



# Establishment of native tropical timber trees in monoculture and mixed-species plantations: Small-scale effects on tree performance and insect herbivory

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## ABSTRACT

Plantations of native timber species established on former pasture are a potential strategy to reduce the logging pressure on remnant natural forests in the tropics. Such plantations may help to mitigate or reverse the negative impacts of land degradation, and they may contribute to the long-term livelihood of livestock farmers. Planting native trees is, however, perceived as a risky activity due to limited knowledge of their performance and due to marked losses of newly established seedlings attributed to insect pests. Our study focuses on the small-scale effects of environmental heterogeneity, tree diversity and insecticide treatment on the performance of three native Central American timber species two years after establishment, and on damage inflicted by insect herbivores. Growth, survival and herbivore leaf damage were quantified for *Anacardium excelsum* (Anacardiaceae), *Cedrela odorata* (Meliaceae) and *Tabebuia rosea* (Bignoniaceae) planted in an experiment in Panama as (1) monocultures, (2) mixed stands, and (3) mixed stands protected by insecticides. Our study revealed that small-scale effects can have a substantial impact on the success of timber trees planted on former pasture. Growth performance and survival of the three species was strongly affected by small-scale environmental heterogeneity, which was expressed as significant differences in growth and survival among different plantation plots at the same study site. Establishment of trees in mixed stands did not have significant effects on tree survival and growth compared to pure stands, although it reduced herbivore pressure in one of the studied tree species. All tree species grew best and suffered lowest leaf damage when protected by insecticides, indicating a general influence of insect herbivory on growth of newly established trees. In contrast to growth performance, survival was not significantly affected by different management practices or herbivory. The large variability among plots in tree survival and growth, and also in the effects of management practices such as planting design and insecticide treatment, emphasizes the importance of small-scale environmental heterogeneity on tree survival and growth.

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## 1. Introduction

Smallholders and communities strongly contribute to deforestation in Central America (FAO, 2009; Scherr et al., 2003). Large-scale initiatives for biodiversity conservation and ecosystem restoration (Hartley, 2002; Lamb et al., 2005; Paquette and Messier, 2010) must therefore consider local-scale smallholder needs (Barrance et al., 2003; Lamb et al., 2005; Montagnini, 2001). Reforestation is a potential strategy to reduce the logging pressure on remnant natural forests, while considering local socio-economic interests (Dijk and Savenije, 2009; Paquette and Messier, 2010). Small-scale landholders, however, perceive tree planting as a risky activity. Compared to harvesting or logging old timber trees in natural

forests, benefits of timber plantations are only achieved in the long term (Dagang and Nair, 2003; Garen et al., 2009; Günter et al., 2009; Lamb et al., 2005). Furthermore, substantial losses of seedlings in new plantations are attributed to insect herbivores. To protect trees from expected herbivore attack, half of the Panamanian farmers interviewed in a recent study applied pesticides (Garen et al., 2009), but until now there is little evidence for the effectiveness of these products under prevailing field conditions. In addition, small-scale site conditions may substantially influence survival and productivity of timber species (Firn et al., 2007; Forrester et al., 2005; Potvin and Gotelli, 2008), as well as plant traits related to defense against herbivores such as leaf palatability, leaf morphology and chemistry (Basset, 1996; Molina-Montenegro et al., 2006). Accordingly, small-scale site conditions might limit accurate assessments of the effects of particular management strategies (Boyden et al., 2005; Forrester et al., 2006; Fridley, 2003). Thus, approaches must be found to ensure that reforestation is made attractive to small-scale

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landholders and that site-specific methodologies are developed for farmers (Lamb et al., 2005).

Since the 1980s, scientific interest has increasingly focused on appropriate strategies for forest plantations to provide multiple ecosystem services and a broader range of goods while meeting the economical demand for high timber productivity (Kelty, 2006; Paquette and Messier, 2010). Whereas former plantation forestry has traditionally concentrated on monocultures based on a few well-known exotic tree species (Evans and Turnbull, 2004; Kelty, 2006; Lamb et al., 2005), recent research has emphasized the potential advantages of native instead of exotic species, planted in mixed stands rather than in monocultures (Erskine et al., 2006; Hartley, 2002; Lamb et al., 2005; Piotta et al., 2010). Native tree species may have more positive effects on the environment, fulfill traditional services to local landholders, and require less financial investment by eliminating dependency on external seed sources and foreign technologies. Mixed stands may lead to product diversification with different rotation cycles while providing a system for growing high value timber (Kelty, 2006). They have the potential to restore degraded areas by improved nutrient cycling and increased soil fertility (Binkley et al., 1992; Guariguata et al., 1995; Montagnini, 2000), and to enhance the biodiversity conservation value of a stand (Hartley, 2002; ITTO/IUCN, 2009). Likewise, mixed species plantations may lead to higher stand-level productivity compared to monocultures as a consequence of positive ecological interactions among different timber species (complementarity, facilitation) (Erskine et al., 2006; Forrester et al., 2006; Pretzsch and Schütze, 2009) and reduced negative impacts of insect herbivores and diseases (Jactel and Brockerhoff, 2007 and references therein; Nichols et al., 2006). Lowered herbivore impact may be due to 'associational resistance' (Tahvanainen and Root, 1972), which might be attributed to chemical interferences (Finch and Collier, 2000), a reduced host plant density ('resource hypothesis') (Root, 1973) and quality ('specialist diet-mixing hypothesis') (Mody et al., 2007) for oligophagous species, and an increased number and diversity of natural enemies due to a more complex and heterogeneous environment ('enemy hypothesis') (Root, 1973).

For tropical ecosystems, most studies of the effects of pests have either focused on comparisons between monocultures and complex natural forests (Kelty, 2006), or on intercropping in agro-ecosystems (Cook et al., 2007). Studies comparing the susceptibility to pest attacks of unprotected and insecticide-protected standardized experimental stands, and of monocultures and low-diversity mixtures are comparably scarce (Jactel et al., 2005; Kelty, 2006; Koricheva et al., 2006).

Here we present results from a study of the reforestation potential of three native Central American timber species in a heterogeneous pasture environment. We tested different management practices by establishing trees in monocultures, 3-species mixtures, and 3-species mixtures protected by insecticides. We considered the influence of small-scale environmental heterogeneity by selecting experimental plots that represented differing, locally prevailing environmental conditions. The aims of the study were (1) to compare the species-specific development of newly planted timber trees on former pasture, (2) to test how different management practices influence the specific survival and growth of the timber saplings, and (3) to assess the effect of different management practices on herbivore damage to the timber species. We hypothesized that (i) survival and growth performance differs among saplings grown in monocultures and mixed stands due to differing interactions among trees, that (ii) survival and growth performance of saplings in the insecticide-protected stands are enhanced compared to monocultures and unprotected mixed stands due to a suppression of insect pests, and that (iii) saplings in mixed stands suffer lower insect herbivore damage than individuals growing in monocultures due to associational resistance

through tree diversification, while lowest injury appears in mixtures protected by insecticides.

## 2. Materials and methods

### 2.1. Study site and tree species

The study was conducted at an experimental site in Sardinilla, Province Colon, Central Panama (9°19'30"N, 79°38'00"W, elevation around 70 m a.s.l.). The former original forest, classified as semideciduous lowland forest and probably similar to the Barro Colorado Island forest (9°9'0"N, 79°51'0"W) (Leigh et al., 1996), was logged in 1952/53 (Potvin et al., 2004). The site was used for agriculture for two years and then converted into pasture for cattle farming by seeding grasses (Scherer-Lorenzen et al., 2007). The soils are derived from Tertiary limestone and other sedimentary rocks. The upper slopes are covered with clayey Typic Tropudalfs and grade into clayey Aquic Tropudalfs in the lower slopes (Potvin et al., 2004). Mean annual precipitation at nearby Salamanca is around 2200 mm, with a mean precipitation of around 50 mm per month during the dry season (January–April), and around 255 mm per month during the rainy season (May–December) (ACP, 2009). Annual daily temperature ranges between a minimum of 21.7 °C and a maximum of 33.1 °C (Scherer-Lorenzen et al., 2007). Climatic conditions during the study period were characterized by comparison of precipitation in 2006–2008 with long-term average precipitation calculated over a 1967–2005 base period (ACP, 2009; Plath et al., 2011).

The three timber species used in this study are *Tabebuia rosea* Bertol. (Bignoniaceae), *Anacardium excelsum* Bertero & Balb. ex Kunth (Anacardiaceae), and *Cedrela odorata* L. (Meliaceae). They were selected for their (1) commercial importance on a regional, national and international scale, (2) comparability with an already established improved afforestation system on the experimental site, and (3) their availability as tree seedlings in local nurseries. All three species are native to the study region and of high timber-value (ACP, 2005). Their growth is characterized as intermediate (*A. excelsum*) to fast (*C. odorata*, *T. rosea*). Beyond their timber value, they provide a variety of other goods and services (Herrera and Morales, 1993; Longwood, 1971). *T. rosea* has been used as an ornamental and shade tree, but it can be planted with success in commercial plantations. The wood is moderately resistant to fungi and susceptible to termite and marine borers (Herrera and Morales, 1993; Longwood, 1971), but little is known on insect herbivores damaging living trees. *A. excelsum* grows in a wide range of soils and climatic conditions. The wood of this species is moderately light, naturally durable and easily accepts preservatives that protect against termites and fungi. It is used for general construction and carpentry (Fournier, 2003; Hartshorn and Gentry, 1991). Seedlings are shade tolerant during early stages of development but need more light for survival and growth in later stages. Seedling survival may be strongly reduced by insect herbivores, fungal diseases, and poor environmental conditions (Fournier, 2003). *C. odorata* is a light demanding, long-lived pioneer that tolerates shade only temporarily (Carpenter et al., 2004). It is widely planted in the tropics and grows best in regions with very fertile and well-drained soils. When established in plantations, *C. odorata* seedlings seldom escape attack by the mahogany shootborer *Hypsipyla grandella* Zeller (e.g. Cole and Ewel, 2006; Menalled et al., 1998).

### 2.2. Planting design

Experimental reforestation plots were established on former pasture as pasture-afforestation (PA) plantations at the Sardinilla site in August 2006. Potted seedlings of *T. rosea*, *A. excelsum* and *C.*

*odorata* were raised in a PRORENA (Proyecto de Reforestación con Especies Nativas) nursery for three months before being planted on the pasture. To support tree establishment, 15 g of 12–72–12 N–P–K granular fertilizer was applied to each seedling at the time of planting 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. The seedlings were planted at a density of 36 trees per 100 m<sup>2</sup>, using a standardized six by six Latin square design with a planting distance of 2 m. Tree individuals were arranged in three different planting schemes: (1) monocultures for all three timber species, (2) mixed stands comprising the three species (management measure ‘tree diversity’), and (3) mixed stands protected by the insecticide/nematicide carbofuran (carbamate, Furadan 10 GR, 5–25 g/tree depending on the effective area of canopy shade) applied to the soil every two months, and by the insecticide cypermethrin (pyrethroid, Arribo EC 20 or 6 EC, 1.2 g/l spray solution) applied to the foliage every two weeks after planting (management measure ‘insecticide treatment’). The three planting schemes were merged in one locality as a coherent plot. Five replicates of this plot (PA1–PA5) were planted at different sites within the Sardinilla experimental area, encompassing variable environmental conditions (Table 1). Competing vegetation (tall grasses and woody successional vegetation) was cleared with machetes every 3 months during the rainy season in the plots PA2–PA5. In PA1, concomitant vegetation (short grass- and herb-layer) was mown approximately every 4 weeks.

2.3. Plot characterization

To quantify environmental variation among the plots, chemical and physical soil properties as well as biomass of herbaceous vegetation were determined in May 2009. Soil was sampled from 5 uniformly distributed locations in each planting scheme of all five replicated plots. Samples were taken from 0 to 5 cm, 5 to 10 cm and 15 to 20 cm soil depth using a cylindrical corer. They were dried at 65 °C to weight constancy before quantification of pH, N, and C concentration. Soil properties were analyzed blending the five samples for each soil depth and planting scheme in the five plots. Soil pH was determined in soil water solution according to NF ISO 10390 (2005) using a Metrohm 780 pH meter (Metrohm Schweiz AG, Zofingen, Switzerland). Analyses of total N and C concentration were conducted using a Flash EA 1112 Series elemental analyzer (Thermo Italy, Rhodano, Italy). Soil moisture was measured as the proportion of water per soil sample, calculated from the weight before and after drying. Living and dead aboveground herbaceous vegetation was uniformly sampled with a 0.5 m × 0.5 m square grid in the center of each planting scheme of all five plots and dried at 65 °C to weight constancy before determination of dry biomass.

2.4. Tree survival and growth

Survival of the three timber species *T. rosea*, *A. excelsum* and *C. odorata* was calculated for each species on an annual basis as the number of saplings surviving the initial phase of two years (from August 2006 to August 2008), divided by the number of saplings planted in 2006. Sapling growth was quantified twice on an annual basis. As measures of tree growth, total height (from the soil to the uppermost point in the tree crown) and basal stem diameter (diameter at 10 cm above soil surface) of all timber saplings were taken.

2.5. Leaf herbivory

Herbivory was measured two years after tree planting in August 2008. Leaf damage on the timber saplings was quantified for all individuals in both the unprotected mixed stands and the mixed

**Table 1** Soil and vegetation characteristics (mean ± SE) of the five pasture–afforestation plots (PA). Contrasting letters a, b, c refer to significant differences between plots or soil depths (D1 = 0–5 cm, D2 = 5–10 cm, D3 = 15–20 cm) for the specific trait.<sup>a</sup>

Trait	PA1	PA2	PA3	PA4	PA5
Slope (%)	3.24 (±0.29)	4.73 (±0.45)	3.01 (±0.54)	7.46 (±0.33)	4.04 (±0.38)
Elevation (m)	77.56 (±0.84)	73.24 (±0.49)	75.96 (±0.23)	73.22 (±0.79)	68.26 (±0.21)
Nitrogen concentration (%)					
D1 (±SE)	0.65 (±0.03)	0.69 (±0.04)	0.66 (±0.07)	0.68 (±0.04)	0.68 (±0.06)
D2 (±SE)	0.42 (±0.04)	0.37 (±0.03)	0.49 (±0.03)	0.52 (±0.05)	0.46 (±0.05)
D3 (±SE)	0.33 (±0.02)	0.23 (±0.02)	0.29 (±0.03)	0.28 (±0.03)	0.35 (±0.05)
Carbon concentration (%)					
D1 (±SE)	7.18 (±0.44)	8.68 (±0.59)	7.33 (±0.82)	7.79 (±0.57)	8.32 (±0.60)
D2 (±SE)	4.75 (±0.48)	5.10 (±0.35)	4.74 (±0.70)	6.06 (±0.78)	5.93 (±0.52)
D3 (±SE)	3.79 (±0.33)	3.43 (±0.23)	3.30 (±0.32)	3.38 (±0.38)	4.71 (±0.53)
pH					
D1 (±SE)	5.25 (±0.11)	5.68 (±0.08)	5.82 (±0.12)	5.93 (±0.09)	5.52 (±0.12)
D2 (±SE)	5.23 (±0.11)	5.75 (±0.17)	5.83 (±0.09)	6.16 (±0.36)	5.74 (±0.14)
D3 (±SE)	5.24 (±0.14)	5.94 (±0.11)	5.97 (±0.13)	5.67 (±0.19)	6.17 (±0.20)
Moisture (%)					
D1 (±SE)	38.28 (±0.60)	29.54 (±0.79)	25.05 (±0.41)	30.13 (±0.81)	30.83 (±0.86)
D2 (±SE)	37.34 (±0.50)	29.27 (±0.75)	25.09 (±0.53)	30.83 (±0.82)	31.39 (±0.49)
D3 (±SE)	37.73 (±0.77)	31.76 (±0.81)	27.17 (±0.35)	28.87 (±0.57)	32.33 (±0.42)
Biomass alive (g) (±SE)	59.50 (±6.71)	205.70 (±84.37)	75.30 (±15.04)	97.20 (±28.55)	89.00 (±10.01)
Biomass dead (g) (±SE)	66.30 (±19.58)	123.40 (±26.39)	110.30 (±11.21)	193.90 (±37.97)	164.80 (±29.38)
Height (cm)	5.00 (±0.00)	49.00 (±20.88)	17.00 (±3.00)	17.00 (±3.61)	19.00 (±3.67)

<sup>a</sup> Analysis of soil characteristics was carried out with two-way repeated measures ANOVA; vegetation traits were analyzed by one-way ANOVA; LSD post hoc test, p < 0.05.

Plot:  $F_{4,20} = 1.165, p = 0.356$   
 Depth:  $F_{2,40} = 140.581, p < 0.001$ ; D1<sup>a</sup> > D2<sup>b</sup> > D3<sup>c</sup>  
 Plot:  $F_{4,20} = 1.332, p = 0.292$   
 Depth:  $F_{2,40} = 134.855, p < 0.001$ ; D1<sup>a</sup> > D2<sup>b</sup> > D3<sup>c</sup>  
 Plot:  $F_{4,20} = 7.449, p = 0.001$ ; PA2<sup>a</sup>, PA3<sup>a</sup>, PA4<sup>a</sup>, PA5<sup>a</sup> > PA1<sup>b</sup>  
 Depth:  $F_{2,40} = 1.548, p = 0.225$   
 Plot:  $F_{4,20} = 26.819, p < 0.001$ ; PA1<sup>a</sup> > PA2<sup>b</sup>, PA4<sup>b</sup>, PA5<sup>b</sup> > PA3<sup>c</sup>  
 Depth:  $F_{2,40} = 1.754, p = 0.186$   
 Plot:  $F_{4,20} = 1.547, p = 0.227$   
 Plot:  $F_{4,20} = 4.301, p = 0.011$ ; PA2<sup>a</sup>, PA3<sup>a</sup>, PA4<sup>a</sup>, PA5<sup>a</sup> > PA1<sup>b</sup>  
 Plot:  $F_{4,20} = 5.564, p = 0.004$ ; PA2<sup>a</sup> > PA3<sup>ab</sup>, PA4<sup>b</sup>, PA5<sup>ab</sup> > PA1<sup>c</sup>

stands protected by insecticides. In the monoculture, six saplings from the outer edge and six saplings from the inner area were randomly selected. Due to low survival (<50%) and resulting reduced sample size for *C. odorata*, quantification of herbivory focused on *T. rosea* and *A. excelsum*. Herbivore damage was exclusively quantified for mature leaves, which were characterized by dark green color and high toughness compared to soft young leaves.

*T. rosea* has digitate leaves consisting of five leaflets of unequal size. The foliage is shed during the dry season, hence, all leaves available on the sapling developed in the actual growing season. From each sapling eight mature leaves were arbitrarily collected. From saplings with lower numbers of mature leaves, all of them were collected. *A. excelsum* has simple, lanceolate-shaped leaves without stipules. The foliage is only partially shed in the dry season, but the top leaves on a shoot in August always developed during the actual growing season. From each sapling, the first fifteen fully developed leaves in the top foliage layer were collected and subsequent analyses focused on the mature leaves within the leaf sample. Leaves were photographed at the day of collection under natural light in the field laboratory with a digital camera (Panasonic, Lumix DMC-LZ3) using a standardized, established procedure (Mody and Linsenmair, 2004). Leaves were spread out on a grey colored plastic board, covered with a hinged lid of transparent, non-reflecting glass, and photographed from a fixed distance, without flash and with a consistent resolution. For high-throughput quantitative analysis of leaf damage, digital photographs were analyzed using a custom-built software tool (W. Einhäuser, unpublished data). This software discriminates leaves from background based on the first principal axis in color space and an automated thresholding procedure. In *T. rosea*, subleaves were separated by an iterative erosion/dilation procedure, and analyzed individually. Fractional leaf damage was assessed by comparing the segmented leaf to its convex hull and absolute damage by additional comparison to the automatically detected reference plate. The analysis was verified by visual inspection and corrected using in-built procedures if needed. Impartiality of manual processing was assured by randomized photograph selection and blinding of photograph identity. Individual leaf damage measurements were averaged to obtain a measure of herbivory for every sapling studied.

## 2.6. Statistical analyses

Prior to analysis, data were transformed where necessary to meet the assumptions of normality and heteroscedasticity for parametric tests. Plot characteristics were arcsin-transformed (soil C and N, soil moisture) or log-transformed (soil pH, biomass, vegetation height). Growth measurement values were square root-transformed. Herbivore damage was arcsin-transformed.

Comparisons of soil properties were conducted using two-way repeated measures ANOVA, with soil depth as within-subject repeated factor and plots as between-subject factor. Biomass and height of herbaceous vegetation in the plots were compared by one-way ANOVA. Survival was compared for the three timber species, and for the three planting schemes for each species using contingency chi-square tests. Comparisons between species and effects of planting schemes on timber sapling growth were assessed by four-way repeated measures ANOVA, with year as within-subject repeated factor and species, planting scheme and plot as between-subject factors. Intraspecific comparison of sapling growth for each species among the three planting schemes was analyzed using a three-way repeated measures ANOVA with year as within-subject repeated factor, and planting scheme and plot as between-subject factors. Herbivore damage was analyzed by two-way ANOVA, with planting scheme and plot as between-subject factors. For multiple comparisons in ANOVA analyses, LSD *post hoc* tests were applied.

The magnitude of each experimental effect ( $\hat{\delta}^2$ ) was estimated following Winer et al. (1991).

All statistical analyses were conducted with SPSS 16.0 for Mac OS X (2007; SPSS, Chicago, IL, USA). For clarity, all figures show untransformed data.

## 3. Results

### 3.1. Plot characterization

The five pasture-afforestation plots (PA1–PA5) differed significantly in soil moisture and soil pH as well as dead biomass and height of concomitant herbaceous vegetation (Table 1). Soil moisture was highest in plot 1, followed by plots 2, 4 and 5, while lowest values were measured in plot 3. Likewise, plot 1 was characterized by a significantly lower soil pH than all other plots, which were characterized by similar pH values. No significant changes occurred over the depth gradient in soil moisture and pH. Nitrogen and carbon concentration were consistently highest in the 5 cm surface layer and lowest in the deepest level at 20 cm, but showed no differences among the single plots. Similarly, alive biomass was not significantly different among the plots, although visual inspection indicated particularly high growth in herbaceous vegetation in plot 2, documented by the relatively high mean value of alive biomass. Dead biomass as well as vegetation height were significantly lower in the mown plot 1 than in the remaining plots (Table 1).

### 3.2. Tree survival

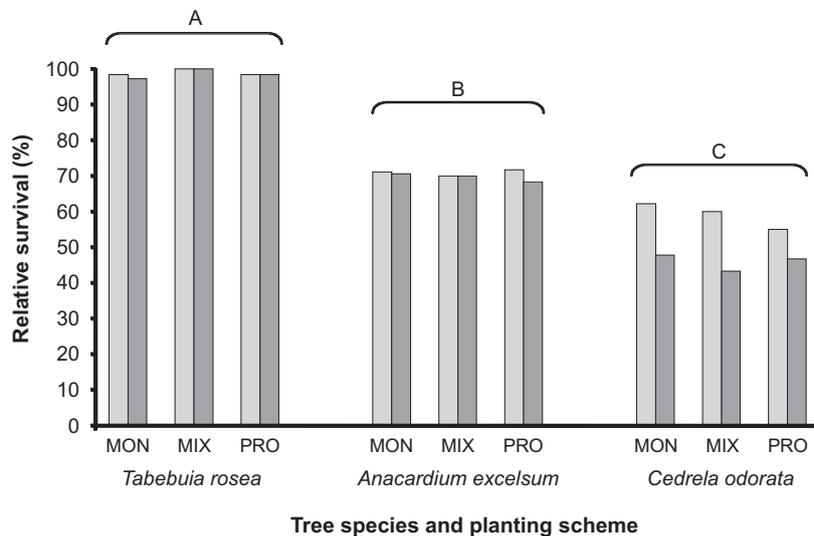
Survival differed significantly among the three timber species *T. rosea*, *A. excelsum* and *C. odorata* ( $\chi^2(2) = 20.4$ ,  $p < 0.001$ ), but it was not significantly affected by planting scheme for any of the species studied (*T. rosea*:  $\chi^2(2) = 1.81$ ,  $p = 0.40$ ; *A. excelsum*:  $\chi^2(2) = 0.11$ ,  $p = 0.95$ , *C. odorata*:  $\chi^2(2) = 1.69$ ,  $p = 0.43$ ) (Fig. 1). In *T. rosea*, almost all individuals survived during the first two years after establishment (98%,  $n = 294$ ). In contrast, *C. odorata* exhibited the lowest survival (46.7%,  $n = 140$ ) with more than half of all planted individuals dying within this time period. Survival of *A. excelsum* was intermediate (70%,  $n = 210$ ). In all three timber species, sapling mortality mainly occurred in the first year after establishment.

Plot effects significantly influenced survival of *A. excelsum* ( $\chi^2(4) = 28.73$ ,  $p < 0.001$ ) and *C. odorata* ( $\chi^2(4) = 19.69$ ,  $p = 0.001$ ) two years after establishment. In *A. excelsum*, highest survival was found in plot 1 (90.0%), followed by plots 2, 3 and 4 (75.0%, 73.3% and 65.0%, respectively), while most individuals died in plot 5 (46.7%). In *C. odorata*, saplings showed higher survival in plot 5 (71.2%) than in plots 1, 2, 3 and 4 (40.0%, 36.7%, 45.0% and 40.0%, respectively). No plot effects were found for *T. rosea* survival ( $p > 0.05$ ).

### 3.3. Tree growth

Two years after establishment, sapling height and stem diameter significantly differed between the three timber species (Fig. 2, Table 2). The species main effect explained more than one quarter of the overall variation in tree height ( $\bar{h} = 26\%$ ) and 13% of variation in stem diameter (Table 2). On average for all three planting schemes, *T. rosea* grew higher ( $\bar{h} = 261.8 \pm 5.8$  cm), and exhibited larger stem diameters ( $\bar{sd} = 47.6 \pm 1.0$  mm) than *A. excelsum* ( $\bar{h} = 159.4 \pm 5.7$  cm,  $\bar{sd} = 37.0 \pm 1.4$  mm) and *C. odorata* ( $\bar{h} = 140.4 \pm 7.2$  cm,  $\bar{sd} = 36.9 \pm 1.6$  mm) ( $p < 0.001$  for both traits). *A. excelsum* and *C. odorata* significantly varied for both sapling height and stem diameter ( $p = 0.005$  and  $p = 0.033$ , respectively).

Management practices strongly affected overall mean values of height and basal stem diameter (Table 2). Intraspecific comparisons of tree growth among the management practices revealed

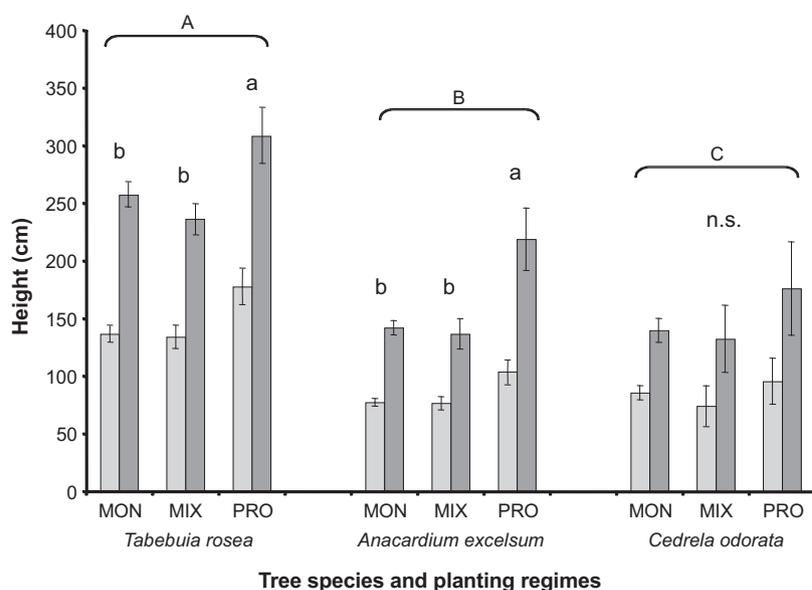


**Fig. 1.** Relative survival of the timber species *Tabebuia rosea*, *Anacardium excelsum* and *Cedrela odorata* one year (light grey bars) and two years (dark grey bars) after establishment. Saplings were planted in monocultures (MON), in 3-species-mixtures (MIX) or in 3-species-mixtures protected by insecticides (PRO). Contrasting letters refer to significant differences between species in total relative survival in all three planting schemes ( $\chi^2$ -test,  $p < 0.05$ ).

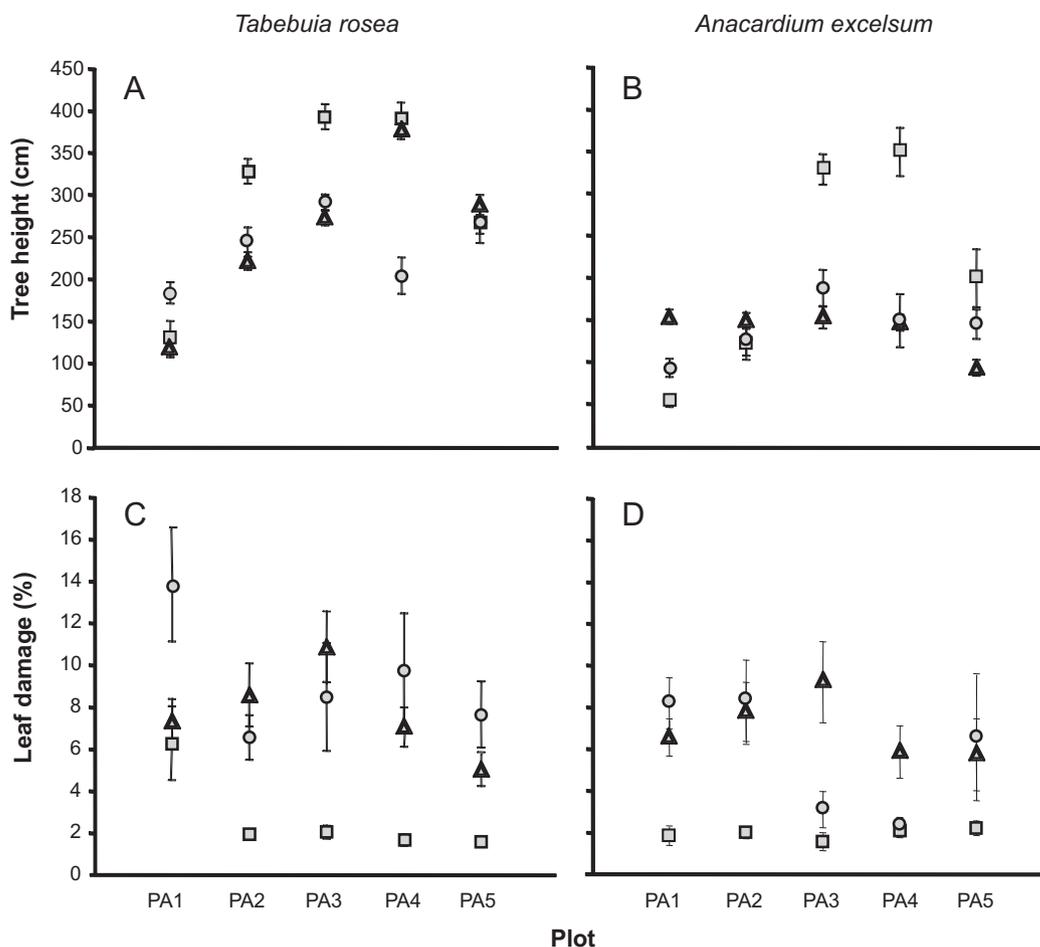
significant effects of ‘insecticide treatment’ in each timber species, whereas ‘tree diversity’ had no significant effect on tree growth performance. *T. rosea* showed significantly better growth performance in the insecticide-protected planting schemes compared to both monocultures and mixtures as assessed for height ( $F_{2,278} = 13.68$ ,  $p < 0.001$ ) and basal stem diameter ( $F_{2,278} = 12.45$ ,  $p < 0.001$ ). In contrast, no differences were found between monocultures and mixed stands ( $p > 0.05$ ) (Fig. 2). Similar results were found for *A. excelsum*, which grew higher and exhibited larger stem diameters in insecticide-protected stands compared to both monocultures and mixtures (height:  $F_{2,195} = 14.31$ ,  $p < 0.001$ ; basal stem diameter:  $F_{2,195} = 15.28$ ,  $p < 0.001$ ). No differences in tree height and stem diameter were found between monocultures and mixed stands (Fig. 2). *C. odorata* showed a similar growth pattern with higher mean height and basal stem diameter in the insecticide-protected stands than in monocultures and mixed stands, but these differ-

ences were not significant ( $F_{2,124} = 1.81$ ,  $p = 0.169$ ). As basal stem diameter was strongly correlated to tree height in both years (year 1:  $R^2 = 0.90$ ,  $p < 0.001$ , year 2:  $R^2 = 0.91$ ,  $p < 0.001$ ), and statistical analyses revealed the same significant differences between planting schemes, tree height is illustrated exemplarily for both growth parameters in Fig. 2.

Plot effects were strong for overall mean values of height and basal stem diameter, explaining 22% of the overall variation of the respective dependent variables (Table 2). Saplings of the three timber species grew best in plot 4 and plot 3, followed by plot 5 and plot 2. Lowest performance of tree individuals was observed in plot 1 for both growth traits (height:  $PA4^a$ ,  $PA3^a > PA5^b$ ,  $PA2^b > PA1^c$ ; stem diameter:  $PA4^a$ ,  $PA3^a > PA5^b > PA2^c > PA1^d$ ) (Table 2). A significant species-plot interaction revealed a varying plot effect on growth performance of the individual timber species (Table 2). Likewise, plots influenced the effects of ‘insecticide treatment’ and



**Fig. 2.** Tree height (mean  $\pm$  SE) of *Tabebuia rosea*, *Anacardium excelsum* and *Cedrela odorata* one year (light grey bars) and two years (dark grey bars) after establishment. Saplings were planted in monocultures (MON), in 3-species-mixtures (MIX) or in 3-species-mixtures protected by insecticides (PRO). Contrasting capital letters refer to significant differences between species in total mean height of all three treatments, small letters to significant differences among planting schemes for each single species; n.s. = non significant (GLM, LSD post hoc test,  $p < 0.05$ ).



**Fig. 3.** Mean tree height ( $\pm$ SE) and mean leaf damage ( $\pm$ SE) of *Tabebuia rosea* (A and C) and *Anacardium excelsum* (B and D) in the three different planting schemes unprotected monoculture ( $\blacktriangle$ ), unprotected mixture ( $\odot$ ) and insecticide-protected mixture ( $\square$ ) for each of the five replicated plots (PA1–PA5).

'tree diversity' on species performance as indicated by a significant planting scheme–plot interaction (Table 2). First, protected saplings of *T. rosea* in plot 1 exhibited much lower growth than unprotected or protected saplings in all other plots, and protected saplings in plot 5 were not benefiting from protection compared to unprotected saplings in the same plot (Fig. 3A). In *A. excelsum*, protected saplings in plots 1, 2, and 5 exhibited much lower growth performance than those in plot 3 and plot 4 (Fig. 3B). Second, saplings

of *T. rosea* growing in plot 1 showed better growth performance in mixed stands compared to monocultures, whereas in plot 4 growth in the monoculture was higher than in mixed stands (Fig. 3A). Similarly, *A. excelsum* growing in plot 5 performed better in mixed stands than in monocultures, whereas in plot 1 saplings growing in monocultures outperformed individuals planted in mixed stands (Fig. 3B).

### 3.4. Leaf herbivory

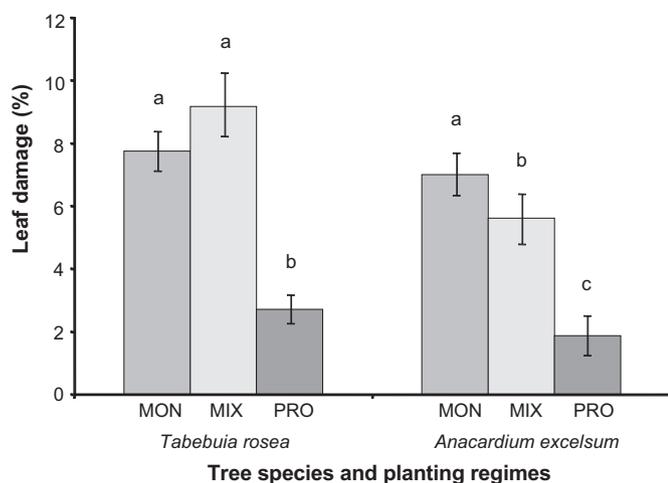
Management practices significantly affected herbivore leaf damage in both timber species analyzed (*T. rosea*:  $F_{2,159} = 41.48$ ,  $p < 0.001$ , *A. excelsum*:  $F_{2,143} = 29.04$ ,  $p < 0.001$ ), explaining 24% of the overall variation of herbivore damage in *A. excelsum* and 29% in *T. rosea*. Consistently in both species, saplings suffered less herbivory in the insecticide-protected mixed stands than in monocultures as well as in unprotected mixed stands ( $p < 0.001$  for both species) (Fig. 4). In *T. rosea*, no differences were found between monocultures and unprotected mixed stands ( $p = 0.340$ ). In contrast, leaf damage in *A. excelsum* additionally differed between mixed stands and monocultures. It was significantly lower in unprotected mixed stands than in monocultures ( $p = 0.029$ ) (Fig. 4).

Plot effects explained additional 5% of overall variation in herbivory in *T. rosea* ( $F_{4,159} = 4.69$ ,  $p = 0.001$ ), whereas no significant plot effects were found for herbivory in *A. excelsum* ( $F_{4,143} = 2.25$ ,  $p = 0.066$ ). A significant planting scheme–plot interaction in *A. excelsum* ( $F_{8,143} = 2.53$ ,  $p = 0.013$ ) revealed an influence of plots on herbivore damage in the single planting schemes for this timber

**Table 2**

Effects of tree species, planting scheme and plot on the two measured growth traits height and basal stem diameter, using a repeated measures ANOVA. The value  $\hat{\omega}_i^2$  gives the magnitude effect of the respective factor and its interactions.

	df	F	p	$\hat{\omega}_i^2$
<i>Height growth</i>				
Species	2	226.99	<0.001	0.255
Planting scheme	2	21.06	<0.001	0.023
Plot	4	97.88	<0.001	0.219
Species $\times$ planting scheme	4	0.36	0.840	–0.002
Species $\times$ plot	8	5.17	<0.001	0.019
Planting scheme $\times$ plot	8	20.42	<0.001	0.088
Error	597			
<i>Stem diameter growth</i>				
Species	2	92.47	<0.001	0.132
Planting scheme	2	20.91	<0.001	0.029
Plot	4	76.36	<0.001	0.217
Species $\times$ planting scheme	4	1.23	0.299	0.001
Species $\times$ plot	8	4.93	<0.001	0.023
Planting scheme $\times$ plot	8	20.22	<0.001	0.111
Error	597			



**Fig. 4.** Herbivore damage (mean  $\pm$  SE) of mature leaves of *Tabebuia rosea* and *Anacardium excelsum* two years after establishment. Saplings were planted in monocultures (MON), in 3-species-mixtures (MIX) or in 3-species-mixtures protected by insecticides (PRO). Contrasting letters refer to significant differences among conspecific trees growing in different planting schemes (GLM, LSD *post hoc* test,  $p < 0.05$ ).

species. No significant planting scheme–plot interaction was found for herbivory patterns in *T. rosea* ( $F_{8,159} = 1.84$ ,  $p = 0.074$ ). Referring to unprotected stands, saplings of both species growing in plot 1 suffered higher herbivory in the mixed planting scheme than in the monoculture (Fig. 3C and D). In contrast, saplings of both *T. rosea* and *A. excelsum* in plot 3 exhibited higher leaf damage in monocultures than in mixed stands. In plot 2, leaves of *T. rosea* saplings were more heavily injured in monocultures than in mixed stands, whereas the opposite was found in plots 4 and 5, with higher herbivory in the mixed planting scheme compared to the monocultures (Fig. 3C). In contrast, *A. excelsum* suffered higher leaf damage in the monocultures than in the mixed stands in plots 3 and 4 (Fig. 3D).

## 4. Discussion

### 4.1. Effects on tree survival

Timber tree survival appeared to be strongly influenced by species-specific traits and by local site conditions, which was expressed by differing survival rates among the single plots for *A. excelsum* and *C. odorata*. No effects on tree survival were found for the management practices ‘insecticide treatment’ and ‘tree diversity’.

Survival of *T. rosea* in our plantation is in line to former studies in Sardinilla (Potvin and Gotelli, 2008). Regarding survival data of *T. rosea* from other studies in the area of nearby Barro Colorado Island, our results are comparable to findings from forests (Condit et al., 1995; Welden et al., 1991), or showed a 30% higher survival than reported from other mixed plantation systems (Wishnie et al., 2002). In contrast, the same studies (except Wishnie et al., 2002) reported higher survival for *A. excelsum* and particularly for *C. odorata*. This finding suggests that *T. rosea* may have a high aptitude to survive across differing local (plot heterogeneity) and larger-scaled environmental conditions (forest and plantation), whereas successful establishment of *A. excelsum* and *C. odorata* is restricted to a narrower range of environmental properties such as water availability and soil quality (Fournier, 2003; Gerhardt, 1998; Plath et al., 2011).

### 4.2. Effects on tree growth

Growth performance of newly established timber trees was clearly affected by ‘insecticide treatment’ but not by ‘tree diversity’. Small-scale plot heterogeneity had strong direct effects on growth performance, and it also influenced the effects of the two studied management practices on tree growth.

Sapling growth was significantly higher (*T. rosea*, *A. excelsum*) in the insecticide-protected stands than in unprotected monocultures and mixed stands. This finding indicates that the general finding of negative effects of insect herbivores on tree growth (Coley and Barone, 1996; Nair, 2007) also applies to timber seedlings newly established on former pastures. Hence, it supports the farmers’ perception that insects play a major role for a successful establishment of native timber trees on former pastures (Garen et al., 2009).

The similar growth performance of establishing timber trees in monocultures and mixed stands suggests that the selected species neither benefited from complementary interactions nor were they impaired by intra- or interspecific competition during the establishment phase. The expression of complementary and competitive interactions in tree stands generally depends on species-specific plant traits, the combination of planted species and the availability of limiting resources at a planting site (Forrester et al., 2005; Grant et al., 2006; Rothe and Binkley, 2001). It may become more important with increasing resource utilization during tree development (Delagrange et al., 2008; Forrester et al., 2006; Stanley and Montagnini, 1999). This assumption is supported by findings from a five-years old plantation at the same study site in Sardinilla (Potvin and Gotelli, 2008; Potvin and Dutilleul, 2009). The study revealed that trees growing in varying 3-species mixtures (comprising one to three of our study species; for details see Healy et al., 2008) exhibited enhanced tree growth and productivity, respectively, compared to monocultures. However, Potvin and Gotelli (2008) focused on the overall effect of different diversity levels of functional groups rather than on species-specific plant traits and the related development under certain combinations. Further studies reported that the effect of tree diversity on growth performance may be positive (Erskinie et al., 2006) or negative (Firn et al., 2007), and it often appears to be substantially associated to differential species performance. That is, some species may grow better in mixed stands, whereas others might exhibit better growth performance in monocultures than in mixtures (Piotto et al., 2003; Redondo-Brenes and Montagnini, 2006).

Small-scale heterogeneity of site conditions strongly affected growth performance as was expressed by significant differences in growth among plantation plots at the same study site. The overall comparisons between species and plot effects on sapling growth revealed that soil moisture (and presumably related soil characteristics) may influence tree growth, as decreasing tree height among the plots (PA3, PA4 > PA2, PA5 > PA1) generally corresponded to increasing soil moisture (PA3 < PA2, PA4, PA5 < PA1) (see also Delagrange et al., 2008; Healy et al., 2008; Plath et al., 2011). Furthermore, growth performance might be influenced by soil pH, as all tree species showed lowest growth in plot 1, characterized by lowest soil pH values. Concomitant vegetation in this regularly mown plot consists only of a short grass- and herb-layer, without the tall grasses and woody successional vegetation found in all other plots, and comes close to actively used pastures. The relatively low pH value might be attributed to this vegetation type, as is described for other tropical alfisols, where vegetation-removal before cultivation affected soil properties and resulted in decreased soil pH (Lal, 1987).

Besides the direct impact of small-scale environmental heterogeneity on tree growth, strong planting scheme–plot interactions in our study suggest that small-scale environmental heterogeneity may (1) lead to differing effectiveness of plant protection by insect

ticides (Felsot and Lew, 1989; Harris, 1972) and (2) contribute to variable outcomes of mixed versus pure planting schemes (Fig. 3) (Piotto, 2008; Rothe and Binkley, 2001).

First, small-scale heterogeneity of site conditions strongly influenced the effects of 'insecticide treatment', expressed by significant variation in growth performance of insecticide-protected saplings among plots of both *T. rosea* (Fig. 3A) and *A. excelsum* (Fig. 3B). These findings suggest that small-scale environmental conditions may affect relevant herbivory effects and that insecticide treatment does not necessarily enhance tree performance and productivity (Grafton-Cardwell et al., 1998; Wylie, 2001), but that specific environmental conditions have to be met. Second, small-scale environmental heterogeneity strongly influenced the effects of 'tree diversity', expressed by the finding that in some plots saplings in monoculture outperformed saplings of the same species in mixed stands, whereas in other plots saplings exhibited better growth performance in mixtures than in monocultures. Hence, intraspecific disparities of growth performance in differing tree diversity levels may occur as a consequence of individual responses to environmental conditions, and complementary and competitive interactions in both intra- and interspecific terms may depend on the interactions of several growth resources and site variables (Forrester et al., 2005; Rothe and Binkley, 2001).

#### 4.3. Effects on herbivory

Management practices and small-scale plot heterogeneity significantly affected herbivore leaf damage in *T. rosea* and *A. excelsum*. Saplings planted in the insecticide-protected mixed stands suffered significantly lower leaf damage than those growing in unprotected mixed stands and monocultures. The lower leaf damage of protected trees provides empirical evidence that protection from herbivores can improve the performance of timber trees in the first two years after establishment (Kumar et al., 2005; Powell et al., 2009). The effects of pure versus mixed planting on herbivory varied among tree species and plots. Saplings of *T. rosea* showed similar leaf damage patterns in both unprotected types of stands. In contrast, saplings of *A. excelsum* suffered higher herbivore damage in monocultures than in mixed stands. These differing results indicate that in low-diversity mixed stands, ecological interrelations underlying the resource- and the enemy-hypothesis do not necessarily promote mutual associational resistance, but may rather function species-specifically. Mixed stands might benefit *A. excelsum* by reducing the herbivore pressure, for example, via a lower host plant density ('resource hypothesis') (Jones, 2001) or quality ('specialist diet-mixing hypothesis') (Mody et al., 2007) for oligophagous species, or via an increased number and diversity of natural enemies due to a more complex and heterogeneous environment ('enemy hypothesis') (Riihimäki et al., 2005). Variation in herbivory among unprotected planting schemes was, however, not strong enough to affect tree growth performance in *A. excelsum*. Hence, none of the two species benefited from 'associational resistance' in the mixed stands in the first two years after establishment.

The strong plot effects in our study suggest that small-scale environmental heterogeneity may not only influence survival and growth performance, but might also have direct impact on a plant's tolerance to herbivory (Wise and Abrahamson, 2007) and affect plant defense characteristics (Basset, 1996; Lau et al., 2008; Molina-Montenegro et al., 2006). For example, herbivore damage to *A. excelsum* substantially varied between plots (Fig. 3D). Saplings in unprotected mixed stands may suffer lower (plots 3 and 4), similar (plots 2 and 5) or higher (plot 1) herbivory than in monocultures (Fig. 3D) (see also Koricheva et al., 2006), which was reflected by significant planting scheme–plot interactions for this timber species. Likewise, plot effects on herbivory in *T. rosea* are presumably attributable to the markedly higher overall herbivory in plot 1

compared to all other plots. Individuals of *T. rosea* growing under the unsuitable conditions in plot 1 (see above) might be more susceptible to herbivore attack due to reduced development of defense traits, and increased herbivore attack in turn might increase the impairment of the sapling (Hartley, 2002; Herms and Mattson, 1992). It is assumable that both insect herbivores and environmental conditions mutually contributed to an impeded development of *T. rosea* in plot 1.

Contrary to growth performance, survival of the timber species tested was apparently not influenced by herbivory as indicated by similar survival patterns in all planting schemes including the insecticide-protected stands. For *T. rosea* and *A. excelsum*, no pest insects are known (Fournier, 2003) that regularly kill these host plants. In contrast, *C. odorata* is highly vulnerable to infestations by the shootborer *H. grandella* Zeller (Lepidoptera, Pyralidae), and seldom escapes its severe attacks (Navarro et al., 2004; Pérez-Salicrup and Esquivel, 2008). Damage by *H. grandella* generally retards or impedes height growth of *C. odorata*, particularly in saplings and younger trees (Griffiths, 2001; Pérez-Salicrup and Esquivel, 2008; Taveras et al., 2004). Our results on survival support the assumption that *H. grandella* rarely causes the death of *C. odorata* (Newton et al., 1993), but we cannot exclude that it affected growth performance of this timber species in our study plots.

## 5. Conclusions

Our study revealed local site conditions as key determinant of successful establishment of small-scale plantations in the tropics. Local-scale environmental heterogeneity influenced species-specific survival and growth performance, effects of management practices including tree-stand diversification and insecticide treatment, as well as herbivore damage to the timber saplings. Species-specific traits and their interaction with small-scale environmental conditions appeared to be more important for tree establishment and initial productivity than tree diversification. Tree diversification showed also ambiguous effects on herbivore damage, with reduced herbivory in mixed stands compared to monocultures occurring in *A. excelsum* but not in *T. rosea*. Whereas insecticide application was not effective under all site conditions, it enhanced tree growth in the majority of cases for all studied timber species, indicating that insect herbivory is generally of relevance for timber tree establishment on former tropical pastures. The finding that tree growth may be affected by very local environmental heterogeneity illustrates problems local landholders are facing when establishing small-scale plantations. In contrast to large-scale commercial plantations, where locally reduced productivity can be balanced through more suitable spots within the same stand, small-scale landholders have to find the best solution concerning tree species and management practices for a specific restricted area disposable for reforestation activities. Smallholders aiming at establishing productive and sustainable plantations are therefore particularly reliant on information about suitable timber species and their specific site and management requirements. Although our results need to be validated for a wider range of biotic and abiotic environmental conditions, we propose *T. rosea* as a promising tree species to be considered for reforestation in the tropics, particularly in its native range in Central America.

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