (MRD), as well as the number of trunks (TN) and resprouts (RN) were recorded for each individual. Afterwards, Eqs. (4)–(8) were calculated for each individual. For this dataset the following criterion was used for measuring RN: when there were between 0 and 20 resprouts, the exact number was recorded. When there were > 20, the number was recorded as "+20". In such cases, a value of 25 was used for statistical analyses. These ranges were selected following previous studies (e.g. Flinn et al., 1992; Kunst et al., 2000; Casillo et al., 2006; Zizka et al., 2014). For eight species (three shrubs, three trees and two shrub/trees) trunk counts (TN) were missed in the original sampling, therefore they were calculated based on a representative sample (N = 152; Appendix A), and not on the plants sampled at burnt sites. Regression analyses of this representative sample showed no significant relationship between trunk diameter and TN, therefore a single mean value was used for each of these eight species.

Because the main purpose of Dataset 1 was to establish the relationship between the RV and the RCIs, field measurements did not include non-resprouting individuals (i.e. RN = 0, therefore making RV and RCIs be zero). In contrast, for Dataset 2 non-resprouting individuals were included as a proxy of the survival rate of each species. Comparisons of the response variables (i.e. RCIs, ECRD and RN) between species were based on Dataset 2.

Given that resprouting capacity may vary considerably depending on fire severity (i.e. aboveground and belowground organic matter consumption from fire; Keeley, 2009) (Bellingham and Sparrow, 2000; Keeley, 2006), variables indicative of fire severity were measured in and around each sampled individual of both datasets (Moreno and

Oechel, 1989; Pérez and Moreno, 1998; Henig-Sever et al., 2001; Keeley, 2009; Catry et al., 2010). The following variables were measured in each individual:

Minimum standing diameter: the diameter of the thinnest burned trunk that remained standing was measured and values were assigned to the following intervals: 1 = 0–5 mm; 2 = 5–10 mm; 3 = 10–20 mm; 4 = 20–30 mm; 5 = +30 mm. Intervals were defined based on bibliography (e.g. Anderson, 1982; Moreno and Oechel, 1989) and on previous field observations by the authors.

State of bark: the state of the bark after the fire was classified as follows:

1 = Burned (when the bark was black due to the fire but remained mostly attached to the trunk)
2 = Loose (when the bark, in addition to being black, appeared detached due to fire damage)

State of soil: the state of soil surrounding each individual was classified as:

1 = normal colour or slightly blackish (i.e. burned) on the surface
2 = blackish colour, burned up to 1 cm in depth
3 = presence of white ashes on the surface, burned more than 1 cm in depth

We then calculated a composite fire severity value for each individual by adding the scores recorded for the three variables mentioned above. Based on their frequency, the severity values were grouped *a posteriori* into four categories, which were used as levels of severity in the analyses. Additionally, the 'Percentage of plant affected by fire' was estimated visually, and classified *a posteriori* as fully affected (i.e. 100% of plant affected) or not fully affected (i.e. < 100% of plant affected). Both composite fire severity and percentage affected by fire (with their corresponding levels) were used as fixed factors in the statistical analyses (see below). Values originally recorded and their corresponding *a posteriori* values of both variables are presented in Appendix B.

2.4. Data analysis

2.4.1. Analysis of Dataset 1
We explored the relationship between the RCIs and RV (Dataset 1) at the species and growth form levels through linear regressions, using log-transformed data. A linear model was used to evaluate if severity and growth form (and their interactions) affected the performance of the RCIs; percentage affected by fire was not included in the analysis because almost all individuals had a value of 100%. Model selection was based on the Akaike criterion (Akaike, 1972). The adjustment of the models was made using the *nlme* R-package (Pinheiro et al., 2013).

2.4.2. Analysis of Datset 2
To explore the differences in the response variables (RCI 1, RCI 2, ECRD and RN) between species, Dataset 2 was analysed through generalised linear models, considering a normal distribution model for variables RCI 1, RCI 2 and ECRD (using log-transformed data); and Poisson distribution for RN. The models considered species, severity and percentage of plant affected by fire as factors. Because there is a relationship between resprouting capacity and ECTD (i.e. larger plants have more resources to resprout), this latter variable was included in the model, as well as its interaction with species. The models also considered the heterogeneity of variances due to species. Model selection was based on the Akaike criterion (Akaike, 1972). The adjustment of the models was made using *nlme* (Pinheiro et al., 2013) and *lme4* (Bates et al., 2015) R-packages. The relationship between the RCIs and ECTD was analysed through standardised major axis regression (Warton et al., 2006) using the *smatr* R-package (Warton et al., 2012). The

relationship between ECTD and survival was analysed through logistic regression. Differences between growth forms were explored through *a posteriori* contrast analysis (i.e. lineal combination of the parameters of the model), grouping species by growth form in three different positions along the full range of diameters of the full Dataset 2 considering deciles one, five (the median value of the data) and nine of the ECTD. Analyses were performed using InfoStat Version 2017p (Di Rienzo et al., 2017) and R (R Core Team, 2019). For completeness, and with the purpose of depicting the physiognomic differences between the studied growth forms, summary values of independent variables ECTD and TN were compiled based on empirical data (i.e. not modelled) and presented in Appendix C.

3. Results

3.1. Relationship between the resprouting vigour (RV) and the proposed resprouting capacity indices (RCI 1 and RCI 2)

Regression analyses of Dataset 1 (N = 192) showed a highly significant relationship between RV and the two proposed RCIs for the three studied growth forms, with R^2 values ranging between 0.76 and 0.92 and $P < 0.0001$ (Fig. 2). Furthermore, at the species level RV was also highly related to the two RCIs, with the only exceptions of *Prosopis torquata* ($R^2 = 0.63$, $P = 0.11$ for RCI1; $R^2 = 0.58$, $P = 0.14$ for RCI 2) and *Senegalia praecox* ($R^2 = 0.33$, $P = 0.14$ for RCI 2) (Appendix D). The composite fire severity had no significant effect on the relationship between the RCIs and the RV (Appendix E), indicating that the level of severity did not affect the performance of the proposed indices. Furthermore, the growth form did not have an effect on the performance of RCI 1, but it did have an effect on RCI 2 (Appendix E), indicating that estimations for trees and tree/shrubs are more accurate than for shrubs, therefore comparisons between growth forms (i.e. contrast analysis) for RCI 2 are not reported.

3.2. Differences between species in the RCIs and their components

All the studied species were able to resprout after the fire; however, they showed considerable differences in their resprouting capacity, as captured by both RCI 1 and RCI 2 (Fig. 3). RCI 1 indicated that *Celtis ehrenbergiana* was the species with the highest resprouting, followed by *P. flexuosa*, *Vachellia aroma*, *P. chilensis* and *Aloysia gratissima*, whereas *Lycium* sp. had the lowest capacity (Fig. 3). For RCI 2, within-growth form comparison showed that for trees *P. chilensis* resprouted the most, followed by *Z. mistol* and *A. quebracho-blanco*. For tree/shrubs, *C. ehrenbergiana* had the highest resprouting and *S. gilliesii* the lowest; and for shrubs, *L. divaricata* resprouted the most, followed by *Maytenus spinosa*; while *Lycium* sp. had the lowest resprouting (Fig. 3).

Despite the rank order of species showed some variations between the two indices (Fig. 4; Appendix F), the overall pattern was similar and highly correlated (Spearman correlation coefficient, $\rho = 0.70$, $P = 0.002$).

Regarding individual components of RCIs, species differed considerably in their ECRD and RN (Fig. 5). *C. ehrenbergiana* had the largest ECRD, followed by *P. chilensis* and *P. flexuosa*, whereas *S. gilliesii* had the smallest ECRD (Fig. 5). RN was highest in *C. ehrenbergiana*, followed by *Castela coccinea*; and was lowest for *S. gilliesii* (Fig. 5).

3.3. Survival percentage at the species level

Although most individuals resprouted, three species in particular had significantly lower survival percentages than expected by chance (i.e. ± 3 deviations of the expected value of 92%; Chi-square = 139.46; $P < 0.0001$; N = 854; see details in Appendix G), namely *S. gilliesii* (64%; n = 36), *C. praecox* (67%; n = 60) and *P. flexuosa* (82%; n = 61). The ranking of species according to their survival percentage differed considerably from that of RCIs (Fig. 4;
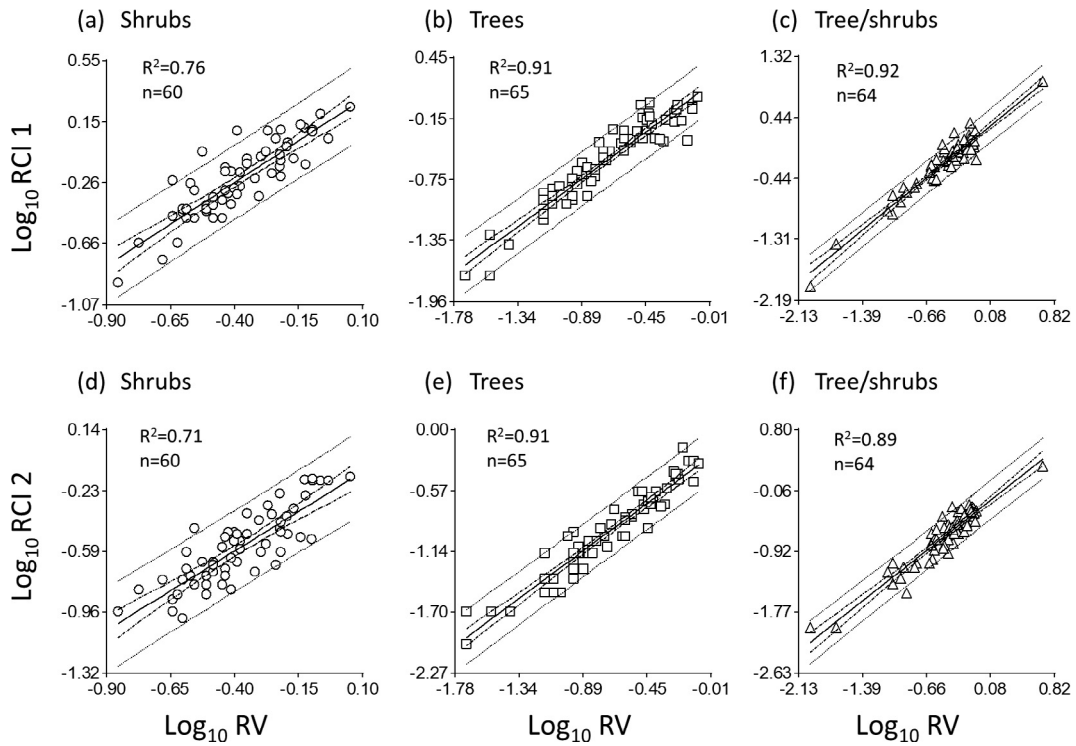
Fig. 2. Regression analysis of Dataset 1 showing the relationship between the two proposed Resprouting Capacity Indices (RCI 1 and RCI 2) and the Resprouting Vigour (RV), with their respective regression coefficients for each of the three studied growth forms (4 shrubs, n = 60; 4 trees, n = 65; 5 tree/shrubs, n = 64). $P < 0.0001$ for all relationships. Three cases with externally studentised residuals larger than four were excluded from the analysis. In each chart the solid line indicates the adjusted value, the dashed lines indicate the 95% prediction values, and the dotted lines indicate the 95% confidence interval. Data was log transformed for the analysis.
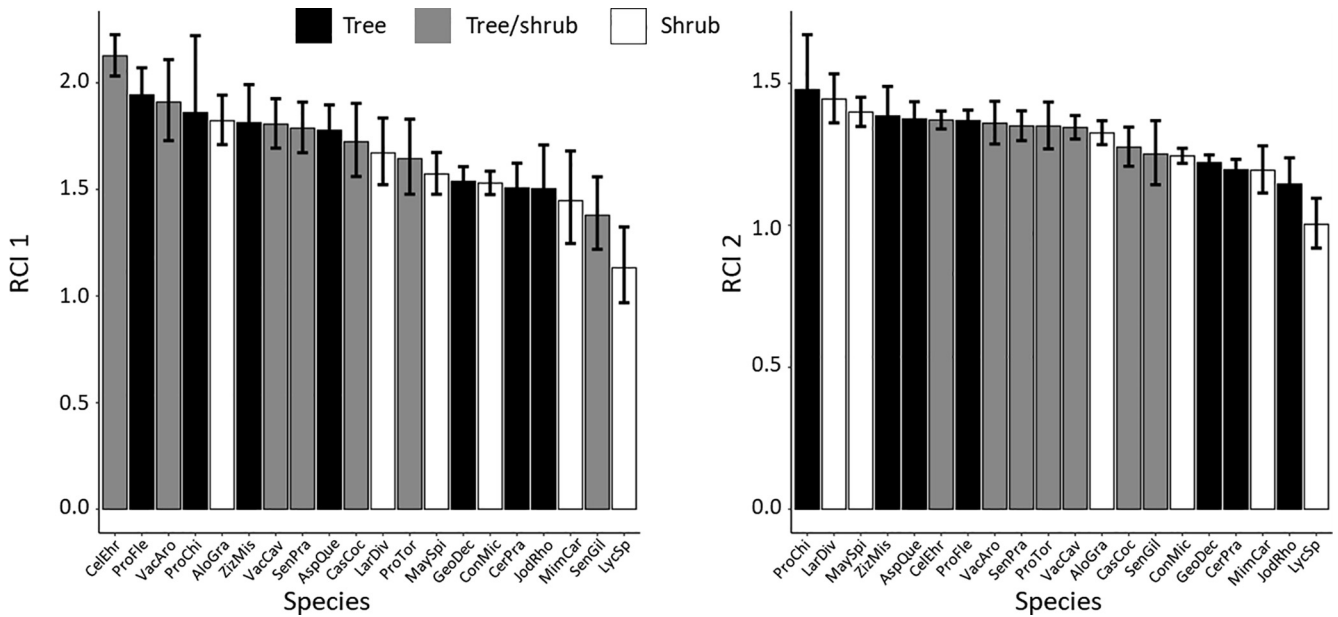

Fig. 3. Comparison between species of the two proposed Resprouting Capacity Indices: (a) RCI 1; and (b) RCI 2, for the 20 studied species (6 shrubs, white bars; 7 trees, black bars; and 7 tree/shrubs, grey bars). Whiskers indicate 95% confidence interval. Species names in alphabetical order (number of sampled individuals in parenthesis): AloGra = *Aloysia gratissima* (n = 60); AspQue = *Aspidosperma quebracho-blanco* (n = 57); CasCoc = *Castela coccinea* (n = 31); CelEhr = *Celtis ehrenbergiana* (n = 64); CerPra = *Cercidium praecox* (n = 60); ConMic = *Condalia microphylla* (n = 62); GeoDec = *Geoffroea decorticans* (n = 56); JodRho = *Jodina rhombifolia* (n = 14); LarDiv = *Larrea divaricata* (n = 35); LycSp. = *Lycium* sp. (n = 56); MaySpi = *Maytenus spinosa* (n = 27); MimCar = *Mimozyganthus carinatus* (n = 30); ProChi = *Prosopis chilensis* (n = 14); ProFle = *P. flexuosa* (n = 61); ProTor = *P. torquata* (n = 35); SenGil = *Senegalia gilliesii* (n = 35); SenPra = *S. praecox* (n = 27); VacAro = *Vachellia aroma* (n = 51); VacCav = *V. caven* (n = 60); ZizMis = *Ziziphus mistol* (n = 19).
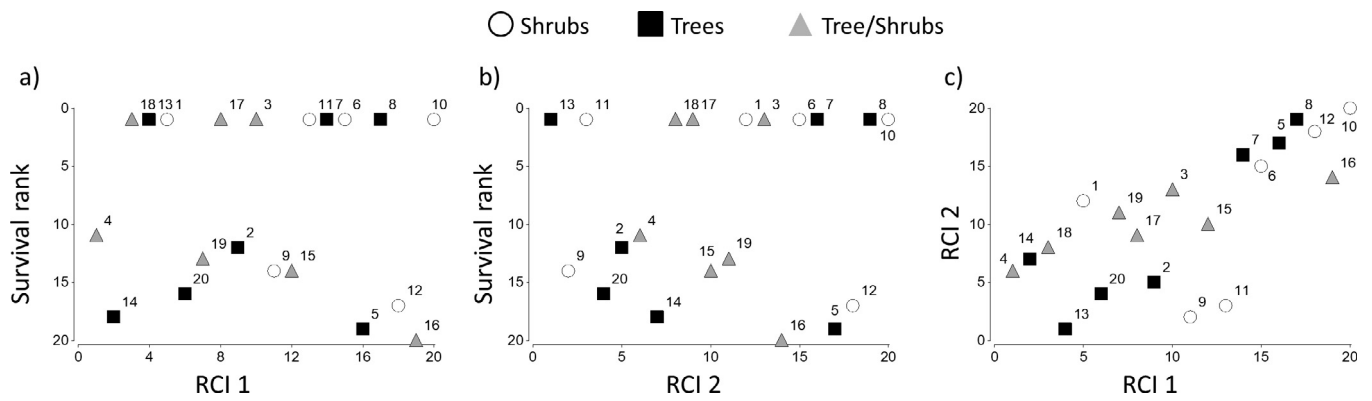
Fig. 4. Relationship between the rankings of resprouting capacity obtained for the 20 studied species (6 shrubs, 7 trees and 7 tree/shrubs) with the two proposed quantitative Resprouting Capacity Indices (RCI 1 and RCI 2), and the ranking obtained with survival percentage (inverted scale in *y* axis in (a) and (b)), which is a measure of resprouting capacity based on a qualitative binary classification of resprouting success (i.e. yes/no), for the same species. Species names (ordered by growth form): Shrubs; 1. *Aloysia gratissima* (n = 60); 2. *Condalia microphylla* (n = 62); 3. *Larrea divaricata* (n = 35); 4. *Lycium* sp. (n = 56); 5. *Maytenus spinosa* (n = 27); 6. *Mimozyganthus carinatus* (n = 30). Trees: 7. *Aspidosperma quebracho-blanco* (n = 57); 8. *Cercidium praecox* (n = 60); 9. *Geoffroea decorticans* (n = 56); 10. *Jodina rhombifolia* (n = 14); 11. *Prosopis chilensis* (n = 14); 12. *P. flexuosa* (n = 61); 13. *Ziziphus mistol* (n = 19). Tree/shrubs: 14. *Castela coccinea* (n = 31); 15. *Celtis ehrenbergiana* (n = 64); 16. *Senegalia gilliesii* (n = 35); 17. *S. praecox* (n = 27); 18. *Prosopis torquata* (n = 35); 19. *Vachellia aroma* (n = 51); 20. *V. caven* (n = 60).

Appendix F) and was not correlated (ρ = -0.10; P = 0.69 for RCI 1 and ρ = 0.04; P > 0.87 for RCI 2). This was especially noticeable for *Lycium* sp., which was ranked first in terms of survival percentage, but it was ranked 20th according to the RCIs (Fig. 4). The main reason for this is that this species had usually very thin resprouts, therefore although they may be numerous, their composite diameter is relatively low compared to the composite trunk diameter.

3.4. Differences between growth forms

Trees and tree/shrubs differed significantly from shrubs regarding RCI 1 for all three deciles analysed, but showed no significant differences between them (Table 3). Furthermore, ECRD differed between trees and shrubs for the three deciles, and between trees and tree/shrubs for D1 and D9; whereas shrubs did not differ from tree/shrubs (Table 3). RN differed between trees and shrubs for all deciles, while it differed between trees and tree/shrubs only for D9, and showed no differences between shrubs and tree/shrubs (Table 3). Finally, mean values of ECTD for shrubs was 48.37 mm, for tree/shrubs 69.04 mm and for trees 99.64 mm; moreover, mean TN for shrubs was 3.01, for tree/shrubs 2.08 and for trees 1.38 (Appendix C).
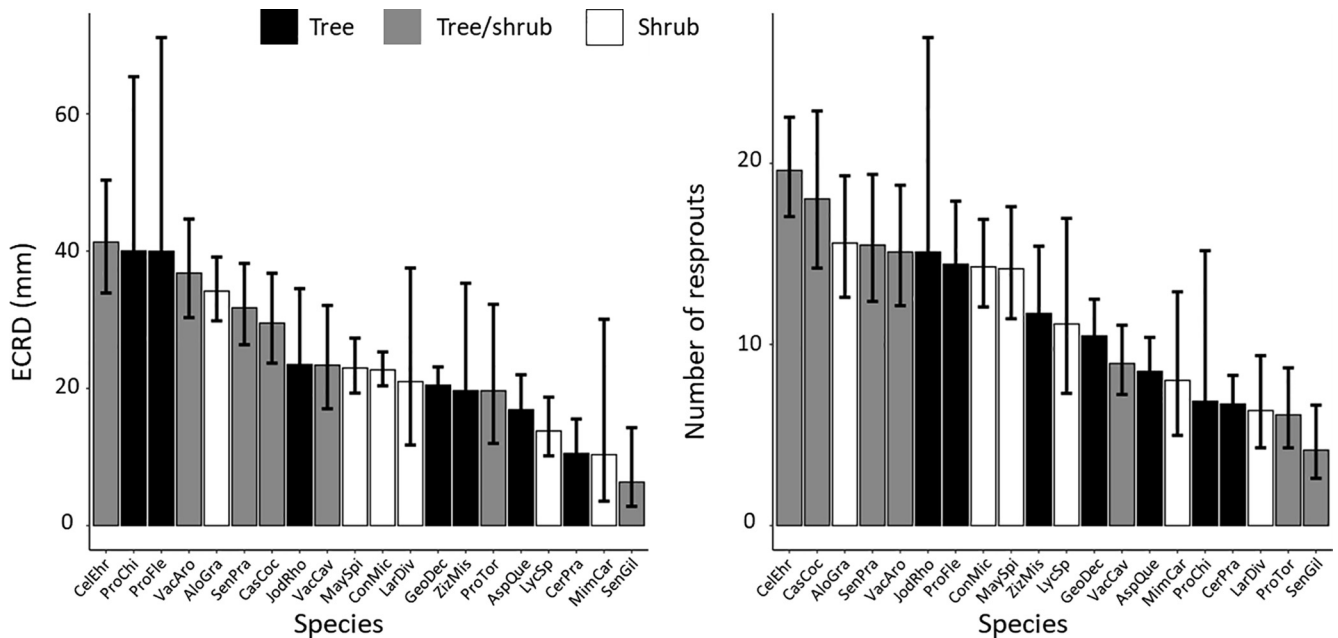

Fig. 5. Comparison between species of the response variables: (a) Estimated Composite Resprout Diameter (ECRD), and (b) Resprout Number, for the 20 studied species (6 shrubs, white bars; 7 trees, black bars; and 7 tree/shrubs, grey bars). Whiskers indicate 95% confidence interval. Species names in alphabetical order (number of sampled individuals in parenthesis): AloGra = *Aloysia gratissima* (n = 60); AspQue = *Aspidosperma quebracho-blanco* (n = 57); CasCoc = *Castela coccinea* (n = 31); CelEhr = *Celtis ehrenbergiana* (n = 64); CerPra = *Cercidium praecox* (n = 60); ConMic = *Condalia microphylla* (n = 62); GeoDec = *Geoffroea decorticans* (n = 56); JodRho = *Jodina rhombifolia* (n = 14); LarDiv = *Larrea divaricata* (n = 35); LycSp. = *Lycium* sp. (n = 56); MaySpi = *Maytenus spinosa* (n = 27); MimCar = *Mimozyganthus carinatus* (n = 30); ProChi = *Prosopis chilensis* (n = 14); ProFle = *P. flexuosa* (n = 61); ProTor = *P. torquata* (n = 35); SenGil = *Senegalia gilliesii* (n = 35); SenPra = *S. praecox* (n = 27); VacAro = *Vachellia aroma* (n = 51); VacCav = *V. caven* (n = 60); ZizMis = *Ziziphus mistol* (n = 19).

Table 3

Contrast analysis comparing the Resprouting Capacity Index 1 (RCI 1), the Estimated Composite Resprout Diameter (ECRD; mm) and the Resprout Number (RN) between the three studied growth forms (shrubs, n = 6; trees, n = 7; and tree/shrubs, n = 7), with their corresponding estimated values. RCI 2 was not compared due to the effect of growth form on the performance of the index (see main text for details). Comparisons were made at three different points in the range of values of the Estimated Composite Trunk Diameter registered for the full Dataset 2, namely deciles one (D1), five (D5 = median) and nine (D9) of the data. *P* values highlighted in bold indicate significant differences between growth forms (α = 0.05). The variables RCI 1 and ECRD were analysed considering a normal distribution, while RN considering a Poisson distribution (see details in Methods).

Variable		DF	Trees vs. shrubs		Trees vs. tree/shrubs		Shrubs vs. tree/shrubs		Estimated values		
			F-value	*P*-value	F-value	*P*-value	F-value	*P*-value	Trees	Shrubs	Tree/shrubs
RCI 1	D1	1	11.90	**6.0E-04**	1.50	0.221	24.460	**< 0.0001**	2.341	1.948	2.487
	D5	1	48.15	**< 0.0001**	0.14	0.708	58.690	**< 0.0001**	1.766	1.418	1.783
	D9	1	24.75	**< 0.0001**	1.90	0.169	11.800	**6.0E-04**	1.214	0.931	1.147
RCI 2	D1								1.613	1.530	1.699
	D5								1.351	1.219	1.351
	D9								1.068	0.902	0.997
ECRD	D1	1	16.467	**1.0E-04**	7.210	**0.0074**	2.595	0.108	12.468	5.798	8.007
	D5	1	5.071	**0.0246**	0.418	0.5177	2.890	0.090	9.203	7.362	8.719
	D9	1	15.380	**1.0E-04**	16.218	**1.0E-04**	0.054	0.815	6.152	10.105	9.763
RN			Z-value								
	D1	1	0.390	**0.6970**	0.913	0.361	−0.580	0.562	9.482	8.816	8.046
	D5	1	−1.334	**0.1820**	−0.715	0.475	−0.844	0.398	10.354	11.943	11.065
	D9	1	−2.493	**0.0147**	−3.205	**1.35E-03**	−0.304	0.761	11.634	17.862	16.883

3.5. Influence of plant size (ECTD)

At the growth form level, both RCIs showed a decreasing pattern with increasing values of ECTD (Table 3). For RCI 1, tree/shrubs had the highest values of resprouting for deciles D1 and D5, whereas trees had higher resprouting in decile D9 (Table 3; Appendix H). A similar pattern was observed for ECRD in trees, but the opposite was observed in tree/shrubs and shrubs. Moreover, RN also increased with increasing values of ECTD for all three growth forms (Table 3). For ECRD, trees had the highest values for D1 and D5, and shrubs for D9. For RN trees had the highest value for D1 and shrubs for D5 and D9 (Table 3).

At the species level, all the studied species showed a decreasing resprouting capacity as their ECTD increased for both proposed indices (Fig. 6). However, regression slopes differed among species both for RCI 1 (SMA regression, Likelihood Ratio = 94.7; P = 4.82e-12) and RCI 2 (Likelihood Ratio = 154.4; P = < 2.22e-16) (Fig. 6). Furthermore, survival was significantly and negatively associated with ECTD (β ± S.E. = −0.078 ± 0.012; Wald test z = −6.63; P = 3.48e-11; N = 854; Appendix I), showing an 8.1% decrease in the chances of survival for every centimetre of increase in ECTD.

4. Discussion

4.1. Relationship between the resprouting vigour and the proposed resprouting capacity indices

The analysis of Dataset 1 showed that the two proposed indices, RCI 1 (the ratio of the estimated composite resprout diameter to the estimated composite trunk diameter), and RCI 2 (the ratio of the main resprout diameter to the main trunk diameter), had a consistent relationship with the RV, both at the growth form level (Fig. 2) and at the species level (Appendix D). This results support the use of the indices as reliable estimators of resprouting capacity. The non-significant relationship observed in *P. torquata* for the two RCIs, and in *S. praecox* for RCI 2 (Appendix D), despite both showed relatively high R² values, could be explained by the low number of replicates of these two species. Further measurements will help confirm the performance of the proposed RCIs for said species. Our results indicate that despite the variability in the number and diameter of resprouts and trunks between and within species, the allometric relationship between their respective estimated composite diameters (ECRD and ECTD) is closely linked to the relationship between the diameter of the main resprout and the main trunk, as has been shown for a limited number of tree species by Schafer and Just (2014).

The proposed RCIs provide a simple and accurate quantitative measure of resprouting capacity at the individual level, allowing a large
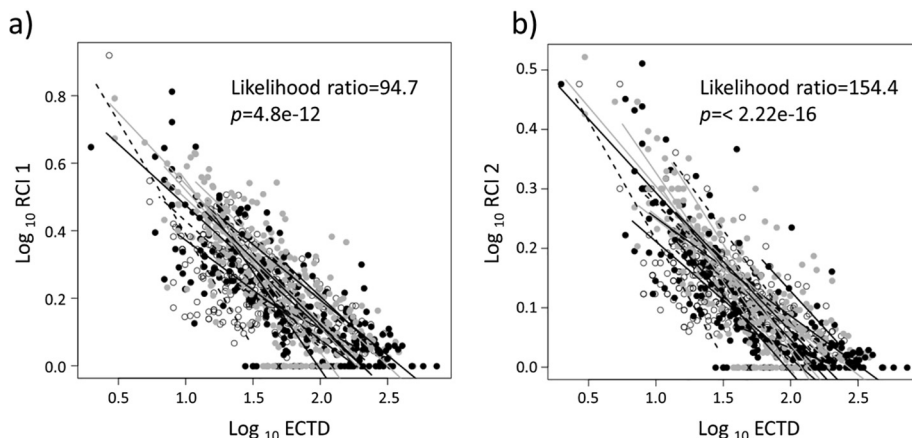

Fig. 6. Standardised Major Axis analysis showing the relationship between the Estimated Composite Trunk Diameter (ECTD) and the two proposed Resprouting Capacity Indices: a) RCI 1); and b) RCI 2. All sampled individuals are depicted (N = 854), with their corresponding growth form and respective regression lines for each species indicated as follows: shrubs (n = 270) = empty circles, dashed lines; trees (n = 281) = black filled circles, black solid lines; tree/shrubs (n = 303) = grey circles, grey lines. Log transformation of data was properly managed to include non-resprouting individuals (i.e. zero values) in the analyses.

number of species to be measured in a short time, therefore constituting a robust option for standardized intra- and inter-specific comparisons between different floras.

The fact that the present study includes more species than previous quantitative studies allows us to draw more robust conclusions about the allometric relationships of the above-ground plant tissues before and after the fire. In addition to the intrinsic value of the indices to assess the resprouting capacity of species after a fire, the allometric relationships presented here may be valuable in predicting and/or modelling the potential response of the studied species before a fire occurs (Lloret et al., 2003; Reyes and Casal, 2008; Vesk and Yen, 2019). The combination of information on the resprouting capacity and life-history traits of species (e.g. growth form, age, size, etc), and community-level aspects such as availability of fuel (as indicator of potential intensity of fire) can help delineating vegetation management actions to prevent or minimize the socio-ecological impact of fires (Keeley, 2006; Baeza and Vallejo, 2008; Rodríguez Trejo, 2008; Keeley et al., 2009).

Moreover, the proposed RCIs have additional advantages with respect to other protocols: 1) pre-fire plant height can be more difficult to estimate if a considerable portion of the burnt plant has been consumed, whereas an accurate measure of burnt trunk diameter can be recorded even if most of the plant has been consumed; and 2) the diameter of trunks and resprouts are easier to measure compared to the variables used in other studies, such as plant height. For example, in floras with tall trees and/or shrubs, and/or in areas of dense vegetation and/or rugged terrain, plant height can be impractical or time-consuming to measure, often involving for example transport of special devices through thick and thorny vegetation and/or steep slopes.

4.2. Practical recommendations for comparative ecology

Although both RCIs show a close relationship with each other and with the RV, either could be more appropriate depending on the situation. First, if the number of species to be studied is low, then RCI 1 is probably the best option, since it provides more accuracy than RCI 2. But if the number of species is large, then RCI 2 could be a more practical option in terms of time and logistics, although, given that RCI 2 was affected by growth form in its estimation of RV, comparisons between growth forms should be taken with caution, or be focused on the intra-growth form level. On the other hand, aspects related to the resprouting patterns of the species may also be relevant to decide between one index or the other. For example, for species with a single trunk and many resprouts (could be hundreds) RCI 2 is more practical but could underestimate the resprouting capacity more than RCI 1 with respect to RV, since it does not consider TN and RN, while RCI 1 does. Conversely, in the less likely case of species with many trunks but one (or very few) resprouts, RCI 2 could overestimate resprouting capacity more than RCI 1. Therefore, there is a trade-off between simplicity and accuracy that depends mainly on the objectives and scale of the study (e.g. number of species), and on the resprouting characteristics of the studied species.

Another important point to consider when measuring resprouting capacity is the time of measurement after the disturbance. Although some of the variables commonly used when assessing resprouting capacity may not change considerably from one year to the next (e.g. the number and diameter of burned trunks), others may do (e.g. number and diameter of resprouts, plant height and/or aboveground biomass; Montès et al., 2004; Falster and Westoby, 2005; Neke et al., 2006; Zizka et al., 2014). Therefore time since disturbance should be acknowledged when interpreting the results and/or if comparisons between species or populations are to be made. It is worth mentioning that this shortcoming is common to most methods for assessing resprouting capacity, such as the survival rate (see further in the text).

4.3. Differences between species in the RCIs and its components

This is one of a few studies that quantitatively measures and compares the post-fire resprouting capacity of a large number of species of different growth forms and sizes. The fact that all the studied species were capable of resprouting one growing season after the fire is supported by previous studies both in the Chaco region (Bóo et al., 1997; Moglia and Jofre, 1998; Kunst et al., 2000; Martínez Carretero and Dalmasso, 2002; Tálamo and Caziani, 2003; Gurvich et al., 2005; Casillo et al., 2006; Torres et al., 2014; Herrero et al., 2016), and other (semi-) arid regions (Flinn et al., 1992; Dacy and Fulbright, 2009; Zizka et al., 2014). The considerable inter-species variability observed in the RCIs and their components (Figs. 3 and 5) is also consistent with previous more restricted studies (Biurrum et al., 1983; Bóo et al., 1997; Moglia and Jofre, 1998), although with some variations in the relative resprouting capacity between species. The high variability at the intra-species level, especially regarding ECRD and RN (Fig. 5) could be an indication that other aspects such as the characteristics of fires (i.e. location, altitude, season, area), the disturbance history (e.g. herbivory) at the sampling sites, and microsite level features (e.g. terrain slope and aspect, or soil depth), which were beyond the scope of this study, could affect resprouting capacity (Clarke et al., 2005; Fulbright et al., 2011).

4.4. Survival percentage at the species level

Species ranking based on survival percentage, which is often used as a measure of resprouting capacity (e.g. Lloret and López-Soria, 1993; Lloret et al., 1999; Wright and Clarke, 2007), showed considerable differences when compared to the two proposed RCIs (Fig. 4). For example, ten species had 100% survival, and therefore were ranked first (Fig. 4; Appendix F), whereas -with the exception of *Lycium* sp., which was last for both RCIs- these ten species were ranked between 3 and 17 by RCI 1, and between 1 and 19 by RCI 2 (Fig. 4; Appendix F), indicating that the RCIs provided a much higher level of disaggregation regarding inter-species differences in resprouting capacity. Furthermore, the observed pattern support the hypothesis that the main strategies for plant survival to fire, namely avoidance of mortality and/or tolerance via resprouting (Jackson et al., 1999; Hoffmann and Solbrig, 2003) can follow decoupled trajectories (Bond and Van Wilgen, 1996; Jackson et al., 1999; Del Tredici, 2001; Bond and Midgley, 2001).

It should be noted that plant survival through resprouting is not necessarily evident one growing season since the last fire occurrence, since factors such as fire intensity, fire season and plant size may prevent resprouting in the first months after the fire (Rundel et al., 1987; Moreno and Oechel, 1991; Drewa, 2003). Conversely, it is possible that individuals presenting resprouts after the first growing season will not survive into subsequent seasons (Moreno and Oechel, 1991; Haggerty, 1994; Moreira et al., 2012). Therefore, resprouting capacity may be under- or overestimated when assessed only one growing season since the fire event, as in the present work.

4.5. Differences between growth forms

As can be deduced from the values of ECRD and RN in Table 3, shrubs and tree/shrubs tended to produce more resprouts of smaller diameter compared to trees, which is in agreement with previous studies on woody species in semi-arid environments (Hoffmann and Solbrig, 2003; Zizka et al., 2014). Although trees had a larger ECRD than shrubs and tree/shrubs for D1 and D5 (Table 3), the total resprouting capacity (i.e. RCI 1) for these sizes was higher in tree/shrubs than in trees; whereas shrubs had lower values in all sizes. This indicates that the increase in ECRD in relation to the increase in ECTD is lower in shrubs compared to the other growth forms (see further below). These allometric variations have been reported elsewhere (e.g. Hodgkinson, 1998; Vesk, 2006; Zizka et al., 2014) and are indicative of different strategies of growth forms to respond to fire and other

selective pressures (Kruger, 2017; Archibald et al., 2019).

4.6. Influence of plant size

Resprouting capacity showed a consistent decreasing pattern with increasing ECTD, both at the species level (Fig. 6) and growth form level (Table 3; Appendix H) indicating that even when the ECRD increases with increasing ECTD, as was the case for shrubs and tree/shrubs (Table 3), it does not compensate the increase in ECTD. The pattern observed at the growth form level is consistent with previous reports suggesting a maximum resprouting capacity in the early years of plant life (Kayll and Gimingham, 1965; Keeley, 1986; Bell and Pate, 1996; Bond and Van Wilgen, 1996; Ojeda, 1998; Del Tredici, 2001; Bond and Midgley, 2001; Vesk, 2006). The increasing resprouting capacity -from low at the early seedling and sapling stages to maximum capacity at young-to-mature stages- could be related to the increasing extent of the plant's root system as the plant matures (Hobbs and Mooney, 1985). Afterwards, the adventitious buds responsible for sprouting become buried by woody tissues as the plant ages, although a combination of life-history, (onto)genetic, physiological and anatomical factors may be involved in limiting the lifespan of buds (Hodgkinson, 1998; Del Tredici, 2001; Keeley, 2006; Clarke et al., 2013).

The loss of resprouting capacity with aging could also partly explain the negative relationship between survival percentage and ECTD (Appendix I). However, to some extent the pattern found here is contradictory to other studies on woody species from semi-arid environments, savannas and temperate forests (Jackson et al., 1999; Bond and Midgley, 2001), and even for some species of the Chaco forest (e.g. *A. quebracho-blanco*, *V. aroma*, *Z. mistol* and *Propsopis* sp.; Morello and Saravia Toledo, 1959). One possible explanation is that many woody species (especially trees) tend to grow in height to avoid disturbances such as fire and herbivory (Bond and Van Wilgen, 1996); if these species succeed in avoiding the disturbance, then the selective advantage of resprouting capacity decreases (Hoffmann and Solbrig, 2003; Clarke et al., 2013). Hence, if the canopy of individuals of greater size is reached by fire (i.e., if they are "*top-killed*"), survival chances are lower than in smaller individuals that still preserve a high resprouting capacity due to ontogenetic factors (Vesk, 2006). At the species level, differences in the regression slopes (Fig. 6) may indicate differences in strategies, in which the size-resprouting capacity relationship can be adjusted to different curves than that found at the growth form level (e.g. Hodgkinson, 1998). These trade-offs have been described, for example, for species of savanna ecosystems (Bond and Van Wilgen, 1996) and involve evolutionary aspects related to the historical fire regime and to changes in plant cover over time due to environmental and anthropogenic factors.

4.7. Data limitations

Legislation in Córdoba Province strictly regulates de use of fire in rural areas (Ley 8571, 1999), making large-scale experimental studies with fire logistically difficult to carry out, especially in remote areas such as our study area. Therefore, one of the main challenges in a study with many species, such as the one presented here, is finding appropriate burned sites that are both logistically accessible and have appropriate vegetation characteristics necessary for the study. This often limits the possibilities of achieving fully balanced data for all species and/or growth forms, as could be achieved in a manipulated field experiment. For example, some species were difficult to find and therefore were underrepresented (e.g. *J. rhombifolia* had only two specimens in Dataset 1 and 14 in Dataset 2), and consequently the robustness of the results was diminished for such species. Furthermore, in unmanipulated studies such as ours the characteristics of fire events, as well as aspects at the microsite level (mentioned earlier in Section 4.3) may differ considerably, adding variability to the data and calling for precaution

in the interpretation and extrapolation of results to draw broader patterns and conclusions. Future studies under more controlled conditions would be highly valuable to contrast with our results.

Despite these constraints, we believe that the proposed indices can be a very useful tool for comparative studies in fire ecology. Furthermore, the results presented here provide unprecedented and valuable information on the resprouting patterns of dominant species from an extensive region such as the Chaco, where fire is a highly relevant socio-ecological factor. In this sense, we hope that our study will serve to promote comparative studies both in the Chaco and in other fire-prone regions. This would allow, on the one hand, testing the proposed indices; and on the other hand, increasing the number of studied species, which has an implicit benefit for delineating appropriate fire management policies and actions in particular regions.

CRediT authorship contribution statement

Pedro Jaureguiberry: Conceptualization, Methodology, Writing - review & editing. **Aníbal Cuchietti:** Conceptualization, Methodology. **Lucas D. Gorné:** Methodology, Formal analysis. **Gustavo A. Bertone:** Conceptualization, Methodology. **Sandra Díaz:** Supervision, Conceptualization, Writing - review & editing.

Declaration of Competing Interest

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

Acknowledgements

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118267.

References

Akaike, H., 1972. Use of an information theoretic quantity for statistical model identification. In: Proceedings of the 5th Hawaii International Conference on System Sciences, North Hollywood, USA, pp. 249–250.

Anderson, H.E., 1982. Aids to determining fuel models for estimating fire behavior. Ogden, Utah.

Archibald, S., Hempson, G.P., Lehmann, C., 2019. A unified framework for plant life-history strategies shaped by fire and herbivory. New Phytol.

Argañaraz, J.P., Gavier-Pizarro, G., Zak, M.R., Bellis, L.M., 2015a. Fire Regime, Climate, and Vegetation in the Sierras de Córdoba, Argentina. Fire Ecology 11, 55–73.

Argañaraz, J.P., Pizarro, G.G., Zak, M., Landi, M.A., Bellis, L.M., 2015b. Human and biophysical drivers of fires in Semiarid Chaco mountains of Central Argentina. Sci. Total Environ. 520, 1–12.

Baeza, M.J., Vallejo, V.R., 2008. Vegetation recovery after fuel management in Mediterranean shrublands. Appl. Veg. Sci. 11, 151–158.

Barchuk, A.H., Campos, E.B., Oviedo, C., Díaz, M.D.P., 2006. Supervivencia y crecimiento de plántulas de especies leñosas del Chaco Árido sometidas a remoción de la biomasa aérea. Ecologia Austral 16, 47–61.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models using lme4. J. Stat. Softw. 67, 1–48.

Bell, T., Pate, J., 1996. Growth and Fire Response of Selected Epacridaceae of South-Western Australia. Aust. J. Bot. 44, 509–526.

Bellingham, P.J., Sparrow, A.D., 2000. Resprouting as a life history strategy in woody plant communities. Oikos 89, 409–416.

Biurrum, F., Ferrando, C., Pagliari, E., Namur, P., 1983. Reacción vegetativa de algunas especies leñosas de los Llanos de La Rioja en relación al tipo de daño provocado por un incendio accidental. In: Taller de arbustos forrajeros para zonas áridas y semiáridas, Orientación Gáafica Editoral, Mendoza, pp. 36–44.

Boletta, P.E., Ravelo, A.C., Planchuelo, A.M., Grilli, M., 2006. Assessing deforestation in the Argentine Chaco. For. Ecol. Manage. 228, 108–114.

Bond, W., Midgley, J., 2001. Ecology of sprouting in woody plants: the persistence niche. Trends Ecol. Evol. 16, 45–51.

Bond, W., Midgley, J., 2003. The evolutionary ecology of sprouting in woody plants. Int. J. Plant Sci. 164, S103–S114.

Bond, W.J., Van Wilgen, B.W. 1996. Fire and Plants. Chapman & Hall, London.

Bóo, R., Peláez, D.V., Bunting, S., Mayor, M., Elía, O., 1997. Effect of fire on woody species in central semi-arid Argentina. J. Arid Environ. 32, 259–269.

Bravo, S., Kunst, C., Grau, R., Aráoz, E., 2010. Fire–rainfall relationships in Argentine Chaco savannas. J. Arid Environ. 74, 1319–1323.

Bravo, S., Kunst, C., Leiva, M., Ledesma, R., 2014. Response of hardwood tree re-generation to surface fires, western Chaco region, Argentina. For. Ecol. Manage. 326, 36–45.

Burrows, N.D., 1985. Reducing the abundance of Banksia grandis in the jarrah forest by the use of controlled fire. Austral. Forest. 48, 63–70.

Cabido, M., Acosta, A., Carranza, M., Díaz, S., 1992. La vegetación del Chaco Árido en el W de la provincia de Córdoba, Argentina. Documents Phytosociologiques 14, 447–456.

Cabrera, A.L., 1976. Regiones fitogeográficas argentinas. (E. F. Ferreira Sobral, Ed.). Enciclopedia Argentina de Agricultura y Jardinería 1–85.

Capitanelli, J., 1979. Clima. In: Vázquez, J., Miatello, R., Roque, M. (Eds.), Geografía Física de la Provincia de Córdoba, Editorial Boldt, Buenos Aires, pp. 45–138.

Casals, P., Valor, T., Rios, A.I., Shipley, B., 2018. Leaf and bark functional traits predict resprouting strategies of understory woody species after prescribed fires. For. Ecol. Manage. 429, 158–174.

Casillo, J., Kunst, C., Ledesma, R., Godoy, J., 2006. Control de Celtis spp (Tala) mediante fuego prescripto. In: Actas Ecofuego, Centro de Investigación y Extensión Forestal Andino Patagónico, Esquel, Chubut, pp. 185–188.

Catry, F.X.X., Rego, F., Moreira, F., Fernandes, P.M.M., Pausas, J.G.G., 2010. Post-fire tree mortality in mixed forests of central Portugal. For. Ecol. Manage. 260, 1184–1192.

Clarke, P.J., Knox, K.J.E., Wills, K.E., Campbell, M., 2005. Landscape patterns of woody plant response to crown fire: Disturbance and productivity influence sprouting ability. J. Ecol. 93, 544–555.

Clarke, P.J., Lawes, M.J., Midgley, J.J., Lamont, B.B., Ojeda, F., Burrows, G.E., Enright, N.J., Knox, K.J.E., 2013. Resprouting as a key functional trait: How buds, protection and resources drive persistence after fire. New Phytol. 197, 19–35.

Conti, G., Díaz, S., 2013. Plant functional diversity and carbon storage - an empirical test in semi-arid forest ecosystems. J. Ecol. 101, 18–28.

Cruz, A., Pérez, B., Moreno, J.M., 2003. Plant stored reserves do not drive resprouting of the lignotuberous shrub Erica australis. New Phytol. 157, 251–261.

Dacy, E.C., Fulbright, T.E., 2009. Survival of sprouting shrubs following summer fire : effects of morphological and spatial characteristics. Rangeland Ecol. Manage. 62, 179–185.

Demaio, P., Karlin, U.O., Medina, M., 2002. Árboles nativos del centro de Argentina. L.O. L.A., Buenos Aires, Argentina.

Díaz, S., Cabido, M., Casanoves, F., 1998. Plant functional traits and environmental filters at a regional scale. J. Veg. Sci. 9, 113–122.

Drewa, P.B., 2003. Effects of fire season and intensity on Prosopis glandulosa Torr. var. glandulosa. Int. J. Wildland Fire 12, 147–157.

Falster, D.S., Westoby, M., 2005. Tradeoffs between height growth rate, stem persistence and maximum height among plant species in a post-fire succession. Oikos 111, 57–66.

Flinn, R.C., Scifres, C.J., Archer, S.R., Robert, C., Charles, J., Steven, R., 1992. Variation in basal sprouting in co-occurring shrubs : implications for stand dynamics. J. Veg. Sci. 3, 125–128.

Fulbright, T.E., Dacy, E.C., Drawe, D.L., 2011. Does browsing reduce shrub survival and vigor following summer fires? Acta Oecologica 37, 10–15.

Giorgis, M., Cingolani, A., Chiarini, F., 2011. Composición florística del Bosque Chaqueño Serrano de la provincia de Córdoba, Argentina. Kurtziana 36, 9–43.

Giorgis, M.A., López, M.L., Rivero, D., Cingolani, A.M., 2015. Cambios climáticos en las sierras de Córdoba (Argentina) durante el holoceno. Aportes a las reconstrucciones climáticas a través del análisis de silicofitolitos del sitio arqueológico El Alto 3. Boletín de la Sociedad Argentina de Botánica 50, 361–375.

Gittins, C., Ghermandi, L., Bran, D., 2011. Studying the post-fire performance of tussock grasses in Patagonia: Survival, biomass production and early competition. J. Arid Environ. 75, 986–990.

Grau, H.R., Gasparri, N.I., Aide, T.M., 2005. Agriculture expansion and deforestation in seasonally dry forests of north-west Argentina. Environ. Conserv. 32, 140.

Gurvich, D.E., Enrico, L., Cingolani, A.M., 2005. Linking plant functional traits with post fire sprouting vigour in woody species in central Argentina. Austral Ecol. 30, pp. 789–796.

Haggerty, P., 1994. Damage and recovery in southern Sierra Nevada foothill oak wood-land after a severe ground fire. Madroño 41, 185–198.

Henig-Sever, N., Poliakov, D., Broza, M., 2001. A novel method for estimation of wild fire intensity based on ash pH and soil microarthropod community. Pedobiologia 45, 98–106.

Herrero, M., Torres, R., Renison, D., 2016. Do Wildfires Promote Woody Species Invasion in a Fire-Adapted Ecosystem? Post-fire Resprouting of Native and Non-native Woody Plants in Central Argentina. Environ. Manage. 57, 308–317.

Higgins, S.I., Bond, W.J., Trollope, W.S.W., 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. J. Ecol. 88, 213–229.

Hobbs, R., Mooney, H., 1985. Vegetative regrowth following cutting in the shrub Baccharis pilularis ssp. Consanguinea (DC) CB Wolf. Am. J. Bot. 72, 514–519.

Hodgkinson, K.C., 1998. Sprouting success of shrubs after fire: height-dependent re-lationships for different strategies. Oecologia 115, 64–72.

Hoffmann, W.A., Solbrig, O.T., 2003. The role of topkill in the differential response of savanna woody species to fire. For. Ecol. Manage. 180, 273–286.

Jackson, J.F., Adams, D.C., Jackson, U.B., 1999. Allometry of constitutive defense: A model and a comparative test with tree bark and fire regime. Am. Nat. 153, 614–632.

Kayll, A.A., Gimingham, C., 1965. Vegetative regeneration of calluna vulgaris after fire. J. Ecol. 53, 729–734.

Keeley, J.E., 2009. Fire intensity, fire severity and burn severity: A brief review and suggested usage. Int. J. Wildland Fire 18, 116–126.

Keeley, J.E., 2006. Fire severity and plant age in postfire resprouting of woody plants in sage scrub and chaparral. Madroño 53, 373–379.

Keeley, J.E., 1986. Resilience of Mediterranean shrub communities to fires. In: Dell, B., Hopkins, A., Lamont, B.B. (Eds.), Resilience in Mediterranean-type ecosystems, Dr. W Junk Publishers, Dordrecht, pp. 95–112.

Keeley, J.E., Aplet, G.H., Christensen, N.L., Conard, S.G., Johnson, E.A, Omi, P.N., Peterson, D.L., Swetnam, T.W., 2009. Ecological Foundations for Fire Management in North American Forest and Shrubland Ecosystems.

Kruger, L., 2017. Woody plant traits and life-history strategies across disturbance gra-dients and biome boundaries in the Hluhluwe–iMfolozi Park. In: Cromsigt, J., Archibald, S., Owen-Smith, N., (Eds.), Conserving Africa's mega-diversity in the Anthropocene: the Hluhluwe–iMfolozi Park story, Cambridge University Press, Cambridge, UK, pp. 189–210.

Kruger, L., Midgley, J., Cowling, R., 1997. Resprouters vs reseeders in South African forest trees; a model based on forest canopy height. Funct. Ecol. 11, 101–105.

Kunst, C., Bravo, S., Moscovich, F., Herrera, J., Godoy, J., Vélez, S., 2000. Control de tusca (Acacia aroma Gill. ap. H. et A.) mediante fuego prescripto. Revista Argentina de Producción Animal 20, 199–213.

Kunst, C., Bravo, S., Panigatti, J., 2003. Fuego en los Ecosistemas Argentinos. Ediciones INTA, Santiago del Estero.

Ley 8571, 1999. Manejo del fuego. Boletín Oficial de la Provincia de Córdoba, 11 de mayo de 1999, Córdoba, Argentina.

Lloret, F., López-Soria, L., 1993. Resprouting of Erica multiflora after experimental fire treatments. J. Veg. Sci. 4, 367–374.

Lloret, F., Pausas, J.G., Vilà, M., 2003. Responses of Mediterranean plant species to dif-ferent fire frequencies in Garraf Natural Park (Catalonia, Spain): field observations and modelling. Plant Ecol. 167, 223–235.

Lloret, F., Verdú, M., Flores-Hernández, N., Valiente-Banuet, A., 1999. Fire and re-sprouting in Mediterranean ecosystems: insights from an external biogeographical region, the mexical shrubland. Am. J. Bot. 86, 1655–1661.

Loehle, C., 2000. Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. Am. Nat. 156, 14–33.

MacDonald, J.E., Powell, G.R., 1983. Relationships between stump sprouting and parent-tree diameter in sugar maple in the 1st year following clear-cutting. Can. J. For. Res. 13, 390–394.

Martínez Carretero, E., Dalmasso, A., 2002. MCarretero_Response to cutting_larrea.PDF. Appl. Veg. Sci. 5, 127–133.

Miglietta, S., 1994. Patrón de ocurrencia de incendios y su efecto sobre la vegetación en el bosque serrano de Córdoba.

Moglia, M., Jofre, G., 1998. Respuestas al desmonte de las especies lenosas en un bosque de quebracho blanco (Aspidosperma quebracho blanco Schletcht) y algarrobo (Prosopis flexuosa) in the Province of San Luis (Argentina). Phyton 63, 257–265.

Montès, N., Ballini, C., Bonin, G., Faures, J., 2004. A comparative study of aboveground biomass of three Mediterranean species in a post-fire succession. Acta Oecologica 25, 1–6.

Moreira, B., Tormo, J., Pausas, J.G., 2012. To resprout or not to resprout: factors driving intraspecific variability in resprouting. Oikos 121, 1577–1584.

Morello, J., Potomastro, J., Sancholuz, L., Blanco, C., 1985. Estudio macroecológico de los Llanos de La Rioja. Serie del cincuentenario de la Administración de Parques Nacionales 1–53.

Morello, J., Saravia Toledo, C., 1959. El Bosque Chaqueño I. Paisaje primitivo, paisaje natural y paisaje cultural en el oriente de Salta. Revista Agronómica del Noroeste Argentino 3, 5–79.

Moreno, J.M., Oechel, W., 1989. A simple method for estimating fire intensity after a burn in California chaparral. Acta Oecologica 10, 57–68.

Moreno, J.M., Oechel, W.C., 1991. Fire intensity and herbivory effects on postfire re-sprouting of Adenostoma fasciculatum in southern California chaparral. Oecologia 85, 429–433.

Neke, K.S., Owen-Smith, N., Witkowski, E.T.F., 2006. Comparative resprouting response of Savanna woody plant species following harvesting: the value of persistence. For. Ecol. Manage. 232, 114–123.

Noble, I.R., Slatyer, R.O., 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43, 5–21.

Ojeda, F., 1998. Biogeography of seeder and resprouter Erica species in the Cape Floristic Region—Where are the resprouters? Biol. J. Linn. Soc. 9, 331–347.

Pausas, J.G., Bradstock, R.A., Keith, D.A., Keeley, J.E., Hoffman, W., Kenny, B., Lloret, F., Trabaud, L., 2004. Plant functional traits in relation to fire in crown-fire ecosystems. Ecology 85, 1085–1100.

Pausas, J.G., Keeley, J.E., 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. New Phytol. 204, 55–65.

Pausas, J.G., Pratt, R.B., Keeley, J.E., Jacobsen, A.L., Ramirez, A.R., Vilagrosa, A., Paula, S., Kaneakua-Pia, I.N., Davis, S.D., 2016. Towards understanding resprouting at the global scale. New Phytol. 209, 945–954.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., De Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., Ter Steege, H., Van Der Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 61, 167–234.

Pérez, B., Moreno, J.M., 1998. Methods for quantifying fire severity in shrubland-fires. Plant Ecol. 139, 91–101.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., the R Core team. 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-120, http://CRAN.R-project.org/package=nlme. 1–339.

R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Reyes, O., Casal, M., 2008. Regeneration models and plant regenerative types related to the intensity of fire in Atlantic shrubland and woodland species. J. Veg. Sci. 19, 575–583.

Di Rienzo, J.A., Casanoves, F., Balzarini, M.G., Gonzalez, L., Tablada, M., Robledo, C.W., 2017. InfoStat versión 2017.

Rodríguez Trejo, D.A., 2008. Fire regimes, fire ecology, and fire management in Mexico. AMBIO: J. Human Environ. 37, 548–556.

Rundel, P., Baker, G., Parsons, D., Stohlgren, T., 1987. Postfire demography of re-sprouting and seedling establishment by Adenostoma fasciculatum in the California chaparral. In: Tenhunen, J., Catarino, F., Lange, O., Oechel, W. (Eds.), Plant Response to Stress – Functional Analysis in Mediterranean Ecosystems. NATO Advanced Science Institute Series, Springer, New York, pp. 575–596.

Schafer, J.L., Just, M.G., 2014. Size Dependency of Post-Disturbance Recovery of Multi-Stemmed Resprouting Trees (C. Carcaillet, Ed.). PLoS One 9, e105600.

Schwilk, D.W., Ackerly, D.D., 2005. Is there a cost to resprouting? Seedling growth rate and drought tolerance in sprouting and nonsprouting Ceanothus (Rhamnaceae). Am.

J. Bot. 92, 404–410.

Tálamo, A., Caziani, S., 2003. Variation in woody vegetation among sites with different disturbance histories in the Argentine Chaco. For. Ecol. Manage. 184, 79–92.

Torres, R.C., Giorgis, M.A., Trillo, C., Volkmann, L., Demaio, P., Heredia, J., Renison, D., 2014. Post-fire recovery occurs overwhelmingly by resprouting in the Chaco Serrano forest of Central Argentina. Austral Ecol. 39, 346–354.

Del Tredici, P., 2001. Sprouting in Temperate Trees: A morphological and ecological review. The Botanical Rev. 67, 121–140.

Vesk, P., 2006. Plant size and resprouting ability: trading tolerance and avoidance of damage? J. Ecol. 94, 1027–1034.

Vesk, P., Warton, D., Westoby, M., 2004. Sprouting by semi-arid plants: testing a di-chotomy and predictive traits. Oikos 107, 72–89.

Vesk, P., Westoby, M., 2004. Sprouting ability across diverse disturbances and vegetation types worldwide. J. Ecol. 92, 310–320.

Vesk, P.A., Yen, J.D.L., 2019. Plant resprouting: How many sprouts and how deep? Flexible modelling of multi-species experimental disturbances. Perspect. Plant Ecol., Evol. Systemat. 41, 125497.

Warton, D.I., Duursma, R.A., Falster, D.S., Taskinen, S., 2012. smatr 3– an R package for estimation and inference about allometric lines. Methods Ecol. Evol. 3, 257–259.

Warton, D.I., Wright, I.J., Falster, D.S., Westoby, M., 2006. Bivariate line-fitting methods for allometry. Biol. Rev. 81, 259–291.

Wells, P., 1969. The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. Evolution 23, 264–267.

Wright, B.R., Clarke, P.J., 2007. Resprouting responses of Acacia shrubs in the Western Desert of Australia – fire severity, interval and season influence survival. Int. J. Wildland Fire 16, 317.

Zizka, A., Govender, N., Higgins, S.I., 2014. How to tell a shrub from a tree: A life-history perspective from a South African savanna. Austral Ecol. 39, 767–778.

Zuloaga, F., Morrone, O., Belgrano, M.J., 2008. Catalogue of the Vascular Plants of the Southern Cone (Argentina, Southern Brazil, Chile, Paraguay, and Uruguay). Missouri Botanical Garden Press.