
ARTICLE

RESEARCH ARTICLE

Effect of anthropogenic disturbances on leaf traits of woody species from a subtropical dry forest of Argentina

Efectos de las perturbaciones antropogénicas sobre rasgos foliares de especies leñosas de un bosque seco subtropical de Argentina

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Abstract: *Aim of study:* To assess the effects of forest disturbances on two foliar attributes, leaf area (LA) and specific leaf area (SLA), of woody species in a semi-arid Chaco forest of Argentina. Disturbances are represented as different combinations of land management practices (removal of vegetation, logging, and fire). We evaluated intraspecific variation in LA and SLA of six native woody species using a quantitative approach. We also explored the effect of growth form (tree/shrub) and leaf periodicity (perennial/deciduous) on plant responses to disturbances, considering that these traits may determine variations in their behavior in response to such disturbances. *Area of study:* Subtropical semi-arid Chaco, Santiago del Estero Province, Argentina, South America. *Material and methods:* Leaves of mature individuals were measured in forests with three different land management histories: undisturbed for four decades (RC); rolled and subjected to selective wood extraction eight years before sampling (Rch+L); and rolled and followed by fire eight years before sampling (Rch+F). For each site, we measured 10 mature individuals of each of the six species studied, recording the maximum height and diameter at breast height (DBH), and harvested 20 leaves from each to measure leaf area (LA) and specific leaf area (SLA). *Main results:* All species significantly increased their LA and SLA in disturbed forests. Tree species had larger LA than shrubs, while shrubs exhibited higher SLA. Both traits presented higher values in deciduous species compared to perennial species, indicating that, after disturbances, these species could better capture released resources by increasing their foliar area. The community-weighted mean (CWM) of LA was highest in the Rch+L forest, likely reflecting the effect of increased light availability. Additionally, all disturbed forests showed a higher CWM of SLA. *Research highlights:* The changes observed in leaf traits at the species level, such as higher LA and SLA, which result in higher LA and SLA at the community level, suggest the adoption of more acquisitive strategies in disturbed communities, promoting higher resource capture and facilitating leaf tissue recovery. This may influence ecosystem functions, such as litter decomposition, productivity, and resource allocation for growth and reproduction. Monitoring foliar responses to disturbances in Chaco forests is critical for guiding sustainable management and conservation practices.

Keywords: Chaco forest; disturbance effects; intraspecific variability.

Resumen: *Objetivo del estudio:* Evaluar los efectos de las perturbaciones forestales sobre dos rasgos foliares, el área foliar (AF) y el área foliar específica (AFE), de especies leñosas en un bosque chaqueño semiárido de Argentina. Las perturbaciones se representan como diferentes combinaciones de prácticas de manejo del suelo (remoción de la vegetación, aprovechamiento maderero e incendio). Evaluamos la variación intraespecífica en AF y AFE de seis especies leñosas nativas mediante un enfoque cuantitativo. También exploramos el efecto de la forma de crecimiento (árbol/arbusto) y la periodicidad foliar (perenne/caducifolio) sobre las respuestas de las plantas a las perturbaciones, considerando que estas características pueden determinar variaciones en su comportamiento frente a tales perturbaciones. *Área de estudio:* Chaco semiárido subtropical, provincia de Santiago del Estero, Argentina. *Material y métodos:* Se midieron hojas de individuos maduros en bosques con diferentes historias de manejo del suelo: sin perturbaciones durante cuatro décadas (RC); rolado y sometido a extracción selectiva de madera ocho años antes del muestreo (Rol+A); y rolado seguido de incendio ocho años antes del muestreo (Rol+F). Para cada sitio, medimos 10 individuos maduros de cada una de las seis especies estudiadas, registrando la altura máxima y el diámetro a la altura del pecho (DAP) y recolectamos 20 hojas de cada uno para medir el área foliar (AF) y el área foliar específica (AFE). *Resultados principales:* Todas las especies aumentaron significativamente su área foliar (AF) y área foliar específica (AFE) en bosques perturbados. Las especies arbóreas presentaron un AF mayor que los arbustos, mientras que estos últimos exhibieron una mayor AFE. Ambos rasgos mostraron valores más altos en especies caducifolias en comparación con las perennes, lo que indica que, tras las perturbaciones, estas especies podrían captar mejor los recursos liberados al aumentar su área foliar. La media ponderada por la comunidad (CWM, por sus siglas en inglés) del AF fue mayor en el bosque Rol+A, probablemente reflejando el efecto del aumento en la disponibilidad de luz. Además, todos los bosques perturbados mostraron una CWM más alta de AFE. *Aspectos destacados de la investigación:* Los cambios observados en los rasgos foliares a nivel de especie, como el aumento del área foliar (AF) y del área foliar específica (AFE), que resultan en un mayor AF y AFE a nivel comunitario, sugieren la adopción de estrategias más adquisitivas en comunidades perturbadas, fomentando una mayor captación de recursos y facilitando la recuperación del tejido foliar. Esto puede influir en funciones ecosistémicas, como la descomposición de la hojarasca, la productividad y la asignación de recursos para el crecimiento y la reproducción. Monitorear las respuestas foliares a las perturbaciones en los bosques chaqueños es fundamental para orientar prácticas de manejo sostenible y conservación.

Palabras clave: bosque chaqueño; efectos de los disturbios; variabilidad intraespecífica.

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Supplementary information ↓

1. INTRODUCTION

The increasing demand for food and other goods by the human population has led to the intensification of land use in various regions of the planet, resulting in changes to or replacements of the main types of vegetation cover (Táلامo et al., 2003, 2009; Kunst et al., 2014; Barati et al., 2023). These changes in the ecosystem's properties and processes can be described and analyzed by a functional ecology approach that evaluates the changes in certain plant traits directly related to them (Chapin et al., 2003; Perez-Harguindeguy et al., 2013). The functional traits of plants include morphological and physiological features that can be easily measured or estimated and are known as "response traits" when they change after alterations in environmental factors such as nutrient and water availability. Also, they could be "effect traits" when they exert an influence over such ecosystem processes as primary productivity,

evapotranspiration, and decomposition, among others (Díaz & Cabido, 2001; Lavorel & Garnier, 2002; Suding et al., 2008). Some functional traits, such as leaf area (LA) and specific leaf area (SLA), are typically considered both response and effect traits. LA and SLA have been commonly studied in many species of the world because they are considered good indicators of environmental changes generated by both climate and human activities (Lloret et al., 2005; Arnan et al., 2007; Perez-Harguindeguy et al., 2013; Salgado-Negret & Paz, 2015). LA (the size of an individual leaf) is a plant trait relevant for light interception and has important consequences for the energy and water balance of the leaves (Díaz et al., 2016). SLA is the ratio between the dry weight and the area of a leaf, and usually exhibits a negative correlation with leaf longevity and assimilation rate, presenting typically lower values in perennial than in deciduous leaves (Reich et al., 1997; Ackerly et al., 2002).

The variation in functional trait values depends on species' genetic diversity and phenotypic plasticity, which influence their ability to adapt to environmental changes at different scales (Jung et al., 2010; Kichenin et al., 2013; Salgado-Negret & Paz, 2015; Vilà-Cabrera et al., 2015; Turcotte & Levine, 2016; Zuo et al., 2016). In functional ecology, the specific value of a trait under certain environmental conditions is called an attribute. The variation among different species and within the same species (intraspecific), or a combination of both, determines changes in these attributes at the community level. In particular, intraspecific variation allows us to estimate the response of organisms to climatic and environmental changes (Kichenin et al., 2013; Zuo et al., 2016).

The community-weighted mean (CWM) is an indicator of the expected value for a trait in the community when a sample is taken randomly (Garnier et al., 2004). It is usually based on the relative abundances of the species and their attributes in a community. A change in the CWM of a functional trait might be considered indicative of environmental alterations affecting the functional structure of a plant community (Díaz & Cabido, 1997; Vandewalle et al., 2010; Pérez-Harguindeguy et al., 2022). Its value is a good indicator of plant responses to environmental disturbances (del Corro, 2023). It may also reflect changes in resource availability resulting from disturbances related to exploitation activities (Conti & Díaz et al., 2013; Loto & Bravo, 2020) and represent valuable information for delineating forest sustainable management plans.

In woody species, the values of leaf traits (e.g., LA and SLA, among others) are associated with allometric traits (height) (de la Riva et al., 2014) and with different ecological strategies related to resource capture, tolerance against different stress levels, and biomass production, among others (Pérez-Harguindeguy et al., 2013). Under low or absent disturbance frequency, the plant species of more conservative strategies (low leaf area, higher wood density, among others) dominate in forest communities. Frequently, high disturbance intensities promote the dominance of rapid-growth early successional species with more acquisitive attributes such as high specific leaf area and nitrogen concentration (Carreño-Rocabado et al., 2012; Conti & Díaz, 2013; Maeshiro et al., 2013; Schönbeck et al., 2015).

In Argentina, subtropical dry forests cover several ecoregions, including the Dry Chaco. This ecoregion is characterized by xerophilous forests adapted to semi-arid conditions with seasonal dry periods (Oyarzabal et al., 2018). The semiarid Chaco is a subregion of the Dry Chaco (Morello et al., 2012) where, like in other subtropical and tropical forests of the world, the extensive livestock and deforestation for the implementation of cultivated pasture and legume crops have caused drastic changes at the landscape level, deeply modifying the native forest structure (Casar et al., 2016) since the beginning of colonization. More recently, silvopastoral systems were implemented involving livestock activities, shrubby stratum removal, and tropical grass sown (Chiossone et al., 2014). These systems also involve the use of roller-chopping (Casar et al., 2016; Borrás et al., 2017), which consists of a metal cylinder that passes over small woody vegetation to reduce the volume of the shrubby layer and allow native or tropical grasses to be planted (Steinaker et al., 2016). They are often combined with prescribed fires to remove the largest volumes of woody waste (Kunst et al., 2012, 2014). The traditional forest

exploitation in the Chaco region consists of extracting the best individuals for sawn wood, poles, and those without forest aptitude for uses of lesser value, such as firewood or charcoal (Rueda et al., 2015; Loto, 2021). The forest logging generally exceeds natural regeneration and tree growth possibilities, and after decades of overexploitation, extensive forest areas could be affected by degradation and biodiversity loss (Morello et al., 2009).

Encroached areas with native vegetation are considered an alternative low productivity state (Coria et al., 2023), and roller-chopping and prescribed fires are commonly employed in the region as a sequential combination of disturbances to reduce the volume of shrubby vegetation (Ledesma et al., 2018; Coria et al., 2021). The synergism among disturbances could harm local communities that depend on forests for their subsistence (Costanza & Neuman, 1997; Morello et al., 2009) and affect the structure and natural dynamics of these vegetation units (Bravo et al., 2010; Herrero et al., 2015; Kunst et al., 2016; Ferraina et al., 2022; Steinaker et al., 2016). The Chaco region forests are characterized by a high resilience to traditional disturbances (Táلامo et al., 2013). The practices as livestock, rolling-chopping, and prescribed fires, could alter diversity and promote changes in edaphic properties and vegetation structure, affecting the dynamics and balance between communities dominated by woody plants and those dominated by herbaceous plants (Adámoli et al., 1990; Bravo et al., 2001, 2010; Morello et al., 2006). Changes in forest structure and species composition can generate alterations in the provision of ecosystem services and goods for rural communities (Táلامo et al., 2003, 2009; Kunst et al., 2014; Pellegrini et al., 2021; Ferraina et al., 2022).

Despite there is some background information on the variation of leaf attributes in woody species in response to environmental changes and/or disturbance gradients in the Chaco region (Trigo 2018; Santacruz García et al., 2019, 2021; Loto & Bravo, 2020), most of these studies analyzed changes in foliar attributes as categorical plant traits. Loto & Bravo (2020) have demonstrated that more disturbed forests are experiencing changes mainly related to the shrubby stratum species composition, the diminishing of the forest structure, and the predominance of species with herbaceous leaves, relating these findings to the higher disturbance recurrence in comparison to a protected area from the same biogeographical region. Conversely, these authors have determined the dominance of species with perennial coriaceous leaves in a protected area from the Chaco region, with better hydric balance. On the other hand, Santacruz García et al. (2019, 2021) informed that shrubby species from the native Chaco region forest are more flammable and have a better biochemical response to fires and resprouting capacity than tree species, which could be related to their dominance in highly disturbed environments. In these antecedents, foliar traits were evaluated as a categorical approach; therefore, quantitative analyses are desirable to improve the comprehension of the role of foliar periodicity and growth habit in the plant responses to disturbances (Bravo et al., 2022). The objective of our work was to assess the effects of forest disturbances on foliar attributes (LA and SLA) of woody species in the semi-arid Chaco of Argentina. Disturbances are represented as different combinations of land management practices (removal of vegetation, logging, and fire) (Kunst et al., 2016; Bravo et al., 2022). We evaluated intraspecific variation in leaf area (LA) and specific leaf area (SLA) of six native woody species using a quantitative approach. We also explored the effect of growth form (tree/shrub) and leaf periodicity (perennial/deciduous) on plant responses to disturbances, considering that these traits may determine variations in their behavior in response to such disturbances (Loto, 2021).

We tested the hypothesis that there is an intraspecific variability in LA and SLA of the species studied that could be implicated in their response to forest disturbances since these events produce physical and biological changes with potential effect on the species' resilience and ecosystem services (Kichenin et al., 2013; Salgado-Negret & Paz, 2015; Vilà-Cabrera et al., 2015; Zuo et al., 2016).

2. MATERIAL AND METHODS

2.1. Study area and species selection

The study area is located in the semi-arid Chaco Region of Argentina, in the province of Santiago del Estero (Fig. 1). The climate is seasonal semiarid with an annual precipitation of 640 mm (average of years 1912–2012; [INTA 2012](#)) that mostly occurs between October and April. The mean temperatures are 26.9 °C for the hottest month (January) and 12.4 °C for the coolest month (July) (SMN, 1992). The native vegetation comprises a mosaic of forests, shrublands, savannas, and grasslands ([Giorgis et al., 2013](#); [Cabido et al., 2018](#); [Oyarzabal et al., 2018](#)). Soils belong to the order Entisols, suborder Eutric Regosol ([Lorenz, 1995](#)).

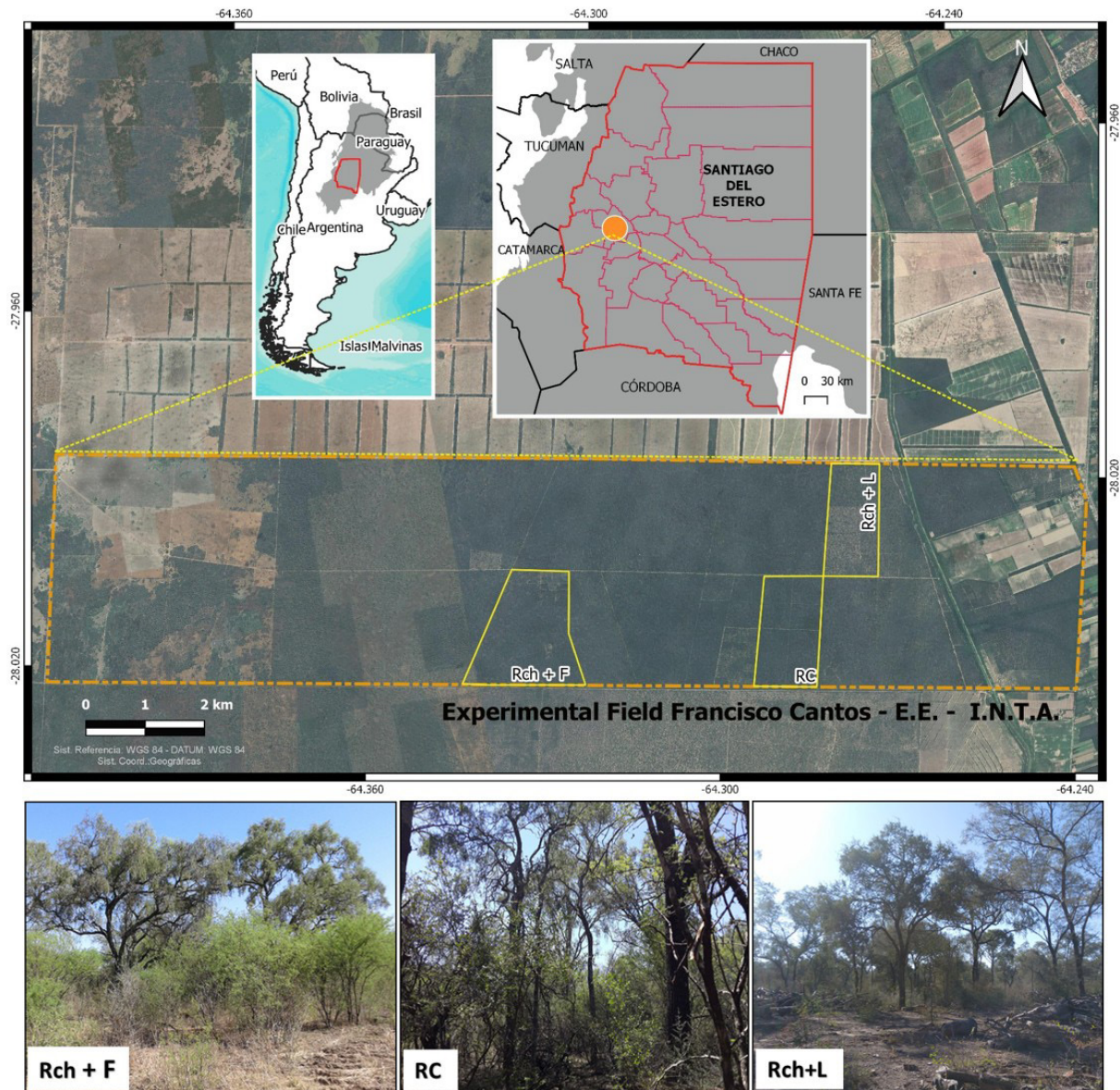


Figure 1. Top: Location of the study area in the Francisco Cantos Experimental Field, Province of Santiago del Estero, Argentina. The minimum and maximum distances between treatments were 1 km and 5 km, respectively. Bottom: Sampling sites, where Rch + F = forests with roller-chopping and fire; RC = reference condition forest; Rch + L = forests with roller-chopping and logging.

The forest presents three strata: the higher stratum is dominated by *Aspidosperma quebracho-blanco* Schltdl. (quebracho blanco) and *Schinopsis lorentzii* (Griseb.) Engl. (quebracho colorado) that can reach heights of more than 20 m. The medium stratum is represented by *Sarcomphalus mistol* (Griseb.) Hauenschild (mistol), *Neltuma nigra* (Griseb) C.E. Hughes & G.P. Lewis (algarrobo negro), *Neltuma ruscifolia* (Griseb) C.E. Hughes & G.P. Lewis (vinal) and *Parkinsonia praecox* (Ruiz & Pav. Ex Hook.) Hawkins (brea) that can reach up to 12 m in height. The lower stratum is characterized by shrubby species, including *Senegalia gilliesii* (Steud.). Seigler & Ebinger (teatín), *Celtis ehrenbergiana* (Klotzsch) Liebm. (tala), *Atamisquea emarginata* Miers ex Hook. & Arn. (atamisqui), *Condalia microphylla* Cav. (piquillín), *Castela coccinea* Griseb. (mistol del zorro), and *Schinus fasciculatus* (Griseb.) I.M. Johnst. (molle) that can reach up to 7 m in height (Araujo et al., 2008; Giménez et al., 2011).

The sampling sites are located at the Francisco Cantos Experimental Station, which belongs to the National Institute of Agricultural Technology of Argentina (INTA), Santiago del Estero province (28° 03' LS; 64° 15' LW; 169 m.a.s.l.) (Fig. 1). Sampling sites were delimited using satellite images and through surveys of the personnel in charge of these areas. Three types of native forests with different management histories were selected: A- undisturbed forests for the last four decades, reference condition (RC); B- forests with roller-chopping and logging (Rch+L); and C- forests with roller-chopping and fire (Rch + F) (Fig. 1). The minimum and maximum distances between forests were 1 km and 5 km respectively.

The RC forest, which has not experienced disturbances in the last four decades, presents three forest strata and the typical species composition of the semiarid Chaco region (Araujo et al., 2008; Loto & Bravo, 2020). The Rch + L forest was managed using a mechanical vegetation removal method known as “low intensity roller-chopping” and then logged for wood extraction destined for fuel, applying a conservative criterion that reduced only 30% of the basal area (Navall et al., 2008; Ledesma et al., 2018). Roller-chopping involves passing a 2.5 m wide cylinder over the shrubby stratum, which reduces plant cover. In the Rch + F forest, vegetation was sequentially subjected to roller-chopping and prescribed fire, also in 2008, to promote grass regrowth, followed by burning to eliminate woody residues (Kunst et al., 2016). Additionally, other wildfires were identified in the Rch + F forest through scars on standing trees (Bravo et al., 2008), although the dates are uncertain. The anthropogenic disturbances recognized in this work correspond to these forest management practices (Ibañez-Moro et al., 2024). The environmental conditions of the sampling sites are shown in Table 1.

Table 1. Values of environmental variables in different forest with different land uses at the Francisco Cantos Experimental Field, Santiago del Estero province, Argentina

	RC	Rch+L	Rch+F
Number of individuals	519	438	539
Maximum canopy height (m)	25	17	21
DBH (cm)	6.44 ± 9.53	4.21 ± 9.45	4.27 ± 9.31
PAR (μmol m ⁻² s ⁻¹)	594.5 ± 412.85 a	1,054.83 ± 300.78 b	578.08 ± 189.3 a
Soil pH (relation 1:2,5)	6.12 ± 0.61 a	5.62 ± 0.27 a	5.53 ± 0.26 a
Soil Conductivity (dS m ⁻¹)	1.42 ± 0.49 b	0.78 ± 0.62 ab	0.44 ± 0.15 a
Soil Organic Carbon (%)	2.71 ± 1.80 a	2.36 ± 0.19 a	2.52 ± 0.23 a
Soil bulk density (g cm ⁻³)	0.93 ± 0.07 a	1.00 ± 0.03 ab	1.03 ± 0.04 b

Mean values ± sd. RC (reference condition forest), Rch + L (roller-chopping and logging forest), and Rch + F (roller-chopping and fire). DBH (diameter at breast height), Photosynthetic Active Radiation (PAR). Different letters indicate significant differences at $p < 0.05$.

To characterize the effects of disturbances on soil properties and nutrient availability, 18 soil samples were collected from each site using a 5 cm diameter auger to a depth of 10 cm. The samples were oven-dried at 105 °C for 48 hours and then weighed to determine bulk density. In the laboratory, pH (in a 1:2.5 aqueous solution), electrical conductivity, and percentage of organic carbon were analyzed. Additionally, to indicate canopy openness caused by disturbances, photosynthetically active radiation (PAR) was measured at each site using a linear quantum sensor, taking 12 readings per site at a height of 1.30 m between 11:30 a.m. and 2:30 p.m. in mid-September 2016. PAR was used as an indicator of irradiance and was related to biomass production and canopy structure.

The species selected for this study were: three trees: *Aspidosperma quebracho-blanco* (quebracho blanco), *Sarcomphalus mistol* (mistol), both perennials, *Schinopsis lorentzii* (quebracho colorado), deciduous, and three shrubs: *Celtis erhenbergiana* (tala), deciduous, *Atamisquea emarginata* (atamisqui), and *Schinus fasciculatus* (molle), both perennials. The botanical family of these species and their growth habit are shown in Table 2. The selection of species is based on their representativeness and dominance in the different forest strata from the Chaco region (Araujo et al., 2008; Giménez et al., 2011).

Table 2. Botanical family, growth habit, and leaf periodicity of the six species included in this study at the Francisco Cantos Experimental Field, Santiago del Estero province, Argentina

Species	Botanical family	Growth habits	Leaf periodicity
<i>Aspidosperma quebracho-blanco</i>	Apocynaceae	tree	perennial
<i>Schinopsis lorentzii</i>	Anacardiaceae	tree	deciduous
<i>Sarcomphalus mistol</i>	Rhamnaceae	tree	perennial
<i>Celtis erhenbergiana</i>	Celtidaceae	shrub	deciduous
<i>Atamisquea emarginata</i>	Capparaceae	shrub	perennial
<i>Schinus fasciculatus</i>	Anacardiaceae	shrub	perennial

2.2. Leaf trait measurement

At each forest condition (Fig.1), ten mature and healthy individuals for each of the six species were selected (60 individuals in total per site). For tree species, we randomly selected individuals with a diameter at breast height (DBH) above 10 cm. The trees at each forest type were selected randomly, with a minimum distance of 30 m between individuals of each species. At each tree or shrub, 20 completely developed and fully exposed to sunlight leaves were collected from each individual to analyze LA and SLA, following the methodology proposed by Pérez-Harguindeguy et al. (2013). Leaves were stored in hermetic bags under moist conditions until laboratory analysis. Fresh leaves, along with petioles and rachis, were scanned using a desktop scanner and then dried in an oven at 60 °C for 48 to 72 hours until a constant weight was achieved. The dry weight of each leaf was measured using a precision balance with 0.0001 g accuracy. LA was determined using ImageJ© software (Di Rienzo et al., 2016), and SLA was calculated by dividing the individual leaf area by its dry weight, expressed in mm²·mg⁻¹ (Pérez-Harguindeguy et al., 2013). Leaf phenology for each species was established based on data published by the Darwinion Institute of Botany (<http://www.darwin.edu.ar>) and analyzed as a categorical variable.

2.3. Species cover measurement

With the objective of describing community structure and tree and shrub species abundance, in four plots in the RC and Rch + F and three plots in Rch + L we recorded the tallest tree (maximum height, m). We also identified each individual of each species and measured its diameter at the breast height (DBH). These cover values (Supplementary material Table S1) were used later to calculate CWM at the site level, for each leaf trait (see below).

2.4. Data analysis

Differences on soil properties and PAR measurements between sites were compared by using ANOVA statistical analysis. To evaluate the intraspecific variation of LA and SLA of species across forests with different management histories (RC, Rch + L, Rch + F) and their relationship with leaf periodicity and growth habit, ANOVA was performed. We considered the foliar traits as response variables and analyzed the differences among species at different sites. To analyze the relationship between leaf periodicity and growth form to the variables LA and SLA, the average values of all individuals from all species were considered, grouped according to whether they were evergreen or deciduous, and whether they were trees or shrubs. The normality of residuals was assessed using the Shapiro-Wilk test, and the homogeneity of variances was assessed using a residual scatter plot against expected values. We conducted Fisher's LSD test for ex-post comparisons, considering a significance level of $p < 0.05$. Values are expressed as the mean of standard deviation. For all analyses, the statistical program InfoStat version 2016 was used (Di Rienzo et al., 2016). The CWMs for LA and SLA were calculated using Formula 1, which represents the average value of a given trait in the plant community weighted by species abundance. CWM was calculated by F Diversity Statistical software (Di Rienzo et al., 2016).

$$CWM = \sum_{i=1}^s w_i x_i$$

where CWM (trait x) is the CWM for trait "X"; S is the total number of woody species in the community at each site, W_i represents the relative cover of species "i" calculated as the sum of the DBH of each species; X_i is the value of the trait in species "i" (Casanoves et al., 2011). Differences between CWM's for the two leaf traits between sites were evaluated by ANOVA and Fisher's LSD test for ex-post comparisons, considering a significance level of $p < 0.05$.

3. RESULTS

The total number of woody individuals, DBH and the maximum canopy height were lower in the Rch + L treatment. The maximum number of individuals was found in the Rch + F forest, while the maximum height and DBH were registered in the RC forest (Table 1). We did not find a consistent pattern for differences between sites in the soil properties analyzed. Photosynthetic active radiation (PAR) was higher in the Rch + L treatment (Table 1), with no differences between RC and Rch + F. There were significant differences in soil conductivity and soil bulk density between the RC and the Rch + F treatments. Results showed no differences neither for soil pH, nor for soil organic carbon between sites.

All species tested showed differences in LA between the RC and at least one disturbed forest. The highest LA values were consistently found in the Rch + L forest (Fig. 2A). Species such as *A. quebracho-blanco*, *S. lorentzii*, *S. mistol*, and *C. ehrenbergiana* increased their LA by 25% and 44% both disturbed forests compared to the RC site. Among other shrubs, *A. emarginata* displayed a higher LA only in the Rch+F forest, while *S. fasciculatus* showed a greater LA in the Rch + L forest, with no significant differences between RC and Rch + F. Overall, the Rch + L forest exhibited the highest LA values.

Regarding the SLA, all species exhibited higher values (between 25 and 35%, Fig. 2B) in disturbed forests compared to the reference control (RC). Notably, *S. mistol*, *A. emarginata*, and *C. ehrenbergiana* exhibited significant differences among all the sites studied (Fig. 2B), while *S. mistol* and *A. emarginata* had the highest SLA values in the Rch + F forest, *C. ehrenbergiana* reached its maximum values in the Rch + L forest. On the other hand, the species *A. quebracho-blanco*, *S. lorentzii*, and *S. fasciculatus* showed non-significant differences in SLA among the disturbed forests (Fig. 2B).

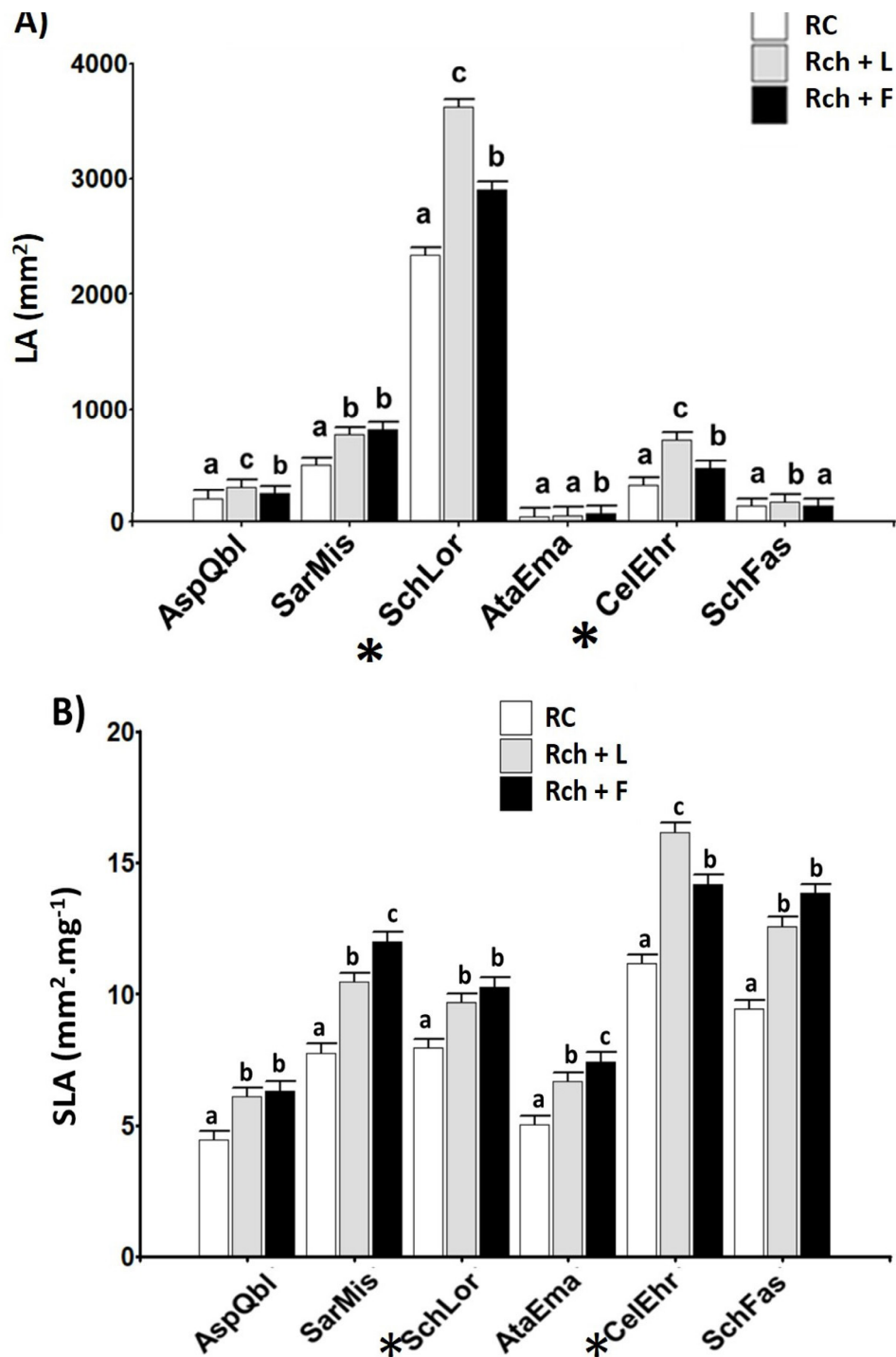


Figure 2. Intraspecific variation of: a) leaf area (LA) and, b) specific leaf area (SLA) of six native woody species of the Argentine Chaco region in forests with different histories of disturbances. Mean values + S.E. (standard error). Tree species = AspQbl: *Aspidosperma quebracho-blanco*, SarMis: *Sarcophagus mistol*, SchLor: *Schinopsis lorentzii*. Shrub species = CelEhr: *Celtis ehrenbergiana*, AtaEma: *Atamisquea emarginata*, and SchFas: *Schinus fasciculatus*. Asterisks indicate deciduous species (species without an asterisk are perennial). RC: reference condition forest, Rch + L: forest with roller-chopping and logging, Rch + F: forest with roller-chopping and fire. Different letters indicate significant differences among the mean values of each site ($p < 0.05$).

Considering the leaf periodicity and habit of the studied species, LA and SLA were significantly higher in the deciduous species (*S. lorentzii*, *C. ehrenbergiana*) than in the perennial (*A. quebracho-blanco*, *S. mistol*, *A. emarginata*) (Fig. 3A and B). Regarding the growth habit, the LA was significantly higher in tree species than in shrubby species (Fig. 4A), while SLA was significantly higher in shrubs than in tree species (Fig. 4B).

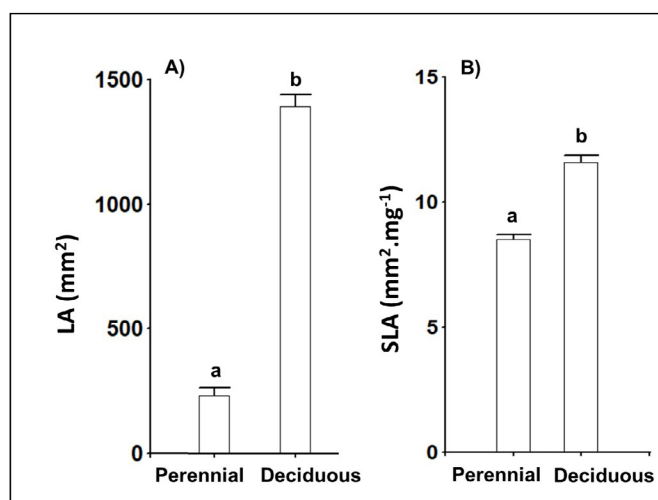


Figure 3. Relationships between leaf periodicity (perennial or deciduous) and the mean values of the two morphological leaf traits analyzed: a) leaf area (LA) and, b) specific leaf area (SLA) of six native woody species of the Argentine Chaco region in forests with different histories of disturbances. Mean values + S.E. (standard error). Different letters indicate significant differences ($p < 0.05$).

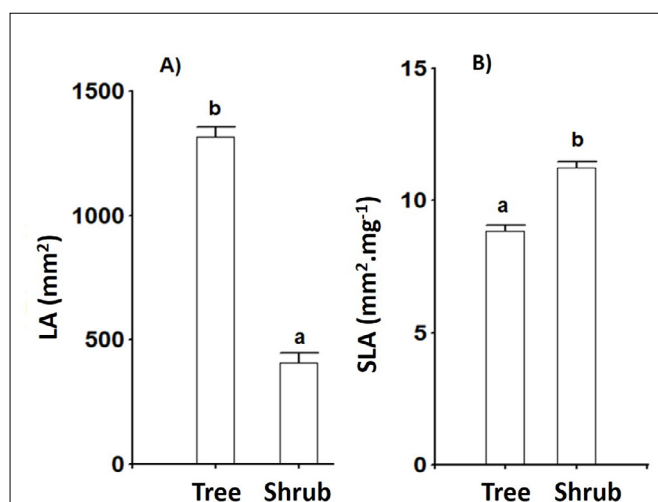


Figure 4. Relationship between the growth habit (tree or shrub) and the mean values of the morphological leaf traits analyzed: a) leaf area (LA) and, b) specific leaf area (SLA) of six native woody species of the Argentine Chaco region in forests with different histories of disturbances. Mean values + S.E. (standard Error). Different letters indicate significant differences ($p < 0.05$).

At the community level (CWM's), the LA was significantly higher in the Rch + L forest than in the RC forest and Rch + F forest. The CWM for SLA was significantly higher in both disturbed forests than in RC, without significant differences among them (Table 3).

Table 3. Community weighted mean (CWM) values for leaf traits in relation to forest types at the Francisco Cantos Experimental Field, Santiago del Estero province, Argentina

	RC	Rch+L	Rch+F
CWM LA (mm ²)	587.71 ± 138.73 a	997.33 ± 199.26 b	523.16 ± 212.26 a
CWM SLA (mm ² .mg ⁻¹)	6.5 ± 0.39 a	8.85 ± 0.66 b	8.72 ± 0.62 b

Community weighted mean (CWM) plus standard deviation (SD) for leaf area (LA) and specific leaf area (SLA) in forests under different management practices. RC reference condition; Rch + L = forest with roller-chopping and logging; Rch + F forest with roller-chopping and fire. Different letters indicate significant differences between sites, for each variable ($p < 0.05$).

4. DISCUSSION

This work analyzed the changes in LA and SLA in six native woody species from the Chaco region of Argentina, in response to different combinations of disturbances commonly applied in the management of native forests (Kunst et al., 2016; Ledesma et al., 2018). Leaf trait (LA and SLA) responses showed consistent patterns regardless of plant growth form (trees/shrubs) and leaf habit (deciduous/evergreen). All species exhibited significant increases in LA and SLA in disturbed environments, suggesting phenotypic plasticity as a response to the release of resources such as light and nutrients generated by disturbances (Pérez-Harguindeguy et al., 2013; Kitzberger et al., 2014). Changes in leaf attributes suggest changes from more conservative to more acquisitive strategies, making individuals more efficient at capturing such resources. These changes could contribute to the resilience of plant communities in the face of such events (Táلامo et al., 2015). LA and SLA are traits mainly related to the allocation of resources to photosynthesis rather than to supporting structures or height growth (de la Riva et al., 2016; Casals et al., 2018). Therefore, the increase in LA and SLA observed in the studied species after disturbances could represent a functional advantage by enhancing nutrient uptake and light interception (de la Riva et al., 2016) in disturbed environments, which in turn may have positive effects on energy and water balance (Díaz et al., 2016).

Poorter & Rozendal (2008) suggested that the increase in LA after a disturbance could be a response to shading and outcompeting by neighboring species. This response can be considered efficient during the initial phases after the disturbance, when competition for resources decreases (de la Riva, 2016; Casals et al., 2018). On the other hand, some authors report the formation of small leaves after a disturbance as a strategy to reduce the degree of insolation of the leaf blade (Ackerly et al., 2002), which does not seem to be the case for the native Chaco species studied here.

The economic leaf traits depend on soil properties, especially nutrient supply, as well as on climatic conditions reflected in precipitation (Joswig et al., 2022). In this context, detailed measurement of soil variables is essential to detect functional changes in leaf attributes such as leaf area and specific leaf area. Our soil parameter results across different sites agree with those reported by Anriquez et al. (2005), who found that soil quality indicators were not significantly affected by the treatments applied, a fact attributable to the low intensity of rolling and associated practices. These values fall within the normal range for soils in the semi-arid Chaco region, validating the representativeness of our data and underscoring the importance of considering them to interpret the observed foliar dynamics.

The increase in LA observed in disturbed forests suggests the formation of larger and thinner lamina even in species with coriaceous and perennial leaves, such as *A. quebracho-blanco* and *S. fasciculatus*. Higher LA values observed in *S. lorentzii*, *A. quebracho-blanco*, *C. ehrenbergiana*, and *S. fasciculatus* in the Rch + L forest seem to indicate a greater allocation of resources towards photosynthetic tissues in response to the significantly higher levels of radiation detected at this sampling site. Leaf size is a trait influenced by light and nutrients like N and P availability (Albanesi et al., 2013; González et al., 2014). Because in our study we did not find differences on soil organic carbon, the increase in LA on the six native species from the Chaco region forests could be a response to the release of space and solar radiation levels. This acquisitive strategy, as observed in the foliar traits of the studied species, could have a positive effect on certain ecological processes, such as primary productivity and litter decomposition. The efficient capture of resources in fast-growing tissues, such as leaves, may help prevent losses due to runoff and soil erosion, while also accelerating nutrient cycling (Lecerf & Chauvet, 2008; Jung et al., 2010; Carreño-Rocabado et al., 2012; Conti & Diaz, 2013; Vaieretti et al., 2021).

The SLA has been demonstrated to be negatively correlated with leaf lifespan and foliar thickness, and positively correlated with Nitrogen content and assimilation rates (Pérez-Harguindeguy et al., 2013; Gray et al., 2019). Species with low SLA have smaller, thicker leaves with longer lifespans; therefore,

they could contribute to higher nutrient retention in foliage and litter but slow down the foliar decomposition rate at the community level (de la Riva et al., 2016). Hoffmann et al. (2005) considered that lower SLA in tree species from savannas in the Cerrado, Brazil, is related to better water-use efficiency, which can be a key factor in the survival in burnt areas.

However, in this study, even those perennial species such as *A. quebracho-blanco*, *S. mistol*, *A. emarginata*, and *S. fasciculatus* showed an increase in SLA in disturbed environments, suggesting a shift toward a more acquisitive strategy under conditions of greater resource availability. The higher SLA in perennial species such as *S. mistol*, *A. emarginata*, and *S. fasciculatus*, in the Rch + F forest, suggests the possibility of investing nutrients potentially released by fire, in bigger and thinner leaves that eventually favor a higher photosynthetic rate. This response could increase photosynthetic efficiency, promoting the dominance of these species in disturbed environments (Giorgis et al., 2021). In this work, both pioneers, such as *C. erenbergiana* and *S. fasciculatus* (with a short lifespan), and late-successional species *S. lorentzii*, *A. quebracho-blanco* (with a long lifespan), adopted a more acquisitive strategy by increasing their LA and SLA in disturbed forests. As for the case of LA, the maximum values of SLA observed in tree species (*S. lorentzii* and *S. mistol*) in the disturbed forests might indicate that these species could be responding positively to a release of space and sunlight by investing in bigger, less dense leaves. Long-term effects of wildfire on soil stoichiometry were demonstrated to be present, in some cases, more than 10 years after the fire event (Francos et al., 2018; Kong et al., 2018).

At the woody community level, the CWMs of LA and SLA appear to be reliable indicators of environmental changes resulting from disturbances in the Chaco forests (Santacruz et al., 2021). The values of CWMs of LA and SLA observed in disturbed forests suggest that the acquisitive strategy identified at the species level also reflects a community-level response to environmental changes (Ackerly et al., 2002; Baraloto et al., 2010; Santacruz et al., 2021). Notably, the Rch + L presented the highest CWM for LA, which corresponds with the significantly higher level of photosynthetically active radiation (PAR) measured at this site as a result of biomass removal and the consequent site openness. The absence of significant differences in the CWM of SLA among forests managed with different disturbance combinations may be related to changes in species dominance or composition that avoid identifying a particular bias in each forest type. According to the biomass-ratio hypothesis (Grime, 1998), both relative cover as well as plant attributes influence the functional characteristics of plant communities, including the CWMs of different traits. Nevertheless, in these forests, not only was the relative cover affected as a consequence of disturbance (del Corro, 2023), but also, and probably more interesting, the attributes of the dominant species. The dominance of shrubs in disturbed forests of the Chaco region (Ledesma et al., 2018) could represent a plant community response that buffers the changes generated by disturbances removing dominant canopy species, typically of slow growth rates, or inducing architectural changes in these species towards shrubby forms due to increased resprouting (del Corro, 2023).

5. CONCLUSIONS

Our results showed that the six woody species analysed responded to disturbances by increasing their LA and SLA, independently of their growth form (trees or shrubs) or leaf longevity (deciduous or evergreen). Moreover, the changes observed in LA and SLA at the species level were also detected at the community level. These functional changes could be effective indicators of the environmental changes caused by anthropogenic disturbances, remarking also a potential effect on changing community properties and processes.

Supplementary information ↑

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Supplementary material

Table 1: Accompanies the paper on *Forest System's* website.

Data availability

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

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Authorship contribution statement

Florencia Inés del Corro: Conceptualization, Investigation, Methodology, Formal analysis, Writing – original draft, Writing – review & editing.

Lucas Enrico: Methodology, Formal analysis, Writing – review & editing, Visualization.

Sandra Josefina Bravo: Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing, Visualization.

Competing interests

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.

Statement on the use of Artificial Intelligence

Not applicable.

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