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**Determinants of insect herbivory and growth of native timber trees on tropical pastures**

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"In many areas, the realm of the wet tropical forest has already changed [...] from the monotonous oil palm expanses of much of Sumatra and Borneo, the silent, overhunted forest fragments of West Africa, to the horizon-spanning cattle ranches and soy fields of Mato Grosso ('the great wood')."

Yadvinder Malhi

The productivity, metabolism and carbon cycle of tropical forest vegetation

**Für meinen Großvater, Karlhans Herrmann und meine ganze Familie**

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## 1 Summary

Across Latin America, agricultural expansion causes deforestation and land degradation. Reforestation is a promising strategy for ecosystem recovery but has to consider land-holder perspectives, especially the need for cattle herding, which is a central part of the rural Latin American economy. Reforestation of pastures with native timber- and multipurpose companion trees holds potential to reconcile the improvement of small-scale farmers livelihoods with the restoration of ecosystem services and biodiversity. Yet, successful reforestation is often hindered by lacking knowledge on ecological requirements of tree species and favorable planting systems as well as on and insect herbivory, which constitutes a severe threat to reforestation efforts in the tropics.

The present PhD study focused on bottom-up and top-down effects on insect herbivory and associated growth of native timber trees on a former pasture in Central Panama. Using the promising native Central American timber tree species *Tabebuia rosea* as focus tree, we studied tree performance in two innovative planting systems: First, the pasture afforestation system, consisting of high density plantings of *T. rosea*, *Anacardium excelsum*, and *Cedrela odorata*, planted either in monocultures, three-species mixtures, or three-species mixtures treated with insecticides during the first two years after plantation establishment. Second, the silvopastoral system, where *T. rosea* was planted at low density either solitary or surrounded by five individuals of a companion tree species, either *Guazuma ulmifolia* or the leguminose *Gliricidia sepium*. We furthermore examined the effects of planting schemes, tree characteristics and ant presence on insect herbivory on *T. rosea*.

The study revealed that directions of associational effects varied between herbivore species. The lepidopteran *Eulepte gastralis*, a key pest of *T. rosea*, responded positively to resource dilution, resulting in higher levels of infestation by this herbivore in the silvopastoral system and in mixtures of the pasture afforestation system than in monocultures of the latter planting system. As *E. gastralis* is responsible for most of the leaf damage of *T. rosea*, total herbivory was higher in mixtures than in monocultures. Contrastingly, the second most relevant herbivore on *T. rosea*, the chrysomelid beetle *Walterianella inscripta*, responded positively to resource concentration. This species was practically absent from the silvopastoral system but caused major damage on *T. rosea* monocultures. *W. inscripta* was further positively associated with tree height and leaf nitrogen content. Companion trees,

which were thought to reduce herbivory by decreasing tree apparency, did not affect herbivory on *T. rosea*. However, *T. rosea* trees growing surrounded by the companion tree *G. ulmifolia* had a lower leaf mass to area ratio, increased leaf water content, and lower  $\delta^{13}\text{C}$  than *T. rosea* trees growing surrounded by *G. sepium*, all indicating shading of *T. rosea* by *G. ulmifolia*. Concurrently, stem diameter growth of *T. rosea* trees accompanied by *G. sepium* was as high as that of solitary trees, whereas it was reduced for *T. rosea* trees growing with *G. ulmifolia*. Companion planting with *G. sepium* did not increase nitrogen content of *T. rosea* leaves.

Ant abundance was occasionally high at baits mounted to tree trunks of *T. rosea* but ants were scarce in the tree crowns, accounting for only 2% of the arthropod assemblages. The ground nesting *Ectatomma ruidum* was the most abundant ant species, and its presence at baits was negatively related to damage by *E. gastralis*. Ant exclusion, however, did not significantly affect leaf damage, although abundance of *W. inscripta* was slightly reduced on ant-excluded branches as long as *W. inscripta* population size was seasonally low.

The study further revealed that tree growth and survival were species-specific and strongly affected by small-scale environmental variation. Concordant with results from the silvopastoral system, planting schemes and associated tree neighbor identity had strong effects on tree growth in the pasture afforestation system. The direction of the effect varied with the involved species: whereas *T. rosea* and *C. odorata* benefitted from heterospecific neighbors, *A. excelsum* grew better in monocultures. Early insecticide treatment benefitted *A. excelsum* and *T. rosea*, as both species displayed a larger stem diameter after five years of growth in insecticide protected mixtures than in unprotected mixtures or monocultures. Stem diameter growth of *C. odorata* was in contrast smallest in in insecticide protected mixtures. The species probably suffered from strong overshadowing by its large neighbors in this planting scheme.

Growth of *T. rosea* in monocultures and of *A. excelsum* in protected mixtures was enhanced at plot borders, suggesting the planting of small patches of native timber trees within pastures as a promising reforestation strategy in Latin America. Although herbivory proved to be a limiting factor for tree growth, negative associational effects of heterospecific tree neighbors on herbivory can be outweighed by direct positive effects on tree growth. In silvopastoral systems, planting of companion trees together with a central timber tree can support timber tree growth, depending on adequate species selection.

In conclusion we found useful information on the relevance of bottom-up and top-down effects on insect herbivores on reforested tropical pastures and on the growth performance of three native timber tree species suitable for pasture reforestation in two innovative planting systems. The findings emphasize the importance of tree-tree interactions in species mixtures and companion plantings for successful tree growth, with differing outcomes depending on species identity.

## 2 Zusammenfassung

Die steigende lokale und globale Nachfrage nach Lebensmitteln führt in Lateinamerika zu fortschreitender Ausdehnung der landwirtschaftlich genutzten Fläche, zu Entwaldung und zu raschem Verlust von Bodenqualität. Aufforstung ist ein vielversprechendes Mittel zur Wiederherstellung von Ökosystemfunktionen, wenn die Interessen von Grundbesitzern hinreichend zur Kenntnis genommen werden. Besonders wichtig in Lateinamerika ist die Berücksichtigung der Rinderhaltung, welche eine zentrale Stellung in der ländlichen Wirtschaft innehat. Eine Möglichkeit den Lebensunterhalt von Kleinbauern zu verbessern, und gleichzeitig Ökosystemfunktionen und Biodiversität wiederherzustellen, ist die Aufforstung degradierter Weideflächen mit einheimischen Bäumen. Allerdings fehlt es hierzu an Wissen über ökologische Ansprüche der einheimischen Baumarten sowie an geeigneten Pflanzsystemen. Zudem verhindert in den Tropen oftmals durch Insekten verursachte Herbivorie das erfolgreiche Anpflanzen von Bäumen.

Ziel der vorliegenden Doktorarbeit war die Untersuchung von sowohl 'Bottom-up' als auch 'Top-down' Faktoren, welche einen Einfluss auf Herbivorie und Baumwachstum auf einer ehemaligen Weide in Zentral-Panama haben könnten. Fokussierend auf die vielversprechende einheimische Baumart *Tabebuia rosea* untersuchten wir zwei speziell designte Pflanzsysteme: ein Weide-Aufforstungssystem mit hoher Pflanzdichte und ein Waldweidesystem (silvopastorales System). Im Weide-Aufforstungssystem wurden *T. rosea*, *Anacardium excelsum* und *Cedrela odorata* in Monokulturen oder 3-Arten Mischkulturen, gepflanzt. Weiterhin etablierten wir 3-Arten Mischkulturen in denen, innerhalb der ersten zwei Jahre nach dem Pflanzen Insektizide angewandt wurden. Im Hinblick auf die Etablierung von Bauminseln innerhalb von Weiden wurden sowohl Misch- als auch Monokulturen kleinflächig gepflanzt. Im silvopastoralen System wurde *T. rosea* in geringer Dichte gemeinsam mit fünf Individuen einer Begleitbaumart, entweder *Guazuma ulmifolia* oder die Leguminose *Gliricidia sepium*, gepflanzt. Hierbei wurden die Begleitbäume kreisförmig um den Zentralbaum herum angeordnet. Wir untersuchten Mortalität und Wachstum von *T. rosea*, *A. excelsum* und *C. odorata* sowie die Effekte von Pflanzsystemen, Baumeigenschaften und Ameisen auf die Herbivorie von *T. rosea*.

Die Studie hat ergeben, dass die realisierten Pflanzsysteme unterschiedlich auf verschiedene herbivore Insekten wirken. Der bedeutendste Schädling auf *T. rosea*, der Falter

*Eulepte gastralis*, reagierte positiv auf geringe Wirtsbaumdichten. Als Resultat war der Befall mit *E. gastralis* höher im silvopastoralen System und in Mischkulturen des Weide-Aufforstungssystems als in Monokulturen. Da *E. gastralis* den grössten Teil des Blattschadens verursachte, war zudem der Gesamtblattschaden höher in Misch- als in Monokulturen. Im Gegensatz dazu reagierte der zweite wichtige Schädling auf *T. rosea*, der Blattkäfer *Walterianella inscripta*, positiv auf hohe Wirtsbaumdichten. Die Spezies fehlte praktisch im silvopastoralen System, verursachte jedoch beträchtlichen Schaden in Monokulturen von *T. rosea*. Es bestand weiterhin ein positiver Zusammenhang zwischen *W. inscripta* und der Höhe der Bäume sowie dem Blattstickstoffgehalt.

Entgegen der Annahme, dass die Auffindbarkeit von Zentralbäumen für herbivore Insekten durch Begleitbäume reduziert wird, führte die Anwesenheit von Begleitbäumen nicht zur Reduktion des Blattschadens des Zentralbaumes. Allerdings deuteten Blatteigenschaften auf eine höhere Beschattung hin, wenn der Zentralbaum von *G. ulmifolia* umgeben war, als wenn er von *G. sepium* umgeben war oder alleine wuchs. Diese hohe Beschattung war möglicherweise die Ursache dafür, dass der Zentralbaum *T. rosea* besser wuchs, wenn er von *G. sepium* umgeben war oder alleine stand, als wenn er von *G. ulmifolia* umgeben war. Die Pflanzung von *G. sepium* als Begleitbaum erhöhte allerdings den Stickstoffgehalt von *T. rosea* Blättern nicht.

Obwohl die Häufigkeit von Ameisen an Ködern am Stamm von *T. rosea* gelegentlich hoch war, blieben Ameisen in den Baumkronen selten. Insgesamt betrug der Ameisenanteil in den Arthropodengemeinschaften ca. 2%. Die häufigste Ameisenart war die bodennistende Spezies *Ectatomma ruidum*. Das Vorkommen dieser Art am Köder war negativ mit dem durch *E. gastralis* verursachten Blattschaden korreliert. Der Ausschluss von Ameisen führte jedoch nicht zu einer signifikanten Verringerung des Blattschadens. Solange *W. inscripta* selten war, war das Vorkommen dieses Schädlings höher auf ameisenfreien Ästen.

Als weiteres Ergebnis dieser Arbeit stellte sich heraus, das Baumwachstum und Mortalität artspezifisch waren und stark durch Standortfaktoren beeinflusst wurden. In Übereinstimmung mit den Ergebnissen des silvopastoralen Systems beeinflussten Nachbarbäume den Fokusbaum stark. Dieser Einfluss unterschied sich jedoch von Art zu Art. *Tabebuia rosea* und *C. odorata* profitierten von heterospezifischen Nachbarn, während *A. excelsum* besser in Monokulturen wuchs. Insektizideinsatz in den ersten beiden Jahren begünstigte das Wachstum von *A. excelsum* und *T. rosea*. Der Stammdurchmesser beider

Arten war auch nach fünf Jahren noch grösser in Insektizid-behandelten Mischkulturen als in unbehandelten Mischkulturen und Monokulturen. Im Gegensatz dazu wies *C. odorata* das geringste Stammwachstum von Jahr drei bis Jahr fünf in Insektizid-behandelten Mischkulturen auf. Eine mögliche Ursache ist die Beschattung von *C. odorata* durch grosse Nachbarbäume in diesen Kulturen.

Das Wachstum von *T. rosea* in Monokulturen sowie das Wachstum von *A. excelsum* in Insektizid-behandelten Mischkulturen war besser am Rande der Plots. Dies deutet darauf hin, dass die Pflanzung kleiner Bauminseln innerhalb des Weidelandes eine aussichtsvolle Aufforstungsstrategie in Lateinamerika sein könnte. Obwohl Herbivorie das Baumwachstum stark einschränkte, können negative, den Blattschaden erhöhende Wirkungen von Nachbarbäumen durch direkte positive Wirkungen der Nachbarbäume auf das Baumwachstum kompensiert werden. In silvopastoralen Systemen kann die Pflanzung von Begleitbäumen dem Wachstum eines Zentralbaumes zuträglich sein, falls eine günstige Artenkombination gewählt wird.

Insgesamt erbrachte die vorliegende Doktorarbeit nützliche Informationen über die Bedeutung von Bottom-up und Top-down Faktoren für herbivore Insekten und das Wachstum einheimischer Baumarten in speziell für die Aufforstung von degradierten, tropischer Weideflächen designten Pflanzsystemen. Die Ergebnisse unterstreichen die Bedeutung von Interaktionen zwischen Nachbarbäumen in Mischkulturen und in silvopastoralen Systemen.

### 3 General Introduction

#### 3.1 Reforestation of degraded tropical pastures in the context of land use change

Worldwide, the area of primary forests and semi-natural forests continues to decline at a rate of - 0.13% of total forest area per year, as a result of different combinations of proximate causes and underlying driving factors (Geist & Lambin 2002, FAO 2010). In Latin America, two opposing processes of land-use change are simultaneously occurring. First, the increasing global demand for food leads to agricultural expansion and deforestation to create farmland, mostly for cash crops (*e.g.* soybean) and cattle ranching (Grau & Aide 2008, Barona *et al.* 2010). Second, rural-urban migration results in farmland abandonment that may promote ecosystem recovery on marginal lands (Rudel *et al.* 2002, Grau & Aide 2008). However, increased urban-based demands for agricultural produce further elevate the pressure on natural habitats and accelerate forest loss (DeFries *et al.* 2010). Whereas agricultural expansion sustains economic interests of corporations and small-scale farmers, resulting deforestation threatens tropical forests and grasslands that get diminished and become degraded and fragmented (FAO 2010). This causes the loss of biological diversity and ecosystem services, such as protection of soil and water resources and carbon storage (Dirzo & Raven 2003, Asner *et al.* 2010, FAO 2010). In Latin America, cattle herding comprises a central part of the economy, due to a strong international demand and its relevance for small-scale farmers, who depend on cattle as it combines low risks and financial flexibility (Wassenaar *et al.* 2007, FAO 2009b). As a result, 27% of the land area in Latin America is covered by cattle pastures (FAO 2009b).

A powerful approach to counteract negative environmental and socioeconomic effects of agricultural expansion is ecological restoration, aiming at the recovery of degraded ecosystem characteristics (Benayas & Bullock 2012). Yet, in order to be contrivable in rural landscapes, ecological restoration has to reconcile measures of conservation with agricultural use and landholder needs (Lamb *et al.* 2005). One such concept is to integrate reforestation with agricultural use in the form of agroforestry systems that combine the growing of trees and shrubs with crops or pasture or both (Dagang & Nair 2003, Murgueitio *et al.* 2011, Benayas & Bullock 2012). Particularly useful in Latin America might be carefully designed silvopastoral reforestations that combine native trees and pastures, like native timber trees

associated with multipurpose companion trees (Plath *et al.* 2011a), or woodland islets within the agricultural land (Benayas *et al.* 2008). Such integrated reforestation on farmland provides resources and habitat for plant and animal species and increases landscape connectivity (Harvey *et al.* 2006, Dorrough *et al.* 2012). Tree plantings on farms might furthermore serve as starting point for the re-establishment of woodland after the abandonment of land in the course of rural-urban migration (Muniz-Castro *et al.* 2006, Grau & Aide 2008). However, knowledge on performance of trees in silvopastoral systems or plantations is relatively poor, particularly with native timber tree species.

### **3.2 Growth performance of native timber trees in different planting systems**

One central aspect of integrated reforestation systems is the use of indigenous tree species, which additionally to their ecological function provide a variety of valuable goods and services to local communities, such as fodder and shade for cattle, fruits, firewood, timber, and medicinal uses (Garen *et al.* 2011, Hall *et al.* 2011a). Native trees support higher levels of species richness compared to plantations of exotic tree species (Bremer & Farley 2010) and can further be grown from locally available seeds, which reduces the dependence on external sources (Folgarait *et al.* 1995). To further increase benefits of reforestations, planting native tree species in mixtures might be expedient, as interactions between different species can evocate positive effects on tree performance as well as on the environment (Erskine *et al.* 2006, Kelty 2006). If tree species are combined that have a complementary resource use (*e.g.* through a stratified canopy or a differing use of soil nutrients), mixtures can lead to higher productivity (Kelty 1992). Heterospecific neighbors might furthermore actively facilitate growth through nitrogen fixation (Forrester *et al.* 2006, Daudin & Sierra 2008) and allow the harvest of different woods at varying rotations (Kelty 2006).

However, reforestation, particularly with native species, is associated with hindrances and risks. Farmers often forgo tree planting because money, labor, and time have to be invested and pasture use has to be curtailed during tree establishment (Dagang & Nair 2003). Successful establishment of native tree plantations is often also impeded by inappropriate site-species matching and lack of knowledge about species-specific ecological requirements

(Hall *et al.* 2011b). Furthermore, insect herbivory reduces growth and can increase tree mortality (Piotto *et al.* 2003, Eichhorn *et al.* 2010, Massad 2012). Hence, in order to design successful planting methods, research has to provide necessary information on ecological requirements of native tree species, favorable planting systems, and the determinants of insect herbivory.

### **3.3 Herbivory on tropical timber trees and bottom-up control of insect herbivores**

Insect herbivory has detrimental effects on tree growth in tropical reforestations (Plath *et al.* 2011b, Massad 2012) and can decrease tree survival, by injuring leaf tissue and thereby facilitating infections or by retarding tree growth and thereby causing the tree to become overshadowed (Eichhorn *et al.* 2010). Insect herbivore communities and their impacts on plants are simultaneously influenced by bottom-up factors like plant defenses and environmental characteristics and top-down factors like predation and parasitism as well as by stochastic processes (Albarracin & Stiling 2006, Shrewsbury & Raupp 2006, Barber & Marquis 2011). Therefore, host tree characteristics have to be regarded simultaneously with the biotic and abiotic tree environment to understand the ecological interactions relevant for successful growth of native timber trees (Walker & Jones 2001).

Considering bottom-up effects, plant defense strategies can be divided into two categories: resistance, which reduces the amount of damage incurred, and tolerance, which reduces the negative impact of damage on plant fitness (Leimu & Koricheva 2006). Plant resistance can be mediated by morphological and chemical plant traits that reduce herbivore preference (antixenosis) or performance (antibiosis) (Leimu & Koricheva 2006).

In addition, characteristics of neighboring plants and vegetation complexity can have tremendous impacts on herbivory of the focus plant as well as on plant traits (Agrawal *et al.* 2006, Jactel & Brockerhoff 2007, Brenes-Arguedas *et al.* 2009). Regarding tree stand diversity, heterospecific neighbors can either increase ('associational resistance') or decrease ('associational susceptibility') resistance of focal plants to herbivore attacks (Tahvanainen & Root 1972, Barbosa *et al.* 2009). Overall, associational resistance seems to be predominant as a vast majority of studies demonstrates that trees growing in mixed stands incur less damage than trees growing in monospecific stands (Letourneau *et al.* 2011). Associational resistance

might be caused by visual or chemical interference, which hinders host plant localization, feeding or ovipositioning (Finch & Collier 2000). Furthermore, species mixtures might also lower herbivore pressure by reducing host plant density or by increasing the abundance of antagonist species (Root 1973). In silvopastoral reforestations, associational resistance might be relevant where heterospecific companion trees have potential to protect the central timber tree from herbivorous insects by reducing 'tree apparency' (Barbosa *et al.* 2009). Thereby the probability of specialist herbivores to find, remain, or reproduce on the host gets diminished (Barbosa *et al.* 2009).

In contrast to associational resistance, associational susceptibility might occur when key pests are generalist feeders that benefit from a wider diet range in more diverse plant communities or if generalist herbivores spread from attractive plants in the vicinity (Brown & Ewel 1987, White & Whitham 2000, Unsicker *et al.* 2008). In any case, the biology of the herbivore insect, *e.g.* its diet breadth and mobility, plays a crucial role in determining the insects' responses to tree stand diversity (Mody *et al.* 2007, Bar-Yam & Morse 2011).

### **3.4 Top-down control of insect herbivores**

Top-down control refers to the predation pressure or parasitism exhibited by natural antagonists of herbivores, such as ants, spiders, and parasitoid wasps and dipterans. It is a process that has been described for various herbivore-plant systems and is applied in biological control of *e.g.* scale insects, lepidopteran larvae, and beetles (Schmale *et al.* 2006, Tschamtkke *et al.* 2008, Pedigo & Rice 2009, Mody *et al.* 2011). In tropical ecosystems, the strength of biological interactions, including herbivory and insect predation or parasitism, is generally more pronounced than in temperate regions (Schemske *et al.* 2009). Hence, the potential for top-down control is high.

Ants supposedly play a key role as arthropod antagonists, as they are common in almost all terrestrial tropical habitats of low- and mid-elevation (Hölldobler & Wilson 1990) and can reduce herbivory rates or herbivore density, ultimately increasing plant fitness in many cases (Rosumek *et al.* 2009). A lot of evidence derives from studies on myrmecophytic plants, which produce nesting sites and are continuously inhabited by ant colonies, and from

myrmecophilic plants, which attract ants with food sources like extrafloral nectaries (Rico-Gray & Oliveira 2007). It was also demonstrated that arboreal ants can be major general predators in tropical tree crowns (Floren *et al.* 2002). Yet, even if ant-plant interactions are routinely positive, the magnitude of the effects is variable (Chamberlain & Holland 2009). Furthermore, the protective effects of ants vary between ant species (Fraser *et al.* 2001, Mody & Linsenmair 2004) and the composition of the ant assemblage visiting the plant (Cuautle & Rico-Gray 2003). Generally, local abundance and diversity of antagonists are considered to be very important for natural top-down control of insect herbivores (Costamagna & Landis 2006, Letourneau & Bothwell 2008). For ants, abundance and diversity are related to tree cover and can be significantly lower in disturbed habitats (Philpott & Armbrecht 2006, Bihn *et al.* 2008, Bisseleua *et al.* 2009). For native timber trees planted on former tropical pastures, information on the extent and the most important determinants of top-down control of insect herbivores is scarce and the role of ants as herbivore antagonists is poorly understood.

### 3.5 Objectives

The aim of the present PhD thesis was to obtain quantitative information on effects of bottom-up and top-down control of insect herbivores on leaf damage and associated growth of native timber trees on degraded tropical pastures. Two different planting systems were established on a former pasture in Central Panama: a silvopastoral system and a pasture afforestation system. Within the silvopastoral system, trees were established at low density, either solitarily or surrounded by companion trees. Within the pasture afforestation system, trees were established in monocultures, three-species mixtures protected by insecticides, and untreated three-species mixtures. To encompass differing environmental conditions the silvopastoral system was replicated three times and the pasture afforestation system five times across the study site. Due to their ecological and economic value we selected three native Central American timber tree species for study: *Tabebuia rosea* Bertol. (Bignoniaceae), *Anacardium excelsum* (Betero and Blab. ex Kunth) Skeels (Anacardiaceae), and *Cedrela odorata* L. (Meliaceae). Because of its good growth performance and suitability for reforestation, *T. rosea* was chosen as focal tree to assess determinants of insect herbivory.

The first objective of the study was to quantify bottom-up control of insect herbivores by assessing how leaf and tree characteristics as well as planting schemes and resulting neighbor identity affect herbivore abundance and resulting leaf damage. Associational effects of stand diversity and neighbor identity on herbivory were tested by comparing herbivory and the level of specialization of key herbivores among *T. rosea* trees growing in monocultures and in three-species mixtures (chapter 4). In the silvopastoral system, associational effects were tested by comparing herbivory among solitary *T. rosea* trees and *T. rosea* trees in companion planting with either *Guazuma ulmifolia* Lam. (Malvaceae) or the nitrogen-fixing *Gliricidia sepium* (Jacq.) Kunth ex Walp. (Fabaceae) (chapter 5). To simultaneously test how association with companion trees affects tree characteristics and how tree characteristics affect herbivory, we quantified the effects of companion trees on leaf chemistry and structure as well as on phenology and related these tree characteristics to herbivore abundance and leaf damage (chapter 5).

The second objective was to experimentally investigate top-down factors influencing arthropod assemblages and herbivory of native timber trees planted on former pasture. We assessed the effects of ants on arthropod assemblages, herbivore abundance, and herbivory of *T. rosea* by recording ant abundance and diversity and by conducting an ant-exclusion experiment (chapter 6).

The third objective was to investigate the growth performance of the selected tree species in different planting schemes. Specifically, we tested in the pasture afforestation system how tree species identity, tree stand diversity, and plant protection by insecticides, applied in the first and second year of plantation establishment, affect tree survival and growth after five years (chapter 7). We furthermore compared timber tree survival and growth at plot borders to plot centers to investigate how border effects affect tree performance in small patches of trees within pastures (chapter 7). In the silvopastoral system we assessed the effects of companion trees on growth of *T. rosea* and measured  $\delta^{15}\text{N}$  and N content of *T. rosea* leaves to test whether companion planting of *G. sepium* facilitates timber tree growth through increasing the content of available nitrogen in the soil (chapter 5).

Implications of the findings for the reforestation of tropical pastures with native timber tree species are discussed in the context of a sustainable world food system

## 4 Associational resistance and associational susceptibility: specialist herbivores show contrasting responses to tree stand diversification<sup>1</sup>

### 4.1 Abstract

Heterospecific neighbors may reduce damage to a focal plant by lowering specialist herbivore loads (associational resistance hypothesis), or enhance damage by increasing generalist herbivore loads (associational susceptibility hypothesis). We tested the associational effects of tree diversity on herbivory patterns of the tropical focal tree *Tabebuia rosea* in an experimental plantation setup, which contained tree monocultures and mixed stands. We found higher herbivore damage to *T. rosea* at higher tree diversity, indicating that *T. rosea* did not benefit from associational resistance but rather experienced associational susceptibility. The specific consideration of the two dominant insect herbivore species of *T. rosea*, the specialist chrysomelid *Walterianella inscripta* and the specialist pyralid *Eulepte gastralis*, facilitated understanding of the detected damage patterns. Tree diversity exerted opposite effects on tree infestation by the two herbivores. These findings point to resource concentration effects for the chrysomelid beetle (favored by tree monoculture) and to resource dilution effects for the pyralid caterpillar (favored by tree mixture) as underlying mechanisms of herbivore distribution. A strong contribution of the pyralid to overall damage patterns in diversified stands suggests that associational susceptibility may not necessarily be related to higher abundances of generalist herbivores but may also result from specialized herbivores affected by resource dilution effects. Thus, the identity and biology of herbivore species has to be taken into account when attempting to predict damage patterns in forest ecosystems.

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<sup>1</sup> Based on Plath M, S Dorn, J Riedel, H Barrios, and K Mody (2012). *Oecologia* 169: 477-487. Author contributions: J Riedel collected and analyzed the data on leaf damage in year 3 (Fig. 4.3).

## 4.2 Introduction

Vegetation complexity and characteristics of neighboring plants may strongly affect interactions between herbivores and a focal host plant, and specific associations can either decrease or increase the susceptibility of plants to herbivores (Agrawal *et al.* 2006, Lewinsohn & Roslin 2008, Barbosa *et al.* 2009). Derived from these observations, the ‘associational resistance hypothesis’ predicts that a plant, in addition to its specific morphological and chemical defense traits (Coley & Barone 1996, Schoonhoven *et al.* 2005, Gutbrodt *et al.* 2011), might experience ‘associational resistance’ to herbivores by growing in close proximity to other plant species (Tahvanainen & Root 1972). Several factors may contribute to associational resistance, including chemical and physical interference of neighboring plant species as well as greater abundances and diversity of natural enemies (Hambäck & Beckerman 2003). In particular, host density is predicted to have strong effects on specialist herbivores as formulated in the resource concentration hypothesis (Root 1973). This hypothesis states that specialist herbivore loads increase with higher densities of the host plant in a given area unit, as specialist herbivores may locate their host plant more easily and stay longer in patches with high host plant densities.

In contrast, the ‘associational susceptibility hypothesis’ predicts that plants in diverse stands may suffer more from herbivore attack than plants in single-species stands (Brown & Ewel 1987). This phenomenon is expected to occur when the principal pests are generalist herbivores (Jactel & Brockerhoff 2007), which benefit from the broader diet range available in diverse plant communities (Unsicker *et al.* 2008). Associational susceptibility may also occur when the focal plant is a less-preferred host growing in close proximity to a highly preferred host (Atsatt & Odowd 1976), which allows a spill-over of generalist herbivores after depletion of the favored host plant (White & Whitham 2000).

Information concerning the effects of stand diversification on insect pests mainly stems from agricultural systems (Andow 1991, Tschamntke *et al.* 2005). The existing studies accounting for forest systems reveal contrasting results, demonstrating that mixed stands can suffer lower, higher, or similar pest damage compared to single-species stands (Koricheva *et al.* 2006, Jactel & Brockerhoff 2007, Kaitaniemi *et al.* 2007, Vehvilainen *et al.* 2007, Plath *et al.* 2011b). Reflecting the opposite predictions of the hypotheses on ‘associational resistance’ and ‘associational susceptibility’, these equivocal results emphasize that the net effects of

diversification in forest systems may only be understood when the spatial arrangement of the focal plant and characteristics of the principal herbivores are studied in concert. Hence, the identification of the key herbivores responsible for the damage, their level of host plant specialization, and the relative proportions of damage they cause may improve our understanding of the mechanisms that govern the direction of resource and associational effects on herbivore–plant interactions in forest systems.

Information on the biology of insect pests in forest systems can help to disentangle the causes of insect pest outbreaks, and hence, to improve the delivery of forest ecosystem services (Hambäck & Beckerman 2003, Butler *et al.* 2007, Tylianakis *et al.* 2007). Such information is particularly required for Central America, where forest plantations with native tree species are increasingly considered as an eligible strategy to mitigate the negative impacts of deforestation and land degradation (Lamb *et al.* 2005, Brockerhoff *et al.* 2008, Hall *et al.* 2011a). However, although insect pests frequently impede the successful establishment of forest plantations, the key insect species associated with tree species native to Central America are virtually unidentified to date (FAO 2009a). To protect trees from expected herbivore attacks, landholders often resort to broad-spectrum pesticides (Garen *et al.* 2009), but until now there is little evidence for the effectiveness of these products under prevailing field conditions. The widespread notion that forest monocultures are susceptible to insect pest attacks has promoted the consideration of stand diversification as sustainable, biodiversity-oriented strategy to control key insect pests in forestry systems (Lamb *et al.* 2005, Koricheva *et al.* 2006 and reference therein). However, the effects of heterospecific tree associations on infestation of a focal host tree by key herbivores have rarely been compared to effects of monocultures or to conventional protection by insecticides.

In the present study, we examined the effects of tree stand diversification on leaf herbivory (associational effects) of a focal native timber tree, *Tabebuia rosea* Bertol. (Bignoniaceae), growing in monoculture and in three-species mixtures in an experimental plantation setup in Panama. Insecticide application was used in additional treatments to achieve baseline information on reduction of herbivore damage through conventional protection measures. We concurrently identified the principal herbivore for each stand type, determined its level of host plant specialization and assessed the effect of individual stand types on the herbivores' densities (resource effects) and on related herbivore impact on *T. rosea*.

According to the described resource-related associational effects on specialist and generalist herbivores, we expected to identify one or several specialist herbivores as key herbivores in the monocultures. The specialist herbivores were expected to accumulate in higher densities in monocultures compared to mixed stands. We further expected to identify one or several generalist key herbivores in mixed-species stands, occurring in higher densities in mixed stands compared to monocultures. We hypothesized that specialist key herbivores contribute most to overall damage of *T. rosea* in monocultures, and that generalist herbivores are responsible for principal damage in mixed plantings.

Specifically, we addressed the following questions: (1) Does tree stand diversification affect herbivory of *T. rosea*? (2) Does the identity of key herbivores and their level of host specialization differ among stand types? (3) Do different stand types affect the densities of the specific key herbivores and their contribution to herbivory of *T. rosea*?

## **4.3 Materials and methods**

### **4.3.1 Study site and planting design**

Three tree species native to Central America were planted in an experimental planting system on former pasture in Sardinilla, Province Colon, Central Panama (9°19'30" N, 79°38'00"W, elevation around 70 m a.s.l.) in August 2006 (for details on study site, see Plath et al. (2011a)). The selected tree species were *Tabebuia rosea*, *Anacardium excelsum* (Bertero and Balb. ex Kunth) Skeels (Anacardiaceae) and *Cedrela odorata* L. (Meliaceae). The three tree species co-occur in natural Panamanian forest ecosystems (Croat 1978), and are of regional economical importance because of their suitability for reforestation activities and as valuable timber (ITTO 2006, Wishnie *et al.* 2007, van Breugel *et al.* 2011).

Potted seedlings of each tree species were raised in a PRORENA (Proyecto de Reforestación con Especies Nativas) nursery for 3 months before being planted on the pasture. To support tree establishment, 15 g of 12-72-12 N-P-K granular fertilizer was applied 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. Concomitant

vegetation in the plots was trimmed with machetes to 10 cm height every 3 months during the rainy season (average vegetation height across plots before cutting  $21 \pm 5$  cm) to allow for unconstrained localization of the host trees by insect herbivores (average tree height across plots at study onset: *T. rosea*  $84 \pm 2$  cm, *A. excelsum*  $55 \pm 2$  cm, *C. odorata*  $46 \pm 1$  cm).

Seedlings of *T. rosea*, *A. excelsum* and *C. odorata* were planted in stands of 36 trees, using a standardized 6 x 6 Latin square design with a planting distance of 2 m. Tree individuals were arranged in five planting schemes: (1–3) monocultures for all three timber species, (4) 3-species mixed stands, and (5) 3-species mixed stands protected by the insecticide cypermethrin (pyrethroid, Arribo EC 20 or 6 EC, 1.2 g/l spray solution; applied biweekly to the foliage) and the insecticide/nematicide carbofuran (carbamate, Furadan 10 GR, 5–25 g/tree depending on the effective canopy area; applied bimonthly to the soil). The five planting schemes were arranged at one locality, which defined a coherent plot. This plot was replicated five times at different locations across the study site.

#### 4.3.2 Insect survey

Insect counts were conducted for all timber trees on a biweekly basis from April 2007 (year 1) to April 2008 (year 2). No survey was conducted at the end of December of year 1 and in the middle of February of year 2. Insect abundance was assessed by a visual census of all insects on a tree's trunk and every leaf during day and night within a 24-h period. Detected individuals of adult Coleoptera and of larval Lepidoptera were assigned to morphospecies, which were deposited in a reference collection created on the basis of previous survey samplings. Individuals of species sampled for the first time, or individuals not immediately assignable to a morphospecies, were collected, preserved in 70% ethanol, and allocated to the reference collection.

The sequence of planting schemes surveyed within each plot was changed randomly. All 36 trees were sampled in the unprotected mixed and in the insecticide-protected mixed stands (12 individuals per tree species). In the monoculture stands, surveys were carried out on 12 trees for each timber species, which were randomly selected before starting the insect assessments. To obtain planting positions comparable to the mixed stands, six trees from the

edge and six trees from the inner area were investigated. The same tree individuals were surveyed during the whole study period. According to this sampling scheme, a total of 540 trees were surveyed at the beginning of the investigation, with 60 trees per species in each of the three planting schemes containing a particular tree species. The number of surveyed trees declined over time as a consequence of tree mortality (*T. rosea* = 1.5%, *A. excelsum* = 30.4%, *C. odorata* = 54.1%), which was not affected by planting schemes or herbivore impact (Plath *et al.* 2011b). Final analyses included all trees that survived until the end of the sampling period.

#### 4.3.3 Identification of key herbivores and their feeding specialization

Key herbivores were defined as the most abundant herbivore species found for each unprotected planting scheme on the focal host tree *T. rosea*. Species identification relied on comparisons of the collected morphospecies with reference collections at Panamanian institutions (Fairchild Museum, University of Panama, Smithsonian Tropical Research Institute), and on consultation with experts for the respective taxonomic groups. Key herbivores were confirmed to feed on *T. rosea* by determining their acceptance of *T. rosea* in no-choice feeding experiments. Feeding tests were conducted by offering leaf discs (18 mm diameter) of one young and one mature leaf of the same tree individual in a Petri dish (90 mm diameter; inlaid with a moistened filter paper) to single individuals of the key herbivore species for 24 h. Leaf discs were replaced 12 h after initiation of the test with fresh discs from another tree individual. Each herbivore individual (*i.e.* adult Coleoptera or larval Lepidoptera) was exclusively used for a single feeding test.

As a measure of specialization, we determined the acceptance of the two remaining study tree species (*A. excelsum* and *C. odorata*) and of two tree species occurring across the study site in the vicinity of the experimental tree stands (*Gliricidia sepium* (Jacq.) Kunth ex Walp (Fabaceae) and *Guazuma ulmifolia* Lam. (Sterculiaceae)) by the key herbivores. The studied trees belong to five phylogenetically distant plant families in four plant orders (*T. rosea*: Scrophulariales; *A. excelsum*, *C. odorata*: Sapindales; *G. sepium*: Fabales; *G. ulmifolia*: Malvales). In the context of our study, we classified the key herbivores as specialist

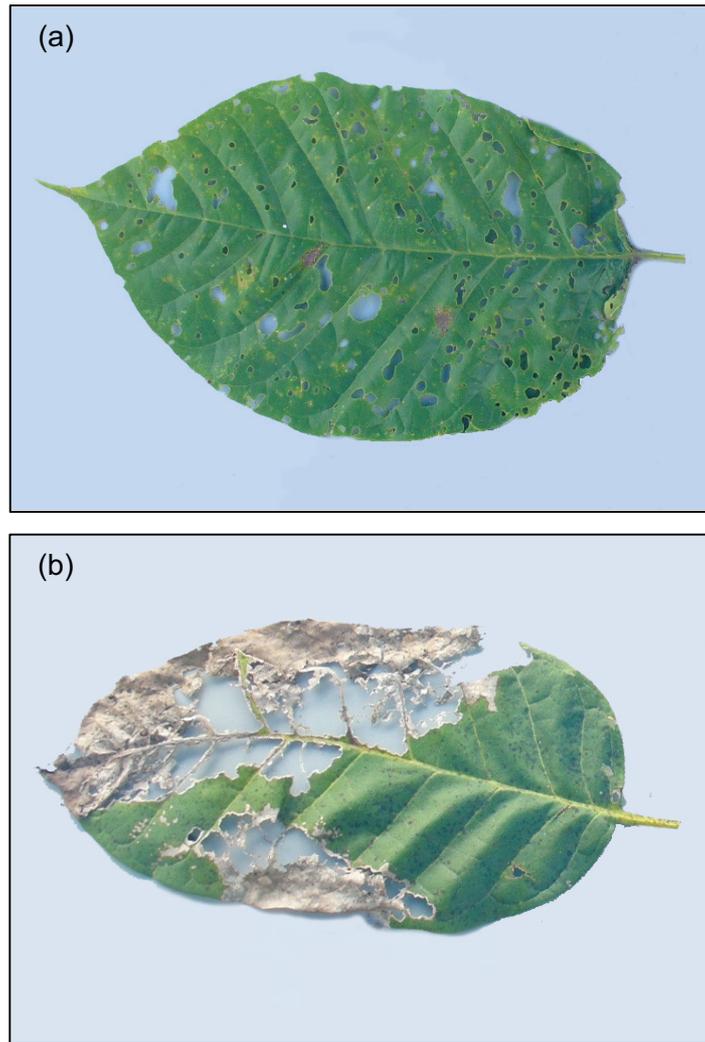
herbivores of *T. rosea* when (1) they exclusively fed on *T. rosea* leaves and rejected to feed on any of the four other tree species, and (2) more than 95% of all recorded individuals were found on *T. rosea*. In comparison, we categorized herbivores as generalists when they fed on two or more of the five tree species (see also Basset *et al.* 1996, Novotny *et al.* 2002, Unsicker *et al.* 2006). We used this definition of specialization to assess whether the herbivores may profit from our specific tree stand diversification design by a broadened diet range, which may apply for species using at least two of the study trees but not for species restricted to *T. rosea*

#### 4.3.4 Leaf herbivory

Leaf damage was measured at the end of the growing season in December of year 1 and reassessed in December of year 3 (2009). In year 1, the first 15 fully developed leaves in the top foliage layer were selected from each *T. rosea* individual and damage was quantified for the complete mature leaves (separated into five leaflets), which were characterized by dark green color and high toughness compared to soft young leaves. In total, 1,862 leaves were analyzed (monocultures:  $N = 642$ ; unprotected mixed stands:  $N = 625$ ; insecticide-protected mixed stands:  $N = 595$ ), with an average of 10.8 leaves per tree individual. No significant differences in the number of analyzed leaves per tree were found among the individual stand types (Kruskal–Wallis:  $H_{2,172} = 1.39$ ,  $P > 0.05$ ). Leaves were photographed with a digital camera (Panasonic, Lumix DMC-LZ3) without removal from trees using a standardized, established procedure (Mody & Linsenmair 2004). Leaves were spread out on a gray-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 in the shade of a tarpaulin. For high-throughput quantitative analysis of leaf damage, digital photographs were analyzed using a custom-built software tool (Plath *et al.* 2011b). Individual leaf damage was calculated as the percent leaf area removed from the total leaf area by herbivores, including leaf fragments discolored due to herbivore feeding (for details, see Plath *et al.* 2011b). Reassessment of leaf damage in year 3 was conducted for 60 *T. rosea* individuals (average tree height  $339 \pm 13$  cm), selected by randomly choosing six trees from each monoculture and unprotected mixed stand per plot. From each selected tree, ten leaves

were haphazardly collected, and leaf damage was determined for the fourth leaflet of all mature leaves (five to ten mature leaves, average 7.5 leaves per tree; damage to the fourth leaflet was found to be representative for damage to all five leaflets, J. Riedel unpublished data). Leaflets were photographed with a digital camera (Canon Powershot A630) as described above, with the exception that leaves had been removed from the tree and photographing took place in the laboratory. Digital photographs were analyzed using the graphics package Adobe Photoshop (v.12.0.4). Leaf damage was quantified by referring to the pixel number of reference areas, which were photographed together with the leaves. The missing parts of the leaflets were accordingly determined, after outlining them in the photograph. The percentage area removed by herbivores was computed from missing and total leaf area. In both year 1 and year 3, values of individual leaf damage were averaged for every tree. Leaves that were completely eaten or dropped after herbivore damage were not considered.

To estimate the contribution of key herbivore groups to total leaf damage, each leaf was screened for prevailing damage types, which were small-hole feeding by chrysomelids (Fig. 4.1a) and large-scale skeletonization by lepidopteran larvae (Fig. 4.1b), in year 1. The contribution of each damage type to total damage was then assessed by assigning the percent damaged leaf area that each type contributed to total damaged leaf area to 1 of 7 categories: 0 = no contribution, 1 = 1–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–99%, 6 = 100% contribution to total damage. Damage that could not be assigned to either damage type was considered as a third type of damage (*i.e.* ‘damage by other herbivores’). The proportion of leaf damage attributed to each damage type was averaged for each studied tree.



**Fig. 4.1** Symptoms of damage by **a** the chrysomelid beetle *Walterianella inscripta* and **b** the pyralid caterpillar *Eulepte gastralis* on leaflets of *Tabebuia rosea*.

#### 4.3.5 Data analysis

Herbivore damage was arcsin-transformed to account for non-normal or heteroscedastic error terms in the analyses. The number of individuals of each key herbivore was calculated for each tree individual and survey event, using the average insect number found in day and night samples to consider possible double counts of less mobile herbivores such as caterpillars. As a measure of tree infestation by the key herbivores, herbivore density was assessed as the total individual number per tree found in all surveys until mid-December of year 1, divided by the respective total leaf number at that time. Leaf counts considered

mature and fully expanded young leaves. Herbivore density was log-transformed after adding 0.01 to each value to retain zero counts in the analysis (Zuur *et al.* 2009).

The effects of planting schemes on herbivore damage were assessed using linear mixed effect models with herbivore damage and herbivore densities, respectively, as response variables, planting schemes as fixed factors and plot as a random factor, accounting for the nesting of planting schemes within plots. The effect of planting schemes on herbivore densities was tested in two stages. First, the effect of insecticide application was analyzed by comparing infested (density > 0) and non-infested tree individuals (density = 0) for the three planting schemes to consider the zero-inflated count data within the insecticide-protected mixed stands. Binomial data were analyzed in a generalized linear mixed effect model using penalized quasi-likelihood. Second, the effects of stand diversification (monocultures vs. unprotected mixed stands) on herbivore density were subsequently analyzed using a linear mixed effect model. To evaluate the potential impact of tree architecture on herbivore densities, tree height (measured at the end of the growing season in December of year 1) was used as a covariate. False discovery rate control was applied for multiple tests following linear mixed effect models (Verhoeven *et al.* 2005). Pearson correlation analyses were conducted to test the relationship between tree height and herbivore densities of the identified key herbivores as well as between herbivore densities and overall herbivore damage in each planting scheme. The relationship between overall leaf damage and key herbivore density was assessed by Spearman rank correlation analyses. Correlation analyses included all trees that survived until the end of the study period in the individual planting schemes (monocultures:  $N = 59$ ; unprotected mixed stands:  $N = 60$ ; insecticide-protected mixed stands:  $N = 59$ ). The effect of tree mortality (*i.e.* decreased tree density) on herbivore densities in the individual planting schemes was tested with Pearson correlations, relating the total number of living tree individuals (*i.e.* *T. rosea* individuals in monocultures with  $N = 33$ – $36$ , and individuals of all three timber species in the unprotected mixed stands with  $N = 22$ – $32$ ) to the respective mean herbivore densities for each planting scheme and plot at the end of the growing season in December of year 1 (see supplementary material 4.1). The effects of planting schemes on the contribution of the key herbivores to total herbivore damage were compared using Kruskal–Wallis tests followed by Dunn’s *post hoc* tests.

Linear mixed effect models were performed using R 2.13.0 (2011; The R Foundation for Statistical Computing). Non-parametric *post hoc* tests were computed with SsS 1.1a (1998;

Rubissoftware, Eichenau, Germany). All remaining statistical analyses were conducted with SPSS 19.0.0 for Mac OS X (2010; IBM SPSS Statistics, Chicago, IL, USA). For clarity, all figures show untransformed data.

## 4.4 Results

### 4.4.1 Identification of key herbivores

We identified two key herbivores, which were numerically dominant on *T. rosea* across the unprotected planting schemes: the chrysomelid beetle *Walterianella inscripta* Jacoby ( $N = 2,209$  adult individuals; no larvae occurred on the shoot system of *T. rosea*) and the pyralid caterpillar *Eulepte gastralis* Guenée ( $N = 2,036$ ), representing 36.8% of all beetles and 88.9% of all caterpillars observed during all surveys on the three timber species. The total abundances of *W. inscripta* and *E. gastralis* significantly differed between the timber species (*W. inscripta*:  $\chi^2_2 = 6,450.0$ ,  $P < 0.001$ ; *E. gastralis*:  $\chi^2_2 = 6,090.0$ ,  $P < 0.001$ ), and specimens of both herbivore species were almost exclusively found on *T. rosea* (*W. inscripta*  $\geq 98.7\%$ ; *E. gastralis*  $\geq 99.9\%$ ). Both *W. inscripta* and *E. gastralis* were classified as specialist herbivores of *T. rosea* according to the given definition (see "Materials and methods"). All tested individuals of either herbivore (*W. inscripta*:  $N = 15$ ; *E. gastralis*:  $N = 14$  per tree species) that showed feeding activity ( $N = 13$  for each species) fed exclusively on *T. rosea*.

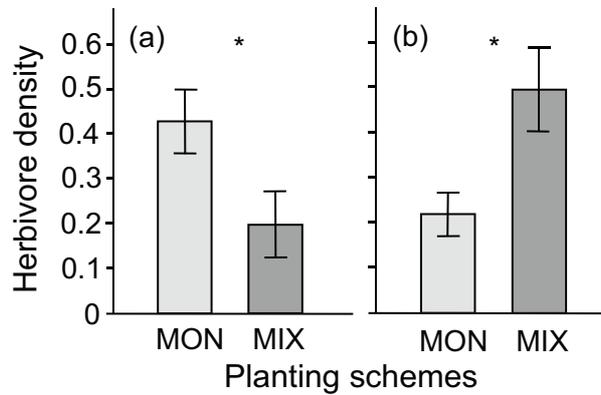
Across all individual stand types, total individual numbers of *W. inscripta* and *E. gastralis* exceeded individual numbers of the third most abundant herbivore species that was found and confirmed to feed on *T. rosea* by factors of 8 and 9, respectively. This third-ranked species was another chrysomelid of the genus *Walterianella* ( $N = 245$ ). *W. inscripta* was the most abundant herbivore species in the monocultures ( $N = 1,629$ ), exhibiting three times higher individual numbers than *E. gastralis* ( $N = 556$ ), the second most abundant herbivore in this planting scheme. In contrast, *E. gastralis* was the most abundant herbivore in the unprotected mixed stands ( $N = 1,432$ ), where *W. inscripta* was the second most abundant herbivore ( $N = 473$ ). In the protected stands, both herbivores were rare (*W. inscripta*:  $N = 107$ ; *E. gastralis*:  $N = 48$ ).

Both *W. inscripta* and *E. gastralis* showed a strong temporal variation in abundance. Either species was rare at the beginning of the rainy season (total  $N < 10$  individuals). Abundance of *W. inscripta* peaked in the middle of the rainy season (September/October), and then gradually decreased until complete disappearance in the dry season (January). Abundance of *E. gastralis* peaked in October and again in January of the following year. Subsequently, *E. gastralis* was found in low numbers until the end of the study period (see also supplementary material 4.2).

#### 4.4.2 Tree infestation

The number of tree individuals infested by *W. inscripta* or *E. gastralis* was significantly different among planting schemes (*W. inscripta*:  $F_{2,8} = 14.86$ ,  $P = 0.002$ ; *E. gastralis*:  $F_{2,8} = 29.19$ ,  $P < 0.001$ ) (see also supplementary material 4.3). It was significantly lower in the insecticide-protected mixed stands (*W. inscripta*:  $N = 24$ ; *E. gastralis*:  $N = 4$ ) than in the monocultures (*W. inscripta*:  $N = 55$ ,  $P = 0.001$ ; *E. gastralis*:  $N = 48$ ,  $P < 0.001$ ) and in the unprotected mixed stands (*W. inscripta*:  $N = 48$ ,  $P = 0.005$ ; *E. gastralis*:  $N = 55$ ,  $P < 0.001$ ). The number of infested trees was not different for monocultures and unprotected mixed stands for either herbivore species ( $P < 0.05$ ).

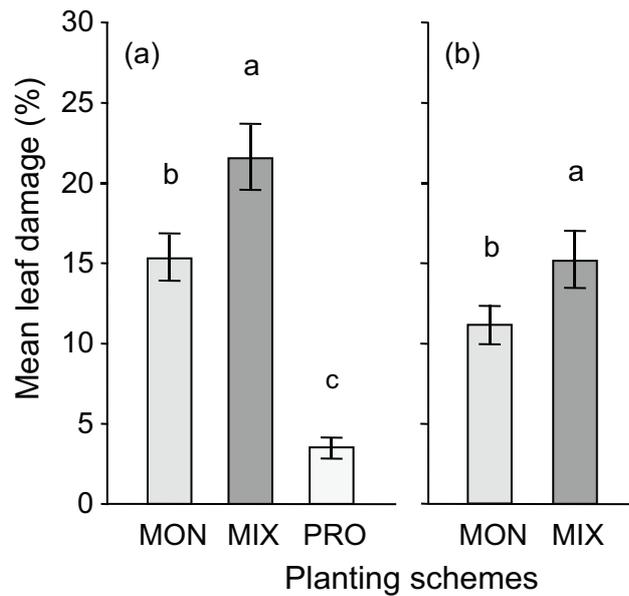
Densities of *W. inscripta* and *E. gastralis* on *T. rosea* were significantly different among monocultures and unprotected mixed stands. For *W. inscripta*, density was significantly higher in the monocultures than in the unprotected mixed stands ( $F_{1,4} = 12.60$ ,  $P = 0.024$ ) (Fig. 4.2a; see also supplementary material 4.4). Tree height strongly influenced the densities of *W. inscripta* ( $F_{1,108} = 10.55$ ,  $P = 0.002$ ). Tree height was positively correlated to the densities of *W. inscripta* in the monocultures ( $R = 0.36$ ,  $P = 0.005$ ) and in the unprotected mixed stands ( $R = 0.36$ ,  $P = 0.005$ ). In contrast, density of *E. gastralis* was significantly higher in the unprotected mixed stands than in the monocultures ( $F_{1,4} = 8.49$ ,  $P = 0.044$ ) (Fig. 4.2b; see also supplementary material 4.4). Tree height had no significant influence on the density of *E. gastralis* ( $F_{1,108} = 0.06$ ,  $P = 0.809$ ). Tree mortality showed no significant correlation with the density of either herbivore in the monocultures (*W. inscripta*:  $R = -0.422$ ,  $P = 0.479$ ; *E. gastralis*:  $R = 0.242$ ,  $P = 0.695$ ) or in the unprotected mixed stands (*W. inscripta*:  $R = -0.060$ ,  $P = 0.924$ ; *E. gastralis*:  $R = 0.378$ ,  $P = 0.530$ ).



**Fig. 4.2** Densities (mean  $\pm$  SE) of **a** *Walterianella inscripta* beetles and **b** *Eulepte gastralis* caterpillars on the host tree *Tabebuia rosea* growing in monocultures (MON), and in 3-species mixed stands (MIX). Densities were calculated as total number of individuals per leaf for either herbivore. Tree number per planting scheme: MON = 59, MIX = 60. Linear mixed effect model, \* $P < 0.05$ .

#### 4.4.3 Leaf herbivory and contribution of herbivore species to damage patterns

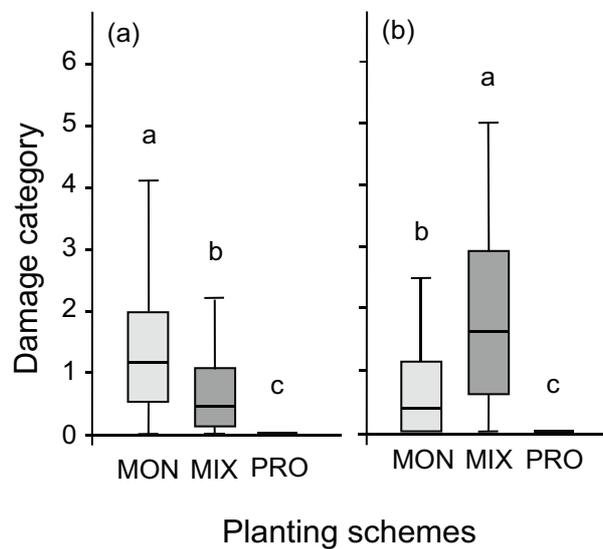
Leaf damage to *T. rosea* was significantly affected by planting schemes in year 1 and year 3 (year 1:  $F_{2,8} = 61.38$ ,  $P < 0.001$ ; year 3:  $F_{1,4} = 9.27$ ,  $P = 0.038$ ) (Fig. 4.3). In year 1, damage was significantly higher in the unprotected mixed stands than in the monocultures ( $P = 0.037$ ). Damage was lowest in the insecticide-protected mixed stands, which differed significantly from the monocultures and from the unprotected mixed stands (for both  $P < 0.001$ ) (Fig. 4.3a). Similarly to year 1, leaf damage in year 3 was significantly higher in the unprotected mixed stands than in the monocultures ( $P = 0.038$ , see above) (Fig. 4.3b).



**Fig. 4.3** Herbivore damage (mean  $\pm$  SE) of mature leaves of *Tabebuia rosea* at the end of the growth period in December of **a** year 1 and **b** year 3. Saplings of *T. rosea* were planted in monocultures (MON), in 3-species mixed stands (MIX), or in 3-species mixed stands protected by insecticides (PRO). Contrasting letters above bars refer to significant differences among conspecific trees growing in different planting schemes (after false discovery rate control of pairwise comparisons in (a); linear mixed effect model,  $P < 0.05$ ). Number of analyzed leaves per planting scheme: year 1: MON = 642, MIX=625, PRO=595; year 3: MON=219, MIX=198. PRO exclusively assessed for year 1.

The prevailing damage types on *T. rosea* leaves, small hole feeding damage and large-scale skeletonization, were assigned to *W. inscripta* and to *E. gastralis*, respectively, as only very few individuals of comparable hole-feeders or other potential skeletonizers were observed during the whole study (see above: "Identification of key herbivores"; and M. Plath, personal observation). An analysis based on this classification revealed that both herbivores significantly contributed to herbivory, but to different extents in the individual stand types. The contribution of *W. inscripta* to overall leaf damage was significantly different between the three planting schemes ( $H_{2,175} = 70.10$ ,  $P < 0.001$ ). It was significantly higher in the monocultures than in the mixed stands ( $Q = 2.77$ ,  $P < 0.05$ ) (Fig. 4.4a). In the insecticide-protected mixed stands, leaf damage inflicted by *W. inscripta* was significantly lower than in the monocultures ( $Q = 8.23$ ,  $P < 0.05$ ) and in the unprotected mixed stands ( $Q = 5.36$ ,  $P < 0.05$ ). Correspondingly, overall leaf damage was positively correlated with the density of *W. inscripta* in the monocultures ( $R_s = 0.30$ ,  $P = 0.024$ ). No significant correlation was found in the unprotected ( $R_s = 0.10$ ,  $P = 0.450$ ) and in the protected mixed stands ( $R_s = -0.10$ ,  $P =$

0.461). The contribution of *E. gastralis* to overall leaf damage also differed significantly between the three planting schemes ( $H_{2,175} = 78.94, P < 0.001$ ). In contrast to damage by *W. inscripta*, it was significantly higher in the unprotected mixed stands than in the monocultures ( $Q = 3.85, P < 0.05$ ) (Fig. 4.4b). In the insecticide-protected mixed stands, leaf damage inflicted by *E. gastralis* was significantly lower than in the monocultures ( $Q = 5.02, P < 0.05$ ) and in the unprotected mixed stands ( $Q = 8.85, P < 0.05$ ). Correspondingly, overall leaf damage in the unprotected mixed stands was positively correlated with the density of *E. gastralis* ( $R_s = 0.41, P < 0.001$ ), whereas no such correlation was found in the monocultures ( $R_s = 0.11, P = 0.410$ ) and in the protected mixed stands ( $R_s = 0.19, P = 0.161$ ).



**Fig. 4.4** Average contribution of **a** *Walterianella inscripta* beetles and **b** *Eulepte gastralis* caterpillars to total damage of mature leaves of the host tree *Tabebuia rosea* growing in monocultures (MON), in 3-species mixed stands (MIX), or in 3-species mixed stands protected by insecticides (PRO). Herbivore damage was measured in categories: 0 = no contribution, 1 = 1–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–99%, 6 = 100% contribution to total damage. Box-whisker plots show minimum, first quartile, median, third quartile and maximum. Outliers and extreme values are not shown for clarity. Contrasting letters above box-plots refer to significant differences among the three planting schemes (Kruskal–Wallis test, Dunn’s *post hoc* test,  $P < 0.05$ ). Number of analyzed leaves per planting scheme: MON = 642, MIX = 625, PRO = 595.

## 4.5 Discussion

Host tree association significantly affected herbivore damage as well as the densities and impact of key herbivores on the tropical timber tree *T. rosea* in an experimental plantation setup on degraded pasture. Two findings shed new light on ecological hypotheses. First, contrary to the ‘resource concentration hypothesis’, we found that certain specialist herbivores may respond positively to resource dilution and accumulate on host trees growing in heterospecific stands rather than in conspecific stands. Second, contrary to the ‘associational susceptibility hypothesis’, higher herbivore damage to a focal host tree in heterospecific stands compared to conspecific stands is not necessarily related to generalist herbivores. In fact, it may substantially depend on a single or few specialist herbivores.

The finding that overall herbivore damage was higher in mixed stands than in monocultures indicates that *T. rosea* did not benefit from associational resistance but rather experienced associational susceptibility at higher tree diversity. This result contradicts reports from other systems, where a decrease in herbivory was noted with increasing plant diversity both for herbs (Andow 1991, Unsicker *et al.* 2006) and for trees (Jactel & Brockerhoff 2007, Kaitaniemi *et al.* 2007, Sobek *et al.* 2009). Many studies attribute high herbivore damage in monocultures to specialist herbivores and consider resource concentration effects (Root 1973) as an explanation for the detected herbivory patterns (see reviews of Andow 1991, Jactel *et al.* 2005). The resource concentration hypothesis predicts that specialist herbivores accumulate in large and dense patches of host plants and that, in turn, damage by specialist herbivores decreases with increasing plant diversity.

However, a positive relationship between tree diversity and herbivore damage as found in our study was also reported in some recent studies on herbivore–tree interactions (Vehvilainen *et al.* 2007, Schuldt *et al.* 2010). In these studies, the positive relationship between tree diversity and herbivore damage was assumed to reflect an increased impact of generalist herbivores, which exceeds the impact of specialist herbivores in monocultures as predicted by the hypothesis of ‘associational susceptibility’ (White & Whitham 2000, see also Jactel & Brockerhoff 2007). Referring to these assumptions, and considering the herbivory patterns found in our study, the higher herbivore damage in the (unprotected) mixed stands was expected to reflect an increased impact of generalist herbivores,

counterbalancing the impact of specialist herbivores in the monocultures.

Our results showed that herbivory in the monocultures was mediated by the specialist chrysomelid beetle *W. inscripta*, confirming the expectation that monocultures are favoring specialists. However, contrary to expectations, herbivory in the unprotected mixed stands was not mainly affected by generalist herbivores, but was predominantly influenced by another specialist, the pyralid caterpillar *E. gastralis*. Hence, higher tree diversity may not necessarily reduce specialist infestation, but can even promote host plant colonization and related damage by specialized herbivores (Yamamura & Yano 1999, but see Otway *et al.* 2005, Sholes 2008). The strong contribution of *E. gastralis* to overall damage in the mixed stands demonstrates that associational susceptibility is not necessarily related to higher abundances of generalist herbivores but can substantially depend on one (or more) specialized herbivores. Thus, the direction of associational effects is strongly governed by the specific herbivore responsible for the damage, as *W. inscripta* and *E. gastralis* differed crucially in their species-specific responses to the spatial arrangement of the focal host tree, leading to their opposite impacts on *T. rosea* within the different stand types.

Density of *W. inscripta* on *T. rosea*, and accordingly the contribution to leaf damage by the beetle, was highest in the monocultures and it was relatively low at higher tree diversity (*i.e.* in unprotected mixed stands), following the predictions of the resource concentration hypothesis. The close proximity of unrelated tree species to *T. rosea* in the mixed stands may have influenced colonization of *T. rosea* by *W. inscripta* by physically and/or chemically masking the focal host species (Agrawal *et al.* 2006, Barbosa *et al.* 2009). In contrast to mixed stands, the accumulation of *T. rosea* in monocultures provides not only a higher resource quantity but may also enhance the beetle's opportunity to switch between host tree individuals to attain higher quality food by 'intraspecific dietary mixing' (Mody *et al.* 2007). These factors likely led to a reduced emigration rate and, consequently, to an aggregated herbivore distribution within the monoculture stands. A preference of *W. inscripta* for taller tree individuals was indicated by the positive correlation between tree height and beetle density. Faster growing tree individuals may invest more resources into growth and may hence be less defended than slower growing conspecifics (Herms & Mattson 1992, Dobbertin 2005). The highly mobile *W. inscripta* may actively choose and aggregate on such less defended individuals. However, the factors decisively determining host tree choice need further investigation as information on the biology of *W. inscripta* is so far lacking. In fact,

the present study appears to be the first that identifies *W. inscripta* as a key herbivore on *T. rosea* in tropical afforestation systems.

In contrast to *W. inscripta*, density and impact of *E. gastralis* on *T. rosea* was positively related to tree diversity. This finding contradicts the resource concentration hypothesis, and indicates that tree diversity affected the distribution patterns of *E. gastralis* via a resource dilution effect (Yamamura 2002, Otway *et al.* 2005). As *E. gastralis* caterpillars complete development on the same tree individual on which oviposition occurs (Hernández & Briceño 1999), their distribution on host tree individuals is expected to strongly depend on the host location and oviposition behavior of the adult female moth (Root & Kareiva 1984, Stöckli *et al.* 2008a). Our results suggest that ovipositing females of *E. gastralis* prefer tree individuals growing in heterospecific stands, irrespective of their height. Previous studies on other lepidopteran species suggest that such selective behavior may enhance the probability for successful development and survival of the offspring (Hern *et al.* 1996, Doak *et al.* 2006, Bonebrake *et al.* 2010). By selecting host trees in the mixed stands, and therefore more isolated hosts compared to the monocultures, the female *E. gastralis* moth may search for ‘competitor-free space’, thereby accessing resources for their offspring that are less exploited by other herbivores such as *W. inscripta* (Root & Kareiva 1984, see also Fisher *et al.* 2000, Tack *et al.* 2009 for intra-guild competition for resources). Avoidance of oviposition in monocultures by *E. gastralis* moths may also represent a search for ‘enemy-free space’ (Pöykkö 2011 and references therein), as a more complex vegetation and larger distances between host tree individuals can impede host localization by key enemies of a focal herbivore (Gols & Harvey 2009, Randlkofer *et al.* 2010, Mody *et al.* 2011). As herbivore egg numbers or effects of antagonists on immature stages were not quantified in our study, we cannot exclude the possibility that the lower density of *E. gastralis* caterpillars observed in monocultures may also be related to higher rates of predation or parasitism in this stand type (Gingras *et al.* 2003, Randlkofer *et al.* 2010). The potential of natural enemies to reduce *E. gastralis* populations is indicated by a study from a Venezuelan forest reserve, which states that the abundance of this important herbivore of *T. rosea* is generally kept at low levels by parasitoids and predators (Hernández & Briceño 1998, 1999).

The finding that generalist herbivores were not abundant in the mixed stands was surprising, particularly when considering coleopterans. A comprehensive study by Novotny *et al.* (2010) on host specialization of tropical forest insect herbivores revealed that the

dominating adult leaf chewers (such as beetles) on a specific plant species are generalists, whereas larval leaf chewers were rather found to be specialists. However, tree diversity and structural heterogeneity in our plantation were low compared to natural forests, possibly leading to low numbers of generalist herbivores. This explanation is supported, for example, by observations from a subtropical forest in China, indicating that increased plant diversity is related to increased herbivory by polyphagous herbivores (Schuldt *et al.* 2010).

Levels of herbivore leaf damage in unprotected mixed stands in our study amounted to 22 and 15% at 1 and 3 years after establishment, respectively. These values are high compared to available data from various tree species in natural tropical ecosystems and also compared to previous results from *T. rosea* in plantations. They indicate that *T. rosea* may experience comparably high insect damage when growing in tree plantations, at least when associated with the “wrong” neighbors (Barbosa *et al.* 2009). Leaf damage in tropical forests ranged from 11% for shade tolerant to 14% for tropical dry forest trees in a meta-study comprising many different tree species (Coley & Barone 1996), and in savannas from 15 to nearly 0% across 25 adult-size tree species in Brazil (Marquis *et al.* 2001) and from 9 to 3% across 9 tree species from the sapling-stage size class in Ivory Coast (Unsicker & Mody 2005). Previous studies reporting herbivore damage specifically for *T. rosea* grown in Panamanian plantations may have underestimated herbivory, with 3% leaf damage in 1-year-old monocultures (Paul *et al.* 2012) and 9% in unprotected 2-year-old mixed stands (Plath *et al.* 2011b). Both studies quantified damage earlier in the season than the current study, which is the first to assess the key herbivores and their temporal abundance patterns (see supplementary material 4.2 for temporal abundance patterns). In fact, both key herbivores reach their maximum abundance in the late rainy season, rendering their full contribution to damage only observable at this later point in time. From an applied point of view, our results emphasize that consideration of key herbivores and of their species-specific responses to management strategies may crucially enhance the establishment of new tree plantations. Compared to monocultures, mixed stands are regarded as a strategy to reduce negative impacts of insect herbivores in plantation forestry (Wagner *et al.* 1996, Montagnini & Jordan 2005, Kelty 2006). Our results, however, indicate that this assumption is not unequivocally true. The contrasting responses of the two key herbivores to individual stand types point to a possible trade-off even when specialist herbivores dominate, as each unprotected stand type favored another key herbivore. The low infestation and reduced damage of *T. rosea* in the

insecticide-protected mixed stands suggest that the application of insecticides may represent a possible measure supporting the establishment of high-value timber species. This assumption is supported by findings from a study in the same experimental plots (Plath *et al.* 2011b) revealing that growth of *T. rosea* saplings was significantly higher in the insecticide-protected stands than in the unprotected monocultures and mixed stands. However, successful tree protection by insecticides often depends on the herbivore species (e.g. Newton *et al.* 1993, Wylie 2001 for chemical control of the pyralid moth *Hypsipyla* spp.), and on specific small-scale environmental conditions (Plath *et al.* 2011b). Moreover, application of insecticides can have detrimental effects on natural enemies of herbivores (Pedigo & Rice 2009). Thus, insecticides cannot be regarded as a miracle cure solving all herbivore-related obstacles in tropical plantation establishment.

## Conclusions

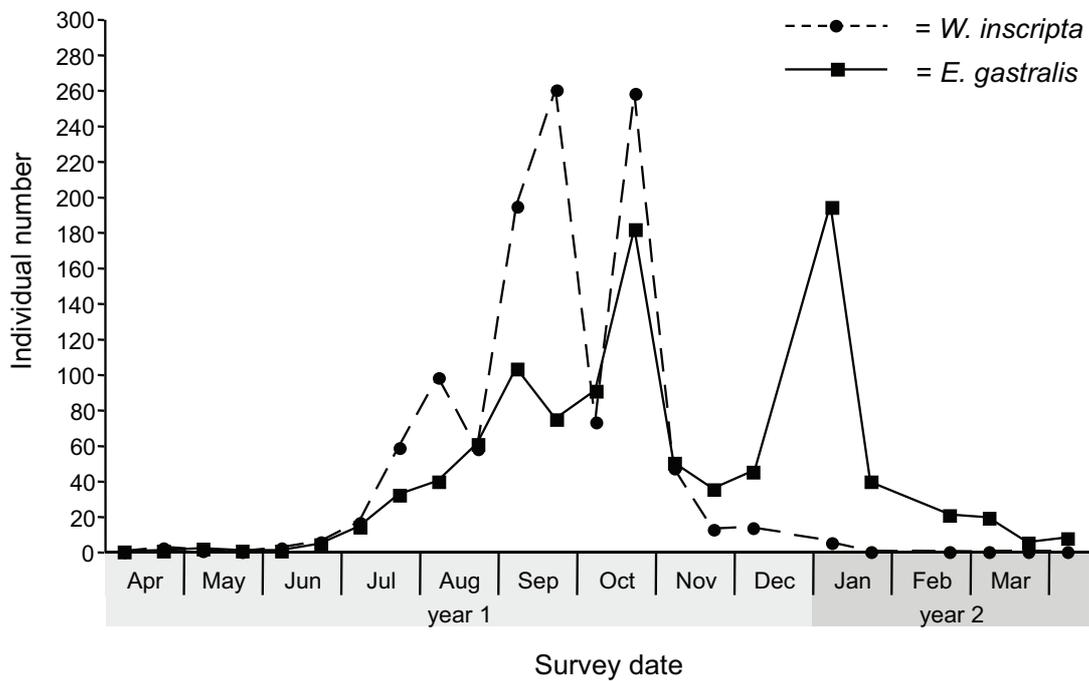
Our results reveal that stand diversification can lead to opposite responses of key herbivores of tropical tree plantations. By considering the individual key herbivore species, we were able to explain the seemingly contradictory coexistence of associational resistance and of associational susceptibility to specialist herbivores. Because tree diversity is regarded as an important tool for sustainable pest management in tree plantations, it is important to explicitly consider the dominant herbivore species as well as their biology and responses to the spatial arrangement of host and non-host trees during the plantation establishment process. Considering species-specific herbivore traits can enhance our understanding of so far neglected associational effects (*i.e.* associational susceptibility mediated by specialist herbivores), and may help to disentangle the causes of insect outbreaks, to develop sustainable forest management strategies, and to improve the delivery of forest ecosystem services.

### Supplementary material 4.1

Total number of alive tree individuals in monocultures of *Tabebuia rosea* (MON) and in 3-species mixed stands (MIX) of the timber species *T. rosea*, *Anacardium excelsum* and *Cedrela odorata*, as well as the mean densities (i.e. mean number of individuals per leaf) of larval *Eulepte gastralis* (Lepidoptera: Pyralidae) and of adult *Walterianella inscripta* (Coleoptera: Chrysomelidae) for each planting scheme and plot at the end of the growing season in December of year 1.

	Treatment	No. of trees	Density	
			<i>W. inscripta</i>	<i>E. gastralis</i>
Plot 1	MON	35	0.180	0.761
	MIX	28	0.458	1.175
Plot 2	MON	36	0.201	0.104
	MIX	24	0.101	0.442
Plot 3	MON	33	0.719	0.046
	MIX	27	0.263	0.203
Plot 4	MON	36	0.940	0.110
	MIX	22	0.114	0.218
Plot 5	MON	36	0.088	0.107
	MIX	32	0.059	0.428

Supplementary material 4.2



Abundance patterns of the pyralid *Eulepte gastralis* and the chrysomelid *Walterianella inscripta* on the host tree *Tabebuia rosea* during a one-year survey period in the experimental tree plantation. Total individual number (mean for day and night counts) of the respective survey date is shown. Note that no survey was conducted at the end of December in year 1 and in the middle of February in year 2. For *E. gastralis* a maximum larval development time of 15 days has been described (Hernández & Briceño 1999), indicating that several generations occurred during our study period. This finding suggests a polyvoltine life cycle of *E. gastralis* (for further details on the biology of *E. gastralis* see also Hernández and Briceño (1998) and Hernández *et al.* (1999)). For *W. inscripta*, information on life history is generally lacking. As no chrysomelid larvae were detected on *T. rosea* during the study period, no statement can be made whether the observed beetles belonged to one very long-living generation or to several generations.

### Supplementary material 4.3

Effects of insecticide application on herbivore densities (individuals per leaf) of *Walterianella inscripta* and *Eulepte gastralis* on the focal host tree *Tabebuia rosea*. *T. rosea* was planted in monocultures (MON), in unprotected 3-species mixed stands in association with *Anacardium excelsum* and *Cedrela odorata* (MIX), and in insecticide-protected 3-species mixed stands (PRO). Effects were tested using binomial data (infested trees: herbivore densities > 0; non-infested trees: herbivore densities = 0) in a generalized linear mixed effect model as penalized quasi-likelihood approach with planting schemes as fixed factor and plot as a random factor, accounting for the nesting of planting schemes within plots. Results are given for (a) overall comparisons, and (b) multiple comparisons between individual planting schemes. Significant effects ( $P < 0.05$ ) are shown in italics (after false discovery rate control of pairwise comparisons); numDF = numerator degrees of freedom, denDF = denominator degrees of freedom. Tree number per planting scheme: MON = 59, MIX = 60, PRO = 59.

	numDF	denDF	<i>F</i>	<i>P</i>
<b>(a) Overall treatment effect</b>				
<i>W. inscripta</i>	2	8	14.860937	<i>0.002</i>
<i>E. gastralis</i>	2	8	29.18934	<i>&lt; 0.001</i>
<b>(b) Multiple comparisons</b>				
		<b>DF</b>	<b><i>T</i></b>	<b><i>P</i></b>
<i>W. inscripta</i>				
MON versus PRO		8	-4.983278	<i>0.001</i>
MIX versus PRO		8	-3.806497	<i>0.005</i>
MON versus MIX		8	1.925897	0.090
<i>E. gastralis</i>				
MON versus PRO		8	-6.586357	<i>&lt; 0.001</i>
MIX versus PRO		8	-7.135759	<i>&lt; 0.001</i>
MON versus MIX		8	-1.596065	0.149

#### Supplementary material 4.4

Effects of stand diversification on herbivore densities (individuals per leaf) of *Walterianella inscripta* and *Eulepte gastralis* on the focal host tree *Tabebuia rosea* growing in monoculture and 3-species mixed stands (*T. rosea* in association with *Anacardium excelsum* and *Cedrela odorata*). Effects were tested using a linear mixed effect model with herbivore densities as response variable, planting schemes as fixed factor and plot as a random factor, accounting for the nesting of planting schemes within plots. To evaluate the potential impact of tree architecture on herbivore densities, tree height (measured at the end of the growing season in December of year 1) was used as a covariate. Significant effects ( $P < 0.05$ ) are shown in italics; numDF = numerator degrees of freedom, denDF = denominator degrees of freedom. Tree number per planting scheme: MON = 59, MIX = 60.

	<b>numDF</b>	<b>denDF</b>	<b><i>F</i></b>	<b><i>P</i></b>
<i>W. inscripta</i>				
Tree height	1	108	10.55	<i>0.002</i>
Treatment	1	4	12.60	<i>0.024</i>
<i>E. gastralis</i>				
Tree height	1	108	0.06	0.809
Treatment	1	4	8.49	<i>0.044</i>

## 5 Growth, herbivore distribution, and herbivore damage of timber trees in a tropical silvopastoral reforestation system<sup>2</sup>

### 5.1 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 reforestation, 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.

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<sup>2</sup> Riedel J, S Dorn, M Plath, and K Mody (2012). Annals of Forest Science DOI: 10.1007/s13595-012-0239-7.

## 5.2 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 2009b). 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 & 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 & Sinclair 2001, Harvey *et al.* 2011). Nevertheless, studies on tree growth in tropical silvopastoral reforestation systems are scarce (but see Hall *et al.* (2011a) 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 & 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 & 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 & Coley 2011), remain, and reproduce on the host surrounded by companion trees (Barbosa *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.

## **5.3 Materials and methods**

### **5.3.1 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 & 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).

### 5.3.2 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).

### 5.3.3 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 two 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<sub>C</sub> = height of companion tree

H<sub>T</sub> = height of timber tree

N<sub>C</sub> = number of companion trees planted (*i.e.* 5).

#### 5.3.4 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.

### 5.3.5 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.

#### 5.3.6 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<sub>2</sub>-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  $\delta^{15}\text{N}$  ratios, which served to test whether the timber tree *T. rosea* accumulates nitrogen fixed by the companion tree *G. sepium* (Daudin & Sierra 2008). Additionally,  $\delta^{13}\text{C}$  ratios were measured to assess drought stress experienced by *T. rosea* (Mody *et al.* 2009). Nitrogen content,  $\delta^{15}\text{N}$

values, and  $\delta^{13}\text{C}$  values were determined using a Flash EA 1112 Series elemental analyzer (Thermo Italy, Rhodano, Italy) coupled to a Finnigan MAT Deltaplus 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;  $\text{mg}/\text{cm}^2$ ) 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  $65^\circ\text{C}$  for 5 days. LMA was computed by dividing the area of each leaflet (obtained during herbivory measurements, see above) by its dry mass. Values of leaf characteristics were averaged for each tree.

### 5.3.7 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 reddishbrown 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.

### 5.3.8 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.

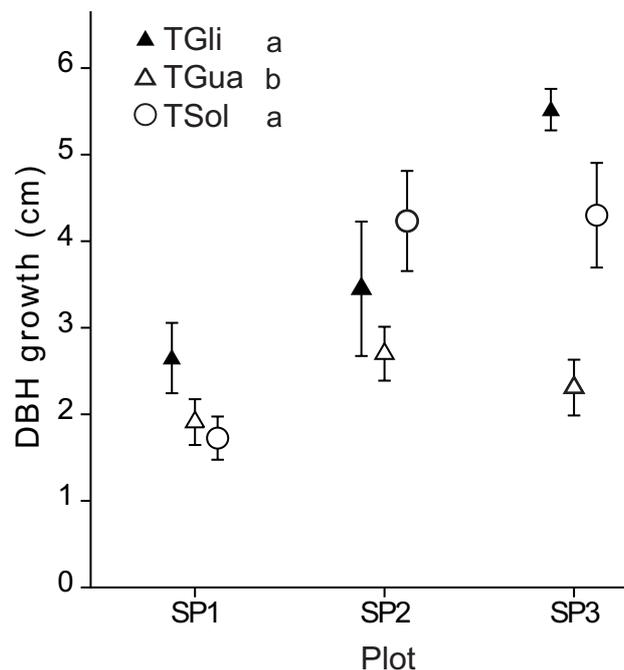
The link between herbivory and tree growth was tested by two-way ANCOVA, with planting regime and plot as fixed between-subject factors, DBH growth of *T. rosea* from year 4 to year 5 as the response variable, and leaf damage in year 4 as the covariate.

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.

## 5.4 Results

### 5.4.1 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 ( $F_{8,37} = 8.16$ ;  $P < 0.001$ ). 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. 5.1). 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. 5.1). 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.



**Fig. 5.1** 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 solitarily (TSol). Contrasting letters a, b refer to significant differences between planting regimes (ANOVA, LSD *post hoc* test with false discovery rate correction).

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 5.1). 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 × plot interactions (Table 5.1). Tree height was not significantly affected by the planting regime 5 years after tree establishment, but it varied significantly among plots (Table 5.1). Trees were significantly smaller in SP1 than in SP2 and SP3, but these plot effects did not interact with planting regimes (Table 5.1).

**Table 5.1** Effects of planting regimes and plots on growth and leaf characteristics of the timber tree *Tabebuia rosea* (mean ± SE for each variable). Trees were growing surrounded by *Gliricidia sepium* (TGli), surrounded by *Guazuma ulmifolia* (TGua), or solitarily (TSol). Significant effects are shown in bold.

	Planting regime			Statistics*
	TGli	TGua	TSol	
<b>Tree size</b>				
Final DBH (cm) year 5	5.30 ± 0.51	4.06 ± 0.34	4.72 ± 0.52	<b>Model:</b> $F_{8,56} = 4.60$ ; $P < 0.001$ <b>Regime:</b> $F_{2,56} = 3.14$ ; $P = 0.051$ <b>Plot:</b> $F_{2,56} = 11.38$ ; $P < 0.001$ (SP3 > SP2, SP1) <b>Regime x Plot:</b> $F_{4,56} = 2.89$ ; $P = 0.030$
Final height (m) year 5	4.57 ± 0.33	4.29 ± 0.30	4.01 ± 0.33	<b>Model:</b> $F_{8,56} = 3.26$ ; $P = 0.004$ <b>Regime:</b> $F_{2,58} = 1.23$ ; $P = 0.301$ <b>Plot:</b> $F_{2,58} = 9.31$ ; $P < 0.001$ (SP3 > SP2, SP1) <b>Regime x Plot:</b> $F_{4,58} = 1.80$ ; $P = 0.142$
<b>Leaf characteristics</b>				
Leaf $\delta^{13}\text{C}$ (‰) year 4	- 29.60 ± 0.16	- 30.20 ± 0.18	- 29.50 ± 0.14	<b>Model:</b> $F_{8,57} = 1.96$ ; $P = 0.069$ <b>Regime:</b> $F_{2,57} = 5.09$ ; $P = 0.009$ (TGli, TSol > TGua) <b>Plot:</b> $F_{2,57} = 0.11$ ; $P = 0.895$ <b>Regime x Plot:</b> $F_{4,57} = 1.16$ ; $P = 0.337$
Leaf $\delta^{15}\text{N}$ (‰) year 4	0.88 ± 0.24	0.90 ± 0.21	0.90 ± 0.30	<b>Model:</b> $F_{8,57} = 0.55$ ; $P = 0.818$ <b>Regime:</b> $F_{2,57} = 0.01$ ; $P = 0.995$ <b>Plot:</b> $F_{2,57} = 1.36$ ; $P = 0.264$ <b>Regime x Plot:</b> $F_{4,57} = 0.47$ ; $P = 0.760$

table continued on next page

	Planting regime			Statistics*
	TGli	TGua	TSol	
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 x 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: $F_{8,57} = 1.75$ ; $P = 0.108$ <b>Regime:</b> $F_{2,57} = 4.63$ ; $P = 0.014$ (TGua > TGli) Plot: $F_{2,57} = 1.89$ ; $P = 0.161$ Regime x Plot: $F_{2,57} = 0.32$ ; $P = 0.866$
LMA (mg/cm <sup>2</sup> ) year 4	11.88 ± 0.22	10.41 ± 0.41	12.12 ± 0.23	<b>Model:</b> $F_{8,56} = 3.95$ ; $P = 0.001$ <b>Regime:</b> $F_{2,56} = 9.55$ ; $P < 0.001$ (TGli, TSol > TGua) Plot: $F_{2,56} = 0.78$ ; $P = 0.462$ Regime x Plot: $F_{4,56} = 2.34$ ; $P = 0.066$
<b>Phenology</b>				
Value year 3	14.3 ± 0.6	13.4 ± 0.6	14.0 ± 0.8	Regime: $H_2 = 1.25$ ; $P = 0.536$ <b>Plot:</b> $H_2 = 7.71$ ; $P = 0.021$ (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: $H_2 = 4.26$ ; $P = 0.119$

\*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.

The companion tree species differed significantly in their size and in the related shielding of the timber trees. *G. ulmifolia* attained a larger DBH, height, and shielding factor than *G. sepium* in year 5 (Table 5.2).

**Table 5.2** Growth and shielding (mean  $\pm$  SE) of the companion tree species *Gliricidia sepium* and *Guazuma ulmifolia*. Significant effects are shown in bold.

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

\*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.

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 5.3).

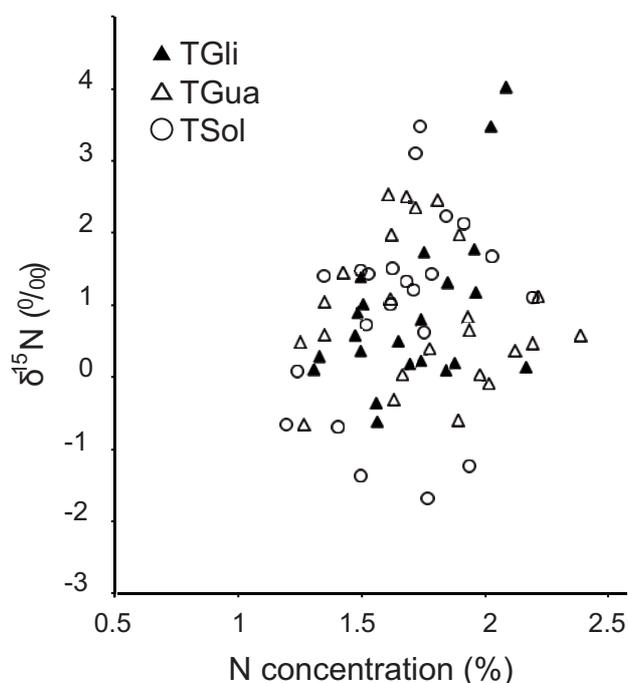
**Table 5.3** Effects of shielding by companion trees and plots on DBH growth of the timber tree *Tabebuia rosea*. Timber trees were growing surrounded by *Gliricidia sepium* (TGli) or surrounded by *Guazuma ulmifolia* (TGua). Significant effects are shown in bold.

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

\*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.

#### 5.4.2 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 5.1).  $\delta^{13}\text{C}$  values were significantly lower in TGua trees than in TGli trees and 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  $\delta^{13}\text{C}$  values, planting regimes had no significant impact on  $\delta^{15}\text{N}$  values and nitrogen content in *T. rosea* leaves (Table 5.1). Furthermore, there was no difference in the relationship between nitrogen content and  $\delta^{15}\text{N}$  values of *T. rosea* leaves between planting regimes (Fig. 5.2), which indicates that the nitrogen-fixing *G. sepium* companion trees had no significant effect on nitrogen content of *T. rosea* leaves.



**Fig. 5.2** Relation between nitrogen content (%) and  $\delta^{15}\text{N}$  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)

Leaf water content and LMA were significantly affected by planting regimes (Table 5.1). 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 5.1).

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 5.1). 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 ( $R_s = 0.29$ ;  $P = 0.018$ ).

#### 5.4.3 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 5.4).

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 5.4). 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 5.4). In contrast, no such significant relation was found between infestation by *W. inscripta* and total leaf damage in year 1 (Table 5.4). In year 4, leaf damage was not significantly affected by planting regimes or plots (Table 5.4). 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 5.4).

The effect of tree height on *W. inscripta* damage approached significance (Table 5.4). 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 5.4).

**Table 5.4** Effects of planting regimes and plots on leaf damage and herbivore infestation of the timber tree *Tabebuia rosea* (mean  $\pm$  SE for each variable) and effects of planting regimes, plots and leaf damage on DBH growth of *T. rosea*. Trees were growing surrounded by *Gliricidia sepium* (TGli), surrounded by *Guazuma ulmifolia* (TGua), or solitarily (TSol). Significant effects are shown in bold.

	Planting regime			Statistics*
	TGli	TGua	TSol	
<b>Herbivore infestation (individuals/leaf)</b>				
<i>E. gastralis</i> year 1	0.71 $\pm$ 0.3	0.80 $\pm$ 0.2	0.84 $\pm$ 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 x Plot: $F_{4,57} = 1.27$ ; $P = 0.294$
<i>W. inscripta</i> year 1	0.05 $\pm$ 0.01	0.14 $\pm$ 0.06	0.07 $\pm$ 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 x Plot: $F_{4,57} = 0.33$ ; $P = 0.858$
<i>W. inscripta</i> year 3	0.07 $\pm$ 0.04	0.02 $\pm$ 0.01	0.04 $\pm$ 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 x Plot: $F_{4,58} = 1.18$ ; $P = 0.328$
<i>W. inscripta</i> year 4	0.04 $\pm$ 0.01	0.09 $\pm$ 0.07	0.05 $\pm$ 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 x Plot: $F_{4,58} = 0.95$ ; $P = 0.442$
<b>Leaf damage</b>				
Leaf damage year 1	17.13 $\pm$ 3.4	15.8 $\pm$ 3.0	19.9 $\pm$ 2.6	<b>Model:</b> $F_{10,54} = 3.28$ ; $P = 0.002$ Regime: $F_{2,54} = 1.90$ ; $P = 0.159$ Plot: $F_{2,54} = 0.69$ ; $P = 0.509$ Regime x Plot: $F_{4,54} = 1.91$ ; $P = 0.123$ <b>Density <i>E. gastralis</i>:</b> $F_{1,54} = 10.04$ ; $P = 0.003$ Density <i>W. inscripta</i> : $F_{1,54} = 3.02$ ; $P = 0.088$ 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 x Plot: $V = 0.14$ ; $F_{12,165} = 0.67$ ; $P = 0.781$ Tree height: $V = 0.13$ ; $F_{3,53} = 2.66$ ; $P = 0.057$ <b>Leaf nitrogen:</b> $V = 0.18$ ; $F_{3,53} = 3.78$ ; $P = 0.016$
Leaf damage year 4, Overall model				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 x Plot: $F_{4,56} = 1.25$ ; $P = 0.300$ Leaf nitrogen: $F_{1,56} = 2.25$ ; $P = 0.139$
Total leaf damage year 4	15.1 $\pm$ 3.6	13.0 $\pm$ 1.6	19.3 $\pm$ 2.2	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 x Plot: $F_{4,56} = 1.26$ ; $P = 0.297$ Leaf nitrogen: $F_{1,56} = 2.16$ ; $P = 0.148$
<i>E. gastralis</i> leaf damage year 4	11.3 $\pm$ 3.7	8.6 $\pm$ 1.6	14.7 $\pm$ 2.3	

table continued on next page

	Planting regime			Statistics*
	TGli	TGua	TSol	
<i>W. inscripta</i> leaf damage year 4	1.32 ± 0.4	1.07 ± 0.4	0.86 ± 0.4	<b>Model:</b> $F_{10,55} = 3.05$ ; $P = 0.004$ <b>Regime:</b> $F_{2,55} = 1.65$ ; $P = 0.201$ <b>Plot:</b> $F_{2,55} = 3.40$ ; $P = 0.040$ <b>Regime x Plot:</b> $F_{4,55} = 0.68$ ; $P = 0.612$ <b>Tree height:</b> $F_{1,55} = 3.86$ ; $P = 0.055$ <b>Leaf nitrogen:</b> $F_{1,55} = 6.09$ ; $P = 0.017$
<b>Effect of leaf damage on DBH growth</b>				
DBH growth (cm) year 4-5	2.09 ± 0.2	1.58 ± 0.13	2.16 ± 0.2	<b>Model:</b> $F_{9,52} = 2.18$ ; $P = 0.038$ <b>Regime:</b> $F_{2,52} = 2.04$ ; $P = 0.140$ <b>Plot:</b> $F_{2,52} = 3.75$ ; $P = 0.030$ <b>Regime x Plot:</b> $F_{4,52} = 1.86$ ; $P = 0.132$ <b>Total leaf damage year 4:</b> $F_{1,52} = 0.44$ ; $P = 0.512$

\*Leaf damage of 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 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 test-statistic and separate univariate ANOVAs were conducted as follow-up analysis to assess effects of the covariates on the dependent variables separately.

## 5.5 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 (Chamailard *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 (Stöckli *et al.* 2008b) 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 & 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 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 belowground interactions through root exudates or interconnected mycelial networks (Sierra & 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 (Plath *et al.* 2011b, Massad 2012). 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.

## 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.

## 6 Effects of ants on arthropod assemblages of a native timber tree in a tropical reforestation plantation<sup>3</sup>

### 6.1 Abstract

Successful reforestation of tropical pastures can be facilitated or impeded depending on the interactions between native timber trees and arthropod communities. We assessed arthropod abundance on *Tabebuia rosea* (Bignoniaceae), a Central American extrafloral nectary-bearing timber tree, in a plantation of native trees on former pasture in Panama, and we excluded ants from branches of *T. rosea* to determine ant impact on arthropod assemblages and on leaf damage. The trees' ant fauna was dominated by ground-nesting species and ants were scarce in tree crowns, constituting only 2% of all arthropods collected by branch beating. Leaf damage was principally caused by caterpillars (mainly the pyralid *Eulepte gastralis*) and by beetles (mainly the chrysomelid *Walterianella inscripta*). Sugar baits at tree trunks revealed that rewarding food resources recruited high ant numbers to some tree individuals. Activity of the dominant ant, *Ectatomma ruidum*, at baits was negatively related to leaf damage by *E. gastralis*, suggesting that trees might be better protected from this herbivore when ant abundance is high. Exclusion of ants resulted in increased beetle diversity. The key herbivore *W. inscripta* was significantly more abundant on ant-exclusion branches at the beginning but not towards the end of the rainy season, when beetle density increased. Overall-leaf damage and arthropod abundance were not significantly affected by ant exclusion. In conclusion, ant abundance on native timber trees in plantations recently established on former pasture can be low, and ant assemblages may be dominated by ground-nesting generalist species, as shown in this study. This may explain the lacking protection of the timber trees from insect herbivory by ants. Increased protection of establishing timber trees by ants probably requires plantation management measures that increase the abundance of more specialized tree-visiting and tree-nesting ants.

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<sup>3</sup> Based on Riedel J, S Dorn, G Brand, H Barrios, and K Mody (2012). Journal of Applied Entomology DOI: 10.1111/jen.12009.

## 6.2 Introduction

The establishment of native timber trees on degraded pastures may improve rural livelihoods (Garen *et al.* 2011), while simultaneously supporting biodiversity (Lamb 1998), and improving soil quality (Montagnini 2001). However, tree re-establishment on deforested land is often severely hindered by insect herbivores, which impede the growth of native trees in plantations (Massad *et al.* 2011, Plath *et al.* 2011b). Top-down control by natural antagonists such as predatory ants may be a promising component of a locally realizable pest management strategy (Way & Khoo 1992, Agarwal *et al.* 2007).

Ants are an essential part of tropical biodiversity and are common in virtually all types of terrestrial tropical habitats of low- and mid-elevation (Hölldobler & Wilson 1990). They are major predators of arthropods (Floren *et al.* 2002) and their presence can contribute to indirect plant resistance, benefiting plants by reducing herbivory and enhancing plant fitness (Rosumek *et al.* 2009). However, the costs and benefits of the interactions between plants and ants are highly conditional (Chamberlain & Holland 2009) and many studies have failed to find beneficial effects of ants (e.g. Freitas *et al.* 2000, Piñol *et al.* 2012).

For tropical timber tree plantations, particularly for native timber trees, the role of ants in plant protection is poorly understood. However, weaver ants (*Oecophylla smaragdina*) can reduce damage by shoot borers (*Hypsipyla robusta*; Lepidoptera: Pyralidae) to mahogany (*Swietenia* spp.) and African mahogany (*Khaya senegalensis*) in plantations in the Paleotropics (Lim *et al.* 2008, Van Mele 2008, Peng *et al.* 2011). In the Neotropics, ant genera that were found to be protective for cocoa trees and therefore may also protect timber trees against insect herbivory, include *Azteca* spp. and *Ectatomma* spp. (Majer & Delabie 1993). Some evidence exists that ants may play a particularly important role in the protection of myrmecophilic timber trees such as *Cordia* spp., which attract ants either via domatia (Pringle *et al.* 2011), or by extrafloral nectaries (EFNs; (Rico-Gray & Oliveira 2007).

In this study our objectives were to (1) record the arthropod assemblages of *Tabebuia rosea* (Bertol.) DC. (Lamiales: Bignoniaceae), which is an EFN-bearing native timber tree promising for reforestation activities due to low mortality, fast initial growth and high timber value (Wishnie *et al.* 2007, Plath *et al.* 2011a), and (2) to investigate the effects of ants on arthropod assemblages and on leaf damage. Therefore we recorded the abundance and diversity of the ant fauna present on *T. rosea* and examined the abundance of different

arthropod orders, feeding guilds and major herbivores concurrently with the amount of leaf damage on ant-exclusion and ant-accessible control branches. We tested the following predictions: (2a) the structure of arthropod assemblages is affected by ant presence, and (2b) herbivore abundance and associated leaf damage are reduced by ant presence.

## 6.3 Materials and methods

### 6.3.1 Study site and species

The study was conducted in a native tree plantation in Sardinilla, Central Panama (9°19'30"N, 79°38'00"W, elevation 70 m a.s.l.), during the rainy season from June to October 2010. The climate at the study site is semi-humid tropical with a mean annual temperature of 25.2° C and a mean annual precipitation of 2289 mm (Wolf *et al.* 2011). During the study period the mean monthly precipitation at Sardinilla site was 243 mm. The annual daily temperature varies between an annual daily minimum of 21.7°C and an annual daily maximum of 33.1°C (Scherer-Lorenzen *et al.* 2007). The original vegetation consisted of semi-deciduous lowland forest on clayey soil, which was logged in 1952/53. Following two years of agricultural use, the site was converted to pasture and grazed by cattle for approximately 50 years (Potvin *et al.* 2004). The site is currently surrounded by grazed cattle pasture and by plots of a native tree plantation that was set up in 2001 (Potvin *et al.* 2004).

The timber tree *T. rosea* is a deciduous species attaining a size of 25-30 m with a native distribution range from Southern Mexico to Venezuela, which occurs naturally in tropical wet-, moist-, and dry forests and is also extensively cultivated throughout the tropics (Gentry 1973). *Tabebuia rosea* bears scale-like extrafloral nectaries that secrete a modest amount of nectar on the surfaces of its palmate, five-foliolate leaves and on young stems (Diaz-Castelazo *et al.* 2005). The principal leaf flushing takes place in the early rainy season, and leaves are shed during the dry season (Gentry 1970). The two most relevant foliar herbivores of *T. rosea* are larvae of *Eulepte gastralis* (Lepidoptera: Pyralidae) and adults of *Walterianella inscripta* (Coleoptera: Chrysomelidae) (Plath *et al.* 2012).

### 6.3.2 Experimental design

The experiment was established in June before the beginning of leaf flush and continued for 12 weeks until the end of the main growing period of the *T. rosea* trees. The key activity period of the most important herbivores of *T. rosea* and also the peak of the rainy season were therefore incorporated into the study period (Plath et al. 2012). The experiment was conducted on 31 four-year-old *T. rosea* trees, ranging in size from 3.5 to 8 m total height, which were situated in five different reforestation plots of the native tree plantation at an average minimum distance of 8.3 m ( $\pm 0.3$  SE). The reforestation plots consisted of three timber species, *T. rosea*, *Anacardium excelsum* (Anacardiaceae) and *Cedrela odorata* (Meliaceae), planted at a tree-to-tree distance of two meters in a regular Latin square design that assured heterospecific next neighbor trees. Two branches similar in within-crown position and in size were chosen from each tree and randomly assigned to one of two treatments: (1) ant-exclusion branches, which were banded at their base with a 10 cm wide tape treated with sticky insect glue, and (2) ant-accessible control branches without sticky barriers. Throughout the experiment the sticky barriers were controlled every two to five days and were renewed if necessary. Occasionally leaves of surrounding trees had to be cut to prevent uncontrolled ant access to the study branches. Exclusion treatments affected ant abundance in a consistent way, as ants were significantly less abundant on ant-exclusion than on control branches, with a total of only three ant individuals collected from the 31 exclusion branches compared to 37 individuals on control branches (paired samples Wilcoxon test,  $P < 0.05$ ).

### 6.3.3 Arthropod sampling and processing

Arthropods on the study branches were sampled at three dates (3/4 August, 30 August to 1 September, and 13 to 15 September) during day and night with a beating tray. The tray (0.5 m x 0.5 m) was positioned directly below the sample branch, which was then shaken for eight seconds. All arthropods in the tray were collected in an ethanol containing plastic container mounted to the bottom of the tray. To standardize the observations, the number of leaves per branch sampled by beating was counted each time. To avoid sampling interference (*i.e.*

collecting fewer individuals from the second branch because insects had escaped due to shaking of the first branch) ant-exclusion and control branches were sampled at a random order on two consecutive days or nights, respectively. Arthropod numbers of each branch were standardized to the number of sampled leaves.

All arthropods were determined to order and beetles were determined to family and morphospecies after Borror *et al.* (1989). Ants were determined to genus and morphospecies after Hölldobler & Wilson (1990), Bolton (2003), and Fernández (2003). Where possible, taxonomic experts were consulted for identification of beetle and ant species. The arthropod taxa were grouped into eight feeding guilds according to Moran & Southwood (1982): leaf chewers, leaf sap suckers, scavengers, predatory insects, spiders, parasitoids, tourists, and ants (diverse feeding habits; often generalist predators). In calculating predator-prey ratios, the first three guilds were considered to be prey, whereas predatory insects, spiders, and parasitoids were considered to be predators. Ants (their occurrence was experimentally manipulated) and tourists (including dipterans) were excluded from the analysis of predator-prey ratios.

To analyze the diversity of coleopteran morphospecies the abundance-based coverage estimator of species richness (ACE; (Chao *et al.* 2000), and the inverse Simpson index (Magurran 2004) were calculated for ant-exclusion and control branches using the software EstimateS Mac 8.2.0. (Colwell 2009).

#### 6.3.4 Ant activity

To estimate potential ant activity per study tree, we quantified the number of ant individuals and species every other week at carbohydrate baits mounted to the tree trunks. The baits consisted of cut-open Eppendorf tubes (2 ml) filled with saturated sucrose solution and cotton. The cotton protruded as a wick to the tree trunk and made the solution available to ants (Blüthgen *et al.* 2006). One bait per tree was attached to the trunk at 1.60 m height, below the sticky barriers. We counted all ant individuals within a radius of 5 cm around each bait in six sampling events, consisting of a night and a day assessment. For each species not readily identifiable in the field, one to three reference specimens (depending on the number of ant individuals at the bait) were collected and stored in 75% ethanol for later identification.

Due to the slow recruitment of ants to the baits, which was observed during preliminary tests, recordings of ant individual numbers started two hours after mounting the bait. To ensure comparably consistent weather conditions and high ant activity, ant counts were conducted between 2000 h and 2100 h for the night-assessments and between 0830 h and 0930 h of the consecutive morning for the day-assessments.

### 6.3.5 Measurement of leaf damage

Three months after the beginning of the experiment, insect herbivore damage to ant-exclusion and control branches was quantified for twelve randomly collected leaves of each branch. All collected leaves were screened for caterpillars, which were counted and weighted. For leaf damage measurements the fourth leaflet of every leaf was used. If the fourth leaflet was completely missing whereas the petiole remained, we considered the leaflet to have suffered 100% herbivory. If the fourth leaflet was almost completely missing whereas some small parts remained, we estimated the damaged area by considering the area of the second leaflet, which is similar in size and shape. If the leaf naturally had only four leaflets (which was exceptionally the case), we measured the second leaflet instead. All analyzed leaflets were photographed with a digital camera (Canon Powershot A630) using a standardized procedure (Mody & Linsenmair 2004): 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. Leaf damage measurements were performed with a leaf scanner (LI-3100C Leaf Area Meter, LI-COR Biosciences, Lincoln) by comparing the area of the actual leaflet with the area of a template of the intact leaflet, which was drawn and cut from paper. To assess the amount of leaf surface damage caused by the leaf-skeletonizer *E. gastralis* and by leaf miners, the damaged areas were successively removed. The remaining area of the leaflet was subsequently re-measured. Additional damage was classified as (1) further damage from caterpillars, (2) damage caused by chrysomelid beetles, (3) leaf-curling damage caused by thrips, and (4) damage that could not be clearly identified or assigned to the mentioned damage categories. The contribution of these four damage classes to overall leaf damage was quantified by estimating the proportion of each damage type to the nearest 10% of total leaf area using the digital photographs. Subsequently the

surface damage by *E. gastralis* and the further caterpillar damage were combined as caterpillar damage. To characterize leaf damage of each branch the mean damage of twelve leaflets was used. The proportion of leaf damage attributed to each category of damage was averaged for each branch.

### 6.3.6 Statistical analysis

Prior to analysis data were transformed to meet the assumptions of normality and heteroscedasticity where necessary. Percentage data (leaf damage and proportion of specific arthropod taxa) were arcsin-transformed. Arthropod densities and ant activity at the baits were  $\log_{10}(x+1)$  transformed. Non-parametric tests were applied whenever assumptions of parametric testing were not met.

Total leaf damage, specific leaf damage categories, total arthropod densities, and ACE of exclusion and control branches of each tree were compared with paired samples t-tests, whereas the abundance of specific herbivore taxa, feeding guilds, and predator-prey ratios were compared between treatments with paired samples Wilcoxon tests. To analyze the change of arthropod assemblage composition over time, arthropod densities and proportion of individuals of the arthropod orders were tested with one-way repeated-measures ANOVA, using sampling as within subject factor and tree as fixed between subject factor. The change of the density of *W. inscripta* over time was compared between samplings by Friedman's ANOVA, using paired Wilcoxon tests as *post hoc* tests, to which false discovery rate correction was applied.

Ant visitation was compared between trees (using the total number of ant individuals per tree recorded at the twelve day and night assessments) by Friedman's ANOVA and ant activity at the baits was correlated with ant abundance on ant accessible control branches with Spearman's correlation. Total ant activity and tree size, as well as activity of *E. ruidum* and tree height, were related to leaf damage of ant accessible control branches with multiple linear regression (forced entry). The abundance of the predator guilds 'spiders' and 'parasitoids' were separately related to total ant activity and activity of *E. ruidum* with linear regression.

Statistical analysis was done with SPSS 20.0 for Mac OS X (2010 SPSS, Chicago, IL, USA). For clarity, figures show untransformed data.

## 6.4 Results

### 6.4.1 Arthropod assemblage composition

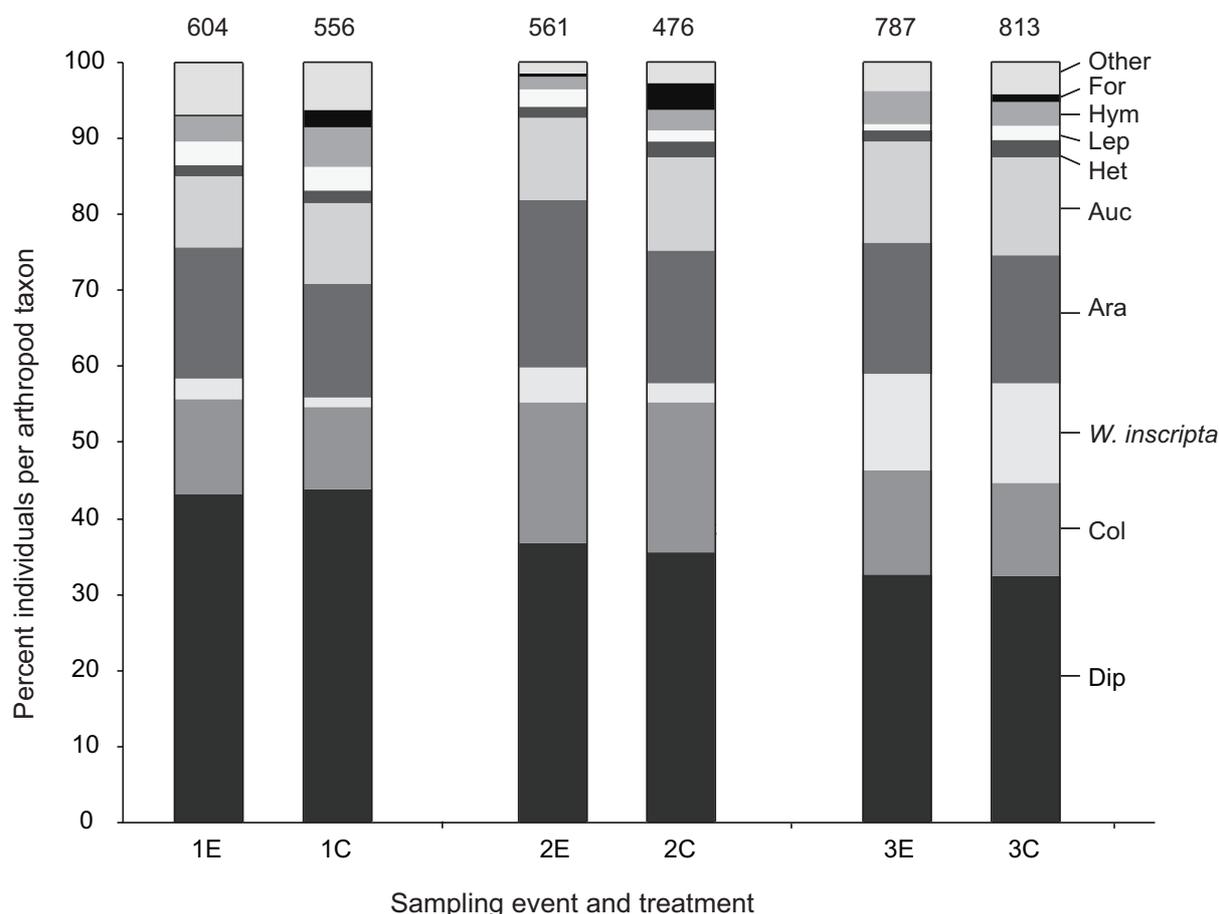
A total of 3797 arthropods were sampled from ant-exclusion and control branches (Fig. 6.1). The most abundant taxa were Diptera (37%), Coleoptera (21%), Araneae (18%), and ‘Auchenorrhyncha’ (12%). Arthropod numbers increased and the composition of arthropod assemblages changed during the course of the experiment and with the progression of the rainy season. The mean arthropod density (individuals per leaf) increased significantly from  $0.85 \pm 0.06$  (mean  $\pm$  SE) at the first sampling event at the beginning of August and  $0.84 \pm 0.09$  at the second sampling event at the end of August, to  $1.4 \pm 0.09$  at the third sampling event in mid-September ( $F_{2, 58} = 23.8$ ,  $P < 0.001$ ). The proportion of Coleoptera increased significantly from 14% in the first sampling event to 24% in the second sampling and 26 % in the third sampling ( $F_{2, 58} = 19.1$ ,  $P < 0.001$ ), while the proportion of Diptera decreased significantly from 42% in the first sampling event to 35% in the second sampling and 32% in the third sampling ( $F_{2, 58} = 5.1$ ,  $P < 0.001$ ).

### 6.4.2 Ant abundance and diversity

Ant abundance at baits revealed that almost all trees were visited by ants (only one tree did not yield any ants at baits), and that ant visitation was significantly different between trees ( $\chi^2_{30} = 183.7$ ,  $P < 0.001$ ; total ant numbers ranging from 0 to 226 individuals). The median ant number at each bait ranged from 0 to 17.5 on different trees.

The contribution of ants to the total arthropod number in branch samples was generally remarkably low: of 1845 arthropod individuals sampled from the freely accessible control branches ( $N = 31$  trees), only 37 (2%) were ants (Fig. 6.1), and from half of the study trees no

ants at all were collected in branch samples. The total number of ants collected from control branches during the beating-tray samplings was positively correlated with the number of ants observed at baits (Spearman's correlation,  $N = 31$ ,  $R_s = 0.43$ ,  $P = 0.02$ ).



**Fig. 6.1** Composition of arthropod assemblages on ant-exclusion (E) and control (C) branches of *Tabebuia rosea* at three sampling events. Day and night samplings are combined. Columns indicate the percentage the specimens of a taxon contribute to the total sampled arthropod number of that treatment and sampling. Numbers above the columns indicate the total number of individuals. Dip = Diptera, Col = Coleoptera without *Walterianella inscripta* (*W. inscripta*), Ara = Araneae, Auc = Auchenorrhyncha, Het = Heteroptera; Lep = Lepidoptera, Hym = Hymenoptera without Formicidae, For = Formicidae.

The ants detected at the baits belonged to ten ant species (Table 5). The most abundant species was *E. ruidum* (67% of 1545 individuals), followed by *Camponotus abdominalis* (7%), *Camponotus* sp. 1 (7%), and *Solenopsis geminata* (6.5%). Some species were encountered at the baits only a few times, but in high abundance, which is shown in low

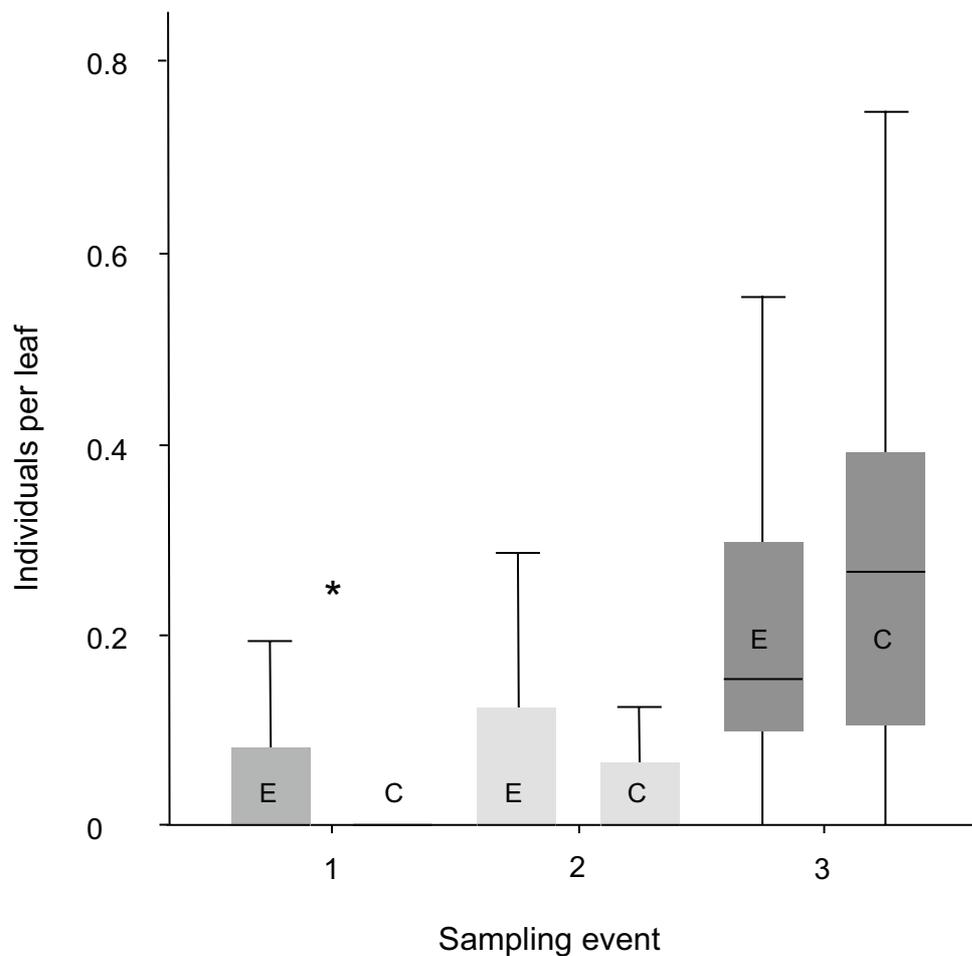
incidence values for numerically dominant ant species (e.g. *S. geminata*; Table 5). The ant species composition at the baits partially differed between day and night: *Camponotus* sp. 1 and *Camponotus lindigi* were rather found by day (73% of 107 and 100% of 19 individuals, respectively) and *C. abdominalis* by night (100% of 108 individuals), whereas *E. ruidum* was found equally at day and night (52% of 1034 individuals by day compared to 48% at night). The ants sampled from the branches belonged to six species in four sub-families (Table 5). Again, the most abundant species was *E. ruidum*, accounting for 48% of 40 sampled individuals, followed by *Camponotus* sp. 1 (25%).

**Table 6.1** Diversity and abundance of ants collected from *Tabebuia rosea* branches and recorded at carbohydrate baits on the tree trunks. Total individual numbers (percentages in brackets) are shown. Incidence values represent the percentage of ant counts in which a single species was present at a bait in relation to the total number of ant counts ( $N = 372$ )

Sub-family	Species	Individuals		Incidence
		Branch samples	Baits	
Ectatomminae	<i>Ectatomma ruidum</i>	19 (47.5)	1034 (67)	39
	<i>Gnamptogenys</i> sp. 1	0	30 (2)	0.3
Formicinae	<i>Camponotus abdominalis</i>	2 (5)	108 (7)	6.0
	<i>Camponotus lindigi</i>	4 (10)	19 (1.2)	2.7
	<i>Camponotus</i> sp. 1	10 (25)	107 (6.9)	6.7
	<i>Paratrechina</i> sp. 1	1 (2.5)	57 (3.7)	2.4
Myrmicinae	<i>Cyphomyrmex</i> sp. 1	0	4 (0.3)	0.3
	<i>Pheidole</i> sp. 1	0	50 (3.2)	0.5
	<i>Solenopsis geminata</i>	1 (2.5)	100 (6.5)	1.1
Pseudomyrmecinae	<i>Pseudomyrmex gracilis</i>	1 (2.5)	1 (0.1)	0.3
Unknown		2 (5)	35 (2.3)	3.2
Total		40	1545	62.1

### 6.4.3 Effects of ants on arthropod assemblage composition and herbivores

Exclusion treatments were associated with significant changes in beetle diversity: on the ant-exclusion branches 85 morphospecies were found in total, with an estimated number of 186 species (ACE, abundance-based coverage estimator of species richness) and a Simpson Index of 7.52, whereas on the control branches only 72 morphospecies were found, with an estimated number of 158 species (ACE) and a Simpson Index of 7.02. On average, the ACE of the ant-exclusion branches was significantly greater ( $31.2 \pm 5.9$ ) than that of the control branches ( $21.8 \pm 3.5$ ;  $t_{30} = -2.12$ ,  $P < 0.05$ ). One of the key herbivores of *T. rosea*, *W. inscripta*, accounted for 33% of the sampled beetles. The density of *W. inscripta* was significantly higher on ant-exclusion branches than on control branches in the first sampling ( $Z = -2.62$ ,  $P < 0.01$ , Fig. 6.2) but there were no significant differences between the two treatments in the second and third sampling (all  $P > 0.05$ ), at which times the individual numbers of *W. inscripta* were higher. The change in the density of *W. inscripta* over the three months of the experiment was significant ( $\chi^2_2 = 24.05$ ,  $P < 0.001$ ); in the third sampling the density was significantly higher than in the first- and second sampling (paired samples Wilcoxon test as *post-hoc* test,  $N = 31$ , all  $P < 0.001$ ). Temporary effects of exclusion treatments were also found for spiders, which were significantly more abundant on ant-exclusion branches than on control branches in the second sampling ( $Z = -2.08$ ,  $P < 0.05$ ).



**Fig. 6.2** Abundance of the chrysomelid beetle *Walterianella inscripta* on exclusion and control branches of *Tabebuia rosea* at three branch sampling events. Horizontal lines represent the distribution median, boxes represent lower and upper quartiles, whiskers represent 1.5 interquartile range. For clarity, outliers and extreme values are not shown. A significant effect (paired samples Wilcoxon test,  $Z = -2.62$ ,  $P < 0.01$ ) between exclusion (E) and control (C) treatment was found in the first sampling and is indicated with an asterisk.

The density of *E. gastralis*, the second key herbivore of *T. rosea*, was low at the caterpillar census during leaf collection in October and did not differ significantly between treatments (ant-exclusion branches: 20 individuals per 372 leaves; control branches: 10 individuals per 372 leaves;  $Z = -0.29$ ,  $P > 0.05$ ).

#### 6.4.4 Effects of ants on leaf damage

Total leaf damage amounted to  $7.4 \pm 0.4\%$  (mean  $\pm$  SE) for leaves of the ant-accessible control branches and  $8.2 \pm 0.5\%$  for leaves of the ant-exclusion branches. Damage by caterpillars was the prevalent damage type ( $3.7 \pm 0.4\%$  of leaf area vs.  $4.5 \pm 0.5\%$ ) for both ant-accessible and ant-exclusion branches, respectively, followed by chrysomelid damage ( $1.8 \pm 0.2\%$  vs.  $1.5 \pm 0.1\%$ ) and damage by leaf curling insects ( $1.4 \pm 0.1\%$  vs.  $1.3 \pm 0.1\%$ ). Damage by leaf miners was negligible ( $0.05 \pm 0.03\%$  vs.  $0.02 \pm 0.01\%$ ).

Neither the difference in total leaf damage between the treatments was significant ( $t_{30} = 0.5$ ,  $P > 0.05$ ) nor were the differences in the contribution of specific leaf damage classes to overall herbivory (all  $P > 0.05$ ). However, multiple linear regression analysis revealed that increasing activity of *E. ruidum* at the baits was negatively related to the average caterpillar leaf damage of the control branches ( $R^2 = 0.31$ ,  $F_{1,29} = 6.17$ ,  $P = 0.006$ , coefficient<sub>*E. ruidum*</sub> = -0.54,  $t = -3.44$ ,  $P = 0.002$ ). In contrast, chrysomelid damage was not significantly related to total ant activity ( $P > 0.05$ ) or *E. ruidum* activity ( $P > 0.05$ ) but to tree height, which explained 32% of the variation in chrysomelid damage ( $R^2 = 0.32$ ,  $F_{1,29} = 6.44$ ,  $P = 0.005$ , coefficient<sub>tree height</sub> = 0.53,  $t = 3.33$ ,  $P = 0.002$ ).

#### 6.4.5 Effects of ant exclusion on arthropod guild composition

The most abundant feeding subguild other than tourists were predators represented by spiders (18% of 3797 individuals), followed by leaf sap suckers (15%) and leaf chewers (13%). scavengers (7%), insect predators (4%), and parasitoids (4%) were less abundant. Exclusion of ants did not change the feeding guild composition considerably. With the exception of the changes in the abundance of spiders and ants mentioned above no significant differences in feeding guild composition were recorded (paired samples Wilcoxon test, all  $P > 0.05$ ). The mean predator-prey ratios were higher on the exclusion branches in all samplings (Table 6), but these differences were not statistically significant (all  $P > 0.05$ ). The abundance of spiders on the control branches was neither significantly related to the total ant activity at the baits ( $R^2 = 0.01$ ,  $F_{1,29} = 0.27$ ,  $P > 0.05$ ) nor to the activity of *E. ruidum* at the baits ( $R^2 = 0.1$ ,  $F_{1,29} = 3.7$ ,  $P > 0.05$ ). The abundance of parasitic wasps was also neither

significantly related to total ant activity at the baits ( $R^2 = 0.05$ ,  $F_{1,29} = 1.45$ ,  $P > 0.05$ ) nor to the activity of *E. ruidum* at the baits ( $R^2 = 0.06$ ,  $F_{1,29} = 1.7$ ,  $P > 0.05$ ).

**Table 6.2** Predator-prey ratio (mean  $\pm$  SE) on ant exclusion and on control branches of *Tabebuia rosea* with *P*-values of the corresponding *t*-test. Shown are the mean values of the three sampling events and the mean value of all samplings combined

Sampling	Predator/prey		<i>P</i> -value
	Exclusion	Control	
1	1.42 $\pm$ 0.26	1.12 $\pm$ 0.16	0.35
2	1.23 $\pm$ 0.20	0.76 $\pm$ 0.09	0.14
3	0.80 $\pm$ 0.78	0.79 $\pm$ 0.13	0.94
Total	1.11 $\pm$ 0.12	0.89 $\pm$ 0.08	0.26

## 6.5 Discussion

This study showed that arboreal ant assemblages in plantations of native timber trees recently established on former pasture can be dominated by ground-nesting generalist species such as *E. ruidum* and that ant abundance in the tree crowns can be surprisingly low. Initially, as long as herbivore densities were low, ant exclusion reduced the density of the chrysomelid beetle *W. inscripta*, a key herbivore of *T. rosea*, but not later in the season. Leaf damage was negatively related to the activity of *E. ruidum* at baits at the tree trunk, and both *W. inscripta* and the second key herbivore, the pyralid caterpillar *E. gastralis*, substantially contributed to this damage. Ant exclusion did not cause major changes of the arthropod assemblages of *T. rosea*, however, spiders were more abundant in one of the samplings where ants were absent. Overall, effects of ants on co-existing arthropods and on herbivory were weak, probably due to the low ant individual number and foraging characteristics of the dominating generalist ant species.

### 6.5.1 Low ant abundance in the tree crowns of *Tabebuia rosea*

Ants were rare in the tree crowns; they comprised only 2% of the sampled arthropod individuals on untreated control branches. This result contrasts with findings from other forested tropical habitats where ants constituted up to 94% of arthropods in fogging samples from canopies (Davidson *et al.* 2003). Compared to the tropical semi-deciduous lowland forest that originally covered the study site, the recently reforested pastures represent a still disturbed ecosystem. The observed low ant abundance and dominance of ground-nesting generalist species such as *E. ruidum* and *S. geminata* may therefore be a consequence of a long history of intensive land use as cattle pasture, and of the comparatively low habitat diversity and complexity of the young plantation ecosystem. It was also found that ant species richness is negatively related to tree density and tree species richness (Bisseleua *et al.* 2009) and that ant species richness and abundance can be reduced in agroecosystems or secondary forests compared to intact forests (Floren & Linsenmair 2005, Philpott & Armbrrecht 2006, Bihn *et al.* 2008). An additional explanation for the absence of arboreal ants is that, due to the young age of the trees, nesting sites such as epiphytes or wood cavities had not yet been established (Blüthgen *et al.* 2000). The dominating ground-nesting ants may systematically approach the tree crowns only in low numbers to search on the leaves for occasionally occurring arthropod prey and to regularly extract the extrafloral nectar (Mody & Linsenmair 2003).

The dominant ant species in our study was *E. ruidum*, which is reported to be tolerant to habitat disturbance and to inhabit open-pasture habitats (Zelikova & Breed 2008). *Ectatomma ruidum* is a common, omnivorous ant that forages solitarily and feeds on extrafloral nectar as well as on small insects (Ibarra-Nunez *et al.* 2001, McGlynn *et al.* 2010). Although it is ground-nesting and also forages mainly on the ground (Levings & Franks 1982), it was among the prevailing species in studies that detected ant-mediated plant protection (Bentley 1976, de la Fuente & Marquis 1999). In contrast to potentially beneficial ants, leafcutter ants that can be highly detrimental for tree plantations (Massad 2012) were never observed in our experimental plots, although *Atta* spp. occurred in the vicinity of the plantation (JR and KM, personal observation).

### 6.5.2 Effects of ants on leaf damage and major herbivores

In this study the accessibility of branches of *T. rosea* for ants had no significant effect on several parameters characterizing herbivory or herbivore occurrence, including (1) total leaf damage and (2) the density of *E. gastralis* caterpillars. This contrasts findings from other studies, which have detected plant protection mediated by some of the ant species found on *T. rosea* in our study. The most abundant ant species in our study, *E. ruidum*, might be an effective plant mutualist, as it provided protection for tropical trees (*Stryphnodendron microstachyum*, Fabaceae) (de la Fuente & Marquis 1999) as well as herbaceous plants (*Phaseolus vulgaris*, Fabaceae) (Bentley 1976). For the second and third most abundant identified species, *C. abdominalis* and *S. geminata*, a protective effect for plants can also be assumed. *Camponotus abdominalis* was a dominant ant species on *Turnera ulmifolia* (Turneraceae) (Cuautle & Rico-Gray 2003), where ant presence reduced herbivory and increased fruit set. *Solenopsis geminata* can colonize disturbed ecosystems quickly and has been considered a keystone predator in agroecosystems (Risch & Carroll 1982). Hence, the lack of tree protection by ants in our study might not only be due to the absence of protective ant species from the study site, but also to a low recruitment of the available ant species to the studied tree crowns. The resulting low ant abundance was probably a major determinant of missing protection, as a critical, species-dependent number of ants is necessary to provide protection services to trees (Di Giusto *et al.* 2001), and this threshold was probably not reached on most tree individuals.

Leaf damage by *E. gastralis* caterpillars was the predominant type of damage observed in our study, and *E. gastralis* damage decreased significantly with increasing activity of *E. ruidum*, measured as ant abundance at baits. This possibly indicates that *E. ruidum* can have a protective effect on *T. rosea*, if it is recruited to trees in sufficiently high numbers. As *E. gastralis* caterpillars complete their development on the same tree on which oviposition has occurred (Hernández & Briceño 1999), tree infestation is possibly not only directly affected by ant aggression towards feeding caterpillars (Floren *et al.* 2002)(Floren *et al.* 2002), but also indirectly modified if female *E. gastralis* moths show oviposition preference (Stöckli *et al.* 2008a, Plath *et al.* 2012) for trees with lower ant abundance.

Besides ant activity, herbivore density may have a strong influence on the protection services provided by ants (Philpott *et al.* 2008). This aspect of ant-mediated protection is

illustrated by the response of leaf beetle damage, in particular by *W. inscripta*. As long as this chrysomelid occurred in moderate densities, for example in the first sampling, ant presence significantly reduced its abundance on the trees. However, as its densities increased, this effect disappeared.

The results of this study further suggest that factors other than ants may have a large influence on the leaf damage experienced by *T. rosea* under field conditions. In the case of *W. inscripta*, leaf damage increased with tree height. Vertical stratification of herbivores is common in tropical forests (Lewinsohn *et al.* 2005). However, tree height *per se* probably does not influence herbivory directly, but rather may be related to other plant or environmental factors affecting herbivore distribution such as tree age, light environment, or exposure to rain and wind (Ruhnke *et al.* 2009), pointing to the existence of tree- and herbivore-species related interactions (Unsicker & Mody 2005). This finding highlights the necessity of examining the abundance and damage caused by different herbivores separately, as each herbivore group may be individually influenced by different parameters.

### 6.5.3 Effects of ants on arthropod assemblages

In this study, not all arthropod groups responded to ant exclusion in the same way. This result supports findings from other ant exclusion experiments (Mody & Linsenmair 2004, Philpott *et al.* 2004). The estimated richness (ACE) of beetle morphospecies was significantly higher on ant-excluded than on freely accessible branches. This lower beetle diversity on the ant-accessible control branches probably reflects the predatory or disturbing role of the ants, which reduces the beetle assemblages to ant-tolerating species.

The spider number in the second sampling significantly increased in the absence of ants. An increase in spider numbers upon ant exclusion has frequently been reported (Mooney 2007, Piovia-Scott 2011), although ants can also have facilitative effects on spiders (Schuch *et al.* 2008). However, possible explanations for an increase in spider density upon ant absence are reduced competition with ants for shared prey (Sanders & Platner 2007), or a decrease in intraguild predation (Moya-Laraño & Wise 2007). Similarly to spiders, other predaceous or parasitic arthropods could benefit from reduced competition if ants are absent

(Mody *et al.* 2011), leading to higher proportions of non-ant herbivore antagonists on exclusion branches. The finding that ants, spiders and parasitoids together (control branches) were slightly more efficient in reducing herbivore densities and their effects on plants than spiders and parasitoids alone (exclusion branches) corroborates the suggestion that the positive, protective effect of ants for plants is generally stronger than their negative, predator-reducing effect (Offenberg *et al.* 2005). It thereby supports the notion that complementarity effects within the predator guild may play an important role in determining overall levels of herbivory (Blüthgen & Klein 2011).

## Conclusions

Our study revealed that ant abundance on native timber trees planted on a former tropical pasture was remarkably low but also varied greatly among individual trees in the first years after tree establishment. The low ant abundance and the dominance of ground-nesting generalist ant species may explain why observed effects of ants on tree-dwelling arthropods and tree damage by insect herbivores were generally weak. Increased protection of establishing timber trees by ants probably requires management measures - including the planting of myrmecophilic timber species - that increase the abundance of more specialized tree-visiting and tree-nesting ants.

## 7 Time matters: temporally changing effects of planting schemes and insecticide treatment on timber tree performance on former pasture<sup>4</sup>

### 7.1 Abstract

Reforestation of former pastures with native timber trees holds potential to improve small-scale farmers livelihoods while supporting ecosystem functioning and biological diversity. To promote successful reforestation with native tree species, more knowledge is needed, particularly on effects of species identity, tree diversity, and insecticide application on tree survival and growth at different time periods after plantation establishment. We assessed these effects for three native Central American timber species and compared results gained two and five years after tree establishment. Survival, stem diameter, and tree height were quantified for *Tabebuia rosea*, *Anacardium excelsum*, and *Cedrela odorata*, planted in (1) monocultures, (2) three-species mixtures, and (3) three-species mixtures treated with insecticides during the first two years of seedling establishment. We further tested how survival and growth performance were affected by the individual tree position within reforestation plots to account for border effects in small-scale tree patches in pasture-afforestations. Survival was significantly affected by tree species identity with highest survival in *T. rosea* and lowest survival in *C. odorata*. Tree growth was affected by tree species identity, tree diversity, insecticide treatment, plots, and border effects, but these effects strongly varied across the individual tree species. Interspecific analyses revealed significant differences between species. *A. excelsum* trees attained the largest and *C. odorata* the smallest size after five years of growth. Intraspecific analyses revealed that DBH growth of *T. rosea* was greater in mixtures and protected mixtures than in monocultures, indicating that intraspecific competition reduced growth of this species. *A. excelsum* achieved equal DBH growth in all planting schemes, whereas its height growth was highest in monocultures, indicating that *A. excelsum* profited from conspecific neighbor trees. *C. odorata* attained highest DBH growth in unprotected mixtures and lowest DBH growth in protected mixtures,

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<sup>4</sup> Riedel J, S Dorn, M Plath, C Potvin, and K Mody, submitted.

suggesting that *C. odorata* benefits from heterospecific neighbors that are not supported by insect control and do not lead to strong overshadowing. Positive border effects, *i.e.* a significantly enhanced growth at the border of a plot, were found for *T. rosea* in monocultures and *A. excelsum* in protected mixtures. These results suggest small patches of native timber trees planted on former pasture as a promising reforestation strategy in Latin America. Insecticide treatment during the establishment phase can result in a larger tree size but does not necessarily enhance tree growth in later years. Depending on tree species, either mixtures or monocultures may provide the best growing results for establishing trees.

## 7.2 Introduction

The ongoing worldwide deforestation has resulted in large-scale land degradation with associated losses of biological diversity and reduced ecosystem services, including carbon storage, and soil and water quality (Dirzo & Raven 2003, FAO 2010). Although processes of land-use change are complex, the conversion of forests to agricultural land and pastures has been identified as the greatest direct driver of deforestation in Latin America, with now 27% of the land surface being used as cattle pastures (Geist & Lambin 2002, FAO 2009b). To restore ecological functions and biodiversity, reforestation of degraded tropical landscapes is imperative but has to reconcile tree planting with agricultural use and landholder needs in order to be contrivable in rural landscapes (Lamb *et al.* 2005). Examples are silvopastoral reforestations that combine native timber trees and pastures (Dagang & Nair 2003, Wishnie *et al.* 2007, Riedel *et al.* 2012b), intensive silvopastoral systems (Murgueitio *et al.* 2011), or the creation of woodland islets within the agricultural land (Benayas *et al.* 2008). Such integrated reforestation on cultivated land is of conservation value as tree cover on farmland supports biological diversity by increasing landscape connectivity and by providing resources and habitat for plant and animal species (Harvey *et al.* 2006, Dorrough *et al.* 2012). Trees on farms might furthermore serve as starting point for the re-establishment of woodland after the abandonment of land in the course of rural-urban migration (Muniz-Castro *et al.* 2006, Grau & Aide 2008).

However, planting trees on pastures requires an investment, and such investment is risky unless it can be based on knowledge about species ecology and performance under different environmental conditions and planting systems (Hall *et al.* 2011a, Plath *et al.* 2011b, a). For tropical reforestation, planting mixtures of native tree species that provide a variety of goods and services of traditional and/or marketable value (*e.g.* timber) is considered particularly promising (Hall *et al.* 2011a). Local landholders frequently maintain native trees on farmland as scattered remnant trees, as plantings around houses, or in live fences (Harvey *et al.* 2011) to traditionally gain fodder, shade, timber and firewood.

Compared to monocultures, species mixtures might lead to higher tree performance due to favorable interactions among different tree species that reduce competition or increase facilitation or pest suppression (Forrester *et al.* 2005, Plath *et al.* 2011b). Mixtures also have the potential to enhance biodiversity conservation (Hartley 2002) as well as to improve soil fertility and nutrient cycling (Montagnini 2000). If trees are sold, product diversification through mixed stands may likewise reduce the farmers' economic risk of fluctuating price levels on local or regional markets (Kelty 2006). However, the success of mixtures and the outcome of species interactions are highly variable and strongly depend on the selection of compatible species and appropriate planting sites (Forrester *et al.* 2005). Furthermore, both competitive and complementary tree-to-tree interactions can change over time and with increased resource utilization (Stanley & Montagnini 1999, Delagrange *et al.* 2008).

Herbivory is assumed to be lower in species mixtures (associational resistance (Barbosa *et al.* 2009, Letourneau *et al.* 2011) but neighbor effects depend on species characteristics of the relevant herbivores, such as host plant specialization and mobility (Jactel & Brockerhoff 2007, Plath *et al.* 2012). To protect tree seedlings from herbivores many farmers regularly apply pesticides (Garen *et al.* 2009), but information on good practices and effectiveness of those pesticides under field conditions is scarce (Plath *et al.* 2011b). As pesticides are costly and can have negative environmental effects, their application should be optimally planned. Since tree seedlings are particularly vulnerable to insect pests (Massad 2012), a potential strategy might be to apply pesticides only during the early phases of tree establishment. However, no information exists about the effectiveness of this strategy in tropical reforestations with native trees.

Integrating patches of trees into pastures is of high potential relevance for the reforestation of agricultural landscapes (Benayas *et al.* 2008). Yet, in this situation a high proportion of

overall reforested area is covered by border area. The preponderance of border area leads to small-scale variation in environmental conditions and resource competition, which may induce differing tree growth between plot borders and plot center (edge effects, *e.g.* Roberts and Harrington (2008)). If trees grow better in the plot center a larger patch size might be preferable, whereas if trees grow better at the plot border smaller patches or management measures such as thinning might be beneficial.

Here we present results from a study on the reforestation potential of three native Central American timber species during the first five years after their establishment on former pasture. We tested different management practices by planting the three species in small-scale monocultures as well as in three-species mixtures with and without insecticide protection. Specifically, we addressed the following questions: (1) How do tree species identity and tree diversity affect timber tree survival and growth five years after tree establishment? (2) How does plant protection by insecticides, applied in the first and second year of plantation establishment, affect tree survival and growth in subsequent years? (3) How does tree survival and growth of trees at the plot border compare to that in the plot center, and (4) how do border effects differ between tree species and planting schemes?

## 7.3 Materials and methods

### 7.3.1 Study site and species

The study was conducted in a native tree plantation in Sardinilla, Central Panama (9°19'30"N, 79°38'00"W, elevation 70 m a.s.l.). The study site is characterized by a semi-humid, tropical climate with a mean annual precipitation of 2289 mm, a mean annual temperature of 25.2°C, and a dry season from January to April (Wolf *et al.* 2011). The site was originally covered by moist tropical forest, on soils that have a high clay content and are derived from Tertiary limestone (Potvin *et al.* 2004). After forest logging in 1952/53, the site was used for agriculture for two years and was subsequently converted into pasture (Potvin *et al.* 2004).

The timber species studied are *Tabebuia rosea* Bertol. (Bignoniaceae), *Anacardium excelsum* (Betero and Blab. ex Kunth) Skeels (Anacardiaceae), and *Cedrela odorata* L.

(Meliaceae), which are all native to Panama (Gentry 1973, Fournier 2003). Species were selected for their commercial value, for their comparability with an already existing surrounding plantation at the study site, and for the availability of seedlings provided by local nurseries. *T. rosea* naturally grows in tropical wet-, moist-, and dry forests and is also extensively cultivated (Gentry 1973). This species yields valuable, high density (0.48-0.60 g cm<sup>-3</sup>) timber, and it can reach a total height of 25-30 m and a stem diameter at breast height (DBH) of 1 m (Fournier 2003, AgroForestryTreeDatabase 2009). Delagrange *et al.* (2008) reported an annual growth rate of 3.4% and Elias and Potvin (2003) classified *T. rosea* as shade-tolerant, non-pioneer species, according to observed growth patterns in forest gaps. Major herbivores of *T. rosea* are *Eulepte gastralis* (Lepidoptera: Pyralidae) and *Walterianella inscripta* (Coleoptera: Chrysomelidae) (Plath *et al.* 2012).

*A. excelsum* occurs in a wide range of soils and climates and has comparably light wood of 0.38 g cm<sup>-3</sup> (McCulloh *et al.* 2012). With an annual growth rate of 5.9% (Delagrange *et al.* 2008) it is classified as pioneer species (Elias & Potvin 2003) that can reach a height of 45 m and a DBH of 3 m (Fournier 2003). To our knowledge there are no reports available characterizing the key herbivores of *A. excelsum*.

*C. odorata* is a valuable timber species of medium wood density (0.42-0.63 cm<sup>-3</sup>) that is cultivated throughout the tropics and generally grows up to 35 m height and 0.6 m DBH with an annual growth rate of around 2.3% (Fournier 2003, Wishnie *et al.* 2007). Sufficient fertility, drainage and aeration of the soil as well as high light levels are imperative for the successful growth of this species (Ricker *et al.* 2000, Dünisch *et al.* 2002, AgroForestryTreeDatabase 2009). Specifications on habitat requirements are inconsistent, classifying *C. odorata* either as shade tolerant non-pioneer species (Elias & Potvin 2003) or as a light demanding 'long-lived-pioneer' (Ricker *et al.* 2000, Carpenter *et al.* 2004). The most serious pest of *C. odorata* is the mahogany shootborer *Hypsipyla grandella* (Lepidoptera: Pyralidae) (Cole & Ewel 2006).

### 7.3.2 Planting design and insecticide treatment

The studied planting schemes were established on former pasture in August 2006 at an existing plantation site, where experimental reforestation activities have taken place since

2001 (Potvin *et al.* 2004). Trees were established as seedlings, which had been raised for three months in a PRORENA (Proyecto de Reforestación con Especies Nativas) nursery before planting. Granular fertilizer (15 g; 12-72-12 N-P-K) was applied to each seedling before and two months after planting. Trees were grown at a distance of 2 m, with a density of 36 trees per 100 m<sup>2</sup> using a standardized six by six Latin square design in three different planting schemes: (1) monocultures (treatment ‘monoculture’), (2) mixed stands of the three species (treatment ‘mixture’), and (3) mixed stands of the three species treated with insecticides during the first two years of the study (treatment ‘protected mixture’). In the latter planting scheme, trees were treated with the insecticide and nematicide carbofuran (carbamate, Furadan 10 GR, 5-25g/tree depending on the effective canopy area), which was applied to the soil every two months, and with the insecticide cypermethrin (pyrethroid, Arribo EC 20 or 6 EC, 1.2 g/l spray solution), which was applied to the foliage every two weeks. Mixed stands consisted of 12 individuals per species, resulting in a total of 36 trees, whereas monocultures consisted of 36 individuals of the same species. The three planting schemes were arranged in one locality as a coherent plot. Plots were replicated five times within the Sardinilla study site, encompassing variable soil moisture, soil pH, soil nitrogen content and collateral vegetation (Plath *et al.* 2011b). In plot 1 concomitant vegetation (short grasses and herbs) was mown approximately once a month, whereas in plots 2-5 competing vegetation (tall grasses and woody successional vegetation) was cleared during the rainy season, every two months during the first two study years and 1-2 times per year from year 3 to year 5.

### 7.3.3 Tree survival and growth

Survival was calculated as the number of trees present after five years divided by the number of trees planted in 2006. Tree size was quantified for each species on an annual basis in August, with the exception of the final measurement in year 5, where tree size and survival were recorded in November (see Plath *et al.* 2011b for results of the first two years). In years 3, 4, and 5 tree size was measured by quantifying (1) stem diameter at 130 cm above soil surface (DBH), (2) basal stem diameter at 20 cm above soil surface, (3) total height (from the

soil to the uppermost point in the tree crown), and (4) crown diameter. Crown diameter was calculated as the average of two measurements of crown diameter (north-south and east-west). Growth of timber trees was determined as the difference in DBH (DBH growth) and in height (height growth) between year 5 and year 3. Some few tree individuals were excluded from the analysis as they suffered major damage, mainly by cattle that entered the plantation inadvertently on a single occasion (*T. rosea*:  $N = 2$ , *A. excelsum*:  $N = 8$ , *C. odorata*:  $N = 3$ ).

#### 7.3.4 Data analysis

Survival was compared among the three timber species and for each timber species between the three planting schemes and five plots by contingency chi-square tests. Survival of trees growing at the plot border was compared with survival of trees growing at the plot center by separate chi-square tests for each species and planting scheme. Pearson and Spearman correlations were conducted to test for possible relations between all size parameters measured. Results revealed significant positive correlations between DBH, basal stem diameter, crown diameter, and height for all species (all  $P < 0.001$ ). Subsequent analyses were therefore restricted to DBH and tree height as growth measures.

Effects of tree species identity, planting schemes, and plots on DBH and height growth from year 3 to 5 and on final values of DBH and tree height in year 5 were assessed by three-way ANOVAs, testing for species, planting scheme, plot, and interaction terms (Morin *et al.* 2011, Plath *et al.* 2011b). Intraspecific comparisons of DBH growth, height growth, and final values of DBH and height in the three planting schemes and five plots were conducted by two-way ANOVAs, testing for planting scheme, plot, and interaction terms. Effects of within-plot position (plot border versus plot center) on DBH and height growth as well as on final values of DBH and height were assessed separately for each species and planting scheme by two-way ANOVAs, testing for plot and tree position at plot center or plot border and interaction terms. LSD *post hoc* tests, to which false discovery rate correction was applied (Verhoeven *et al.* 2005), were applied for multiple comparisons subsequent to ANOVA analyses. Analyses were done with SPSS 20.0 for Mac OS X (2010 SPSS, Chicago, IL, USA).

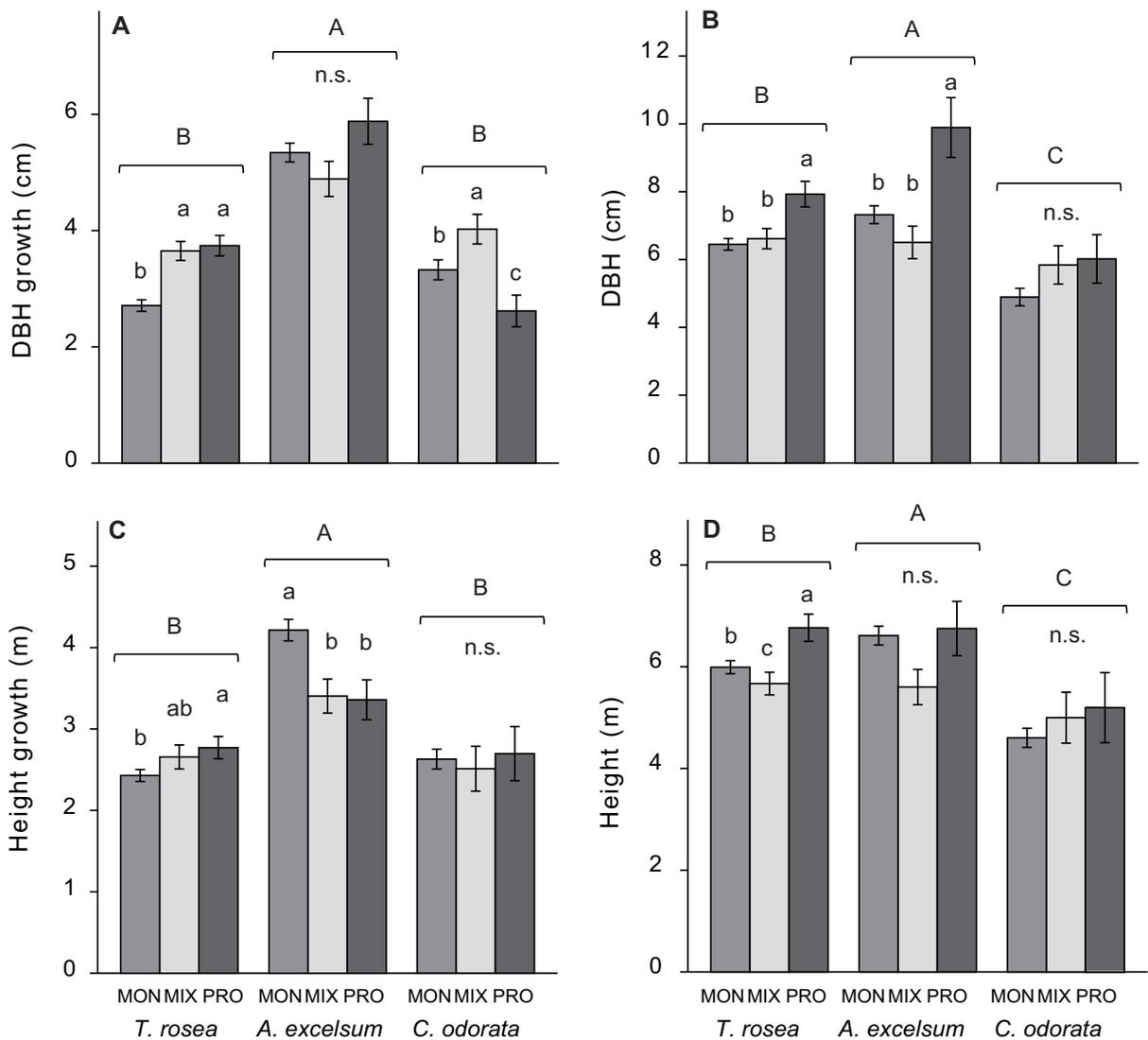
## 7.4 Results

### 7.4.1 Tree survival after 5 years

Five years after establishment, tree survival differed significantly among species ( $\chi^2 (2) = 264.55, P < 0.001$ ). It was highest for *T. rosea* (95.6% of 298 trees), intermediate for *A. excelsum* (64.7% of 292 trees) and lowest for *C. odorata* (31.6% of 297 trees). Planting schemes did not significantly affect survival of any of the tree species studied (*T. rosea*:  $\chi^2_2 = 4.17, P = 0.124$ ; *A. excelsum*:  $\chi^2_2 = 0.18, P = 0.913$ ; *C. odorata*:  $\chi^2_2 = 0.40, P = 0.820$ ). In contrast, survival of each tree species differed significantly across the individual plots (*T. rosea*:  $\chi^2_4 = 21.16, P < 0.001$ ; *A. excelsum*:  $\chi^2_4 = 27.92, P < 0.001$ ; *C. odorata* ( $\chi^2_4 = 35.58, P < 0.001$ ). Survival of *T. rosea* was relatively low in plot 1 (85%) compared to its survival in the remaining plots ranging between 98.3% and 100%. Survival of *A. excelsum* was highest in plot 1 (83.3%), followed by plot 2, plot 3, and plot 4 (71.7%, 69.5%, 58.5%). Lowest survival of *A. excelsum* was found in plot 5 (40.0%). Survival of *C. odorata* was comparably higher in plot 5 (62.7%) than in the remaining plots 1-4 (16.7% to 28.8%).

### 7.4.2 Effects of species identity, tree diversity, and insecticide treatment on tree growth

Tree species identity and planting schemes significantly affected tree growth (Table 7.1). Growth of stem diameter at breast height (DBH) and height growth from year 3 to year 5 varied significantly between species (Fig. 7.1). DBH growth and height growth of *A. excelsum* were significantly higher than of *T. rosea* and *C. odorata*, which did not significantly differ from each other (Fig. 7.1). Concordantly, final measures of DBH and height in year 5 differed significantly among species (Table 7.1). Final DBH and final height of *A. excelsum* were significantly higher than of *T. rosea* and *C. odorata* and final DBH and final height of *T. rosea* were significantly greater than final DBH and height of *C. odorata*.



### Tree species and planting schemes

**Fig. 7.1** Mean ( $\pm$  SE) growth of diameter at breast height between year 3 and year 5 (DBH; A), final DBH achieved in year 5 (B), height growth between year 3 and year 5 (C) and final height achieved in year 5 (D) by *Tabebuia rosea*, *Anacardium excelsum* and *Cedrela odorata*. Trees were grown in unprotected monocultures (MON), unprotected 3-species-mixtures (MIX), or in 3-species-mixtures protected by insecticides (PRO). Contrasting capital letters refer to significant differences between species over all three treatments; contrasting small letters refer to significant differences among planting schemes for each single species; n. s. = non significant (ANOVA, LSD *post hoc* test,  $P < 0.05$ ).

Planting schemes had no significant effects on DBH growth and height growth across species, but strongly affected final tree size measures in year 5 (Table 7.1). Across species, final DBH was significantly higher in protected mixtures than in unprotected mixtures and in monocultures. No differences were found between unprotected mixtures and monocultures. Furthermore, final height of all tree individuals was significantly greater in protected mixtures than in unprotected mixtures and monocultures and greater in monocultures than in unprotected mixtures.

**Table 7.1** Effects of species identity, planting schemes (monocultures (Mon), mixed cultures (Mix), and mixed cultures protected with insecticides (Pro)) and plots (P1-5) on growth measures of the timber trees *Tabebuia rosea* (Tab), *Anacardium excelsum* (Anac), and *Cedrela odorata* (Ced). Contrasting letters refer to significant differences in the *post hoc* tests for the respective between-subject factors\*. Significant differences are highlighted in bold. DBH = diameter at breast height.

		<b>Df</b>	<b>F</b>	<b>P</b>	<b>Post hoc</b>
DBH growth	Species	2	80.37	<b>&lt; 0.001</b>	Anac <sup>a</sup> > Tab <sup>b</sup> , Ced <sup>b</sup>
	Planting scheme	2	2.26	0.106	
	Plot	4	1.90	0.110	
	Species x planting scheme	4	5.97	<b>&lt; 0.001</b>	
	Species x plot	8	2.99	<b>0.003</b>	
	Planting scheme x plot	8	0.97	0.458	
	Species x planting scheme x plot	12	1.76	0.053	
	Error	438			
	Height growth	Species	2	39.14	<b>&lt; 0.001</b>
Planting scheme		2	1.91	0.150	
Plot		4	19.63	<b>&lt; 0.001</b>	P3 <sup>a</sup> > P2 <sup>b</sup> , P5 <sup>bc</sup> , P4 <sup>cd</sup> , P1 <sup>d</sup>
Species x planting scheme		4	7.72	<b>&lt; 0.001</b>	
Species x plot		8	1.41	0.190	
Planting scheme x plot		8	6.61	<b>&lt; 0.001</b>	
Species x planting scheme x plot		15	2.90	<b>&lt; 0.001</b>	
Error		521			

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		<b>Df</b>	<b>F</b>	<b>P</b>	<b>Post hoc</b>
Final DBH	Species	2	19.42	<b>&lt; 0.001</b>	Anac <sup>a</sup> > Tab <sup>b</sup> > Ced <sup>c</sup>
	Planting scheme	2	9.12	<b>&lt; 0.001</b>	Pro <sup>a</sup> > Mix <sup>b</sup> , Mon <sup>b</sup>
		4	35.39	<b>&lt; 0.001</b>	P4 <sup>a</sup> , P3 <sup>a</sup> > P5 <sup>b</sup> , P2 <sup>b</sup> > P1 <sup>c</sup>
	Plot				
	Species x planting scheme	4	1.85	0.118	
	Species x plot	8	3.82	<b>&lt; 0.001</b>	
	Planting scheme x plot	8	11.81	<b>&lt; 0.001</b>	
	Species x planting scheme x plot	14	3.87	<b>&lt; 0.001</b>	
Error	515				
Final height	Species	2	21.23	<b>&lt; 0.001</b>	Anac <sup>a</sup> > Tab <sup>b</sup> > Ced <sup>c</sup>
	Planting scheme	2	4.26	0.015	Pro <sup>a</sup> > Mon <sup>b</sup> > Mix <sup>c</sup>
		4	67.44	<b>&lt; 0.001</b>	P3 <sup>a</sup> > P4 <sup>b</sup> > P5 <sup>c</sup> , P2 <sup>c</sup> > P1 <sup>d</sup>
	Plot				
	Species x planting scheme	4	2.66	0.032	
	Species x plot	8	4.05	<b>&lt; 0.001</b>	
	Planting scheme x plot	8	16.89	<b>&lt; 0.001</b>	
	Species x planting scheme x plot	15	5.00	<b>&lt; 0.001</b>	
Error	523				

\*Statistical analysis was done by three-way ANOVAs, testing for species, planting scheme plot, and interaction terms. Significant ANOVAs were followed by *LSD post hoc* tests, to which false discovery rate correction (Verhoeven *et al.* 2005) was applied.

Intraspecific analyses revealed significant differences among planting schemes for all individual tree size measures considered (Table 7.2). For *T. rosea*, DBH growth from year 3 to year 5 was significantly higher in unprotected and protected mixtures than in monocultures, whereas no significant difference was found for *T. rosea* individuals in unprotected and protected mixtures (Fig. 7.1A). Height growth of *T. rosea* was significantly higher in protected mixtures compared to monocultures and intermediate in unprotected mixtures (Fig. 7.1C). Final DBH in year 5 was significantly higher in protected mixtures than in unprotected mixtures and monocultures (Fig. 7.1B), whereas no difference was found between the unprotected tree stands. Final height of *T. rosea* was highest in protected mixtures, intermediate in monocultures, and lowest in unprotected mixtures (Fig. 7.1D).

For *A. excelsum*, height growth was significantly greater in monocultures than in protected and unprotected mixtures, which did not significantly differ from each other (Fig. 7.1C). In

contrast, DBH growth of *A. excelsum* was not significantly affected by planting scheme (Fig. 7.1A). Final DBH of *A. excelsum* was significantly higher in protected mixtures than in unprotected mixtures and monocultures but did not differ between the unprotected stands (Fig. 7.1B). In contrast, final height of *A. excelsum* was not significantly affected by planting schemes (Fig. 7.1D).

For *C. odorata*, DBH growth differed significantly between planting schemes (Fig. 7.1A). DBH growth was highest in unprotected mixtures, intermediate in monocultures and lowest in protected mixtures. In contrast to DBH growth, height growth (Fig. 7.1C), final DBH (Fig. 7.1B), and final height (Fig. 7.1D) of *C. odorata* were not affected by planting schemes.

Tree growth differed furthermore significantly between the individual plots across and within the three tree species (Table 7.1, Table 7.2). Overall mean values of final DBH and final height achieved after five years were greatest in plot 3 and plot 4. Final size measures were generally reduced in plot 1 (Table 7.1). Significant interaction effects demonstrated how planting scheme effects on tree growth were related to plot characteristics (Table 7.1, Table 7.2).

**Table 7.2** Intraspecific effects of planting schemes (monocultures (Mon), mixed cultures (Mix), and mixed cultures protected with insecticides (Pro)) and plots (P1-5) on growth measures of the timber trees *Tabebuia rosea*, *Anacardium excelsum*, and *Cedrela odorata*. Contrasting letters refer to significant differences in the *post hoc* tests for the respective between-subject factors\*. Significant differences are highlighted in bold. DBH = diameter at breast height.

		df	F	P	Post hoc
<b><i>T. rosea</i></b>					
DBH growth	Planting scheme	2	23.37	<b>&lt; 0.001</b>	Pro <sup>a</sup> , Mix <sup>a</sup> > Mon <sup>b</sup>
	Plot	4	17.68	<b>&lt; 0.001</b>	P2 <sup>a</sup> , P3 <sup>a</sup> > P5 <sup>b</sup> > P4 <sup>c</sup> , P1 <sup>c</sup>
	Planting scheme x plot	8	3.31	<b>&lt; 0.001</b>	
	Error	251			
Height growth	Planting scheme	2	4.84	<b>0.009</b>	Pro <sup>a</sup> , Mix <sup>ab</sup> , Mon <sup>b</sup>
	Plot	4	21.97	<b>&lt; 0.001</b>	P5 <sup>a</sup> P3 <sup>a</sup> , P2 <sup>a</sup> > P4 <sup>b</sup> > P1 <sup>c</sup>
	Planting scheme x plot	8	1.92	<b>&lt; 0.001</b>	
	Error	268			
Final DBH	Planting scheme	2	21.13	<b>&lt; 0.001</b>	Pro <sup>a</sup> > Mix <sup>b</sup> , Mon <sup>b</sup>
	Plot	4	69.99	<b>&lt; 0.001</b>	P5 <sup>a</sup> P4 <sup>a</sup> , P3 <sup>a</sup> > P2 <sup>b</sup> > P1 <sup>c</sup>
	Planting scheme x plot	8	7.08	<b>&lt; 0.001</b>	
	Error	269			
Final height	Planting scheme	2	18.70	<b>&lt; 0.001</b>	Pro <sup>a</sup> > Mon <sup>b</sup> > Mix <sup>c</sup>
	Plot	4	96.25	<b>&lt; 0.001</b>	P5 <sup>a</sup> P4 <sup>a</sup> , P3 <sup>a</sup> > P2 <sup>b</sup> > P1 <sup>c</sup>
	Planting scheme x plot	8	8.50	<b>&lt; 0.001</b>	
	Error	269			
<b><i>A. excelsum</i></b>					
DBH growth	Planting scheme	2	2.02	0.136	
	Plot	4	0.32	0.867	
	Planting scheme x plot	7	1.19	0.315	
	Error	136			
Height growth	Planting scheme	2	8.01	<b>&lt; 0.001</b>	Mon <sup>a</sup> > Mix <sup>b</sup> , Pro <sup>b</sup>
	Plot	4	5.77	<b>&lt; 0.001</b>	n. s.
	Planting scheme x plot	8	4.76	<b>&lt; 0.001</b>	
	Error	174			
Final DBH	Planting scheme	2	4.30	<b>0.015</b>	Pro <sup>a</sup> > Mon <sup>b</sup> , Mix <sup>b</sup>
	Plot	4	12.17	<b>&lt; 0.001</b>	P4 <sup>a</sup> , P3 <sup>a</sup> > P5 <sup>b</sup> , P2 <sup>b</sup> , P1 <sup>b</sup>
	Planting scheme x plot	8	6.20	<b>&lt; 0.001</b>	
	Error	168			
Final height	Planting scheme	2	2.02	0.136	
	Plot	4	16.49	<b>&lt; 0.001</b>	P3 <sup>a</sup> , P4 <sup>ab</sup> , P2 <sup>bc</sup> , P5 <sup>c</sup> , P1 <sup>c</sup>
	Planting scheme x plot	8	10.28	<b>&lt; 0.001</b>	
	Error	174			

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		df	F	P	Post hoc
<b><i>C. odorata</i></b>					
DBH growth	Planting scheme	2	4.50	<b>0.016</b>	Mix <sup>a</sup> > Mon <sup>b</sup> > Pro <sup>c</sup>
	Plot	4	0.88	0.482	
	Planting scheme x plot	5	0.98	0.439	
	Error	51			
Height growth	Planting scheme	2	0.52	0.595	
	Plot	4	7.15	< 0.001	P3 <sup>a</sup> P5 <sup>ab</sup> , P2 <sup>bc</sup> , P4 <sup>bc</sup> , P1 <sup>c</sup>
	Planting scheme x plot	7	3.51	0.003	
	Error	79			
Final DBH	Planting scheme	2	1.50	0.230	
	Plot	4	7.43	< <b>0.001</b>	P3 <sup>a</sup> > P5 <sup>b</sup> , P4 <sup>b</sup> , P2 <sup>b</sup> > P1 <sup>c</sup>
	Planting scheme x plot	6	3.77	<b>0.002</b>	
	Error	78			
Final height	Planting scheme	2	0.19	0.824	
	Plot	4	20.11	< <b>0.001</b>	P3 <sup>a</sup> > P5 <sup>b</sup> , P4 <sup>b</sup> , P2 <sup>b</sup> > P1 <sup>c</sup>
	Planting scheme x plot	7	10.57	< <b>0.001</b>	
	Error	80			

\*Statistical analysis was done by two-way ANOVAs, testing for planting scheme, plot, and interaction terms. Significant ANOVAs were followed by *LSD post hoc* tests, to which false discovery rate correction (Verhoeven *et al.* 2005) was applied. In *post hoc* tests contrasting letters refer to significant differences, whereas n. s. means that no significant differences were found.

#### 7.4.3 Border effects on tree survival and growth

The position of tree individuals within plots did not affect survival (all  $P > 0.05$ ) but had strong influence on tree growth depending on tree species identity and planting scheme. In *T. rosea*, individuals in monocultures exhibited significantly lower DBH growth when planted in the plot center ( $2.38 \text{ cm} \pm 1.5 \text{ (SE)}$ ) compared to individuals planted at the plot border ( $2.97 \pm 1.3$ ;  $F_{1,148} = 10.30$ ,  $P = 0.002$ ). Similarly in protected mixtures, DBH growth of *A. excelsum* was significantly reduced for individuals planted in the plot center ( $4.79 \pm 0.5$ ) compared to those planted at the plot border ( $6.97 \pm 0.5$ ;  $F_{1,20} = 8.75$ ,  $P = 0.008$ ). In contrast to the positive border effects in *T. rosea* and *A. excelsum*, individuals of *C. odorata* in monocultures exhibited a significantly greater height in the plot center than at the plot border ( $3.02 \pm 0.2$  vs.  $2.28 \pm 0.2$ ;  $F_{1,49} = 11.01$ ,  $P = 0.002$ ). Remaining comparisons of DBH and

height growth, and of final values of DBH and height among plot center and plot border revealed no significant differences (all  $P > 0.05$ ).

## 7.5 Discussion

We studied effects of species identity, tree diversity, and insecticide application on survival and growth of three native timber tree species planted on former pasture during the first five years after plantation establishment. We furthermore tested how the individual tree position within plots (border effects) affected tree growth in reforestation patches. Survival differed significantly among tree species and between plantation plots, but it was neither affected by planting schemes nor by position within the plot. Growth differed between species and was also affected by planting schemes, plots, and border effects.

### 7.5.1 Effects of tree species identity

Survival after five years was highest in *T. rosea* (96%), intermediate in *A. excelsum* (65%), and lowest in *C. odorata* (32%). The high survival of *T. rosea* was similar to that reported from other native tree plantations in Panama (van Breugel *et al.* 2011) and from the primary forest on nearby Barro Colorado Island (BCI; Condit *et al.* 1995). In contrast, survival of *A. excelsum* was comparably lower in our study than the survival recorded by Condit *et al.* (1995) on BCI. The observed low survival of *C. odorata* was even lower than observations from other reforestation trials (Carpenter *et al.* 2004, van Breugel *et al.* 2011). These findings suggest that *T. rosea* may be able to tolerate a wider range of environmental conditions than the latter two species (Plath *et al.* 2011b). The low survival of *C. odorata* furthermore supports the view that this species has very specific environmental requirements. The net photosynthesis of *C. odorata* increases with potassium and water content of the soil (Dünisch *et al.* 2002). Accordingly, van Breugel *et al.* (2011) observed the highest survival of *C. odorata* in sites with high amounts of rainfall and high soil fertility. In our study, the low survival of *C. odorata* in the plot with the lowest soil pH (plot 1, (Plath *et al.* 2011b)) might

therefore be related to insufficient availability of nutrients at this location. Our finding that species-specific survival rates of *T. rosea*, *A. excelsum*, and *C. odorata* were not affected by tree diversity is in agreement with another study conducted in the vicinity of our plantation, which also reported no effects of tree diversity on timber tree survival in plantations (Potvin & Gotelli 2008).

Regarding tree growth, we observed a change in size patterns five years after tree establishment compared to size patterns in the first two growth years (Plath *et al.* 2011b). Whereas *T. rosea* was the tallest species with the largest diameter at breast height (DBH) two years after tree establishment, its growth from year 3 to year 5 was as low as that of *C. odorata*. In contrast, the growth of *A. excelsum* increased between year 3 and 5, rendering *A. excelsum* the tallest tree species with the largest DBH five years after tree planting. Our results thereby emphasize that measures of tree performance should span an adequate period of time to account for changes in growth patterns and to draw reliable conclusions about species performance and their suitability for reforestation. Patterns of tree growth and associated traits may change during the individual life cycle (Dalling *et al.* 2004, Delagrange *et al.* 2008) and with stand development and concurrent alteration in resource use patterns (Filipescu & Comeau 2007, Cavard *et al.* 2011). Whereas *T. rosea* is a shade-tolerant, non-pioneer species, characterized by its high-density wood and slow growth, *A. excelsum* is a fast growing pioneer species characterized by its low-density wood and fast growth (van Gelder *et al.* 2006, Delagrange *et al.* 2008). Therefore the size and growth patterns recorded in year 5 agree better with the life-history traits and the successional status of the studied tree species predicted by literature than the pattern recorded two years after establishment. Concerning *C. odorata*, our results support the view that *C. odorata* grows best in open or slightly shaded conditions (Ricker *et al.* 2000, Gyimah & Nakao 2007) and can be considered as a long-lived pioneer (Carpenter *et al.* 2004), as its DBH growth from year 3 to 5 was lowest in protected mixtures, the planting scheme with the tallest trees, intermediate in monocultures, where its conspecific neighbours were comparably small, and highest in unprotected mixtures.

### 7.5.2 Effects of tree diversity

In contrast to species identity and plots, tree diversity did not significantly affect tree survival, but had significant effects on tree growth, which varied among the studied species. *T. rosea* and *C. odorata* benefitted from stand diversification, with a significantly higher DBH growth between year 3 and year 5 in unprotected mixtures than in monocultures. Underlying mechanisms might be a weaker interspecific competition in mixed stands than intraspecific competition in monocultures due to differential resource utilization (competitive reduction, Forrester *et al.* 2005), or enhanced accessibility of light due to initiating canopy stratification (Erskine *et al.* 2006, Grant *et al.* 2006). Following this reasoning, the reduced growth of *T. rosea* in monocultures was probably mediated by stronger intraspecific competition for light with its direct conspecific neighbors (Potvin & Gotelli 2008). For *C. odorata*, in contrast, competition for light was probably lower in monocultures due to the small size of the conspecific neighbour trees. Hence, the beneficial effect of mixtures was possibly caused by a reduction of irradiance or by partitioning of belowground resources (Forrester *et al.* 2005, Gyimah & Nakao 2007). In fact, *C. odorata* is efficient in acquiring nutrients and produces more biomass in species mixtures than in monocultures (Oelmann *et al.* 2010). These findings demonstrate that for different species, positive effects of neighbour identity on tree growth can be caused by different mechanisms.

In contrast to *C. odorata* and *T. rosea*, stand diversification showed no significant effect on DBH growth of *A. excelsum* from year 3 to 5, which was equally high in all planting schemes, while its height growth during this time was largest in monocultures. This suggests that competitive relationships in a conspecific environment can be more favorable for *A. excelsum* than for the other two tree species studied. However, even if mixtures enhance the performance of only a selection of planted timber tree species, higher biodiversity and the possibility to harvest timber of different species on varying rotations can favor their establishment (Lamb *et al.* 2005, Kelty 2006).

### 7.5.3 Effects of insecticide treatment

Effects of insecticide treatment found during the first two years after establishment at the same study site (see Plath *et al.*, 2011b) were still visible in year 5. Final DBH and final height of *T. rosea* as well as final DBH of *A. excelsum* were highest in protected mixtures. As growth from year 3 to 5 of *T. rosea* and *A. excelsum* did not differ between protected and unprotected mixtures, their larger size probably reflects the increased growth during the years of insecticide treatment (year 1 and 2). However, as strategic insecticide treatment during the first two years of growth may lead to longer-term differences in tree size, it may be an expedient management strategy, especially since trees are particularly vulnerable to herbivore attack during the sapling stage (Plath *et al.* 2011b, Plath *et al.* 2012), and because the abundance of herbivore-antagonists, which could possibly exert top-down control on herbivores, can be very low in recently established plantations on former pasture (Riedel *et al.* 2012a). Insecticide treatment did not benefit *C. odorata*, which had the lowest DBH growth in protected mixtures and showed no differences in height growth, final height, or final DBH 5 years after establishment between protected and unprotected mixtures. As it was the tree species with the lowest growth performance among all species studied, the negative effect of strong shading by larger neighbor trees was probably more relevant than a potential reduction of herbivore damage, particularly for a light-demanding species such as *C. odorata* (Alvarez-Clare & Kitajima 2009, Easdale *et al.* 2012).

### 7.5.4 Border effects and implications for pasture reforestation

The individual tree position within plots strongly affected tree growth, but the direction of this effect varied among tree species and planting schemes. Height growth of *C. odorata* was greater in the center than at the plot borders of monoculture plots, possibly indicating positive effects of neighboring trees on microclimate, light conditions, or pest infestation (Hauxwell *et al.* 2001 and references therein, Gyimah & Nakao 2007). Contrastingly, *T. rosea* in monocultures and *A. excelsum* in protected mixtures showed a significantly reduced DBH growth in the plot center, illustrating the variable influence of inter - and intraspecific

competition for light on the performance of the two timber species (Riedel *et al.* 2012b, Zhang *et al.* 2012). The finding that DBH growth of *T. rosea* differed between plot border and plot center in monocultures but not in unprotected or protected mixtures supports the previous reasoning that for this species intraspecific competition in monocultures was more detrimental than possible interspecific competition in mixed stands.

*A. excelsum*, on the other hand, may have encountered more adverse conditions in the center of protected mixture plots, compared to the plot border. This was probably caused by higher interspecific competition for light, as *T. rosea* exhibited greatest final DBH and final height in this planting scheme. Water shortage was probably not the cause of the reduced growth of *A. excelsum* trees in the plot center of protected mixtures, since *A. excelsum* has higher mean water use rates than *C. odorata* and *T. rosea* (Kunert *et al.* 2010), and because soil nutrient concentrations at the study site are high, belowground competition for nutrients was possibly also less relevant (Oelmann *et al.* 2010, Plath *et al.* 2011b).

In contrast to Holl *et al.* (2011), who reasoned that abiotic conditions might be more stressful at plot borders for species with relatively low light saturation points, both the climax species *T. rosea* and the pioneer *A. excelsum* exhibited equal or better growth at plot borders. This demonstrates that for the planting of trees in small patches within pastures, the small size of the reforestation plots does not hinder successful tree growth. Furthermore, increasing light availability through selective thinning in the plot center might be advantageous for tree growth.

## Conclusions

Survival of native timber tree species planted on a former pasture in Panama was highly species-specific and affected by small-scale environmental heterogeneity. Tree diversity and insecticide application during the first two years after establishment had no longer-term effect on timber tree survival five years after establishment, but had significant longer-term effects on tree growth of the individual tree species. Early insecticide treatment led to a larger size of *T. rosea* and *A. excelsum* five years after planting but did not enhance new tree growth in later years. Depending on tree species, both mixtures and monocultures may provide the best growing results for establishing trees, indicating that tree stand diversification may not only

support competitive reduction (*T. rosea*, *C. odorata*) but may likewise lead to strong interspecific competition for individual species (*A. excelsum*). However, due to the additional benefits of species mixtures, this planting scheme seems to be a generally promising reforestation system of degraded pastures. Small size of reforestation plots does not hinder tree growth but can be beneficial for different tree species, probably due to increased light availability at the borders of the plots.

## 8 General Discussion

Restoration of degraded tropical pastures requires tree planting systems that integrate landholder needs. In the tropics, especially Latin America, cattle pastures comprise a huge part of land use, rendering planting of native timber trees on degraded pastures a promising strategy of ecological restoration. Reforestation, however, is often impeded by lack of knowledge on species-specific ecological requirements, favorable planting systems, and insect herbivory. The aim of this work was to generate quantitative information on determinants of insect herbivory and on the effects of planting schemes on associated growth of native timber trees on degraded tropical pastures.

We found that bottom-up factors of host tree association had strong but opposing effects on the two main herbivores of *Tabebuia rosea*, the lepidopteran *Eulepte gastralis* and the coleopteran *Walterianella inscripta*. Top-down effects by ants on insect herbivory were weak, as exclusion of ants produced only marginal effects on arthropod assemblages and herbivory. Ants comprised only 2% of the arthropod assemblages in the tree crowns of *T. rosea* and ant assemblages were dominated by ground nesting species, such as *Ectatomma ruidum* and *Camponotus lindigi*. Tree survival was species-specific, with *T. rosea* having the highest survival after five years and *Cedrela odorata* having the lowest survival. Tree growth was affected by tree species identity, tree diversity, insecticide treatment, plots, and border effects, but these effects differed among tree species. Companion trees supported or impeded growth of *T. rosea* in the silvopastoral system, depending on the companion tree species identity.

### 8.1 Bottom-up control of insect herbivores

Overall, *E. gastralis* followed by *W. inscripta* were the most relevant herbivores of *T. rosea* in both the pasture afforestation system and the silvopastoral system. The two herbivores showed opposing reactions to tree stand diversity and host tree density. In the pasture afforestation system, *E. gastralis* was more abundant and contributed more to total leaf damage in mixed stands, whereas *W. inscripta* was more abundant and contributed more

to leaf damage in monocultures (Plath *et al.* 2012). In the silvopastoral system, companion trees did not significantly reduce herbivory of *T. rosea*, even though trees growing with *G. ulmifolia* had the lowest leaf damage in both studied years. Possibly companion trees did not disrupt host plant finding sufficiently to decrease herbivory (Barbosa *et al.* 2009, Finch & Collier 2012). However, rather than olfactory or visual barriers by companion trees, the general design of the silvopastoral system, that is to say the low density of host trees, seems to play a crucial role, as density of *E. gastralis* was higher in the silvopastoral system than in the high density pasture afforestation system. Contrastingly, density of *W. inscripta* was much lower in the silvopastoral system than in the pasture afforestation system.

In the case of *E. gastralis*, infestation probably depends on the host location and oviposition behavior of the female moth, as *E. gastralis* caterpillars complete their development on the same tree individual on which oviposition has occurred (Hernández & Briceño 1999). In agreement, *E. gastralis* larvae did not discriminate in dual-choice feeding tests between leaves from *T. rosea* trees, which varied in infestation in the field (J. Riedel, unpublished data). Interactions between herbivore species might be relevant, as the moths might prefer low density arrangements of host trees, such as mixed stands or silvopastoral systems, in search of 'competitor free space' (Root & Kareiva 1984, Murphy 2004, Tack *et al.* 2009, Plath *et al.* 2012, Wielgoss *et al.* 2012).

An alternative explanation for the resource dilution strategy of *E. gastralis* is the search for 'enemy free space' (Pöykkö 2011), as host localization by antagonist species might be hindered by complex vegetation patterns and larger distances between the focal trees in mixtures (Randlkofer *et al.* 2010, Mody *et al.* 2011). However, even though parasitism of *E. gastralis* caterpillars is high at the study site (approx. 25%), no differences in parasitism were found between mixtures and monocultures (J. Riedel, unpublished data). Furthermore, ants had only mediocre effects on herbivory at the study site (see next chapter). As such, the reduced competition with other herbivores in low density tree stands is a more probable explanation for the high infestation of *T. rosea* trees with *E. gastralis* in mixtures of the pasture afforestation system and in the silvopastoral system, than reduced impact of natural enemies of the herbivores. Hence, contradictory to the resource concentration hypothesis (Root 1973), specialists may respond positively to resource dilution (Yamamura 2002, Otway *et al.* 2005). Accordingly, *T. rosea* experienced associational susceptibility to *E. gastralis* when growing in mixed stands together with *Anacardium excelsum* and *C. odorata*.

Leaf and tree characteristics had detectable effects only on *W. inscripta*, which was positively associated with tree height and leaf nitrogen content. These highly mobile herbivores might be attracted to conspicuous large trees and actively feed on those that present fresh leaves and associated high quality foliage (Basset 1991, Jordano & Gomariz 1994, Coley & Barone 1996, Ruhnke *et al.* 2009).

After five years, trees growing in mixtures treated with insecticides during the first two years after plantation establishment were still larger than trees growing in untreated mixtures and monocultures, highlighting the large and detrimental effect of herbivory on tree growth at the study site. This finding is in accordance with studies demonstrating the strength of biotic interactions in the tropics (Andrew & Hughes 2005, Schemske *et al.* 2009) and pronounced effects of herbivory on growth and survival of tropical trees (Eichhorn *et al.* 2010, Massad 2012). However, herbivory affects tree growth together with direct tree-to-tree interactions and local site conditions (Hambäck & Beckerman 2003, Baraza *et al.* 2010, Chaneton *et al.* 2010). While herbivory of *T. rosea* proved to be lower in monocultures than in mixed stands of the pasture afforestation system (Plath *et al.* 2011b, Plath *et al.* 2012), stem diameter growth of *T. rosea* from year 3 to year 5 was higher in mixtures than in monocultures. This result indicates that at the study site, negative associational effects of heterospecific tree neighbors on herbivory can be outweighed by direct positive effects on tree growth. Therefore effects of planting schemes and associated tree neighbor identity on herbivory have to be considered jointly with competitive and facilitative effects of tree-to-tree interactions on tree growth.

## **8.2 Top-down control of insect herbivores**

The presence of ants can benefit plants by reducing herbivory and enhancing plant fitness (Rosumek *et al.* 2009). Ants may prevent herbivores from oviposition (Freitas & Oliveira 1996, Adandonon *et al.* 2009), actively prey on herbivores (Floren *et al.* 2002, Agarwal *et al.* 2007), or reduce herbivory by molesting herbivores and decreasing feeding activity (de la Fuente & Marquis 1999). Contrastingly, ants can also have indirect negative effects on plants, by exhibiting antagonistic effects on parasitoids (Mody *et al.* 2011) or spiders (Mody &

Linsenmair 2004). However, ant effects on herbivory and plant performance appear to be generally positive, although the magnitude of protective effects is variable (Chamberlain & Holland 2009, Rosumek *et al.* 2009). The extent of ant-mediated plant protection depends *i.a.* on ant species richness and on adequate predator-prey ratios (Di Giusto *et al.* 2001, Chamberlain & Holland 2009).

Our study site was originally covered by lowland tropical rain forest but this forest was logged in 1951-1952 (Potvin *et al.* 2004). Following two years of agriculture the site has been used as cattle pasture for over fifty years, before in 2006 the plantation was established. The site is hence a highly disturbed habitat, characterized by low habitat complexity. Accordingly, ant assemblages were dominated by a few ground-nesting species that are tolerant to habitat disturbance and frequently inhabit open pasture habitats, such as *E. ruidum* or *S. geminata* (Way *et al.* 2002, Zelikova & Breed 2008). Our study has shown that although ants were sparse in the tree crowns, visitation by *E. ruidum* slightly decreased leaf damage exerted by *E. gastralis*, the main lepidopteran herbivore of *T. rosea*, and that *E. ruidum* might therefore be an effective plant mutualist. However, in spite of the potential of *E. ruidum* as herbivore antagonist and although nest density and presence of *E. ruidum* were high at the study site (see Appendix) it did not provide sufficient predation pressure to decrease foliar herbivory on *T. rosea*. One explanation might be that the moderate amounts of extrafloral nectar that *T. rosea* produces (Diaz-Castelazo *et al.* 2005) did not suffice to attract effectual ant numbers to the trees (Di Giusto *et al.* 2001).

Furthermore, arboreal ants, which can be effective plant mutualists (Floren *et al.* 2002), were greatly absent from the plantation. It remains to be tested whether *T. rosea* receives ant-mediated protection in more natural habitats, such as forests. In the young plantation, necessary habitat requirements of arboreal ants, such as nesting sites like epiphytes or wood cavities, had not yet been established (Blüthgen *et al.* 2000). However, whether arboreal ants become a relevant top-down factor in the future depends on their occurrence on remaining trees and fragments from the original forest or on their re-introduction into the habitat from the nearest forest, via connecting elements such as living fences or alleys. Top-down control of insect herbivores by ants hence may gain importance when ant numbers on trees increase in parallel to resources for tree-dwelling ants on growing trees, if it is possible for arboreal ants to immigrate into the reforestation from nearby forest fragments.

### 8.3 Growth performance in different planting systems

The performance of the three native timber tree species planted at the study site was highly species-specific. After five years, *T. rosea* showed the highest survival and an intermediate size, *A. excelsum* had intermediate survival and the largest size, and *C. odorata* was the smallest species with the lowest survival. Survival and growth were further affected by local site conditions, but the direction of the effect depended on species identity (for example *T. rosea* had its lowest survival in plot 1, which was characterized by high soil moisture and low soil pH (Plath *et al.* 2011b), where *A. excelsum* had its highest survival). Tree growth, on the other hand, was generally reduced in plot 1. These results demonstrate that different species react differently to small-scale environmental variability and highlight that detailed knowledge on species-specific requirements is necessary before recommending a species to growers. Due to their valuable wood, additional values, and native status in Central America, all three species can be recommended for reforestation in the region. However, *C. odorata* is a very delicate species with very specific requirements, that should only be planted on adequate, fertile, well-drained soils with sufficient aeration (Dünisch *et al.* 2002, AgroForestryTreeDatabase 2009, Plath *et al.* 2011b, van Breugel *et al.* 2011). Furthermore, thought has to be given on which planting systems to implement, as the three species showed opposite reactions to management measures. *T. rosea* and *C. odorata* benefitted from stand diversification, possibly due to competitive reduction (Forrester *et al.* 2005), whereas *A. excelsum* seems to benefit rather from conspecific than from heterospecific competitors. Accordingly, *A. excelsum* benefitted from the reduced abundance of large, heterospecific neighbors, when growing at plot borders in protected mixtures and *T. odorata* benefitted from plot borders when growing in monocultures. Holl *et al.* (2011) raised the concern that abiotic conditions, specifically high irradiance, might be more stressful at the borders of small tree patches. In agreement with this argument, *C. odorata* showed better growth in plot centers of monocultures, because its small, conspecific neighbors did not produce much shade. Whether small patch size provides an advantage or hindrance to tree growth, depends on species characteristics, such as *e.g.* the light saturation point (Holl *et al.* 2011). Furthermore, robust species, like *T. rosea* and *A. excelsum*, that have a good growth and likely become limited by access to light, can be planted in small patches within pastures, and they will benefit from increased light at plot borders. For large species, like *A. excelsum*

that can grow up to 45m in height (Fournier 2003), additional management measures to provide sufficient space might be advantageous.

In the silvopastoral system, growth of *T. rosea* was supported by companion planting with *G. sepium* but hindered by companion planting with *G. ulmifolia*. This finding contrasts the results obtained for the first two years of growth, when trees were still smaller. At that time, companion trees did neither have facilitative nor competitive effects on the growth of *T. rosea* (Plath *et al.* 2011a). After five years, companion planting with *G. sepium* did still not increase the nitrogen content and  $\delta^{15}\text{N}$  values of *T. rosea* leaves, but the large size of *G. ulmifolia* companion trees was associated with reduced growth of trees growing accompanied by this species. Lower LMA and  $\delta^{13}\text{C}$  values, and significantly higher water content of *T. rosea* leaves, indicated reduced water stress and higher shading of trees growing surrounded by *G. ulmifolia* (Mody *et al.* 2009, Daas-Ghrib *et al.* 2011, Gutbrodt *et al.* 2012). As *T. rosea* is highly light demanding (Potvin & Gotelli 2008), the decreased light availability has probably retarded its growth in this planting scheme. Even though *G. sepium* did still not facilitate nitrogen uptake of *T. rosea* five years after tree planting, it turned out to be a very beneficial companion tree. Stem diameter growth of *T. rosea* trees growing with *G. sepium* was as high as that of solitary trees, whereas it was reduced for *T. rosea* trees growing with *G. ulmifolia*. Furthermore, *G. sepium* provides many goods to farmers, including fodder for cattle in the dry season and firewood (Wishnie *et al.* 2007, Akinnifesi *et al.* 2010, Harvey *et al.* 2011). In fact, companion planting with any species that does not impede tree growth of the central tree is advantageous as companion trees can shield the central tree from cattle and might reduce fencing costs (Love *et al.* 2009). Our findings on effects of companion trees on timber trees lead to two principal conclusions: (1) tree-to-tree interactions in companion plantings might become more pronounced with stand development and concurrent alteration of tree and resource use patterns (Dalling *et al.* 2004, Filipescu & Comeau 2007, Delagrange *et al.* 2008, Cavard *et al.* 2011). (2) Whether companion trees support or impede the growth of a central tree depends on the selection of an appropriate companion tree species. At the study site, *G. sepium* was a favorable companion tree for *T. rosea*.

## 8.4 Implications for the reforestation of tropical pastures

We investigated determinants of insect herbivory and tree growth for three native Central American timber tree species in two innovative planting systems using native tree species: (1) the silvopastoral system, which combines timber trees with multipurpose companion trees, and (2) the pasture afforestation system, which is designed to plant mixtures or monocultures of timber trees, possibly in small patches within the pastures. These planting systems might be applicable in different settings across Central America, and potentially across the world's tropics, if implemented with different tree species. The study has been conducted at one study site within an agricultural landscape in Panama. Although small-scale variability in environmental characteristics was high across the study site, care should be taken when extrapolating our findings to other sites, as variation between sites can be high (van Breugel 2011). Herbivory and local site conditions proved to be very important factors determining the success of the planting systems. We further demonstrated that tree-to-tree interactions can be favorable for example in species mixtures of *T. rosea* or *C. odorata*, or in companion plantings of *T. rosea* with *G. sepium* in silvopastoral reforestations. However, we have shown that biotic interactions between trees and between trees and herbivores were highly species-specific. Interactions between species might change at different locations, rendering different combinations of trees more favorable at other sites. Hence, knowledge has to be expanded to include further tree species and test the outcome of the proposed planting systems at various sites differing in climatic and soil characteristics. Furthermore, herbivory should be evaluated at a larger scale to test whether *E. gastralis* and *W. inscripta* are relevant across Central America and whether they are specialists across multiple sites. The potential for top-down control should be assessed in a forest to gain insight on the effects of ants on herbivory of *T. rosea* at a less degraded site.

Overall, to fulfill the world's increasing demand of food products, it is imperative for a sustainable world food system to integrate conservation into agricultural areas and the complete anthropogenic biome, which covers the majority of the earth's land surface (Ellis 2011). Interest in native tree species is increasing (Hall 2011). However, as deforestation proceeds, knowledge gained from scientific studies has to be tested for practical applicability, and sociologic factors limiting deforestation have to be investigated (Garen 2011). Findings have to be communicated to small-scale farmers, stakeholders, and to policy makers.

Ultimately, whether research on reforestation systems contributes to conservation and land restoration, depends on financial and practical support of people willing to plant trees in intelligently designed reforestation systems.

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## 10 Appendix

### Ant diversity in different planting systems of a tropical, native timber tree plantation on former pasture

This appendix (App.) is the basis for a further manuscript focusing on ant diversity.

#### App. 1. Objectives

- (1) To record ant diversity of a tropical native timber tree plantation on former pasture
- (2) To compare ant abundance at baits, and nest density of the ant species *Ectatomma ruidum* and *Camponotus lindigi* among different planting schemes of a pasture afforestation system and a silvopastoral system

#### App. 2. Methods

##### App. 2.1 Study site and species

The study was conducted from July 2009 (year 1) to November 2011 (year 3) in a native tree plantation in Sardinilla, Central Panama (9°19'30"N, 79°38'00"W, elevation 70 m a. s. l.), about 40 km north of Panama city and 30 km north-east of Barro Colorado Island. The climate at the study site is semi-humid tropical with a mean annual temperature of 25.2° C, a mean annual precipitation of 2289 mm and a dry season from January to April (134 ± 19 days) (Wolf *et al.* 2011). The semi-deciduous lowland rainforest previously covering the study site was logged in 1952/53 and after two years of agricultural use the site was converted into pasture and grazed by cattle for almost 50 years (Potvin *et al.* 2004).

The selected focal timber species, *Tabebuia rosea* Bertol. (Bignoniaceae), is a native, commercially valuable timber tree that has good growth potential across different environmental conditions and is suitable for pasture reforestation (for details see Plath *et al.* 2011a, b and references therein). It is a deciduous tree attaining a size of 25-30 m with a natural distribution range from Southern Mexico to Venezuela, which occurs naturally in

tropical wet-, moist-, and dry forests and is also extensively cultivated throughout the tropics (Gentry 1973, Wishnie *et al.* 2007). *Tabebuia rosea* bears scale-like extrafloral nectaries that secrete a modest amount of nectar on the surfaces of its palmate, five-foliolate leaves and on young stems (Diaz-Castelazo *et al.* 2005). The principal leaf flushing takes place in the early rainy season, and leaves are shed during the dry season (Gentry 1970).

## **App. 2.2 Planting design**

The native tree plantation was established on former pasture in August 2006 in an area where experimental reforestation activities took place since 2001 (Potvin *et al.* 2004). Trees were planted as 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. We established two planting systems: a pasture afforestation system and a silvopastoral system.

Within the pasture afforestation system, *T. rosea* was planted either in monoculture or in three species mixture together with the native timber trees *Anacardium excelsum* (Betero and Blab. ex Kunth) Skeels (Anacardiaceae) and *Cedrela odorata* L. (Meliaceae). Trees were established in stands of 36 trees (distance between trees = 2 m) using a standardized six by six Latin square design. Mixed stands consisted of 12 individuals per species, whereas monocultures consisted of 36 individuals of the same species. Mixed and monoculture stands were arranged in one locality as a coherent plot, which was replicated five times within the Sardinilla study site (PA1-PA5).

Within the silvopastoral system, seedlings of *T. rosea* were established at low density (distance between trees = 9 m) in three different planting schemes: (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 schemes, five conspecific companion seedlings were planted circularly around the central timber tree at a distance of 1.5 m. Planting schemes consisted of eight *T. rosea* individuals that were randomly arranged within a coherent plot. This plot was

replicated three times (SP1-SP3), resulting in a total of 24 timber tree individuals per planting scheme.

In both systems, local site conditions, including soil moisture, soil pH, soil nitrogen content and collateral vegetation, varied notably across plots (Plath *et al.* 2011a, b). In PA1 and SP1 concomitant vegetation (short grasses and herbs) was mown approximately once a month, whereas in PA2-5, SP2 and SP3 competing vegetation (tall grasses and woody successional vegetation) was cleared, every two months in the first two years of plantation establishment and 1-2 times per year during the rainy season in the study years.

### **App. 2.3 Assessment of ant assemblages**

In the pasture afforestation system, ants were sampled from six randomly selected *T. rosea* trees per tree stand, resulting in a total of 60 sampled trees, 30 trees in mixed stands and 30 trees in monoculture stands. In the silvopastoral system, ants were sampled on all surviving *T. rosea* trees. Incidental tree mortality resulted in a total of 24 (TGua), 23 (TSol), and 22 (TGli) sampled trees. Ant assemblages were assessed by recording ant abundance at sugar and tuna baits. Furthermore, we recorded the nest density of two dominant ant species, *Ectatomma ruidum* Roger and *Camponotus lindigi* Mayr. Ants were determined to genus and (morpho)species after Hölldobler and Wilson (1990), Bolton (1994), and Fernández (2003). Where possible, taxonomic experts were consulted for identification of ant species.

#### **App. 2.3.1 Ant samplings from branches of *T. rosea***

Ants were sampled from the tree crowns of the study trees at four dates in year 1 (09-22 July, 19 August to 1 September, 28 September to 2 October, 27-30 October) and at two dates in year 2 (24-27 August, 20-22 September) during day and night with a beating tray. The tray (0.5 m x 0.5 m) was positioned directly below the sample branch, which was then shaken for approximately eight seconds. All ants in the tray were collected in an ethanol containing plastic container mounted to the bottom of the tray. Ant numbers of each branch were standardized to the number of sampled leaves.

### **App. 2.3.2 Abundance of bark dwelling ants recorded with branch traps**

We recorded the abundance of bark dwelling ants by using branch eclector traps, which consisted of a ring of black duct tape, fitted tightly around a branch, a plastic funnel, and a container (Stuntz *et al.* 1999, Koponen 2004). The duct tape was treated with FLUON (polytetrafluorethylene, PTFE) to create a slippery surface. The funnel was hung beneath, leading into a plastic container filled with saturated NaCl solution as preservation liquid. The container had an overflow hole below the lid, which was covered with gauze. Traps were hung up between 26 and 28 July of year 2 and left in the tree crowns of the study trees for 13-14 days.

### **App. 2.3.3 Ant activity at baits**

To estimate the potential ant activity per study tree, we quantified the abundance of each ant (morpho)species by using baits mounted to the tree trunks. In year 1, we placed a set of two types of baits in the tree crowns of the study *T. rosea* trees. Baits consisted of either 4 g of tuna ('nitrogen bait') or a piece of cotton soaked in 4 ml saturated sucrose solution ('sugar bait'), and were put on a wooden plate with an area of 10 cm<sup>2</sup>, which was attached horizontally to the branch using a thin wire. The maximum distance between the two baits was 20 cm. We observed the baits during the day, 30 min, 1 h, 2 h, and 3 h after bait placement and recorded number of ant species and individuals present on the wooden plate. Recordings took place during two weeks in July/August of year 1. As recruitment of ants to the baits was slow, we used the recording of ant individual numbers 2 h after mounting the bait for statistical analysis and as the standard recording time in subsequent assessments.

Based on the experience of year 1, we adjusted the measurement method and quantified ant abundance at baits in year 2 by using sugar baits that consisted of cut-open Eppendorf tubes (2 ml) filled with saturated sucrose solution and cotton (Blüthgen *et al.* 2006, Riedel *et al.* 2012). The cotton protruded as a wick to the tree trunk and made the solution available to ants. One bait per tree was attached to the trunk at 1.60 m height. We counted all ant individuals within a radius of 5 cm around each bait in four sampling events (4 August, 31 August to 1 September, 17/18 September, 10 November), consisting of a night and a day

assessment. To ensure comparably consistent weather conditions and high ant activity, ant counts were conducted between 20:00 h and 22:00 h for the night-assessments and between 07:00 h and 10:30 h for the day-assessments. Ant activity was re-assessed in October/November of year 3 (31 October to 3 November) by conducting one sampling at day and night, using the same method as in year 2.

Occasionally, individual numbers of *Soleonopsis geminata* were exceedingly high. Counting was then discontinued at 50 individuals, and abundance was recorded as 50 individuals, taking into account an underestimation of total abundance of this species. For each ant species not readily identifiable in the field, one to three reference specimens (depending on the number of ant individuals at the bait) were collected per bait and stored in 75% ethanol for later identification. In case a single ant specimen escaped without prior identification of the genus, it was listed as "unknown species".

#### **App. 2.3.4 Nest density of *E. ruidum* and *C. lindigi***

Nest density of two dominant ant species, *E. ruidum* and *C. lindigi*, was recorded in the pasture afforestation system and in the silvopastoral system by attracting ants with sugar baits as described above. Baits were directly attached to the trunks of *T. rosea* 40 cm above the ground. Ant workers departing from the baits were followed to their nests within a radius of 60 cm around the examined *T. rosea* tree and the number of nest entrances in the resulting 'observation circle' was recorded. Two hours after mounting the bait, each observation circle was then observed for 20 minutes. As the typical structure of *E. ruidum* nests has been described as having only one entrance (Levings & Franks 1982), each nest entrance was counted as one colony, unless the distance between entrances was below 10 cm. In pasture afforestation plots, nests were recorded around the stems of 12 randomly selected *T. rosea* trees, whereas in silvopastoral plots nests were recorded around each *T. rosea* tree. Of each colony one to four reference specimens were collected and preserved in 75% ethanol.

## App. 2.4 Data analysis

To compare ant activity at baits among planting schemes we used the sum of the recorded individual numbers of all sampling events. Ant activity and nest density were compared among planting schemes with Kruskal-Wallis tests (silvopastoral system) and *U*-tests (pasture afforestation system), separately for total ant abundance and abundance of the three dominant species, *S. geminata*, *E. ruidum*, and *C. lindigi*. Significant Kruskal-Wallis tests were followed by *U*-tests as *post-hoc* tests, to which false discovery rate correction was applied (Verhoeven *et al.* 2005). Total ant abundance as well as abundance of *E. ruidum* and *C. lindigi* at baits were compared among sugar baits and nitrogen baits by using paired Wilcoxon tests. Nest densities of *E. ruidum* and *C. lindigi* were related to each other using Spearman's correlation. Nest densities were compared among the silvopastoral system and the pasture afforestation system by using *U*-tests.

## App. 3. Results

### App. 3.1 Effects of tree planting systems on ant abundance

In total we collected 943 ant individuals belonging to 26 (morpho)species by branch sampling in year 1 and year 2, and 272 ant individuals belonging to 18 (morpho)species with branch traps in year 2 (Table App. 1).

At baits mounted to trunks of *Tabebuia rosea*, we observed a total of 6325 ant individuals, which belonged to 19 (morpho)species in 11 genera and 6 sub-families (Table App. 1). The ant assemblage recorded by baiting was dominated by three species: *Solenopsis geminata*, *Ectatomma ruidum*, and *Camponotus lindigi* (Table App. 1). *Solenopsis geminata* had the highest individual numbers but comparably low incidence, meaning that it was observed at the baits at few times but each time with high individual numbers (Table App. 1).

**Table App. 1.** Diversity and abundance of ants collected from *Tabebuia rosea* by branch sampling and branch traps and recorded at baits on the tree trunks. Total individual numbers (percentages in brackets) are shown. Incidence values represent the percentage of ant counts in which a single species was present at a bait in relation to the total number of assessments.

Sub-family	species	Branch samples	Branch traps	Baits	
				Individuals	Incidence
Formicinae	<i>Brachymyrmex</i> sp. 1	8 (0.85)	0	0	0
	<i>Camponotus abdominalis</i>	8 (0.85)	7 (2.57)	275 (4.35)	0.046
	<i>Camponotus lindigi</i>	377 (39.98)	31 (11.40)	583 (9.22)	0.138
	<i>Camponotus</i> sp. 2	95 (10.07)	13 (4.78)	76 (1.20)	0.027
	<i>Camponotus</i> sp. 3	17 (1.80)	0	3 (0.05)	0.002
	<i>Camponotus</i> sp. 4	1 (0.11)	0	0	0
	<i>Camponotus</i> sp. 5	0	0	10 (0.16)	0.001
	<i>Camponotus</i> sp.	0	0	15 (0.24)	0.007
	<i>Paratrechina</i> sp. 1	3 (0.32)	0	20 (0.32)	0.004
Myrmicinae	<i>Crematogaster</i> sp. 1	25 (2.65)	0	33 (0.52)	0.001
	<i>Crematogaster</i> sp. 2	3 (0.32)	1 (0.37)	30 (0.47)	0.008
	<i>Crematogaster</i> sp.	0	0	120 (1.90)	0.008
	<i>Monomorium</i> sp. 1	3 (0.32)	0	0	0
	<i>Monomorium</i> sp. 2	1 (0.11)	0	0	0
	<i>Cyphomyrmex</i> sp. 1	1 (0.11)	2 (0.74)	0	0
	<i>Pheidole</i> sp. 1	16 (1.70)	1 (0.37)	26 (0.41)	0.005
	<i>Pheidole</i> sp. 2	2 (0.21)	2 (0.74)	0	0
	<i>Pheidole</i> sp. 4	1 (0.11)	0	0	0
	<i>Pheidole</i> sp.	0	3 (1.10)	91 (1.44)	0.006
	<i>Solenopsis geminata</i>	27 (2.86)	0	2733 (43.21)	0.066
	<i>Solenopsis</i> sp. 1	5 (0.53)	0	5 (0.08)	0.001
	<i>Strumigenys</i> sp. 1	1 (0.11)	0	0	0
	<i>Wasmania auropunctata</i>	0	1 (0.37)	2 (0.03)	0.001
	Ponerinae	<i>Hypoponera</i> sp. 1	1 (0.11)	0	0
Proceratinae	<i>Discothyrea</i> sp. 1	0	0	1 (0.02)	0.001
Pseudomyrmecinae	<i>Pseudomyrmex gracilis</i>	31 (3.29)	17 (6.25)	9 (0.14)	0.005
	<i>P. occultatus</i>	1 (0.11)	1 (0.37)	0	0
	<i>Pseudomyrmex</i> sp. 1	12 (1.27)	4 (1.47)	12 (0.19)	0.005
Dolichoderinae	<i>Azteca</i> sp. 1	0	0	23 (0.36)	0.001
	<i>Azteca</i> sp. 2	1 = (0.11)	0	0	0
	<i>Dolichoderus bispinosus</i>	8 (0.85)	1 (0.37)	39 (0.62)	0.003
	<i>Tapinoma</i> sp. 1	1 (0.11)	0	0	0
Ecitoninae	<i>Eciton burchellii</i>	0	3 (1.10)	0	0
Ectatomminae	<i>Ectatomma ruidum</i>	269 (28.53)	166 (61.03)	2119 (33.50)	0.283
unknown		25 (2.65)	2 (0.74)	100 (1.58)	0.014
TOTAL (Individuals)		943	272	6325	0.542
TOTAL (Species)		26	15	19	

In the pasture afforestation system, total number of ant individuals at baits in year 2 was three times as high in monocultures than in mixed tree stands, and total ant abundance cumulated over all three years was twice as high in monocultures than in mixed tree stands (Table App. 2). Among individual ant species, abundance of *C. lindigi* was marginally higher in mixed tree stands than in monocultures in year 1, and abundance of *E. ruidum* was more than twice as high in monocultures than in mixed tree stands in year 2 (Table App. 2). Considering bait types, total ant activity did not differ between sugar and tuna baits ( $Z = -0.714$ ,  $P = 0.475$ ). Concordantly, we found no significant differences among sugar and tuna baits regarding activity of the individual species *E. ruidum* ( $Z = -1.72$ ,  $P = 0.086$ ) and *C. lindigi* ( $Z = -0.57$ ,  $P = 0.567$ ). *Solenopsis geminata* was not observed at either bait type in year 1.

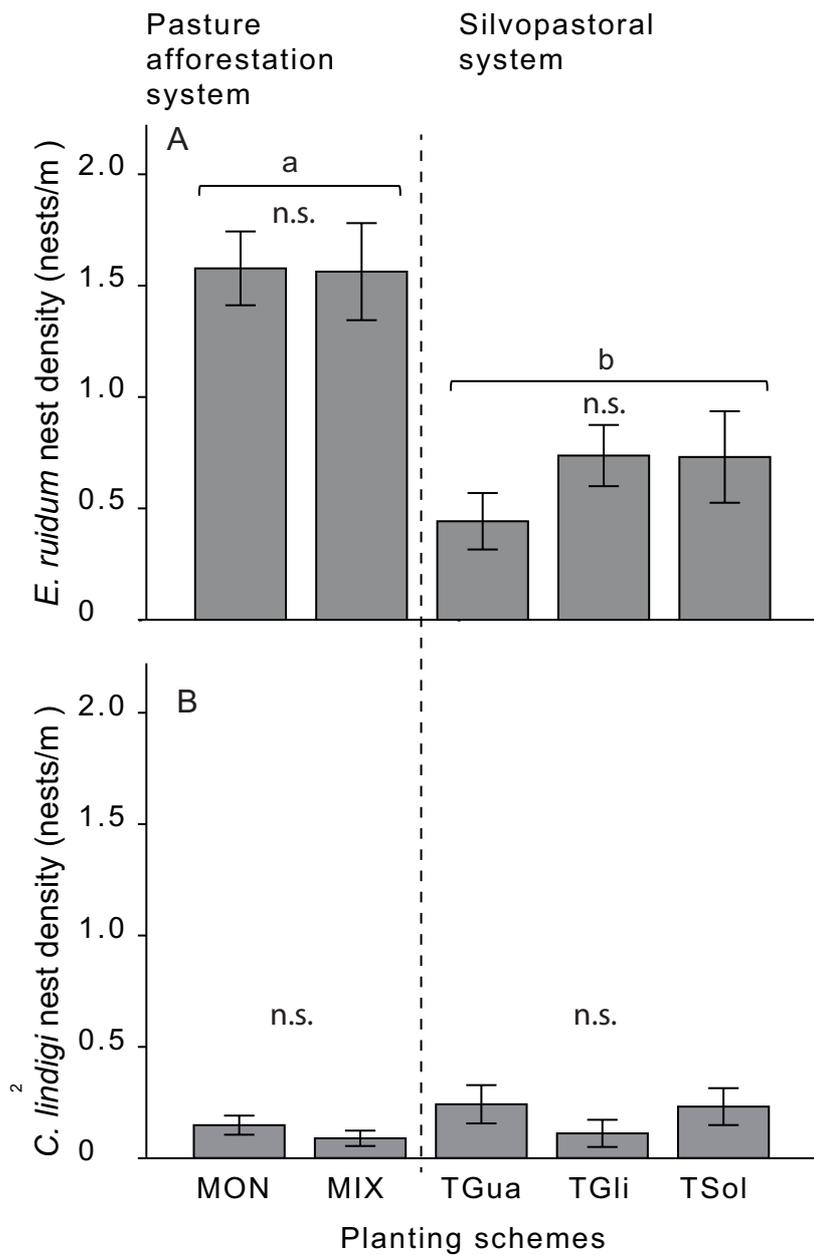
In the silvopastoral system, mean values of overall ant activity were lower on *T. rosea* trees growing solitarily than on *T. rosea* trees surrounded by *Guazuma ulmifolia*, or surrounded by *Gliricidia sepium* (Table App. 2). This difference was significant in year 3, and when considering the ant activity cumulated over all three years (Table App. 2). The abundance of individual ant species did not differ significantly among planting schemes. Considering bait types, we found a significantly higher total ant activity at sugar baits than at tuna baits ( $Z = -2.31$ ,  $P = 0.021$ ). In agreement, activity of *E. ruidum* was significantly higher at sugar than at tuna baits ( $Z = -2.67$ ,  $P = 0.008$ ). Activity of *C. lindigi* did not differ between the two bait types ( $Z = -1.45$ ,  $P = 0.148$ ).

**Table App. 2.** Effects of planting schemes on ant activity at baits (number of individuals) on tree trunks of *Tabebuia rosea* trees ( $N = 129$ ). In the pasture afforestation system, planting schemes represent monocultures of *T. rosea* (MON), and three-species mixtures of *T. rosea*, *Anacardium excelsum*, and *Cedrela odorata* (MIX). In the silvopastoral system, planting schemes refer to *T. rosea* trees growing surrounded by *Guazuma ulmifolia* (TGua), surrounded by *Gliricidia sepium* (TGli), or solitarily (TSol).

System	Year	Taxon	Planting scheme			Statistics	
			MON	MIX			
Pasture afforestation	year 1	Total	66	45		$U = 430.5, P = 0.764$	
		<i>E. ruidum</i>	30	6		$U = 365.0, P = 0.097$	
		<i>C. lindigi</i>	31	37		$U = 431.0, P = 0.047$	
		<i>S. geminata</i>	0	0			
	year 2	Total	1508	504		$U = 193.0, P < 0.001$	
		<i>E. ruidum</i>	746	302		$U = 315.0, P = 0.041$	
		<i>C. lindigi</i>	37	80		$U = 381.5, P = 0.211$	
		<i>S. geminata</i>	666	48		$U = 385.0, P = 0.104$	
	year 3	Total	203	246		$U = 404.5, P = 0.498$	
		<i>E. ruidum</i>	144	149		$U = 439.5, P = 0.868$	
		<i>C. lindigi</i>	3	4		$U = 449.5, P = 0.986$	
		<i>S. geminata</i>	0	50		$U = 435.0, P = 0.317$	
	TOTAL		1777	795		$U = 194.0, P < 0.001$	
	Silvopastoral	year 1	Total	122	109	40	$H = 5.82, P = 0.055$
			<i>E. ruidum</i>	35	32	21	$H = 0.40, P = 0.819$
			<i>C. lindigi</i>	65	51	18	$H = 3.01, P = 0.222$
<i>S. geminata</i>			0	0	0		
year 2		Total	1107	812	641	$H = 3.80, P = 0.150$	
		<i>E. ruidum</i>	180	196	51	$H = 2.23, P = 0.328$	
		<i>C. lindigi</i>	47	88	76	$H = 1.69, P = 0.430$	
		<i>S. geminata</i>	726	440	461	$H = 0.23, P = 0.891$	
year 3		Total	470	324	128	$H = 11.76, P = 0.003;$ $TGua^a, TGli^a > TSol^b$	
		<i>E. ruidum</i>	129	53	45	$H = 1.22, P = 0.543$	
		<i>C. lindigi</i>	13	12	21	$H = 4.03, P = 0.133$	
		<i>S. geminata</i>	148	173	21	$H = 2.13, P = 0.344$	
TOTAL			1699	1245	809	$H = 9.95, P = 0.007;$ $TGua^a, TGli^a > TSol^b$	

### App. 3.2 Effects of tree planting systems on nest density of *E. ruidum* and *C. lindigi*

Mean nest density of *E. ruidum* ranged between 0.44 nests/m<sup>2</sup> and 1.58 nests/m<sup>2</sup>, with an overall mean of 1.23 nests/m<sup>2</sup> (Fig. App. 1 A). Mean nest density of *C. lindigi* was lower and ranged between 0.09 nests/m<sup>2</sup> and 0.23 nests/m<sup>2</sup>, with an overall mean of 0.15 nests/m<sup>2</sup> (Fig. App. 1 B). In the pasture afforestation system, nest densities of *E. ruidum* ( $U = 1655.5$ ,  $P = 0.437$ ) and *C. lindigi* ( $U = 1680$ ,  $P = 0.285$ ) did not differ among mixed tree stands and monocultures but were significantly and negatively related to one another ( $R = -0.297$ ,  $P = 0.001$ ). In the silvopastoral system, nest densities of *E. ruidum* ( $H = 2.23$ ,  $P = 0.328$ ) and *C. lindigi* ( $H = 1.83$ ,  $P = 0.401$ ) did not differ between planting schemes and were not interrelated ( $R = -0.04$ ,  $P = 0.778$ ). Overall, nest density of *E. ruidum* was significantly higher in the pasture afforestation system than in the silvopastoral system ( $U = 2548$ ,  $P < 0.001$ ), whereas nest density of *C. lindigi* did not differ between the two planting systems ( $U = 3792$ ,  $P = 0.134$ ).



**Figure App. 1** Mean ( $\pm$  SE) nest density of *Ectatomma ruidum* (A) and *Camponotus lindigi* (B) in different planting schemes. In the pasture afforestation system, two planting schemes were established: monocultures of *Tabebuia rosea* and three-species mixtures of *T. rosea*, *Anacardium excelsum*, and *Cedrela odorata*. In the silvopastoral system, planting schemes included *T. rosea* trees surrounded by *Guazuma ulmifolia* (TGua), surrounded by *Gliricidia sepium* (TGli), or growing solitarily (TSol)

#### App. 4 Conclusions

- (1) We identified a total of 30 ant species belonging to eight sub-families in a tropical native timber tree plantation on former pasture in Central America. Numerically dominant were the three ant species *Ectatomma ruidum*, *Camponotus lindigi*, and *Solenopsis geminata*.
- (2) Ant abundance at baits cumulated over three observation years was higher in monocultures than in mixed tree stands in the pasture afforestation system, and it was higher on *Tabebuia rosea* trees surrounded by companion trees than on *T. rosea* trees growing solitarily in the silvopastoral system.  
Nest density of the ant species *E. ruidum* and *C. lindigi* did not differ among planting schemes within either reforestation system. Comparing the pasture afforestation with the silvopastoral system, we found a much higher nest density of *E. ruidum* in the pasture afforestation system, which is characterized by a higher timber tree density.

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