

## Original article

# Anthropogenic disturbance impact on the stem growth of *Prosopis flexuosa* DC forests in the Monte desert of Argentina: A dendroecological approach



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## ABSTRACT

Anthropogenic disturbance acts globally as an ecological process with long-term implication on the ecosystem equilibrium. In the central-western Argentina (Desierto del Monte Central: DMC), the desert *Prosopis flexuosa* woodlands has been intervened by man with differential incidence, e.g. through logging, fire and grazing. Despite recognizing a history of disturbances in these forests, the local removal of trees and its incidence in the stem growth of the surviving trees is still poorly known. Dendroecological methods were applied to 10 plots distributed along a landform gradient, aiming to analyze how disturbance, together with possible modulation effects of the spatial variability on growth, can influence forest dynamics. Tree removal was an intensive practice during the second half of the 20th century in the DCM, in synchrony with the expansion of wine-growing activity. Our results suggest that removal of *P. flexuosa* individuals in any considered plot was the main driver of changes in the forest dynamics. This argument is based on the weak climatic incidence in years considered critical with respect to the beginning of abrupt tree-growth releases. This disturbance impact seemed to be landform-dependent, as suggested by the higher relative basal area values at mesic sites in relation to sites linked to drier landforms. The presented findings represent the first attempt in reconstructing the disturbance regime experienced by the DMC *P. flexuosa* woodlands. Our research contributes to interpret how logging practices coupled with landform-related heterogeneities may influence the forest dynamics at desert environments, providing elements for implementing policies for conservation and management of these natural resources.

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## 1. Introduction

Semi-arid lands, covering about 40% of Earth land surface and inhabited by approximately a third of the total world population, are fragile ecosystems threatened by extreme climatic events and natural/anthropogenic disturbances (Noy-Meir, 1973; Whitford, 2002; Asner et al., 2004). In these environments, water availability determines plant spatial distribution and growth, influencing

the ecosystem dynamics (Noy-Meir, 1973; Whitford, 2002). In this sense, water scarcity (long-lasting drought episodes) as well as water excess (flooding) can induce massive tree mortality through disruptions of the conducting system and root asphyxia, respectively (Stromberg et al., 1993; Allen et al., 2010).

Human pressure (e.g. grazing, wood extraction) and climatic variability overlaps in their influence on long-term semi-arid forests dynamics (Whitford, 2002). Therefore, the determination of the degree of influence of these variables could greatly improve our understanding of dryland forest ecology, further contributing in establishing and advancing in restoration and conservation programs (Swetnam et al., 1999; Ellis and Ramankutty, 2008).

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Dendrochronology may provide information of disturbance regimes in temperate woodlands (e.g. Henry and Swan, 1974; Östlund and Linderson, 1995; Nowacki and Abrams, 1997). In these environments, from an ecological viewpoint, it is widely accepted that a disturbance could modify the plant–plant interaction (e.g. competition for light), with resulting abrupt changes in radial growth patterns (release/suppression pulse: Nowacki and Abrams, 1997; Rubino and McCarthy, 2004). More recently, tree-ring analysis successfully reconstructed tropical and subtropical forest disturbance history (e.g. Grau et al., 2003; Baker et al., 2005). However, likely due to the disagreement about the role of competition in shaping the desert tree growth (e.g.: Grime, 1977; Fowler, 1986), it has been recent that the application of dendrochronological methods proved its utility in analyzing semi-arid forest disturbances. Nevertheless, tree-ring studies of forest disturbance in drylands are still scarce and, with few exceptions (Dussart et al., 1998; Bogino et al., 2015), mainly performed on conifer forests from the Northern Hemisphere (e.g. Black and Abrams, 2005; Py et al., 2006; Rozas et al., 2011).

The Monte Desert biome (a South American subtropical warm temperate desert in western Argentina; Morello, 1958; Abraham et al., 2009) experienced disturbance episodes with a differential degree of intensity, particularly during the 20th century (Abraham and Prieto, 1991, 1999; Rojas et al., 2009; Villagra et al., 2009; Contreras et al., 2011; Cesca et al., 2014). Studies performed in the central area of these territories (Desierto del Monte Central, hereafter DMC) dealt with human activity and its influence on the vegetation dynamics, particularly those in which the algarrobo tree (*Prosopis flexuosa* DC) dominates. Grazing, seasonal-distributed livestock, and homesteads spatial scattering modified the natural biogeochemical cycles, groundwater quality and plant cover in these forests (Aranibar et al., 2011; Goirán et al., 2012; Meglioli et al., 2014). Moreover, it has been suggested that wood extraction, as dead wood removal and pruning of *P. flexuosa* multi-stemmed trees, affected pollinator abundance, seed production and tree growth (Vázquez et al., 2011; Alvarez et al., 2013).

The abovementioned analyses constitute progress in the understanding of human impacts on the DMC natural dynamics. Nevertheless, the influence of tree-removal on the stem growth of remaining individuals has not been studied yet in the algarrobo forest. Due to the ecological and cultural importance of this desert tree (Alvarez and Villagra, 2009), the analysis of the species growth dynamics in response to anthropogenic-induced disturbance will contribute to develop plans oriented towards the management and conservation of these natural resources.

In this contribution we examined the influence of tree-removal on the radial stem growth of *P. flexuosa* forest stands distributed along a landform gradient (river, paleo-river, lowland, and inter-dune units; Goudie, 2004) in the DMC. We hypothesized that disturbance, rather than climate, has produced changes in the growth patterns of the *P. flexuosa* woodlands from central Argentina, as evidenced from significant episodes of growth deviations during the 20th century. Furthermore, as the ecosystem response to disturbance varies along environmental gradient, we conjectured that landform heterogeneity at the DMC potentially represents a modulating factor contributing to the species post-disturbance growth expressions (Harmon et al., 1984; Bisigato et al., 2009). Therefore, the objectives of this research were to i) analyze the disturbance history in areas of the DMC *P. flexuosa* woodlands through annual resolution dating of tree-removal events, ii) link tree-cutting episodes and climatic variability to stem growth releases, and iii) examine the presence of possible landform-dependent response in the species growth to logging activity. Through this study, we aimed to contribute with information that serves to delineate sustainable management policies of the regional *P. flexuosa* woodlands, and globally to achieve a

more refined knowledge about the incidence of disturbances in dry hardwood forest dynamic ecosystems.

## 2. Material and methods

### 2.1. Sites description and sampling

The study area belongs to the DMC Phytogeographic Province located in the central-western Argentina (Mendoza Province, Fig. 1). Along this Province, shrub steppes dominated by *Larrea* spp. (Zygophyllaceae) are the typical landscapes, and *Prosopis* spp. occurs in open woodlands where groundwater is accessible (Cabrera, 1976). Climate is arid to semi-arid, with mean annual precipitation of 155 mm, and large seasonally and daily temperature amplitude (Morello, 1958; Abraham et al., 2009; Fig. 1).

This research is devoted to disentangle the synergic effect of climate, disturbance and spatial heterogeneity upon the *P. flexuosa* growth dynamics. Thus, sample design followed geographical and logistic criteria, due to the high DMC spatial heterogeneity, as well as woodland extent and landowner agreements.

Ten plots distributed along six *P. flexuosa* woodlands were analyzed (Fig. 1). These plots are located in a landform gradient that broadly represents the landscape of this arid region (see Piraino et al., 2015 for a brief description of the sampled woodlands). For this reason, the structure of these forests shows particular stand features, as indicated in Tables 1 and 2. However, common species appear on all sites, most notably the tree *P. flexuosa* with shrubby and low arboreal associates such as *Larrea divaricata* Cav., *Geoffroea decorticans* (Hook. & Arn.), *Capparis atamisquea* Kuntze, and *Bulnesia retama* (Hook.) Griseb.

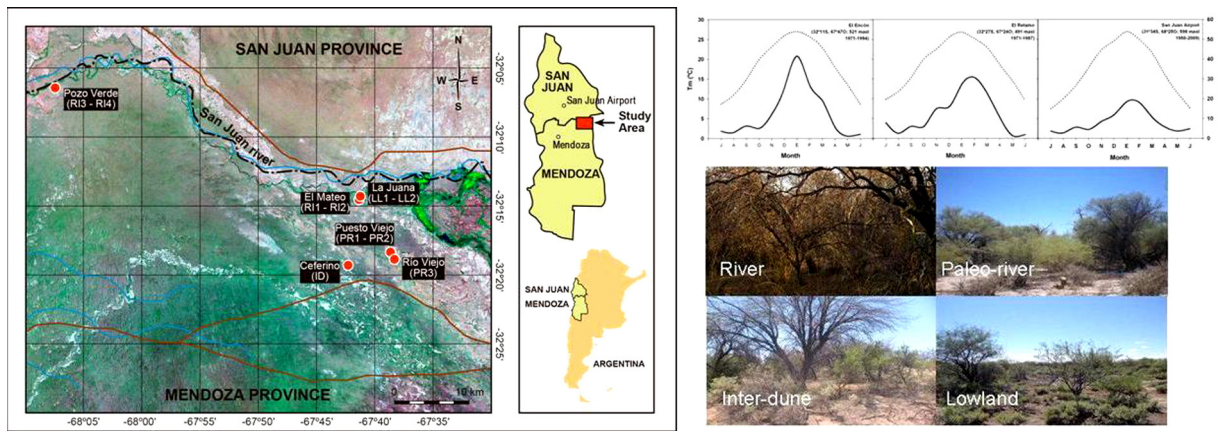
At each site, 1–2 plots of 1000 m<sup>2</sup> (50 m × 20 m) were established. The dendrochronological sampling involved all the stumps and the live trees placed as far as 15 m from the selected deadwood material. This distance has been considered in relation to previous studies regarding the intraspecific competition of *P. flexuosa* forests at the northern distribution of the species range (Catalán, 2000).

Within the plots, a total of 128 *P. flexuosa* individuals (28 stumps and 100 living trees) were sampled. Additionally, 30 stumps of the same species were randomly sampled among the selected forest stands. Two cores per living tree were extracted with a gas-powered drill (TED 262R, Tanaka Kogyo Co. Ltd, Chiba, Japan). Dead *P. flexuosa* wood material (stumps) was sampled by cutting stem disks by means of a chainsaw. All samples were extracted at about 50 cm above ground and stored in laboratory to proper further preparation for analysis.

### 2.2. Dendroecological methods

Increment cored wood samples were glued on wooden supports and polished with progressive finer sandpaper (from 80 up to 2000 grit). An EPSON Perfection flatbed scanner was used to scan cores with a resolution of 1200 dpi. Tree-ring widths were identified, dated and measured from pith to bark to the nearest 0.01 mm resolution through the facilities of the IPWin4 Image Analysis software (v4.5, Media Cybernetics, USA). Concerning stumps, two radii per sample were measured. In order to calendar date the disturbance events, individual stump ring series were cross-dated against the corresponding tree-ring site chronologies derived from living *P. flexuosa* trees (Piraino et al., 2015), and their data quality resulted from this comparison was validated by statistical control through the COFECHA program (Holmes, 1983). Then, annual ring values corresponding to the same stump were averaged to obtain a single tree-ring series representative of each logged tree.

Radial growth of individual trees was transformed into basal area increment (BAI). BAI provides a more accurate approximation



**Fig. 1.** Geographical location of the sampled sites and the gauge station (left), Ombrothermic diagram (according to Bagnouls and Gaussen, 1953) (upper right), and examples of the sampled landform units (lower right). Tm = monthly air temperature; P = monthly total rainfall. Gray dot line refers to monthly mean air temperature, and black solid line to monthly total rainfall.

**Table 1**  
Environmental and geographical settings of the sampled sites.

Site	Landform Unit	Altitude	Latitude (°S)	Longitude (°W)
El Mateo	River	512	32° 14' 31.4"	67° 41' 21.8"
Pozo Verde	River	534	32° 06' 26.6"	68° 07' 26.4"
Puesto Viejo	Paleo-river	500	32° 18' 20.4"	67° 38' 39.5"
Río Viejo	Paleo-river	497	32° 18' 51.9"	67° 38' 18.1"
Ceferino	Inter-dune valley	511	32° 19' 17.1"	67° 42' 17.0"
La Juana	Lowland	512	32° 14' 18.3"	67° 41' 14.7"

**Table 2**  
Stand structure characteristics of the analyzed plots. Stand density referred to *P. flexuosa* density; BA: mean annual basal area value; Dbase: mean tree basal diameter; H: mean tree height; N trees and N stumps represent sample depth at each plot.

Plot	Site	Period	Stand density (n/ha)	BA (m <sup>2</sup> /ha)	Dbase (cm)	H (m)	N trees	N stumps
RI1	El Mateo	1923–2010	280	2.08	30.4	4.1	10	4
RI2	El Mateo	1951–2010	340	2.11	18.3	3.9	19	5
RI3	Pozo Verde	1942–2011	130	3.56	65.6	5.2	9	2
RI4	Pozo Verde	1962–2011	90	2.01	63.4	5.1	4	2
PR1	Puesto Viejo	1960–2010	200	2.23	29.8	3.9	5	2
PR2	Puesto Viejo	1940–2010	100	3.46	44.2	3.8	4	3
PR3	Río Viejo	1957–2010	250	3.27	20	2.7	12	4
ID	Ceferino	1918–2011	110	3.99	35.4	7.1	5	3
LL1	La Juana	1947–2010	120	1.78	18.9	4.1	7	1
LL2	La Juana	1943–2010	60	1.73	14.8	3.8	5	2

of the annual tree growth than ring widths, by minimizing the age- and size-related trends (Visser, 1995; Biondi and Qeadan, 2008). We computed the basal area (BA) in square centimeters for each tree and year as follows:

$$BA = \pi \times r^2$$

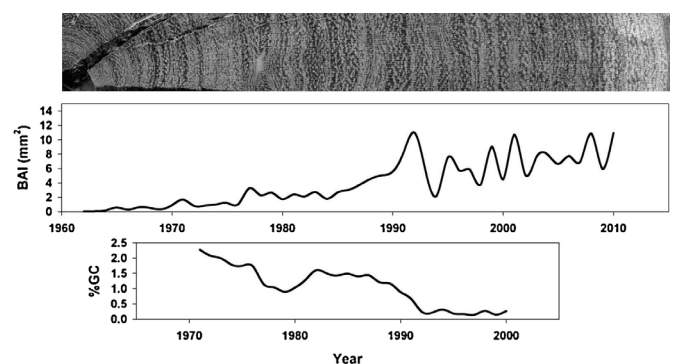
where, r is the tree-ring width of a given year. Then, we obtained the increment expressed in basal area for a year y as follows:

$$BAI_y = (BA_y - BA_{y-1})$$

being, BA<sub>y</sub> and BA<sub>y-1</sub> the basal area values at the year y and at the previous year, respectively

Changes in radial growth patterns following tree-removal (e.g. Fig. 2) were analyzed through the percent-growth change method (%GC; Nowacki and Abrams, 1997). This method detects releases by comparing average radial growth for successive periods, identifying peak growth-change values above a minimum threshold (Nowacki and Abrams, 1997). The percent-growth change method is represented by the formula:

$$\%GC = [(M2 - M1)/M1] \times 100$$



**Fig. 2.** Core of *P. flexuosa* living tree (top), basal area index chronology (middle), and post-disturbance growth changes curve (bottom).

where %GC is percent-growth change for a single year, while M1 and M2 are the mean radial growth preceding and following the examined year (Nowacki and Abrams, 1997). We selected a 10-year moving average window for the parameters M1 and M2, since this length allows averaging out short-term growth responses

related to climate whilst capturing intermediate-length growth changes associated with disturbance (Nowacki and Abrams, 1997). An abrupt positive change in stem growth was recognized as a release when %GC > 125% for at least three consecutive years.

### 2.3. Abiotic influence upon stem growth changes

To ensure that peaks in growth change are independent of an improving climatic condition, we considered growing season (previous year October–current year March average; Giantomasi et al., 2012) precipitation as potential abiotic driver. This time-window was chosen since rainfall along the whole period is strongly correlated to the species cambial activity at the DMC (Giantomasi et al., 2012). Data, spanning the 1950–2011 period, was obtained from the San Juan Airport gauge station (31°34'S; 68°25'W; 598 m a.s.l.), and has been successfully used in previous dendroclimatological studies of *P. flexuosa* (Piraino et al., 2015; Piraino and Roig, 2016).

Two different analyses were performed. First, plot-level %GC chronologies were matched by simple correlation functions against “precipitation difference” ( $P_{diff}$ ), adapted from the “PDSI differences” originally proposed by Nowacki and Abrams (1997).  $P_{diff}$  was calculated as follows:

$$P_{diff} = P_2 - P_1$$

where  $P_2 - P_1$  are the following and preceding 10-yr means value of growing season rainfall amount of a given year. Due to the strong autocorrelation in both %GC and  $P_{diff}$  series, the effective number of degrees of freedom was calculated, in order to avoid any possible overestimation of the correlation function results (Oort and Yienger, 1996).

Then, the possible relation between rapid environmental and BAI changes was examined through pointer year analysis (Schweingruber et al., 1990). Since we were interested in possible overlap between stem growth release pulses and pointer years, we focused our attention only to positive values of the latter. We followed the “normalization in a moving window” method (Cropper, 1979), selecting a 9-years long window through the common period between 1950 and 2000. A given year was recognized as a pointer one when at least 50% of the analyzed trees exhibited a change in the stem growth greater than 50%. Calculations were performed through the WEISER software (Gonzalez, 2001). Pointer year occurrence was then yearly compared to growth releases. Finally, the influence of water availability upon pointer years was evaluated through Superposed Epoch Analysis (SEA; Grissino-Mayer, 1995). As in desert systems the occurrence of sporadic precipitation events may translate into abrupt plant growth (“pulse-reserve paradigm”: Noy-Meir, 1973), SEA was used since it allows a direct comparison among rainfall and stem growth pulses (e.g. Morales and Villalba, 2012). In this case, raw precipitation data, instead of  $P_{diff}$ , was considered. Event years were established corresponding to pointer ones, and a 9-year precipitation window (4 years before and 4 years after the event) was selected. For each event, windows were superimposed and averaged. The mean rainfall pattern for the selected years was statistically examined for significance (95% bootstrap confidence intervals) through 1000 Monte Carlo random simulations (Mooney and Duval, 1993). SEA was performed through the facilities of the EVENT software (Holmes and Swetnam, 1994).

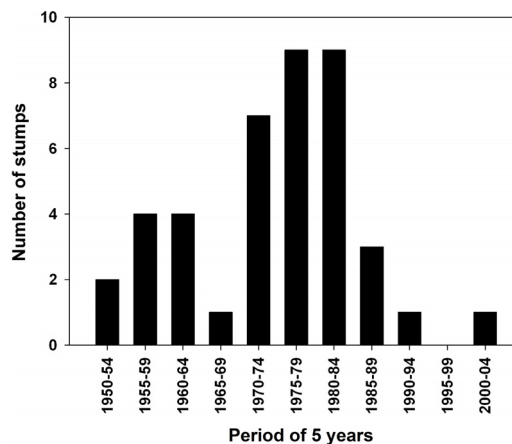
### 2.4. Landform-dependent stem growth following disturbance

The possible influence of landform heterogeneity upon the post-disturbance stem growth was examined through relative BAI ( $BAI_{rel}$ ; Reinhardt and Ryan, 1988; Valor et al., 2013; Keyser and Brown, 2014). As a unitless variable,  $BAI_{rel}$  allows each tree to serve as its own control (Reinhardt and Ryan 1988; Valor et al., 2013).

**Table 3**

Mean Pearson correlation moment (lower and higher intervals between parentheses) among stump ring chronologies and references site chronologies (Piraino et al., 2015). Values are significant at the  $p < 0.05$  level.

Site	Pearson $r$
El Mateo	0.51 (0.40–0.70)
Pozo Verde	0.48 (0.36–0.61)
Puesto Viejo	0.45 (0.40–0.57)
Río Viejo	0.48 (0.44–0.52)
Ceferino	0.39 (0.36–0.41)
La Juana	0.46 (0.43–0.48)



**Fig. 3.** Chronological distribution of the tree-removal episodes, at a 5-years timescale, according to the dendrochronological analysis of *P. flexuosa* deadwood.

$BAI_{rel}$  values higher (lower) than 1 indicate an increase (decrease) in the stem growth compared to pre-disturbance growth rates. The last shared tree-removal episode among the selected plots (1979–1984 period) was considered as the first year of analysis. Annual BAI of the sampled trees was averaged by plot, thus providing plot-level BAI chronologies. Then, mean BAI of the 5 years previous thinning ( $BAI_{pre}$ ) was computed. Finally, at each plot  $BAI_{rel}$  was calculated as the ratio between annual BAI increment from 1 up to 15 years after thinning and  $BAI_{pre}$ .  $BAI_{pre}$  and  $BAI_{rel}$  time periods were respectively selected to minimize the possible influence of previous disturbance events on the stem growth and to analyze plot-level chronologies composed by at least 75% of the sampled trees per year. Parametric ANOVA was used to examine the modulation exerted by landform heterogeneity upon the post-disturbance stem growth. Since annual  $BAI_{rel}$  values lacked of normality, the data was transformed by the Box-Cox methodology (Box and Cox, 1964). Statistical analyses were computed through R software (R Development Core Team, 2011).

## 3. Results

### 3.1. Disturbance event patterns

Through dendrochronological methods, a total of 41 *P. flexuosa* stumps distributed along the 6 considered populations were successfully dated (Table 3). Pearson correlation moment between deadwood ring series and the respective site chronologies ranked among 0.39 and 0.70, with the highest values recorded at river and paleo-river environments (Table 3).

According to cross-dating results, tree removal took place between 1953 and 2000, with a peak during the 1970s and the first half of the 1980s (Fig. 3). Indeed, 39% of the analyzed stumps correspond to trees cut in the 1970–79 period, followed by logging

**Table 4**

Proportion of trees showing growth releases by percent-growth change method (%Released Trees) and mean length of liberation pulses (Mean%GC length) according to examined landform units.

Landformunit	%Released Trees	Mean%GC length
River	58	8
Paleo-river	81	7
Lowland	60	4.9
Inter-dune	40	7.5
Total	61	7.1

events at 1980–89 (29%), 1950–59 (15%), 1960–69 (12%), and the 1990–99 and the post-2000 decades (both corresponding to 2%).

### 3.2. Disturbance impact on radial growth

Among the 80 analyzed trees, 49 (61% of total sampled living individuals; Table 4) experienced growth releases. At the landform-scale, the percentage of trees showing releases oscillated between 40% (inter-dune) and 81% (paleo-river) (Table 4). Mean%GC length corresponded to 7.1 years (Table 4), ranking from 4.9 (lowland) to 8 years (river).

Along the 10 sampled plots, almost all the detected release pulses were distributed following disturbance events, suggesting a temporal synchronicity between tree-removal episodes and stem growth changes (Fig. 4). At the river and paleo-river environments, the first disturbance events occurred during the 1950s and the 1960s (e.g. RI1, RI2 and PR3 plots) and concomitantly trees experienced stem growth releases. Then, during the 1970s and the 1980 decades the abovementioned stands were highly exploited, and a great percentage of sampled trees showed positive abrupt changes in the stem growth (Fig. 4).

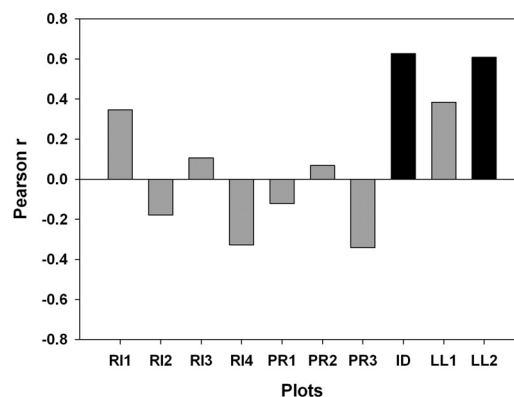
On the other hand, less clear results seemed to emerge at the lowland and, particularly, inter-dune landforms. In this sense, it is worth mentioning that 2 *P. flexuosa* individuals belonging to the LL1 plot showed release pulses during the 1960s and the 1970s, apparently decoupled from a tree-removal episode. Finally, at the ID plot, trees were logged during the 1970 and the 1980s, but positive changes in the stem growth only occurred until the beginning of the 1980s decade (Fig. 4).

### 3.3. Precipitation influence on tree growth releases

Correlation function analyses indicated that rainfall is poorly linked to the modulation of the stem growth changes among the selected stands. Indeed, this biotic factor significantly influenced the %GC at the  $p < 0.05$  level only at the ID ( $r = 0.63$ ) and the LL2 ( $r = 0.61$ ) plots (Fig. 5).

A total of 87 pointer years were recorded along the examined plots (Table 5). At the river unit, pointer years corresponded to growth releases between 4% (RI2) and 15% (RI4). At the paleo-river stands, the percentage of coincidence between both indices ranked among 8% (PR2) and 12% (PR1). Finally, at the ID and the LL1 plots pointer years poorly matched with release pulses (9% and 12%), while only at the LL2 plot where the coincidence among pointer years and stem growth releases presented a particularly high value (46%).

SEA indicated that pointer years were not related to climatic conditions during previous or following years, as evidenced by the lack of statistically significant results emerged for any of the analyzed plots (Fig. 6).



**Fig. 5.** Correlation functions between growing season (previous year October–current year March average)  $P_{diff}$  and plot-level %GC chronologies. Black bars indicate significance at  $p < 0.05$ .

### 3.4. Landform-dependent BAI response to disturbance

Multiple comparisons of means performed on transformed  $BAI_{rel}$  series suggested a possible influence of landform heterogeneity upon the stem growth response to anthropogenic disturbance (one-way ANOVA,  $F = 7.45$ ;  $p < 0.001$ ,  $df = 3$ ). Furthermore, mean  $BAI_{rel}$  values of the 15 years following tree removal are statistically higher (at the  $p < 0.05$  level) at the river/paleo-river units than at lowland/inter-dune valley landforms (data not shown).

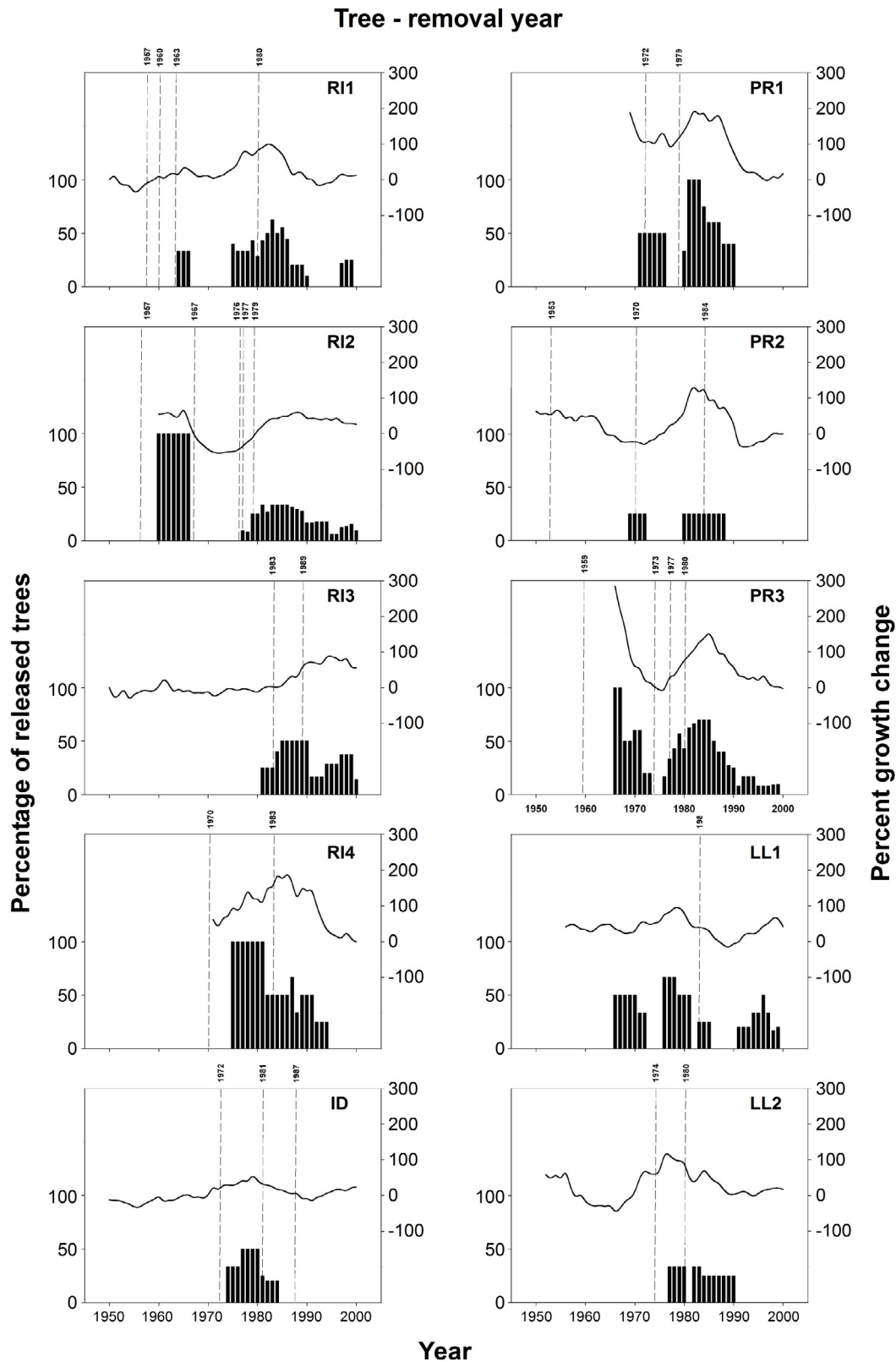
## 4. Discussion

In this research, we explored the anthropogenic disturbance effect on the radial growth dynamics of a desert hardwood tree species, providing information about possible landform-dependent response of stem growth to tree removal. The outstanding bark and sapwood long-lasting conservation of deadwood (many stumps were cut during the 1950s and 1960s decades) allowed the identification of the year's logging growth ring, thus proving the suitability of *P. flexuosa* stumps to infer disturbance regimes.

Along the 10 analyzed plots, the number of stumps ranks between 2 (RI3, RI4 and PR1) and 4 (RI1 and PR3), excluding RI2 (5) and LL1 (1). In exceptional cases, buried stumps showed some wood decay, raveling the dendrochronological dating. This could suggest that at the LL1 plot, possibly more than a single tree-removal event could have took place. Therefore, we can assume a relative homogenous time-distributed anthropogenic disturbance among the examined plots.

Correlation analyses performed among deadwood ring series and the reference chronologies brought different results within and among sites. This can reflect both the high variability in the species radial growth, as well as the DMC landform heterogeneity and its influence on the species growth patterns (Villalba et al., 2000; Piraino et al., 2015).

According to the cross-dating results, tree removal took place in the second half of the 20th century, predominantly during the 1970s and the first half of the 1980s decades. Unfortunately, we could not match our results to historical documents, lacking for the study area. Nevertheless, our findings reflect the DMC *P. flexuosa* forest exploitation history. Indeed, from 1945 until the first half of 1980s, these woodlands were cut to obtain poles and posts for development of vineyards (Richard-Jorba, 2008). Then, wood demand decreased by the introduction of substitutes originating from cultivated woods, which probably reduced the demand for algarrobo woods used for vineyards and consequently this factor influenced a decline in disturbance events since the 1990s.



**Fig. 4.** Temporal distribution of disturbance events (vertical lines), liberation pulses (black bars), and plot-level %GC chronologies.

Correlations between %GC and  $P_{diff}$  likely confirmed the documented *P. flexuosa* landform-dependent dendroclimatological signal (Piraino et al., 2015). Nevertheless, the weak temporal synchronicity among %GC and pointer years, and particularly the lack of significant results emerged from SEA, suggested a negligible abi-

otic control upon the species stem growth changes, thus indicating that tree-removal was probably the main driver of release pulses. This result is sound with dendroecological analysis performed for *P. caldenia* stands located near the studied area, showing that growth

**Table 5**

Pointer years (asterisks) temporal distribution. Red asterisk indicates years where both pointer year and %GC occurred (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

Plot	RI1	RI2	RI3	RI4	PR1	PR2	PR3	ID	LL1	LL2
1950									*	*
1951									*	*
1952	*									
1953								*		*
1954	*		*					*		
1955	*	*		*		*		*	*	
1956		*				*				
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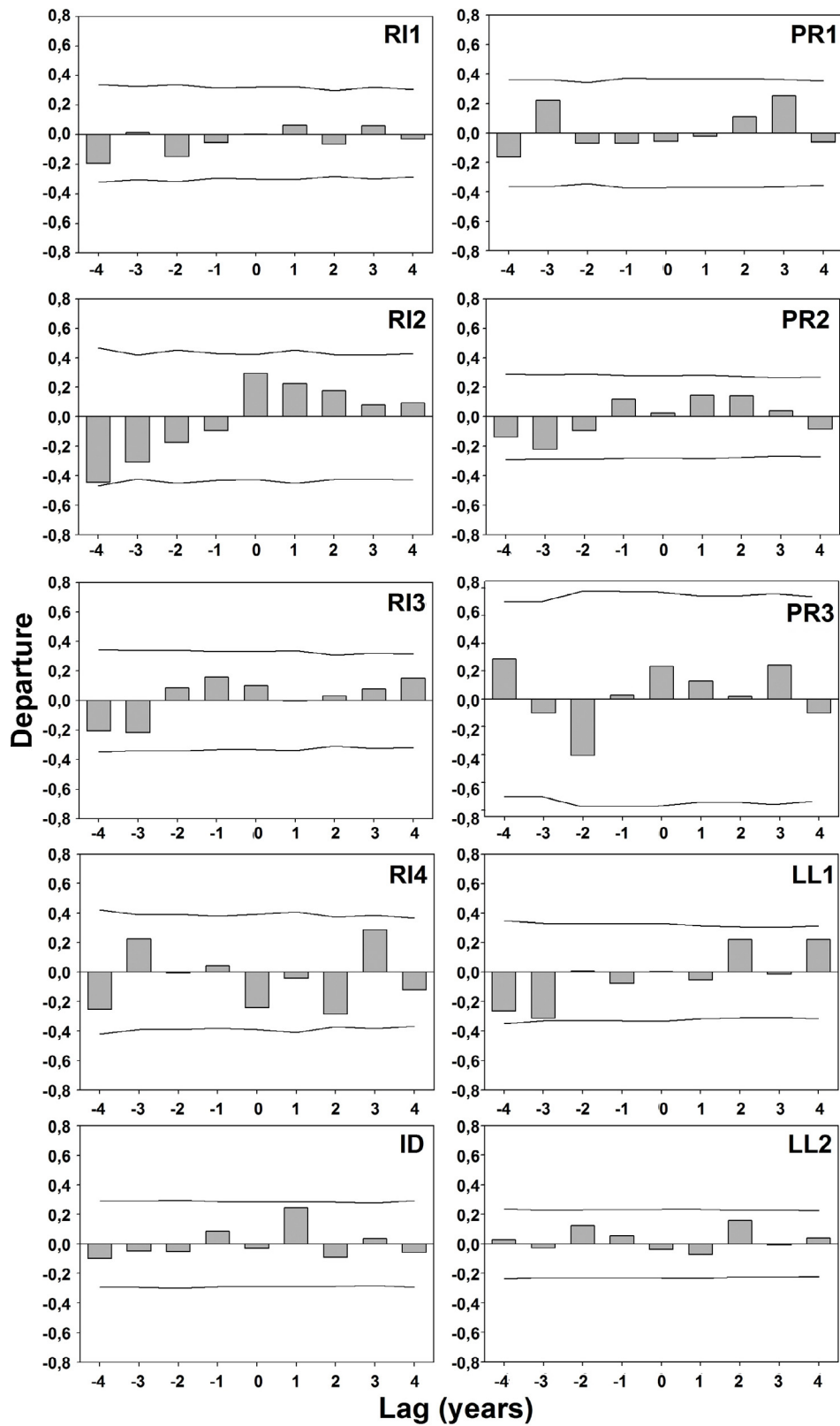
releases are related to influence of disturbances (fire) rather than climatic variability (Bogino et al., 2015).

From an ecological point of view, the tree-removal effects on the species stem growth are likely consequence of belowground competition for water (Fowler, 1986). Although there is no previous evidence of the role of this biotic factor in shaping the DMC *P. flexuosa* dynamics, reports for competition regulation of forest growth are found for the Arid Chaco woodlands (Catalán, 2000). Since the aforementioned Phytogeographic Provinces share similar environmental conditions, which translate into a common species dendroclimatological signal (Giantomasi et al., 2013), we can presume the existence of tree competition in the studied area.

*P. flexuosa* is a facultative phreatophyte species characterized by a dimorphic root system, with a taproot reaching water-table at 6–15 m depth and superficial roots distributed at approximately

0.6 m depth (Guevara et al., 2010). The removal of *P. flexuosa* trees may create resource-rich patches (e.g. higher nutrients or water availability), which can be exploited by the superficial root system of neighboring trees.

Our findings confirmed the positive response of stem growth to tree-removals in a semi-arid environment. In dry areas of NW China it has been observed that radial growth of *Picea crassifolia* Kom. increased following thinning, while selective cutting enhanced the growth of planted *Pinus halepensis* Mill. trees from the Iberian Peninsula (He et al., 2010; Navarro et al., 2010; Ruano et al., 2013). Regarding the *Prosopis* genus, there are records of the positive effect of tree-removal (thinning) on the radial growth dynamics. Logging of young *P. glandulosa* var. *glandulosa* trees incremented the branch and basal diameters three and nine years following thinning, respectively (Meyer and Felker, 1990; Patch and Felker,



**Fig. 6.** Superposed epoch analysis (SEA) comparing growing season precipitation departures during the growth event-years, corresponding to pointer years. The X-axis represents a 9-year window, starting 4 years previous and ending 4 years after the growth event (year 0). The time intervals used to run SEA analysis were 1950–2011. Dotted lines: 95% confidence interval.

1997a,b). An experimental pruning on multi-stemmed DMC *P. flexuosa* trees improved the tree shape in the short run, while stem

diameter growth significantly increased five years after removing branches (Alvarez et al., 2013).



Despite the relative low sample depth at lowland and inter-dune environments, the presented results brought interesting hints regarding possible landform-related responses of the *P. flexuosa* growth to tree removal. Indeed, according to the highest values of  $BAI_{rel}$ , disturbance was apparently more influential at river/paleo-river environments than in any other landform here considered. This probably reflects the DMC spatial heterogeneity, which in turns influences the hydrological balance, and possibly the growth and stand setting characteristics of the selected forests (Spurr and Barnes, 1980; Bisigato et al., 2009). In this sense, river and paleo-river landforms can be considered as relatively mesic, high-density units, due to the presence of active/inactive streams. On the other hand, at inter-dune and lowland, stand growth and density both reflected the sporadic contribution of rainwaters, thus representing more xeric environments (Roig et al., 1992). Therefore, differences in water availability can explain the strongest effect of disturbance in the river/paleo-river environments, where tree-removal in denser stands can translate into higher water supply and consequently enhance carbohydrate productivity, hence favoring stem growth.

To our knowledge, no research analyzed the modulation effect of spatial heterogeneity upon the post-disturbance stem growth in desert woodlands. Thus, in the search for an environmental analogue, we compared our findings to similar studies performed in Mediterranean forests (Pérez-de-Lis et al., 2011; Rozas et al., 2011; Ruano et al., 2013). Thinning and wildfire influenced the *Pinus canariensis* growth according to microtopographic differences (Pérez-de-Lis et al., 2011; Rozas et al., 2011). On the opposite, differences in aspect did not regulate the *Pinus halepensis* growth response to pre-commercial thinning (Ruano et al., 2013).

## 5. Conclusions

In this research, we explored the *P. flexuosa* growth response to logging-induced disturbance. We found that tree-removal, rather than incremental pulses of precipitation, drove the occurrence of growth release, and that this disturbance differently shaped the forest dynamics in a possible link with the landscape typology. Knowledge of these reactions was based on local silvicultural practices (e.g. Alvarez et al., 2013), but the results here achieved project these observations at large spatial scale, further improving the management of these natural resources.

Presently, the DMC woodlands are protected following conservation and management criteria. Although relatively limited in sample depths, our observations suggest that forest exploitation should be landform-related. Tree-removal could be concentrated in river and paleo-river environments, where logging disturbance had the strongest effect on the *P. flexuosa* stem growth dynamics. On the other hand, and following previous researches (Vázquez et al., 2011; Alvarez et al., 2013), at the inter-dune and lowland units, forests should be managed through pruning and removal of dead wood remnants. Furthermore, the dendroecological analyses derived from this research could be extended to other areas of the DMC that have suffered any degree of deforestation (Villagra et al., 2009). The present results demonstrated the utility of tree-ring analysis in reconstructing disturbance history and its influence on the growth dynamics of desert hardwood forests.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.dendro.2017.01.001>.

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