Transplanting native tree seedlings to enrich tropical live fences: an ecological and socio-economic analysis

Beatriz D. Fuentealba · Miguel Martínez-Ramos

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Abstract The enrichment of live fences with native tree species has been proposed as a conservation strategy in agricultural landscapes; however, little research has explored ways to do this in tropical areas. This study examines selection of native tree species, effects of damage caused by mammals (mainly cattle) in performance (survival and growth) of transplanted seedlings, and cost-benefit balances as critical steps to enrich tropical live fences. Seven native tree species, with ecological and socio-economic importance, were selected in a Mexican agricultural landscape to grow as seedlings, and six of them were transplanted into live fences of cattle ranches with different levels of cattle activity (none/moderate/high). Costs associated with propagation and seedling protection in the field were calculated, and performance and damage in seedlings were measured over 2 years. We developed an index to identify species with the best performance and lowest costs in sites with cattle activity. Our results showed that damage, caused mainly by cattle, reduced the performance of transplanted seedlings. The effect of this damage varied depending on its severity (level and frequency) and the identity and life history of species. All selected species performed well

B. D. Fuentealba (🖂) · M. Martínez-Ramos

Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Antigua Carretera a Pátzcuaro No. 8701 Col. San José de La Huerta, C. P. 58190, Morelia, Michoacán, Mexico e-mail: beatrizfud@cieco.unam.mx in the site without cattle access. *Dendropanax arboreus* was the best species at site with moderate cattle activity, and *Trema micrantha* and *Saurauia scabrida* at site with high cattle activity. These species are recommended for enriching live fences because of good cost-benefit balance. This approach could be an important quantitative method to select species useful not only in agroforestry but also in restoration projects, which normally remain under the pressure of domestic and wild animals.

Keywords Seedling demography · Mexico · Tropical pastures · Herbivory · Cattle damage

Introduction

Livestock is considered one of the most ecologically degrading land uses in tropical landscapes because it converts large areas of highly biodiverse rainforest into pastures dominated by a few grass species used for extensive grazing of cattle (Ospina et al. 2012). High cattle stocking rates cause compaction, erosion, and impoverishment of tropical soils (Buschbacher et al. 1988; Martínez and Zinck 2004). In addition, livestock contributes about 20 % of global greenhouse gas emissions (O'Mara 2011), with methane being the main contributor (Lassey 2007). All these environmental impacts are likely to increase because global demand for meat and dairy products is growing

(Speedy 2003; Walker et al. 2009). Therefore, there is an urgent need to find strategies to increase native biodiversity and mitigate environmental problems inside tropical production systems, especially cattle ones, without affecting productivity and incomes for farmers (Harvey et al. 2008a; Chazdon et al. 2009; Murgueito et al. 2011).

Live fences (also called living fences or live fences posts), defined as "fences established by planting large cuttings, that easily produce roots and on which several strings of wire are attached with the obvious purpose of keeping livestock in or out" (sensu Budowski 1987), are widely employed in tropical areas (Harvey et al. 2005; Maldonado et al. 2008). It has been recognized that live fences may play an important ecological role as providers of resources and habitat for native plants and animals, especially generalist species (Estrada et al. 2000; Harvey et al. 2005; Pulido-Santacruz and Renjifo 2011), and as features that enhance landscape connectivity (Chacón-León and Harvey 2006). However, such features usually are established with a limited number of tree species that are ease to propagate (Zahawi 2005; Harvey et al. 2004, 2008b; Maldonado et al. 2008). In this context, enriching live fences with native tree species has been proposed as an important strategy to improve their ecological value and their contribution to conserve biodiversity in agricultural landscapes (Harvey et al. 2005, 2008a; Murgueito et al. 2011).

Enriching tropical live fences already established with valuable native woody species could increase their conservation importance at both local and landscape scales (Chacón-León and Harvey 2006), and at the same time, provide benefits to people (Harvey et al. 2005). Several woody species supply timber (e.g. for construction and fence-posts) or nontimber forest products (e.g. firewood, fodder, fruits, fiber, etc.) to local farmers (Harvey et al. 2005, 2011; Suárez et al. 2011). Additionally, tree species established in grazing areas provide diverse ecosystem services; for instance, litter-fall and deep roots of trees improve the fertility of soils (Dagang and Nair 2003; Sánchez-Cárdenas et al. 2008), and shade provided during the dry season (Harvey et al. 2005) reduce heat stress in cattle, enhancing dairy production (Betancourt et al. 2003; Hernández-Rodríguez and Ponce-Ceballo 2004). Therefore, it is important to identify criteria to select suitable native species to enrich live fences, which not only consider their conservation value but also their socio-economic value; the last is critical to promote the acceptance of species among local farmers (Beer et al. 2003; Suárez et al. 2011).

The conservation value of plant species is associated with its native origin and rarity in the landscape, and it is better if have a role in maintaining wildlife (e.g. pollinated and/or dispersed by animals; Rodrigues et al. 2009; Suárez et al. 2011). The socioeconomic value of species usually is reflected by one or several local names, and it is associated with local uses of species (Turner 1988; de Lucena et al. 2007). Additionally, it is important to include species with local farmer preference (Beer et al. 2003; Wishnie et al. 2007), and the monetary costs associated with the production and establishment of seedlings. To our knowledge, few native tree species have been tested for the enrichment of live fences in tropical areas (Love et al. 2009). Therefore, it is important to confirm that species with conservation and socio-economic value can also grow and survive as seedlings in conditions prevailing in live fences.

From an ecological perspective, live fences can be considered as disturbed areas, but with better environmental conditions than open pastures for the establishment of transplanted tree seedlings (Love et al. 2009). Shade provided by trees creates a favorable microclimate at ground level with more humidity, less temperature and light radiation than open pastures (Belsky et al. 1993). The shade also could reduce competition with grasses for tree seedlings (Holl 2002). Additionally, in active pastures, herbivorous mammals (especially cattle, as well as rabbits and moles) damage tree seedlings and saplings, affecting their survival and growth (Holl and Quiros-Nietzen 1999; Griscom et al. 2005, 2009). However, the barbed wire used in live fences could provide protection to trees from cattle damage (Love et al. 2009). Consequently, to enrich live fences, it is necessary to identify tree species that tolerate disturbed conditions (compared to those prevailing in conserved forest environments), but not as extreme as those found in open pastures.

From a socio-economic perspective, enrichment has to include perspectives of farmers and land owners because they make all the decisions about live fence management (Harvey et al. 2008b). For instance, live fences are compatible with cattle production because their establishment is cheap, requires low maintenance inputs, and their lineal design not reduce effective grazing areas (Harvey et al. 2005). In agroforestry projects, farmers usually prefer multipurpose tree species because they provide more benefits at similar establishment cost (McDonald et al. 2003; Mekoya et al. 2008). However, some timber species are more appreciated despite their slow growth and high costs because they give greater profits when the timber is sold (Beer et al. 2003; Wishnie et al. 2007). Therefore, the cost-benefit balance is a key question in selecting valuable native tree species for enriching live fences, especially when seedlings of some species may need special and expensive protection to provide expected benefits.

In this paper, the selection of species and effects of cattle damage, and calculate cost-benefit balances as critical steps in enriching tropical live fences with native tree species have been examined. We used a case study conducted in a tropical region (in western of Mexico) to assess the suitability of six tree native species for the enrichment of live fences in cattle pastures. These species differ in their ecological attributes and socioeconomic properties. The economic costs (to propagate and transplant seedlings) and the first year performance (survival and growth) of transplanted seedlings under three levels of cattle activity have been included. In particular, following questions have been answered in this study: Does cattle and other mammal damage (MD) affect the initial performance of native tree species transplanted into live fences? If so, are these effects dependent on ecological attributes of the species? Do costs of seedling production vary among species? If so, what cause such variation? Which species has the best performance in live fences with the lower costs? To answer the last question, we used an index that integrated ecological and economic metrics to discuss the convenience of using selected species in the enrichment of live fences.

Materials and methods

This study was conducted in Hueytamalco (19°58'N, 97°18'W), in west-central Mexico, between 500 and 900 m.a.s.l. The climate is warm and humid, with rainfall all year, a mean monthly temperature of 21.7 °C and mean annual precipitation of 2,700 mm (INIFAP unpublished data). In the area, soils are mainly Andosols of volcanic origin and high fertility (Sánchez-Beltrán 1984). The landscape has been highly transformed by

agricultural activities. Cattle pastures have covered almost 40 % (around 140 km²) of the region since at least 40 years ago; old-growth forest has been reduced to <10 % of its historical cover, secondary forest covers 8 %, and the remaining land is under diverse agricultural use (Hernández-Tejada 2004; INEGI 2007).

In this region, cattle ranches are mainly characterized by extensive grazing, moderate stocking rates (1.6 U animals ha⁻¹) and crosses of Cebu and European breeds, which are sold as calves in the meat market. Ranch areas measure on average 70 (\pm 9) ha and, depending on the incomes of the owner, pastures are dominated by native (*Axonopus* sp.) or exotic (*Cynodon nlemfuensis*, *Brachiaria brizantha* cv. insurgente) grasses. Live fences are set in almost all ranches to divide grazing areas. Stakes of *Bursera simaruba* and *Gliricidia sepium* are the most commonly used for the establishment of live fences (*personal observation*).

Criteria used to select native tree species

Tree species were considered native when they were found in old-growth or secondary forest within the study area and no information existed about possible exotic origin. We used the following criteria to select potential native tree species for enriching live fences: (a) conservation value: if species was rare in the landscape, or it is included in red lists of endangered species or have restricted geographical distribution, (b) functional value: if species provided food to wildlife (i.e. fleshy fruits), shade and habitat to wildlife (evergreen habit), and/or improved soil fertility (e.g. high production of litter-fall), (c) cultural value: if species had a common local name, and it was useful to local farmers (provide shade to cattle, fodder, timber and/or firewood), and (d) availability: if species was found in disturbed environments but with adult trees in secondary or old-growth forests. To assess these criteria, we use the database generated for woody species in our study area by a team of researchers from the National Autonomous University of Mexico (Ibarra-Manríquez and Paz unpublished data).

Attributes of selected species

Seven native tree species were selected based on the above criteria (Table 1). All species were evergreen and found in disturbed environments. Only one species

Table 1 Attributes of seven native tree species in the area of Hueytamalco, Mexico, selected for their cultivation under nursery conditions	ea of Hueytamalco, Mexi	co, selected for their cu	ltivatior	n under m	ursery co	ondition	IS		
Species (Family)	Local name	Abundance (Habitat) GD EF	GD	EF	ΓΩ	LU RS WD	MD	SW	SW Fruit type (fruiting season)
Saurauia scabrida (Hemsl.) (Actindaceae)	Ixlahuate	Medium (OGF, SF)	RE	F,E	f	Νb	NP 0.38 ^b 0.9	0.9	F (Sep-Oct)
Dendropanax arboreus (L.) Decne. & Planch. (Araliaceae)	Temalcuahui	Medium (SF)	WD	F,E	sh	ЧN	0.45 ^b	9.0^{d}	F (June–July)
Alchornea latifolia Sw. (Euphorbiaceae)	Jicarillo o Guajillo	High (OGF, SF)	WD	F, L,E	sh, t	Νb	0.42^{b}	34^{d}	AS (April-May)
Matudaea trinervia Lundell (Hammamelidaceae) ^a	Quebracho	High (OGF)	RE	L,E	t, w	ЧN	0.61^{b}	61	F (June)
Ficus turrialbana Burger (Moraceae)	Higuera de hoja ancha	Low (OGF)	RE	F,E	sh	ЧN	0.48^{b}	1.2	F (May–July)
Heliocarpus appendiculatus Turcz (Tiliaceae)	Jonote	Medium (SF)	WD	L,E	t, w	Ь	0.19^{c}	1.5^{d}	D (March-May)
Trema micrantha (L.) Blume (Ulmaceae)	Matacaballo	Low (SF)	WD	WD F, L, E t, f	t, f	Р	0.31°	3.0^{d}	0.31 ^c 3.0 ^d F (March–Nov)
Growing habitat (obtained from Ibarra-Manriquez unpublished data): OGF old-growth forest, SF secondary forest, GD geographic distribution (RE restricted, WS widespread); EF ecological function (L litter, F food for wildlife, E evergreen); LU local uses (f fodder, sh shade for cattle, t timber, w firewood). Attributes: LH life history (P pioneer, NP non-pioneer); WD wood density ($o \ cm^{-2}$). SW dry seed weight (mo). Fruch tone: F fleshy AS seeded with aril D dry finite: finiting method indicated in narmonesis.	l data): OGF old-growth for uses (f fodder, sh shade fo shv AS seeds with aril D	est, SF secondary forest, est, T secondary forest, u firew transfer to the transfer the transfer the transfer the transfer the transfer the transfer transfer the transfer transfer the transfer t	<i>GD</i> geog ood). At indicate	raphic dist tributes: L	ribution H life hi thesis	(RE res story (F	tricted, W pioneer,	S wides]	pread); EF ecological 1-pioneer); WD wood
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Species vulnerable (NOM-059-SEMARNAT 2001)

Ibarra-Manríquez and Oyama (1992)

^c Williamson and Wiemann (2010)

^b Paz unpublished data

protected under Mexican law (Matudaea trinervia in NOM-059-SEMARNAT 2001) due to its geographic rarity. We included two species typically categorized as pioneers (strongly light-demanding, short-lived species) along with a fast-growing but long-lived species (Alchornea latifolia) considered "almost pioneer" (McDonald et al. 2003). Also, we included four species categorized as non-pioneer (shade-tolerant, slow-growing, and long-lived species).

Production of seedlings in nursery and associated costs

Seedlings of selected species were raised in a local greenhouse. According to the fruiting season of each species (Table 1), mature fruits were collected from at least five healthy adult trees growing in the study area. Seeds were cleaned up by hand and germinated in groups of 30-50 per species (depending on seed size), in plastic boxes (15 cm length \times 12 cm wide \times 2 cm deep) filled with a mixed substrate (nursery soil with 1/4 sand and 1/3 vermiculite). Boxes were monitored every 2 days to record the emergence of seedlings and watered as necessary. Once the cotyledons expanded, seedlings were transplanted to individual black plastic tubes of 380 cm³ with a mixed substrate (nursery soil with 1/3 vermiculite and 1/5 fertilizer Organodel Jardín[®]). Seedlings were watered as necessary. Nonpioneer species were grown in 50 % shade conditions until 1 month before transplant.

We considered a seedling ready for transplanting when it reached at least 25 cm height and it looked healthy. The number of seedlings ready for transplantation varied per species according to their total emergence and survivorship in the greenhouse. Total emergence was the proportion of sowed seeds which emerged as seedlings, and survivorship was the proportion of emerged seedlings which were ready for transplanting in July 2011. The time (days) in the greenhouse for each species depended on the date of seed collection and the growth rate of seedlings. Seedlings of non-pioneer species remained in the greenhouse for 286-328 days, and it was necessary to transfer them from tubes to individual black plastic bags (1.5 L), while the pioneer species remained in the greenhouse for only 60-65 days. Therefore, initial seedling size at the transplantation date differed among species (Table 2).

Species	CAL	Height (ci	n)		Root colla	r diameter (cm)	
		Initial	12 months	20 months	Initial	12 months	20 months
Al Tm Ha Ss Da	None	27 ^a	218	395	0.3 ^a	3.1	5.5
	Moderate		44	50		0.7	0.9
	High		24	30	50 0.7 30 0.6 459 0.4^a 73 0.7 90 1.0 532 0.5^b 83 0.9 31 0.7 0.10 1.2 91 1.4 334 0.8^c 3.0 135 1.8 43 1.1	0.8	
Tm	Moderate High None 28 Moderate High None 45 Moderate High None 55 Moderate High None 55 Moderate High	28 ^a	260	459	0.4^{a}	3.0	5.6
	Moderate		65	73	$\begin{array}{cccccccccccccccccccccccccccccccccccc$		
	High		65	90		1.0	1.6
На	None	45 ^b	300	532	0.5 ^b	5.1	9.2
	Moderate		74	4 83 0.9 1 2 31 0.7 0	1.2		
	High		22	31		0.7	0.8
Ss	None	58 ^c	190	315	0.8°	2.9	4.5
	Moderate		96	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	1.5		
	High		66		1.8		
Da	None	51 ^c	187	334	0.8°	3.0	4.8
	Moderate		100	135		1.8	2.2
	High		48	43		1.1	1.2
Ft	None	71 ^d	162	190	1.4 ^d	2.8	3.4
	Moderate		85	87		1.9	2.1
	High		42	46		1.4	1.6

Table 2 Mean size values of experimental seedlings at the initial (time 0), twelve (12 months) and twenty (20 months) months after their transplantation at Hueytamalco, Mexico

Seedlings correspond to six native tree species transplanted into pasture fields with none, moderate and high cattle activity (CAL). Size was measured as seedlings height and root collar diameter. Mean initial size was the same for all sites. Letters indicate significant differences (p < 0.05) among mean initial size among species. Species acronyms: Al Alchornea latifolia, Tm Trema micrantha, Ha Heliocarpus appendiculatus, Ss Saurauia scabrida, Da Dendropanax arboreus, Ft Ficus turrialbana

Transplantation of seedlings into live fences

By July 2011, not enough seedlings of *Matudaea trinervia* were ready for transplanting; so, only seedlings of six of our studied species were used for their transplantation inside three active cattle ranches. The ranches were representative of cattle management in the study area (Table 3), and also they reflected a gradient of accessibility and levels of cattle activity: none (site 1), moderate (site 2) and high (site 3). Although these levels had no replicates, we were able to compare seedling performance of the six native tree species under different live fence scenarios, which we believe represent typical conditions for tree seedling growing in cattle ranches.

The transplanting area changed in each site. At site 1, seedlings were transplanted to an abandoned pasture area without cattle access. Here, about 10 years before our experiment, *Cedrela odorata* trees were planted in rows (with 5 m between trees) and we used these rows

to mimic live fences. The density of climber plants was higher, and the pasture coverage was lower than in other two sites. At site 2, seedlings were transplanted parallel to six live fences, which were used mainly to separate pasture field from the nearby fallow vegetation (around 10-12 years old), where seedlings were transplanted. This site was considered as moderate level of cattle activity because the stocking rate was low (~ 0.5 animal ha^{-1}), and transplanted seedlings were protected partially from cattle damage by live fences with barbed wires (previously laid by the field owner). At site 3, seedlings were transplanted parallel to five live fences used mainly to delimit pairs of adjacent pasture fields. This site was considered to have high levels of cattle activity because the stocking rate was 1.25 animal ha^{-1} and cattle had access to the transplanting areas.

At all sites, the transplanting areas were cleared to reduce competition from grasses and climber plants. Then seedlings were planted randomly with respect to species and spaced at 2.5 m intervals. At site 1, the

Ranch	Altitude (masl)	Land relief	Pastures	Grazing area (ha)	Cattle heads (ha)	Productive purpose	Access to cattle	Planting area
Site 1	590	Hilly	Exotic grass	80	2.3	Meat	No	1,200 m ²
(Llagostera)								
Site 2	570	Hilly	Native grass	>1,000	0.5	Meat	Moderate	700 m
(Margaritas)								(living fences)
Site 3	800	Hilly	Native grass	40	1.2	Meat	High	700 m
(Xalteno)								(living fences)

Table 3 Characteristics of the three cattle ranches used in the seedling transplanting experiments at Hueytamalco, Mexico

transplanting area covered ~ 1,200 m². At sites 2 and 3, the transplanting areas were established parallel to live fences, in strips 1.5 m wide and covering a total area of 930 m². Extra care provided to transplanted seedlings included a manual weeding (every 3 months) around the seedlings stem and provision of mechanical support (using a wood stick) when trees grow inclined.

At the transplanting period (July 2011), we measured crown width diameter (maximum and minimum) and root collar diameter (RGD) of each seedling (initial size). Then after, we recorded survival, crown diameter, RGD, and damage of each surviving seedling during October 2011, January, April, and July 2012, and March 2013. The damage caused by cattle was recorded as trampling when stem of the seedlings was broken and as browsing (feed upon crown of plants by nibbling) when the tip of the stem was ripped or dry (Love et al. 2009). When the tip of stem had a clean cut, it was recorded as MD (Holl and Quiros-Nietzen 1999). All visible injuries on the stem and foliage of the seedlings were recorded as other damage (OD).

Data and statistical analysis

Survival and growth rates were calculated 12 and 20 months after transplantation. For each species, site and time, survivorship probability was calculated dividing the number of living seedlings by the initial number of transplanted seedlings. Growth was measured as a relative growth rate (RGR) to include differences in initial seedling size among species (Table 2). RGR was calculated as [ln(FS) – ln(IS)]/t, where FS is the final size, IS is the initial size and t is the time in days from the transplanting date to the last census date. RGR was calculated using both crown diameters (RGC, cm cm⁻¹ day⁻¹) and RGDs (mm mm⁻¹ day⁻¹).

Damage was quantified using two metrics: (1) level of damage was calculated by site as the proportion of

living plants 20 months after transplanting which had: only MD (which include cattle damage), only OD, mammal and other damage (M&O) or without damage (WD). (2) The frequency of damage (FD) was calculated per seedling as $FD_i = nf_i/tf_i$, where nf_i is the number of times that *i* damage was registered, tf_i is the number of censuses conducted (five in our study) and *i* is the type of damage (mammal damage, including cattle damage—MD—or other damage—OD). Additionally, the proportion of seedlings browsed and trampled by cattle from all records identified as MD was calculated.

Between sites, we compared the level of MD, OD and seedlings WD using general linear models (GLM), with a binomial error and a logistic link function (Crawley 1993). The frequencies of MD (FMD) were normalized using angular transformation and they were compared among species, and among and within sites using ANOVA. Bonferroni post hoc tests were used to identify significant differences among sites and species (p < 0.05). As well, seedling survival and growth rates were compared among sites (joining all species) using GLM logistic analysis for survival and ANOVA for growth.

Within sites, we tested the effects of initial size, FMD, and species identity on survival using GLM logistic analysis. Differences in growth were tested using analysis of covariance (ANCOVA). In these analyses, species was a categorical factor with six levels and initial size and FMD were co-variables. Initial seedling size (root collar area and crown area at transplanting date) was normalized with log-transformation. Bonferroni post hoc tests were used to identify significant differences among species (p < 0.05).

To test the relationship between survival and growth rates with attributes of species: wood density and seed weight, within each site, single linear regression analyses were used. We tested differences in survival (GLM logistic analysis) and growth (ANOVA) between life histories (pioneer vs. non-pioneer species). Finally, we used all data to evaluate the effects of life history (pioneer vs. non-pioneer species), FMD, and their interaction on survival and growth of each seedling species using ANCOVA. In these analyses, survival was normalized using angular transformation. All statistical analyses were conducted using SPSS 15.0.

To integrate the survival and growth rates of seedlings into a single performance index per species and site, we modified the integral response index (IRI) used by Román-Dañobeytia et al. (2012) as follows: IRI = [survival (%) × RGD (mm mm⁻¹ day⁻¹)]/IRI_{max}. We included IRI_{max} as the maximum value of IRI recorded among all species in all sites to obtain an index value between 0 (worst performance) and 1 (best). The species performance was calculated 12 and 20 months after transplantation.

Cost calculations

The economic costs of seedling production included those related to propagation in the greenhouse, seedling transplantation to the field, and the protection of seedlings from cattle damage. Propagation costs were calculated per seedling as money invested in labor and materials to harvest seeds and to nurture seedlings in the greenhouse. These costs varied according to species and fruit availability, ease of seed extraction, and total emergence and seedling survivorship in the greenhouse. To estimate propagation costs under optimal nursery conditions, we used the highest percentage of germination reported in the literature for our study species to recalculate this cost. Transplantation costs were calculated as money invested in seedling transportation from the greenhouse to the field, and labor required for land preparation and planting.

Finally, for each study site we calculated the money invested in labor and materials used for weeding and to provide protection to transplanted seedlings. At site 1, protection costs included the building of a fence with four lines of barbed wire around the planting area to exclude cattle. Costs of fence maintenance (replace wood posts and adjusted barbed wire) were included only for those species that, on average, were smaller than 2.5 m height 1 year after transplantation, assuming that trees higher than this size were resistant to herbivory caused by cattle. At site 2, protection costs included only the maintenance of the barbed wire (laid along the live fences), because in this case it was not required replacement of wood posts. At site 3, no protection was provided. All labor invested in greenhouse and field was converted to work days (8 h) and paid for at 11 US dollars per day/person. Construction costs for the greenhouse were not included because they were the same for all species.

Species selection index

To integrate species performance, which we used as an indicator of potential species benefits, and economic costs in a single metric we developed a species selection index (SSI). The SSI was based on cost index proposed by Martínez-Ramos and García-Orth (2007), and it was calculated per species and included: (a) propagation and transplanting costs (PC) per seedling, (b) costs of care (CC) per transplanted seedlings with (CC_p) and without protection (CC_{np}) from cattle damage, and (c) performance (growth and survival) of transplanted seedlings per unit of time quantified by IRI, described above. The SSI compares performance (IRI_p) and costs $(PC + CC_p)$ of seedlings protected from cattle damage with performance (IRI_{np}) and costs $(PC + CC_{np})$ of seedlings nonprotected, as follows:

$$SSI = (IRI_p/IRI_{np}) \times [PC + CC_{np}/(PC + CC_p)]$$
(1)

If the value of SSI is higher than 1, it means that protection costs (CC_p) were compensated by a better species performance due to protection (IRI_p/ IRI_{np} > 1). However, if the value of SSI is lower than 1, it means that seedling performance with and without protection was similar (IRI_{np} \approx IRI_p) and that investment in seedling protection is not required. In this study, SSI was calculated under moderate cattle activity (site 2), and under high cattle activity (site 3). Seedlings free of cattle activity (site 1) were used to calculate IRI_p and CC_p. All costs, IRI and SSI were calculated for 12 and 20 months after transplantation.

Results

Damage from cattle and other mammals

Total MD suffered by transplanted seedlings over 20 months increased with level of cattle activity (Fig. 1a). The percentage of living seedlings with MD was lower in the absence of cattle (5 % in site 1)

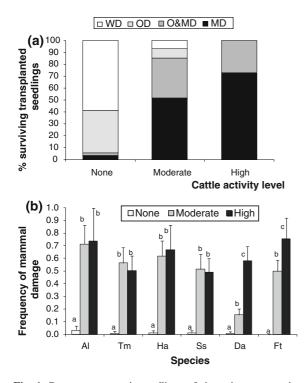


Fig. 1 Damage patterns in seedlings of six native tree species transplanted into live fences under three levels of cattle activity in Hueytamalco, Mexico. a Percentage of surviving seedlings in categories of damage type and cattle activity level, 20 months after transplanting, b frequency of mammal damage per species and cattle activity level; 0 indicates that none seedling was damaged over time and 1 that all seedlings endured damage all around the study. The total number of surviving transplanted seedlings by cattle activity level was: none = 206, moderate = 176, high = 99. Damage types: MD seedlings with damage caused by mammals (including cattle damage), OD with damage not caused by mammals, O&MD with damage caused by mammal or cattle, and by other cause, WD without damage. In b bars sharing different letters indicate significant differences (p < 0.05) among cattle activity levels for same species. Species acronyms: Al Alchornea latifolia, Tm Trema micrantha, Ha Heliocarpus appendiculatus, Ss Saurauia scabrida, Da Dendropanax arboreus, Ft Ficus turrialbana; species are ordered from smaller (left) to higher size (right) at the time of transplantation

than under moderate cattle activity (85 % in site 2), and this was lower than under high cattle activity (100 % in site-3; $\chi^2_{(2)} = 99.0$, p < 0.01); whereas, the level of damage due other causes was the same in all sites ($\chi^2_{(2)} = 5.7$, n.s). The FMD showed the same pattern ($F_{(2,477)} = 428.6$, p < 0.01). Browsing was the main damage caused by cattle affecting more than 90 % of all damaged seedling per site.

Cattle (and other mammals) had no preference for browsing on specific species. At each site, species with the highest and lowest FMD were different. However, our results enabled us to group the species (Fig. 1b) into those showing high and similar FMD under moderate and high cattle activity (sites 2 and 3; *A. latifolia*, *H. appendiculatus, Saurauia scabrida* and *Trema micrantha*), and those with significantly highest FMD only at the site with higher cattle activity (site 3; *Dendropanax arboreus* and *Ficus turrialbana*).

Mammal damage and seedling performance

Survival and growth of transplanted seedlings decreased with cattle activity. Overall, 20 months after transplantation, mean (±s.e) survival probability in absence of cattle was higher (0.85 ± 0.02) than under moderate cattle activity (0.72 ± 0.03), and this higher than under high cattle activity (0.40 ± 0.05; $\chi^2_{(2)} = 105.4$, p < 0.01). Mean RGC showed same trend with higher growth in absence of cattle (0.0031 ± 0.0001 cm cm⁻¹ day⁻¹) than under moderate (0.0001 ± 0.0002; $F_{2,476} = 229, p < 0.01$). Regarding RGD, it was similar at moderate (0.0011 ± 0.0001 mm mm⁻¹ day⁻¹) and high (0.0010 ± 0.0001) cattle activity levels, but lower than in absence of cattle (0.0034 ± 0.0001; $F_{2,477} = 278, p < 0.01$).

Mammal damage, initial seedling size and species identity had significant effects on survival and growth of transplanted seedlings within sites 20 months after transplantation (Table 4). Overall, MD did neither affect species survival nor RGC in absence of cattle, but it had a strong negative effect at the sites with moderate and high cattle activity. In contrast, growth in RGD showed the opposite trend and was independent of MD under high cattle activity. At all sites, survival of seedlings increased and growth (RGD) decreased with initial size (Table 4). Species identity influenced survival at sites with cattle activity and growth at all sites. Overall, considering effects of initial size and MD, T. micrantha was the fastest and F. turrialbana the slowest growing species considering RGC, while H. appendiculatus showed the higher reduction in survival and growth (RGD) at sites with middle and high cattle activity (site 2 and 3).

Differences in survival and growth among species were reflected for the IRI (Fig. 2). Twelve and twenty months after transplantation, all species showed highest IRI in the absence of cattle, while most species showed the lowest IRI at the site with high cattle activity. *H. appendiculatus* performed best in the

Response variable	CAL	FMD	ISS	SI	Contrast among species	WD	LH
	None	n.s.	87.7 (1.2)**	n.s.	1	n.s.	n.s.
Survival	Moderate	$15.8 (-1.4)^{**}$	$44.0 (1.5)^{**}$	34.8**	$6^{a}, 5^{ab}, 4^{b}, 1^{b}, 3^{bc}, 2^{c}$	30.2 (8.71)**	$32.1 (NP > P)^{**}$
	High	27.9 (-7.3)**	$21.1 (1.8)^{**}$	38.2**	$4^{a}, 6^{b}, 5^{b}, 2^{b}, 1^{c}, 3^{c}$	n.s.	$23.6 (NP > P)^{**}$
	None	n.s.	$26.9 (-0.002)^{**}$	13.0^{**}	2 ^a , 3 ^a , 1 ^{ab} , 4 ^{bc} , 5 ^c , 6 ^d	n.s.	$7.9 (P > NP)^*$
RGC	Moderate	$21.1 (-0.001)^{**}$	n.s.	7.3*	$1^{a}, 3^{a}, 4^{a}, 5^{a}, 2^{ab}, 6^{b}$	n.s.	n.s.
	High	$13.2 (-0.002)^{**}$	n.s.	20.8^{**}	2 ^a , 4 ^{ab} , 1 ^{abc} , 3 ^{bc} , 5 ^c , 6 ^c	n.s.	n.s.
	None	$7.9 (-0.001)^{**}$	59.2 (-0.002)**	17.6^{**}	$3^{a}, 5^{b}, 1^{bc}, 2^{bc}, 4^{bc}, 6^{c}$	n.s.	$16.7 (P > NP)^*$
RGD	Moderate	$31.4 (-0.001)^{**}$	$27.5 (-0.001)^{**}$	2.8^{**}	$5^{a}, 1^{ab}, 6^{ab}, 4^{ab}, 3^{ab}, 2^{b}$	n.s.	n.s.
	High	n.s.	13.7 (-0.002)**	6.1^{**}	$4^{a}, 2^{ab}, 1^{ab}, 6^{ab}, 5^{b}, 3^{b}$	n.s.	n.s.

continuous factor (FMD, ISS and WD), or the direction of the difference between pioneer and non-pioneer species is shown in parentheses. Species: 1 A. latifolia, 2 T. micrantha. 3 H. appendiculatus, 4 S. scabrida, 5 D. arboreus, 6 F. turrialbana. In the "contrast among species" column, species are ordered (from left to right) in decreasing order of the corresponding rate; different letters indicate significant differences (p < 0.05)

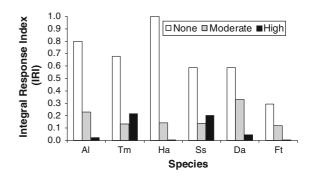


Fig. 2 Integral response index (IRI) per species and cattle activity level for seedlings of native tree species, 20 months after transplantation, into three levels of cattle activity at Hueytamalco, Mexico. IRI integrates survival and growth measures and varies between 0 (lowest performance) and 1 (highest performance). Pioneer species (P): Ha H. appendiculatus, Tm T. micrantha, AlA. latifolia; non-pioneer species (NP): Ss S. scabrida, Da D. arboreus, Ft F. turrialbana, species ordered from smaller (left) to higher mean height (right) at the time of transplantation

absence of cattle, D. arboreus in moderate cattle activity and T. micrantha and S. scabrida at the site with high cattle activity. F. turrialbana had a poor performance at all sites, even in absence of cattle.

Seedling performance and attributes of species

Survival or growth of seedling species did not show any relation with seed weight. In the absence of cattle, pioneer species exhibited higher growth than nonpioneer species; meanwhile, under cattle activity nonpioneer species had better survival than pioneer species (Table 4). Wood density only had a positive effect on survival when cattle activity was moderate (Table 4).

The MD had a general negative effect on seedling survival and growth, independently of species life history (Fig. 3). Overall, non-pioneer species had a better survival probability than pioneer species ($F_{1,15} = 4.6$, p < 0.05; Fig. 3a), while pioneer species showed higher growth than non-pioneer ones (RGD: $F_{1,14} = 20.4$, p < 0.01; RGC:F_{1.15} = 10.3 p < 0.01). In most species, at high frequencies of damage there were negative values in RGC, but not in RGD.

Costs of propagation and transplantation of seedlings

Total seedling emergence in the greenhouse varied widely among species (Table 5), ranging from 19 %

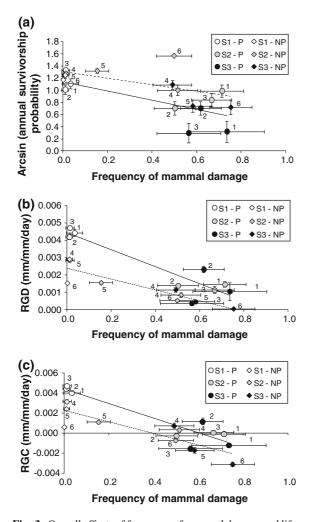


Fig. 3 Overall effects of frequency of mammal damage and lifehistory (pioneer vs. no-pioneer species) on seedlings performance of six native tree species transplanted into three ranches of Hueytamalco, Mexico. a Survival probability (angular transformed), b relative growth rate of root collar diameter (RGD), and c relative growth rate of crown diameter (RGC). S1 absence of cattle, S2 moderate cattle activity, and S3 high cattle activity. P Pioneer species (1, 2, 3), NP Non-pioneer species (4, 5, 6); 1 A. latifolia, 2 T. micrantha, 3 H. appendiculatus, 4 S. scabrida, 5 D. arboreus, 6 F. turrialbana. Solid line indicates adjusted linear regression for pioneer species and dotted line that for non-pioneer ones. Equations of adjusted regression were, for pioneer species: Survival = $-0.763 \times FMD + 1.14$ (R²: 0.48), RGD = $0.0048 \times \text{FMD} + 0.004$ (R²: 0.85), and RGC = $-0.0073 \times$ FMD + 0.004 (R^2 : 0.86); and for non-pioneer species: Survival = $-0.534 \times FMD + 1.31$ (R^{2}) : 0.32), RGD = $-0.0031 \times \text{FMD} + 0.002 \text{ (R}^2: 0.81)$, and RGC = $-0.0058 \times$ $FMD + 0.002 (R^2: 0.74)$

for *H. appendiculatus* to 78 % for *F. turrialbana*, being the lowest emergence for species sown in April 2011. Low seedling emergence values increased the

propagation costs; when these costs were recalculated assuming the highest seed germination reported in the literature, the propagation costs decreased between 5 and 30 %.

Pioneer species were cheaper to propagate than non-pioneer ones. Pioneer species required less time in greenhouse to reach a desirable size for transplantation, although mortality rate of most non-pioneer species tended to be lower than that of pioneer ones (Table 5a). Among pioneer species, A. latifolia was the most expensive and had the highest mortality. Similarly, S. scabrida and M. trinervia showed the highest mortality among non-pioneer species and were the most expensive within this group. Finally, propagation costs of seedlings were higher than transplantation and protection costs (Table 5b), although this varied among sites and species. For pioneer species, propagation represented 41 % of total costs in absence of cattle, and 64 % for sites with cattle activity; for non-pioneer species these percentages were 56 and 78 %, respectively.

Index of species selection

Similar results in SSI values after 12 and 20 months of transplantation were found. *D. arboreus* was the only species with an optimum SSI value (near to 1). This value was recorded under moderate cattle activity (Table 6). Under high cattle activity, SSI was very high for most species and it increased over time; this was particularly noticeable for the case of *H. appendiculatus*. Only *T. micrantha* and *S. scabrida* showed similar and relatively low SSI values (around 2). *F. turrialbana* showed the biggest difference in SSI between moderate and high cattle activity.

Discussion

As expected, cattle and other MD reduced survival and growth of seedlings. However, the effect varied depending on the severity (level and frequency) of this damage, and with the identity and life history of the studied native tree species. The life history of the species was also important determinant of the costs of seedling propagation. Additionally, our results suggested that increasing seedling size before transplantation improves the probability of seedling survival in the field.

0.0

0.0

1.5 0.33

3

Table 5 Components of costs associated with propagation of seedlings of seven native tree species in (a) greenhouse conditions, and (b) transplantation and protection (first and second year) of seedlings into live fences at cattle ranches of Hueytamalco, Mexico

(a) Propagation in greenhouse							
Components	$Al^{(P)}$	Tm ^(P)	Ha ^(P)	Ss ^(NP)	Da ^(NP)	Ft ^(NP)	Mt ^(NP)
Number of seeds collected ^a	713	345	626	568	419	264	702
Total seedling emergence (%)	20 (82) ^b	36 (70) ^c	19 (50) ^d	66	44 (70) ^e	78	57
Mortality rate per month (%)	19.9	13.0	10.6	11.3	5.7	6.4	9.4
Months in greenhouse	$3^{\rm f}$	$3^{\rm f}$	$3^{\rm f}$	9 ^g	12 ^h	12 ^h	12 ^h
Cost of materials (collect, germination, maintenance) ^a	95	86	83	212	118	129	223
Labor (\$11.2/day/person) ^a	11.5	7.5	10.5	28	17.5	19	32
Propagation costs per seedling in dollars	$2.22 - 1.6^{i}$	$1.68 - 1.5^{i}$	$2.02 - 1.6^{i}$	5.3	3.17-3.1 ⁱ	3.4	5.9
(b) Transplantation and protection costs							
			None		Moderate		High
Transplantation costs per seedling			1.38		0.73		0.63
(transportation, land preparing and planting)							

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Materials	first	vear	j

Materials first year ^j	100.7	9.7
Materials second year ^j	3.0	3.0
Workdays (weeding and set protection)-first year ^j	12	4
Workdays (weeding and maintenance of protection)-second year ^j	$6(2)^{l}$	2.5
Protection costs per seedling ^k	$1.7 (1.3)^{1}$	0.53

Pioneer species (P): Ha H. appendiculatus, Tm T. micrantha, Al A. latifolia; non-pioneer species (NP): Ss S. scabrida, Da D. arboreus, Ft F. turrialbana, Mt M. trinervia. All costs are expressed in US dollars. Total seedling emergence in the greenhouse, and maximum germination percentage reported in literature (in parentheses) are provided: ^dVázquez-Yanes and Orozco-Segovia (1982), ^cSilvera et al. (2003), ^bFrancis and Rodríguez (1993), ^eNiembro-Rocas (2003). ⁱPropagation costs recalculated with maximum germination reported in literature. Starting germination month: April 2011 (^f), October 2010 (^g) and July 2010 (^h). ^aLabor costs needed to produce 100 seedlings ready to transplant. ^jCalculates for 120 seedlings seeded. ^kDoes not include transplantation costs. ¹Protection costs for Ha and Tm, species with a mean height bigger than 2.5 m 1 year after transplantation, is indicated in parenthesis

Our SSI and the criteria used to select species were useful to target species with the potential to enrich the biodiversity of live fences in active cattle pastures. In particular, we suggest D. arboreus as a good candidate under moderate cattle activity, since it had the lowest SSI. The pioneer T. micrantha and the non-pioneer S. scabrida, which showed better resprouting ability than other species and withstood cattle damage better, can be good candidates too.

Mammal damage, species attributes and seedling performance

In the absence of cattle, seedlings of all selected species performed well during 20 months after transplantation. All species had the highest survival and growth rates and the lowest levels of MD (5 %). Under this scenario, seedlings growth rates were related to life history of species. Pioneer species usually had softer wood and showed higher growth than the nonpioneer ones, previous studies have also observed the same (McDonald et al. 2003; Román-Dañobeytia et al. 2012).

In contrast, under conditions of cattle activity, browsing suffered by seedlings severely limited their growth, and pioneer species endured higher mortality than non-pioneer ones. This result could be associated with the general pattern that tropical non-pioneer tree species have denser wood which give them more mechanical resistance to damage than pioneer ones with softer wood (Lugo and Zimmerman 2003; Poorter et al. 2008). Also, seedlings of non-pioneer species may survive to defoliation because they have carbohydrate reserves stored in stems and roots that enable them to cope with leaf area losses (Green and Juniper 2004; Myers and Kitajima 2007). Under the prevailing conditions in study area, initially bigger transplanted seedlings had better survival probabilities

Al	Tm	На	Ss	Da	Ft
2.3 (2.4)	3.5 (2.5)	4.9 (4.2)	3.4 (3.6)	1.3 (1.3)	1.8 (2.3)
20.1 (9.2)	1.9 (1.8)	86.8 (15.8)	2.1 (2.3)	8.2 (7.1)	34.2 (21.4)
	2.3 (2.4)	2.3 (2.4) 3.5 (2.5)	2.3 (2.4) 3.5 (2.5) 4.9 (4.2)	2.3 (2.4) 3.5 (2.5) 4.9 (4.2) 3.4 (3.6)	2.3 (2.4) 3.5 (2.5) 4.9 (4.2) 3.4 (3.6) 1.3 (1.3)

SSI values are shown for twelve (in parenthesis) and 20 months after transplantation. SSI_{2-1} values were obtained comparing performance and costs under moderate and no cattle activity (site 2 and site 1), and SSI_{3-1} comparing high and no cattle activity (site 3 and site 1). Pioneer species: Al *A. latifolia*, Tm *T. micrantha*, Ha *H. appendiculatus*; and non-pioneer species: Ss *S. scabrida*, Da *D. arboreus*, Ft *F. turrialbana*, Mt *M. trinervia*. Species ordered from smaller (left) to higher size (right) at the time of transplantation

but slower growth than smaller ones, as observed in previous studies with tropical tree species (Poorter 1999; Martínez-Garza et al. 2011). These results indicate that transplanting big seedlings (at least 50 cm height) is a basic procedure in the process of enriching live fences. Additionally, we found that transplanted seedlings received some protection from the available live fences because, overall, only 7 % or less of them experienced trampling, which was much lower than the 35 % reported by Love et al. (2009) in open pastures.

Species tolerance to mammal damage and resprouting ability

Our results showed that seedling response and tolerance to MD depended on level and frequency of this damage. At low frequencies (absence of cattle), growth but not survivorship was affected, suggesting some general tolerance of seedlings for losing photosynthetic tissues. This result agrees with studies that simulated small levels of herbivory on seedlings of tree species (Hughes 1976; Valio 2001). In contrast, at high damage frequencies (particularly under high cattle activity) growth was severely reduced and seedlings did not recover their photosynthetic tissues (they showed negative growth values) and endured high mortality rates. Holl and Quiros-Nietzen (1999) found similar effects of MD on seedlings transplanted into abandoned pastures. A review by Bellingham (2000) indicated that resprouting ability of the plants (i.e. recovery of plant tissues) depends on the severity and frequency of disturbance. After low levels of defoliation, plants can usually recover, but when disturbance are frequent and/or severe, it is energetically impossible to maintain the reserves necessary to recover (Lopez-Toledo et al. 2012).

Under high level of cattle activity, T. micrantha and S. scabrida showed high resprouting ability (indicated by positive crown growth), and they performed better than the others species as indicated by the IRI (Fig. 2). From six species, the resprouting ability has been only reported for T. micrantha. This species is more tolerant to the loss of tissues than other pioneer species (Dalling and Hubbell 2002), and their seedlings have shown high growth plasticity when their apex is removed (Valio 2001). In general, differences in resprouting strategies of tree species are not yet well understood (Vesk 2006), and it is associated with the species identity. Resprouting ability is an important trait for tree species growing into live fences, especially if the species are palatable and can be used as fodder to cattle (Beer et al. 2003). From six species, three (H. appendiculatus, T. micrantha and S. scabrida) have fodder potential and could be palatable for favorable chemical-nutritional status (Luviano Elías 2012; Jiménez-Ferrer et al. 2008).

Costs of seedling propagation and protection

The most important difference in production costs among species was associated with their RGR, which determined the time required (and labor invested) in the greenhouse to be ready for transplantation. RGR is an intrinsic attribute of plant species (Poorter 1999; Poorter et al. 2008) that is necessary to consider in the selection of potential tree species for enriching live fences. The propagation cost may be more expensive if slow-growing species are chosen against fastgrowing ones; therefore, these selected slow-growing species must be those with highly valuable properties to local farmers (e.g. timber or fodder species). Furthermore, to make propagation costs of native tree species affordable, more knowledge is needed to increase the percentage of seedling emergence (especially in pioneer species) and survivorship under greenhouse conditions. This implies also the training of specialized personnel to reduce costs.

Under the technical protocol followed in the present study, the propagation costs were much higher (1.5–5.9 USD) than those reported by Zahawi and Holl (2009) for seedlings of native tree species produced in a local commercial greenhouse (0.15–0.25 USD). In contrast, our costs for transplanting and seedling care in the field, except in site 1, were cheaper than the 0.8–1.2 USD per seedling calculated by Zahawi and Holl (2009), and <36 % of total costs indicated by Vieira et al. (2009). Probably, seedlings growing in live fence conditions (i.e. more shade and humidity, and with low pasture competition) require less labor for maintenance, even though they needed protection from cattle damage.

Target species for enriching live fences

Our SSI was useful for integrating performance of transplanting seedlings (which can be taken as an indicator of the potential benefits of the species) and the associated propagation, transplanting and protection costs. Also, SSI may provide some general management suggestions.

Trema micrantha could be a good option for enriching live fences. It showed the highest resprouting ability and a good growth even under high levels of cattle activity, and the survival could increase using bigger seedlings. This species also has been identified as potential fodder tree and good element for restoration (Vázquez-Yanes 1998; Luviano Elías 2012). D. arboreus and S. scabrida can also be considered for enriching live fences. D. arboreus had the best performance at the site with moderate cattle activity but with poor resprouting ability so required some protection, and it has been identified as an important multipurpose tree and it do not seem a palatable species (McDonald et al. 2003). S. scabrida is a less well-known tropical tree species but it has been identified as a potential fodder tree (Jiménez-Ferrer et al. 2008; Luviano Elías 2012). This species had a good resprouting ability and high survival in field, but their seedlings endured high mortality in the greenhouse and were the most expensive to propagate.

Alchornea latifolia could be transplanted into live fences but not under high cattle activity because it endured more MD than we expected (similar to those identified as fodder species) and low resprouting ability. This species has been recognized as a good element for restoration (Vázquez-Yanes et al. 2001) but with few local uses (McDonald et al. 2003), which could reduce its potential acceptance for local farmers. Finally, F. turrialbana is a valuable species to local farmers and could be transplanted into live fences under moderate cattle activity, but expecting a low performance. Based on the experiences of local farmers, it is important to explore and refine the vegetative propagation (by stakes) of this species. For some species, stakes could be a better option than seedlings to enrich live fences in active pastures (Zahawi and Holl 2009) but is necessary to carry out cost-benefit analyses as illustrated here with the SSI index.

We do not recommend the transplantation of *H. appendiculatus* into live fences. It showed very poor performance, limited resprouting ability and high mortality at the sites with cattle activity in response to the high MD endured. This species has been identified as a potential fodder tree (Luviano Elías 2012) but with low tolerance to defoliation as have been observed in seedlings under natural conditions (Núñez-Farfán and Dirzo 1991). However, this species had an exceptional survival and growth in absence of cattle, and we recommend establishing in areas without access for cattle.

Enrich live fences would be a valuable strategy to increase biodiversity in highly transformed tropical landscapes dominated by cattle systems, but this required new efforts and tools. Our study shows that selecting and establishing native tree species into live fences is possible, at least in the first 2 years, especially in sites with low and moderate cattle activity. However, more knowledge is necessary about the acceptance from local farmers, and benefits producing by these native trees to farmers and local biodiversity. Additionally, cost-benefit evaluation is a mandatory procedure to include the social-economic perspective when native species are selected to agroforestry and restoration projects.

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