

Growth, herbivore distribution, and herbivore damage of timber trees in a tropical silvopastoral reforestation system

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Abstract

• **Context** The reforestation of degraded tropical pastures requires innovative tree planting systems that consider land user needs.

• **Aim** We established a silvopastoral reforestation system and assessed the effects of companion trees on the native timber tree *Tabebuia rosea* in Panama. Timber tree individuals were established in (1) solitary plantings (TSol) or in companion plantings with (2) *Guazuma ulmifolia* (TGua) or (3) the nitrogen-fixing *Gliricidia sepium* (TGli).

• **Methods** We quantified growth characteristics and herbivory of *T. rosea*, and analyzed leaf chemistry (including the stable isotopes $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) and structure (leaf mass per area).

• **Results** Companion trees significantly affected stem diameter growth of *T. rosea*. Stem diameter growth was as high in TGli trees as in TSol trees but was reduced in TGua trees. Furthermore, TGua trees had higher leaf water content, and

lower $\delta^{13}\text{C}$ and lower leaf mass-to-area ratio than TGli trees, suggesting there were effects of shading by *G. ulmifolia* on *T. rosea*. Herbivory was high but not affected by planting regimes. Leafing phenology did not differ between planting regimes and *G. sepium* did not increase nitrogen content in *T. rosea* leaves.

• **Conclusion** Companion tree planting can support timber tree growth in silvopastoral reforestations, but adequate species selection is crucial for successful implementation of this planting system. Tree–tree interactions seem to be more relevant for timber tree growth than herbivory in the studied system.

Keywords Associational resistance · Insect herbivores · Plant apparency · Restoration · Smallholder forestry · Timber plantations

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Conducted the fieldwork: JR, MP, KM
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1 Introduction

Progress has been made towards reversing the overall trend of global forest area loss (−0.13 % of total forest area per year from 2000 to 2010 compared to −0.2 % per year from 1990 to 2000), but world forest cover continues to decline with most of the net loss taking place in tropical countries (FAO 2010). In Latin America, a major cause of deforestation is forest clearance for agriculture and livestock grazing (Barona et al. 2010 and references therein). Cattle ranching is a dominant part of the rural economy in Latin America, with about 27 % of the land area in Latin America and the Caribbean covered by pastures (FAO 2009). Farmers, in particular smallholders of limited means, depend on cattle despite of the comparatively low income that it generates due to a combination of low risks and high economic flexibility (Wassenaar et al. 2007). As an important element of the rural economy, cattle ranching will continue to constitute a large component of land use in Latin America,

rendering reforestation and conservation initiatives that are compatible with ranching activities particularly promising (Garen et al. 2011). Silvopastoral reforestation systems that combine timber trees, fodder trees, and pasture can accomplish the dual goals of forest reestablishment and enhancement of actively used rangeland landscape. They may provide a wide range of environmental benefits including enhanced biodiversity through resource provisioning and increased landscape connectivity while generating economic benefits for the farmers that support incentives for their implementation (Cajas-Giron and Sinclair 2001; Murgueitio et al. 2011).

Latin American pastures frequently include scattered remnant trees and live fences, which are maintained to provide fodder, shade, timber, and firewood (Cajas-Giron and Sinclair 2001; Harvey et al. 2011). Nevertheless, studies on tree growth in tropical silvopastoral reforestation systems are scarce (but see Hall et al. 2011 for an overview of studies on reforestation with native trees).

We established a silvopastoral reforestation system designed to optimally meet the needs of farmers by combining high-value timber and multipurpose companion trees planted on pasture. The companion trees were planted circularly around a central timber tree to possibly support timber tree growth and to provide additional benefits such as fodder and shade for livestock during the dry season (Dagang and Nair 2003). The selected tree species included a nitrogen-fixing companion tree species to possibly enhance soil fertility through increased nitrogen content available for the timber species (Daudin and Sierra 2008). Shading of the central timber tree by the companion trees may alter light and soil water availability (Brenes-Arguedas et al. 2009; Myster 2012), thereby affecting light- and drought-related growth and differentiation processes (Gutbrodt et al. 2011; Rüger et al. 2011). Furthermore, neighboring heterospecific companion trees might protect the central timber tree from herbivorous insects according to the resource concentration hypothesis (Root 1973) by increasing associational resistance via a reduced probability of specialist herbivores to find (tree apparency; see Endara and Coley 2011), remain, and reproduce on the host surrounded by companion trees (Barbosa et al. 2009; Jactel et al. 2009).

In the present study, we examined the effects of the different companion tree species on the focal timber tree *Tabebuia rosea* and assessed its leaf traits and tree characteristics as potential determinants of tree resistance to herbivore damage. Specifically, we tested the following predictions: (A) Growth of timber trees surrounded by multipurpose companion tree species differs from growth of solitary individuals and depends on the companion tree species chosen. (B) Companion tree species affect microclimate and competitive conditions, resulting in differing leaf characteristics and phenology of the central timber trees across the different planting regimes. (C) Companion planting with a legume tree species increases leaf nitrogen content of the timber species. (D)

Associational effects lead to differences in insect herbivory and infestation between planting regimes.

2 Materials and methods

2.1 Study site and tree species

The study was conducted from April 2007 (year 1) to November 2011 (year 5) at an experimental plantation site in Sardinilla, Central Panama (9°19'30"N, 79°38'00"W, elevation 70 m.a.s.l.). The local climate is semi-humid tropical, with a mean annual temperature of 25.2 °C, a mean annual precipitation of 2,289 mm, and a pronounced dry season from January to April (134±19 days; Wolf et al. 2011). The original vegetation consisted of semi-deciduous lowland forest on clayey soil (Potvin et al. 2004). The forest was logged in 1952/1953, and after 2 years of agricultural use the site was converted into pasture and grazed by cattle for almost 50 years (Potvin et al. 2004).

We selected *Tabebuia rosea* Bertol. (Bignoniaceae) as focal timber tree due to its forest restoration potential, commercial importance, and good growth performance (for details see Plath et al. 2011a, b and references therein). *T. rosea* is a deciduous species with a natural distribution range from Southern Mexico to Venezuela. It attains a size of 25–30 m. The digitate leaves consist of five leaflets and are shed during the dry season (Gentry 1970).

The companion tree species *Gliricidia sepium* (Jacq.) Kunth ex Walp. (Fabaceae) and *Guazuma ulmifolia* Lam. (Malvaceae), also native to Central America, are planted frequently as traditional multipurpose trees (Cajas-Giron and Sinclair 2001). *G. sepium* is a nitrogen-fixing tree commonly used in tropical agroforestry. It has the ability to grow well and reclaim soil on degraded lands, and it is often used as living fence and as protein-rich fodder (Wishnie et al. 2007). *G. ulmifolia* is a pioneer tree that is valued as fodder for cattle, fuelwood, charcoal, and for traditional medicine (Senthil 2009). It is fast growing and was found to dominate both naturally grown as well as manipulated forest regeneration from pasture in Panama (Griscom et al. 2009).

2.2 Planting design

The experimental silvopastoral system was established on former pasture in August 2006 by using potted seedlings, which were raised for 3 months in a PRORENA (Proyecto de Reforestación con Especies Nativas) nursery before being planted. To assist tree establishment, granular fertilizer (15 g 12–72–12 N–P–K) was applied to the bottom of each planting hole and covered with soil before planting and again 2 months after planting to each seedling on the soil surface. Seedlings of the timber species *T. rosea* were established at a minimal

distance of 9 m from one another in three different planting regimes: (1) *T. rosea* trees surrounded by the legume companion species *G. sepium* (TGli), (2) *T. rosea* trees surrounded by the companion species *G. ulmifolia* (TGua), and (3) solitary *T. rosea* trees (TSol). In the first two planting regimes, five conspecific companion seedlings were planted circularly around the central timber tree at a distance of 1.5 m. Each planting regime consisted of eight *T. rosea* individuals, and all three planting regimes were randomly arranged in one locality as a coherent plot. This plot was replicated three times (SP1–SP3) within the Sardinilla study site, resulting in a total of 24 timber tree individuals per planting regime. Local site conditions, including soil moisture, soil pH, soil nitrogen content, and collateral vegetation, varied notably across the three plots (Plath et al. 2011a). In plot SP1, concomitant vegetation (short grasses and herbs) was mown approximately once a month throughout the research period. In plots SP2 and SP3, competing vegetation (tall grasses and woody successional vegetation) was cleared during the rainy season, every 3 months during the first two study years and at least once a year in the study years 3 to 5. The three plots were surrounded by grazed cattle pasture and by plots of a native tree plantation that was set up in 2001 (Potvin et al. 2004).

2.3 Tree growth

Growth of *T. rosea* was quantified for the 5 years after tree establishment (see Plath et al. 2011a for results of the first 2 years). As measures of growth of *T. rosea*, stem diameter at 130 cm above soil surface (DBH) and total height (from the ground to the uppermost point in the tree crown) were quantified. Assessment of DBH was restricted to years 3 to 5 due to the small size of the trees in years 1 and 2. Growth of *T. rosea* was determined as the difference in DBH between year 5 and year 3 (DBH growth). An intermediate value of DBH growth was calculated as the difference in DBH between year 5 and year 4 to relate timber tree growth to herbivory, which was assessed in year 4. Growth of companion trees was determined as DBH and total height of the companion trees measured in year 5. Relations between growth measures were tested separately for each species by Pearson correlations, which revealed that growth measures were significantly and positively correlated for each species (all $P < 0.01$).

Both companion tree species branch from the ground up to the top and have a dense crown. Therefore, companion tree size as characterized by height and stem diameter provides a good proxy for shielding of the timber trees by the companion trees. As a measure of potential reduction of timber tree apparency to insect herbivores, a shielding factor (S) was computed that accounted (1) for height differences between timber trees and surrounding companion trees and

(2) for the number of companion trees (which varied due to incidental companion tree mortality):

$$S = \frac{\left(\frac{H_{C1}}{H_T} + \frac{H_{C2}}{H_T} + \frac{H_{C3}}{H_T} + \frac{H_{C4}}{H_T} + \frac{H_{C5}}{H_T} \right)}{N_C}$$

with

- S Shielding factor
- H_C Height of companion tree
- H_T Height of timber tree
- N_C Number of companion trees planted (i.e., 5).

2.4 Insect survey

Larvae of *Eulepte gastralis* Guenée (Lepidoptera: Pyralidae) and adults of *Walterianella inscripta* Jacoby (Coleoptera: Chrysomelidae) are the two most relevant herbivores of *T. rosea* in high-density reforestation plots at the same study site (Plath et al. 2012). To assess their specific abundance and main activity period in the studied silvopastoral reforestation system, insect counts were conducted for all timber trees in the first two study years on a biweekly basis from April of year 1 to April of year 2, except from end of December of year 1 to mid-February of year 2 when *T. rosea* was seasonally leafless. Insect abundance was assessed by a visual census of all individuals present on leaf, branch, and trunk surfaces of each tree during day and night within a 24-h period. Tree infestation by *E. gastralis* and *W. inscripta* was quantified as herbivore density, which was calculated as the total number of individuals per tree, summed over all surveys until mid-December of year 1, and divided by the total leaf number of the tree at this date. Leaf counts included mature and fully expanded young leaves.

In years 3 and 4, abundance of the chrysomelid beetle *W. inscripta* was reassessed during its maximum incidence from July to October. As a complete sampling of the whole trees was no longer feasible due to increased tree size, we collected the beetles during the day (between 0700 h and 1730 h) and night (between 2000 h and 2400 h) by standardized beating-tray sampling of one branch per tree. The tray (0.5 × 0.5 m) was positioned directly below the randomly chosen branch, which was then shaken for 8 s to dislodge the beetles. Beetles were collected in an ethanol-containing plastic bottle mounted to the bottom of the tray. To standardize observations, the number of leaves per branch was counted each time. Beating-tray sampling was carried out at monthly intervals from July to October in year 3 and from August to October in year 4. Quantitative assessment of *E. gastralis* larvae was not feasible in years 3 and 4, as they feed confined within leaves and only incidentally fall into a beating tray upon branch shaking.

2.5 Leaf herbivory

Herbivore damage was measured in November of year 1 (15 months after tree planting) and of year 4, subsequent to the peak of the rainy season. Because *T. rosea* sheds its leaves in the dry season, analyzed leaves developed during the vegetation period of the respective year. Total leaf damage was quantified in year 1 and year 4. In year 4, we additionally quantified the leaf damage caused by the key herbivores *E. gastralis* and *W. inscripta*. Symptoms of damage by either key herbivore species *E. gastralis* and *W. inscripta* were assigned according to Plath et al. (2012). Large-scale skeletonization, including continuously missing and necrotic areas, was characterized as damage by *E. gastralis* larvae, whereas small holes in the leaf were characterized as damage by *W. inscripta*. Damage that could not be assigned to either key herbivore was considered as “damage by other herbivores”.

In year 1, we selected the first 15 fully developed leaves in the top foliage layer of each *T. rosea* tree and quantified the damage of the mature leaves, which were characterized by their toughness and dark green color ($N=524$ leaves, average=7.7 leaves per tree). Rather than applying destructive sampling by cutting leaves from the young trees, leaves were photographed in situ with a digital camera (Panasonic, Lumix DMC-LZ3) using a standardized and established procedure (Mody et al. 2007). Leaves were spread out under a plane of non-reflecting plexiglass to even the surface and photographed together with a reference area, without flash, and from a fixed distance in the shade of a tarpaulin. Digital photographs were analyzed using a custom-built software tool (Plath et al. 2011b).

In year 4, the methodological approach to assess herbivory was changed due to increased tree size and to obtain samples for leaf parameter analysis. We collected a random sample of 10 mature leaves ($N=661$ leaves, average=9.7 leaves per tree, depending on the availability of mature leaves) from each *T. rosea* tree. Directly after collection, leaflets were photographed. Missing leaf area was calculated with a leaf area meter (LI-3100C Leaf Area Meter; LI-COR Biosciences, Lincoln, NE, USA) by comparing the area of the actual leaflet with the area of a paper template of the intact leaf. The contribution of *E. gastralis* and *W. inscripta* to the total missing area was quantified by estimating the proportion of each damage type to the nearest 10 % of total leaf area. Damage to the leaf surface by *E. gastralis* (necrosis) was measured by analyzing the digital photos with Adobe Photoshop. The proportion of leaf damage attributed to each type of damage was averaged for each studied tree in both years.

2.6 Leaf characteristics

C–N elementary and stable isotope analyses were conducted for *T. rosea* leaves to assess the effects of companion trees

on drought stress for the focal timber trees, to estimate nitrogen transfer from the N_2 -fixing companion tree *G. sepium* to *T. rosea*, and to determine the relationship between foliar nitrogen content and herbivory. Therefore, two mature leaves per tree were randomly taken from the dried leaf samples collected in year 4. For representative measurements, we used the fourth of the five *T. rosea* leaflets when available, or otherwise the second leaflet as the first alternative, or the third one as the second alternative. Leaflets were ground separately into a homogenous powder using a Retsch ball mill (MM 200; Retsch GmbH, Haan, Germany) to quantify total nitrogen content and $\delta^{15}N$ ratios, which served to test whether the timber tree *T. rosea* accumulates nitrogen fixed by the companion tree *G. sepium* (Daudin and Sierra 2008). Additionally, $\delta^{13}C$ ratios were measured to assess drought stress experienced by *T. rosea* (Mody et al. 2009). Nitrogen content, $\delta^{15}N$ values, and $\delta^{13}C$ values were determined using a Flash EA 1112 Series elemental analyzer (Thermo Italy, Rhodano, Italy) coupled to a Finnigan MAT Delta^{plus} XP isotope ratio mass spectrometer (IRMS; Finnigan MAT, Bremen, Germany) via a six-port valve and a ConFlo III, following the procedure described by Werner and Brand (2001). In addition to leaf nitrogen and carbon analyses, we calculated leaf water content (%) and leaf mass-to-area ratio (LMA; mg/cm^2) for each leaflet used in herbivory assessments in year 4 (see below). To determine water content, all leaflets were weighed immediately after collection and again after drying at 65 °C for 5 days. LMA was computed by dividing the area of each leaflet (obtained during herbivory measurements, see below) by its dry mass. Values of leaf characteristics were averaged for each tree.

2.7 Leafing phenology

The phenology of the trees was recorded in year 3 (four times) and in year 4 (five times). Recording of phenology started in May and continued until leaf expansion was complete on at least 90 % of the trees (by the end of July). At each assessment, the individual trees were categorized based on a scoring system that considered five phenological stages: buds are closed (value=1); first tips of leaves are visible (value=2); leaves have emerged but are still reddish brown and folded (value=3); leaves are unfolded, bright green, and soft (value=4); and leaves are mature, dark green, and hardened (value=5). The cumulative value from all assessments from a single year was used to characterize the phenological property of a tree from that year, with high values indicating early leaf expansion.

2.8 Statistical analysis

Prior to analysis, percentage data (leaf damage, leaf nitrogen content, and leaf water) were arcsine-transformed (no relevant difference was found compared to logit-transformed data). In

all models, we tested main effects and interactions of explanatory variables. Effects of planting regimes and plots were assessed by two-way ANOVAs, using planting regime and plot as fixed between-subject factors. Response variables were DBH growth, final DBH (i.e., DBH 5 years after establishment), final height, and herbivore infestation of *T. rosea*, as well as nitrogen content, $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, water content, and LMA of *T. rosea* leaves. Growth traits and shielding of the companion tree species *G. sepium* and *G. ulmifolia* were analyzed using the mean value of the five individuals surrounding a single timber tree. Mean values were then compared by two-way ANOVA, using species and plot as fixed between-subject factors. To relate shielding exerted by companion trees to timber tree growth, one-way ANCOVAs, with plot as between-subject factor, shielding as the covariate, and DBH growth as the response variable, were conducted for each companion tree treatment. Subsequent to ANOVA analyses, LSD post hoc tests followed by false discovery rate correction (Verhoeven et al. 2005) were applied to test for differences between treatment levels.

Phenological rank values were compared between planting regimes and plots by Kruskal–Wallis tests, followed by *U* tests, to which false discovery rate correction was applied. The relationship between phenological values of the different years was assessed by Spearman's rank correlation.

Leaf damage of *T. rosea* in year 1 was analyzed by two-way ANCOVA, using planting regime and plot as fixed between-subject factors and density of *E. gastralis* and *W. inscripta* as covariates. Leaf damage of *T. rosea* in year 4 was analyzed by two-way MANCOVA, using planting regime and plot as fixed between-subject factors; total leaf damage, *E. gastralis* leaf damage, and *W. inscripta* leaf damage as dependent variables; and tree height and leaf nitrogen content as covariates. Pillai's trace (*V*) was used as the test statistic, and separate univariate ANOVA was conducted as follow-up analysis to separately assess effects of fixed factors and covariates on the dependent variables.

The link between herbivory and tree growth was tested by two-way ANCOVA, with planting regime and plot as fixed between-subject factors, DBH growth of *T. rosea* from year 4 to year 5 as the response variable, and leaf damage in year 4 as the covariate.

Statistical analyses were performed using the software SPSS 20.0 for Mac OS X (2010 SPSS, Chicago, IL, USA). For clarity, all figures show untransformed data.

3 Results

3.1 Effects of companion trees on timber tree growth

Stem diameter (DBH) growth from year 3 to year 5 of the timber tree *T. rosea* was affected by planting regimes and

plots (ANOVA, $F_{8,37}=8.16$; $P<0.001$). The growth differed significantly between planting regimes ($F_{2,37}=10.58$, $P<0.001$), and effects of planting regimes differed significantly between plots (planting regime \times plot interaction— $F_{4,37}=3.88$; $P=0.010$). DBH growth of TGli trees was higher than DBH growth of TGua trees in all plots, and it was higher than DBH growth of TSol trees in SP1 and SP3 (Fig. 1). TGli trees and TSol trees showed a significantly higher DBH growth than TGua trees, whereas growth differences between TGli trees and TSol trees were not significant (LSD post hoc test, $P_{\text{TGli/TGua}}<0.001$; $P_{\text{TSol/TGua}}=0.004$; $P_{\text{TGli/TSol}}=0.226$; Fig. 1). Furthermore, DBH growth was significantly different between plots ($F_{2,37}=16.09$, $P<0.001$). It was significantly lower in SP1 than in SP2 and SP3.

Corresponding to differences in DBH increase from year 3 to year 5, final DBH of *T. rosea* trees attained after 5 years varied between planting regimes and plots (Table 1). Final DBH was higher for TGli trees than for TGua trees, and trees growing in SP3 attained a significantly higher final DBH than trees growing in SP1 and SP2. No significant difference in final DBH was found between SP1 and SP2. Effects of planting regimes on final DBH varied between plots, as indicated by significant planting regime \times plot interactions (Table 1).

Tree height was not significantly affected by the planting regime 5 years after tree establishment, but it varied significantly among plots (Table 1). Trees were significantly smaller in SP1 than in SP2 and SP3, but these plot effects did not interact with planting regimes (Table 1).

The companion tree species differed significantly in their size and in the related shielding of the timber trees. *G.*

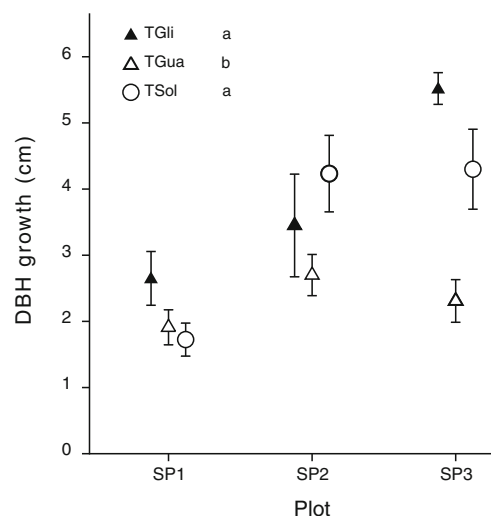


Fig. 1 Mean (\pm SE) DBH growth of *Tabebuia rosea* between year 3 and year 5 in three planting regimes and plots (SP1–SP3). Planting regimes included *T. rosea* trees growing surrounded by *Gliricidia sepium* (TGli), surrounded by *Guazuma ulmifolia* (TGua), or solitary (TSol). Contrasting letters *a*, *b* refer to significant differences between planting regimes (ANOVA, LSD post hoc test with false discovery rate correction)

Table 1 Effects of planting regimes and plots on growth and leaf characteristics of the timber tree *Tabebuia rosea* (mean±SE for each variable)

	Planting regime			Statistics ^a
	TGli	TGua	TSol	
Tree size				
Final DBH (cm) year 5	5.30±0.51	4.06±0.34	4.72±0.52	Model: $F_{8,56}=4.60$; $P<0.001$ Regime: $F_{2,56}=3.14$; $P=0.051$ Plot: $F_{2,56}=11.38$; $P<0.001$ (SP3>SP2, SP1) Regime×Plot: $F_{4,56}=2.89$; $P=0.030$
Final height (m) year 5	4.57±0.33	4.29±0.30	4.01±0.33	Model: $F_{8,56}=3.26$; $P=0.004$ Regime: $F_{2,58}=1.23$; $P=0.301$ Plot: $F_{2,58}=9.31$; $P<0.001$ (SP3>SP2, SP1) Regime×Plot: $F_{4,58}=1.80$; $P=0.142$
Leaf characteristics				
Leaf $\delta^{13}\text{C}$ (‰) year 4	-29.60±0.16	-30.20±0.18	-29.50±0.14	Model: $F_{8,57}=1.96$; $P=0.069$ Regime: $F_{2,57}=5.09$; $P=0.009$ (TGli, TSol>TGua) Plot: $F_{2,57}=0.11$; $P=0.895$ Regime×Plot: $F_{4,57}=1.16$; $P=0.337$
Leaf $\delta^{15}\text{N}$ (‰) year 4	0.88±0.24	0.90±0.21	0.90±0.30	Model: $F_{8,57}=0.55$; $P=0.818$ Regime: $F_{2,57}=0.01$; $P=0.995$ Plot: $F_{2,57}=1.36$; $P=0.264$ Regime×Plot: $F_{4,57}=0.47$; $P=0.760$
Leaf nitrogen (%) year 4	1.71±0.05	1.76±0.07	1.66±0.06	Model: $F_{8,57}=0.95$; $P=0.483$ Regime: $F_{2,57}=0.63$; $P=0.535$ Plot: $F_{2,57}=2.53$; $P=0.088$ Regime×Plot: $F_{4,57}=0.33$; $P=0.860$
Leaf water (%) year 4	58.04±0.77	61.38±0.80	59.66±0.79	Model: $F_{8,57}=1.75$; $P=0.108$ Regime: $F_{2,57}=4.63$; $P=0.014$ (TGua>TGli) Plot: $F_{2,57}=1.89$; $P=0.161$ Regime×Plot: $F_{2,57}=0.32$; $P=0.866$
LMA (mg/cm ²) year 4	11.88±0.22	10.41±0.41	12.12±0.23	Model: $F_{8,56}=3.95$; $P=0.001$ Regime: $F_{2,56}=9.55$; $P<0.001$ (TGli, TSol>TGua) Plot: $F_{2,56}=0.78$; $P=0.462$ Regime×Plot: $F_{4,56}=2.34$; $P=0.066$
Phenology				
Value year 3	14.3±0.6	13.4±0.6	14.0±0.8	Regime: $H_2=1.25$; $P=0.536$ Plot: $H_2=7.71$; $P=0.021$ (SP2>SP3)
Value year 4	17.1±0.8	14.4±0.9	15.5±1.0	Regime: $H_2=5.66$; $P=0.059$ Plot: $H_2=4.26$; $P=0.119$

Trees were growing surrounded by *Gliricidia sepium* (TGli), surrounded by *Guazuma ulmifolia* (TGua), or solitarily (TSol). Significant effects are shown in bold

^a Statistical analysis of tree growth, leaf characteristics, and herbivore infestation was by two-way ANOVAs, using planting regime and plot as fixed between-subject factors. Significant ANOVAs (shown in bold) were followed by LSD post hoc tests (shown in brackets), to which false discovery rate correction (Verhoeven et al. 2005) was applied. Phenological rank values were analyzed by Kruskal–Wallis tests

ulmifolia attained a larger DBH, height, and shielding factor than *G. sepium* in year 5 (Table 2). DBH growth of TGua trees was not significantly related to the shielding exerted by its *G. ulmifolia* companion trees, but within the TGli treatment shielding was significantly negatively related to DBH growth of the central *T. rosea* trees (Table 3).

3.2 Effects of companion trees on leaf characteristics and phenology

The $\delta^{13}\text{C}$ values of mature leaves of *T. rosea* differed significantly among planting regimes (Table 1). $\delta^{13}\text{C}$ values were significantly lower in TGua trees than in TGli trees and

Table 2 Growth and shielding (mean±SE) of the companion tree species *Gliricidia sepium* and *Guazuma ulmifolia*

	Companion tree species		Statistics
	<i>G. sepium</i>	<i>G. ulmifolia</i>	
DBH (cm)	3.94±0.24	6.36±0.49	Model: $F_{5,39}=7.41$; $P<0.001$ Species: $F_{1,39}=20.66$, $P<0.001$ Plot: $F_{2,37}=4.85$, $P=0.013$ (SP3>SP2, SP1) Species×Plot: $F_{2,39}=1.28$, $P=0.289$
Height (m)	4.51±0.14	5.74±0.34	Model: $F_{5,39}=4.36$; $P=0.003$ Species: $F_{1,39}=13.38$, $P=0.001$ Plot: $F_{2,39}=4.10$, $P=0.024$ (SP2>SP1) Species×Plot: $F_{2,39}=0.83$, $P=0.443$
Shielding	1.0±0.1	1.3±0.1	Model: $F_{5,39}=3.74$; $P=0.007$ Species: $F_{1,39}=8.64$, $P=0.006$ Plot: $F_{2,39}=2.43$, $P=0.101$ Species×Plot: $F_{2,39}=3.97$, $P=0.027$

Significant effects are shown in bold. Statistical analysis of companion tree DBH, height, and shielding was by two-way ANOVAs, using species and plot as fixed between-subject factors. Significant ANOVAs (shown in bold) were followed by LSD post hoc tests (shown in brackets), to which false discovery rate correction (Verhoeven et al. 2005) was applied

in TSol trees, indicating reduced water stress for TGua tree individuals, whereas no differences were found between TGli trees and TSol trees. In contrast to $\delta^{13}C$ values, planting regimes had no significant impact on $\delta^{15}N$ values and nitrogen content in *T. rosea* leaves (Table 1). Furthermore, there was no difference in the relationship between nitrogen content and $\delta^{15}N$ values of *T. rosea* leaves between planting regimes (Fig. 2), which indicates that the nitrogen-fixing *G. sepium* companion trees had no significant effect on nitrogen content of *T. rosea* leaves.

Leaf water content and LMA were significantly affected by planting regimes (Table 1). Leaf water content was significantly higher in TGua trees than in TGli trees. No differences

were found between TSol trees and trees surrounded by *G. ulmifolia* or *G. sepium*. LMA was significantly lower in TGua trees than in TGli trees and TSol trees (Table 1).

Leafing phenology varied markedly among the individual *T. rosea* trees, with up to 60 days of difference among different trees in finishing leaf expansion. Leafing phenology was not significantly affected by planting regimes, although differences approached significance in year 4 (Kruskal–Wallis test, Table 1). In both studied years, TGua trees terminated leaf expansion later than TGli trees and TSol trees, i.e., TGua trees had the lowest phenological values. Phenological values from year 3 were significantly correlated with phenological values from year 4 ($R=0.29$; $P=0.018$).

Table 3 Effects of shielding by companion trees and plots on DBH growth of the timber tree *Tabebuia rosea*

		Statistics ^a		
		df	F	P
DBH growth				
TGua	Model	3	0.92	0.457
	Shielding	1	0.32	0.582
	Plot	2	1.23	0.322
	Error	14		
TGli	Model	3	15.21	< 0.001
	Shielding	1	9.66	0.010
	Plot	2	3.22	0.079
	Error	11		

Timber trees were growing surrounded by *Guazuma ulmifolia* (TGua) or surrounded by *Gliricidia sepium* (TGli). Significant effects are shown in bold

^a DBH (stem diameter at breast height) growth was analyzed separately for TGua trees and TGli trees by one-way ANCOVA, using plot as fixed between-subject factor and shielding as covariate

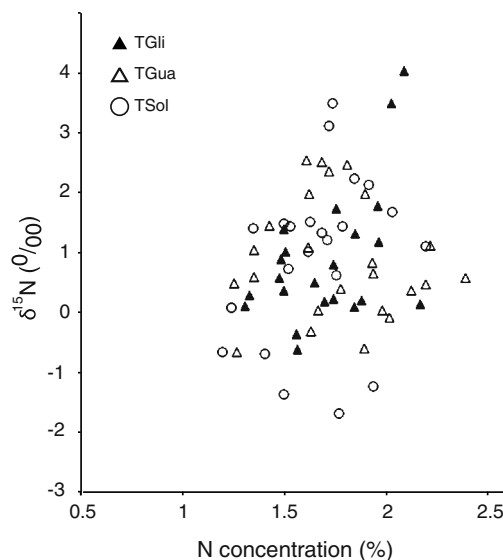


Fig. 2 Relation between nitrogen content (%) and $\delta^{15}N$ in mature leaves of *Tabebuia rosea* in year 4. *Tabebuia rosea* was growing surrounded by *Gliricidia sepium* (TGli), surrounded by *Guazuma ulmifolia* (TGua), or solitarily (TSol)

3.3 Timber tree infestation by key insect herbivores and herbivory

The lepidopteran key herbivore *E. gastralis* was considerably more abundant on *T. rosea* than the coleopteran key herbivore *W. inscripta* in the studied time period between year 1 and year 2 (total individuals—*E. gastralis*=1,391; *W. inscripta*=61 individuals). Consistently throughout all assessments, no significant differences in herbivore densities among planting regimes were found (Table 4).

Total damage of mature *T. rosea* leaves ranged from 13 % to 20 % and was highest for TSol trees, intermediate for TGli trees, and lowest for TGua trees in both year 1 and year 4, though these differences were not significant (Table 4). In year 1, neither planting regime nor plot had a significant effect on total leaf damage, but density of *E. gastralis* was positively related to total leaf damage (Table 4). In contrast, no such significant relation was found between infestation by *W. inscripta* and total leaf damage in year 1 (Table 4). In year 4, leaf damage was not significantly affected by planting regimes or plots (Table 4). Damage by *E. gastralis* was the most relevant damage type in all the planting regimes. Damage by *W. inscripta* was consistently low and positively related to leaf nitrogen content (Table 4). The effect of tree height on *W. inscripta* damage approached significance (Table 4).

There was no detectable association between herbivory and tree growth, as the covariate leaf damage in year 4 did not significantly affect DBH growth from year 4 to year 5 (Table 4).

4 Discussion

We found that companion trees significantly affected growth and some leaf characteristics but not leafing phenology of the timber tree *T. rosea* 3 to 5 years after establishment of an experimental silvopastoral reforestation system. Facilitation of timber tree growth via enhanced nitrogen uptake in the presence of legume companion trees was not detected. Herbivore abundance and resulting damage to timber trees was not related to companion trees.

Stem diameter growth of *T. rosea* trees surrounded by the companion tree *G. sepium* (TGli trees) was significantly higher than stem diameter growth of *T. rosea* trees surrounded by the companion tree *G. ulmifolia* (TGua trees). Additionally, stem diameter growth was significantly reduced for TGua trees compared to solitary trees (TSol trees). In contrast, we found a trend of higher mean stem diameter growth of TGli trees than of TSol trees. This suggests that the companion tree *G. sepium* can enhance timber tree

growth, as stem diameter growth of *T. rosea* individuals accompanied by *G. sepium* was at least as high or higher than that of trees in other planting regimes. In a nutshell, our findings thus indicate that companion trees planted circularly around a timber tree can impede or enhance the timber tree's growth.

The variable effects of the different companion tree species may be attributed to their individual growth performance and its related impact on timber tree growth. Light availability, for instance, represents a key factor for growth of tropical trees (Rüger et al. 2011). As the companion tree species in our study differed in their size, with *G. ulmifolia* being taller and attaining larger DBH than *G. sepium*, decreased light availability due to shading by *G. ulmifolia* companion trees could have caused reduced timber tree growth. The interpretation that *G. ulmifolia* companion trees affected the growth of the focal timber trees by altering the light or thermal environment of the timber trees is supported by the differing timber tree leaf characteristics that were observed in the individual planting regimes. Variation in $\delta^{13}\text{C}$ values is known to occur across and within tree populations (Chamaillard et al. 2011). In our study, the significantly lower $\delta^{13}\text{C}$ values in TGua trees compared to TGli and TSol trees indicate that TGua trees experienced lower drought stress, possibly due to the assumed shadier environment, as $\delta^{13}\text{C}$ values increase along with increasing water shortage (Gutbrodt et al. 2012) unless drought intensity is very severe (Mody et al. 2009). Moreover, leaf mass per area (LMA) is positively related to irradiance (Daas-Ghrib et al. 2011). Hence, the reduced LMA and increased water content of leaves of TGua trees also corroborate the explanation that the timber trees were exposed to a shadier, less sun-exposed environment in the presence of *G. ulmifolia* companion trees. In contrast to the leaf characteristics, $\delta^{13}\text{C}$, LMA, and water content, leafing phenology of *T. rosea* did not respond strongly to companion trees since no differences in leafing phenology between planting regimes were detected. Effects of planting regimes on leafing phenology were possibly obscured by a substantial influence of tree genotype (Stoekli et al. 2008) and site conditions (Valdez-Hernandez et al. 2010), which render leafing phenology a distinct individual tree characteristic that is relatively stable across years (Mopper 2005). However, as leafing phenology is also affected by light (Graham et al. 2003) and water availability (Itioka and Yamauti 2004), a successive change in leafing phenology due to companion tree influence can gradually be expected to occur along with increasingly differing environmental conditions in the different planting regimes.

Besides exposure to sun, availability of nutrients such as nitrogen can strongly affect growth of tropical timber trees (Merino et al. 2003). In our experiment, we expected increased nitrogen uptake and concomitant enhanced growth

Table 4 Effects of planting regimes and plots on leaf damage and herbivore infestation of the timber tree *Tabebuia rosea* (mean±SE for each variable) and effects of planting regimes, plots, and leaf damage on DBH growth of *T. rosea*

	Planting regime			Statistics ^a
	TGli	TGua	TSol	
Herbivore infestation (individuals/leaf)				
<i>E. gastralis</i> year 1	0.71±0.3	0.80±0.2	0.84±0.2	Model: $F_{8,57}=0.88$; $P=0.537$ Regime: $F_{2,57}=0.06$; $P=0.944$ Plot: $F_{2,57}=0.85$; $P=0.433$ Regime×Plot: $F_{4,57}=1.27$; $P=0.294$
<i>W. inscripta</i> year 1	0.05±0.01	0.14±0.06	0.07±0.02	Model: $F_{8,57}=0.97$; $P=0.471$ Regime: $F_{2,57}=0.94$; $P=0.397$ Plot: $F_{2,57}=2.21$; $P=0.119$ Regime×Plot: $F_{4,57}=0.33$; $P=0.858$
<i>W. inscripta</i> year 3	0.07±0.04	0.02±0.01	0.04±0.02	Model: $F_{8,58}=1.43$; $P=0.205$ Regime: $F_{2,58}=1.66$; $P=0.200$ Plot: $F_{2,58}=2.38$; $P=0.102$ Regime×Plot: $F_{4,58}=1.18$; $P=0.328$
<i>W. inscripta</i> year 4	0.04±0.01	0.09±0.07	0.05±0.01	Model: $F_{8,58}=0.68$; $P=0.705$ Regime: $F_{2,58}=0.39$; $P=0.678$ Plot: $F_{2,58}=0.16$; $P=0.850$ Regime×Plot: $F_{4,58}=0.95$; $P=0.442$
Leaf damage				
Leaf damage year 1	17.13±3.4	15.8±3.0	19.9±2.6	Model: $F_{10,54}=3.28$; $P=0.002$ Regime: $F_{2,54}=1.90$; $P=0.159$ Plot: $F_{2,54}=0.69$; $P=0.509$ Regime×Plot: $F_{4,54}=1.91$; $P=0.123$ Density <i>E. gastralis</i>: $F_{1,54}=10.04$; $P=0.003$ Density <i>W. inscripta</i>: $F_{1,54}=3.02$; $P=0.088$
Leaf damage year 4, overall model				Regime: $V=0.18$; $F_{6,108}=1.76$; $P=0.114$ Plot: $V=0.19$; $F_{6,108}=1.92$; $P=0.084$ Regime×Plot: $V=0.14$; $F_{12,165}=0.67$; $P=0.781$ Tree height: $V=0.13$; $F_{3,53}=2.66$; $P=0.057$ Leaf nitrogen: $V=0.18$; $F_{3,53}=3.78$; $P=0.016$
Total leaf damage year 4	15.1±3.6	13.0±1.6	19.3±2.2	Model: $F_{9,56}=1.23$; $P=0.297$ Regime: $F_{2,56}=2.44$; $P=0.096$ Plot: $F_{2,56}=0.12$; $P=0.886$ Regime×Plot: $F_{4,56}=1.25$; $P=0.300$ Leaf nitrogen: $F_{1,56}=2.25$; $P=0.139$
<i>E. gastralis</i> leaf damage year 4	11.3±3.7	8.6±1.6	14.7±2.3	Model: $F_{9,56}=1.36$; $P=0.228$ Regime: $F_{2,56}=2.44$; $P=0.096$ Plot: $F_{2,56}=0.26$; $P=0.773$ Regime×Plot: $F_{4,56}=1.26$; $P=0.297$ Leaf nitrogen: $F_{1,56}=2.16$; $P=0.148$
<i>W. inscripta</i> leaf damage year 4	1.32±0.4	1.07±0.4	0.86±0.4	Model: $F_{10,55}=3.05$; $P=0.004$ Regime: $F_{2,55}=1.65$; $P=0.201$ Plot: $F_{2,55}=3.40$; $P=0.040$ Regime×Plot: $F_{4,55}=0.68$; $P=0.612$ Tree height: $F_{1,55}=3.86$; $P=0.055$ Leaf nitrogen: $F_{1,55}=6.09$; $P=0.017$

Table 4 (continued)

	Planting regime			Statistics ^a
	TGli	TGua	TSol	
Effect of leaf damage on DBH growth				
DBH growth (cm) year 4–5	2.09±0.2	1.58±0.13	2.16±0.2	Model: $F_{9,52}=2.18$; $P=0.038$ Regime: $F_{2,52}=2.04$; $P=0.140$ Plot: $F_{2,52}=3.75$; $P=0.030$ Regime×Plot: $F_{4,52}=1.86$; $P=0.132$ Total leaf damage year 4: $F_{1,52}=0.44$; $P=0.512$

Trees were growing surrounded by *Gliricidia sepium* (TGli), surrounded by *Guazuma ulmifolia* (TGua), or solitarily (TSol). Significant effects are shown in bold

^a Leaf damage of year 1 was analyzed by two-way ANCOVA, using planting regime and plot as fixed between-subject factors and density of *Eulepte gastralis* and *Walterianella inscripta* as covariates. Leaf damage of year 4 was analyzed by two-way MANCOVA using total leaf damage, *E. gastralis* leaf damage, and *W. inscripta* leaf damage as dependent variables; planting regime and plot as fixed between-subject factors; and tree height and leaf nitrogen content as covariates. Pillai's trace (V) was used as a test statistic and separate univariate ANOVAs were conducted as follow-up analysis to assess effects of the covariates on the dependent variables separately

of TGli trees as a consequence of nitrogen fixation by *G. sepium*, which was found to fix nitrogen within 2 years of planting (Plath et al. 2011a). However, as nitrogen concentrations and $\delta^{15}\text{N}$ values of mature leaves of TGli trees were not significantly different from TGua trees and TSol trees, our findings suggest that even 4 years after plantation establishment atmospheric nitrogen fixed by *G. sepium* is not bioavailable in quantities that enhance nitrogen content of *T. rosea* leaves. The lack of detectable nitrogen transfer may be related to missing direct below-ground interactions through root exudates or interconnected mycelial networks (Sierra and Nygren 2006) or to an absence of indirect interactions actually driven by the decomposition of nitrogen-enriched *G. sepium* biomass (Kurppa et al. 2010).

Insect herbivory can have strong negative effects on tree growth in tropical reforestation (Massad 2012; Plath et al. 2011b). In our study, however, the differences in tree growth between planting regimes were not strongly related to key herbivore abundance, and herbivory did not differ between planting regimes. These findings support the observation that the key herbivores and resulting damage were not responding to the presence of companion trees but rather to the general planting design of the silvopastoral reforestation system, namely to the low density of timber host trees. Compared to a nearby high-density timber plantation at the same study site (Plath et al. 2012), the abundance of the lepidopteran key herbivore *E. gastralis* was markedly higher in the silvopastoral reforestation system (0.6–0.9 individuals/leaf) than in the high-density plantations (0.2–0.5 individuals/leaf). This higher abundance of *E. gastralis* on host trees growing at low density in the silvopastoral reforestation system strongly supports the assumption that *E. gastralis* follows a resource-dilution strategy to avoid enemies or competition (Plath et al. 2012), and it rendered *T. rosea* timber trees in the silvopastoral reforestation system susceptible

to damage by *E. gastralis* (76–85 % contribution to total leaf damage). In contrast to *E. gastralis*, abundance of the coleopteran key herbivore *W. inscripta* was much lower in the silvopastoral reforestation system (0.06 to 0.12 individuals/leaf) than in the high-density plantations (0.2 to 0.4 individuals/leaf). Furthermore, *W. inscripta* tended to respond positively to tree height, suggesting that resource apparency might affect infestation by this herbivore. These indications support the view that tree infestation by *W. inscripta* is positively affected by resource concentration (Plath et al. 2012), and they suggest that silvopastoral planting designs can serve as a strategy to reduce damage by these herbivores.

5 Conclusions

Companion plantings of multipurpose and timber trees can support the reforestation of rangeland with native tree species. However, adequate species selection is crucial for the successful implementation of the proposed planting system. *G. sepium* was found to be a promising species for companion planting with the timber tree *T. rosea*. Even without the effect of an enhanced nitrogen uptake by the timber tree in the presence of *G. sepium*, companion planting with *G. sepium* can enhance timber tree growth. In contrast, *G. ulmifolia* was not a suitable companion tree for *T. rosea*, as it impeded timber tree growth. However, planting *G. ulmifolia* as companion tree reduced water stress in *T. rosea* compared to timber tree individuals growing solitarily or in combination with *G. sepium*. In the context of increasing drought and rising temperatures through climate change, companion trees that lead to a shadier environment could provide a more pronounced benefit for silvopastoral reforestations.

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