ESTABLISHMENT OF SILVOPASTORAL SYSTEMS IN DEGRADED, GRAZED PASTURES: TREE SEEDLING SURVIVAL AND FORAGE PRODUCTION UNDER TREES IN PANAMA

By

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To my Mother and Father, whose boundless love gives me life
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ESTABLISHMENT OF SILVOPASTORAL SYSTEMS IN DEGRADED, GRAZED PASTURES: TREE SEEDLING SURVIVAL AND FORAGE PRODUCTION UNDER TREES IN PANAMA

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Silvopastoral systems that integrate trees on animal production units are reported to be a promising land-use activity. Research on methods of integrating trees into smallholder pasture systems for development of such systems in the tropics has, however, received little attention. In Panama, smallholder pastures are abundant across the landscape, but they are often extensive, degraded, overgrazed, and of low productivity. Based on the premise that integration of silvopastoral systems on degraded pastures might be an effective technology that is accessible and affordable for small-scale producers, this research was carried out on-farm for two years in central Panama to help devise best management practices for optimizing tree-seedling survival, reducing competition between seedlings and herbaceous vegetation, and managing effects of large trees on forage.

Three experiments were conducted. The first one examined seedling survivorship and herbivory of three tree species (Anacardium occidentale, Bombacopsis quinata, and Tectona grandis) planted in three configurations (grouped in diagonals, in lines, and along fences). The second experiment examined the effects of herbaceous vegetation on the establishment of tree
seedlings. Seedling growth and biomass distribution to shoots and roots were evaluated in relation to four herbaceous removal regimes, which included removal of surrounding vegetation both above- and belowground. In the third experiment that focused on the effects of large, dispersed trees on forage characteristics, two tree species, *Anacardium occidentale* and *Tectona grandis*, were evaluated for their effects in terms of mass, digestibility, and botanical composition of the forage underneath.

Research results revealed that *Anacardium occidentale* seedlings survived best in grazed pastures and the fence planting configuration resulted in the lowest seedling survival. Seedling herbivory was greatest for *Bombacopsis quinata*, and cattle and leaf-cutter ants (*Atta* spp.) were the herbivores that browsed seedlings most. Tree seedlings performed differently under the different herbaceous vegetation removal regimes. *Bombacopsis quinata* grew best overall and maintained a consistent root:shoot ratio during the two years of study. However, *Anacardium occidentale* performed better than the other species in terms of biomass allocation to shoots. Similarly, the effects of large trees on understory forage varied with tree species. Forage mass under *T. grandis* was suppressed in comparison to *A. occidentale*. Conversely, forage digestibility was lower under *A. occidentale* than under *T. grandis*. Finally, while forage botanical composition was uniform (with a greater proportion of grass) under *T. grandis* across distances from tree stem, under *A. occidentale*, proportions of botanical composition were more varied and comprised more legume than grass.

These results can be used for development of recommendations and guidelines on tree species selection, planting configuration, grazing, weeding, and forage management for successfully integrating silvopastoral systems into smallholder pastures in Panama.
CHAPTER 1
INTRODUCTION

In Panama, pastureland covers about 1.3 million hectares, constituting more than 20% of the landscape. Existing pastures are extensive, low in productivity, commonly under some degree of degradation, and practically devoid of trees. Although high-intensity technologies and management technologies such as use of feed lots and supplemental, processed feeds exist to augment productivity, these are untenable for most producers. New production strategies that can be easily accessed, implemented, and afforded by producers must be sought. Silvopastoral systems – the integration of trees into livestock systems – are considered to be one such approach with the potential to address the problem of increasing degradation of existing pastures in Panama. Based on the premise that tree integration on degraded pastures can augment soil health, forage production, and environmental services, silvopastoral systems, might be an effective technology that is accessible and affordable for producers. Several management aspects of silvopastoral systems have, however, not been researched and therefore remain unknown. It was in this context that the present study was undertaken.

The study, exploratory in nature, involved applied, on-farm research to devise appropriate means of establishing silvopastoral systems on degraded pastures and to investigate how best to integrate tree seedlings into grazed, degraded pastures in Panama. Major areas of investigation included appropriate tree species and their optimal planting configuration in terms of seedling survival and seedling herbivory. Consequences of large trees on pastures in terms of effects on forage mass, forage digestibility, and forage botanical composition; and interactions between herbaceous vegetation and establishing seedlings as they pertain to removal of herbaceous material around seedlings were also investigated.
Three species, chosen by participating farmers, were used in the study: *Anacardium occidentale* (cashew), *Tectona grandis* (teak), and *Bombacopsis quinata* (tropical cedar). *Anacardium occidentale* is a locally abundant species that is valued for the marketable, well-priced nut it produces and for its fruit, which is consumed by farm families and livestock. *Tectona grandis* is arguably the most valuable tropical hardwood species that has been heavily promoted throughout Panama in reforestation efforts and as a plantation species. Producers perceive *T. grandis* as a commodity species that can provide added income from the pasture to the household. *Bombacopsis quinata* is a multi-purpose, native hardwood species that is used locally in live and dead fences, furniture making, and in construction.

The overall objective of this research was to gain knowledge of some of the bases of silvopastoral system establishment in degraded, grazed pastures. Through monitoring seedlings for survival and herbivory over two years, manipulating herbaceous vegetation and tree seedlings above- and belowground, and testing forage characteristics close to and far from isolated trees, the study was also aimed at understanding some of the interactions that occur in silvopastoral systems in extensive pastures in Panama.

The study sought to examine particular assumptions regarding the use and performance of *A. occidentale, T. grandis*, and *B. quinata* in silvopastoral systems as well as the impact of these species on pasture. Specifically, the following general hypotheses were tested:

- The pattern in which tree seedlings are planted in pasture (planting configuration) impacts the survival and herbivory of seedlings.
- Differences exist among tree species in terms of their performance under different planting configurations in silvopastoral systems.
- Removal of herbaceous vegetation around establishing seedlings has positive effects on seedling survival.
- Isolated, large trees impact mass, digestibility, and botanical composition of the understory forage.
This dissertation is presented in six chapters. Following this introductory chapter, Chapter 2 expands upon the problem statement providing an in-depth discussion and background to the drivers behind land use in Panama today and presenting the overall context for the motivation behind the research presented. Chapter 2 also includes a review of the relevant silvopastoral system literature as well as tree species and research site descriptions. Chapters 3, 4, and 5 present the experiments conducted in this research. Chapter 3 comprises the presentation of the experiment and its results that examined seedling survival and herbivory of three tree species on five farms in extensive pastures in Central Panama. Chapter 4 provides the results from the study that examined the consequences of dispersed, large trees on forage characteristics in pasture. Chapter 5 presents the results from the experiment that studied the effects of above- and belowground vegetation removal on tree seedling growth in a controlled field site. Each of the three chapters includes an explanation of the experimental methodology, a review of the pertinent literature, a description of the study results, and a discussion of the findings. Finally, Chapter 6 provides a synthesis of the results of the experiments, implications for the on-farm integration of trees into extensive pastures, and recommendations for future research based on the outcomes of the research.
Agroforestry

Agroforestry entails the deliberate growing of woody perennials on the same unit of land as agricultural crops and/or animals in some form of special mixture or sequence that results in a significant interaction of woody and non-woody components (Nair, 1993). There is evidence of the implementation of agroforestry systems dating 10,000 years before present (Miller and Nair, 2006; Gakis et al., 2004). Widespread study of these traditional practices has grown during the 20th century. Researchers who seek appropriate technologies to respond to growing food needs, diminishing global ecological health, and the rise in land degradation have embraced agroforestry practices as a suite of systems with the potential to meet some of these demands (Huxley, 1999). Some of these systems include alley cropping for soil improvement, fodder production for livestock and dispersed trees in pasture for enhancing animal production, fallow enhancement for soil enrichment, home gardens for food and nutritional security, and others (Nair, 1993). Silvopastoral systems, a type of agroforestry, involve the interaction of woody perennials, forages, and livestock. The three components in the system are intentionally managed for optimal interactions aimed at augmenting agricultural production and environmental services (Sharrow, 1999). Silvopastoral systems will be discussed further in this chapter.

Benefits of Agroforestry Systems

Agroforestry systems such as improved fallows, alley cropping, and silvopasture offer benefits for agricultural production and environmental enhancement. Benefits from improved fallows involve the augmentation of soil physical and chemical properties through the short-term planting of soil-improving tree species. These can be an answer to exhausted soils or degraded...
Alley cropping is the combining of woody perennials and annual crops in fields with the aim of enhancing crop production through enriched nutrient cycling (Jordan, 2004).

Improvement in agricultural production through agroforestry systems is based in part on the contribution of woody species to enhanced nutrient cycling. The woody perennial component of the systems may provide multiple services to crops and/or forage by accessing belowground resources in lower soil columns through deep roots. Likewise, increased capture of light can enrich the overall production of the system (Ong et al., 1996). In some cases, the woody component may provide needed soil moisture to neighboring vegetation by excising moisture from deep soil sources and redistributing it near the soil surface, a debated phenomenon known as hydraulic lift (Burgess et al., 1998; Emerman and Dawson, 1996).

**Relevance of Agroforestry in Panama**

Currently well-known and implemented agroforestry systems in Panama include home gardens, live fences, dispersed trees in pastures and crop fields as well as to a lesser extent coffee (*Coffea* spp.) and cocoa (*Theobroma cacao*) shaded perennial systems. Although certain systems such as live fences are extensively used in Panama, agroforestry systems have not been holistically embraced by Panamanian land managers as an alternative for improving agricultural production. However, the existing multitude of agroforestry systems are in fact relevant to Panama in that they have the capacity to address important challenges that the agricultural and environmental sectors face today, including issues of burning, deforestation, and land degradation.

Three current deleterious situations include 1.) burning for plot clearing and short-term soil enhancement, 2.) deforestation for pasture creation, and 3.) pasture degradation. These situations are highly detrimental to the natural resource base and agroecological conditions in the
short-term and in the long-term. Pasture degradation and creation are among the leading causes of deforestation. As such, integration of silvopastoral systems into existing agricultural enterprises can potentially enable farmers to reduce the degradation of their farms (Serrao and Toledo, 1990). Benefits and characteristics of silvopastoral systems will be discussed in detail in the next section.

**Silvopastoral Systems**

As noted above, silvopastoral systems, a form of agroforestry, include land-use practices that involve woody perennials, forage plants, and livestock simultaneously during a period of time to enhance production and/or the environment. One type of silvopastoral system, cut-and-carry fodder banks entails the growing of forages in a confined space. Forages are harvested and taken to livestock as opposed to being directly grazed. Another type of silvopastoral system includes grazed systems. These may involve the establishment of high quality fodder banks which are protected from herbivory at most times but are periodically grazed by cattle. Another grazed system includes dispersed tree systems in which trees grow on pasture at different stand densities but trees are not directly grazed. However, depending on the tree species, livestock commonly graze fallen fruits, seeds, nuts, and foliage. Each of these systems offers different advantages and benefits for agricultural production.

From improved microclimate to increased productivity, there is a multiplicity of production and conservation benefits reported by researchers that occur in silvopastoral systems. Garret et al. (2004) suggest multiple objectives are achievable through the implementation of silvopastoral systems. They postulate that social, environmental, and economic benefits can be obtained through improving forage quality, increasing timber production, sequestering carbon, reducing contaminant run-off, enriching wildlife habitat, and improving landowner income. For example, studies in semiarid northeastern Brazil conclude that maintaining 30% of tree cover
when converting forest vegetation to pasture increased forage and beef production in comparison to areas with no remaining trees (Araujo Filho 1990 as cited by Menezes et al. 2002). Although researchers agree on the benefits offered by silvopastoral systems, there is a great deal of research that needs to be carried out in order to make appropriate recommendations for silvopastoral systems in terms of tree density, forage cultivars, and animal stocking rates.

Although several aspects of agroforestry systems in general and silvopastoral systems in particular have been studied, the following brief review of literature will highlight general topics of silvopastoral system research which are included in this particular study. In the following chapters, specific reviews of literature address the topics in greater detail.

**Choice of Tree Component**

Species selection for the tree component in a silvopastoral system is vital in that the unique characteristics of each species including rooting habit, litter quality, canopy architecture, allelopathy, radiation interception, and other traits can have decisive impacts on the nature and outcome of the system and its parts. Research has yet to identify and ubiquitously recommend appropriate tree species to be used in temperate or tropical pasture systems. However, Garret et al. (2004) agree that properties such as canopy density, species phenology, vigor, and growth habit are crucial characteristics to be identified for the integration of a tree component into silvopastoral systems. Likewise, Cajas-Giron and Sinclair (2001) suggest that the canopy strata which trees occupy as well as the products they offer in terms of leaf forage, fruits, and other products are key determinants for the choice of tree species in silvopastoral systems.

Some studies have been conducted testing pine species (*Pinus* spp.). For example, in a modeling study by Ares et al. (2003) based on data from long-term silvopastoral studies in the southern U.S.A., it was found that growth of southern pines (*Pinus* spp.), was sensitive to understory composition. Also, differences in grazing, fertilization, and tree population density
significantly affected the growth of the studied pine stands. Similarly, in New Zealand, Chang and Mead (2003) in an eight-year study found radiata pine (*Pinus radiata*) diameter growth to be sensitive to understory forage composition although tree height was not significantly affected at the end of the experiment. Moreover, in a study looking at broad-leaved species, Teklehaimanot et al. (2002) found significant differences in growth between sycamore (*Acer psuedoplatanus*) and alder (*Alnus rubra*) in a study in North Wales. They attributed these differences to species amenability to spacing and/or different levels of nitrogen availability in the soil. However, neither species had a significant effect on sheep and lamb stocking rates in terms of productive capacity.

**Microclimate**

Within a silvopastoral system, the multiple effects of microclimate created by the tree component and the understory vegetation can have positive and negative impacts on production as a whole as well as on the individual parts of the system. Microclimate characteristics and potential consequences were studied by Menezes et al. (2002) in semiarid Brazil using two unique tree species (*Ziziphus joazeiro* and *Prosopis juliflora*) and buffel grass (*Cenchrus ciliaris*) as the primary understory vegetation. They found that microclimate effects on pasture soil differed by tree species. The results of their study provide an excellent example of the microclimatic effects of trees on pasture and highlights how these can differ by species (Table 2.1).

As seen in the Menezes et al. (2002) experiment, canopy radiation interception and therefore canopy architecture can play an important role in the effects of the tree component on understory vegetation. In West Virginia, Feldhake (2001) studied the effects of black locust (*Robinia pseudoacacia*) canopy on a tall fescue (*Festuca arundinacea*) pasture. He studied photosynthetically active radiation (PAR), red/far-red ratio, and soil temperatures and found that
under increasingly cloudy conditions (25% PAR), % PAR under black locust canopy relative to open field PAR doubled. Moreover, the author posited that the presence of the black locust canopy reduced the extent of extreme conditions that the understory vegetation had to endure and therefore to which it must adapt – which he asserted may be beneficial. He concluded that increased radiation use efficiency of the forage under diffuse light conditions as opposed to direct sun increased forage production. Feldhake (2001) also found a significant difference in soil temperature when comparing open-field and under-canopy temperatures. During a mid-day reading, there was a difference of 6.5°C in soil temperature under the two scenarios with equivalent soil moisture. In response to a 10% decrease in soil moisture, soil temperature in the open field increased 12°C while under the black locust canopy soil surface temperature increased 2°C. According to Feldhake (2001), temperature conditions under the black locust canopy were consistently within the appropriate range for tall fescue. Feldhake (2002) also found significant differences in night temperatures in an on-farm silvopastoral system. His research results showed that average below canopy nighttime temperatures in a southern West Virginia 35-yr-old, 17-m-tall mixed conifer site with orchardgrass (*Dactylis glomerata*) understory was 11.5°C higher than open field temperatures. Results from the Feldhake experiments demonstrate the potential for the use of trees to moderate extreme temperatures that can be disadvantageous for forage plants in pasture systems.

Contrary to the findings of Feldhake (2001; 2002), Dulormne et al. (2004) found no significant differences between air temperatures or humidity under the tree canopy of a *Gliricidia sepium-Dichanthium aristatum* silvopastoral system and *Dichanthium aristatum* open field in Guadeloupe. However, there was a significant difference in wind speed between the two system types. On the other hand, grass growth in the wet season was significantly greater in the
open field. However, during the dry season, there was no significant difference observed for grass dry matter production between the two field types. Likewise, in the dry season no significant difference was found between treatments in terms of soil porosity among the three tested soil. However, interestingly, Dulormne et al. reported that in a previous study (Tournebize, 1994) carried out on the same study site, it was observed that air temperature and humidity were in fact higher under the *Gliricidia sepium* canopy. Nevertheless, the authors note that in the previous study, the canopy of *G. sepium* was far larger (covering the entire interrow) than the current canopy studied and therefore may have resulted in these different findings. The comparison of these two studies illustrates how different management schemes can affect the interactions among silvopastoral system components. They also highlight the importance for research to address how different management types can result in distinct agronomic and physiological outcomes.

**Forage component – Recent Studies on Forage Vegetation in Silvopastoral Systems**

As mentioned in the microclimate section, the varied characteristics of tree species can influence the overall productive outcome of a silvopastoral system. Positive and negative effects can occur belowground between the forage plant and tree component as well as aboveground through shading and fallen leaf litter.

A vivid example of the dynamic effects of tree-forage interactions was found in an experiment carried out in Australia studying the raintree *Samanea saman* in a dispersed tree silvopastoral system. Durr and Rangel (2002) looked at forage growth proximate to the *S. saman* canopy. The authors sampled biomass accumulation under the canopy, at the drip line, and in open field. They found no significant difference in aboveground biomass accumulation between the drip line and open field samples. However, under the canopy, aboveground biomass averaged 90% more than the drip line and open field samples (found to be significantly
different). Another part of this experiment examined the botanical composition of the forage species in the different canopy regions and found important contrasts that could explain the sizable differences in aboveground accumulation in the different canopy zones. The below canopy zone which was found to have overwhelmingly greater abundance of aboveground biomass was dominated by *Panicum maximum*, an important tropical forage species. The drip line was populated by a mix of *P. maximum* and *Urochloa mosambicensis* and the open field was dominated by *U. mosambicensis*. This species specialization by canopy region was generally static most of the year except during the dry season when there was an increase in *U. mosambicensis* at the drip line. This study illustrates how understory forage species can differ in preferences for proximity to tree crowns, another important element in the design and research of silvopastoral systems.

Kallenbach et al. (2006) addressed a similar issue in Missouri, USA, looking at forage growth, nutritional quality, and livestock performance under young mixed stands of pitch pine (*Pinus rigida*), loblolly pine (*Pinus taeda*), and black walnut (*Juglans nigra*). Their experiment produced diverse results. Using pasture blocks with and without trees, they measured forage abundance over two years and found that pasture without trees consistently produced more forage than the pasture with trees. Yet, there were apparent seasonal differences of less forage abundance in the treeless pastures which the authors speculate can be attributed to the buffering of temperature and wind in the treed pastures.

**Summary**

Forage is a principal component of silvopastoral systems. Its abundance or scarcity can be the determining factor in the productivity of a farming system. Forage species that demonstrate shade tolerance and effective rooting abilities may provide greater advantages when used in silvopastoral systems. Likewise, tree species without highly competitive tendencies that are not
especially sensitive to effects of understory competition may be preferential for silvopastoral systems. It is plausible that, given the appropriate companion components and management, forage productivity can be enhanced through the integration of silvopastoral systems in livestock farming systems. Considering the need to develop alternatives to present day, traditional agriculture in the interest of ecosystem health and farm productivity and survival, agroforestry is one option for farmers. Silvopastoral systems in particular offer viable options for agricultural improvement and ecosystem health through the integration of woody perennials into farming systems. Specific, specialized research is needed on silvopastoral systems in the tropics due to the importance of synergy among system components and that these be optimal for the success of the systems.

**Land Use and Land Use Change in Panama: A Background to the Impetus for the Presented Research**

**Introduction**

This section discusses historical, human, ecological, and social drivers behind present day land use. The aim of the discussion is to illustrate the motivations behind the research reported in this dissertation, which was devised in response to contemporary Panamanian realities of land use change, degradation, and indications of declining agricultural productivity. Factors contributing to land use change are multifaceted, not only made up of modern agro-ecological realities but are also a result of the natural history of the isthmus and the land use practices applied by pre-colonial populations, Spanish colonists, and 20th century homesteaders. Such historical factors coupled with current socioeconomic conditions transcend and shape today’s land use issues. In order to understand these situations and thereby shed light on the conception of this research, this section will convey the development of the Panamanian isthmus, pre-historic land use, the legacies of fire and savanna crops left by pre-colonial populations and
colonists, consequences of the introduction of cattle on to the landscape, and the nature of land use today.

**Emergence of the Isthmus**

Three million years ago, the Panamanian isthmus emerged connecting Central America and South America. The occurrence had profound impacts on regional terrestrial and marine ecology including the definitive separation of the Atlantic and Pacific Oceans (Coates, 1997). The connection of the Americas through the emergence of the isthmus also gave way to the Great American Faunal Exchange (Webb, 1997).

With the rise of the isthmus, a mountain range was formed, a feature that creates one of the central pieces of Panama’s topography (Figure 2.1). The resulting *cordillera central* is the central mountain range that moves through Mesoamerica and continues into Panama creating two prominent and distinct climatic and ecological zones. These include what are known as the Pacific seasonal region and the wet Atlantic region. Historically, this geographic and climatic distinction has had a decisive impact on the ecological, agricultural, and human development of Panama. The unique eco-climatic regions created by the central range continue to influence land use today.

Two unique precipitation zones are created in part by the predominant directions of trade winds. These generally blow from northeast to southwest causing areas north and east of mountain ranges to be wet, and those south and west of mountain systems to be drier. This occurs in Panama consequent to the presence of the central mountain range. The phenomenon is also known as an orographic rain shadow. Murphy and Lugo (1995) site Panama as a primary example of this geographical contrast in precipitation patterns. They state, “The Pacific coast of Panama, supporting semideciduous forest, receives about 1780 mm of annual rainfall whereas the evergreen forest of the Caribbean coast receives over 3300 mm. On the Caribbean side,
minimum monthly rainfall is normally $\geq 38$ mm while the Pacific coast receives $< 13$ mm during the cooler months of February and March.” This situation results in the northern part of the country being subject to continuous, very humid conditions throughout the year (3000 to 4000 mm) while the southern plains and mountains of the country are seasonally dry during five to six months of the year (Murphy and Lugo, 1995).

Contrasting precipitation and topography have brought about the development of unique ecological zones (Piperno and Pearsall, 1998). On the north side (Atlantic), there are steep slopes, dense forest canopy, abundant fast-moving rivers, few mangroves, and extensive wetlands. On the south side, there are dry, wide plains; moderate mountain slopes; extensive rivers; mangrove forests; and varied seasonal forest types (ANAM, 2000).

**Development of Human Land Use in Panama**

Today, land use is a product of land occupation, manipulation, and cultivation by human civilizations over millennia coupled with the demands of political and economic changes experienced during the 20th century. To understand what is going on today in terms of land use, food production, and conservation, it is crucial that one become familiar with the history of the landscape.

Panama’s topographical and ecological contrasts play a key role in the nature of the natural and human transformation of the landscape and development of land use on the isthmus. The unique ecological zones were fundamental to the development of human civilization during the pre-colonial period in Panama. The flatter, drier southern side of the country with more abundant river systems was favored by pre-colonial populations for farming, fishing, hunting, and general existence. The very wet inhospitable, adverse conditions of the northern side of the country presented greater challenges to survival than the southern coast (Linares, 1980). Although the wet north coast presented challenges, some populations did live there. However,
their agricultural practices were profoundly distinct in that very small plots were slashed, soon abandoned, and left for long fallow periods whereas southern populations developed expansive crop savannas (Cooke, 1997).

Research reveals that pre-colonial populations in Panama began to use fire to manipulate forests and augment abundance of desirable forest products during the period of 11,000 yr BP. Panamanian agriculture commenced in the period of 7,000 yr BP coinciding with the introduction of maize (*Zea mays*) to the isthmus (Piperno and Pearsall, 1998) and was rapidly widespread by 2000 BP. In fact, it is reported that at the time of the Spanish arrival to the isthmus (early 16th century), much of the southern flatlands was void of forest cover as a result of the widespread use of fire and agricultural practices by pre-colonial populations as anthropogenic savannas dominated the landscape (Jaen, 1985). However, the arrival of the Spanish in the 16th century changed land use and land cover dramatically. Notably, the Spanish conquest provoked a significant decrease in the pre-colonial population and a concomitant recovery of forests on the landscape (Cooke, 1997).

**Introduction of Cattle and Land Use Change**

In 1521, Spanish merchants began to import cattle (Heckadon-Moreno, 1997) to graze Panama’s former savannas and recovering forests. Introduction of cattle to the isthmus marked a crucial turning point for the landscape as cattle counteracted forest recovery and impeded fallow regrowth. Limiting forest regrowth was important to Spanish colonists for two reasons: it facilitated the creation of extensive haciendas and controlled the invasive natural landscape (Jaen, 1985).

Following initial colonial settlement, the northern region was comparatively unpopulated and became densely forested with a marked recovery of forests along the alluvial coastal plain. The mountainous region, populated by descendants of indigenous groups escaped from slavery,
was cultivated in the traditional indigenous slash-and-burn system. The southern plains were
dominated by European settlers engaged in agriculture and cattle raising. The eastern region of
the country was sparsely populated by communities of escaped slave populations. However, by
the 18th century demographic changes spurred amplification of the anthropogenic savannas.
Settlers used cattle, fire, and traditional agricultural practices in tandem to increase space for land
settlement. The combined use of these was fundamental to population expansion and land
incursion. Agricultural area doubled between the beginning of the 17th century and the end of
the 19th century in the central provinces (Jaen, 1985). Characteristics of the rural Panamanian
landscape changed little from the 19th century through the early 20th century (Figure 2.2). Today,
of Panama’s 7.5M ha of land area, approximately 2.25M ha are covered by forest, 1.5M ha are
covered by pasture, and 0.5M ha are devoted to crops (Figure 2.3).

**Frontier Expansion and Green Revolution in Panama**

Today, Panama’s rural human and ecological landscape resembles in some ways that of the early 20th century. However, certain developments have modified this situation. Firstly,
provision of basic medical care during the 20th century augmented the expansion of the human
population base (Heckadon-Moreno, 1997). In response to the new, growing population,
forested areas of the southern region neighboring the principle areas of commerce and cultivation
were expanded into including the southern portion of the Azuero Peninsula and the province of
Chiriqui (Heckadon, 1983; Jaen, 1985). Also, the population boom provoked an important rural-
to-rural migration that vastly expanded the agricultural frontier into 400 yr old forests (Herrera,
1986).

**Impacts of the Green Revolution**

The time at which rural-to-rural migration and large-scale expansion began (beginning in
the late 1950s) coincided with the initiation of the green revolution and heightened concurrently
with the spread of green revolution practices. For the rural sector in Panama, widespread rural migration and the green revolution worked in concert as each circumstance mutually fueled the other (Priestley, 1982). These conditions, coupled with a fervent State-sponsored campaign (the “Conquer the Atlantic” campaign set forth by ruling General Omar Torrijos) to facilitate the relocation of peoples from areas of burgeoning population growth and land scarcity into the hinterlands, spawned a massive migration into forests (Dagang et al., 2003). Government-sponsored migration into forest lands initiated multiple new agricultural frontiers, opening new lands for cultivation and pasture creation, and in some cases, application of green revolution practices (mechanization, synthetic inputs, new crop varieties, etc.). Green revolution practices enabled farmers to increase agricultural production capacity and concomitantly continue expansion into forests (Priestley, 1982). For example, between 1950 and 1970, the area devoted to pasture production doubled (Jaen, 1985). Increased food production facilitated an increase in family size thus provoking greater population growth and consequent further migration and expansion of the frontiers (Figure 1.1).

**Land Use in Panama Today**

Panama’s landowners and occupiers consist of peoples who own or occupy small, medium, or large parcels of land. In Panama, generally a small parcel can comprise 0.5 – 30 ha; a medium-sized farm may be considered 31 – 120 ha; and a large farm may comprise more than approximately 120 ha. Due to a multitude of global and national social, economic, and political issues, the Panamanian agricultural economy has suffered in the past ten years which has provoked important changes in land use and a transformation of the landscape (Dagang, 2004). During this period, many small farms have been sold to medium and large farmers permitting the consolidation of large landholdings (Figure 2.4). While these small farms traditionally maintained a diversity of crops and livestock, larger owners generally choose to cultivate
monocrops and/or engage in single-species livestock raising. Some smallholders who have sold their land have moved to urban areas to seek wage labor opportunities while others move to an agricultural frontier area to continue traditional farming (Rudolf, 1999) and pasture creation, among these are the agricultural frontiers initiated in the 1960s during the green revolution and the campaign to “Conquer the Atlantic.” Changes in farmer populations and parcel size resulting from socioeconomic and political transformations have resulted in important alterations of the landscape and land use patterns. The new, changed (and still transforming) Panamanian agricultural landscape comprises medium and large-scale farming on the southern plains and into the piedmont, dwindling small farmer population in the southern mountains, small farming on degraded lands in the northwest, aggressive frontier expansion into the wet north and into the east, abutting protected areas and indigenous reserves.

Today, smallholder farmers and some large landowners on the frontiers are moving into the less populated areas of the wet north and extreme eastern regions of the country. However, the newly migrating farmers have met different challenges than their predecessors. Frontier expansion has become more tenuous due to a diminishing supply of unclaimed land and increased demand for it by a larger population. Expansion is being limited by the preservation status of protected areas and by the country’s autonomous indigenous reserves. Conflicts among populations for rights to land occupation and use have arisen and ignited social discord (Benjamin and Quintero, 2005). Such diminishing supply of available land and the consistent outward migration to agricultural frontiers are gradually prompting some producers to think about how to reap greater production from their land but in a manner that will not damage their limited commodity. This research was conceived and conducted to respond to this need.
Cattle Ranching in Panama

The changing landscape is dominated by cattle ranching and pasture proliferation. Increasing cattle population and concomitant expansion of pastureland calls for a greater focus and increased emphasis of research on pasture productivity within the context of growing land scarcity as mentioned above. To embrace this situation optimally, it is vital that the dynamics of today’s land use, dominated by pasture and cattle, be understood. The following sections discuss these issues.

Ranching Importance and Benefits

Cattle ranching is pervasive throughout Panama and plays a strong cultural and ecological role on the isthmus. Cattle and pasture are dominating features throughout the landscape (Table 2.1). Generally, cattle are highly valued within Panamanian society and ranching is an activity that symbolizes wealth. Ranchers are generally regarded as influential community members and important stakeholders (Dagang et al., 2003).

In addition to its cultural relevance, there are multiple incentives for raising cattle. Firstly, raising cattle has traditionally been a more profitable and stable investment than many banking ventures, providing salaried sectors of society with a steady, low-risk investment. According to the National Bank of Panama, a 6-month investment in cattle can produce as much as 20% in earnings on initial investment as compared to typical certificate of deposit interest rates (Banco Nacional, 2003). Secondly, raising cattle is commonly embraced by city dwellers, who choose to maintain strong ties with the countryside. To strengthen these connections, contribute to kinship welfare, and simultaneously earn income on a stable investment, salaried city dwellers will invest in cattle to achieve these multiple objectives (Dagang and Nair, 2003). Thirdly, cattle provide emergency funds for farmers during moments of critical need such as family illness, school initiation, and other expenses. Fourthly, in contrast to other agricultural endeavors, cattle
can provide immediate liquidity at key moments for their owners as opposed to crops which can only be cashed in at harvest time. Fifthly, cattle provide the means for farmers without land title or other property to attain credit. When producers do not hold title to their farm, cattle can be used as collateral to obtain bank loans. Sixthly, cattle are used as a vehicle for land claim. For instance, in regions of unoccupied land, forests are cleared for crop planting and after harvest are seeded to grass (Joly, 1989). Then, cattle are introduced onto these lands for land claim. The law recognizes use of land for cattle, not forest, as justification for land claim. As such clearing forest and creating pastures for cattle fulfill two general objectives for squatters and homesteaders: to inhibit the regrowth of forest, and to demonstrate to government land title inspectors that requirements have been met for legal land claim (Villalobos, 2003).

**Economic Importance of Cattle**

Cattle represent an important part of the national economy particularly for the rural sector which constitutes half of the Panamanian population. Cattle sales contributed more than $111 million to the national economy in 2000 (Table 2.2). This amount comprised 19% of the agricultural contribution to the GDP, more than any other agricultural activity. These figures do not include the contributions of the dairy industry to the economy in which annual milk sales averaged approximately $30M. In addition, of the 503 corregimientos\(^1\) surveyed in the 2000 agricultural census, 268 corregimientos produced more than $100,000 each in cattle activities and 14 corregimientos produced more than $1M in cattle sales during the year 2000 - marking significant contributions to the rural economy.

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\(^1\) A “corregimiento” is the smallest political division recognized by the State. For example, corregimientos comprise towns, districts comprise corregimientos, and provinces comprise districts.
Pasture Proliferation

The prominence and importance of cattle ranching is reflected in the vast areas occupied by cattle in Panama. Of the 7.5M ha that constitute the country of Panama, approximately 1.5M ha are cattle pasture. These 1.5M ha makeup approximately 20% of Panama’s total land mass and 71% of all agricultural land in Panama (Censo, 2001). Approximately half of the corregimientos nationwide are covered by 40% or more with pasture and 112 of these corregimientos are covered by more than 70% of pasture (Figure 2.5). Traditionally pastures are extensive, maintain less than one head of cattle per hectare, are often degraded, covered by naturalized grasses, managed non-intensively, and may have both flat and sloped topography.

Changing Nature of Ranching

Raising cattle has traditionally been a low-input activity. However, certain sectors of the cattle industry are changing due to changes in economic globalization and a future that speaks of the need to have to compete with imports. The agricultural sector has received incentives to intensify cattle production. Laws 24 and 25 of 2001, including the “Programa para la Reconversión Agropecuaria (Agricultural Conversion Program),” provide low interest loans, reimbursements, and other assistance for farmers interested in improving their production techniques. This program is sponsored by the Inter-American Development Bank and part of the effort reimburses farmers on their investments in advanced agricultural technology. These programs are geared toward large farming enterprises.

The goal of these laws is to equip and prepare farmers to compete with their counterparts in other parts of the world in light of the imminent reduction of tariffs and assorted free trade agreements Panama has pending (Gordon, 2001). In addition, recent law that mandates grading of meat quality is slowly catalyzing changes in the meat industry particularly in terms of animal genetics, nutrition, management, and investment. These changes have the potential to bear
significant effects on the ecological consequences of cattle ranching particularly in the reduction of the use of extensive pastures. One of the emphases of these changes has been the reduction of space in which cattle are raised i.e. the promotion of feed lots and stabling of cattle for fattening in shorter time periods as opposed to the traditional system of grazing cattle during 3 – 5 years on extensive pastures. However, the programs designed to encourage farmers toward confined fattening (feed lots) programs have not been fruitful. Purchasing of feed which is unsubsidized has not proven cost effective for farmers. In many cases, producers who originally tried these techniques have reverted to extensive pasture fattening or semi-pastured feedlots.

In the past five years farming conditions have begun to change as a result of the oscillating economic situation and government programs geared toward improving agricultural productivity nationwide and activity-wide. On some farms, pastures are beginning to be managed more intensively through improvement in animal genetics, feed supplementation, and pasture improvement (17% of pastureland has been planted with improved grasses and 97% of corregimientos report having some type of improved grasses). However, these types of changes require costly monetary investments. As a result, small-scale ranchers who raise cattle in an extensive nature have been obliged in many cases to withdraw from the ranching business. It has become more difficult economically to raise cattle extensively, due to declining productivity and the increased cost of living. This implies that large areas of land are used that are costly to maintain and that because cattle are fattened on pasture as opposed to feedlots, the cattle are older when they are sold and thus the quality of the meat is low and money earned is less. Hence, the traditional system requires more time for production and, today, renders fewer earnings. It is projected that the change in technology use and intensification may render a marked reduction in small-scale cattle farmers and only those farmers able to access credit and
invest in technology for farm improvement will prevail (Name, 2002). Due to the inaccessibility of advanced technologies for some farmers and in other cases the inability to expand landholdings, coupled with the existing need to improve traditional farming practices both for land health and income, it is necessary to seek alternatives to agricultural practices employed today. Agroforestry systems may be an alternative to traditional farming practices; silvopastoral systems may be particularly important in the context of improving traditional cattle and pasture management.

**Conclusion**

Pre-historic peoples have left a vivid, indelible legacy of fire and savanna-like crop fields on the Panamanian landscape. Introduction of cattle by the Spanish solidified the perpetuation of the pre-historic legacies and added cattle to these to become an established trio of legacy land use practices which have been embraced in their entirety by land use managers of the 20th and 21st centuries. The nature of land use today pillared by deforestation, pasture creation, and cattle insertion has begun to confront its limits in that the supply of remaining unclaimed forest for deforestation is diminishing and the existing pastures which in some cases have been worked for centuries and in other cases during millennia exist in various stages of degradation. The research presented in this dissertation was carried out in response to this land use crisis in Panama and seeks to take a closer look at the potential of silvopastoral systems as an alternative for land managers and their farms.

**Research Site Description**

**Location**

Panama lies between Costa Rica and Colombia on the Central American isthmus. The study site lies in the center of the country on the southern coast and is located in the corregimiento of Rio Grande, in the Penonomé district of the province of Coclé (08.31°N,
80.21°W) (Figure 2.6). The corregimiento of Rio Grande consists of extensive flatlands with a landscape dominated by rice fields and cattle pastures. These lands are known to have been inhabited and cultivated prior to colonial settlement, by pre-Columbian peoples, and were among the first cultivated and grazed during the arrival of Spanish settlers (Jaen, 1985).

**Ecology**

Rio Grande forms part of the dry tropical forest life zone (as described by Holdridge, 1967) that characterizes Panama’s central Pacific flatlands. Dry forest zones are primarily climatically determined and occur on a range of soil types. As depicted by Murphy and Lugo (1995), Central American tropical dry forest occurs in the lowlands and temperature varies little throughout the year. Seasons, therefore, are noted by changes in precipitation regimes. In the case of Rio Grande, centuries and perhaps millennia of anthropogenic land use has eliminated the native landscape. The corregimiento of Rio Grande lies approximately between 0 and 25 masl. Local soil types are classified as chromic luvisols and dystric nitosols (ultisols and alfisols) (FAO, 1972; Nair, 1993). Specifically, Matthews and Guzman (1955) classify soils in the study site area as pertaining to “Chumico sandy clay loam.” Soil pH ranges from 4.3 to 5.9 and percentage of soil organic matter ranges from 1.61 to 4.02.

**Climate**

There are two well-defined climatic seasons on Panama’s southern coast – the wet season and the dry season. In the last ten years in Rio Grande, the dry season has extended from January to June and the wet season from July to December (observations from farmers). During the wet season, 93% of the annual precipitation occurs. However, the corregimiento of Rio Grande is situated in a well known microclimate called the *Arco Seco* or dry arc of Panama’s central provinces in which a semi-circular area of the country’s central plains receives less
precipitation than the surrounding areas just a short distance away. Rio Grande receives between 900 to 1200 mm precipitation annually. Temperature ranges from 25 to 31°C.

**Local Farming Systems**

In Rio Grande, the dominant agricultural activities include growing rice (*Oryza sativa*) and corn (*Zea mays*), and raising beef and dual purpose cattle. Most producers are semi-subsistence in which they produce for household sustenance as well as market a portion of their products. Although the community is relatively small, there are a wide range and diversity of producer types, including:

- day laborers who rent out their labor to farmers for a wage,
- day laborers who also cultivate small parcels for home consumption,
- smallholder farmers of crops who are almost entirely of a subsistence nature,
- smallholder farmers of crops and cattle who are almost entirely subsistence farmers,
- medium-scale farmers with crops for home and market,
- medium-scale farmers with crops for home and cattle for market,
- medium-scale farmers with crops for market and cattle for market, and
- large-scale farmers with rice and cattle for market.

Cattle include dairy, beef, and dual-purpose. Market crops include corn, rice, and some seasonal peppers. The studies reported in this dissertation were undertaken within the context of the local farming systems in Rio Grande. The five farms where the trials took place encompassed a range of production types.

**Species Descriptions**

In the experiments presented in this dissertation, three species of woody perennials were studied. These include *Tectona grandis*, *Bombacopsis quinata*, and *Anacardium occidentale*. These species were selected by the farmers who were involved in the study. Of the three species, *Tectona grandis* is the only non-native species and was chosen by the farmers on the basis of the high price of its timber. *Bombacopsis quinata* was chosen based on the strong wood it produces and its versatile utility on-farm. *Anacardium occidentale* was chosen for two of the products it
bares, its fruit and nut. The following information presented here provides a broad background of the characteristics of these species. Because these species are studied closely throughout this work, it is important to have a complete understanding of their defining characteristics. The information available on each of the species is disparate. According to the available literature, it is apparent that *Tectona grandis* has been studied and probed more extensively than either *Anacardium occidentale* or *Bombacopsis quinata*, as such the length of each species review is correspondingly unique.

**Tectona grandis**

**Origin, Natural Habitat, and Environment**

Teak (*Tectona grandis* L.) is native to Southeast Asia and parts of the Indian subcontinent. In the Philippines, it is also regarded as a naturalized species. Teak occurs naturally as part of an assemblage of mixed forest species in its natural habitat. Although teak occurs naturally in diverse ecological settings, moist deciduous forest is regarded as being its original, native habitat (Kadambi, 1972) and develops best on fertile, well drained soils. In Thailand, teak is found at altitudes between 100 and 1000 masl while in Indonesia, teak occurs in rainfall ranges of 1500 to 2500 mm. However, rainfall for optimum growth is regarded to range from 1500 to 2000 mm yet trees will tolerate minimum precipitation of 500 mm with a maximum of 5000 mm and temperatures between 2° and 48°C. Due to the species’ plasticity in a range of conditions and proven adaptability, it has been planted throughout tropical Africa, the Americas, and other parts of Asia. Likewise, it is known to have been planted in plantations on the Indian subcontinent and in Burma since the middle of the 19th century. Kadambi (1972) notes that experimentation with teak planting began in Panama in the 1920s.
**Uses**

Teak gained its worldwide reputation initially as a prized wood due to its excellent performance as a material for shipbuilding. Its hue, texture, and durability make it a desired wood throughout the world (Bailey and Harjanto, 2005; Husen and Pal, 2006), for furniture making, cabinetry, wharf construction, and for railcars. The qualities that make teak a formidable wood species for these crafts include termite resistance, strength, appearance, water resistance, and workability. Teak wood has been known to last intact for more than five centuries (Kadambi, 1972).

**Botany**

Part of the Verbenaceae family, teak leaves are large, elliptical, and obovate with tapering petioles. They produce abundant white flowers and the fruit takes the form of a hard berry-nut. Seeds have four inner cells with an additional central cavity. Generally regarded as hardy, teak trees are light-demanding, deciduous, and when mature become quite large, some known to reach more than 40 m in height. Mature teak trees in favorable conditions can be generally characterized by a tall, straight, cylindrical bole. The phenological cycle of the species consists of the initiation of leaf senescence commensurate with the onset of the local dry season (in the case of Panama this occurs in January). Leaves emerge in May while flowering initiates in September in Panama. Numerous white flowers abound during the dry season in Panama as teak trees defoliate entirely during this period.

**Germination and Establishment**

Seed germination is epigeous. One fruit can produce up to 4 seedlings resulting from the multi-cavity fruit as mentioned above. Leaves are small during the initial growing season while the seedling taproot can elongate up to 30 cm during this period. The taproot is known to reach 60 to 90 cm during the second and third growing seasons. Lack of light, drought, overhead drip,
excessive grazing, and resource competition from weeds are the known leading barriers to germination and establishment of teak seedlings (Kadambi, 1972).

Adaptability and Performance

Abundant fruit production and a multi-cavity fruit enable teak to proliferate throughout the landscape. Likewise, teak’s well-documented plasticity and adaptability to diverse and, in some cases, adverse conditions have also enabled its expansion throughout the tropics. In a study by Piotto et al. (2003), teak was one of two exotic species compared with seven native species for performance factors in Costa Rica. Teak was among the highest performing species in terms of mean annual increment, a key growth marker. Both in height and DBH, teak was among the highest producers. However, teak exhibited higher variability across plantations and management strategies than its native counterparts. It also demonstrated a comparatively high rate of bifurcation. The authors concluded that exotic species were promising; but, for optimal timber production, they required more intensive management schemes compared to native species.

In a similar study, Piotto et al. (2004) compared the survival and growth of 13 native species in mixed and single-species plantations with teak under dry forest conditions on the Costa Rican Pacific coast. The native species were equally divided into slow-growth species and fast-growth species. In the slow-growing category, teak rated second to Dalbergia retusa in a single-species plantation with a survival rate of 90%. Similarly, compared to the species in the fast-growing category, teak was second to Pseudosamanea guachapele (92%) in a mixed species plantation in terms of survival percentage. After 58 months of growth, teak surpassed all slow-growth species in height and DBH. In comparison with the fast-growing species, teak was second to S. parahyba in height and DBH. However, despite these promising characteristics demonstrated in multiple research studies, Perez and Kanninen (2005) claim that in Costa Rica
and in several other Central American countries, teak plantations have not reached anticipated levels of productivity.

**Rooting and Competition**

Teak in its juvenile stage exhibits aggressive rooting habits characterized by one or two well-developed tap roots and extensive lateral roots located just below the soil surface. The taproot is known to develop into a series of vertical roots. Root competition from neighboring vegetation and other teak trees in plantation conditions markedly hampers teak growth (Kadambi, 1972). Teak’s sensitivity to root competition presents considerable problems at the plantation level as numerous population density studies have shown the superiority of planting teak plantations sparsely. In a root distribution study, Divakara et al. (2001) tested interspecific root competition between bamboo (*Bambusa arundinacea*) and teak by tracing $^{32}$P uptake. They found that when $^{32}$P was applied at 25 cm depth, teak uptake of P increased exponentially as lateral distance to bamboo increased. However, when $^{32}$P was applied at 50 cm depth, teak P uptake declined as lateral distance to bamboo clumps increased. Although these two species are well-known for being highly competitive belowground, this study may indicate teak’s ability to specialize in upper soil horizon P uptake when faced with a fierce competitor such as bamboo. Similarly, Shankar et al. (1998) note that in a 35-yr-old taungya field, the competitive presence of introduced teak may have inhibited the invasion of the site by nonnative and weedy surface-rooted species.

**Burning**

One way in which plantation owners have sought to ameliorate teak’s sensitivity to surrounding vegetation is through burning. Teak is known to benefit from fire. Burning provokes a rejuvenation of tree vigor, increased growth (height and diameter), and in plantation
situations a renewed uniformity within the plantation (Kadambi, 1972). Ultimately, teak’s fire
hardiness allows it to prevail over its neighbors for survival.

**Potential benefits of teak plantations**

There is much controversy over the introduction of exotic species into foreign landscapes and the consequences for the environment and wildlife. Studies and cases of negative impacts of the effects of exotic species abound. In Panama, there are numerous testimonies based on empirical evidence to the negative effects of teak plantations there. Some of these impacts include erosion on slopes due to the large, slow decomposing leaf litter left following the dry season and teak’s ability to inhibit the growth of understory vegetation to a certain degree particularly under a closed canopy. There are also claims in Panama that teak plantations do not provide wildlife habitat. For example, in their work on comparisons of wildlife habitat in Tanzania, Hinde et al. (2001) found teak plantations to be favorable for ‘gleaner’ wildlife species. Also in Tanzania, Jenkins et al. (2003) found wildlife use of teak plantations to depend on plantation age, distance to food sources, and animal type. Younger plantations maintained wildlife communities similar to those of native opened woodland. However, the authors stress the need for these plantations to have direct connectivity with natural areas for wildlife to benefit.

As teak plantations were shown to provide habitat for some large mammals, Saha (2001) found no significant difference in plant diversity in a comparison study of vegetation composition in a secondary forest (30 to 35 yr) and in a teak plantation (16 to 18 yr). Overall, for the two land-use types, species richness was similar as were seedling density and the abundance of animal dispersed species. However, Saha indicates that the plantations tested possessed dissimilar composition and structure in comparison to the secondary forest.
An alternative use of teak plantations may be for carbon sequestration and storage. In Panama, Kraenzel et al. (2003) found 20 yr teak plantations could sequester and store 85% as much carbon as did local mature forest. Similarly, litterfall abundance in the teak plantations was similar to that of local forest whereas litter quantity on nearby pasture was 25 to 30% less than that of surrounding forest and the studied teak plantations.

**Bombacopsis quinata (syn. Pochota quinata, Bombacopsis quinatum)**

*Bombacopsis quinata* Jacq. (bombacopsis) is a deciduous species native to the Americas ranging from southern Honduras through Columbia and Venezuela. It is a large tree known to reach 30 to 35 m in height and 1 to 2 m in diameter. Bombacopsis requires a defined dry season and occurs in areas of annual precipitation ranging from 800 to 3000 mm (Cordero et al., 2003). It grows from 0 to 900 masl and is more commonly found on flat land than on hillsides. Bombacopsis prospers in well-drained, neutral or acidic soils and is characterized by a main stem lined with large stems and a fluted base.

Leaves of bombacopsis trees are compound and usually possess 3 to 7 leaflets. Seeds are wind-dispersed. Flowers are pinkish-white and the encapsulated fruits are 4-10 cm long. One of the defining characteristics of bombacopsis is its ability to thrive during extended dry seasons. During 5 to 6 months of the year, bombacopsis is completely deciduous; this period usually coincides with the local dry season. However, precipitation plays an important role in the production capacity and specific gravity of bombacopsis timber (Cordero and Kanninen, 2002).

Timber from this species is prized for its ability to maintain its shape and form during moisture loss. The heartwood is reddish and the sapwood is white in color. It is generally used for exterior and interior construction, furniture, and general carpentry. It is also a highly valued reforestation species for its survival capacity, pest and disease resistance, and proven growth
rate. Bombacopsis has also become a desirable species due to its easy propagation using stumps, bareroots, and by seeding.

In Venezuela and in Costa Rica in the past twenty years, bombacopsis has been planted widely for timber production (Cordero and Kanninen, 2002). In Venezuela, bombacopsis is one of the most important commercial forest species. In the moist deciduous forests of the western plains, it is prominent in the standing stock volume and occurs naturally in prolific stands. In this region, Kammesheidt (1998) found that bombacopsis recovered poorly after being logged which lead to the near disappearance of the species in the studied forests even after more than 19 yr following the logging event. The author attributes this to the small bombacopsis seeds’ need for gap conditions and litter-free soil to germinate. Consequently, Kammesheidt suggests that the often-prescribed timber harvest cycle of 30 yr will be inadequate for the regeneration of the species. In fact, Cordero et al. (2003) recommend a rotation cycle of 50 yr for plantation-grown bombacopsis (to maximize heartwood content).

*Anacardium occidentale*

Cashew (*Anacardium occidentale* L.), a member of the Anacardiaceae family, is a small to medium-sized tree averaging a maximum of 20 m height and 1 m diameter. Cashew is known to grow in regions generally from 0 to 1000 masl with mean annual rainfall between 600 to 1200 mm. Trees can withstand dry periods of up to 9 months and can tolerate infertile, shallow soils (Behrens, 1996).

**Botanical description**

Cashew leaves are oval, average 10 to 20 cm in length, and can measure up to 20 cm in width. Young leaves are reddish or light green and mature into dark green. Flowers are yellowish pink and usually emerge during the middle of the dry season on newly developed shoots. Following pollination, nut growth is vigorous and reaches its maximum size 30 days
after initiation while the fruit (peduncle) develops at a slower rate. Fruit generally requires 70 days to reach maturity (Behrens, 1996).

**Cultivation**

Widespread cashew planting is prevalent in India, Brazil, Indonesia, and Tanzania. Cashew is also frequently found on farms throughout Mesoamerica. In Tanzania, cashew trees are prevalent on small farms whereas in India they are a popular species used in wasteland reclamation. Major et al. (2005) found cashew to be among the most abundant food species in eastern Amazonian homegardens. The prevalence of cashew can be attributed to its hardiness under adverse environmental conditions.

Cashew’s hardiness has been shown to be a product of its ability to capture resources and withstand drought. For example, in Ghana cashew tree planting and production is known today to be expanding rapidly and concern exists over the potential instability that extensive cash crop lands can cause in terms of the consumption of important water and nutrient resources which is thought to be particularly acute in the case of cashew due to its drought hardy nature and its frequent placement on barren lands in this case in forest-savanna transition zones. In response to this concern, Oguntunde and van de Giesen (2005) investigated cashew water use. Their research addressed the amplification of cashew plantations in West Africa. They found that cashew responded sensitively to certain climatic conditions. For example, under conditions of high radiation and high vapor pressure deficit, stomata were shown to close despite non-limiting soil moisture availability. Therefore, when sensing environmental moisture deficiency cashew restricted its water uptake instead of accessing soil moisture to counter the moisture deficit. The authors concluded that cashew soil water uptake was directly related to climatic conditions rather than soil moisture availability. We may deduce that this apparent mechanism of cashew’s, to
conserve water reserves during periods of moisture deficit, may aid in cashew’s noted ability to withstand drought.

Studies have also been done in Brazil to investigate the physiological drivers behind cashew’s ability to thrive in resource poor conditions. In a study that looked at various physiological characteristics of cashew gas exchange, de Souza et al. (2005), like Oguntunde and van de Giesen (2005), found cashew stomata behavior to be highly influenced by changes in vapor pressure deficit. Prompt stomata closure in response to high vapor pressure deficit was effective in restricting transpiration. The authors concluded that cashew’s ability to quickly and effectively provoke stomata closure lends to cashew’s ability to prosper on drier soils.

Uses

Cashew products and byproducts have a multiplicity of uses and values. From the world market to rural homegardens (Isaac and Nair, 2005; Major, 2005), cashew is grown for the sale of its kernel, for its fruits in industrially produced beverages, and for the nut shell liquid which is used in a range of industries. The nut shell liquid is used abundantly and in a variety of scenarios, including as a substitute for asbestos, in the car industry, as a wood sealant, germicide, and others (Behrens, 1996).

In addition to providing multiple products for the global market, cashew has been shown to provide services for biodiversity restoration as well. In a comparison of single and mixed-species plantation types in Thailand, Kaewkrom et al. (2005) found that the combination of teak, tamarind (*Tamarindus indica*), and cashew was superior in providing habitat for establishment of species from adjacent forests. They found that the diverse nature and multi-strata shading in the tri-species canopy resulted in a reduction in weeds and pioneer species abundance giving way to an acceleration of succession in the understory. The plantation, with the combination of teak, tamarind, and cashew, housed the largest number of native forest tree species compared to other
plantation types. Kaewkrom et al. (2005) also found that the plantations with three species (as opposed to the others having only two or single species) had scaled litter decomposition rates providing a continuous release of nutrients to the soil nutrient pool. Finally, the authors noted that the presence of cashew in the plantations may have played an important role in attracting frugivores thereby potentially enhancing and diversifying the seed bank via the deposition of other forest species seeds by these animals.

In the aforementioned study, Kaewkrom et al. (2005) allude to the role of leaf litter playing an important role in nutrient storage and release. Building on this, Isaac and Nair (2005) carried out one of the few studies that examined the dynamics of cashew leaf litter. They compared cashew, mango (*Mangifera indica*), and jackfruit (*Artocarpus heterophyllus*) leaf litters. Initial characteristics of the cashew litter were different from the others. They found cashew litter to have high nitrogen and cellulose concentrations coupled with intermediate quantities of phenols and low amounts of lignin, relative to the other species. Likewise, of the three species, cashew litter was the fastest to reach 95% decomposition (in 6 months). Soil under cashew litter also held the largest quantities of actinomycetes, bacteria, and fungi relative to the other species in the experiment. Nutrient release (N, P, K) from cashew litter was gradual throughout the 6 months of its decay in which cashew litter released 97% of its N and K nutrients and 94% of P. With these results, Isaac and Nair (2005) conclude that the cashew species can make an excellent component in agroforestry systems due to its ability to provide a steady stream of soil nutrients important to crops.

Researchers are also looking to cashew for use with livestock. In Brazil, Ferreira et al. (2004) tested the use of cashew bagasse (fruit mass and fiber that remains following processing) as an additive to grass silage for livestock feed. The study results showed that the cashew
bagasse had a positive effect on the nutritive composition of the silo and a positive effect on silo conservation quality. In addition to the use of cashew for agricultural purposes, researchers in Cuba are testing cashew for its ability to improve conditions of soils from abandoned mining regions. In one study in Cuba, Izquierdo et al. (2005) tested cashew for its soil reclamation capacity. They found cashew trees rapidly improved the targeted soil physical and biochemical properties, including the improvement of soil electrical conductivity, total organic C concentration, total N, and the reactivation of certain microbial processes in the mined soil. However, while in the above study cashew played an important role in soil amelioration, Ngatunga et al. (2003) found in Tanzania that cashew cultural practices acidified soil. According to Ngatunga et al. (2003), due to the overwhelming infestation of powdery mildew disease in cashew trees, Tanzanian farmers apply large quantities of sulfur to fight this crop killing disease. The abundance of deposited sulfur in the last decade has resulted in the acidification of soils in Tanzania’s cashew producing region. This situation, lowering of pH of farm soils, can have dire consequences as cashew is often intercropped with annual crops which, in the long run, will unlikely be able to withstand the imminent acidification of these soils. Finally, one important new use of cashew under investigation concerns its medicinal properties. In Brazil, Medonça et al. (2005) studied a range of plant species for their ability to kill mosquito larvae. They found that among a range of native species studied, cashew was the most effective at killing the larvae of the dengue-spreading mosquito *Aedes aegypti*.

**Planting Configuration**

In Chapter 3, seedlings of the three species described above were planted in three different planting configurations, which included plantings in lines, grouped on a diagonal, and along fences. Investigation of different planting configurations was based on the premise that cattle browse and treading of tree seedlings may occur differently depending on the organization of
seedlings in the pasture. Prior to the establishment of the experiment, participating farmers noted that cattle tended to congregate along fences and may have an impact on planted tree seedlings. On the other hand, farmers suggested that planting in lines would create alleyways for cattle to move through. They also proposed that the diagonal configuration would create a greater shading effect on the pasture that could benefit cattle during high temperatures. In addition, Teklehaimanot et al. (2002) noted that trees planted in different configurations can impact tree architecture and shading, and can create “micro-woodland” habitat for the benefit of wildlife.
Table 2-1 Results of effects of *Ziziphus joazeiro* and *Prosopis juliflora* trees on buffelgrass pasture in Northeast Brazil.

<table>
<thead>
<tr>
<th>Test as compared to open pasture</th>
<th>Ziziphus joazeiro</th>
<th>Prosopis juliflora</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil moisture</td>
<td>No effect</td>
<td>Less soil moisture than pasture (early season)</td>
</tr>
<tr>
<td>Maximum soil temperatures</td>
<td>Lower</td>
<td>No significant effect</td>
</tr>
<tr>
<td>Maximum air temperatures</td>
<td>Lower</td>
<td>Little effect</td>
</tr>
<tr>
<td>Loss of P from litter under crown</td>
<td>Lower</td>
<td>NA</td>
</tr>
<tr>
<td>Mineralized net N</td>
<td>Greater</td>
<td>Greater than pasture and <em>Z. joazeiro</em></td>
</tr>
<tr>
<td>Crown radiation interception</td>
<td>65-70%</td>
<td>20-30%</td>
</tr>
</tbody>
</table>

Source: Menezes et al., 2002.
Figure 2-1 Topographic map of the Panamanian isthmus.

Figure 2-2 Panama forest cover and areas of deforestation in 1947.

Figure 2-3 Changes in land use and human population in Panama 1961-2003.

Source: Pagiola et al., 2004; FAOSTAT, 2006.
Figure 2-4 Farm sizes and areas in Panama 2000.

Table 2-2 Total farm land, farms with cattle, and area under pasture in Panama, 2000.

<table>
<thead>
<tr>
<th>Province</th>
<th>No. of total farms (1000)</th>
<th>No. of cattle farms</th>
<th>% cattle farms</th>
<th>Total agricultural area (10,000 ha)</th>
<th>Total area in pasture (10,000 ha)</th>
<th>Proportion of agricultural land in pasture (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bocas del Toro</td>
<td>4.72</td>
<td>1,282</td>
<td>27</td>
<td>9.74</td>
<td>3.68</td>
<td>38</td>
</tr>
<tr>
<td>Chiriquí</td>
<td>48.50</td>
<td>7,305</td>
<td>15</td>
<td>42.79</td>
<td>24.60</td>
<td>57</td>
</tr>
<tr>
<td>Coclé</td>
<td>31.22</td>
<td>4,347</td>
<td>14</td>
<td>25.24</td>
<td>10.15</td>
<td>40</td>
</tr>
<tr>
<td>Colon</td>
<td>10.95</td>
<td>2,136</td>
<td>20</td>
<td>16.99</td>
<td>7.63</td>
<td>45</td>
</tr>
<tr>
<td>Darién</td>
<td>5.31</td>
<td>1,543</td>
<td>29</td>
<td>23.23</td>
<td>7.00</td>
<td>30</td>
</tr>
<tr>
<td>Herrera</td>
<td>18.84</td>
<td>4,590</td>
<td>24</td>
<td>19.01</td>
<td>11.64</td>
<td>61</td>
</tr>
<tr>
<td>Los Santos</td>
<td>17.31</td>
<td>5,795</td>
<td>34</td>
<td>30.76</td>
<td>23.20</td>
<td>75</td>
</tr>
<tr>
<td>Panamá</td>
<td>65.86</td>
<td>4,526</td>
<td>7</td>
<td>48.62</td>
<td>20.17</td>
<td>41</td>
</tr>
<tr>
<td>Veraguas</td>
<td>33.72</td>
<td>7,615</td>
<td>23</td>
<td>60.16</td>
<td>30.17</td>
<td>50</td>
</tr>
</tbody>
</table>

Table 2-3 Economic importance of cattle in Panama by province, 2000.

<table>
<thead>
<tr>
<th>Province</th>
<th>Earnings from cattle ($ 1M)</th>
<th>Average household monthly income ($)</th>
<th>Farmstead population</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bocas del Toro</td>
<td>2.63</td>
<td>282.60</td>
<td>23,402</td>
</tr>
<tr>
<td>Coclé</td>
<td>6.44</td>
<td>220.60</td>
<td>113,764</td>
</tr>
<tr>
<td>Colón</td>
<td>4.41</td>
<td>377.60</td>
<td>36,830</td>
</tr>
<tr>
<td>Chiriquí</td>
<td>26.02</td>
<td>302.10</td>
<td>140,909</td>
</tr>
<tr>
<td>Darién</td>
<td>5.28</td>
<td>116.50</td>
<td>21,016</td>
</tr>
<tr>
<td>Herrera</td>
<td>9.56</td>
<td>249.80</td>
<td>55,743</td>
</tr>
<tr>
<td>Los Santos</td>
<td>26.46</td>
<td>235.70</td>
<td>43,684</td>
</tr>
<tr>
<td>Panamá</td>
<td>13.67</td>
<td>540.40</td>
<td>486,201</td>
</tr>
<tr>
<td>Veraguas</td>
<td>16.85</td>
<td>166.90</td>
<td>125,562</td>
</tr>
</tbody>
</table>

Figure 2-5 Proportion of pasture area to total land area by corregimiento in Panama, 2003.

Figure 2-6 Research study site location, Rio Grande corregimiento, Coclé province, Republic of Panama.

Source: [www.lib.utexas.edu/maps/cia00.html](http://www.lib.utexas.edu/maps/cia00.html)
CHAPTER 3
TREE SEEDLING SURVIVAL AND IMPACT OF HERBIVORY ON SILVOPASTORAL SYSTEM ESTABLISHMENT

Introduction

Finding a balance among food production, income generation, and environmental preservation is a growing challenge. Likewise, an increasing world population requires greater products and services from the land base. In light of these realities, it is vital that land use and land management be carried out optimally and efficiently to maximize production of food, income, and environmental integrity. The study presented in this chapter sought to test one aspect, seedling survival and herbivory, of a land management strategy that intends to increase the productive capacity of the land unit, diversify its products, and potentially increase the environmental services it offers.

Considering that more than 20% of Panama is covered by pastures and most of these are degraded and of low productivity, it seems both logical and necessary to focus on improving the services pastures can provide. Being that cattle production in extensive pastures is the most dominant land use system in the country, and considering the growing needs of the human population coupled with the diminishing natural resource base, I focused on testing the integration of fruit and hardwood trees into extensive, degraded pastures. When designing a study to further develop an existing land use system, it is vital that the land strategies already employed be included in the new design. For this reason, this study included the existing system of cattle grazing in extensive, degraded pastures in its structure. Therefore, the experiment was carried out in pastures that were actively grazed by cattle. The inclusion of cattle in experimental pastures was made due to farmer interest, as farmers in Panama are generally not willing to remove cattle from their pastures for the establishment of trees.
Literature Review

Tree Seedling Survival

Some researchers suggest a relationship exists between seedling survival and particular seedling characteristics. Through their research of seedling survival under distinct microenvironments with variation in competition, trenching, light, and soil nutrient availability in the US Southeast, Beckage and Clark (2003) proposed that seed size may be an important factor in seedling survival. In their experiment, small-seeded yellow poplar seedlings \((\textit{Liriodendron tulipifera})\) exhibited far greater growth than larger seeded species. Also, in a study in Costa Rica examining the effects of light gradients on seedlings, Balderrama and Chazdon (2005) relate the importance of size to seedling survival and growth, although in this case seedling size, rather than seed size, was proposed to have had a positive impact upon seedling survival. Balderrama and Chazdon (2005) also suggest that within the importance of seedling size and more importantly seedling height, seedling architecture may play a role in survival within light-compromised environments. However, Benitez-Malvido et al. (2005) found in the Central Amazon that seedlings of \textit{Pouteria caimito} demonstrated an inverse relationship between survivorship and initial seedling height. Also, seedlings of \textit{Chrysophyllum pomiferum} demonstrated a negative relationship between seedling size and height relative growth rate.

Factors contributing to survival and growth of seedlings can be difficult to generalize and seedling responses in terms of survival and growth can be species specific (Benitez-Malvido et al., 2005). Beckage and Clark (2003) found species performed distinctly under different resource situations. In the study, \textit{Liriodendron tulipifera} flourished in high resource environments but did not do well in competitive environments. \textit{Quercus rubra} responded little to competitive environments and responded similarly across treatments. However, Balderrama and Chazdon (2005) found that responses from different tropical species varied more in survival
than in growth across different light availability treatments. *Hyeronima alchorneoides* and *Virola koschnyi* survived under low light situations; however, they did not respond as well as other species in terms of growth in high light conditions. The often studied *Dipteryx panamensis* and *Vochysia guatemalensis* did not exhibit this tradeoff in that they had high survival rates under low light conditions coupled with high growth rates in high light conditions.

Griscom et al. (2005) also found different species to respond distinctly in the field. When comparing *Cedrela odorata, Enterolobium cyclocarpum*, and *Copaifera aromatica*, herbicide application had a greater, significantly positive effect on survival of *C. odorata* seedlings than on other species in the study. Ramirez-Marcial (2003) also assessed survival of different species in anthropogenic environments and found that species growth and response to grazing differed. She found relative height and diameter growth rates of *Liquidambar styraciflora* seedlings were significantly associated with cattle grazing while growth rates of *Cornus disciflora* and *Oreopanax xalapensis* were not.

Another factor that can have differential effects on seedling species is habitat. In fact, Benitez-Malvido et al. (2005) found that the pasture conditions (temperature, humidity, and soil moisture) in their study, unique to the native forest habitat of the seedling species that were studied, may have impeded acclimation of certain species, specifically *Chrysophyllum pomiferum* and *Micropholis venulosa*, to the area. The authors contend that the dramatically different habitat conditions in which the seedlings attempted to establish brought about higher rates of seedling mortality for certain species while other species such as *Pouteria caimito* thrived in pasture conditions but not in forest.

Another relevant factor when considering seedling survival is the effect of existing vegetation on seedling establishment. In a Hawaiian forest, Denslow et al. (2006) found that
existing vegetation severely constrained woody seedling establishment. Presence of grasses impeded growth of the species *Acacia koa*, *Sophora chrysophilla*, and *Dodonea viscosa*. Sanchez and Peco (2004) also suggest that presence of grasses during seedling establishment of *Lavandula stoechas* in Spain negatively impacted seedling growth. They also concluded that grass roots form a belowground layer that functions as a barrier to seedling roots and prevents their penetration into deeper soil layers.

More specifically, Posada et al. (2000) found that different grass types impacted establishing seedlings differently in an abandoned pasture in Colombia. Molassesgrass (*Melinis minutiflora*) permitted significantly greater colonization and growth of woody individuals than kikuyugrass (*Pennisetum clandestinum*). The authors suggest that the stoloniferous growth habit of *P. clandestinum* created a physical barrier that inhibited seed germination and seedling establishment of woody perennials. Similarly, seedlings that achieved germination within the stolon mat suffered due to low light and mechanical damage by fast growing *P. clandestinum* grass shoots. In contrast, the bunch grass *M. minutiflora* allocated less biomass to stolons and had more open surface area between plants which they found to be more conducive to woody perennial seedling establishment.

**Effects of Cattle Grazing**

Effects of cattle grazing such as browsing and treading can have negative impacts on seedling survival. Stammel et al. (2006) studied the emergence and establishment of six tree species under different land management strategies including grazing, and they found that treading effects from cattle tended to have a negative impact on seedling emergence. Moreover, treading caused vegetation removal, soil disturbance, puddling, and desiccation. Likewise, seedlings in a study carried out in a Panamanian pasture by Griscom et al. (2005) encountered negative effects of cattle on seedlings, in which cattle impacted seedling growth and survival by
trampling and browsing seedlings. They found that negative effects from cattle grazing could be species specific. In their study, exclusion of cattle from seedlings had a greater, significantly positive effect on *Enterolobium cyclocarpum* when compared with other species. Also for *Cedrela odorata* seedlings, presence of cattle significantly reduced dry mass across the species. Overall, presence of cattle and absence of herbicides caused the greatest mortality among all seedling treatment combinations in the study. Evans et al. (2004) also found species-specific effects of cattle on seedlings in which cattle avoided grazing *Salix* spp. and only when other forage was scarce would cattle browse this species. Ganskopp and Bohnert (2006) also suggest that cattle will select for high quality forage and that cattle in their study traveled longer distances to access higher quality forage. They make the point that cattle return year after year to the same grazing areas presenting a problem for range managers and causing large areas of pasture to not be used. However, the non-use of some pasture areas by cattle may provide a window of opportunity for the establishment of woody perennials.

Although the research discussed above indicates potential negative effects of cattle grazing on woody perennial establishment, some studies suggest that the presence of cattle can in fact benefit seedling survival. Posada et al. (2000) propose the notion that grazing can serve as a tool for the regeneration of forests on abandoned pastures. They suggest that cattle browse can reduce aggressive grass species in pastures. In addition, they put forth the notion that initial colonization of tropical grasslands is dominated by wind-dispersed species consisting of woody shrubs or small trees that frequently occur in disturbed areas. Establishment of such species, they note, can lead to the shading out of grasses and the creation of suitable microclimates for forest species establishment. Other studies conclude similarly. For example, in a study in Argentina de Villalobos et al. (2005) found that grazing may benefit woody perennial seedling
survival. They contend that grazing caused a reduction in grass biomass above- and
belowground, potentially increasing surface soil moisture and thereby enhancing woody seedling
establishment and growth. In contrast with Stammel et al. (2006), de Villalobos et al. (2005)
contend the creation of gaps by cattle treading may induce periodic woody perennial seedling
establishment. Despite finding negative impacts on seedlings from cattle, Griscom et al. (2005)
also suggest that seedling survival and growth may benefit from cattle through the removal of
competing biomass, which has the potential to increase seedling access to light, water, and
nutrients.

Herbivory

Leaf-cutter ants (*Atta* spp.) are an abundant invertebrate species in tropical ecosystems
(Jaffe and Vilela, 1989) and they function as important selective herbivores throughout the
Neotropics (Rao et al., 2001). These herbivores can have a tremendous impact on the landscape.
Leaf-cutter ant herbivory can reduce plant reproductive potential through decreased seed
production and result in reduced seedling survivorship (Vasconcelos and Cherrett, 1997). In
addition, leaf-cutter ants prefer young leaves over mature leaves thereby hindering regeneration.
Leaf-cutter ants manifest preference for particular species. Rao et al. (2001) found decreased
density of adult trees of preferred species in ant-foraging zones in comparison with ant-free
areas. They suggest that repeated exposure to ant defoliation may induce mortality and trigger a
reduction of species diversity.

Similarly, anthropogenic intervention into natural tropical landscapes has been shown to
increase the density of leaf-cutter ant nests (Jaffe and Vilela, 1989). Impact by *Atta* spp. has
been observed to heighten within human-influenced natural systems. Jaffe and Vilela (1989)
suggest two reasons for the increase in *Atta* populations in human-intervened natural systems.
First, they propose that due to species diversity, abundance of palatable vegetation free of
defense mechanisms is low and may be highly dispersed in forests in comparison to human-affected environments. They argue that the diversity of forest vegetation makes ants susceptible to poisonous plants and consequently may subdue the *Atta* population. Secondly, the authors contend that *Atta* nests require exposure to sunlight. This requirement is often a rarity on the tropical forest floor. However, because human interference is often coupled with the removal of tree cover and a consequent increase in sunlight, these conditions may be advantageous for increases in nest density. Therefore, they propose that proliferation of human-affected landscapes decreases non-desirable plant abundance and concomitantly increases leaf-cutter ant nest density. For example, Terborgh et al. (2006) also examined leaf-cutter and plant presence in a comparison of *Atta* populations on different sized islands and mainland Venezuela. They found that leaf-cutter ants browsed less selectively at high population densities, and were able to generate wide impacts on plant communities. In addition, *Atta* population density was greater on smaller islands resulting in a greater impact on the landscapes of the islands. Rao (2000) attributed this occurrence in part due to an absence of *Atta* predators on small islands, which were too small to maintain populations of predators such as armadillos (*Dasypus novemcinctus*).

As noted above, the effects of herbivory on a landscape can be cross-cutting and intense. Detrimental consequences due to herbivory can occur for different plant species as well as for cohorts of different age classes (Terborgh et al., 2006). However, species responses to herbivory can vary (Midoko-Iponga et al., 2005). Variables such as habitat, seedling height, herbivory intensity, pathogens, competition, and seedling non-structural carbohydrate reserves can influence seedling response to herbivory (Benitez-Malvido et al., 2005). For example, according to Allcock and Hik (2004), habitat played a pivotal role in the response of seedlings to mammalian herbivory in an Australian grassland. In their study, seedlings exposed to herbivores
in grassland were similar in size to seedlings grown in herbivore exclosures in woodlands after three years of observation. The authors deduced that rapid seedling growth in the grassland habitat counterbalanced the negative impacts of herbivory. Seedlings were able to recover from herbivory more quickly due to the potentially higher resource habitat in the grassland, especially regarding light availability. On the other hand, the slower growth rates and recovery time of seedlings in the woodland habitat placed seedlings at greater risk to repeated herbivory and mortality. As it took longer for seedlings to grow their apical meristems beyond the reach of herbivores, their risk to herbivory was observed to be greater and prolonged.

Vasconcelos and Cherrett (1997) also found in their research that taller seedlings experienced less mortality than others. To compound the risk of repeated herbivory and eventual mortality, Haukioja and Koricheva (2000) note that the breaking of apical dominance due to herbivory can result in vigorous vegetative growth leading to higher susceptibility of plants to herbivores. Such induced susceptibility (young leaf growth coupled with shorter seedling stature) can cause seedlings to be more attractive to herbivores.

Hester et al. (2004) also found seedling height to play an important role in response to herbivory, particularly in the case of Pinus sylvestris in a simulated browse greenhouse experiment. They found that slow height growth of browsed P. sylvestris seedlings caused them to remain in a size range susceptible to herbivores in comparison to non-browsed seedlings. However, they concluded slow growth response of P. sylvestris seedlings, including fewer shoots, may make seedlings less desirable to herbivores. Hester et al. (2004) found that Betula pendula and Sorbus aucuparia seedlings responded better to simulated browsing than P. sylvestris with increased biomass above- and belowground. Likewise, Allcock and Hik (2004) found that Eucalyptus albens seedlings experienced greater survival than that of Callitris...
due to Eucalyptus’ ability to rebound from herbivory through hastened re-sprouting. The authors suggested a decline in the *C. glaucophylla* population would occur if sustained grazing were to occur in the study site.

Herbivory intensity and energy reserves may also play an important role in seedling response to herbivory. In an experiment using seedlings species (*Acer rubrum*, *Acer saccharum*, *Quercus rubra*, and *Prunus serotina*) from the US Northeast, Canham et al. (1999) examined the effects of different degrees of manual defoliation on the survival and biomass allocation of seedlings. They found that in response to complete leaf removal, survival declined sharply. They suggested survival was closely tied to total carbohydrate reserves and concentrations of carbohydrate reserves. Although effects of defoliation on carbohydrate reserves were consistent across species, consequences for survival differed by species. Rao et al. (2001) concurred in their conclusions that if seedlings are able to persist through the sapling stage, their survival may likely be due to the accumulation of energy reserves which may better equip them to survive and recover from a defoliation event. Similarly, Haukioja and Koricheva (2000) in their comparison of woody perennials and herbs concurred that plant regrowth following herbivory is dependent on energy and nutrient storage; however, they emphasize that such storage must occur in unthreatened plant organs when herbivory is a factor. Being that mature woody perennials store a small proportion of their biomass in leaves (in comparison with herbs), Haukioja and Koricheva (2000) concluded that woody plants were better suited than herbs to withstand herbivory.

Just as response to herbivory by seedlings can be species-specific, so may herbivores maintain preferences for particular species (as noted to be the case with *Atta* spp.). Hester et al. (2004) contend that herbivore choice can be affected by a multitude of factors, including
individual location, plant morphology, plant chemical composition, and neighboring species. The authors also distinguish preferences among different herbivores. They note that morphological differences among saplings are more important to mammalian herbivores than plant chemistry. However, they propose that secondary chemical composition and morphology may interact to influence herbivore choice.

Tree seedling survival, herbivory, and recovery from herbivory are intricate processes which, according to the research, seem to be impacted by a range of tree species, herbivore, and habitat characteristics. Species characteristics such as seed size, seedling height, and architecture seem to play important roles in a species’ ability to survive. These characteristics coupled with variations in habitat including light availability, moisture, and existing vegetation can result in differences in seedling survival. Similarly, seedling herbivory can also have important impacts on survival. Herbivore preferences can have particularly negative impacts on seedling survival and ability to persist. Also, seedling response to herbivory can be sensitive to species-specific characteristics such as seedling architecture and biomass allocation particularly in the case of storage of non-structural carbohydrates, as well as habitat conditions and herbivory intensity.

Considering that research suggests seedling survival, herbivory, and response to herbivory can be species-specific and taking into account that seedling survival is vital to the establishment of a silvopastoral system (the larger focus of this study), the following research was undertaken to investigate the survival and herbivory of three important tree species used in agricultural systems in Panama.

**Objectives and Hypothesis**

The objective of this study was to assess the potential for the integration of *Anacardium occidentale*, *Bombacopsis quinata*, and *Tectona grandis* seedlings into actively grazed pastures. I hypothesized that cattle herbivory (the grazing or browsing of seedlings by cattle) and treading
would play an important role in seedling survival and that seedling species would be a determining factor for survival and herbivory.

**Methods and Materials**

**Study Site**

This study was conducted on five farms in the Rio Grande corregimiento of Coclé province, Republic of Panama (see Chapter 2 for specific local and regional characteristics). Each on-farm study site consisted of a 2 ha pasture dominated by the naturalized grass *Hyparrhenia rufa*. Pasture stocking rate averaged approximately 0.5 to 1.0 animal unit per ha (one animal unit = \(~ 270 \text{ kg}\)).

**Experimental Design**

A randomized complete block design was used. There were five blocks; one block on each farm. Each block contained a complete set of treatment combinations which comprised a total of 135 seedlings. There were nine treatment combinations consisting of three species and three planting configurations. The species were *Anacardium occidentale*, *Bombacopsis quinata*, and *Tectona grandis*. The planting configurations included seedlings planted in pastures on a diagonal, in lines, and along fences (APPENDIX A). There were fifteen seedlings planted for each treatment combination. Each experimental unit was planted in random locations throughout each pasture.

**Materials**

The three tree species were chosen by farmers participating in the study. The seedlings were acquired through local nurseries. *A. occidentale and B. quinata* seedlings were approximately 180 days in age and measured approximately 30 cm height at the time of planting. In accordance with local and regional planting technique, *T. grandis* was planted using bareroot stalks approximately 180 to 220 days in age.
Establishment

On each farm, a circular area of 1 m diameter was cleared of vegetation manually for each seedling. Holes were dug 30 cm deep and 30 cm in diameter. Seedling nursery bags were removed and seedlings were placed in holes as they were backfilled with the excavated soil. Within each experimental unit, seedlings were planted 3 m apart.

Measurements

Seedlings were surveyed weekly for two years. They were observed for mortality and herbivory. We recorded mortality, potential cause of mortality, sign of herbivory, and source of herbivory. Seedlings were considered dead when their stems had dried and/or when their stems and leaves had disappeared. Cause of mortality was categorized into cattle, leaf-cutter ant (*Atta* spp.), natural, and other. Cattle and leaf-cutter ant effects were distinguished visually.

Herbivory was determined when a portion of a seedling had been removed. Source of herbivory was also categorized into cattle, leaf-cutter ant, and other and were also distinguished visually.

Data Analysis

Statistical analyses were performed using SPSS. A survival analysis was conducted to analyze the seedling mortality and cause of mortality data. The Kaplan-Meier survival probability via the Log Rank test was used to compare the survival curves and source of mortality curves for species and planting configuration. SAS JMP was used to analyze the interaction factors of species and configuration through Cox regression analysis. SAS was used to analyze herbivory data. A two-way analysis of variance was conducted. Tukey’s Honestly Significant Difference test was used to determine mean separations at the .05 significance level. A chi-square analysis and Goodman and Kruskal Tau test were used to analyze source of herbivory data.
Results

Seedling Survival

During the two years of the experiment, the survival analysis revealed 250 of a total of 675 planted seedlings survived, a survival rate of 37%. Survivorship was significantly affected by the planting configuration, species, and planting configuration x species interaction treatments. The Log Rank test revealed significant differences in the survival curves across configuration ($p < 0.001$), species ($p < 0.001$), and planting configuration x species interaction ($p < 0.001$) (Table 3-1).

The survival analysis for species reveals some insight into species performance. For example, much of the total mortality (70%) across species that occurred over the life of the experiment occurred by day 300 (73% of $A. occidentale$, 65% of $B. quinata$, and 73% of $T. grandis$) (Figure 3-1). Likewise, the three species experienced mortality in a similar pattern, in two large events during the first third of the experiment and in smaller increments toward the end of the experiment (Figure 3-2). Also, across species, of those seedlings that died, 27% were $A. occidentale$, 35% were $T. grandis$, and 38% were $B. quinata$. Within species, mortality rates were 51% for $A. occidentale$ seedlings, 67% for $T. grandis$, and 71% for $B. quinata$, amounting to seedling survival rates of 49%, 33%, and 29% for $A. occidentale$, $T. grandis$, and $B. quinata$, respectively.

When examining the results of the interactions between species and planting configuration, the survival analysis reveals that in the diagonal configuration, species performed significantly different ($p < 0.001$). There were a total of 127 seedling deaths in the diagonal configuration which included 19 mortality cases for cashew, 64 for tropical cedar, and 44 for teak. Mean survival time for seedlings planted in the diagonal configuration was 500 days. Similarly, 170 seedling deaths occurred in the fence configuration consisting of 57 mortality cases for cashew,
62 cases for tropical cedar, and 51 cases for teak. Mean survival time for the fence configuration was 451 days. However, the Log Rank test revealed that within the fence configuration there was not a significant effect on survival for species \((p = 0.069)\). Within the line configuration, there were a total of 128 seedling deaths made up of 34 cases for cashew, 39 cases of tropical cedar, and 55 cases for teak. The mean survival time for seedlings planted in the line configuration was 572 days. The line configuration had a significant effect on survival \((p = 0.003)\). The different patterns in which seedling species mortality and risk to mortality occurred over time are illustrated in the survival curves in Figure 3-1.

**Observed Causes of Mortality**

Browsing and treading by cattle were the dominant observed causes of seedling mortality. Of the total 425 seedlings that died, 345 (81.1\% of the total) died due to effects from cattle. Other observed causes of mortality included effects from leaf-cutter ants, natural causes, and from machinery. Using the Log Rank test there were significant differences in the survival curves across the 'causes of mortality' factor, \(p = 0.005\). Survival curves reveal that the mortality cases that occurred due to “natural causes” occurred sooner after planting than the other mortality cases, and 46.5\% of the cases that occurred due to cattle effects expired during the period of 210 – 287 days.

**Herbivory**

The effects of species and planting configuration on herbivory were tested. Of the species, overall \(B.\ quinata\) was browsed most frequently while \(A.\ occidentale\) was browsed least frequently. A significant main effect was captured for species, \(p < 0.0001\). A significant two-way interaction was obtained when examining the configuration x species interaction, \(p < 0.0001\). However, contrary to survival, the main effect for configuration was not significant.
Using the Tukey hsd test, significant differences in herbivory were observed between *B. quinata* and *A. occidentale*. In the diagonal configuration, *B. quinata* experienced significantly greater herbivory than did *A. occidentale*. In the fence configuration, *T. grandis* was browsed significantly more than the other two species. Finally, in the line configuration, *B. quinata* experienced significantly more herbivory than the other two species (APPENDIX B).

**Sources of Herbivory**

Three categories of sources of herbivory were recorded, including cattle, leaf-cutter ants, and other. Overall 68.1% of the herbivory cases occurred due to cattle, 30.5% due to leaf-cutter ants, and 1.5% due to other causes. Among the species, *B. quinata* had the largest proportion of cases of herbivory due to cattle grazing and due to leaf-cutter ants with a total of 57.2% and 56.4%, respectively (Figure 3-3). *A. occidentale* had the largest number of cases for the third category of “other” sources of herbivory. In addition, when using the chi-square test, there was a significant effect for species on source of herbivory, $p < 0.05$. Also, the Goodman and Kruskal Tau test was significant for the species effect on source of herbivory, $\tau = .009, p < 0.05$.

The effect of configuration on source of herbivory was significant at $p < 0.05$. In addition, the Goodman and Kruskal Tau test was significant for configuration at $\tau = .01, p < 0.05$.

Relative to source of herbivory as an outcome, line had the highest proportion of cases for cattle (37.4%) and leaf-cutter ants (39.5%), whereas diagonal and fence were highest for 'other' (37.0%) (Figure 3-4).

**Discussion**

**Seedling Survival**

The overall seedling survival rate of 37% can be regarded as an adequate yield for a field planting trial considering the continuous grazing of cattle and the long-term nature of the study. Mortality occurred at distinct times over the life of the study. High seedling mortality took place
relatively early (1-60 day) while moderately high mortality occurred toward the end of the
experiment (Figure 3.2). This pattern occurred similarly across species. The period right after
transplanting is expected to be a bottleneck for survival due to difficulty of establishment into
existing vegetation (Sanchez and Peco, 2004). The second mortality period occurred between
day 200 and day 320. This period coincided precisely with the local dry season when rainfall
can drop below 13 mm per month (Murphy and Lugo, 1995). Consequently, it is likely that
moisture scarcity played an important role in the persistence of seedlings and their ability to
establish early on. Overall, median seedling mortality occurred at day 286 (in the third month of
the 5-6 month dry season). It is important to note that during the dry season, seedlings
experienced increased threat to survival as during this period moisture stress typically can lead to
seedling mortality; concomitantly, forage scarcity is typical of the dry season period, which can
lead to increased grazing of seedlings by cattle. Thus, during the dry season seedlings were
likely subject to the typical moisture deficits of this period that are reportedly experienced in
natural settings, in addition to the added burden of likely forage-deprived cattle. However, it is
relevant to note that these conditions were not directly measured in this study.

The species treatment was significantly different across the seedling mortality survival
curves and, overall A. occidentale experienced the greatest survivorship among the species
followed by T. grandis and B. quinata, respectively. A. occidentale’s perseverance in the
pastures is reflective of its local abundance. Its ability to withstand prolonged drought
conditions may have aided its survival. Also, its ability to persist and eventually thrive in the
seedling stage was seen in the experiment discussed in Chapter 5. In that study, A. occidentale
seedlings did not experience notable growth in the first year of the experiment but flourished
during the second year. Similarly, T. grandis also suffered less mortality than B. quinata. T.
grandis leaves are less brittle but seemingly equally unpalatable as A. occidentale leaves. These characteristics may have provided T. grandis with an added benefit for survival.

Spatial placement of the planted seedlings may have been key to their survival in terms of planting configuration. This was reflected in the significant effect planting configuration had on survival. It is likely that seedlings were subjected to strong neighboring competition by already existing vegetation in the pasture both above- and belowground. Although seedlings were spaced at equal distances throughout the configuration treatments (3 m x 3 m), seedlings in the fence treatment suffered most such that there were no significant differences among species planted along fences. It is likely that seedlings in the fence treatment were subject to more frequent cattle presence and treading due to the more abundant shade (where cattle tend to congregate) that occurred along fences in comparison to open pasture. Also, competition may have been more intense along fences than in open pasture (in lines and diagonals) as most fences comprised mature, live tree posts and trees with established roots systems and canopies which likely had an advantage over seedlings in acquiring resources, particularly during the dry season. However, it is important to note that competition between large trees and seedlings was not directly measured in this study.

Despite lower total survival in the fence treatment, seedlings planted along fences may have benefited from periodic weeding of fences, which entails the cutting away of all vegetation surrounding live and dead fence posts just prior to and during the dry season. This practice is carried out to avoid the spreading of local human-induced fires into pastures. The elimination of competing grasses and forage vegetation along fences in itself may have provided an advantage to seedlings already negatively affected by on-going cattle presence, shade, and competitive effects of nearby large trees. Likewise, the removal of competing vegetation during a critical
period such as the dry season when available soil moisture is reduced may have had an even more dramatic, important effect on seedling survival in the fence treatment.

Line and diagonal treatments may have been subject to competition as well due to their having a greater abundance of surrounding vegetation as well as having the presence of neighboring seedlings surrounding them in comparison to the fence treatment. However, their greater survival indicates that these configurations provided an advantage for seedling survival. The design of each of these configurations formed alleyways between seedling rows which may have facilitated cattle movement through the configurations and potentially reduced cattle treading and consequent seedling damage. In addition, other studies have proposed that planting seedlings in small groups can reduce cattle damage due to a clustered, island effect that is formed when seedlings are grouped together; creating conditions where cattle may be less apt to graze in contrast to the fence treatment which consisted of one long, accessible row of seedlings.

**Observed Causes of Seedling Mortality**

According to the data, cattle treading and grazing were the primary observed cause of seedling mortality in this experiment. Taken as a whole, 81.1% of seedling mortality was caused by cattle. As reflected in the survival curve, seedling mortality due to “other” circumstances occurred largely during the same brief periods, i.e. the majority of these cases occurred at three particular times. Being that the “other” category included causes of mortality such as those due to accidental cutting by a machete during weeding and being run over by a machine, it seems presumable that the “other” mortality cases would have occurred more or less during the same time period as weeding and presence of machines took place only at specific moments.

Almost half of the seedlings that died due to effects from cattle died between day 210 and day 287 after planting – during the first four months of the lengthy dry season. There may have been two different dynamics behind the seedling mortality during this period. First, available
forage for cattle is scarce during the dry season particularly late in the season when drought is often prolonged. For sustenance, cattle are known to browse any type of living plant during this period; even those plants that are not customarily browsed during the wet season will be consumed when scarcity occurs. Therefore, it seems logical that cattle would act most vigorously upon seedlings precisely at a time when customary forage is unobtainable. However, it is likely that an additional factor influenced seedling mortality during this period. That is, during the dry season period, seedlings were weakened due to moisture scarcity. Effects of cattle such as browsing and treading (which seedlings would normally be able to effectively rebound from in the wet season) may have been too severe in the dry season, and, therefore, led to mortality. This situation is further intensified as seedlings may not have developed an adequate root structure to capture dwindling soil moisture particularly while competing with long-established pasture grasses. Therefore, given the presumably weakened status of seedlings during the dry season coupled with often amplified cattle effects such as grazing and treading, it is not unexpected that mortality would heighten particularly due to cattle during this period.

**Herbivory**

In contrast to seedling survival, seedling herbivory was significantly affected by species but was not significantly affected by planting configuration of seedlings. Additionally, the interaction effect of species and configuration was significant as has been noted in other agroforestry communities (Teklehaimanot et al., 2002). It is interesting to note that species played a significant role in herbivory. This result may provide some insight into the importance of tree species as a driver or determining factor of herbivory in grazed pastures and, consequently, establishment of silvopastoral systems in grazed pastures. At the same time, considering insight gained from the results and in terms of drivers, it could then perhaps be conceived that species (as well as other factors) is a more relevant driver of seedling herbivory.
than is configuration. These broad, potential insights will bear upon the ultimate purpose of this research, i.e., to aid farmers in decisionmaking regarding the establishment of dispersed trees in pasture and the creation of appropriate silvopastoral systems.

Across species, *B. quinata* was indeed browsed most among all of the species. This is not surprising given that *B. quinata* seedlings possess succulent green leaves. However, it is noteworthy that herbivory of *B. quinata* occurred most given that the seedlings in the study experienced leaf senescence and, generally, this species is known to defoliate completely during seasonally dry periods. Hence, although it seems appropriate that *B. quinata* leaves were browsed more often than others given their better palatability, their leaves were not present during at least half of the experimental period. This leads us to believe that *B. quinata* leaves were, in fact, likely browsed quite intensely while they were present.

*B. quinata* was more heavily impacted by herbivory than *A. occidentale*. In contrast to *B. quinata*, *A. occidentale*’s fibrous, brittle leaves were less appetizing to the observed herbivores. This condition was likely a deterrent to the browsing of *A. occidentale* and may have enhanced the herbivory of *B. quinata*. As noted above, this situation may have served as an added advantage for the survival of *A. occidentale*. Furthermore, in the case of *T. grandis*, the texture and herbivores’ lack of preference for *T. grandis* leaves were similar to those of *A. occidentale* which may have lead to those seedlings being browsed less than *B. quinata*.

When examining the results of the post hoc test of the interaction of seedling species and planting configuration on herbivory, significant results varied. *A. occidentale* was shown to be the least desirable to herbivores overall, across configuration treatment interactions. This result was to be expected given the significant main effect of *A. occidentale*. However, the surprising result was that *T. grandis* herbivory was significantly greater in the fence configuration than the
other species. Although leaf growth data were not recorded, it is possible that *T. grandis* benefited from the shade from the live fence in the fence configuration which may have provided an increase in soil moisture along the fence treatment area. Given *T. grandis*’ documented aggressive character and ability to readily dominate available resources in comparison to other species, it is possible that *T. grandis* was able to capture shade-induced moisture increases better than the other species on the fence and consequently increase its leaf growth. Increased leaf growth could have then lead to increased herbivory due to greater leaf presence in comparison to the other species particularly during periods of moisture scarcity. However, it is important to note that soil moisture and leaf growth parameters were not measured in this study.

**Sources of Herbivory**

Similar to the survival study, it was evident that cattle were the observed herbivore that grazed seedlings the most. Cattle are known to graze palatable woody perennials when given the opportunity in both pasture and forest environments (Ramirez-Marcial, 2003). In the case of pasture, cattle herbivory can lead to the local elimination of certain woody perennials in pasturelands. However, prior to the initiation of the experiment, there was the expectation that leaf-cutter ants (*Atta* spp.) would play a more dominant role in the herbivory of seedlings, given the abundance of these in the study site and past farmer experience, particularly in the case of *B. quinata*. It is not surprising though that cattle and leaf-cutter ants browsed *B. quinata* seedlings most often, for the same reasons mentioned above – palatability and texture. In contrast, the undesirability of *A. occidentale* by the leading herbivores (cattle and leaf-cutter ants) led it to be the most browsed by “other” sources. Hence, the results which clearly show significant differences among sources of herbivory demonstrate that species was a main factor that shaped the way in which source of herbivory occurred. Like the survival data, cattle were the greatest overall browsers of seedlings, particularly in the line configuration. It is not understood why
planting configuration may have had a significant effect on herbivory. In fact, prior to the installation of the experiment, it was assumed that fence would have the greatest amount of herbivory being that shade abounds along fences and it is in this area where cattle tend to congregate.

**Conclusion**

Tree-seedling survival is shown to be highly responsive to changes in season, herbivore (cattle) presence, tree species characteristics, configuration, and possibly proximity to large trees (in the case of the fence configuration). Each of these factors played a determining role in the survival and mortality of the seedlings studied in this experiment. The greatest amount of mortality occurred during the first dry season, indicating that if producers can find the means to support the survival of planted seedlings through this period, the total proportion of surviving seedlings could be greater in the long-term. Cattle were the overwhelming predators of seedlings and, if seedling survival is a farmer priority, then cattle should be removed during seedling establishment. However, if cattle are the farmer priority, then seedlings can be grazed and will rebound with a satisfactory survival percentage (37%). As will be manifested in the subsequent chapters, it was found here that tree species is key to seedling survival and herbivory. In all four analyses, species had a significant effect on the outcomes. As noted, characteristics such as aggressive growth type, leaf palatability, shade tolerance, and regrowth ability are a few of the considerations that should be made when selecting appropriate tree species for grazed silvopastoral system establishment. Configuration also played an important role, particularly in terms of seedling mortality where in the fence treatment the most mortality occurred and seedling lifespan was shortest; however, the fence configuration experienced the least amount of herbivory.
The varied results of this experiment are indicators of the delicate balance that occurs in natural systems. Although human-induced systems are often characterized as being less biologically diverse and complex than naturally occurring systems, it has become evident through this study that the integration of silvopasture into pasture systems is in fact complex. The complexity lies in the many factors the system comprises: trees, grasses, and livestock; however, complexity is heightened by competition among the system components, presence of other herbivores, and local conditions. These must also be combined with farmer preferences and land management goals. Given these considerations coupled with the present need to augment the production capability and environmental integrity of agricultural systems, it is important that research on silvopastoral systems be intensified.
Table 3-1 Comparison of effects of planting configuration and species on survival of 675 seedlings planted in five blocks in degraded pastures on-farm over two years in Coclé, Panama.

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</table>
Figure 3-1 Comparison of the survival curves of three tree seedling species (*Anacardium occidentale*, *Bombacopsis quinata*, and *Tectona grandis*) (N = 675) planted in three planting configurations (diagonal, fence, and line) during 900 days in pastures of Rio Grande, Coclé province, Panama.
Figure 3-2 Incidence of mortality among *Anacardium occidentale*, *Bombacopsis quinata*, and *Tectona grandis* seedlings planted in three planting configurations for silvopastoral system establishment in farmers’ fields in Rio Grande, Coclé, Panama.
Figure 3-3 Incidence of herbivory of three species of tree seedlings (N = 225 seedlings per species) browsed by cattle, leaf-cutter ants, or other observed sources during a two-year experiment in grazed on-farm pastures in Rio Grande, Coclé, Panama. The y-axis (Incidence of herbivory) refers to the number of events when seedlings were impacted by herbivores.
Figure 3-4 Incidence of cattle, leaf-cutter ant, and other sources of herbivory of tree seedlings *Anacardium occidentale*, *Bombacopsis quinata*, *Tectona grandis*) planted in three planting configurations in grazed pastures in Rio Grande, Coclé, Panama. The y-axis (Incidence of herbivory) refers to the number of events when seedlings were impacted by herbivores.
CHAPTER 4
EFFECTS OF SCATTERED LARGE TREES IN PASTURES ON A Hyparrhenia rufa-
DOMINATED MIXED SWARD

Introduction

To be able to promote the implementation and use of silvopastoral systems with certainty, it is imperative that the dynamics of the systems and their parts be understood. Garnering knowledge of interactions in silvopastoral systems is of particular importance due to their complexity, as they comprise multiple, multi-dimensional components including trees, crops, and livestock. Within the context of seeking to understand diverse biophysical interactions of silvopastoral systems as a means to work toward the promotion and wider implementation of silvopastoral systems in Panama, this research studied the effects of mature, dispersed trees on forage in extensive degraded pastures. Effects of two species of trees (Anacardium occidentale and Tectona grandis) were assessed on pastures dominated by the naturalized African grass, Hyparrhenia rufa. Analyses included the testing of forage mass, digestibility, and composition along a gradient of distances from mature trees.

Literature Review

Light

A debate abounds concerning the effects of light on forage growth in tree-pasture systems. Belsky (1994) proposed that light is not a primary factor in the growth of perennial species under trees. She found that the environmental conditions under tree canopies were more prominent than the potential effects of competition for light between trees and perennials. Clason (1999) also suggested that canopy shading did not play a role in his research on subtropical forage growth under a mixed pine plantation (Pinus taeda and Pinus echinata) in Louisiana, USA. Rather, he found competition for soil moisture between trees and forage to be a greater determining factor in reduction of forage yields under trees. Ares et al. (2006) also contended
that overstory shade was not a prominent factor affecting forage production under large native pecans (*Carya illinoinensis*) in Kansas, USA. Rather, they attributed fluctuations in forage yield to changes in local climatic conditions. Likewise, in Argentina Fernandez et al. (2006) studied the interactions between *Festuca pallescens* and *Pinus ponderosa*. They found that at a stand density of 350 trees per ha, light levels under the pine canopy and in areas between canopies were similar.

However, disparity exists in this debate. Some researchers conclude that light does in fact have an important effect on forage growth under trees. In fact, in a study in Appalachia, USA testing the performance of orchardgrass (*Dactylis glomerata*) in open pasture, woodlands, and woodland-grass edge sites, Belesky (2005) found a significant relationship between grass dry matter and light availability to grass. Grass dry matter was greatest as leaf of grass growing in transition zone edge sites, suggesting that availability of light in edge sites facilitated grass growth. Similarly, in their research on a mixed forage pasture with dispersed poplar (*Populus* spp.) trees, Douglas et al. (2006) found forage growth was reduced 23% under trees when compared to open pasture. The authors attributed the differences in treatment effects, particularly in terms of season, to differences in light reception below trees and in open pasture. However, other research results (Peri et al., 2002) show that effects of changes in light may vary by forage species. For example, in the study carried out by Douglas et al. (2006), white clover (*Trifolium repens*) was significantly more abundant in open pasture than under trees. On the other hand, orchardgrass composition in pasture was twofold greater under trees than in open pasture while differences were not found in perennial ryegrass (*Lolium perenne*) growth under trees and open pasture. Similarly, Fernandez et al. (2002), studying the effect of overstory *Pinus ponderosa* canopy on the tussock grass *Stipa speciosa* in Argentina concluded that *S. speciosa*
growth was limited as a result of the interception of light by the overstory canopy. They found that as pine stocking rate increased, grass growth decreased.

**Biomass Allocation**

Consistent with the differing results of the effects of light on tree-pasture systems, some research has looked closer at plant responses to diminished light availability in silvopastoral systems. Specifically, changes in grass allocation to above- versus belowground biomass consequent to changes in available light have been examined. Fernandez et al. (2004) examined the changes in biomass allocation of the forage species, *Festuca pallescens*, relative to different shade intensities in Argentina. They deduced that changes in allocation of biomass resulted in increases in leaf production. Under a stand density of 500 pruned pine trees per ha, radiation was reduced by 75%. They proposed that the forage species changed its biomass allocation pattern in response to shading: allocation to storage roots was reduced while allocation to leaves increased. The authors asserted that this change may affect species susceptibility to herbivory. A shift in biomass allocation, from storage organs to leaves, can leave a plant less equipped to respond to herbivory with new growth.

Belesky (2005) concurs that leaf production should not be achieved at the expense of structures contributing to plant persistence. Reduced allocation to roots can also result in reduced drought tolerance due to decreased soil foraging and water uptake by roots, particularly when in competition with tree roots. Moreover, both Belesky (2005) and Fernandez et al. (2002) found shading reduced tiller production in forage grasses.

**Belowground Factors**

Considering the potential effects of reduced light availability on pasture grasses under trees, Rietkerk et al. (1998) suggest that a tradeoff exists between light availability and soil nutrient availability in that although light in the understory often becomes reduced due to
shading by the overstory canopy, trees may confer beneficial effects on understory conditions and vegetation. Silva-Pando et al. (2002) proposed that a relationship existed between shade intensity and soil nutrient availability. Moreover, as suggested by Belsky (1994) and others, factors other than changes in light availability may impact forage growth in tree-pasture systems. Such factors include soil water use (Clason, 1999) and belowground competition for nutrients and space (Ares et al., 2006). In fact, Rietkerk et al. (1998) suggested that tree roots’ zone of influence extended beyond the tree crown implying that tree root systems can have a strong, extensive effect on understory vegetation belowground.

Silva-Pando et al. (2002) also proposed the existence of mechanisms other than light, such as physiological aspects of trees and forage in the understory and overstory, that may affect forage growth. Indeed, Douglas et al. (2006) and Fernandez et al. (2006) found soil water availability to be less under trees than in open pasture. They both suggest that rainfall was captured by trees in the overstory thereby limiting soil moisture content, and consequently, moisture availability to understory vegetation. Also, uptake of water by tree roots might play an important role in limiting the availability of moisture belowground. However, Fernandez et al. (2004) only found a disparity in soil moisture availability between open pasture and under trees during periods of high moisture availability, at which time grasses under trees had better water status than grasses in open pasture. The authors attributed this to lower evaporative demand under the tree canopy.

There is a range and diversity of research and opinions concerning large tree effects on understory forages. There seems to be much debate on which aspects of tree-forage interactions ultimately determine outcomes: light may or may not be a factor, climate, soil moisture, species-
specific traits, and tradeoffs of light reduction and buffering of extreme conditions are considered to play some type of role in impacting characteristics of understory forage.

**Objective and Hypothesis**

The objective of this study was to evaluate and compare the impacts and consequences of large, dispersed trees in pasture on the characteristics of *Hyparrhenia rufa*-dominated forage growing in mixed swards in degraded pastures. Characteristics included forage growth, in vitro organic matter digestibility, and forage composition as characterized by proportions of grass, legumes, weeds, and necromass on the pasture. I hypothesized that along a range of distances relative to stems of trees, influence and impacts of trees on pasture components and characteristics would become reduced with increasing distance from the tree stems.

**Methods and Materials**

**Study Site**

This study was conducted in the sectors of La Calendaria and Los Olivos, Rio Grande corregimiento, Coclé province, Panama (see Chapter 2 for specific local and regional characteristics). Data were gathered from pastures on one farm in each sector. The pasture is dominated by the naturalized African grass *Hyparrhenia rufa* with few naturally occurring legume species. Field burning is a common practice in the area; however, broadleaf herbicide application is rare. Pastures had been grazed by cattle consistently during at least two decades. Mature trees were dispersed throughout the pastures. In the wet season, cattle stocking rate averaged 0.5 to 1.0 AU per ha.

**Experimental Design**

The study consisted of two similar experiments. These experiments were structured as randomized complete block designs. Each experiment was alike except for the tree species that was used; one experiment used *Anacardium occidentale* and the other experiment used *Tectona*
grandis. All experimental design aspects of the study were similar for both experiments. There were three blocks for each species and each block contained all of the treatment combinations. Forage was harvested on a gradient of three distances from tree stems in the four cardinal directions. Distances were formulated according to the crown size of each tree. The radius of each canopy was measured and distances were gauged based on the space pertaining to 50%, 100%, and 200% (identified as 0.5, 1.0, and 2.0 distances) of the radius of each tree canopy (APPENDIX C). Forage samples were harvested randomly within the context of corresponding direction and distance from the tree stem, yielding twelve destructive samples per tree, for both experiments. Sampling of forage mass, digestibility, and botanical composition occurred in May and September of 2002, in May and December of 2001, and in December of 2001, respectively.

**Measurements**

Sample sites were chosen at each distance in each cardinal direction. A metal wire ring, 0.5 m in diameter, was placed in the selected sites and all herbage within the ring was harvested manually (by machete and hand clippers) to ground level. The forage fresh weight was recorded. To evaluate in vitro organic matter digestion (IVOMD), herbage was bagged and oven-dried at 60°C. Dried samples were ground and milled through a 1 mm screen. In vitro organic matter digestion was performed by a modification of the two-stage technique (Moore and Mott, 1974). To assess composition, fresh samples were air dried and separated by hand into pre-established categories of grass, weeds, legume, and necromass. “Grass” was categorized as all green biomass pertaining to the species *Hyparrhenia rufa*. “Weeds” were plants that participating farmers identified as being undesirable or harmful to cattle, and/or not beneficial to or contributing to good pasture and cattle production. These included a variety of plant types, including forbs and shrubs. “Legumes” were categorized as those plants with characteristics that
resembled the Fabaceae family. “Necromass” was all biomass identified as dead material. After forage categorization, samples were bagged and weighed.

Data Analysis

Statistical analyses were performed using SAS and SPSS. Dependent variables (forage mass, IVOMD, and forage botanical composition) were analyzed using the ANOVA procedure. When main effects were significant, Tukey hsd post-hoc test was used to compare means. Orthogonal polynomial contrasts were used to describe the effect of location.

Results

Forage Mass

When analyzing the distance by season interaction for A. occidentale, there was no significant effect on forage mass \((p = 0.641)\), nor was there a significant main effect for the distance variable \((p = 0.76)\) in the case of A. occidentale. There was no significant linear or quadratic effect of distance on mass or its interaction with the season variable (Table 4-1). There was a main effect of season on forage mass \((p < 0.001)\) with wet season obtaining an overall higher mean than dry season. In the post hoc test, we observed that there was a significant seasonal effect within each distance, 50\% \((p = 0.015)\), 100\% \((p = 0.002)\), and 200\% \((p < 0.001)\). Wet season marginal means were greater than dry season marginal means at each distance.

In the analysis of forage mass under Tectona grandis, there was no significant two-way interaction between distance and season \((p = 0.368)\). There was a significant linear effect \((p = 0.001)\) of distance, but the quadratic effect only approached significance \((p = 0.097)\) (Table 4-2). In the post hoc test, distance 2.0 mean forage mass was significantly greater than distance 1.0 \((p = 0.018)\) and distance 0.5 \((p = 0.004)\) (Table 4-3). However, there was no significant main effect for season \((p = 0.926)\) under T. grandis.
Forage Digestibility

Forage digestibility under *A. occidentale* was affected by distance and season ($p = 0.042$ and $p < 0.001$, respectively) but there were no interactions. The post hoc test revealed that forage digestibility was significantly greater at the farthest distance from the tree stem (2.0) than at the 0.5 distance (close to the tree stem) while the drip line (1.0) and 0.5 distances were not significantly different. In addition, in the post hoc analysis of the season variable, wet season digestibility was significantly greater than dry season digestibility at the 0.5 and 2.0 distances from the *A. occidentale* tree stems (Table 4-4).

However, results were different for *T. grandis* forage digestibility. There was no distance effect for *T. grandis* ($p = 0.746$). The season variable was significant at $p < 0.001$ under *T. grandis*. Wet season digestibility was significantly greater than that of the dry season at distances 2.0 ($p = 0.001$) and 0.5 ($p < 0.001$) (Table 4-4).

Forage Composition

Under *A. occidentale*, there were no treatment effects on forage botanical composition. Likewise, under *T. grandis*, the effect of distance on weeds, grass, and legume was not significant. However, results for necromass under *T. grandis* were different from the other forage components in that the effect of distance on necromass was significant ($p = 0.035$). When examining further the comparisons of means of necromass by distance, there was a significant difference between distances 0.5 and 1.0, where necromass at the drip line (distance 1.0) was significantly greater than necromass close to the stem (distance 0.5) ($p = 0.049$). No significant difference was observed in necromass abundance between distances 1.0 and 2.0 ($p = 0.982$) or 0.5 and 2.0 ($p = 0.314$).
Discussion

Forage Mass

Effects of trees on understory forage can vary by season, climate, and soil conditions. In this research, forage mass was affected by distance and season; however, these effects were dependent on tree species. Distance of forage from the tree stem did not have a significant effect on forage mass below *A. occidentale* but did play a role below *T. grandis*. Forage mass was significantly greater at the 2.0 distance than at the 0.5 and 1.0 distances below *T. grandis*. At the same time, seasonal effects influenced forage mass under *A. occidentale* but did not have an effect on *T. grandis* forage. The difference found for forage mass under *A. occidentale* in the dry season and the wet season touches upon the importance of seasonal effects on herbage abundance in tropical pastures. This result was to be expected given the seasonal contrast in moisture availability. Although accurate rainfall data for the study site could not be obtained, records at the nearby recording site show the annual rainfall as about ~ 900-1100 mm, 90% of which is received in eight months during May to December, the remaining 4 months being quite dry. However, results of forage mass under *A. occidentale* should not be generalized across species because although forage mass was significantly higher under *A. occidentale* during the wet season than in the dry season, forage mass did not differ significantly under *T. grandis* between seasons. In fact, forage mass was lower under *T. grandis* in the wet season than in the dry season. Thus, season did not have the same affect on forage mass under the two tree species. The consistency of forage mass abundance under *T. grandis* across seasons contrasted with the sizable increase in forage abundance under *A. occidentale* from the dry season to the wet season; forage mass under *T. grandis* experienced a decrease during the same period (Figure 4-1). These results suggest: 1) dry season conditions augmented forage mass under *T. grandis* while wet season conditions induced a suppressive effect on forage growth under *T. grandis*; or 2) based on
the consistency of forage mass abundance across season, *T. grandis* maintained a steady, suppressive effect on forage throughout the year, regardless of season; and 3) growth performance of forage was different under different tree species.

Increased forage mass under *T. grandis* in the dry season may have been related to two traits pertaining to *T. grandis*: deciduousness and aggressive growth habit. During the dry season, *T. grandis* was completely deciduous. At this time, the entire stem and branches of *T. grandis* individuals are leafless – indicating that *T. grandis* may enter a type of dormancy during this period. If such dormancy occurs, an attenuation of *T. grandis*’ aggressive growth type, including a temporary reduction in belowground resource use, may occur as part of the dormancy process. Relief from *T. grandis*’ highly aggressive growth complemented by increased availability of belowground resources and light may have provided the forage under *T. grandis* with increased access to resources, leading to increased growth and accumulation of forage mass during this period.

However, it is also plausible that the consistency of overall low forage mass abundance under *T. grandis* across seasons and distances may be the consequence of a consistent suppressive effect of the tree species. In this case, the decrease in forage mass in the wet season could have been the result of the intensification of *T. grandis*’ suppressive effect due to an increase in soil moisture, reduced stress, and consequent increase in resource availability to the tree. However, it is important to note that these parameters were not directly measured in this investigation.

The contrasting results of forage growth under *A. occidentale* and *T. grandis* emphasize the difference in effects of individual tree species on forage. Also emphasizing the importance of tree species effect on pasture, forage mass was notably less under *T. grandis* in comparison to
herbage under *A. occidentale* in both the wet and dry seasons. Higher yielding forage performance under *A. occidentale* and the apparent suppression of forage growth under *T. grandis* further accentuates the distinct effects tree species can have on forage.

Species-specific effects were also evident when comparisons were made of results within distances. Like season, distance played a different role in the results by species. Unlike season, distance was not a relevant factor for forage mass under *A. occidentale*; however, under *T. grandis* distance from the tree stem played a role in determining forage abundance. Forage mass at the farthest distance (2.0) was significantly greater than forage mass at the drip line (1.0) and close to the tree stem (0.5) under *T. grandis*. There was no difference between the 0.5 and 1.0 distances, suggesting that the tree had some effect on nearby forage. However, when examining the absolute values of forage mass at different distances under *T. grandis*, the differences are seemingly slight. Nevertheless, decreased forage abundance closer to the *T. grandis* tree stem broadens the argument regarding the aggressive character of this tree species. This is also emphasized by the lack of distance effect of *A. occidentale* on forage.

Differences in distance can be influenced by seasonal effects as well; for example, during the dry season forage mass at the drip line can be buffered from high temperatures and evapotranspiration rates while in the wet season moisture at the drip line is captured by the tree crown. In comparison, open pasture during these periods is exposed to temperature, evapotranspiration, and moisture fluxes. These effects are related to and can be impacted by tree species type. For example, canopy architecture and leaf type can determine the degree of light availability, temperature buffering, and evapotranspiration at the drip line. Also, root systems and belowground performance can differ by species. Rooting ability, root length, root architecture, and biomass allocation to roots can determine species effectiveness at acquiring and
outcompeting grasses for resources at both distances. In fact, Behrens (1996) notes that roots of mature *A. occidentale* trees are known to extend beyond the drip line as much as twice the length of the tree canopy. Species with more effective root systems may be better equipped to outcompete grasses at the drip line and potentially in open pasture.

For a better understanding of the difference in effects of particular tree species on forage, we may consider the impacts of cattle, tree canopy, leaf type, and allelopathy on conditions around trees, and how these can differ by tree species and thereby impact forage. In the case of this experiment, in which forage mass under *A. occidentale* was markedly greater than that under *T. grandis*, it is worthwhile to consider how cattle may impact forage around these species. *A. occidentale* is an abundant producer of large, nutritious fruit which attracts cattle to its immediate surroundings. Also, *A. occidentale* commonly possesses a globular, densely-leafed canopy which casts cool shade, frequently pursued by cattle in extensive, denuded pastures. As such, cattle are lured by shade and fruit to *A. occidentale* trees and thus can often be observed congregating close to these. Such presence of cattle brings the benefits of deposition of dung and urine to trees and surrounding areas. Dung and urine can add organic material and nutrients to the environment thereby benefiting soil and forage under the tree and as well as the tree itself.

Conversely, *T. grandis* does not produce fruits relished by cattle. Also, *T. grandis* does not tend to attract cattle (in this experiment). In this experiment, *T. grandis* trees possessed a conical canopy shape which did not produce shade that was attractive to cattle. In addition, leaf characteristics of the two species are unique. *T. grandis* grows a very large, thick leaf that, when added to the ground following leaf-fall, requires prolonged periods of time to decompose.

**Forage Digestibility**
Forage digestibility proved to respond to overstory presence of trees distinctly from forage mass. In contrast to forage mass, distance was relevant to *A. occidentale* but not to *T. grandis* while season played a role for both species, also unlike the case of forage mass. Overall, it is to be expected that forage digestibility would decrease in the dry season in comparison to the wet season due to desiccation. The season effect was consistent along the three gradients of distance from the tree stem for both species, emphasizing the decisive effect seasonal conditions have on forage digestibility.

For both seasons, digestibility of forage growing under *T. grandis* was consistently and notably greater than that under *A. occidentale* (Figure 4-2). It is possible to attribute the differences in digestibility of the two forages at the 0.5 and 1.0 distances to contrasts in light availability. This suggestion is based on the assumption that due to its dense evergreen canopy (Behrens, 1996), *A. occidentale* limited understory light availability more than *T. grandis* did. When light availability becomes restricted, several changes can occur in plant characteristics such as decreases in plant non-structural carbohydrates, increases in cell wall content, and increases in internode length. Such shifts in plant characteristics, provoked by reductions in light availability, can result in decreases in the digestibility values of forage (Lin et al., 2001).

**Forage Composition**

For each species, distance to tree was tested for their affects on the four forage components: grass, weed, legume, and necromass. Composition of the forage differed by tree species in which composition under *A. occidentale* varied notably in each of the categories. Forage under *A. occidentale* comprised more legume overall than did forage under *T. grandis*, alluding to a benefit for cattle. However, the forage composition under *T. grandis* was highly uniform (Figure 4-3) across distances. Distinct proportional composition of forage under *A. occidentale* and *T. grandis* suggest a potential effect of tree species on forage performance in the
context of composition (Figure 4-4, Figure 4-5). Moreover, such marked consistency of the forage contents across parts under *T. grandis* alludes to the possible lack of relevance of distance from the tree to forage composition in the case of this species, particularly in the case of the proportions of weeds, grass, and legume as part of the total forage composition.

However, distance had a significant effect on necromass under *T. grandis*. This contrast in results as compared to grass, legume, and weeds is quite noteworthy as it is an indicator of a clear forage response to tree presence. The differences in necromass by distance may be an indication of an interaction between forage and trees. Creation of a microclimate beneath and around trees on pasture, including buffering of temperature and reduced evapotranspiration under the tree canopy may maintain forage vigor and prevent the generation of necromass.

**Conclusion**

This study has shown that effects of large trees on pasture can be species-specific and variable, and therefore should not be generalized. The most interesting element of the results presented here is the lack of consistent impact of the distance variable: distance to tree stem did not have a constant, clear main effect on mass, digestibility, or composition of the forage underneath. This may indeed indicate that the simple presence of an isolated tree on pasture is not the determining factor when considering the consequences for effects on forage. Rather, it was season and species that exerted a more prominent influence on variation of forage characteristics.

The greater relevance of season and species is key as Panamanian producers tend to dislike the presence of trees in pastures because they believe that trees, regardless of species, have universal negative effects on forage. In light of the diverse results of this study, it is imperative that research on effects of particular tree species on pasture be continued, in order to formulate a
working framework of recommendations to support farmer decisionmaking in silvopastoral establishment and management.
Table 4-1 Analysis of variance for polynomial orthogonal contrasts of sample mean forage mass comparing the effects of distance and season under dispersed *Anacardium occidentale* trees in Rio Grande, Coclé, Panama.

<table>
<thead>
<tr>
<th>Source</th>
<th>Distance</th>
<th>Type III Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
<th>Partial Eta Squared</th>
</tr>
</thead>
<tbody>
<tr>
<td>distance</td>
<td>Linear</td>
<td>10513.92 2595.903</td>
<td>1</td>
<td>10513.92</td>
<td>3.444</td>
<td>0.077</td>
<td>0.135</td>
</tr>
<tr>
<td></td>
<td>Quadratic</td>
<td></td>
<td>1</td>
<td>2595.903</td>
<td>1.494</td>
<td>0.235</td>
<td>0.064</td>
</tr>
<tr>
<td>distance x season</td>
<td>Linear</td>
<td>1759.341 389.404</td>
<td>1</td>
<td>1759.341</td>
<td>0.576</td>
<td>0.456</td>
<td>0.026</td>
</tr>
<tr>
<td></td>
<td>Quadratic</td>
<td></td>
<td>1</td>
<td>389.404</td>
<td>0.224</td>
<td>0.641</td>
<td>0.01</td>
</tr>
<tr>
<td>Error (distance)</td>
<td>Linear</td>
<td>67157.789 38228.803</td>
<td>22</td>
<td>3052.627</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quadratic</td>
<td></td>
<td>22</td>
<td>1737.673</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>
Table 4-2 Analysis of variance for polynomial orthogonal contrasts of sample mean forage mass comparing the effects of distance and season under dispersed *Tectona grandis* trees in Rio Grande, Coclé, Panama.

<table>
<thead>
<tr>
<th>Source</th>
<th>Distance</th>
<th>Type III Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>Sig.</th>
<th>Partial Eta Squared</th>
</tr>
</thead>
<tbody>
<tr>
<td>distance</td>
<td>Linear</td>
<td>18840.317</td>
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<td>18840.317</td>
<td>12.161</td>
<td>0.001</td>
<td>0.269</td>
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<tr>
<td></td>
<td>Quadratic</td>
<td>1479.516</td>
<td>1</td>
<td>1479.516</td>
<td>2.909</td>
<td>0.097</td>
<td>0.081</td>
</tr>
<tr>
<td>distance x season</td>
<td>Linear</td>
<td>1768.478</td>
<td>2</td>
<td>884.239</td>
<td>0.571</td>
<td>0.571</td>
<td>0.033</td>
</tr>
<tr>
<td></td>
<td>Quadratic</td>
<td>2621.69</td>
<td>2</td>
<td>1310.845</td>
<td>2.578</td>
<td>0.091</td>
<td>0.135</td>
</tr>
<tr>
<td>Error (distance)</td>
<td>Linear</td>
<td>51124.044</td>
<td>33</td>
<td>1549.213</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quadratic</td>
<td>16781.606</td>
<td>33</td>
<td>508.534</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4-3 Post hoc comparisons of mean forage mass at three distances\(^1\) from dispersed *T. grandis* tree stems in grazed, degraded pastures in Rio Grande, Coclé, Panama.

<table>
<thead>
<tr>
<th>(i)Distance</th>
<th>(j)Distance</th>
<th>Mean difference (i-j)</th>
<th>Std. Error</th>
<th>Sig.</th>
<th>95% Confidence Interval for Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Lower bound</td>
</tr>
<tr>
<td>0.5</td>
<td>1</td>
<td>-8.325</td>
<td>4.332</td>
<td>0.178</td>
<td>-19.219</td>
</tr>
<tr>
<td></td>
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<td>9.277</td>
<td>0.004</td>
<td>-55.685</td>
</tr>
<tr>
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<td>4.332</td>
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<tr>
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<td>24.028*</td>
<td>8.164</td>
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\(^1\)The distances were: 0.5 = close to tree, 1.0 = drip line, 2.0 = open pasture.
Table 4-4 Post hoc analysis of forage digestibility across three distances from dispersed Cashew trees (*A. occidentale*) and by two seasons in grazed pastures of Rio Grande, Coclé, Panama.

<table>
<thead>
<tr>
<th>Distance</th>
<th>(i) Season</th>
<th>(j) Season</th>
<th>Mean difference (i-j)</th>
<th>Std. Error</th>
<th>Sig.</th>
<th>Lower bound</th>
<th>Upper bound</th>
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<td>Wet</td>
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<td>1.271</td>
<td>0.000</td>
<td>-8.836</td>
<td>-3.566</td>
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<tr>
<td></td>
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<td>Dry</td>
<td>6.201*</td>
<td>1.271</td>
<td>0.000</td>
<td>3.566</td>
<td>8.836</td>
</tr>
<tr>
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<td>-3.004</td>
<td>1.616</td>
<td>0.076</td>
<td>-6.356</td>
<td>0.347</td>
</tr>
<tr>
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<td>Dry</td>
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<td>1.776</td>
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<td>1.776</td>
<td>0.001</td>
<td>3.213</td>
<td>10.582</td>
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</tbody>
</table>
Figure 4-1 Forage mass under two species (*Anacardium occidentale* and *Tectona grandis*) of isolated, large trees in a *Hyparrhenia rufa*-dominated mixed sward during two seasons in Rio Grande, Coclé, Panama.
Figure 4-2 In vitro organic matter digestibility of forage from *Hyparrhenia rufa* mixed swards under two species (*Anacardium occidentale* and *Tectona grandis*) of large, isolated trees in pastures during two seasons, in Rio Grande, Coclé, Panama.
Figure 4-3 Proportional botanical composition of Hyparrhenia rufa mixed swards at three distances from two species (Anacardium occidentale and Tectona grandis) of large, isolated trees in pastures at the end of the wet season in Rio Grande, Coclé, Panama.
Figure 4-4 Composition of forage categorized by weeds, grass, legume, and necromass across three distances (0.5 (close to tree stem), 1.0 (drip line), 2.0 (open pasture)) from Cashew (*A. occidentale*) tree stems in grazed pastures in Rio Grande, Coclé, Panama.
Figure 4-5 Composition of forage categorized by weeds, grass, legume, and necromass across three distances (0.5 (close to tree stem), 1.0 (drip line), 2.0 (open pasture)) from Teak (T. grandis) tree stems in grazed pastures in Rio Grande, Coclé, Panama.
Introduction

In Panama, there is national interest in improving the welfare of farmers and balancing the costs of agriculture with greater attention toward environmental conservation. Part of this effort is to look at how to increase the environmental sustainability of existing farm fields including the thousands of hectares of extensive pastures that cover the landscape. There is interest on the part of some farmers in integrating trees in or around their pastures. Part of this interest is fueled by the constant, daily needs of farmers for products obtained from trees including fence posts, construction materials, fodder for cattle, food, medicine, and fuelwood. Despite the national interest in improving agricultural sustainability, farmer interest, and farmer need for tree-derived products, practically few efforts are underway in fomenting or developing systems to integrate trees into pastures. Likewise, little research has been done in Panama on appropriate management of tree seedlings that are planted for establishing silvopastoral system of dispersed trees in extensive pastures.

This research aims to examine potential management strategies of tree seedlings planted in pasture, focusing on the tree species: *Anacardium occidentale*, *Bombacopsis quinata*, and *Tectona grandis*. Effects of three herbage removal regimes on growth of field-grown tree seedlings form the focus of the two-year study reported here.

Literature Review

Several experiments have been carried out to assess the extent of interactions between tree seedlings and grasses and other herbaceous vegetation into which tree seedlings have been
planted, the mechanisms that determine such interactions, and the responses of diverse woody species to manipulation of herbaceous vegetation and surrounding conditions.

**Competitive Ability**

Tree seedling and grass interactions are often characterized as competitive, and frequently result in the domination of one type of vegetation or species or age class over another. Research suggests that there are numerous ways in which types of vegetation gain dominance or outcompete one another. For example, in an experiment in Australia that investigated the interactions between tree seedlings and grasses, Florentine and Fox (2003) found that *Eucalyptus victrix* seedlings did not effectively compete with grasses as grasses overcame tree seedlings during the period of establishment. Likewise, in a pot experiment, Sanchez and Peco (2004) interplanted *Lavandula stoechas* subsp. *pedunculata* with Mediterranean perennial grasses. There was a significant difference in seedling survival for pots planted with and without perennial grasses. In pots without grass, 78.36% of tree seedlings survived; in pots planted with grasses, only 7.36% of seedlings survived. It has been suggested that many different plant characteristics can confer a superior competitive advantage to plants, including total plant biomass, development of an elongated tap root, high leaf area, root storage function, and early germination (Casper et al., 2003; Rajaniemi et al, 2003; Harmer and Robertson, 2003; Espigares et al., 2004).

Blair (2001) suggests that size is not paramount to effective ability to compete. Rather, individuals with greater competitive ability are more likely to acquire greater belowground resources regardless of their size. The author tested whether belowground competition in soils with isolated pockets of nutrients is dependent on plant size. Blair concluded that competition for nutrient patches may occur in unique ways, and may depend more on resource patch size and root foraging ability than on plant size. However, Collet et al. (2006) contend that changes in the
spatial dimensions of seedling root growth may be the consequence of direct effects of nearby herbaceous vegetation including allelopathy and mechanical effects. In an experiment involving Quercus petraea seedlings, Collet et al. (2006) studied interactions between seedlings and grasses. They tested seedling performance under grass-removal treatments. Experiment results revealed that seedling branch roots were significantly shorter when grown with grass than without grass. Likewise, at various dates during the four year field experiment, differences in seedling tap root length were statistically significant. Seedling biomass distribution was also affected by the treatments: biomass distribution to roots was more for seedlings grown with grass, compared with those grown without grass. Also, smaller seedlings, as opposed to larger ones, were shown to have allocated more biomass to roots. However, Cahill (2003) found no relationship between belowground competitive ability and root system size in a Canadian grassland experiment.

In accordance with some of the research cited above, Peltzer and Kochy (2001) suggest that the characteristics of a good competitor constitute the ability to withstand suppression by neighbors, effectively exploit available resources, hinder growth of other plants, and grow faster or survive longer at low resource levels. In addition, the authors found that competitive ability may not rely as much on total accumulated plant biomass but rather on growth rate, in addition to the other characteristics mentioned. Through their greenhouse experiment looking at effects of neighbor plants (grasses, shrubs, and intact vegetation), Peltzer and Kochy (2001) found less competition for resources between woody plants than between grasses. Consequently, they suggest that some type of facilitation may occur among woody plants, and this may be the reason behind the occurrence of concentrations of woody plants on the landscape, particularly in savanna conditions.
It has also been suggested that resource and spatial gaps (areas unoccupied by grass roots) in belowground soil layers may better induce tree seedling establishment. Coll et al. (2004) suggest that gaps in soil resource abundance and differences in soil resource distribution in areas of grass growth may be consequent to indirect effects from grass roots induced by high grass root density, creating zones of resource depletion which may induce or detour changes in spatial distribution of tree seedling root systems. Jurena and Archer (2003) propose that roots compete for space, not only resources, belowground. In a field experiment, they tested the establishment of *Prosopis glandulosa* seedlings with *Schizachyrium scoparium* and *Paspalum plicatum* grasses in areas with and without gaps in grass roots belowground, and with and without aboveground gaps of grass. No relationship was found between belowground biomass and aboveground gap size, although aboveground spatial gaps had a positive impact on seedling survival. However, Lindh et al. (2003) found root biomass in aboveground gaps to be notably less than root biomass under closed canopy in a NW US coniferous forest. Yet, Jurena and Archer (2003) found seedling roots preferentially grew in unoccupied spatial gaps belowground. Within these gaps, vertical spatial gaps in the soil had greater impact than horizontal spatial gaps on seedling establishment. Overall, the authors concluded that spatial and temporal differences in competitive intensity among vegetation may bring about diverse windows of opportunity for tree seedling establishment in grasslands. Their conclusion agrees with that of Cahill (2002) and Jose et al. (2004) who argue that competition is not made up of a suite of static interactions rather these can fluctuate in intensity and vary spatially and temporally.

**Competition for Soil Moisture**

As seedlings and grasses have been shown to compete for space, some researchers have found that the most intense interactions and competition among vegetation occur for moisture. Such heightened competition can occur due to drought, increases in biomass of herbaceous
vegetation that provoke decreases in soil moisture content, and other factors that trigger moisture availability deficits (Benayas et al., 2003; Jose et al., 2004; Schenk, 2006).

In an experiment to test the interactions among existing native and invasive forbs, annual and perennial grass species, and blue oak (*Quercus douglasii*) seedlings in a greenhouse, Gordon and Rice (2000) found significant differences in soil water potential in the different competitive neighborhoods over time. The authors proposed that higher soil water depletion rates in the competing neighborhoods might have been due to significantly higher biomass production rates and longer root lengths of the annual grass *Bromus diandria* (non-native) in comparison to the competitive neighborhoods created with the forb *Erodium botrys* (non-native) and with the perennial grass *Nassella pulchra* (native). Blue oak seedling leaf number and leaf area were highest when grown with *N. pulchra*. Root biomass of oak seedlings was lower in treatments involving high density plantings of other species. Blue oak shoot emergence was significantly affected by neighborhood competition; 89% of oak seedlings emerged in a no-neighbors situation and in the case of non-native neighbors planted in low densities 56% of oak seedlings emerged. Water potentials in all treatments had important impacts on oak seedling growth and elongation.

Davis et al. (2005) found different results in an experiment in Minnesota, USA, in which they examined the effects of native and non-native species on oaks as well as effects of moisture on oak (*Quercus ellipsoidalis*) seedling establishment by manipulating moisture and nutrient levels. Results indicated no important impacts were made due to neighboring grass type and, in addition, soil moisture content had a positive, significant effect on seedling growth. Benayas et al. (2003) also investigated the effects of native grasses on oak seedlings by testing, in a pot experiment consisting of native Mediterranean herbaceous vegetation and *Quercus faginea*
seedlings, in which different herbaceous removal treatments were used. Results revealed that in
the treatment that excluded aboveground biomass (regarded as the belowground competition
treatment), biomass of herbaceous vegetation correlated negatively with soil moisture content.
Similarly, soil moisture was lowest for treatments with no competition during the dry season.
However, elimination of herb shoots did not affect seedling survival.

Coll et al. (2004) combined beech (Fagus sylvatica) seedlings and perennial grasses in a
pot experiment, in which, beech seedlings grown alone, free of grasses, increased their initial
height by 87% in contrast to seedlings grown with grasses in which height increased just 1%.
After two growing seasons, diameter and height growth of beech seedlings grown with grasses
were reduced. The authors correlated reduction in seedling diameter with reduced soil water
content, as during both growing seasons treatments involving interplanted seedlings and grass
experienced an important decrease in soil water content. They also noted that grasses were more
efficient at absorbing nutrients than beech seedlings.

It is apparent that there is a wide variety of results and opinions regarding tree seedling-
grass interactions and competition. It has been shown that trees and grasses can utilize different
strategies to outcompete one another for above- and belowground resources and space. It has
also been shown that competition and interactive relationships can change over time and space
and that these will also vary with species and environmental conditions. Evidently, available soil
moisture plays a key role in seedling establishment and may determine species survivorship.

**Root Biomass Allocation**

One way in which plants respond to competition is through shifts in biomass allocation.
To explore this idea, Harmer and Robertson (2003) studied changes in tree seedling root systems
associated with intercropped grasses grown in nursery beds. In their experiment, five of six
seedling species had greater root:shoot ratios when planted with grasses as compared to when
planted without grass. Over time, biomass accumulation increased in roots rather than shoots. Tap root lengths were overall longer for species planted with grasses; however, mean length of the root systems were shorter in the grass treatments. Also in the grass inclusion treatments, tap root made up a larger proportion of total root length for the final harvest, resulting in an increase in root length relative to total root biomass. Yet, significant differences were not found for most of the variables. Authors attributed lack of significance to the short-term nature of the study and the differing emergence and germination dates of the seedlings, and attributed the differences in responses among tree seedlings to the unique responses among different species to grass presence.

In an experiment exploring a similar topic, Nilsson and Orlander (1999) found comparable results when testing Norway spruce (*Picea abies*) seedlings and grasses using treatments of mounding and herbicide. They found spruce seedlings in a grass inclusion treatment allocated greater biomass to roots than in grass exclusion treatments. Additionally, the presence of neighboring grasses brought about increased evapotranspiration in spruce seedlings. Collett et al. (2006) also found increased allocation of biomass to roots in *Quercus petraea* seedlings when seedlings were grown with grasses. However, in a study in New Zealand examining mountain beech (*Nothofagus solandri*) seedlings in forest understory, Platt et al. (2004) found that belowground root trenching and trenching combined with fertilization significantly increased biomass allocation to roots. More literature exists with parallel as well as contrasting results: in some competitive situations, biomass allocation to roots increases and in other situations of competitive exclusion the same result occurs.
Competition for Nutrients (Fertilization Studies)

It seems apparent that competition for moisture and space can create situations of exclusion in which herbaceous vegetation can outcompete woody perennial seedlings, as competition for soil nutrients can be intense for seedlings and herbaceous vegetation. Several studies have examined the effects of fertilization treatments on the interactions between tree seedlings and herbaceous vegetation, some of these include Hangs et al. (2002), Thevathasan et al. (2000), Ramsey et al. (2005), and Platt et al. (2004). For example, in a Canadian boreal environment, Hangs et al. (2002) tested *Populus tremuloides*, *Epilobium angustifolium*, and *Clamagrostis canadensis* (early succession species) in competition with *Picea glauca* and *Pinus banksiana* for N. In the study, the grass species, *Calamagrostis canadensis*, outcompeted *P. glauca* and *P. banksiana* seedlings for N during the establishment phase of tree seedlings and vegetation in a pot experiment. Hangs et al. (2002) concluded that the ability of herbaceous vegetation to efficiently access NH$_4^+$ and NO$_3^-$ more effectively than the other species ensured the grasses with a competitive edge over the tree seedlings. Thevathasan et al. (2005) also looked at the effects of *C. canadensis*, *E. angustifolium*, *P. tremuloides* together with other species on black spruce (*Picea mariana*) based on NO$_3^-$ accumulation rates. The early succession species (also deemed weed species in the literature) benefited most from the accumulated NO$_3^-$. Weeds were able to outcompete black spruce seedlings for resources. In treatments of low weed density, black spruce seedling performance improved.

Ramsey et al. (2002) also tested fertilizer treatments although coupled with an herbicide regime to assess interactions between longleaf pine (*Pinus palustris*) and varied naturalized grasses in Florida, USA. They found fertilization to have a negligible effect on seedling development. The authors postulated that fertilization of seedlings in an old field site potentially reduced seedling survival due to the possible stimulation of surrounding weed growth by
fertilizer. Concurrently, herbaceous weed control significantly increased pine seedling height and root collar diameter. Herbaceous weed control also resulted in higher seedling survival than that of the control after the first growing season. Furthermore, weeding treatments increased the growth of seedlings out of the characteristic *P. palustris* “grass stage.” Platt et al. (2004) combined fertilization with vegetation removal treatments and added root trenching to control herbaceous vegetation growing with mountain beech seedlings (*Nothofagus solandri*). They found that the combination of root trenching and fertilization significantly increased seedling stem diameter 231% and height growth 167% under the same treatment regime in comparison with the seedling control group. However, seedling growth in fertilizer-only treatments (in the absence of trenching and herbaceous vegetation removal) was not significantly higher.

**Microclimate Effects**

An indirect form of interaction between grasses and tree seedlings was tested by Ball et al. (1997; 2002) in New South Wales, Australia, through assessing the effects of grasses on ground-level microclimate. They found that grasses around seedlings caused a change in temperature near to the ground creating a microclimate around seedlings. The microclimate significantly lowered minimum temperatures above the grass surface and consequently lowered tree seedling leaf temperature 13°C, leading to a significant decrease in seedling growth. Concurrently, seedling leaf temperatures increased linearly with increased bare ground area (removal of grass) surrounding the seedling.

**Trenching Effects**

The strategy used by Pratt et al. (2004), root trenching, has been used for research in some cases to form a physical barrier between root systems, unlike treatments such as clipping and herbicide applications, which in most cases only eliminate vegetation interaction superficially. In experiments with mature trees, Ludwig et al. (2004) and Harrington et al. (2003) used
In an East African savanna, Ludwig et al. (2004) trenched mature *Acacia tortilis* trees in an experiment to examine plant-tree interactions within the context of hydraulic lift. They found live grass biomass to be significantly higher in trenched plots. Overall, grass growth benefited from trenching and the reduction in competition. In addition, total aboveground biomass was significantly higher in trenched plots than in control plots.

In a unique study, Harrington et al. (2003) assessed mature woody species’ ability to outcompete native herbaceous vegetation. Mature long leaf pines demonstrated belowground intraspecific competition by limiting longleaf seedling growth nearby through root competition. The authors also suggested that pine needle litter could play a role in curbing the growth of herbaceous vegetation as litter can diminish the penetration of sunlight and moisture to lower layers. During the first two years of the study, there was effective separation of herbaceous and pine roots using trenching. The authors deemed that trenching was effective at reducing competitive interactions among the species. However, in the third year of the study, trenching effects were reduced by pines’ capacity to access soil moisture beyond the trenched areas. At the same time, stand basal area for pine increased substantially and the increased absorption of moisture occurred in proportion to the increase in basal area. The authors found that the presence of pine in the overstory and relative buffering of high surface temperatures did not provide an overall benefit to herbaceous vegetation as increases in pine population caused an increase in competitive interactions above- and belowground.

In contrast to these, Holl (1998) found in an experiment on the effect of trenching on seedling performance in a pasture and a forest in Costa Rica that trenching had a significant effect on root biomass of grasses and shrubs but not on tree seedlings. Grass fine root biomass
was greater than shrub fine root biomass in non-trenched treatments; however, fine root biomass for grasses and shrubs in the trenched treatments were similar. Seedling growth was also greater with grass than with shrubs across treatments.

Also in a tropical setting, Barberis and Tanner (2005) examined the effects of trenching on seedling performance in a semi-evergreen forest in Panama. They evaluated seedling survival and growth in forest gaps and in forest understory in relation to soil moisture, soil nutrient availability, and light availability in both trenched and non-trenched plots. In the study, soil moisture was significantly affected by trenching, by 40% in the dry season and by 2% in the wet season. Also in the dry season, seedlings in trenched plots had greater leaf area than those in non-trenched plots. In terms of overall effects of trenching on soil moisture, the authors generalized that the increase in seedling growth in trenched plots was a function in part of improved soil moisture. However, the authors found soil nutrient availability also played an important role in seedling performance. In fact, trenching was less effective in the understory when seedlings became less limited by nutrients. Like soil moisture and nutrient availability, light availability also played a significant role in seedling performance in trenched and non-trenched plots. According to the results, light gaps were more effective at increasing seedling growth and survival than trenching. The authors suggested that, “the importance of belowground competition in limiting the growth of tropical tree seedlings decreases as soil fertility increases and decreases as drought decreases. We can also generalize that the increases in growth due to gaps are greater than increases due to trenching in wetter and more fertile sites.”

It is evident that interactions between tree seedlings and grasses are extensive, somewhat complex, and not of any consistent pattern. There are numerous variables and scenarios that affect belowground interactions and competition, including soil conditions, species, surrounding
vegetation, climate, regions, ecology, and many others. Existing research alludes to the possible relationships between some of these variables; however, concrete determinations are few.

**Objectives and Hypothesis**

The objective of this study was twofold. One element of the experiment sought to assess whether vegetation surrounding seedlings affected the development of the studied seedlings. The other objective was to use information from this study to provide recommendations to producers regarding species selection and required weeding regimes for trees integrated into pasture systems. I hypothesized that increasing herbage removal would lead to increasing seedling growth, trenched seedlings would prosper over seedlings in the other herbage removal treatments, and *A. occidentale* would be the hardiest species among the three species tested.

**Methods and Materials**

**Study Site**

The study was conducted on La Cabimosa Farm, La Candelaria sector, Rio Grande corregimiento, Coclé province, Panama (see Chapter 2 for specific local and regional characteristics).

**Experimental Design**

A completely randomized design was used with three tree species (listed in the next section) and four levels of herbage removal around seedlings, thus a total of 12 treatment combinations. Tree seedlings were planted in rows of thirty, and treatment combinations were randomly assigned to each row. Treatments included zero removal of herbage around the seedling (control), removal of herbage within a 50 cm diameter around the seedling stem, removal of herbage within a 100 cm diameter around the seedling stem, and removal of herbage within a 100 cm diameter around the seedling stem combined with a backfilled trench around the seedling. There were 10 repetitions for each treatment combination and each season, totaling 

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360 seedlings. To maintain the herbage removal treatments, weeds were clipped to ground level once monthly using a machete.

**Materials**

Three tree species were chosen by participating farmers to be used in the study. The species were *Anacardium occidentale*, *Bombacopsis quinata*, and *Tectona grandis*. All of the seedlings were acquired through a local nursery. The *A. occidentale* and *B. quinata* seedlings were approximately 180 days in age and 30 cm in height at the time of planting. In accordance with local and regional planting technique, *T. grandis* seedlings were planted using bareroot stalks and were approximately 200 days in age.

**Establishment**

On the Cabimosa farm in a fenced field previously used for pasture and seasonal rice production, soil was tilled by tractor in preparation for planting. Most of the standing herbage was removed by tilling; remaining weeds were removed manually using a machete. Holes were dug 3 m apart and measured 30 cm deep by approximately 30 cm wide in rows 3 m apart, resulting in a planting configuration of 3 m x 3 m. Circular trenches were excavated at 100 cm diameter around the seedlings, which were randomly chosen to correspond to the trenching treatment. Within each trench, a single layer of thin black plastic was placed to line the trench and the trench was backfilled. At the time of planting, the nursery bags of *A. occidentale* and *B. quinata* were removed and the root ball with its original soil was placed inside the hole with the previously removed soil which had been loosened and rocks removed prior to planting. *T. grandis* bareroots were planted similarly into the holes and backfilled. Seedlings were planted in June, 2000.
Measurements

Seedlings were harvested 6, 12, and 24 months after planting. Harvesting consisted of the complete uprooting of the seedling. Seedlings were removed from the ground using knives and fingers. Roots were washed to disperse soil particles. Seedlings were weighed fresh and then divided into roots, stem, and leaves. Observations were recorded for the total dry mass weight of each seedling as well as its roots, stems, and leaves separately.

It is notable that data for *T. grandis* in month 24 was unavailable due to seedling mortality. In addition, due to the phenology of *T. grandis* and *B. quinata*, leaf data for these species were often unavailable due to the abscission of its leaves prior to the time of harvest and observation.

Data Analysis

Logarithmic transformations of the data were applied to improve normality of the distribution. Statistical analyses were performed using SAS. Analysis of variance (ANOVA) was conducted. When the ANOVA results indicated a significant effect ($\alpha = 0.05$), a Scheffé test was conducted to carry out multiple comparisons of means. The data used in the analysis consisted of weights per seedling or seedling part.

Results

Herbage Removal

Effects of herbage removal on tree seedlings varied by species and over time as there was an overall significant main effect of the herbage removal treatment variable on seedling biomass (Table 5-1). In the Scheffé comparison of means, the Control and Trench treatments were significantly different while the 50 cm and 100 cm treatments were not (Table 5-2). Overall, the lowest growth occurred in the Control group (Figure 5-1).
Effects of the Species Treatment on Biomass

The three tree species differed significantly in biomass production over time; also there was a significant interaction between species and the repeated measure time. Each species was significantly different at each time, with the exception of teak at 24 months (Table 5-3).

In relationship to the weeding regimes, *A. occidentale* showed the largest fluctuation in responses to weeding regimes, with its highest mean biomass in the 100 cm treatment and the lowest in the Control treatment. Results for *B. quinata* were somewhat similar for the 50 cm and 100 cm treatments. However, *B. quinata* biomass was highest overall in the Trench treatment. At the same time, *B. quinata* had the highest mean biomass of all species in all of the herbage removal treatments except in the 100 cm treatment while *T. grandis* had the lowest mean in all of the treatments.

Between the 6 and 12 month harvests, there was a general decreasing trend in mean biomass for the Control, 50 cm, and Trench treatments. However, in the 100 cm treatment, growth was stagnant overall. Conversely, in the 24 month harvest, overall growth increased sharply (Figure 5.2). It should be noted that in the 24 month harvest, no data was available for *T. grandis* growth due to mortality of *T. grandis* seedlings during this period. In the ANOVA analysis, there was a significant interaction between species and harvest (*p* < 0.0001). When a comparison of means was conducted, at 6 months, 12 months, and 24 months, all of the species were significantly different except for the absence of *T. grandis* in the 24 month harvest. At the 6 and 12 month harvests, *B. quinata* had the highest mean biomass values. However, in month 24, *A. occidentale* had the highest mean of the two species, which was almost twice that of *B. quinata*.
Stem Biomass

There was a significant main effect for herbage removal on stem biomass ($p < 0.0446$). However, there was no significant interaction of herbage removal with the other variables. Similar to the results of total seedling biomass stated above, in a comparison of means test there was a significant difference ($p < 0.0137$) between the Control and the Trench treatments in the stem data. However, the 50 cm and 100 cm treatments were not significantly different.

At the same time, there was a significant interaction effect between species and harvest variables. All of the species were significantly different at month 6 and at month 12, but were not significantly different at month 24. In terms of differences in growth patterns, *A. occidentale* stem growth made little progress during the first year. However, between 12 and 24 months, there was a substantial increase in its stem biomass (Figure 5-3): while the mean stem weight was 62.75 g per seedling at 12 months, it was 836.12 g at 24 months. Furthermore, the stem biomass of *A. occidentale* was about three times the amount of its root biomass during the study. Both *B. quinata* and *T. grandis* stem weight decreased from month 6 to month 12. However, in month 24, *B. quinata* stems rebounded in growth, from a mean weight of 240.5 g in month 6 to 340.02 g in month 24.

Root Biomass

Similar to the stem biomass data, there was a significant interaction between harvest and species in the root biomass data ($p < 0.001$). Root biomass yields were significantly different for each measurement interval (harvest) across species (except *T. grandis* in month 24), unlike the stem data but similar to the overall growth data. For *A. occidentale*, root:stem ratios were 0.405, 1.185, and 0.29 at months 6, 12, and 24, respectively. *B. quinata* root:stem ratios were somewhat consistent over time at 1.185, 1.465, and 1.21 at 6, 12, and 24 months respectively. In contrast, for the first two harvest dates, root biomass of *T. grandis* decreased over time, its
root:stem ratio at the 6 month harvest interval was 3.31 and at the 12 month interval it was 2.0 (Figure 5-4).

**Discussion**

To promote the integration of trees into pasturelands, it is imperative that the dynamics of the interactions between grasses and trees be understood. Of particular importance is the period of seedling establishment to ensure the growth of healthy seedlings within a nascent silvopastoral system. In addition, it is vital that land managers be aware of the management practices required during the tree seedling establishment phase of the system to ensure its longevity and vitality.

In Panama’s southern plains, pastures with few dispersed trees dominate the landscape. Trees remain in pastures for myriad reasons; however, both trees and emerging seedlings are seldom cared for or managed. This study was established primarily to examine the dynamics of seedling establishment in pastures to help land managers interested in successfully establishing a greater number of trees in their pastures.

**Seedling Growth**

In the study, observations were made of total seedling growth (including roots, stems, and leaves - when intact) in response to experimental treatments. Removal of herbage surrounding seedlings had a significant effect on seedling growth. The hypothesis was that the absence of herbage competitors above- and belowground would have beneficial effects on seedling growth; thus, increasing herbage control was expected to have positive effects on seedling growth. However, only the Trench treatment had a significant impact on seedling growth. This may indicate that although herbage was removed aboveground, for example in the 50 cm and 100 cm treatments, herbage continued to have an impact belowground. It can therefore be inferred that herbage removal is only effective when presence of belowground plant components are removed through measures such as systemic herbicide application and rototilling. However, a combined
analysis of the data across herbage removal treatments showed the lowest seedling biomass yields occurred in the Control treatment which included no herbage removal, suggesting that herbage removal treatments were in general effective in increasing seedling growth. This indicates that herbage removal treatments indeed had an effect on seedling biomass accumulation.

The three species tested in the study performed differently throughout the experiment. *A. occidentale* is quite abundant locally in the study site. Its ability to acclimate and thrive within the conditions of the study during the trial may have been to a certain extent an attribute of its inherent adaptation to the area. However, *A. occidentale* experienced difficulties between month 6 and month 12 of the experiment when there was only a small increase in its total biomass production while between months 12 and 24 its growth accelerated. Trenching, coupled with plastic lining, may have hindered *A. occidentale* growth during months 6 and 12. Only when the species was able to penetrate and overcome the plastic barrier, perhaps at or after month 12, was it able to reach its full growth potential. A very similar response occurred in the experiment of Harrington et al. (2003) with longleaf pine.

Across the species, the 6 to 12 month period saw a general decrease in biomass accumulation – an unexpected result which may have occurred due to seasonal variation. The 6 to 12 month period coincided with the local dry season where precipitation can fall below 13 mm monthly (Murphy and Lugo, 1995). The region where the study was conducted, called the *arco seco*, is known to have the driest and most prolonged dry season in the country extending up to 5 months. Hence, the decrease in biomass weights observed may have been a consequence of the severe drought experienced during these months and/or the result of herbivory by local herbivores.
Stem and Root Biomass

Leaf data are not reported in this study due to the lack of availability of leaf biomass for all of the species on all of the harvest dates. *B. quinata* and *T. grandis* are deciduous species; their leaves had often fallen before the harvest dates. In fact, *B. quinata* is known to be devoid of leaves during six months of the year.

Effects of herbage removal differed for stem and root growth. It was expected that herbage removal would have a relevant impact on root growth, as has been observed in diverse studies (Harmer and Robertson, 2003; Coll et al., 2004; Platt et al., 2004). However, herbage removal did not have a significant impact on root growth. On the other hand, stem growth was, in fact, adversely affected by herbage removal. The reasons for this observation are unclear.

Ratios of roots to stem varied distinctly among the species. For example, root:shoot ratio of *A. occidentale* differed from that of the other species and the ratio for the species itself differed over time. The changes in the root:shoot ratio of *A. occidentale* may have been a consequence of the seedlings’ inability to access soil resources in which the inlaid plastic impeded growth of *A. occidentale* roots and their ability to access growth resources. The change in the root:shoot ratio of *A. occidentale* coincided with its marked, accelerated growth between months 12 and 24. This could be attributed to *A. occidentale* roots reaching a region of the soil profile with greater soil resources thereby allowing *A. occidentale* to distribute greater biomass to aboveground growth and forsake increases in belowground growth (Schenk, 2006).

In contrast, *B. quinata* maintained a constant root:shoot ratio throughout the experiment regardless of seasonal fluctuations and treatment effects. A unique trait of *B. quinata* is its ability to thrive under drought conditions for extended time periods. Consistent allocation of more biomass to roots than stems may be one of the adaptation and survival mechanisms of this species. Conversely, *T. grandis* had a “difficult” time in this study, demonstrated by its complete
mortality by month 24. However, during months 6 and 12 the species maintained a high root:shoot ratio, roots accounting for 67 to 77% of total observed biomass; this may also have been an after-effect of being grown from bareroot stalks.

**Conclusion**

This study examined the effects of herbage removal treatments on three tree seedling species over two years. At the initiation of the study, I hypothesized that increasing herbage removal would lead to increases in seedling growth. The experiment results did not provide evidence to validate this hypothesis. However, within this hypothesis, I stated that it was likely that the Trench treatments would have the greatest effect on increasing seedling growth and this hypothesis was confirmed by the results. I also hypothesized that *A. occidentale* would be the hardiest of the three tree species in the experiment. However, this was not demonstrated in the results. In fact, *B. quinata* had the largest overall mean weight. While *A. occidentale* was a close second to *B. quinata*, its performance was less consistent than that of *B. quinata*. Finally, the applied objective of this study was to garner information in order to make recommendations to land managers regarding appropriate herbage removal for establishing seedlings. The study results indicate that herbage removal in general will favor seedling performance; however, the results do not provide a clear result for the appropriate, specific amount of herbage removal to optimize seedling establishment and growth.
Table 5-1 Analysis of the effects of the repeated measures herbage removal (at distances of 50 cm, 100 cm, and 100 cm with trenching, from seedling stem), tree species (*Anacardium occidentale*, *Bombacopsis quinata*, and *Tectona grandis*), and time (6, 12, and 24 months after planting) and their interactions on biomass accumulation of tree seedlings planted on-farm in a non-grazed pasture in Rio Grande, Coclé, Panama.

<table>
<thead>
<tr>
<th>Effect</th>
<th>df</th>
<th>F</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herbage removal</td>
<td>3</td>
<td>2.6</td>
<td>0.0562</td>
</tr>
<tr>
<td>Species</td>
<td>2</td>
<td>118.59</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Species x Herbage removal</td>
<td>6</td>
<td>0.1</td>
<td>0.9962</td>
</tr>
<tr>
<td>Time</td>
<td>1</td>
<td>2.51</td>
<td>0.1152</td>
</tr>
<tr>
<td>Season x Herbage removal</td>
<td>3</td>
<td>1.87</td>
<td>0.1371</td>
</tr>
<tr>
<td>Time x Species</td>
<td>2</td>
<td>110.22</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Time x Species x Herbage removal</td>
<td>6</td>
<td>0.61</td>
<td>0.7212</td>
</tr>
</tbody>
</table>
Table 5-2 Comparisons of the within-subject effects of the repeated measure herbage removal (0 = control (no herbage removal), 50 = herbage removal 50 cm diameter around seedling stem, 100 cm = herbage removal 100 cm diameter around seedling stem, Ditch = herbage removal 100 cm diameter around seedling stem coupled with plastic-lined, back-filled trench 100 cm diameter around seedling stem) on biomass accumulation of tree seedlings planted on-farm in a non-grazed pasture and observed over two years in Rio Grande, Coclé, Panama.

<table>
<thead>
<tr>
<th>Herbage removal</th>
<th>Herbage removal</th>
<th>t</th>
<th>Pr &gt; t</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>100</td>
<td>-0.91</td>
<td>0.3644</td>
</tr>
<tr>
<td>0</td>
<td>50</td>
<td>-0.98</td>
<td>0.3284</td>
</tr>
<tr>
<td>0</td>
<td>Ditch</td>
<td>-2.51</td>
<td>0.0137</td>
</tr>
<tr>
<td>100</td>
<td>50</td>
<td>-0.07</td>
<td>0.942</td>
</tr>
<tr>
<td>100</td>
<td>Ditch</td>
<td>-1.6</td>
<td>0.1124</td>
</tr>
<tr>
<td>50</td>
<td>Ditch</td>
<td>-1.52</td>
<td>0.1303</td>
</tr>
</tbody>
</table>
Table 5-3 Effects of the interactions of three seedling species (Cashew (*Anacardium occidentale*), Tropical cedar (*Bombacopsis quinata*), and Teak (*Tectona grandis*)) with harvest time (6, 12, and 24 months after planting) on biomass accumulation of tree seedlings planted on-farm in a non-grazed pasture in Rio Grande, Coelé, Panama.

<table>
<thead>
<tr>
<th>Species</th>
<th>Species</th>
<th>Time</th>
<th>t</th>
<th>Pr &gt; t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cashew</td>
<td>Tropical cedar</td>
<td>6</td>
<td>-15.26</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Cashew</td>
<td>Teak</td>
<td>6</td>
<td>-4.39</td>
<td>&lt; 0.0001</td>
</tr>
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<td>Tropical cedar</td>
<td>Teak</td>
<td>6</td>
<td>9.57</td>
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</tr>
<tr>
<td>Cashew</td>
<td>Tropical cedar</td>
<td>12</td>
<td>-12.5</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Cashew</td>
<td>Teak</td>
<td>12</td>
<td>11.08</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Tropical cedar</td>
<td>Teak</td>
<td>12</td>
<td>20.29</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Cashew</td>
<td>Tropical cedar</td>
<td>24</td>
<td>2.94</td>
<td>0.004</td>
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</tbody>
</table>
Figure 5-1 Responses of three species of tree seedlings to three understory-herbage-removal treatments during the first two years after tree planting in a field site in Rio Grande, Coclé, Panama.
Figure 5-2 Biomass accumulation of stems and roots of three species of tree seedlings planted for the establishment of silvopastoral systems in a field site in Rio Grande, Coclé, Panama.
Figure 5-3 Changes in seedling biomass accumulation in stems and roots, and root:shoot ratio (numbers above bars) changes during the two-year establishment of silvopastoral systems in pastures in Coelé, Panama.
Figure 5-4 Root:shoot ratios of three species of seedlings across grass removal treatments during the two-year establishment phase of silvopastoral systems planted in pastures in Rio Grande, Coclé, Panama.
CHAPTER 6
SUMMARY AND CONCLUSIONS

The focus of this effort was to address the problems and challenges of improving production efficiency and environmental health that small-scale cattle farmers in Panama face today. The goal was to produce research results that could be readily adopted by farmers and adapted to their production practices on-farm. With this purpose and based on the premise that trees in pastures can augment production and provide beneficial environmental services, this research examined the survival of planted tree seedlings in active pastures, evaluated the interactions between establishing seedlings and surrounding vegetation, and assessed the effects of large trees on forage characteristics in pasture. The principal questions that guided the research were:

1. What are the best means, in terms of tree species and planting configuration design, to establish young tree seedlings into actively grazed pastures?

2. In terms of management strategies, what is the vegetation removal regime that optimizes seedling survival?

3. What is the effect of dispersed trees in pasture on forage characteristics and pasture production?

Experimental Findings

To explore possible responses to the principal research questions, research was carried out on tree seedling survival and herbivory, consequences of large trees on forage, and the interactions between seedlings and grasses.

Seedling Survival and Herbivory

We found that species characteristics played a major role in seedling survival. This was to be expected considering that rooting ability, ability to acquire resources, carbohydrate reserves, growth type, and light needs are characteristics that are critical to the survival of a species, particularly in competitive environments. In the study, planting configuration and tree species
played important roles in seedling survival. Seedlings in open pasture (planted in lines and diagonals) survived better and longer than those planted along fences. On the other hand, incidence of herbivory was overwhelmingly dependent on species type. Species with palatable leaves were browsed far more often than the less palatable ones. Of the three species studied, *Anacardium occidentale*, *Tectona grandis*, and *Bombacopsis quinata*, *A. occidentale*, which is locally abundant, showed greater survival and had least herbivory, and it performed better than the other two species at the end of the two-year study period.

Seedlings were quite sensitive and they responded differently to planting configurations. Seedling mortality was highest in the fence treatment (66%), followed by diagonal (51%) and line (47%). It was also clear that presence of cattle was not conducive to seedling survival. Grazing cattle present a challenge to both increasing seedling survival and diminishing seedling herbivory in grazed pastures. When cattle were present, *A. occidentale* performed markedly better than *T. grandis* and *B. quinata*.

**Effects of Large Trees on Understory Forage**

Three forage characteristics were examined: forage mass, digestibility, and botanical composition. Season and distance had different effects on the two tree species tested, *Anacardium occidentale* and *Tectona grandis*. Season was important to forage growth below and around *A. occidentale* in that across distances forage abundance was greater in the wet season than in the dry season. However, this was not the case for *T. grandis*. Surprisingly, forage mass values were greater in the dry season than in the wet season below and around *T. grandis* crowns. The fact that forage mass values for *T. grandis* were generally low in comparison to those of *A. occidentale*, forage dry season abundance was greater than in the wet season, and forage mass in open pasture was greater than it was at the drip line and close to the stem (unlike *A. occidentale*) indicates that there are potentially relevant interactions occurring.
between the *T. grandis* trees and forage which may be impinging upon forage growth. Hence, season was relevant to forage growth throughout. It was evident, however, that, similar to the results of seedlings survival and herbivory, tree species was key to differences in forage growth.

Unlike forage mass, forage digestibility was impacted by distance and season under *A. occidentale* and only season under *T. grandis*. Tree species had a particularly noteworthy effect on digestibility in that forage under *T. grandis* had consistently better digestibility than that under *A. occidentale*. Even when close to the tree stem, species had important impacts on digestibility, unlike forage mass. However, when moving away from trees and into open pasture, only season became relevant to changes in digestibility.

Forage composition was also highly affected by tree species. Quantity of grass, legume, and weed biomass was sensitive to tree species as their abundance was generally static in the *T. grandis* understory yet varied under *A. occidentale*. Changes in effects did not occur across distances, implying that distance to the tree was irrelevant while the tree species itself was the relevant factor affecting forage composition. However, the amount of necromass (dead material in the forage) was considerably sensitive to distance to *T. grandis* stem in that it increased at the drip line; this observation provides a relevant insight into the relationship between tree presence and forage botanical composition.

**Interactions between Seedlings and Vegetation**

Vegetation removal regimes had varying effects on tree seedling growth. Seedling biomass was affected positively by vegetation removal aboveground. However, a significant increase in seedling growth occurred only when belowground vegetation biomass growth was impeded, indicating the importance of belowground competition on seedlings. The different vegetation removal regimes affected seedling stem growth but did not have significant impacts on root growth. However, interestingly, the different vegetation removal regimes affected
seedlings differently. *A. occidentale* root:shoot ratio fluctuated with vegetation removal while *B. quinata* root:shoot ratio was consistent regardless of season or herbage removal. Overall, *B. quinata* and *T. grandis* allocated more biomass to roots than stems.

**Implications for Implementation**

**Options for Grazing**

In the experiment, cattle were left on pastures to graze in an attempt to imitate the real situations on producers’ farms as producers are reluctant to remove their cattle from pastures to allow for seedling establishment and growth. However, research results revealed that cattle grazing produced deleterious effects on seedlings. Therefore, a quandary exists as to how best to establish seedlings while meeting the needs and desires of producers to allow cattle to graze. One option may include recommending that in the wet season producers exclude cattle from pastures that have been planted with seedlings and that cattle are allowed to graze these pastures only in the dry season. By eliminating grazing in the wet season, seedlings will be allowed seven to eight months to become established and develop their root systems that are important in preparation for potential grazing or herbivory in the dry season, free of the negative effects of cattle. At the same time, generally the wet season is the period when available forage is highly abundant. It is assumed then that a producer could satisfy cattle needs in other pastures leaving the seedling-planted pasture free to grow and develop during the period. Conversely, in the dry season cattle would graze the seedling-planted pasture. In the dry season, when forage availability is generally deficient, the producer is able to access the forage on the seedling-planted pasture. As found in the experiment, the use of deciduous species may benefit seedling survival in active pastures during the dry season as seedlings would be devoid of leaves when cattle are present thereby reducing the potential for herbivory and damage.
Manipulating Forage with Trees

According to the research results, tree presence diminished necromass around trees. Necromass is undesirable in terms of productive capacity and performance of pasture. Therefore, through appropriate use of trees, producers may be able to reduce necromass abundance. Tree spacing and tree crown architecture would be critical to generate this benefit of reduced necromass yet, at the same time it is necessary to balance light availability to forage when considering tree spacing and total tree stem density.

Tree Establishment

The research results show that seedling establishment, the first step in the integration of trees into pastures, is sensitive to presence of neighboring vegetation. For optimal seedling establishment, competition both above- and belowground should be minimized. However, removal of belowground competition is not always feasible for producers due to cost and labor requirements. Response to vegetation removal within 1 m diameter around the seedling stem was beneficial to seedlings in terms of biomass accumulation although results differed by species. Based on this study, weeding within a 50 to 100 cm diameter around seedlings is the recommended regime.

Future Research

The overriding message from this research as it bears upon impacting directions for future research is that: 1. a dispersed tree silvopastoral system can have positive impacts on extensive pasture productivity, and 2. overall, the species used in the system determines whether the system will benefit or negatively affect pasture characteristics.

It is imperative that silvopastoral research be conceived within the scope of improving agricultural productivity. Given the generally low adoption success of silvopastoral systems in Central America, there needs to be a shift in the conception of silvopastoral research. A
systematic framework geared toward addressing producers’ bottom line, agricultural productivity, must be created that will mobilize the transfer of this evidently beneficial technology that is still in the process of being researched, addressed, and adapted to the needs of producers. It is too vital that research address multiple scales of silvopastoral research application – conceiving of systems for small-, medium-, and large-scale cattle producers, as each of these is abundant across the landscape.

Research should focus on tree species, addressing how these affect forage characteristics. Likewise, forage species within the specific context of silvopastoral systems need to be investigated. There should also be a focus on the livestock component of the system, something that was not included in this study. New studies should also examine the environmental impacts of silvopastoral systems including general biodiversity, birds, insects, and carbon sequestration. These studies will be of particular importance as producers begin to enter the global environmental services market. Finally, it is imperative that research broaches a systems approach to silvopastoral systems. Each of the components, tree, forage, and livestock, must be assessed in terms of their interactions with one another and the ultimate effect these interactions have on production.
APPENDIX A

PLANTING CONFIGURATIONS OF THE THREE TREE-SPECIES SEEDLINGS FOR ESTABLISHMENT OF A SILVOPASTORAL SYSTEM IN RIO, GRANDE, COCLÉ, PANAMA

Fence

Line

Diagonal

Fence
### APPENDIX B

**COMPARISONS OF MEANS OF INCIDENCE OF TREE SEEDLING HERBIVORY ACROSS TREE SPECIES AND PLANTING CONFIGURATION**

<table>
<thead>
<tr>
<th>Configuration</th>
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<th>Species (j)</th>
<th>Mean difference (i-j)</th>
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<th>Sig.</th>
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<tr>
<td></td>
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<td>Teak</td>
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<td>1.314</td>
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<td>Tropical cedar</td>
<td>-3.611*</td>
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</tbody>
</table>
APPENDIX C
FORAGE SAMPLING SCHEMATIC OF HERBAGE MASS HARVESTED AT THREE
DISTANCES FROM TREE STEM IN THE FOUR CARDINAL DIRECTIONS CARRIED
OUT UNDER SCATTERED TREES IN PASTURES IN RIO GRANDE, COCLÉ, PANAMA
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BIOGRAPHICAL SKETCH

Aly Dagang was born in Los Angeles, California in 1972. She graduated from the American University in Washington, D.C. in 1994 where she earned her B.A. in international development and Spanish/Latin American studies. After graduation, she worked as an agroforestry extension volunteer in the Peace Corps in Panama until 1998. Following her return to the United States, Aly began her graduate studies in agroforestry at the University of Florida. Currently, she is the Academic Director for the School for International Training in Panama and member of the Alianza para la Conservacion y Desarrollo.