Forest Ecology and Management 261 (2011) 741–750

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

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ARTICLE INFO

Article history:
Received 22 September 2010
Received in revised form
27 November 2010
Accepted 2 December 2010
Available online 28 December 2010

Keywords:
Anacardium excelsum
Cedrela odorata
Insect herbivory
Pasture reforestation
Soil characteristics
Tabebuia rosea

ABSTRACT

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

1. Introduction

Smallholders and communities strongly contribute to deforestation in Central America (FAO, 2009; Scherr et al., 2003). Large-scale initiatives for biodiversity conservation and ecosystem restoration (Hartley, 2002; Lamb et al., 2005; Paquette and Messier, 2010) must therefore consider local-scale smallholder needs (Barrance et al., 2003; Lamb et al., 2005; Montagnini, 2001). Reforestation is a potential strategy to reduce the logging pressure on remnant natural forests, while considering local socio-economic interests (Dijk and Savenije, 2009; Paquette and Messier, 2010). Small-scale landholders, however, perceive tree planting as a risky activity. Compared to harvesting or logging old timber trees in natural forests, benefits of timber plantations are only achieved in the long term (Dagang and Nair, 2003; Garen et al., 2009; Günter et al., 2009; Lamb et al., 2005). Furthermore, substantial losses of seedlings in new plantations are attributed to insect herbivores. To protect trees from expected herbivore attack, half of the Panamanian farmers interviewed in a recent study applied pesticides (Garen et al., 2009), but until now there is little evidence for the effectiveness of these products under prevailing field conditions. In addition, small-scale site conditions may substantially influence survival and productivity of timber species (Firn et al., 2007; Forrester et al., 2005; Potvin and Gotelli, 2008), as well as plant traits related to defense against herbivores such as leaf palatability, leaf morphology and chemistry (Basset, 1996; Molina-Montenegro et al., 2006). Accordingly, small-scale site conditions might limit accurate assessments of the effects of particular management strategies (Boyden et al., 2005; Forrester et al., 2006; Fridley, 2003). Thus, approaches must be found to ensure that reforestation is made attractive to small-scale

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doi:10.1016/j.foreco.2010.12.004

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

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

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

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

2. Materials and methods

2.1. Study site and tree species

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

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

2.2. Planting design

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