University of Alberta

Management of Elephant Grass and Restoration of Moist Evergreen Forest in Abandoned Pastures, Galapagos Islands, Ecuador

by

Sarah Rachel Wilkinson ©

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Abstract

Invasive alien species, often introduced intentionally, are the primary threat to the unique flora of the Galapagos Islands. Abandoned pastures of elephant grass (*Pennisetum purpureum* Schum.) persist within Galapagos National Park, fragmenting and encroaching upon native Scalesia forest. In this study, methods to control elephant grass and enhance restoration of the forest were investigated, as part of a restoration framework for the Scalesia forest zone on the island of Santa Cruz. Four management treatments, one-time cutting, repeated cutting, cutting followed by a one-time herbicide application and cutting followed by repeated herbicide applications, and three restoration treatments, natural recovery, use of hand-collected seed and use of a donor soil seed bank, were tested. Restoration success was measured by a reduction in the cover of elephant grass, absence of other alien species, and an increase in the density and richness of native and endemic species. A restoration strategy will focus on integrating proven methods with an understanding of reference community dynamics and land use management.

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1.0 Introduction

1.1 Biological Invasions

Invasive alien species worldwide have caused humans great inconvenience and economic loss as well as displacing and in some cases eliminating native species. The term alien species, used interchangeably with non-native, exotic and non-indigenous species, is here defined according to the U.S. Congress Office of Technology Assessment (1993) as 'species beyond their native range or natural zone of potential dispersal including all domesticated and feral species and all hybrids except for naturally occurring crosses between native species.' Most alien species pose little threat to native plant communities (Vitousek et al. 1996). For example, 43% of the alien species in the Galapagos Islands are naturalized but only a dozen or so have had obvious negative impacts on the native vegetation (Mauchamp 1997). Invasive species are defined as those 'spreading naturally (without direct assistance of people) in natural and semi-natural habitats, to produce a significant change in terms of composition, structure or ecosystem process' (Cronk and Fuller 1995).

The number of species extinctions caused by biological invasions is likely only second to those resulting from landuse changes; although biological invasions are strongly connected with landuse change (D'Antonio and Vitousek 1992). For example, the chestnut blight, an introduced pathogen, has reduced the American chestnut to the point of extinction in forests of the northeastern U.S. (Vitousek et al. 1996). Alien mammals such as rats and feral cats prey on native wildlife particularly young. The introduced brown tree snake is believed to be the cause of native bird species extinctions on the island of Guam through nest predation (Savidge 1987). Invertebrates are some of the most widespread invaders; Eurasian zebra mussels deplete resources necessary for the survival of native aquatic organisms thereby reducing the productivity of the system (Vitousek et al. 1996).

Plant invaders are more widespread than animal invaders as their propagules are easily transported on equipment, clothing and cargo or in commercial seed (Cronk and Fuller 1995). However, alien plant invasions are generally more difficult to quantify than invasions by other types of organisms. Plant invaders can be identified in the initial invasion stage, particularly in disturbed habitats, but the effects they have on neighbouring organisms are often subtle. Since the potential long-term effects of alien plants on native communities and ecosystems are largely unknown, alien plant invaders have not been actively controlled in natural areas, where human interest is not immediate (Cronk and Fuller 1995). The result for some of these alien species has been population explosion.

It is easier to quantify a loss in agricultural production or a depletion of fish, due to plant invasions, than determine if native species vigour is declining or essential ecosystem functions are being altered. For example, the alien grass *Miscanthus sinensis* reduces the light availability and daily carbon gain of regenerating oak trees in Japan; this significantly slows the rate of encroachment of oak into old field habitats (D'Antonio and Vitousek 1992). The availability of resources such as water and soil nutrients can also be altered. The invasive shrub *Myrica faya* increases nitrogen (N) levels in the severely N limited volcanic soils of dry submontane forests in Hawaii (Ley and D'Antonio 1998). This increase in N reduces regeneration of the native tree *Metrosideros polymorpha* and causes conversion of the habitat to grassland. The ability of European annual grasses to rapidly draw down soil moisture in California grasslands is also considered the major cause of poor oak recruitment (D'Antonio and Vitousek 1992). Lastly, ecosystem functions can directly be altered by invasive alien plants including changes to microclimate, disturbance regimes and geomorphology.

To predict which species are potential invaders, research has focused on identifying key attributes, traits or commonalties that allow alien species to succeed in their new environments (Rejmanek and Richardson 1996; Daehler 1998). Noble and Slatyer (1980) identified three attributes that are most important for determining a species role in plant community development: the method of arrival and persistence, the ability to establish and grow and the time required to reach critical life stages such as sexual maturity. These attributes have also been identified as essential to successful invasion by alien species (Rejmanek and Richardson 1996).

Invasions by alien grass species are of particular interest, as noted in a recent study, due to their vast distribution and their effective growth strategies (D'Antonio and

Vitousek 1992). Alien grass invasions are generally more prevalent outside Europe and Africa perhaps because a large proportion of invasive alien grasses are of African or Eurasian origin. There are four key reasons why grass invasions are of worldwide significance. Grass propagules are actively moved on a global scale for agricultural purposes; alien grasses compete effectively with native species in a wide range of ecosystems; where dominant, grasses can alter ecosystem processes; and many grass species can tolerate or enhance fire causing significant changes in habitat and landuse (D'Antonio and Vitousek 1992).

1.2 Invasibility of Island Communities

1.2.1 Biodiversity

Species rich communities are hypothesized to be less invasible than those that are species poor as few empty niches remain (Crawley 1987; Tilman 1997; Wiser et al. 1998). If species poor communities are more readily invaded, then it is not surprising that islands, which are generally species poor due to dispersal limitations, reduced colonization and high local extinction, have higher rates of invasion and species replacement (Elton 1958; MacArthur and Wilson 1967; Brockie et al. 1988; Vitousek et al. 1996). Furthermore, species poor communities experience less intense competition, due to low species richness, and have simple food chains, thus an impact on one species will affect the community. Island populations and endemic species in general may have low genetic diversity due to low occurrences (Linhart 1995) and therefore be more significantly impacted by alien species (Williamson 1981; Simberloff 1995; Randall 1996). These species may be less able to reinvade a site following disturbance due to the lack of refugia often present on continents where ranges and number of populations are greater (Simberloff 1995). Although commonly touted as theory, little conclusive evidence exists to support the notion that diversity begets stability (Simberloff 1995).

High species diversity is used synonymously with high functional group diversity. A functional group is defined as a group of species, which provide the same or a similar role in a community. It may be the absence of a functional group rather than low species diversity that increases the risk of community invasion (Simberloff 1995). Island floras are often limited to a few taxonomic families, with a high proportion of herbaceous species relative to woody species (D'Antonio and Dudley 1995; Simberloff 1995).

1.2.2 Dispersal and Competition

Dispersal and interspecific competition are thought to limit the establishment of species on Pacific Islands (MacArthur and Wilson 1967). The rate of introduction of alien species relative to the land mass is greater on islands compared to continental areas, particularly as human intervention increases (Simberloff 1995). In Galapagos, the rate of species introduction is approximately 10 a year (Mauchamp 1997), approximately 100,000 times the natural rate of introduction (Porter 1983). As the number of introductions increases, the threat to native communities also increases, as these species are able to fill 'empty niches' proposed to be prevalent on islands. Even allowing for the fact that the recent rate may be more due to detection than introduction, the rate since 1800 has been over two species per year, or 20,000 times the natural rate (Porter 1983).

The competitive ability of island endemics is thought to be low due to their isolated evolution. This is not conclusive, as a few studies have suggested that the high divergence within genera on islands (e.g. *Scalesia*) indicates competition may be more intense (Simberloff 1995). In contrast, species that have been introduced outside of their native environment have increased competitive abilities such as increased seed production and growth than when in their native environment (Crawley 1987; Blossey and Notzold 1995). These differences are likely due to a reduction in natural herbivores and pathogens.

1.2.3 Disturbance

Local disturbance facilitates the introduction, spread and establishment of plant species (Usher 1988; Burke and Grime 1996; Kotanen 1997; Fensham and Cowie 1998). Canopy openings increase the abundance of seed rain and the amount of incident light reaching the forest floor. Soil disturbances bring seed already in the seed bank closer to the surface, and increase the availability of microsites. Animals, including humans, moving through the forest, act as dispersal vectors for a variety of seeds, moving seed to new locations and bringing seed from outside the forest. Most seed deposited into the local seed bank will die but a small portion will persist until favourable germination conditions arise.

Disturbance is often considered to favour or even be a prerequisite for invasion (D'Antonio and Dudley 1995). Islands, especially young ones such as Galapagos, may be more susceptible to invasion as the natural state of their ecosystems is similar to disturbed habitats in their simplicity and comparative paucity of species (Macdonald and Cooper 1995). Disturbance such as fire and natural stand dieback may further increase the risk associated with an invasive species.

1.3 Restoration of Communities

1.3.1 Restoration

Restoration is 'the process of assisting the recovery and management of ecological integrity. Ecological integrity includes a critical range of variability in biodiversity, ecological processes and structures, regional and historical context and sustainable cultural practices.' (Society for Ecological Restoration 1996). Most often the purpose of a restoration initiative is to conserve endangered or threatened habitat. Sometimes only a particular species is of interest due to its rarity or it may be considered a keystone or umbrella species (Pavlik 1998). The purpose of restoring a site may also be to control the establishment of alien species. Restoration could be used as a tool to suppress shade intolerant, alien species and/or to eliminate staging areas of non-native species that are adjacent to undisturbed but threatened native flora (Berger 1993). Restoration alone will not eradicate an undesirable species but it may prevent reinfestation of a community, particularly if coupled with proper management of surrounding areas.

Aronson et al. (1993) theorized that certain thresholds of irreversibility are passed as a community is degraded. If too many of these thresholds are passed, then a system loses its resilience. Only with human inputs can the system be put back on a trajectory towards a pre-disturbance state. At some point, the inputs required to achieve this goal are even too great and this is when alternative land use objectives may be considered.

At this point restoration is not feasible and rehabilitation or reclamation may be considered.

1.3.2 Reference Conditions

The goal of restoring a disturbed site to a replica of its original conditions or to pristine habitat is not easy, and perhaps not possible, to achieve. Reference conditions provide a benchmark for planned activities as well as allowing practitioners to measure the success of a project. There is much to debate on this topic and unfortunately this often stalls, if not halts, the progress of beneficial restoration projects. Recent debates have concluded that while a single end goal cannot be clearly defined, some reference point is required to guide restoration efforts (Pickett and Parker 1994; Aronson et al. 1995). At the very least, adjacent undisturbed communities can be used to define reference conditions, along with historical records, where available. Climate change and use of the land by indigenous peoples over extensive periods of time, however, are difficult to document with any degree of certainty. In the absence of undisturbed conditions, a reference state from a predetermined time period is often chosen.

1.3.3 Measurement of Success

Most often species composition and physiognomy are monitored in restoration and used as a measure of success (Ewel 1987; Pavlik 1998). Species composition is certainly a reflection of the soil, topography and microclimate of a site, however, this measure is only an indicator of short-term success. Ecosystem function must also be restored to achieve desirable restoration goals. This is not to say that attainment of a lesser status is a failure, but clear goals and objectives need to set out at the beginning of a project to allow effective determination of success (Ehrenfeld 2000).

Ewel (1987) has defined five basic parameters for measuring the success of restoration projects: sustainability, invasibility, productivity, biotic interactions and nutrient retention. Restored communities should be self-sustaining (i.e. require no human inputs in the long-term), resistant to invasions by alien species and composed of all key species and functional groups (plants and animals). The restored community should also be as productive as the reference community in terms of biomass and nutrient cycling. These measures exclude the socio-economic and cultural components of a successful restoration (Lamb 1988). Depending on the site location, community is essential to the self-sustainability of the restoration. In a developing nation, recognition of the human need for local resource extraction and the fluctuating availability of resources will strengthen restoration success.

Little is known of the complex interactions between ecosystem components at the landscape level and records do not document all historical events. Thus restoration can be as subjective as it is objective and dependent on the ecologist or practitioner. As long as restoration is approached realistically and clear objectives defined for any given project, worthwhile conservation initiatives to protect natural landscapes can successfully be implemented. At the very least, failures can be clearly identified and lessons learned that are beneficial to understanding community and landscape dynamics (Ewel 1987).

1.4 The Galapagos Islands

1.4.1 Overview

There are 15 main islands and approximately 40 islets in the Galapagos archipelago. The Galapagos National Park (GNP) comprises 97% of the area of the islands with the remaining area towns and rural communities. Galapagos currently has a population of approximately 16,000, located on four islands. The main town, Puerto Ayora on the island of Santa Cruz, supports about two thirds of this population as well as up to 70,000 tourists each year. Tourists come each year to see the unique flora and fauna that have evolved on these isolated islands. Of the 560 native plant species in Galapagos, 32% are endemic including seven genera (Mauchamp 1997). This includes some species of uncertain origin, principally pantropical weeds, which may have arrived naturally or may have been introduced by the earliest human visitors to the islands. This flora supports a variety of endemic fauna including 13 species of Darwin's finches (*Geospiza, Platyspiza, Cactospiza, Camarhynchus* and *Certhidia*) as well as the threatened giant tortoises (*Geochelone elephantopus*) and land iguanas (*Conolophus subcristatus*).

Although earlier visits to the islands by indigenous people from mainland South America have been suggested, the official date of discovery of the archipelago is recognized as 1535 (Jackson 1993). The islands were uninhabited at that time, and no evidence of earlier human use has been found. The first visitors after discovery were mainly buccaneers, passing sailors, whalers and sealers (Jackson 1993). The first settler established on Floreana about 1807 with subsequent groups in 1832 and 1902 following short intervals of unoccupancy; it has been permanently inhabited since 1929. San Cristobal was settled permanently in 1869, Isabela in 1893 and Santa Cruz in the 1920s (Schofield 1989; Jackson 1993).

The Galapagos Islands are a province of Ecuador. The majority of the island's population is residents arriving within the last 25 years. Although the majority is Ecuadorian, a substantial portion of both recent and long-term residents are immigrants from Europe, Australia and the United States. Residents work in the tourism industry or rely on agriculture and fishing for their livelihood. The average annual income in Galapagos is high compared to the mainland of Ecuador at US$457 for a family of four (Falconi 2001). Those in Puerto Ayora and those working in the tourism industry generally earn more than those who rely on agriculture and fishing. All of these industries are seasonal.

The Galapagos National Park Service (GNPS) is responsible for management of lands within the boundaries of the national park. The GNPS has a staff of approximately 40 Ecuadorian park guards, many long-term residents, to achieve its management objectives. The Charles Darwin Research Station (CDRS) conducts research and provides technical advice to the GNPS on a variety of conservation issues as well as providing educational programs for the local and tourist communities. The CDRS is the operational arm of the Charles Darwin Foundation, an international not-for-profit organization based in Quito, Ecuador.

Access to the GNP is limited to designate tourist sites, due to the lack of roads and trails, and to reduce impacts on the natural environment. While official park regulations exist, their interpretation and enforcement is determined by the current, elected GNP managers, which results in inconsistencies. For example, in 1999 cattle grazing was permitted within the national park on Santa Cruz, and small scale unauthorized extraction of resources and grazing occur regularly without objection. An unpredictable political climate in Ecuador, the growing population of Galapagos and a booming eco-tourism industry exacerbates these inconsistencies.

1.4.2 Threats to the Galapagos Flora

The number of reported alien plant species in the Galapagos Islands has increased from 77 in 1971 (Wiggins and Porter 1971) to 460 in 1997 (Charles Darwin Research Station). This increase, as well as the introduction of 11 mammals and hundreds of insect species (Loope et al. 1988), has been directly attributed to the population explosion experienced over the past decade and the subsequent increase in agricultural and tourist activities. Many of these alien species have had a direct impact on the native vegetation, although few quantitative studies have been completed to date. *Lantana camara* L. (lantana) is thought to be responsible for the reduction in the endemic *Lecocarpus pinnatifidus* and the native semi-arid community of Floreana; *Cinchona pubescens* Pav. *ex* Klotzsch (red quinine) and *Psidium guajava* L. (guava) are thought to be responsible for the reduction in *Miconia robinsoniana* Cogn. and the fern-sedge vegetation zones on Santa Cruz (Lawesson 1990).

The majority of alien plant species in the Galapagos are initially introduced, either intentionally or unintentionally, within the agriculture zones. Consequently, alien species are only mainly a concern on the inhabited islands, though tourists visiting more remote islands have been dispersal vectors (Jaramillo 1998). Invasive alien species often escape from cultivated areas and invade the neighbouring parklands. Disturbance of parklands due to grazing by feral animals, fruit and timber extraction and tourism has facilitated the establishment of these species in the past. Invasive alien plants not only displace native species and reduce the aesthetic and conservation value of the islands, but they are a constant nuisance to farmers by reducing land productivity and increasing operational costs. Floreana has the longest history of the presence of a large introduced flora, while agriculture on Santa Cruz was minimal until about 1960 (Moll 1990).

The paucity of the Galapagos flora means niches, that would be occupied by trees and shrubs on the continent are vacant in Galapagos. The higher elevation plant communities tend to have more vacant niches than those at lower elevations due to the increased difficulty in seed dispersal. The lower elevation plant communities are arid and considered harsh environments (high stress or extreme) for plants to establish compared to the moist higher elevation communities (Loope and Mueller-Dombois 1989). Only 5% of the species present in the arid regions are alien compared to 30% in the highlands; this relationship is also affected by the patterns of human development (Tye 1999).

Extinctions on Galapagos have not been well documented, although 30% of the endemic species are thought to be threatened (Tye pers. comm.). The dramatically increased rate of introductions in protected areas due to human disturbance may, however, push the balance in favour of further displacement of native species and eventual extinction of species (Fensham and Cowie 1998). Human assistance, such as the removal of undesirable species, soil remediation, seed bank stocking and fertilizer addition, may be necessary to stimulate community resilience, or the natural ability of a plant community to restore itself to its prior composition, structure and diversity (Robertson and Archie 1990; Aronson et al. 1993; Shimizu 1997).

1.4.3 Scalesia Forest Vegetation Zone

The island of Santa Cruz is divided into four vegetation zones (Figure A.1): littoral, arid, transition, and humid. The humid zone is further subdivided into two subzones, the Scalesia forest and the fern/sedge zone. This research was conducted within the Scalesia forest zone. The Scalesia forest on the north side of Santa Cruz is the last remaining stand of any significance in Galapagos (Itow 1995). Historically, Scalesia forest was found on four islands in the archipelago; however, it has been locally extirpated on the islands of Santiago and San Cristobal. On Santa Cruz and Floreana it is threatened by land clearing and introduced species. Restoration of disturbed Scalesia forest is not only desirable for conservation value in itself, but also as a means of preventing further invasions by alien plants (Shimizu 1997).

The moist evergreen forest in the humid zone is dominated by the tree *Scalesia pedunculata* Hook f. (Asteraceae). There are four tree species within the endemic genera *Scalesia,* all of which are found within the moist, high elevation regions of the islands (Itow 1995). *Scalesia* attains a height of up to 10 metres, with a diameter at breast height of 20-25 cm. *Scalesia* forms an even aged cohort, due to stand level dieback following El Nino events every 10 to 15 years (Hamann 1979; Lawesson 1988). Therefore, stands greater than 15 years old are rarely found. Dieback events occur in a patchy distribution across the island, with some areas of forest experiencing more severe dieback than others. It is hypothesized that prior to major El Nino events (every 10 to 15 years), trees are nearing natural senescence and in a state of reduced vigour. The winds and rain associated with El Ninos therefore may only accelerate, not cause, dieback (Lawesson 1988).

Following dieback, or other disturbances such as periodic fire, *Scalesia* experiences synchronous regeneration, as it does not regenerate under a closed canopy. *Scalesia* has been considered a climax species (e.g., Eliasson 1984), however, it exhibits characteristics typical of pioneer species, such as shade intolerance, rapid growth, secondary wood and heliophilous germination (Van der Werff 1978). *Scalesia* reaches maturity within 3 years (Hamann 1981; Shimizu 1997). Its seed is an achene with a much reduced pappus and it is wind and water dispersed. *Scalesia* seed has only been found within a 10 to 20 m radius of parent plants, suggesting that isolation and speciation have resulted in a loss of dispersal ability typical of most Composites (Eliasson 1984; Shimizu 1997).

Elephant grass is preventing regeneration of the Scalesia forest on Santa Cruz, as it forms a dense canopy that effectively reduces light available for regeneration of native species (Hamann 1984; Moll 1990; Shimizu 1997). Elephant grass, also known as napier grass, is an aggressive African perennial. Qualities that make it a desirable forage (e.g., providing a thick cover in a short period of time and ability to survive the dry season), also contribute to its invasiveness in the islands. In 1988, it was estimated that elephant grass covered 5000 ha of land in the islands (Stone et al. 1988). More recent estimates of its distribution have not been made but visual observations indicate that it is spreading at an exponential rate. Nevertheless, its current area within the Scalesia forest zone of the GNP on Santa Cruz is estimated to be not more than 50 hectares.

Elephant grass was introduced to Santa Cruz in 1967, when a farmer brought cuttings from the Loja region of mainland Ecuador (F. Lleno pers. comm.). Elephant grass pastures remain within the established agriculture zone, as well as within areas of native

Scalesia forest. Elephant grass encroaches on intact forest and small patches can be found in the forest interior where canopy gaps occur. It is not a prolific seeder and depends mainly on vegetative spread by vigorous tillering, stolons and small rhizomes (Duke 1983; Skerman 1990; Cronk and Fuller 1995). A C_4 grass native to Uganda and Zimbabwe, it is currently found in dry to wet regions of the tropical and warm temperate climatic zones (Humphreys 1981; Burton 1993). Elephant grass can tolerate a wide range of conditions from low to high elevation, dry to wet, as well as fire, acidity and excess nutrients; it is not tolerant of frost (Humphreys 1981; Duke 1983; Skerman 1990; Burton 1993; McCann et al. 1997). Ideal conditions for elephant grass include full sun, mean annual precipitation of 1500 mm, sites below 1000 m a.s.l., and deep rich soils such as friable loams that are well drained (Duke 1983; Skerman 1990).

1.5 Research Outline

The research goal was to develop cost-effective methods for restoration of the threatened Scalesia forest on the island of Santa Cruz, Galapagos. As invasive, alien species are the greatest threat to the forest, successful restoration would include methods to manage these species as well as methods to enhance recruitment of native and endemic species. Elephant grass was the alien species of focus in this research due to its dominant presence in the Scalesia forest zone, potential ease of removal and potential threat to the existing community particularly during El Nino years (Chapter 2.). The potential for natural recovery of Scalesia forest following elephant grass management was evaluated (Chapter 3.) as well as the effectiveness of methods to enhance recruitment (Chapter 4.). Within a restoration framework, these proven methods are balanced with an understanding of community dynamics, appropriate land use management and socio-economic considerations to achieve the restoration goal (Chapter 5.).

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2. Assessment of Management Options for the Invasive Species Elephant Grass (*Pennisetum purpureum* Schum.), Galapagos Islands, Ecuador

2.1 Introduction

African pasture grasses have been introduced to the Neotropics to improve forage efficiency (Parsons 1972; Low 1997). Many of these grasses have become persistent where planted preventing recolonization of native forest and in some cases invasive, threatening intact remnants of native forest (Nepstad et al. 1990; Low 1997; Posada et al. 2000). Land originally cleared for pasture is being abandoned and in areas of high conservation value, restoration considered. The more persistent grasses, those that have been present for long periods of time or possess aggressive growth strategies (i.e. perennial with vegetative reproduction), form dense mats that effectively compete with other vegetation (Gerhardt 1993). D'Antonio and Vitousek (1992) summarized that the persistence of grasses is due to effective resource competition, rapid growth rates, loss of native seed bank and poor seed dispersal of natives. Other studies suggest that soil physical and chemical properties such as water holding capacity, nitrogen and phosphorous levels are altered by pasture grasses (Buschbacher et al. 1988; Rhoades et al. 1998; Holl et al. 2000).

Abandoned elephant grass pasture within the Galapagos National Park, Ecuador, results in the fragmentation of native forest and encroachment on intact forest remnants. Elephant grass is preventing regeneration of the Scalesia forest on the islands of Santa Cruz and San Cristobal by forming a dense canopy, thereby effectively reducing light available for regeneration of native species (Hamann 1984; Moll 1990; Shimizu 1997). In 1988, it was estimated that elephant grass covered 5000 ha of land in the islands (Stone et al. 1988). More recent estimates of its distribution have not been made but visual observations indicate that it is spreading at an exponential rate. The removal of elephant grass is necessary to preserve habitat and facilitate restoration. Information on the impacts of invasive grass species is, however, more readily available than on successful methods to manage them.

Elephant grass, also known as napier grass, is an aggressive African perennial. Qualities that make it a desirable forage, providing a thick cover in a short period of time and ability to survive the dry season, also contribute to its invasiveness (Table B.1). Elephant grass is considered invasive in other parts of the world, including Hawaii and the continental U.S.A. (Macdonald et al. 1989; NAEPC 1997). However, it is only considered a serious threat in the Galapagos Islands. It is not a prolific seeder and depends mainly on vegetative spread by vigorous tillering, stolons and small rhizomes (Duke 1983; Skerman 1990; Cronk and Fuller 1995). Detailed information on the reproductive potential of elephant grass does not exist and would be valuable to guide decisions on appropriate control methods (Eliasson and Allen 1997).

An integrated approach to elephant grass management requires consideration of all available methods as well as ecological and socio-economic factors. Activities to manage elephant grass should result in the successful suppression of the species to a pre-determined level to satisfy landuse objectives. In the Galapagos National Park, these objectives focus on the preservation of native habitat, flora and fauna. Consequently, the management objectives for introduced species, as supported by studies of natural areas elsewhere, are: to prevent further introduction of alien species; to contain the spread of alien species already present; and to eventually eradicate all alien species from within the park boundaries and restore native habitat (Macdonald 1990; Cowie and Werner 1993; Cronk and Fuller 1995). Eradication of established alien species is difficult to achieve as most reproduce by seed that is easily spread by wind, water and/or animals. In the case of elephant grass within the Scalesia zone, the management goal is to eliminate it within the national park though not necessarily on the entire island.

Manual and chemical management methods have been employed by the Galapagos National Park Service (GNPS) and the Charles Darwin Research Station (CDRS). Manual methods have been labour intensive and chemical control deemed more appropriate due to efficacy and efficiency of application. The use of herbicides within natural areas, however, is controversial. Control trials in Galapagos with non-selective herbicides have focused on selective application methods, low concentrations and applicator safety (Gardener et al. 1999). Manual and mechanical methods are often promoted as being more environmentally sound options than the use of herbicide. However, they can be less selective in understory vegetation and can cause significant soil disturbance providing opportunities for further invasion (Macdonald et al. 1989; Motooka 1990).

Documentation on the effectiveness of elephant grass control methods is not available. For other species, chemical control has been effective for up to one year, but regeneration from the seed bank, vegetative propagules and neighbouring seed sources has made annual control efforts necessary. It is difficult to determine if the lack of long-term control is due to choice of herbicide, application method or timing, herbicide concentration or a combination of these factors. In Galapagos, glyphosate is the only herbicide that has been tested on elephant grass to date (Wilkinson and Tye 1998). While literature suggests other herbicides may control elephant grass (Skerman 1990; Kline and Duquesnel 1996; Langeland and Stocker 1997), these are not readily available in Galapagos or Ecuador, are toxic to wildlife and/or persistent in the environment. Further experimental trials are required, as most studies on the use of herbicides on invasive species have been conducted in agricultural regions and not in protected areas (Marrs 1985).

2.1.1 Research Objectives

The goal of this study was to ensure that future resources allocated to elephant grass management were put towards proven methods. By beginning with the most obvious and readily available methods of control, this work would hopefully provide baseline data for more focused experiments and eventually lead to large-scale management and restoration initiatives in the Scalesia forest zone on Santa Cruz.

The objectives were, to determine the reproductive potential of elephant grass in the Scalesia forest, to compare the effectiveness of manual and herbicide methods in controlling elephant grass as well as those methods with and without repeated follow-up to suppress regrowth, to quantify the relationship between elephant grass control and the subsequent native recruitment, and to identify the most appropriate measure to monitor in future management programs.

It was predicted that elephant grass was not a prolific seed producer and relied mainly on vegetative reproduction. Manual methods would not effectively kill the roots of elephant grass even with repeated efforts and therefore, herbicides would be required. One-time control attempts whether using manual or herbicide methods would also not effectively suppress elephant grass except in the immediate short-term, and not sufficient to allow successful recruitment of native species. Effective management methods would result in a reduction in elephant grass canopy cover, live basal cover and height, and an increase in dead basal cover and native recruitment.

2.2 Methods

2.2.1 Site Description

Three study sites were established within the Humid Zone on the island of Santa Cruz within a national park (Figure A.1). The Humid Zone is located between 250 and 500 m a.s.l. on the south side and 500 to 750 m a.s.l. on the north side of Santa Cruz (Jackson 1993). Weather station data from the south side of the island (elevation 194 m a.s.l.) indicate an average annual precipitation of 1216 mm and an average annual temperature of 23 °C (Figures A.2 and A.3) (Snell and Rea 2000). The year in which this study was conducted, 1999, was much drier than normal, with a total precipitation of 669 mm and an average monthly temperature of 22.4 °C. At an elevation closer to that of the study sites, 620 m a.s.l., the average annual precipitation is 1845 mm with no obvious peaks or troughs throughout the year, and the average annual temperature 16.9 °C with a peak in April and a trough in September (Itow 1992).

Santa Cruz is one of the oldest islands (2.2 to 2.9 million years) and soil is well weathered. The soils of the Humid Zone are < 1 m deep, contain an admixture of ash and clay, and have a reddish brown hue darkened locally by humification (Laruelle 1966). Soils have an ABC profile with 5 to 13 cm of humus in the upper horizons, and tuff-like material, ash and fragmented basaltic and pyroclastic materials in the C horizon. Base saturations in these soils are of 57 to 74%. The soils at the site were a sandy loam texture (Table A.1).

Study sites were situated within the Scalesia Forest subzone. The forest is dominated by the endemic evergreen tree, *Scalesia pedunculata* Hook f. *Scalesia* comprises 60 to 100% of the canopy, with subcanopy species *Psidium galapageium* Hook f. var.

galapagiem, *Chiococca alba* (L.) Hitchc. and *Zanthoxylum fagara* (L.) Sarg. (Table A.2). A dense shrub and herbaceous layer and an abundance of bryophytes and epiphytes are present. Shrub species are limited to *Tournefortia rufo-sericea* Hook f., *Psychotria rufipes* Hook f., *Cordia* spp., *Croton scouleri* Hook f. var. *grandifolius* and *Sida rhombifolia* L. Native ferns including *Ctenitis pleurois* (Hook f.) Morton, *C. sloani* (Spreng.) Morton, *Blechnum* spp., *Asplenium* spp., *Doryopteris pedata* (L.) Fee var *palmata* and *Dennstaedtia globulifera* dominate the herbaceous layer.

Elephant grass was introduced to Galapagos in 1967, when a farmer brought cuttings from the Loja region of mainland Ecuador (F. Lleno pers. comm.). The specific cultivar present on Santa Cruz is not known. Land was cleared within the Scalesia zone on the north side of the island, elephant grass was planted and the area was lightly grazed for one to two years before national park officials removed cattle. At the time of this study, remaining elephant grass pastures varied in size from 0.5 to 10 hectares. Smaller areas of elephant grass within the forest likely encroached from neighbouring pasture and/or were introduced from seed to the interior and small-scale disturbance facilitated establishment. The Scalesia zone on the north side of Santa Cruz, including abandoned elephant grass pasture, has had limited access, except by park guards, researchers and some local residents who collect fruit and timber and hunt feral animals. At each site, vegetation cover was completely dominated by elephant grass.

2.2.2 Experimental Design

Three abandoned elephant grass pastures were selected within the Scalesia forest zone based on accessibility and similarity of physical conditions (Table A.3). Sites A and B were approximately 500 m apart, and Site C approximately 2 km from them. A randomized complete block design was used. At each site, thirty 10 by 10 m plots were established in a grid pattern. The grid was centred in each pasture to ensure opportunities for seed dispersal from adjacent forest to all plots were similar.

Plots were randomly assigned one of four management treatments to control elephant grass, one-time manual cutting (M), repeated cutting (MR), cutting and one-time herbicide application (H) and cutting with repeated herbicide application (HR); and one of three restoration treatments, natural recovery (NR), the use of hand-collected seed

(HC) and the use of a donor soil seed bank (SS). The twelve treatment combinations were twice replicated at each site. The six remaining plots were assigned control treatments. Response variable values were averaged between replicates to obtain one value per treatment per site. As restoration treatments were not a component of this part of the study, there were three sampling units per management treatment per site.

A two-metre buffer was located between each of the treatment plots and around the perimeter of each site to reduce off-target effects from herbicide treatments and shading of plots. Vegetation within the buffer was cut with machetes or spot sprayed with Roundup.

2.2.3 Treatments

Management treatments were carried out in mid March 1999. Methods were based on CDRS and GNPS experiments, availability of resources and site-specific conditions (i.e. height of grass).

2.2.3.1 Manual Treatments

Elephant grass was cut as close to the ground as possible (5 to 10 cm) using machetes. Grass was actively growing at the time of cutting and seed heads were present. Cut debris was removed by hand and placed to the side of plots. Large, woody debris from the litter layer beneath the elephant grass canopy was removed to prevent inhibition of native regeneration.

Follow-up cutting to control regrowth was carried out in one quarter of the above plots when grass was 0.50 m high (Table B.2). Cutting shorter grass was not effective as young, flexible grass stems remained. Cut debris was not removed as it was labour intensive and would not be feasible in a large-scale restoration project. Debris coverage following cutting was not even and patches of bare ground remained. Grass was cut at a height greater than 0.50 m in June, when appropriate cutting heights were being determined.

2.2.3.2 *Herbicide Treatments*

Half of the manually cut plots received a foliar application of a 2% Roundup (glyphosate) solution, according to manufacturers instructions, when regrowth was 0.25 to 0.30 m high and actively growing. Grass in plots to be sprayed was cut prior to herbicide application, as the grass was almost 3 m in height, and herbicide could not be applied effectively or safely. A 14 L backpack sprayer was used, applying constant pressure and walking at a constant pace in a systematic pattern, with the wind behind. The amount of herbicide used varied for each plot depending on the density of elephant grass (Table B.2). Sprayed plots were not disturbed for at least seven days following application to enhance herbicide absorption (Carey pers. comm.). After seven days all plots, including those that were only manually cut, were scarified with a three pronged hand cultivator to a maximum depth of 2 to 3 cm to prepare the seedbed. Complete tilling of the site was not desirable as this could bury native seed present in the soil seed bank too deep for successful germination and emergence.

Half of the herbicided plots (one quarter of the total treated plots) received repeated spot spraying with a 2% Roundup solution when regrowth reached 0.20 to 0.30 m high (Table B.3). These plots were cut a second time in early June, as grass was too tall to be effectively sprayed.

2.2.3.3 *Control Treatments*

Control treatments consisted of 10 by 10 m plots at each site that had not received any management or restoration. The cover and height of elephant grass and presence/absence of other species were recorded at the beginning of the study. Monitoring did not occur as it was assumed grass height could change with time, however, greater cover could not be achieved and no recruitment other than elephant grass would occur.

2.2.4 Vegetation Measurements

2.2.4.1 Elephant Grass Seed Production and Soil Seed Bank

Ten randomly located, permanent 1-m^2 quadrats were established at each of the sites. Based on initial observations of the time required for an inflorescence to mature and florets to dehisce (assumed time of seed dispersal), quadrats were monitored every 4 weeks for 12 months. Florets were collected from each spike-like inflorescence within a quadrat without damaging the rachis. The assumption that florets were a reasonable indication of seed production was made at the beginning of the study, as the seed grain is permanently attached to the lemma and palea in elephant grass. More detailed dissection of the florets in the field would not have been feasible. Florets were collected in paper bags and counted in the laboratory. The length of each inflorescence was measured. The average monthly floret production per m^2 at each site was calculated from the total florets collected in the 10 quadrats over the year.

Laboratory germination of the first elephant grass florets collected was largely unsuccessful suggesting the initial assumption that most florets contained seed was not valid. The florets present in each quadrat continued to be collected during monitoring, however, 250 mature florets were also collected from each site (not from within quadrats) and cut open to locate the seed grain. Mature florets were identified as non-green (on the brown side) with exert stamens absent. The percent seed production for this subset was calculated and applied to the total number of florets collected at that monitoring period and site to estimate seed production.

To sample the soil seed bank, five systematically randomized, 5-cm diameter and 5-cm deep soil cores were taken (Garcia 1995; Dalling et al. 1998) in each plot in early March following initial cutting of elephant grass. A transect was laid out from a randomly selected point and a sample taken every 2-m. Samples were placed in plastic bags and labelled. Five soil cores were also randomly taken at each donor soil seed bank location within adjacent forest.

In early July, five systematically randomized soil cores were collected by the forest edge. At each site, two randomized transects extended 8 m into the forest and 8 m into pasture and a sample collected every 2 m. A sample was composed of five subsamples taken 0.3 m apart along a line perpendicular to the main transect. Samples were placed in plastic bags and labelled.

Soil samples were spread to a depth of 2.5 cm in containers lined on the bottom with vermiculite, placed under a canopy of approximately 50% cover and kept moist. Caging prevented seed predation by birds and reduced the likelihood of seed rain affecting results. Seedlings were counted and removed every two weeks. Unidentifiable seedlings were not recorded and left until the next monitoring period.

2.2.4.2 Management of Elephant Grass

Monitoring was carried out approximately every three weeks from treatment (mid March) until the end of 1999. In 2000, monitoring was irregular. Grass canopy cover data were collected in January and recruitment density in March 2000, one year following treatments (Table B.4).

Cover was used as an estimate of the success of elephant grass. Two components of cover were measured, canopy and basal. Three randomly located, permanent 1-m^2 quadrats were established in each plot to measure canopy cover. The 1-m^2 quadrat was visually divided into four equal smaller quadrats, and a cover value of 1 to 7 assigned to each of these smaller quadrats (Table B.5). The midpoint of each cover range for the assigned value was used to calculate the average cover for the quadrat.

Basal cover was determined using 100 systematically placed pinpoints in each plot. Starting one metre from the southwest corner, pinpoints were located every metre along five 10 metre transects. At each point, the sampler lowered a pin flag without looking at the ground. Elephant grass basal cover was recorded as live or dead; basal area that did not show signs of growth (i.e. green, moist pith, or shoots) was recorded separately from that which was actively growing.

Height of the tallest natural standing stem within each of the three 1-m^2 elephant grass quadrats was recorded. Height, in conjunction with cover, could indicate the stage at which elephant grass control methods should be implemented to maximize efficacy and regeneration of native species.

The number of individual plants or the density of recruitment, following management treatments was determined for all species except elephant grass. Species were placed into one of four plant groups: native, endemic, alien and those of uncertain origin, according to Porter (1983) and Lawesson et al. (1988).

2.2.5 Statistical Analyses

All data were tested for normality and equality of variance prior to analysis and non-parametric procedures used where appropriate. Correlation analysis was conducted on seed production, floret production and the number and length of inflorescences. A one-way analysis of variance (ANOVA) was used to test for significant differences in measured variables between sites (Zar 1996). Two-way ANOVA was conducted on the density of elephant grass seed in the soil seed bank data to identify differences between pasture, edge and forest and between sites. Post-hoc multiple comparison tests were employed. Paired T-tests were applied to forest edge seed bank data to determine significant differences in elephant grass seed density into the forest versus into pasture.

Two-way ANOVAs were conducted to determine significant differences in measured variables among treatment groups at the final monitoring period (Zar 1996). Post-hoc multiple comparison tests were employed. Kendall's coefficient of concordance was calculated to determine agreement in treatment ranking between sites. Regression lines were fitted to the data for each treatment group over time. Correlation analysis was used to identify potential redundancies in monitoring effort between measured variables.

2.3 Results

2.3.1 Elephant Grass Seed Production and Soil Seed Bank

The percent of florets with seed varied between 0 and 34% depending on site and month. Seed production was not different between sites confirming invasion potential was equivalent (Table B.6). A significantly greater number of florets and inflorescences were produced at Site B compared to Site A (Table 2.1). Seed production peaked in January or February at each of the sites (Figure 2.1). A smaller peak was also observed in mid August at Site B, while seed production at Sites A and C remained relatively constant at other times of the year. There was no correlation between seed production and floret production, number or length of inflorescences (Table B.7). Floret production was significantly correlated with number and length of inflorescences.

Elephant grass was present in pasture, edge and forest soil seed banks. Seed density was significantly greater by the forest-pasture edge than in pasture or forest alone. The pasture had the lowest seed density (Table 2.2). Site C had a greater density of seed than Site A in both the edge and forest locations, but there was no significant difference in pasture seed density among sites (Table 2.2). At forest edge, seed density was significantly greater at 2 and 8 metres into pasture than into forest (Table 2.3).

2.3.2 Management Treatments

Canopy cover, live basal cover, height and recruitment density, but not dead basal cover, differed with management treatment (Table 2.4). Kendall's coefficient of concordance indicated strong agreement in ranking of management treatments among the three study sites for each variable (Table B.8).

2.3.2.1 Manual versus Herbicide Treatments

Herbicide treatments were not always more effective than manual treatments. At the final monitoring period, elephant grass canopy cover, and live and dead basal cover were similar in M and H treatments (Table 2.4). H treatments did result in a reduction in elephant grass height compared to M treatments. HR treatments had considerably less elephant grass canopy cover, height and live basal cover than all treatments. Dead basal cover was considerably lower in M, MR and H treatments compared to HR treatments and controls, although differences were not significant (Table 2.4).

A one-time application of Roundup stunted elephant grass growth. For all measured variables, H treatments had the same growth pattern as M treatments but slower rates

(Figures 2.2 to 2.6). The trendlines suggest that the height of elephant grass in H treatments would eventually attain the same value as that in M treatments (Figure 2.5). Canopy cover steadily declined in HR treatments but remained constant in MR treatments (Figure 2.2). Declining live basal cover in manual and herbicide treatments suggests little regeneration from seed and reliance on vegetative growth (Figure 2.3). Throughout monitoring, root kill increased in HR treatments and decreased in MR treatments (Figure 2.4).

2.3.2.2 One-time versus Repeated Treatments

Repeated control activities were effective at reducing elephant grass canopy cover and height but their effect on other measures was variable depending on the use of manual or herbicide methods. At the final monitoring period, MR treatments had considerably lower canopy cover and height than M treatments, while there was no difference in live and dead basal cover (Table 2.4). HR treatments had considerably lower canopy cover, height and live basal cover than H treatments, and greater dead basal cover. H treatments had greater elephant grass canopy cover and height than MR treatments, but similar live and dead basal cover.

There was a greater reduction in canopy cover between one-time and repeated treatments when applying herbicide (100 times) than manual cutting (2.3 times). Variability in canopy cover, particularly in the MR treatments, reflects the incongruence between monitoring dates and dates when follow-up control activities were carried out (Figure 2.2). The duration between follow-up treatments whether manual cutting or spot spraying was approximately 2 months; though in MR treatments this steadily declined over the monitoring period indicating an increased elephant grass growth rate (Table B.2). Trendlines suggest that if follow-up activities had continued, the effectiveness of HR treatments would have continued to improve, while that of MR treatments and those without follow-up would have stabilized, the latter around control levels (Figures 2.2 to 2.6).

2.3.3 Native Recruitment Density

Native recruitment was considerably greater in HR treatments throughout monitoring, and significantly so at the final monitoring period, than in other treatments (Figure 2.6). There was no difference in recruitment between M, MR and H treatments; recruitment density in these treatments increased only slightly over the monitoring period. Even in HR treatments abundant native recruitment was not observed until July/August as temperatures cooled and rain increased. Native recruitment in HR treatments increased exponentially, even after follow-up activities ceased in December, while recruitment in one-time application treatments stabilized by July. Native recruitment in MR treatments was increasing towards the final monitoring period (Figure 2.6).

A reduction in canopy cover enhanced native recruitment. Recruitment increased once elephant grass cover was less than 50%. Canopy cover decreased in H and M treatments in October when weather was drier and grass taller, however, this did not improve native recruitment. In MR treatments, the increase in canopy cover from a mean of 39% to 51% between December 1999 and January 2000, and no significant decline in recruitment density, suggests canopy cover was not the only factor affecting growth in these plots. Drier weather, along with reduced growth rates, meant cut debris in MR treatments was reduced and more quickly decomposed.

2.3.4 Evaluation of Management Measures

Canopy cover is the preferred measure of elephant grass control. Canopy cover, live basal cover and height were all strongly positively correlated throughout monitoring suggesting redundancy in effort (Table B.9). Height was not a useful measure of success in repeated treatments as it was maintained at a constant value with management. Recruitment density and dead basal cover were negatively correlated with canopy cover, live basal cover and height, however, only significantly at six and nine months following initial treatments. Recruitment density and dead basal cover had a significant positive correlation only at the end of monitoring. The strength of the correlation among recruitment density and dead basal cover and other variables was increasing towards the end of the study time period.

Basal cover and recruitment density data were time consuming to collect (0.50 h per 100 m^2 plot and 0.33 h per 100 m^2 plot, respectively) compared to canopy cover and height combined (0.20 h per 100 m^2 plot). High canopy cover and height doubled the time required to collect all data.

2.4 Discussion

2.4.1 Reproductive Potential of Elephant Grass

Elephant grass produces a small quantity of seed compared to other aggressive grasses (Maillet 1991; Karl et al. 1999). Environmental conditions that may reduce seed production include insufficient moisture, nutrients and cool temperatures, particularly at night. Tropical grasses also have a high occurrence of immature embryos, as competition within an inflorescence is great (Humphreys 1981). Precipitation in 1999 was half of the ten-year average and temperatures cooler. Seed set may therefore be higher with normal precipitation levels and temperatures. Plant growth in tropical pasture grasses is associated with an increase in inflorescences, due to increased tillering, and generally an increase in seed production (Humphreys 1981). This did not happen in this study, where abundant plant growth was associated with high inflorescence, floret and seed production. However, poor plant growth did not lead to low seed production.

Although we cannot conclude that vegetative reproduction is elephant grass' main mode of reproduction, the results, in conjunction with field observations, support this. Prevailing winds from the southeast may sweep seed across pastures to collect by forest edges, explaining the reduction or absence of seed at upwind locations. Seed was found in interior forest gaps, implying dispersal by humans or animals from the initial pasture. Seed could more easily reach the ground in the absence of dense vegetation. Humphreys (1981) reported that the seed bank of tropical pasture grasses is only important under intensive grazing or cutting. In an abandoned pasture, grass would rely on stolons and tillering to persist even though a seed bank may be present. The literature does suggest that elephant grass relies on vegetative production as it possesses rhizomes and stolons, and the best method of propagation is from cuttings (Duke 1983; Burton 1993; McCann et al. 1996). Elephant grass is well established at the study sites, therefore it is not surprising that the relative contribution of seed versus vegetative growth is low. Poor seed production coupled with low tolerance of shade ensure the rate of elephant grass encroachment is slow but steady, particularly in the absence of large-scale disturbance.

2.4.2 Elephant Grass Management

The cutting of elephant grass stimulated regrowth indicating other management options must be considered. Repeated cutting encouraged more vigorous resprouting than one-time cutting resulting in an increase in effort requirements. Regrowth following cutting is influenced by residual leaf area and carbohydrate reserves in roots and rhizomes. Belyuchenko (1977) reported that cutting elephant grass at any height encouraged plant growth; cutting height only influenced the type of growth. At a cutting height of 5 cm, regrowth from rhizomatous buds occurred. The taller the cutting height the greater the reliance on auxiliary buds. Studies in Florida on a dwarf cultivar of elephant grass found that frequent close cutting increased total dry matter in the first year, but in subsequent years plant vigour was reduced (Chaparro et al. 1995); frequent time intervals were 3 to 6 weeks. Live basal cover decreased in each treatment, indicating little recruitment from seed following the initial cutting, and increases in canopy cover were due to tillering. Wilen and Holt (1996) concluded that while cutting may slow the process of invasion it is inadequate on its own to control an aggressive perennial species.

A one-time application of a non-residual herbicide such as Roundup is not sufficient to kill the roots of aggressive, perennial species (Grossbard and Atkinson 1985). Continual application of Roundup did increase root kill and studies on Roundup have shown successful reduction in perennial grass cover within 1 to 5 years with repeated applications (Abahl et al. 1981; Grossbard and Atkinson 1985). The gradual reduction in required resources coupled with an increase in effectiveness make repeated herbicide application a desirable management option. Herbicide efficacy should be further considered within the context of the island's climate. There were few rain-free, sunny days in the highlands from July to November. Spot spraying occurred under less than ideal conditions though during initial application in March, days were dry and sunny. Elephant grass management can be improved with increased knowledge of appropriate application timing in the highlands and investigation of the selective use of residual herbicides.

The use of pesticides is often undesirable within natural areas. In such situations, repeated cuttings, although labour intensive, could contain elephant grass. In small infestations, this method could be economical and if within close proximity of native seed sources, natural invasion may occur. Although cut debris can act as mulch increasing soil moisture and cooling soil temperatures necessary for germination (Nepstad et al. 1996; Eliasson and Allen 1997), mulch also reduces light penetration and in some cases safe sites. Only if debris is removed will repeated cutting stimulate regeneration of desirable species (Luken 1990). Debris removal and investigation of post-control techniques to enhance recruitment could facilitate results similar to those obtained with repeated herbicide applications. For the method to be feasible, a continued increase in effectiveness would be required to compensate for the increase in labour. The removal of root crowns is extremely labour intensive though would improve the efficacy of no herbicide management options; herbicide use remains the most effective choice.

2.4.3 Native Recruitment

Recruitment occurred in all treatments, though from a management standpoint, only those treatments with follow-up have potential to facilitate restoration. Light and soil moisture are limiting factors to germination and seedling establishment (Aide and Cavalier 1994). The initial cutting and opening of the elephant grass canopy provided a germination cue, though greater than a month exposure was required for successful recruitment. Seedlings established under a canopy though new recruitment was negligible. The trade off between the reduction in cover and the subsequent loss of soil moisture can be an obstacle to an effective management program. By initially clearing elephant grass later, in May or June, when elephant grass growth is less vigorous, precipitation greater and temperatures cooler, recruitment may be enhanced.

The successful establishment of vegetation may assist in suppressing persistent grasses by shading them out (Nepstad et al. 1990; Parrotta 1992; Guariguata et al. 1995; Rhoades et al. 1998; Posada et al. 2000). Native tree plantations in Costa Rica were effective in suppressing pasture grasses including elephant grass and allowing invasion by native vegetation (Parrotta 1992; Gerhardt 1993). Light levels were lower under plantation trees but many native species, as in Galapagos, were shade tolerant, and plantation trees increased seed dispersal by providing perches and roosting sites for birds and bats (Guariguata et al. 1995). Cover crops of domestic fruit and nut trees have provided interim means of income and sped up restoration (Aide et al. 2000). In Galapagos, the majority of tree species introduced for their economic value, including red quinine (*Cinchona pubescens* Klotzsch) and guava (*Psidium guajava* L.), have become serious invaders of native habitats (Lawesson 1990; Mauchamp 1997). Given the mandate not to introduce new species, *Scalesia* is the only native option for shade trees at the study sites as it is a fast growing pioneer species, shade intolerant, and is also the community dominant,

2.4.4 Management Applications

An integrated approach to elephant grass management may involve a variety of methods, depending on the extent of change in soil properties (e.g. due to cultivation system, time since establishment of pasture and grass species), grass growth strategy and availability of local native seed sources. The abundance of invasive tropical grasses in developing regions, where resources and technologies are limited, requires that alternative management strategies to those commonly implemented in developed nations are considered. Studies in Costa Rica, Puerto Rico, Columbia, mainland Ecuador and Brazil have provided innovative ideas in this field (Parrotta 1992; Aide and Cavalier 1994; Guariguata et al. 1995; Rhoades et al. 1998). Cattle and horses have been introduced to abandoned pastures to graze unwanted grasses (Nepstad et al. 1990; Posada et al. 2000). These grazers not only removed grass but also facilitated native regeneration (Nepstad et al. 1990). Posada et al. (2000) found cattle grazing reduced pasture grass biomass by 50%, and resulted in an increase the cover of woody and herbaceous species. The use of cattle or horses would not, however, be an acceptable management option within the Scalesia forest. Cattle favour the fruits of introduced species found within the forest, as native species generally produce small seed without fleshy coverings, and consequently spread the seed of invasive species in their faeces.

The use of fire has been proposed in ecosystems where abandoned pastures exist (Nepstad et al. 1990). The burning of elephant grass pasture followed by the application of herbicide effectively controlled this species in Africa (Tilley 1977). It has also been suggested, however, that if fire were introduced (or reintroduced), invasion would be more rapid (D'Antonio and Vitousek 1992; Marrs 1993; Low 1997; Ley and D'Antonio 1998). Fire or any other large-scale disturbance would favour establishment of perennial species, such as elephant grass. Fire, although historically present in Galapagos through volcanic activity, is not considered a reasonable management option at this time. The lack of knowledge, experience and resources to effectively and safely carry out such a program has led to strong concern regarding liability.

From a conservation management perspective, achieving success will be labour intensive, though effort requirements should decrease with time. It has been argued that root kill is more effective than leaf or stem kill as an indicator of long-term success (Luken 1990). As long as live vegetative propagules remain, control will be required. Implementation of a long-term labour intensive management program can be risky. Over extended periods of time changes in management, fluctuations in the availability of resources, and the development of impatience or complacency among participants, will affect the rigor of monitoring. Less rigor in monitoring increases the likelihood of overlooking new infestations and jeopardizes past control efforts. Less labour intensive methods should be investigated including effective timing of herbicide application, the use of residual herbicides, applied either foliarly or selectively to root crowns following cutting and the use of cover crops. In the short-term, efforts to control elephant grass should focus on continual reduction of cover and small-scale disturbances within intact forest. Lack of a perfect management method should not lead managers to inaction. As long as a seed source and disturbance exists, new satellites of elephant grass will appear each year and inaction, or a 'wait and see' attitude will be detrimental to the conservation of the Scalesia forest on Santa Cruz.

2.5 Conclusions

For the three abandoned elephant grass pastures studied on the island of Santa Cruz, this research concludes:

1. Elephant grass is not a prolific seed producer.
    - Seed was produced year round.
    - Seed production was independent of the number of inflorescences and florets.

2. Cutting of elephant grass, followed by repeated application of Roundup to regrowth was the most effective management method tested.
   - One-time efforts to control elephant grass, whether manual cutting or application of a non-residual herbicide, did not reduce elephant grass canopy cover or height.
   - Repeated follow-up activities, whether cutting or non-residual herbicide application, significantly reduced elephant grass canopy cover and height.
   - The effort required to complete repeated cutting treatments increased with time, while elephant grass canopy cover remained constant.
   - The canopy cover of elephant grass steadily decreased in repeated herbicide application treatments, as did the amount of labour and herbicide required to control regrowth.
3. A continued reduction in elephant grass cover was associated with an increase in native recruitment.
   - Initial clearing of elephant grass would be most appropriate in June or July, as precipitation levels increase and temperatures decrease.
   - Removal of cut debris would improve native recruitment particularly during months of high precipitation in the highlands (i.e. July to November).
4. In the short-term, canopy cover is the most appropriate measure of successful elephant grass control. This should be monitored in conjunction with dead basal cover and native recruitment density to evaluate long-term management programs.

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Table 2.1. Mean monthly (±SE) values per 1-m^2 quadrat of elephant grass at three abandoned pastures in the Scalesia forest, Santa Cruz, Galapagos.

	% Florets with Seed	Number of Seeds	Number of Florets	Number of Inflorescences	Length of Inflorescence
Site A	4.3	13	233[b]	1[b]	11
	(2.2)	(9.14)	(65.52)	(0.19)	(1.80)
Site B	6.1	24	506[a]	2[a]	14
	(1.6)	(6.97)	(101.09)	(0.31)	(1.12)
Site C	6.4	18	273[ab]	1[ab]	13
	(3.0)	(10.98)	(36.56)	(0.19)	(1.24)
P-value	0.79	0.71	0.03	0.05	0.31

Means within a column which do not share a common letter are significantly different at $p \geq 0.05$.

Table 2.2. Mean (±SE) elephant grass density (germinable seed m^{-2}) in the soil seed bank at three locations within three study sites in the Scalesia forest, Santa Cruz, Galapagos.

	Pasture	Forest Edge	Forest
Site A	26	223[a]	51[a]
	(17.63)	(92.73)	(38.55)
Site B	0	1116[ab]	166[ab]
	(0.00)	(333.14)	(42.82)
Site C	4	2868[b]	586[b]
	(4.25)	(1102.42)	(239.75)
Overall	10[a]	1402[b]	268[a]
	(6.12)	(409.51)	(92.04)

Means within a column which do not share a common letter are significantly different at $p \geq 0.05$.

Table 2.3. Paired T-tests for mean elephant grass seed density (germinable seed m^{-2}) 2, 4, 6 and 8 metres along a transect into pasture and forest, Scalesia forest, Santa Cruz, Galapagos.

	2 m		4 m		6 m		8 m	
	Pasture	Forest	Pasture	Forest	Pasture	Forest	Pasture	Forest
Density (+SE)	6.0 (1.7)	1.0 (0.5)	3.0 (1.5)	2.0 (1.1)	10.0 (5.0)	2.0 (1.1)	7.0 (1.7)	1.0 (0.5)
T-test P-value	0.05		0.69		0.20		0.03	

Table 2.4. Measure mean (+SE) per 100-m^2 plot and p-values for ANOVAs at final monitoring period after treatments to manage elephant grass in the Scalesia forest, Santa Cruz, Galapagos.

	Control	Manual Cutting	Repeated Cutting	Herbicide	Repeated Herbicide
Cover (%) $p \geq 0.02$	100^{a} (0.0)	90^{ab} (4.3)	53^{bc} (4.8)	78 (8.0)	2^{c} (0.7)
Height (cm) $p \geq 0.02$	258^{a} (15.2)	168^{ab} (12.2)	37^{bc} (9.2)	134 (10.6)	6^{c} (0.7)
Recruitment Density (# plants) $p \geq 0.04$	0.0^{a} (0.0)	7^{ab} (6.0)	11^{bc} (5.8)	9^{ab} (4.7)	84^{c} (23.7)
Live Basal Cover (%) $p \geq 0.02$	35^{a} (9.0)	24^{a} (1.9)	20^{a} (1.3)	18^{ab} (1.6)	2^{b} (0.4)
Dead Basal Cover (%) $p \geq 0.09$	4^{ab} (2.4)	1^{a} (0.5)	1^{a} (0.2)	2^{a} (0.3)	11^{b} (0.7)

Means within rows which do not share a common letter are significantly different at the $p \geq 0.05$ level.

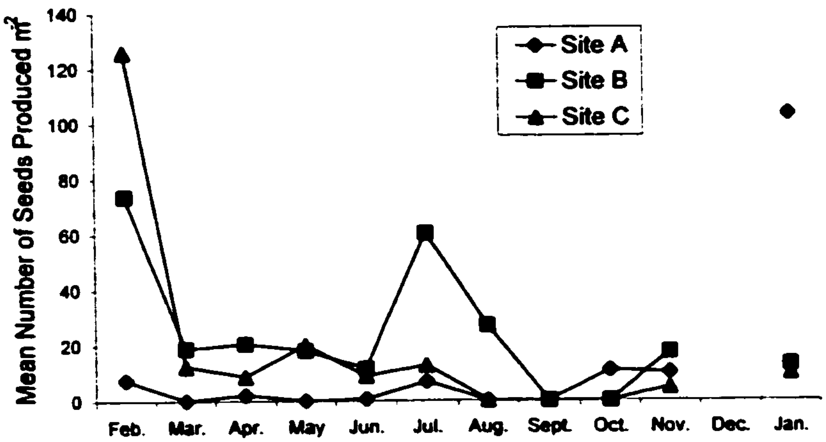

Figure 2.1. Elephant grass seed production at three sites in the Scalesia forest zone, Santa Cruz, Galapagos. Monitored at four-week intervals February 1999 to Janurary 2000.

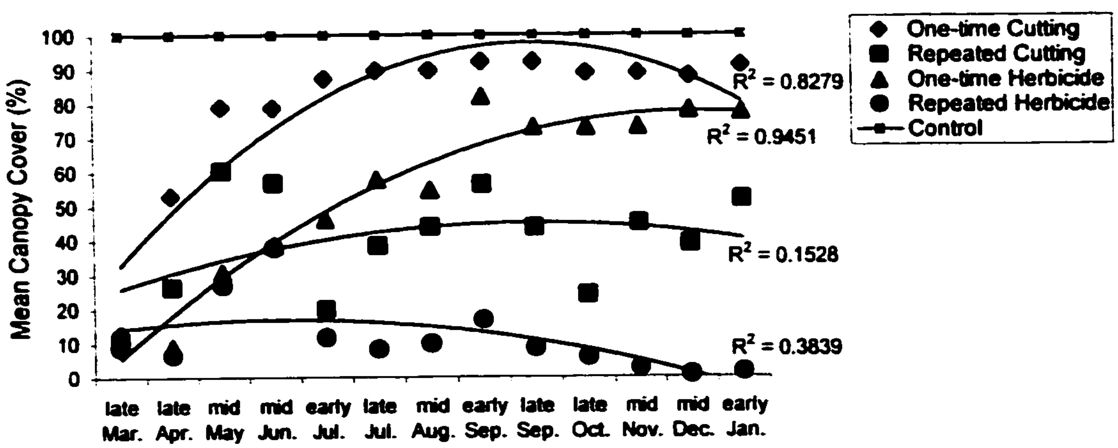

Figure 2.2. Canopy cover of elephant grass following four management treatments to control species in abandoned pasture, Santa Cruz, Galapagos. Monitored March 1999 to January 2000. Second order polynomial trendlines fitted.

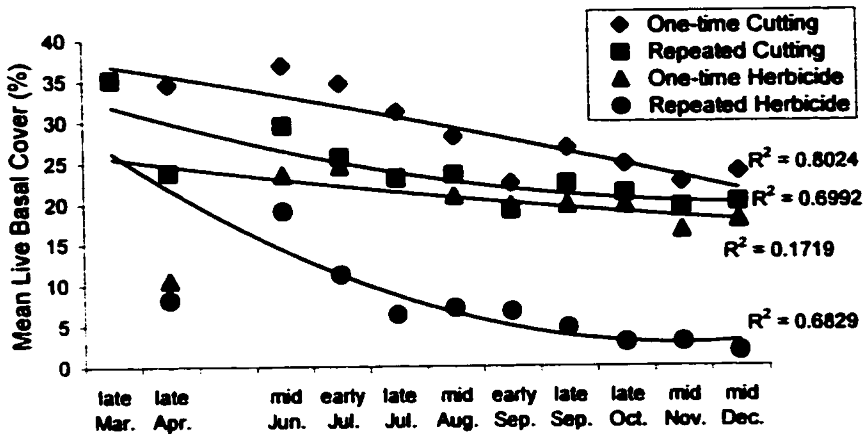

Figure 2.3. Live basal cover of elephant grass following four management treatments to control species in abandoned pasture, Santa Cruz, Galapagos. Monitored March to December 1999. Trendlines fitted.

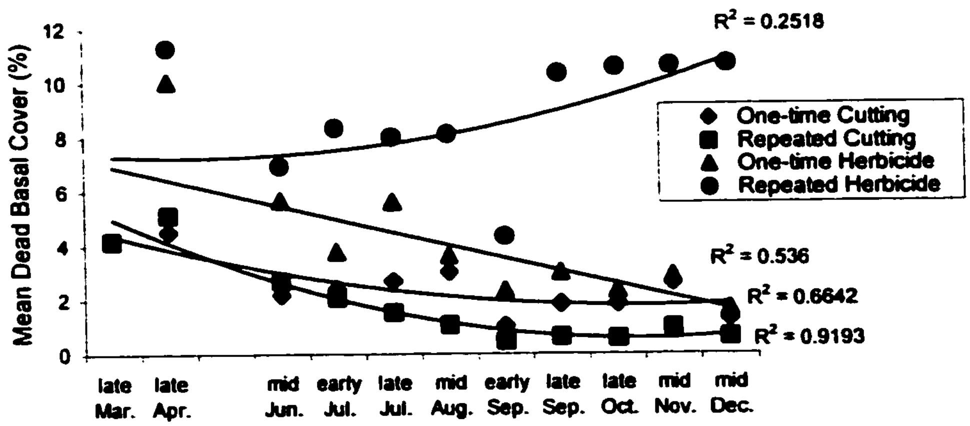

Figure 2.4. Dead basal cover of elephant grass following four management treatments to control species in abandoned pasture, Santa Cruz, Galapagos. Monitored March to December 1999. Trendlines fitted.

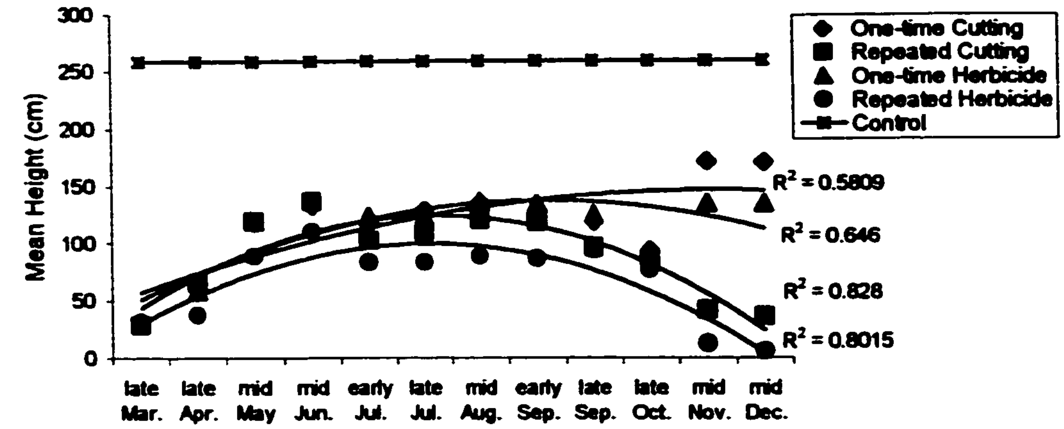

Figure 2.5. Height of elephant grass following four management treatments to control species in abandoned pasture, Santa Cruz, Galapagos. Monitored March to December 1999. Second order polynomial trendlines fitted.

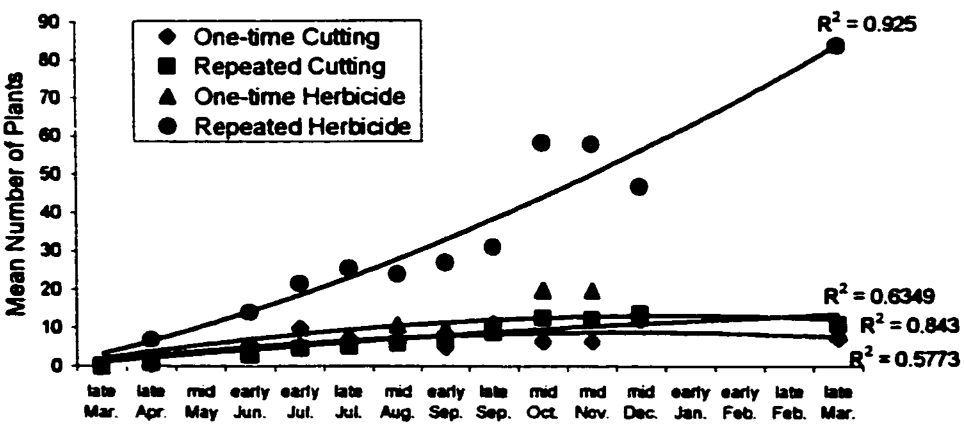

Figure 2.6. Recruitment density following four management treatments to control elephant grass in abandoned pasture, Santa Cruz, Galapagos. Monitored March 1999 to March 2000. Polynomial trendlines fitted.

3. The Potential for Natural Recovery of Scalesia Forest from a Relict Soil Seed Bank 30 Years Following Pasture Abandonment

3.1 Introduction

Restoration efforts can be greatly improved upon if a relict soil seed bank and intact areas of habitat for seed dispersal exist (van der Valk and Pederson 1989; Ray and Brown 1994; Holl 1999; Holl et al. 2000; Wijdeven and Kuzee 2000). Seed from these sources is locally adapted and can germinate quickly given appropriate conditions (Linhart 1995). Species that are required to promote future establishment of the native community by ameliorating soil conditions, providing shade and nutrients may also be favoured (Egler 1954). Few studies have been conducted in the tropics on seed banks of disturbed habitats and the implications for restoration (Garwood 1989; Skoglund 1992; Baskin and Baskin 2001).

A review of tropical seed banks studies concluded that soil seed banks are not as important for recruitment and therefore restoration as in temperate regions (Skogland 1992). This is in part because tropical seed banks are smaller than those in temperate forests. High rates of seed mortality due to predation and disease, and the reliance on ephemeral favourable conditions for germination also reduce the effectiveness of relict seed banks. Seed predation, particularly of woody species, is high in disturbed environments, such as abandoned pastures (Wijdeven and Kuzee 2000). In moist environments, the risk of seed mortality due to fungus also increases (Chambers and MacMahon 1994).

The density of moist tropical forest seed banks can vary from 25 to 10,000 seeds m^{-2}, depending on forest type and depth of sampling (Skoglund 1992). Primary forests in general have less dense seed banks than secondary forests (Saulei and Swaine 1988). These seed banks are dominated by pioneer species often not present in the extant vegetation (Hall and Swaine 1980; Saulei and Swaine 1988; Garwood 1989; Tsuyuzaki and Kanda 1996). In some primary forests, seed banks are dominated in particular by pioneer woody species (Thompson 1989). Long-term dormancy is not thought to be present in these forest species (Garwood 1983; Lawesson 1988; Dalling et al. 1998), however, most woody species experience short-term dormancy due to the ephemeral nature of appropriate germination conditions (Garwood 1983). The variability in seed density and richness of tropical forest seed banks is, therefore, hypothesized to be high within a year, but to be stable between years (Garwood 1989).

The soil seed banks of abandoned pastures are generally larger than those of adjacent tropical forest (Harper 1977; Saulei and Swaine 1988; Skoglund 1992; Tsuyuzaki and Kanda 1996) and are dominated by longer-lived herbaceous species (Uhl and Clark 1983). Some studies have found that these seed banks become dominated by woody species over time (Saulei and Swaine 1988), while in other studies the density of trees and shrubs has remained low compared to undisturbed forest (Ray and Brown 1994; Wijdeven and Kuzee 2000; Holl et al. 2000). The seed banks of abandoned pastures are dominated by pantropical weeds and other opportunistic species, which are wind or water dispersed. Woody species rely on animals and insects for seed dispersal, and the lack of vegetation structure discourages the use of pasture by these vectors. This suggests that late successional species or those with poor dispersal abilities may have to be supplementary seeded to restore a site (Skoglund 1992; Ray and Brown 1994).

Knowledge of the local seed bank allows restorationists to assess the need for native recruitment enhancement through site preparation, seeding and addition of amendments. The study of seed banks can assist in predicting the composition of future plant communities and provide information on vegetation history (Hopkins and Graham 1983; Keddy et al. 1989). They provide reliable information on species composition, however, relative abundances and distribution of species can be unpredictable (van der Valk and Pederson 1989). As well, the importance of a relict seed bank compared to seed rain will decrease with disturbance size and persistence (Skoglund 1992; Ray and Brown 1994). It can be concluded that some form of a seed bank exists following a disturbance and that the seed bank of those sites more recently disturbed will be more similar to the surrounding vegetation than those experiencing persistent or chronic disturbance.

3.1.1 Research Objectives

The objective of this research was to determine the potential for restoration of the native Scalesia forest from the relict soil seed bank of abandoned elephant grass (*Pennisetum purpureum* Schum.) pastures on the island of Santa Cruz. This research compared the richness, composition and density of the soil seed bank in the abandoned pasture to that of the forest edge (more recent disturbance) and forest interior (no disturbance) and predicted that the soil seed bank of the forest edge would be most diverse, and that of the intact forest the least diverse. The forest seed bank was predicted to have the greatest native and endemic richness, while the pasture seed bank would be dominated by alien species and those of uncertain origin.

3.2 Methods

3.2.1 Site Description

The study sites were established within the Humid Zone on the island of Santa Cruz within a national park (Figure A.1). The Humid Zone is located between 250 and 500 m a.s.l. on the south side and 500 to 750 m a.s.l. on the north side of Santa Cruz (Jackson 1993). Weather station data from the south side of the island (elevation 194 m a.s.l.) indicates an average annual precipitation of 1216 mm and an average annual temperature of 23 °C (Figures A.2 and A.3) (Snell and Rea 2000). The year in which this study was conducted, 1999, was much drier than normal, with a total precipitation of 669 mm and an average monthly temperature of 22.4 °C. At an elevation closer to that of the study sites, 620 m a.s.l., the average annual precipitation is 1845 mm with no obvious peaks or troughs throughout the year, and the average annual temperature 16.9 °C with a peak in April and a trough in September (Itow 1992).

Santa Cruz is one of the oldest islands (2.2 to 2.9 million years) and soil is well weathered. The soils of the Humid Zone are < 1 m deep, contain an admixture of ash and clay, and have a reddish brown hue darkened locally by humification (Laruelle 1966). Soils have an ABC profile with 5 to 13 cm of humus in the upper horizons, and tuff-like material, ash and fragmented basaltic and pyroclastic materials in the C horizon.

Base saturations in these soils are of 57 to 74%. The soils at the site were of a sandy loam texture (Table A.1).

Study sites were situated within the Scalesia Forest subzone. The forest is dominated by the endemic evergreen tree, *Scalesia pedunculata* Hook f. *Scalesia* comprises 60 to 100% of the canopy, with subcanopy species *Psidium galapageium* Hook f. var. *galapagiem*, *Chiococca alba* (L.) Hitchc. and *Zanthoxylum fagara* (L.) Sarg. (Table A.2). A dense shrub and herbaceous layer and an abundance of bryophytes and epiphytes are present. Shrub species are limited to *Tournefortia rufo-sericea* Hook f., *Psychotria rufipes* Hook f., *Cordia* spp., *Croton scouleri* Hook f. var. *grandifolius* and *Sida rhombifolia* L. Native ferns including *Ctenitis pleurois* (Hook f.) Morton, *C. sloani* (Spreng.) Morton, *Blechnum* spp., *Asplenium* spp., *Doryopteris pedata* (L.) Fee var *palmata* and *Dennstaedtia globulifera* dominate the herbaceous layer.

Elephant grass was introduced to Galapagos in 1967, when a farmer brought cuttings from the Loja region of mainland Ecuador (F. Lleno pers. comm.). The specific cultivar present on Santa Cruz is not known. Land was cleared within the Scalesia zone on the north side of the island, elephant grass was planted and the area was lightly grazed for one to two years before national park officials removed cattle. At the time of this study, remaining elephant grass pastures varied in size from 0.5 to 10 hectares. Smaller areas of elephant grass within the forest likely encroached from neighbouring pasture and/or were introduced from seed to the interior and small-scale disturbance facilitated establishment. The Scalesia zone on the north side of Santa Cruz, including abandoned elephant grass pasture, has had limited access, except by park guards, researchers and some local residents who collect fruit and timber and hunt feral animals. At each site, vegetation cover was completely dominated by elephant grass.

3.2.2 Experimental Design

Three abandoned elephant grass pastures with adjacent Scalesia forest were selected based on accessibility and similarity of physical conditions (Table A.3). Sites A and B were approximately 500 m apart, and Site C approximately 2 km from them. It was assumed that a relict seed bank existed, although its richness, composition and abundance were unknown. It was also assumed that the seed bank was relatively uniform between sites, as the species pool was identical.

In the pastures, seed bank samples were taken within an existing experimental design. Each pasture contained thirty 10 m by 10 m plots. The grid was centred in each pasture to ensure opportunities for seed dispersal from adjacent forest to plots. Each plot was randomly assigned one of four management treatments to control elephant grass, one-time manual cutting (M), repeated cutting (MR), cutting and one-time herbicide application (H) and cutting with repeated herbicide application (HR); and one of three restoration treatments, natural recovery (NR), the use of hand-collected seed (HC) and the use of a donor soil seed bank (SS). Treatments were replicated twice and the remaining plots were assigned controls. Five 5-cm diameter and 5-cm deep soil cores were collected in each of the treatment plots and results averaged between replicates for a total of 12 samples per site. Sampling occurred in early March 1999 prior to implementation of restoration treatments, but following management treatments to control elephant grass. A systematic random sampling strategy was used. A corner and a metre mark from this corner were randomly chosen. A transect was laid out from this point and a sample taken every 2-m.

In the forest, a judgemental random sampling strategy was employed. In March, eight sampling sites within adjacent Scalesia forest were selected based on the absence of alien species and distance to restoration sites. Sites were between 15 m and 30 m from forest-pasture edge. Five soil cores were randomly taken at each location and results averaged, for a total of eight samples per site.

At the forest edge, samples were collected in July 1999 and using a systematic random sampling strategy. Three transects were randomly established perpendicular to the forest-pasture interface extending 8 m into forest and 8 m into pasture. The start location of each transect was selected using a table of random numbers and paced along the edge of the forest. Five soil cores were taken every 2 m along transects into forest and pasture. These five subsamples were taken 0.3 m apart along a line perpendicular to the main transect (parallel to the forest edge). For this study, only the samples from 4 m and 8 m along the transect were included in the analysis for a sample total of 8 per site.

As these samples were taken approximately 3.5 months following the pasture and forest samples, caution was used in interpreting results.

3.2.3 Seed Bank Monitoring

Samples were spread to a depth of 2 cm in containers lined on the bottom with vermiculite, and kept moist in the Bellavista nursery (194 m a.s.l.). Caging was necessary to prevent seed predation by birds; this also reduced the likelihood of seed rain affecting results. Nursery conditions were drier and warmer than study sites. Samples received an estimated 50% available sunlight, due to a canopy of trees.

Although past studies suggest that seeds which have not germinated within 4 to 5 weeks are non-viable (Dalling et al. 1998) or dormant (Baskin and Baskin 2001), seed bank samples were monitored from March to December 1999. Seed, including new species, germinated up until six months following placement in nursery. Seedlings were counted and removed every two weeks. Unidentifiable seedlings were not recorded and left until the next monitoring period. The initial seedlings were identified with the assistance of Henning Adsersen, a botanist with over 25 years experience studying the flora of Galapagos. Unidentifiable seedlings were grown in the nursery until identification was possible. The number of individual seedlings that emerged was used to calculate the germinable seed density for each species per m^2 of soil.

3.2.4 Statistical Analyses

One-way parametric analysis of variance (ANOVA) was conducted to determine if significant differences in soil seed bank density existed among pasture, forest edge and forest interior (Zar 1996). Species were grouped into four plant groups for all analyses: native, endemic, alien and those of uncertain origin according to Porter (1983) and Lawesson et al. (1988). Jaccard's and Sorenson's similarity indices were used to quantify the similarity in species composition and richness in recruitment among treatments and the native forest.

3.3 Results

The density and richness of the pasture soil seed bank was not significantly different from that of the native forest (Table 3.1). Mean germinable seed density was 5,159 seeds m^{-2}. The pasture had a significantly greater density of native seed, however, 94% of these native propagules were fern spores (Table 3.1). Total species richness was 15 and 13% of the species were trees or shrubs (Table 3.2). The seed bank was dominated by native ferns (4778 m^{-2}), *Oxalis corniculata* L. (217 m^{-2}), *Mecardonia dianthera* (Sw.) Pennell (67 m^{-2}), *Solanum nodiflorum* Jacq. (42 m^{-2}), and *Physalis pubescens* L. (30 m^{-2}) (Table 3.4).

The density and richness of the forest interior seed bank was comparable to that of the pasture. Mean germinable seed density was 7,584 seeds m^{-2}. Total species richness was 14 and 43% of the species were trees or shrubs (Table 3.2). The seed bank was dominated by the endemic forb, *Pilea baurii* Robins. (4209 m^{-2}), native ferns (2412 m^{-2}), *Borreria laevis* (Lam.) Griseb. (344 m^{-2}), elephant grass (268 m^{-2}) and *S. nodiflorum* (149 m^{-2}) (Table 3.4). Ferns and *B. laevis* were the dominant understorey species in intact Scalesia forest, though *B. laevis* was only present in the forest interior seed bank. The forest seed bank had the greatest richness of trees and shrubs, though as a proportion of the total density, edge had the greatest abundance of woody species (9%) and pasture the least (1%). *Scalesia* was only present in the forest interior seed bank, though even there in low abundance (8 germinable seeds m^{-2}).

The forest edge seed bank had a significantly greater germinable seed density than pasture or forest interior (Table 3.1). The seed bank species richness was also the greatest. Total species richness of the seed bank was 18 with 28% of the species trees or shrubs (Table 3.2). Mean germinable seed density was 12,102 seeds m^{-2}. The seed bank was dominated by *P. baurii* (6,561 m^{-2}), native ferns (1,847 m^{-2}), elephant grass (1,401 m^{-2}), *S. nodiflorum* (922 m^{-2}), *O. corniculata* (520 m^{-2}) and *Salvia occidentalis* (340 m^{-2}) (Table 3.4).

The seed bank of the pasture and forest edge were least similar according to both Jaccard's and Sorenson's indices (Table 3.3). The forest interior and edge seed banks were the most similar when based on Sorenson's index which favours dominant species;

the pasture and forest interior seed banks, however, were the most similar according to Jaccard's index which favours rare species.

In summary, the forest edge had the greatest total germinable seed density while the abandoned pasture had the lowest density. Abandoned pasture had a significantly greater density of native seed and a significantly lower density of endemic seed than the forest edge or interior. Ferns comprised the majority of native propagules in the pasture. The forest edge had a greater density of alien species and those of uncertain origin than the forest interior or pasture. Species were not unique to the edge but were in greater densities.

3.4 Discussion

3.4.1 Pasture Seed Bank

A relict seed bank does exist in abandoned elephant grass pasture, however, its composition does not resemble that of the native Scalesia forest. Previous studies in abandoned pastures have found a gradual increase in the native species richness and density with time; in particular an increase in woody species (Uhl et al. 1988; Falinska 1999; Aide et al. 2000). Thirty years following abandonment, the pasture seed bank was dominated by opportunistic species, species often characterized by persistent seed banks.

Many pioneer species, as is the community dominant *Scalesia*, have a transient seed bank strategy according to Thompson and Grime's classification (1979); brief longevity followed by rapid germination (Hall and Swaine 1980; Garwood 1983; Garwood 1989; Skogland 1992). A transient strategy would be beneficial for a species such as *Scalesia* that depends on periodic predictable stand level dieback for synchronous regeneration, while a persistent strategy would be appropriate for slow growing secondary forest species such as *Zanthoxylem fagara* and *Psidium galapageium*, as favourable germination conditions are unpredictable. Transient seed banks decrease with time unless constant seed rain is received. Although, pioneer species are characterized by prolific seed production and efficient seed dispersal by wind or water (Fenner 1987), a dense vegetative canopy in pasture would reduce incorporation (Falinska 1999). Seed of secondary species, on the other hand, is not readily dispersed long-distances (Fenner 1987).

Native species, particularly woody species which may shade out aggressive grasses, were not abundant. *Scalesia* is not adapted to long-distance dispersal, as seed drops below the parent plant (Hamman 1981; Shimizu 1997). However, Seed of many tree and shrub species in the Scalesia forest are actively dispersed by birds (Porter 1983). Seed of herbaceous species may possess awns: bristles or sticky exudations allowing seed to be transported passively on birds' feathers or feet, or seed is eaten and regurgitated or passed through the gut. Few Galapagos finches were actively foraging in elephant grass pasture, except by forest edge. Only once grass was cleared were they observed in the pasture interior. Previous studies have shown that residual perching structures are necessary for seed dispersal in pastures and their presence results in an increase in seed incorporated into the soil seed bank (Guevara and Laborde 1993; Holl 1998).

Native ferns dominated the soil seed bank of the abandoned pasture and Scalesia forest as well as the forest understorey however, their role in forest succession is unknown. Ferns may act as pioneer species, by providing rapid cover and shade thereby facilitating establishment of later successional species. They are, however, also able to persist once a canopy develops. The microscopic fern spores are easily wind and water dispersed, which may increase their propagule rain in abandoned pasture, even though a dense vegetative mat exists. Once established the relative importance of rhizomes for colonization compared to spores may increase (Hill and Silander Jr. 2001) and may explain this study's finding of a decline in spore density in intact forest. Ferns successfully established in an abandoned pasture in Venezuela and were important for building soil organic matter following a disturbance (Rosales et al. 1997). They were, however, poor soil protectors. Slocum (2000) found germination of woody species increased in fern patches, as did overall species richness and density, compared to grassy areas. A reduction in grazing due to the unpalatability of ferns may explain some of this effect.

3.4.2 Scalesia Forest Seed Bank

This study does not support previous work which found tropical moist forest seed banks to be dominated by pioneer woody species (Swaine and Hall 1983; Tsuyuzaki and Kanda 1996; Dalling et al. 1998; Baskin and Baskin 2001). The two species unique to the forest seed bank were opportunistic trees or shrubs, including the community dominant *Scalesia*, however, they were in low abundance. Dominance by woody pioneers may be common in pristine Scalesia forest, however, a relatively small area is covered by this type of forest, and the influence of neighbouring disturbances may be significant. Secondary forests and those in close proximity to disturbance have larger seed banks than primary forests and are dominated by herbaceous species (Young et al. 1987).

3.4.3 Edge Effects in Seed Bank

The forest edge seed bank was sampled later in the year than that of the pasture or forest interior with the possible result of differences in richness, composition and/or density. Although the majority of species found in forest edge seed bank were present in the other sampling locations, the extra three months for seed incorporation to occur may explain the increase in seed density.

The significant increase in seed density and richness by the forest-pasture edge, however, could indicate edge induced effects. Edge induced effects, including increased seed dispersal and vegetative colonization, as well as changes in microclimate and irradiance levels, have been well documented (Williams-Linera 1990; Laurence 1991; Matlock 1994; Restrepo et al. 1999). Although these effects are most often documented at recently disturbed sites, they have been known to persist particularly in forests that experience long disturbance intervals (Matlock 1994). Fruit production is at least initially greater by forest edges than interior following disturbance, due to increased light (Restrepo et al. 1999). An increase in fruit encourages bird foraging in edge habitat, potentially increasing the abundance of bird dispersed plant species such as trees and shrubs (Harvey 2000). As the forest canopy closes in and irradiance is reduced, edge patterns in vegetation are also reduced (Matlock 1994). The gradual invasion of elephant grass into the forest, however, ensures that the canopy remains less dense than in the interior, increasing irradiance, and the potential for dispersal, incorporation and germination.

3.4.4 Seed Bank Dynamics

Seed banks are not static in time or space. Multiple samples would be required to accurately quantify them (Bigwood and Inouye 1988; Gross 1990; Hutchings and Booth 1996; Falinska 1999). Half of the species found in the forest seed bank were present in the aboveground vegetation, while the other half were present in low abundance by the forest edge, or not observed in the forest. Seed is continually added, moved horizontally and vertically, and it senesces (Chambers and MacMahon 1994). Seed may remain in the canopy until it is ready to be dispersed, or it may lie on the forest litter (Chambers and MacMahon 1994), which was removed in this study. Seed banks are also spatially variable; for example, bird dispersed seed is often clumped while seed of wind dispersed species is more uniformly distributed over an area (Chambers and MacMahon 1994).

Tropical forest species have developed seed bank strategies which take advantage of favourable conditions during the rainy season for germination and establishment (Ray and Brown 1994). Native species may use these cues to determine appropriate times for seed ripening and dehiscence. Many herbaceous and woody species produce fruit in the dry season (i.e. late March to early June), but may not set seed until early in the rainy season, when conditions are favourable. For example, *Psychotria rufipes*, a dominant subcanopy species, did not begin to set seed until September. By sampling in March, seed of such species may not be incorporated into the seed bank; later in the year, these species may be present. Other seed (e.g., *Tournefortia*) is incorporated into the seed bank throughout the year, as it is produced year-round. As well, many subcanopy species in the Scalesia forest rely on vegetative growth once established and it is likely that they produce fewer viable seeds (Matlock 1994; Hill and Silander Jr. 2001).

3.4.5 Potential for Restoration from Relict Seed Bank

How reliable are methods to quantify the soil seed bank and therefore indicate a site's potential for natural recovery? Methods used to quantify seed banks in past studies have biased the outcomes (Bigwood and Inouye 1988; Gross 1990; Brown 1992; Falinska 1999). Use of the germinable seed density compared to the actual seed density may limit the ability to predict the future plant community. Falinska (1999) found the seedling emergence method allowed 40% of the species to be identified while the counting of actual seed present resulted in 70 to 80% being identified. Partial shade in nurseries can also prevent germination of sun-loving pioneer species, while enhancing that of shade tolerant species. The lack of predictive capabilities in seed bank studies is not only attributed to temporal and spatial variation, but to germination limitations, such as seed dormancy, predation, lack of safe sites and poor environmental conditions (Ray and Brown 1994; Holl 1999; Holl et al. 2000). Sampling throughout the year, at more sites and using a variety of methods may be required to capture the inherent variability and accurately assess the potential for natural recovery.

Previous research concluded that following a disturbance seed banks are more important for recruitment than seed dispersal (Swaine and Hall 1983; Saulei 1984; Young et al. 1987). This study, however, supports others that found the seed bank to be rapidly depleted following a disturbance and that over time, dispersal becomes increasingly important (Saulei and Swaine 1988; Skogland 1992). As well, some research found woody species to be added to abandoned pasture seed bank with time since disturbance, and overall seed bank diversity increased (Saulei 1984; Janzen 1986; Thompson 1989). Although this was not true at sites described in the present study, following a reduction in elephant grass cover, seed incorporation may significantly increase.

When relying on seed dispersal, clear-cut areas would be at a greater disadvantage than those areas experiencing gradual disturbance, due to a lack of vegetation structure to facilitate incorporation of bird dispersed species. Pasture closest to the forest edge may therefore have the greatest potential for natural recovery. As well, the composition and density of seed rain is unpredictable in time and space, and dependent on adjacent forest communities, which include native and alien species. The role of the seed bank in any future restoration projects will be highly dependent on the time since disturbance, type of disturbance, size of site, degree of isolation and the regeneration strategies of native species.

3.5 Conclusions

For the three abandoned elephant grass pastures and adjacent native Scalesia forest studied on the island of Santa Cruz, this research concludes:

- The soil seed banks of the pasture and native forest were comparable in density and richness. The pasture seed bank, however, contained few functional groups.
- Only the forest seed bank contained the community dominant *Scalesia pedunculata*, as well as moderate abundances of ferns, herbaceous and other woody species.
- Samples need to be taken throughout the year to conclude if forest-pasture edge effects are present. A potential edge effect was substantiated by a significant increase in the density and richness of the soil seed bank. The forest edge seed bank had the greatest density of endemic, uncertain origin and alien species.
- Abandoned pasture is not a reservoir for alien and potentially invasive species; an accumulation of alien seed by the forest edge and interior is a greater threat to intact forest.
- Dominance of the seed bank by opportunistic species of uncertain origin may be a concern, as these species' aggressive colonization strategies may prevent recruitment of the dominant native and endemic species of the Scalesia forest.
- Restoration of abandoned pasture to native Scalesia forest without human assistance is unlikely. The community dominants were missing, therefore manipulation of the seed bank through the addition of propagules is necessary.

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Table 3.1. Mean germinable seed density m^{-2} (±SE) in the soil seed bank of abandoned elephant grass pasture and native Scalesia forest, Santa Cruz, Galapagos.

	Total	Native	Endemic	Uncertain Origin	Alien
Pasture	5159^{b} (408.3)	4851^{a} (408.9)	219^{b} (42.0)	72^{b} (12.7)	9^{b} (6.3)
Forest Edge	12102^{a} (1733.2)	2590^{b} (370.5)	6518^{a} (1462.9)	1423^{a} (330.3)	1529^{a} (378.1)
Forest Interior	7584^{b} (826.2)	2531^{b} (681.0)	4229^{a} (535.6)	548^{b} (167.2)	276^{b} (91.1)

Means within columns that do not share a common letter are significantly different at $p \geq 0.05$.

Table 3.2. Germinable seed species richness m^{-2} by plant group in the soil seed bank of abandoned elephant grass pasture and native Scalesia forest, Santa Cruz, Galapagos.

	Total	Native*	Endemic	Uncertain Origin	Alien	Woody
Pasture	15	6	3	4	2	3
Forest Edge	18	6	3	4	4	5
Forest Interior	14	3	3	3	4	6

* Excluding native ferns, which consisted of at least 4 species in each sampling location.

Table 3.3. Similarity between the soil seed banks of abandoned elephant grass pasture and Scalesia forest (interior and edge), Santa Cruz, Galapagos.

Communities	Common Species	Unique Species	Jaccard's Index	Sorenson's Index
Pasture, Forest	13	6, 3	59	74
Pasture, Edge	14	5, 8	34	68
Forest, Edge	15	1, 7	39	79

Table 3.4. Mean density of germinable seed m^{-2} in soil seed bank of abandoned elephant grass pasture and native Scalesia forest, Santa Cruz, Galapagos. Dash indicates the species was not found at this location.

Family	Species	Origin*	Growth** Form	Abandoned Pasture	Forest Edge	Forest Interior
Apiaceae	*Apium laciniatum*	N	H	7	-	-
Asteraceae	*Gnaphalium purpureum*	U	H	6	-	-
	Scalesia pedunculata	E	T	-	-	8
	Synedrella nodiflora	A	H	-	64	51
Boraginaceae	*Tournefortia rufo-sericea*	E	S	6	64	13
Caryophyllaceae	*Drymaria cordata*	N	H	-	11	-
Commelinaceae	*Commelina diffusa*	N	H	1	85	55
Euphorbiaceae	*Phyllanthus caroliniensis*	N	H	1	-	-
Lamiaceae	*Salvia occidentalis*	U	H	3	340	4
Lauraceae	*Cestrum auriculatum*	A	T	-	32	4
Nyctaginaceae	*Boerhaavia caribaea*	N	H	-	11	-
Oxalidaceae	*Oxalis corniculata*	A	H	217	520	-
Passifloraceae	*Passiflora colinvauxx*	E	V	1	-	-
Piperaceae	*Peperomia galapagensis*	E	E	-	297	-
Poaceae	*Pennisetum purpureum*	A	G	10	1401	268
Rubiaceae	*Galium galapagoense*	N	H	4	-	-
	Borreria laevis	U	H	10	319	344
Rutaceae	*Zanthoxylum fagara*	N	T	-	21	-
Schrophulariaceae	*Mecardonia dianthera*	N	H	67	149	8
Solanaceae	*Browallia americana*	A	H	-	11	-
	Physalis pubescens	N	S	30	159	59
	Solanum nodiflorum	U	S	42	922	149
	Solanum quitensis	A	S	-	-	4
Urticaceae	*Pilea baurii*	E	H	4	6561	4209
Valerianaceae	*Astrephia chaerophylloides*	U	H	-	53	-
Polypodiophyta	*Dennstaedtia spp., Diplazium spp., Pteris spp., Ctenitis spp.*	N	F	4778	1847	2412
	Unidentified species			8	42	4

* N = native, E = endemic, U = uncertain, A = alien

** F = forb, G = grass, S = shrub, T = tree, V = vine, E = epiphyte, F = fern

4. Evaluation of Revegetation Techniques to Facilitate Restoration of Moist Evergreen Forest in Abandoned Pasture, Galapagos Islands

4.1 Introduction

Natural recovery following disturbances is desirable to reduce the financial and human resources required to facilitate restoration (Lugo 1988). Recruitment from the soil seed bank in abandoned tropical pastures is, however, highly unlikely, mainly due to the fast turnover in tropical seed banks (Garwood 1989). Reliance on seed dispersal from remaining areas of native vegetation is risky as there is little control over which species establish and their spatial distribution (Chambers and MacMahon 1994). Short-distance dispersers will be at a disadvantage, or at least require more time to become established. In communities invaded by alien species that form dense ground cover, incorporation of new seed into the soil seed bank may be reduced. Dispersed seed remains in the vegetative or litter layers, which do not provide adequate nutrients, moisture or protection from predators for successful germination and persistence (Chambers and MacMahon 1994). Even if aggressive competitors are removed through cutting or chemical methods, limitations to seed germination are a formidable problem (Posada et al. 2000).

Manipulating regeneration processes to attain the desired community composition, diversity and structure is another option (Hobbs and Huenneke 1992). This can involve two approaches: manipulating the disturbance or manipulating recruitment following disturbance (Keddy et al. 1989). A combination of the two is generally necessary given environmental and resource constraints. In the case of invasive alien species, manipulating the disturbance is not always possible although practices, which prevent further introduction (frequency and intensity) and limit dispersal agents (area), are feasible. Following disturbance, it may be desirable to manage for preferred species and/or undesirable species.

Alternatives to natural recovery include sowing seed collected from native plants, transplanting seedlings or sod and the use of donor soil seed banks. Hand-collected seed has the advantage of allowing management for preferred species whether for morphological or taxonomic attributes. Unfortunately, a native seed source is not always available (Lugo 1988), and even if available, the resources to collect and store sufficient viable seed can be extravagant. The advantage of transplanting is increased recruitment rates by overcoming problems in determining seed viability and inhibition factors. Again, growing (or collecting), maintaining and transplanting seedlings is labour intensive. The use of a donor soil seed bank, although not allowing for the selection of individual species, does increase the likelihood of including a greater diversity of species than natural recovery, hand-collected seed or transplanting. The likelihood of short-distance dispersed seed and short-lived seed being present is particularly increased compared to the relict seed bank as incorporation was likely more recent than on a disturbed site.

Restoration efforts in tropical regions have focussed on removal of stressors such as alien species or human pressures in anticipation that natural re-colonization, or passive restoration will occur (Janzen 1986; Aronson et al. 1993; Posada et al. 2000; Nepstad et al. 1996). Methods that actively enhance recruitment on disturbed sites have generally been limited to planting of tree seedlings (Parrotta 1992; Gerhardt 1993). Seeding has been suggested as an alternative revegetation technique, but has not been rigorously tested (Janzen 1986; Nepstad et al. 1990; Eliason and Allen 1997). Ray and Brown (1994), in one of the few studies undertaken, tested the relative success of seed, seedlings and rooted cuttings of native trees of dry forest. They concluded that seed was the least effective over a 9-month study period, as germination rates were low. Literature on tropical forest seed banks and seed germination does exist (e.g. Garwood 1983, 1989), although it has not been linked to the potential for restoration of abandoned agricultural lands.

The Scalesia forest on the north side of Santa Cruz is the last remaining stand of any significance in Galapagos (Itow 1995). Restoration of disturbed Scalesia forest is not only desirable for conservation value in itself but also as a means of preventing further invasions by alien plants (Shimizu 1997). This moist evergreen forest is dominated by the endemic tree *Scalesia pedunculata* Hook f. (Asteraceae). If re-established *Scalesia* could outcompete alien plants; *Scalesia* is often a superior competitor in the early developmental stages growing up to 3 m in the first year (Itow 1995; Shimizu 1997).

Scalesia reaches sexual maturity within three years (Hamann 1981; Shimizu 1997), although intervals as short as six months have been documented for some species, when grown from seed (Itow and Mueller-Dombois 1988). *Scalesia* seedlings, however, have only been found within a 10 to 20 m radius of parent trees suggesting that isolation and speciation have resulted in a loss of dispersal ability typical of most Composites (Eliasson 1984; Shimizu 1997); thus assistance would be required. The intensive inputs required to maintain a propagation program for woody species, and the poor access to restoration sites, has focused research on alternative restoration methods. There is little information on *Scalesia* seed viability and germination, or that of other native species, however, use of seed may be less labour intensive than the use of seedlings and allow for re-introduction of a greater diversity of species and functional groups.

4.1.1 Research Objectives

The objectives of this study were to assess the feasibility of natural recovery in facilitating restoration of the Scalesia forest following efforts to remove elephant grass in abandoned pasture, and to compare natural recovery to two techniques to enhance native recruitment, the use of hand-collected seed and the use of a donor soil seed bank. It was predicted that natural recovery would not be feasible due to the extensive length of time since initial disturbance, the subsequent loss of a soil seed bank and the poor dispersal abilities of *Scalesia* (See Chapter 3); therefore, assistance would be required to promote native recruitment. Successful revegetation was measured by an increase in the density and richness of native and endemic species, and a reduction in the richness and density of alien species.

4.2 Methods

4.2.1 Site Description

The study sites were established within the Humid Zone on the island of Santa Cruz within a national park (Figure A.1). The Humid Zone is located between 250 and 500 m a.s.l. on the south side and 500 to 750 m a.s.l. on the north side of Santa Cruz (Jackson

1993). Weather station data from the south side of the island (elevation 194 m a.s.l.) indicates an average annual precipitation of 1216 mm and an average annual temperature of 23 °C (Figures A.2 and A.3) (Snell and Rea 2000). The year in which this study was conducted, 1999, was much drier than normal, with a total precipitation of 669 mm and an average monthly temperature of 22.4 °C. At an elevation closer to that of the study sites, 620 m a.s.l., the average annual precipitation is 1845 mm with no obvious peaks or troughs throughout the year, and the average annual temperature 16.9 °C with a peak in April and a trough in September (Itow 1992).

Santa Cruz is one of the oldest islands (2.2 to 2.9 million years) and soil is well weathered. The soils of the Humid Zone are < 1 m deep, contain an admixture of ash and clay, and have a reddish brown hue darkened locally by humification (Laruelle 1966). Soils have an ABC profile with 5 to 13 cm of humus in the upper horizons, and tuff-like material, ash and fragmented basaltic and pyroclastic materials in the C horizon. Base saturations in these soils are of 57 to 74%. The soils at the site were of a sandy loam texture (Table A.1).

Study sites were situated within the Scalesia Forest subzone. The forest is dominated by the endemic evergreen tree, *Scalesia pedunculata* Hook f. *Scalesia* comprises 60 to 100% of the canopy, with subcanopy species *Psidium galapageium* Hook f. var. *galapagiem*, *Chiococca alba* (L.) Hitchc. and *Zanthoxylum fagara* (L.) Sarg. (Table A.2). A dense shrub and herbaceous layer and an abundance of bryophytes and epiphytes are present. Shrub species are limited to *Tournefortia rufo-sericea* Hook f., *Psychotria rufipes* Hook f., *Cordia* spp., *Croton scouleri* Hook f. var. *grandifolius* and *Sida rhombifolia* L. Native ferns including *Ctenitis pleurois* (Hook f.) Morton, *C. sloani* (Spreng.) Morton, *Blechnum* spp., *Asplenium* spp., *Doryopteris pedata* (L.) Fee var *palmata* and *Dennstaedtia globulifera* dominate the herbaceous layer.

Elephant grass was introduced to Galapagos in 1967, when a farmer brought cuttings from the Loja region of mainland Ecuador (F. Lleno pers. comm.). The specific cultivar present on Santa Cruz is not known. Land was cleared within the Scalesia zone on the north side of the island, elephant grass was planted and the area was lightly grazed for one to two years before national park officials removed cattle. At the time of this study, remaining elephant grass pastures varied in size from 0.5 to 10 hectares. Smaller areas of elephant grass within the forest likely encroached from neighbouring pasture and/or were introduced from seed to the interior and small-scale disturbance facilitated establishment. The Scalesia zone on the north side of Santa Cruz, including abandoned elephant grass pasture, has had limited access, except by park guards, researchers and some local residents who collect fruit and timber, and hunt feral animals. At each site, vegetation cover was completely dominated by elephant grass.

4.2.2 Experimental Design

Three abandoned elephant grass pastures were selected within the Scalesia zone based on accessibility and similarity of physical conditions. Sites A and B were approximately 500 m apart, and Site C approximately 2 km from them. A randomized complete block design was used. At each site, thirty 10 by 10 m plots were established in a grid. The grid was centred in each pasture to ensure opportunities for seed dispersal from adjacent forest to plots.

Twelve treatment combinations, composed of four management treatments to control elephant grass and three restoration treatments, were twice replicated at each site. The management treatments were, one-time manual cutting (M), repeated manual cutting (MR), cutting and one-time herbicide application (H), and cutting with repeated herbicide (HR); and the three restoration treatments, natural recovery (NR), the use of hand-collected seed (HC), and the use of a donor soil seed bank (SS). Treatments were replicated twice and the remaining plots were assigned as controls. Response variable values were averaged between replicates to obtain one value per treatment per site.

A two-metre buffer was established between each of the treatment plots and around the perimeter of each site to reduce off-target effects from herbicide treatments and shading of plots. Vegetation within the buffer was cut with machetes and spot sprayed with Roundup.

Three 100 m^2 plots were established in regions of the Scalesia forest that were not invaded by alien plant species. The purpose of these plots was to determine the species richness and abundance of relatively pristine forest habitat. These data were compared to the species richness and relative abundance of species in treated plots at the conclusion of the study. Reference plots were located at least 50 metres from areas invaded by elephant grass to minimize the potential edge effects (Dalling et al. 1998). Studies indicate that edge effects in tropical forests extend to depths of 150 m for canopy species and 500 m for the herbaceous layer (Laurance 1991). Location of the non-invaded plots maximized the distance from each edge where feasible. At some sites, alien species had penetrated into the forest and truly non-invaded plots were difficult to locate. When complete absence of aliens was not possible, plots with few individuals were selected.

4.2.3 Treatments

Restoration treatments were carried out in late March 1999 following management treatments. Refer to Chapter 2. for details on management treatments.

4.2.3.1 Natural Recovery

Natural recovery relies on the presence of a relict soil seed bank and dispersal from neighbouring areas. Assessment of the potential of natural recovery was important to evaluate the economic feasibility of restoration as this is often the least costly method. The use of seed and vegetative propagules already present on-site is preferred as these sources are most adapted to site conditions (Lugo 1988; Linhart 1995). Natural recovery also represented a control to determine if the two other seeding treatments enhanced recruitment.

4.2.3.2 Hand-collected Seed

Beginning in early January 1999, seed was collected from native species in the Scalesia forest surrounding the sites. Three species were in seed during this time period, *Scalesia*, *Tournefortia* and *Paspalum conjugatum* Berguis. Seed collection continued until late March when treatments were carried out. Not more than 50% of the seed from one plant was removed to ensure genetic diversity and sufficient remained for forest regeneration. Unfortunately, insufficient *Scalesia* seed was collected from Site C due to a later and lower seed set. Consequently, Site C was seeded with a mix of seed from all three sites. The flesh was removed from *Tournefortia* berries prior to drying, though the pappus remained on *Scalesia* seed. Seed was dried in the sun for 24 hours and then stored for up to a month.

4.2.3.3 Donor Soil Seed Bank

One m^2 quadrats were selected within the native forest adjacent to each site. Sites for the quadrats were chosen based on absence of alien species, representiveness of Scalesia forest, and distance to restoration sites. The top 5.0 cm of soil within each quadrat was removed and placed in buckets. Soil from the quadrats was mixed to reduce the effects of spatial aggregation of seed in the seed bank. The soil seed bank was spread evenly over plots by hand, immediately following collection.

4.2.3.4 Control

Control treatments consisted of 10 by 10 m plots that had not received any management or restoration. The cover and height of elephant grass and presence/absence of other species were recorded at the beginning of the study. Monitoring did not occur as it was assumed grass height could change with time, however, greater cover could not be achieved and no recruitment other than elephant grass would occur.

4.2.4 Seedbed Preparation and Seeding

The upper portion of the litter layer contained large pieces of thatch and cut debris and was removed by hand to prevent impediment of germination. The lower portion of the litter layer provided ideal conditions for seed germination and likely contained part of the soil seed bank. Stubble from remaining elephant grass root crowns was left on-site following management treatments as removal would have been arduous and not practical as part of a management program (Smith 1985; Morgan pers. comm.). Plots were scarified with a hand cultivator to create safe sites for newly added seed. Complete tilling of the site was not desirable as it may have significantly disturbed the soil seed bank and inhibited the germination of native seed already present. Sites were neither cultivated nor seeded within the first 5-7 days following the application of herbicide to enhance absorption rates (Carey pers. comm.).

Seeding rates were calculated based on the estimated seed viability, the estimated seedling recruitment rate from past studies and the density of the species in reference Scalesia forest. The availability of seed for collection ultimately had an effect on the seeding rate as well. Table C.1 presents this information for each of the three seeded species. Seeding rates per plot were 21,440, 104 and 1,600 seeds for *Scalesia*, *Tournefortia* and *Paspalum*, respectively. In SS treatments a seeding rate of 2.5 x 10^6 cm^3 of soil per plot was applied, based on *Scalesia* germination rates in preliminary seed bank samples.

Seed viability was estimated for each species by recording the percent of seed, from a subset of the total collected seed that germinated in the lab (Table C.2). *Scalesia* seed was collected in March and germination treatments conducted at two different dates in April and July. Seed was placed under three stratification treatments to break dormancy and facilitate germination, room temperature water (18.7 °C), hot water (45.3 °C) and a control (no water). Seed was soaked for 48 hours and then placed on wet paper towel in petri dishes. Petri dishes were set near a north-facing window. Paper towels were changed every two days to prevent fungal growth. When the paper towel was changed, the number of seeds that had germinated was recorded. A portion of the collected *Scalesia* seed was also planted in soil with and without its pappus removed (by hand). The pots were placed in the Bellavista nursery to compare germination rates with those obtained in the laboratory.

Each plot was divided into five 2-m wide strips. Seed was also divided into five equal portions, one for each strip. Within each strip, *Scalesia* was broadcast seeded by hand on a calm day. For species where broadcast seeding was not possible due to insufficient seed (*Tournefortia*) or the fact that the seed was too light (*Paspalum*), seed was spread by hand in random clumps. A thin layer of soil was placed over the patches of seed to reduce desiccation and erosion by wind. The soil seed bank was applied in the same manner. A thin layer of grass cuttings was spread over areas where the bare soil was exposed. The purpose of the mulch was to assist in retaining soil moisture necessary for germination. Mulch depth was not uniform and did not exceed 2.5 cm.

4.2.5 Vegetation Measurements

Species richness or the number of species present was recorded for each plot. The density of recruitment was determined by counting individual plants of each species present in plots. Species were then grouped into four plant groups, native, endemic, alien and those of uncertain origin. Species were grouped according to classification by two checklists, Porter (1983) and Lawesson et al. (1988).

Native species were those that had come naturally to the islands from the neighbouring continental land masses by wind, water, birds (internal or external) or on vegetation mats. Endemic species were those that came by the same modes previously mentioned, however, in isolation they evolved into distinct species from their continental ancestors. Alien species were those that arrived on the islands with human assistance whether intentional or accidental. A date of introduction had been documented. Species of uncertain origin were those that could not be unequivocally confirmed to be native, as they were often pantropical weeds that could have easily come through the assistance of humans, nor alien, without a definite date of introduction. If the checklists did not agree then the species was placed in the uncertain origin group. Only in one instance was there disagreement whether a species was native or endemic; *C. scouleri* was assigned to the native group.

In reference plots, a vegetation inventory was conducted to determine species richness. To determine plant cover, three permanent line transects were laid out in an east-west direction, 1 m from plot edges and through the centre. The proportion of each transect covered by each species was recorded, and the mean cover for each species calculated by averaging the values for the three transects. This was repeated in the dry (March/April) and in the wet seasons (October). Trees were also counted individually to determine density.

4.2.6 Statistical Analyses

All data were tested for normality and equality of variance prior to analysis and non-parametric procedures used where appropriate. One-way ANOVAs were conducted to determine if significant differences in recruitment density and total species richness existed between the twelve management and restoration treatment combinations (Zar 1996). Post-hoc tests were employed. Kendall's coefficient of concordance (*W*) was calculated with each ANOVA to determine if there was agreement in treatment ranking between the three study sites. These analyses were repeated for density and species richness of the native, endemic, uncertain origin and alien plant groups. ANOVA was only performed on data from the final monitoring period approximately one year following implementation of management and restoration treatments. Correlation analysis was carried out between the germinable seed density and richness of the soil seed bank in natural recovery plots and the density and richness of the extant vegetation.

4.3 Results

4.3.1 Management and Restoration Treatments

There was no significant difference in the relict soil seed bank density or richness between plots prior to treatment (Table C.2). An ANOVA indicated significant differences in total recruitment density and species richness between the twelve treatment combinations (Table C.3). Significant results were also found for each of the four plant groups. Post-hoc comparison tests indicated a significant difference in the total and species of uncertain origin recruitment density between the HR/SS and the control treatment, and total richness between the HR/HC and the control treatment.

An interaction effect between management and restoration treatments was assumed from the ANOVA results and graphical presentation of data (Figures 4.1 and 4.2). Therefore, an ANOVA was conducted on restoration treatments within management groups. ANOVA results only indicated significant differences in recruitment density and species richness between the control and restoration treatments (Tables 4.1 to 4.4). Some post-hoc comparison tests produced a p-value close to significant that it could not be casually rejected (Table C.4). These results were obtained for the difference in density of native and species of uncertain origin between MR/SS (Table 4.1) and the control treatment as well as the richness of endemic and uncertain origin species between HR/HC and the control treatment (Table 4.4).

Recruitment density and richness in all plant groups was greatly enhanced following repeated herbicide application management treatments (Figures 4.1 and 4.2). In these treatments, there was not a statistically significant difference in recruitment density or richness among the three restoration methods. Following all other management treatments, however, recruitment was greatest in donor soil seed bank treatments, due to an increase in density of species of uncertain origin. HC treatments had a lower density of species of uncertain origin, resulting in an overall lower density though not a significant difference. Hand-collected seed plots also had a slightly greater density of endemic species than the other restoration methods.

Recruitment in all donor soil seed bank treatments, regardless of management method, continued to increase at a greater rate than the other two restoration treatments, even when repeated management efforts ended in December 1999 (Figure 4.3). In all treatments, a gradual decline in species richness was observed once repeated management ceased (Figure 4.4).

There was no correlation among density or richness of the soil seed bank and that of extant vegetation in the pasture following clearing (Table C.5). Densities of all dominant species and plant groups were greater in the soil seed bank than in the pasture.

4.3.2 Recruitment Composition

4.3.2.1 Natural Recovery

Recruitment in all treatments was dominated by species of uncertain origin. *B. laevis*, a shade tolerant forb, was the dominant in manual and herbicide treatments with or without follow-up. *S. nodiflorum*, a shade intolerant shrub, was a dominant species in herbicide treatments. The density of alien species was also similar between restoration treatments though composition varied. At Sites A and B, the dominant aliens were *Passiflora edulis* Sims, an invasive vine, and *Solanum quitensis* Lam., an invasive shrub. Seedlings of these species were consistently found in or near cattle faeces indicating that cattle rather than restoration methods were responsible for their introduction. *Canna edulis* Ker-Gawl, recently naturalized and a potential invader in the islands, was present in all treatments at Sites A and C indicating local dispersal of seed. *Hibiscus diversifolius* Jacq., another potential invader, established in a few plots at Site C.

4.3.2.2 Hand-collected Seed

Seed treated in July had greater germination success than that treated in April, suggesting an after ripening period was necessary (Table C.6). In July, 38.5% of the seed germinated in room temperature treatments compared to 15.7% in hot water treatments and 19.1% in controls. *Scalesia* seed germination in burial trials was similar to results obtained under laboratory germinations. The presence of the pappus had little effect on seed germination. Germination of *Paspalum* seed was variable with a mean of 50.3% (Table C.6). *Tournefortia* did not germinate in treatments or control.

HC treatments, following repeated herbicide applications, had a greater density of endemic species than the other two restoration treatments (Table 4.2). The density of endemic species, however, was low and therefore had a negligible effect on total recruitment density. There was a significantly greater density of *Scalesia* in HC treatments than natural recovery or SS treatments. The density of *Tournefortia* was significantly greater than in NR treatments, but not SS treatments (Table 4.5).

Scalesia and *Tournefortia* recruitment was most successful at Site A. *Scalesia* achieved a height of over 1.5 metres in one plot while *Tournefortia* reached a metre. There was no *Scalesia* recruitment at Site B and a few seedlings in treatments at Site C. No natural recovery of *Scalesia* was observed, though *Tournefortia* was recorded in these treatments. *Paspalum* only established at Site C and was not observed until February 2000. Seedlings were found in all treatments. *Paspalum* was more abundant in the surrounding forest at this site than at the other two sites.

4.3.2.3 Donor Soil Seed Bank

Some species were dependent on the SS treatment for establishment; for example, *Pilea baurii* Robins. (E), *Jaegaria gracilis* Hook f. (E), *Elaterium carthagenense* Jacq. (N), *Ipomeoa triloba* L. (N), *Plumbago scandens* L. (N), *Trema micrantha* (L.) Blume (QN) and *C. scouleri* (N). Woody vegetation was not abundant, however, across all treatments the richness of woody species was greater in SS treatments. The density of woody vegetation was not significantly different between treatments (Table C.7).

The few alien species present in SS treatments were considered serious invaders; for example, elephant grass, *Cestrum auriculatum* L'Her. and *S. quitensis*. Even though elephant grass propagules were present in the donor soil seed bank, they did not have an effect on elephant grass cover between treatments (Table C.8). Although present in other treatments and sites, the density of *C. auriculatum* was greatly increased in SS treatments at Site C, as was that of the pantropical weed, *Conyza bonariensis* L. The presence of *C. auriculatum*, an invasive tree, in plots reflected its presence in the adjacent forest. Invaded areas were avoided while collecting the donor seed bank, however, it was impossible to find areas at Site C that did not have this species within 10 to 20 metres.

4.3.3 Site Effects

Site had a noticeable effect on species richness, even though forest species pools were identical and relict seed banks similar. Species richness was greater at Site C than the other sites; 22 native species established at Site C compared to 7 and 3 native species at Sites A and B respectively. Much of the variation can be explained by the fact that nine fern species established at Site C while none did at Sites A and B. Up to 16 species established in a plot at Site C compared to a maximum of 10 at Site A and 6 at Site B. The dominant native species were the same between sites.

Species unique to Site C such as *J. gracilis*, *Paspalum*, *Drymaria cordata* (L.) Willd. and numerous ferns, were common in the fern/sedge vegetation zone which bordered the site to the south and east. Site C may also have been planted with elephant grass at a later date than Sites A and B according to locals, or a greater reduction in elephant grass height and basal cover may promote recruitment. If Site C was excluded from the analysis, there would not have been a difference in the proportion of native species between restoration treatments following HR management (Table 4.2). If the high species richness can be attributed to time since disturbance, this would have implications for prioritization of pastures for management and restoration.

The sites were assumed to be similar and soil analyses indicated this (Table A.1). Distance to forest edge and site orientation relative to prevailing winds may have an effect on recruitment (Table A.3). Site A was lower in elevation therefore received less precipitation (pers. obs.), and its soil was shallower and contained more lava rock. Prevailing winds are from the southeast in Galapagos and Site C was the only site that did not have Scalesia forest to its south side.

4.3.4 Similarity to Native Forest

Scalesia was the dominant tree species (21 trees 100 m^{-2}) in the reference forest with subcanopy species of *C. alba* (1 tree 100 m^{-2}), *Z. fagara* (2 trees 100 m^{-2}) and *C. scouleri* (1 tree 100 m^{-2}). The dominant understory species were *Paspalum* (16%), *P. rufipes* (14%), *Tournefortia* (12%), *Ichnanthus nemerous* (Sw.) Doell (11%), *Blechum occidentalis* L. var. *puberulum* Sodiro (11%) and *B. laevis* (10%) (Table C.7). Forty-eight species were counted across all plots, with a mean plot richness of 21 species. The majority of species had a cover of less than 1%, including alien species with the exception of *P. edulis* (3% cover). Reference plot cover and richness was dominated by native and endemic species.

Abundance would not be a useful measure of successful forest restoration after only one year, as canopy and subcanopy species, many slow growing secondary species, have not yet established. Evaluation of restoration success will be based on species richness and composition.

Treatments where a donor soil seed bank was used were most similar in species richness and composition to the native forest. Mean species richness, however, ranged from 2 species following M treatments to 3 following MR treatments, 4 following H treatments and 9 following HR treatments. From a restoration perspective, and given the period of time since initiation of the study, only those treatments that involved repeated management activities would be considered feasible options. Species richness following HR treatments was equivalent between restoration treatments and approached 43% of that of the reference community (Table 4.6). Similarity indices also indicated that no one treatment was more similar than another to the native forest reference plots (Table 4.7). Sorenson's index showed a greater similarity between communities based on dominant rather than rare species.

In reference plots, native species comprised the largest portion of species richness (Table 4.7). Although, native species comprised the second largest portion of total species richness in HR/SS treatments, the percentage was the highest of the three restoration treatments. All treatments had fewer native and endemic species than the reference forest. The majority of endemic species were woody, and native species were woody or ferns. Treatments also had a greater percentage of species of uncertain origin than the native forest. Thus the dominants found in the understory forest vegetation were not found or in very low abundance in treatments with the exception of *B. laevis*. While the percentages may have been high, the mean number of species of uncertain origin in each treatment was similar to that of the native forest. Reference plots had similar alien species richness to treatments, though the majority were only represented by one or two individuals.

4.4 Discussion

4.4.1 Natural Recovery and Germination Limitations

The variability in recruitment density and species composition makes natural recovery unpredictable, and therefore it may not be sufficient to prevent invasions as much bareground could result in the short-term. Small-scale variability in seed banks is known to be particularly high in tropical rainforest (Garwood 1989). The recruitment in hand-collected seed plots was expected to be similar to that of natural recovery plots except for the three species seeded, however, differences resulted. As the Scalesia forest seed bank is assumed not to be persistent for greater than a year (Shimizu 1997; Chapter 3), seed dispersal will be essential for natural recovery in abandoned elephant grass pastures. A number of native forbs and those of uncertain origin that germinated in the field did not germinate from seed bank samples indicating these species may be new additions following the clearing of elephant grass.

Germination limitations, however, are a further obstacle to seed even if successfully dispersed to sites. Differences in species richness, composition and abundance between the soil seed bank and recruitment have been documented in past studies (Ball and Miller 1989; Ray and Brown 1994; Garcia 1995; Falinska 1999). The dominant species are generally represented in both, however, their abundance is often lower in the aboveground vegetation than in the seed bank (Ball and Miller 1989; Tsuyuzaki and Kanda 1996). The lower density in extant vegetation can be a result of insufficient soil moisture and appropriate light quantity and quality, necessary cues for germination in tropical forests (Hall and Swaine 1980). Short-term dormancy may be caused in some species by the ephemeral nature of favourable germination conditions, dictated by wet and dry seasons (Marks 1983; Skoglund 1992). The germination of ferns under nursery conditions, but not in the field, may be a direct result of moisture deficits.

Microsite conditions are important for germination and may be sufficiently variable at the study sites (van der Valk and Pederson 1989; Slocum 2000). Microsite elements are influenced by bioclimatic conditions and therefore are site-specific though could include tree snags, rocks, depth of soil and nutrients. The presence of remnant logs increased seedling establishment in recent studies of abandoned pastures (Slocum 2000; Peterson and Haines 2000); this woody debris may improve N levels (Ley and D'Antonio 1998). In other studies, the use of cattle increased the number of microsites (Janzen 1986; Posada et al. 2000). The observation that *Tournefortia* often germinated in clumps of two to three individuals provides support for the importance of microsite. At the beginning of 2000, a number of species new to the sites established and species previously present established in new plots and/or sites. Availability of microsites may only inhibit establishment in the short-term, and with time the variability in density and species composition may decrease.

4.4.2 Enhancement of Native Recruitment

If dispersal is a limiting factor, use of hand-collected seed and/or a donor soil seed bank is necessary to accelerate restoration. Results demonstrate, however, that a number of obstacles to successful forest restoration exist when applying these methods. Young et al. (1987) summarized the common limitations of seeding success as improper seed placement and coverage, competition, use of non-adapted species, predation of seeds or seedlings, and environmental factors.

Native seed may be adapted to gravity dispersal mechanisms and drop under the parent plant to wait for gaps in the *Scalesia* canopy to establish. The use of a donor soil seed bank may increase the inclusion of these species as well as rare species as seed loss, due to long distance dispersal is eliminated. Another advantage of this restoration method is that vegetative propagules can potentially be collected. A number of forest shrubs (e.g., *Tournefortia* and *Psychotria rufipes*) rely on vegetative reproduction once established. A donor soil seed bank enhanced the relict seed bank thereby increasing the chance of germination success and resulting recruitment density. Increasing the soil seed bank application rate could improve restoration results and speed up the process. Unfortunately, on a large scale this method may not feasible. The 1-m^2 disturbance areas, however small, do increase potential safe sites for invasive alien species.

Scalesia and *Paspalum* readily germinated under controlled conditions, and with further research use of hand-collected seed could be a successful restoration method. Manipulation of site conditions should be considered as low surface soil moisture was apparent until mid 1999 and sites had full sun exposure compared to nursery conditions. Shimizu (1997) suggested sowing *Scalesia* seed at the beginning of the rainy season in December/January. Sowing at the beginning of the growing season has also been suggested as the ideal time when using donor soil seed banks (van der Valk and Pederson 1989). The findings of this study, however, suggest a more appropriate time to sow collected seed would be at the end of the wet season or beginning of the dry season in May or June. Although termed the dry season, the Humid Zone of Santa Cruz receives higher precipitation in form of mist during this season and native species flourish (Itow 1992).

Covering of seed to prevent desiccation could improve establishment rates of small seeded species. In a temperate environment, *Bromus tectorum* was one hundred times more likely to germinate when sown in 9 mm pits than open soil. However, in humid environments, the increased moisture gained from this method can increase the risk of seed loss to pathogens and general seed decomposition (Chambers and MacMahon 1994). Following management treatments, a thick cover of mulch prevented germination and seedling establishment (Chapter 2.). Mulch could be sparingly applied if a maximum depth and cover is maintained.

The timing of soil seed bank collection and addition also affects the species richness, composition and density of restored communities (van der Valk and Pederson 1989). The maturity and germinability of seed once incorporated into the soil seed bank will depend on the species and microsite conditions (Garwood 1989). Ripe *Scalesia* seed heads were present on trees in large quantities during seed collection and for a few months following seeding though establishment rates in the soil seed bank plots were low. Seed may require the rains of 'garua', or the misty season, to be dislodged and incorporated into the soil seed bank. Regeneration within the forest was greatest from late August to October when the rains arrived and temperatures were cooler. The removal of the leaf litter layer while collecting may have reduced seed abundances. Wind and water dispersed seeds may fall onto this layer, which was set aside in the study. In March, *Scalesia* seed may have been on this litter layer waiting for rain for incorporation.

The variation in establishment of hand-seeded species may not only be due to site or seeding factors but the method of seed collection. Local seed is adapted to site-specific conditions and may not germinate and/or establish well if moved to another site (Linhart 1995). *Toumefortia* and *Scalesia* both established well at Site A, but sparsely at Sites B and C. The majority of seed used was from the region surrounding Site A because of variation in seed set. Thus the establishment patterns may reflect this need to use seed from immediately surrounding a restoration site. Other researchers have suggested not collecting seed from more than 100 m away for herbaceous species and 1 km for woody plants, although noting that significant genetic variation can occur at a finer spatial scale (Cooper 1957; Linhart 1995). Endemics are known to have less genetic variability and therefore are more vulnerable to environmental change (Linhart 1995).

The significance of seed predation in abandoned elephant grass pasture is not known. A study in moist lowland forests in Columbia (Aide and Cavelier 1994) found that seed predation was higher in the adjacent forest than in abandoned pasture, suggesting that seed predation is not a limiting factor to forest restoration. In the Amazon (Nepstad et al. 1996) and Costa Rica (Holl and Ludlow 1997; Holl et al. 2000), predation was higher in pastures, but Aide and Cavalier hypothesize that this is only true where rodents, mammals or ants are primary predators. The number of introduced rats in the highlands is not known, though they are a threat to petrel nests on the south side of Cerro Croker, and only a few feral pigs and goats have been observed. Galapagos Doves and Darwin's ground finches, which feed on seeds, were regularly seen on-site and are likely the main seed predators (Bowman 1961; Grant and Grant 1979). The rate of seed erosion and predation was not documented, though the seeds of both *Scalesia* and *Paspalum* are small, light, easily wind dispersed and a potential food source for finches. These causes of seed mortality and loss could be overcome with the use of transplants.

4.4.3 Restoration Success and Management Applications

The goal of restoration in Galapagos is to preserve biodiversity, to preserve populations of endemic and/or rare species and reduce the establishment of invasive alien species. This study can only determine the success of short-term restoration objectives based on species richness and composition. It is a valid conjecture that if these attributes are restored then community structure and function are likely to follow (Jordan et al. 1987). However, multiple parameters, including time, will be required to accurately evaluate restoration projects.

Scalesia and a number of subcanopy trees and shrubs have been identified as key components of the native forest in terms of community dominance and function, and consequently, restoration efforts should focus on them. Propagation of the remaining *Scalesia* trees on San Cristobal for re-establishment of *Scalesia* forest has been attempted (Estupianan 1987). Natural transplants taken from the remaining sites on the island did not establish well on new sites, with or without the use of fertilizer, and with or without nursery care for six months prior to transplanting. These natural transplants were taken from a lower elevation (300 m a.s.l.) than where they were to be planted (600 m a.s.l.), which potentially limited success. Greater success was achieved by growing transplants from seed in a nursery. These transplants were more vigorous, attaining a height of 18.18 cm after 4 months in the nursery, and a survival rate of 73.3% once transplanted.

The establishment of a native plant nursery would be an important component of restoration in the Galapagos Islands, rather than relying solely on seed. Although low germination rates are the greatest factor to overcome, low rates of seedling survival are also a concern. *Scalesia* seedling survival is estimated as high as 5% and as low as 1 % (Hamman 1979; Lawesson 1988). Field establishment rates would be significantly higher if these two phases of mortality were reduced under nursery conditions. Seedlings only require a few months to reach an appropriate height and vigour, if grown under the right conditions (plenty of precipitation and cooler temperatures).

Patches of elephant grass within intact forest, and small pastures surrounded by forest may not require treatments to enhance native recruitment, as relict seed banks likely exist and dispersal is feasible. In small pastures, a species such as *Scalesia* may, however, still be dispersal limited. It may be beneficial to add *Scalesia* seed to a disturbed site, as this *Scalesia* is potentially a keystone species in that it provides the necessary shade for regeneration of shade-intolerant species and maintains soil moisture. For small pastures that are upwind of native forest, and therefore receiving reduced seed rain and/or the absence of a persistent seedbank, use of a donor soil seed bank should be considered. Use of donor soil seed bank can increase recruitment of forbs that provide quick cover. The risk of disturbance within intact forest, however, makes this method only feasible on sites less than 0.5 ha.

At larger sites, with the same aforementioned limitations, seeding of *Scalesia* and other woody species is desirable. Collecting seed from other species need not be the primary focus, as forbs are more likely to naturally recover. Although suggested as being more effective than hand-collected seed or use of a donor soil seed bank, the use of transplants would be costly at poor access sites such as those in this study. Seedlings transported by horse have a high risk of being damaged and large work crews are not desirable, as they can negatively impact sites and often lead to increased future access. Transplants are effective for restoration projects close to road access or on private property. It is hoped that these preliminary findings will stimulate further research.

4.5 Conclusions

For the three abandoned elephant grass pastures and adjacent native Scalesia forest studied on the island of Santa Cruz, this research concludes:

1. Germination of native and alien species from the relict seed bank in abandoned pasture was reduced. Germination limitations will be a significant barrier to restoration of abandoned pastures.

2. The use of a donor soil seed bank was the most effective restoration technique for enhancing recruitment density following one-time and repeated cutting treatments, as well as one-time herbicide applications.
3. Native recruitment was greatest following repeated herbicide applications, however, there was no difference among restoration techniques.
   - Species of uncertain origin dominated all three restoration treatments in terms of density and richness.
   - The use of hand-collected seed significantly increased the density of those endemic species seeded.
5. Natural recovery can provide adequate plant cover to reduce invasions of alien species. However, similarity between the resulting community and the native Scalesia forest would be low.
6. A variety of techniques are required to enhance restoration of Scalesia forest:
   - The use of a donor soil seed bank to increase the density of native and rare species.
   - The use of hand-collected seed to increase the density of endemic and woody species.
   - Increase microsite variability and use of moisture retention methods to enhance all methods.

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Table 4.1. Mean plant density (±SE) by plant group per 100 m^2 one year following natural recovery (NR), use of hand-collected seed (HC) and use of a donor soil seed bank (SS) treatments, Scalesia zone, Santa Cruz, Galapagos. Table presents data for manual management treatments only.

	Cutting			Repeated Cutting			Control
	NR	HC	SS	NR	HC	SS	
Native	0 (0.2)	0 (0.0)	1 (0.9)	1^{ab} (0.6)	1^{ab} (0.7)	3^{a} (0.8)	0^{b} (0.0)
Endemic	0 (0.0)	1 (0.4)	0 (0.0)	0 (0.3)	0 (0.3)	1 (0.4)	0 (0.0)
Uncertain Origin	1 (0.3)	1 (0.3)	18 (17.5)	2^{ab} (0.8)	1^{ab} (0.6)	22^{a} (13.7)	0^{b} (0.0)
Alien	1 (0.8)	1 (0.5)	0 (0.0)	1 (0.9)	0 (0.2)	1 (0.4)	0 (0.0)
Total	2 (1.0)	2 (1.2)	19 (18.3)	4^{ab} (2.0)	2^{ab} (0.6)	26^{a} (14.9)	0^{b} (0.0)

Row means within management treatments which do not share a common letter are significantly different.

Table 4.2. Mean plant density (±SE) by plant group per 100 m^2 one year following natural recovery (NR), use of hand-collected seed (HC) and use of a donor soil seed bank (SS) treatments, Scalesia zone, Santa Cruz, Galapagos. Table presents data for herbicide management treatments only.

	Herbicide			Repeated Herbicide			Control
	NR	HC	SS	NR	HC	SS	
Native	0 (0.2)	0 (0.2)	1 (0.3)	25^{ab} (19.8)	24^{ab} (19.6)	36^{a} (23.0)	0^{b} (0.0)
Endemic	1 (0.7)	3 (2.0)	2 (0.6)	2^{ab} (1.0)	9^{a} (5.9)	4^{ab} (3.7)	0^{b} (0.0)
Uncertain Origin	4 (3.1)	2 (1.3)	14 (11.5)	53 (25.9)	22 (6.3)	58 (35.2)	0 (0.0)
Alien	1 (0.7)	0 (0.3)	0 (0.2)	9 (6.2)	3 (1.4)	6 (2.8)	0 (0.0)
Total	5 (4.3)	5 (3.2)	17 (12.0)	89^{ab} (51.7)	57^{ab} (21.0)	104^{a} (55.1)	0^{a} (0.0)

Row means within management treatments which do not share a common letter are significantly different.

Table 4.3. Mean species richness (±SE) by plant group per 100 m^2 one year following natural recovery (NR), use of hand-collected seed (HC) and use of a donor soil seed bank (SS) treatments, Scalesia zone, Santa Cruz, Galapagos. Table presents data for manual management treatments only.

	Cutting			Repeated Cutting			Control
	NR	HC	SS	NR	HC	SS	
Native	0	0	1	0	0	1	0
	(0.2)	(0.0)	(0.2)	(0.2)	(0.3)	(0.6)	(0.0)
Endemic	0	0	0	0	0	1	0
	(0.0)	(0.2)	(0.0)	(0.3)	(0.3)	(0.3)	(0.0)
Uncertain Origin	0	1	1	1	1	1	0
	(0.2)	(0.3)	(0.6)	(0.6)	(0.3)	(0.8)	(0.0)
Alien	1	0	0	1	0	0	0
	(0.3)	(0.2)	(0.2)	(0.0)	(0.2)	(0.3)	(0.0)
Total	1	1	2	2	2	3	0
	(0.9)	(0.5)	(0.4)	(1.2)	(0.3)	(1.8)	(0.0)

Row means within management treatments which do not share a common letter are significantly different.

Table 4.4. Mean species richness (±SE) by plant group per 100 m^2 one year following natural recovery (NR), use of hand-collected seed (HC) and use of a donor soil seed bank (SS) treatments, Scalesia zone, Santa Cruz, Galapagos. Table presents data for herbicide management treatments only.

	Herbicide			Repeated Herbicide			Control
	NR	HC	SS	NR	HC	SS	
Native	0	0	1	3	3	4	0
	(0.2)	(0.2)	(0.3)	(1.5)	(0.7)	(1.9)	(0.0)
Endemic	0	1	1	1^{ab}	2^{a}	1^{ab}	0^{b}
	(0.3)	(0.6)	(0.3)	(0.3)	(0.3)	(0.8)	(0.0)
Uncertain Origin	1	1	1	4^{ab}	3^{a}	3^{ab}	0^{b}
	(0.8)	(0.3)	(0.8)	(1.0)	(0.6)	(0.6)	(0.0)
Alien	1	0	0	1^{ab}	1^{a}	0^{ab}	0^{b}
	(0.4)	(0.2)	(0.2)	(0.7)	(0.8)	(0.2)	(0.0)
Total	2	2	4	9	9	9	0
	(1.4)	(1.0)	(1.3)	(3.0)	(1.9)	(2.3)	(0.0)

Row means within management treatments which do not share a common letter are significantly different.

Table 4.5. Mean density (±SE) of seeded species following three restoration treatments, natural recovery (NR), use of hand-collected seed (HC) and use of a donor soil seed bank (SS), Scalesia zone, Santa Cruz, Galapagos. Species were only known to be seeded in HC treatments.

	NR	HC	SS	Control
Scalesia pedunculata	0^b	3^a	0^b	0^b
	(0)	(2)	(0.2)	(0)
Tournefortia rufo-sericea	0^b	1^a	1^a	0^b
	(0.2)	(0.4)	(0.2)	(0)
Paspalum conjugatum	1	0	0	0
	(0.4)	(0.1)	(0.1)	(0)

Row means with different letters are significantly different at the p = 0.05 level.

Table 4.6. Comparison of mean species richness (percentage of total) by plant group following repeated herbicide applications and three restoration treatments, natural recovery (NR), use of hand-collected seed (HC) and use of a donor soil seed bank (SS) to reference Scalesia forest, Santa Cruz, Galapagos.

Plant Group	NR	HC	SS	Forest
Native	3	3	4	10
	(36)	(29)	(42)	(48)
Endemic	1	2	1	6
	(6)	(18)	(15)	(30)
Uncertain Origin	4	3	3	3
	(42)	(36)	(34)	(17)
Alien	1	1	0	1
	(8)	(9)	(3)	(6)
Total	9	9	9	21
	(100)	(100)	(100)	(100)

Table 4.7. Similarity between recruitment following three restoration treatments and the native Scalesia forest, Santa Cruz, Galapagos. NR = natural recovery, HC = hand-collected seed and SS = donor soil seed bank.

Communities	Common Species	Unique Species	Jaccard's Index	Sorenson's Index
NR, Forest	15	17, 22	22	48
HC, Forest	15	9, 22	25	49
SS, Forest	17	17, 20	24	48

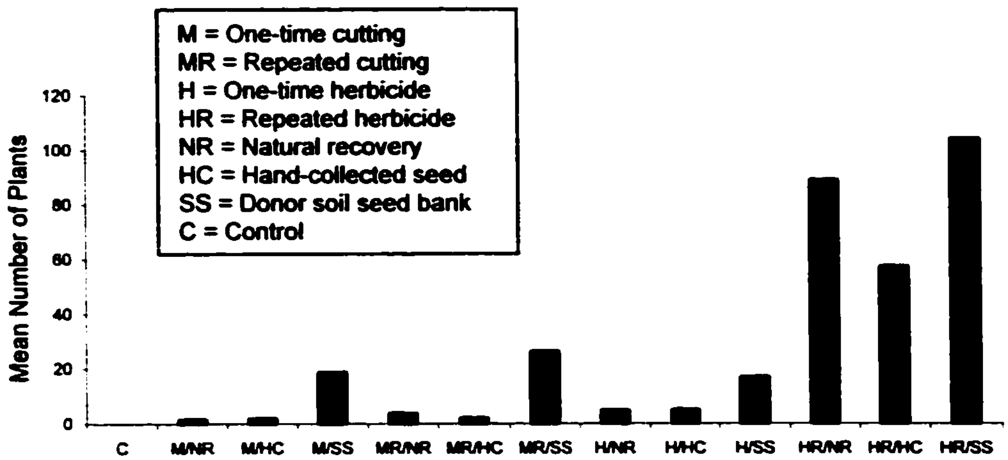

Figure 4.1. Mean density of recruitment 100 m^{-2} following four management and three restoration treatments in abandoned elephant grass pasture, Scalesia zone, Santa Cruz, Galapagos.

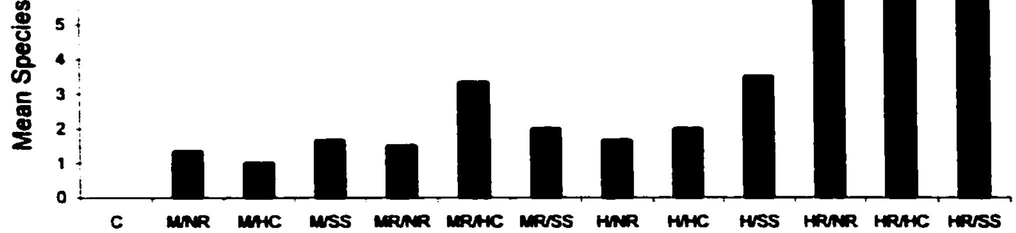

Figure 4.2. Mean species richness 100 m^{-2} following four management and three restoration treatments in abandoned elephant grass pasture, Scalesia zone, Santa Cruz, Galapagos.

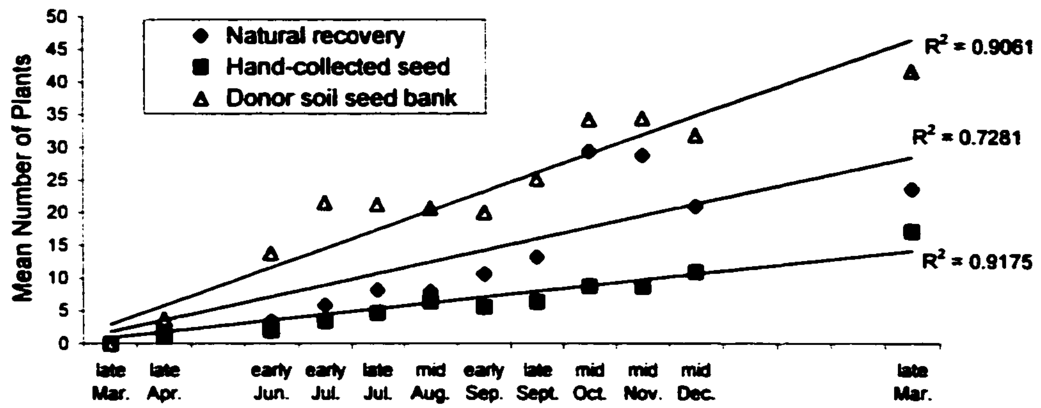

Figure 4.3. Mean density of recruitment 100 m^{-2} following three restoration treatments in the Scalesia forest, Santa Cruz, Galapagos. Monitored March 1999 to March 2000. Linear trendlines fitted through the origin.

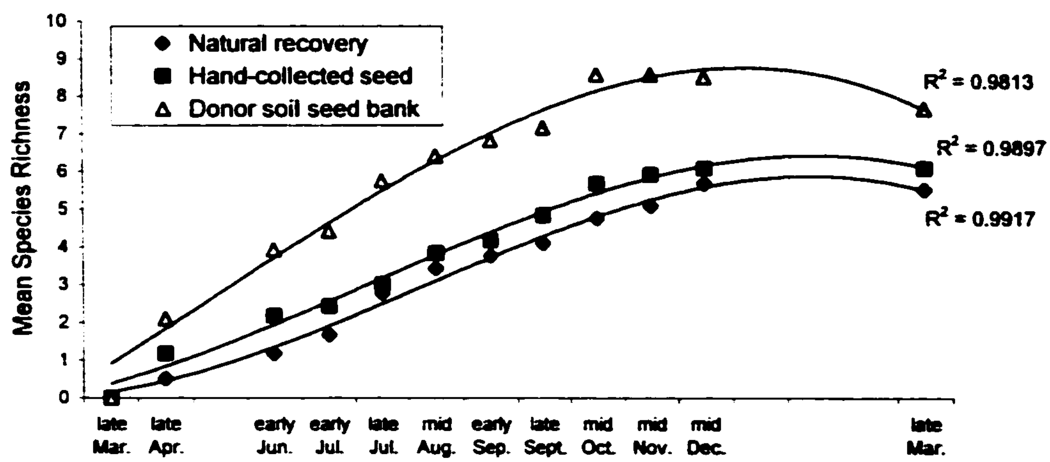

Figure 4.4. Mean species richness 100 m^2 following three restoration treatments in the Scalesia forest, Santa Cruz, Galapagos. Monitored March 1999 to March 2000. Polynomial trendlines fitted through the origin.

5. A Restoration Framework for the Scalesia Forest, Galapagos Islands: An Application of the State-Transition Model

5.1 Introduction

The recognition of dynamic, non-equilibrium ecosystems has resulted in a paradigm shift in restoration ecology, and a focus on systems theories rather than linear paths (Pickett and Parker 1994). Restorationists recognize that vegetation development can be discontinuous, unpredictable and irreversible. Hence, restoration efforts can not confidently direct succession by managing for a desired stage of development, but rather can only hope to reassemble community composition and processes, setting the community on a trajectory towards one or more states within a system of multiple fluctuating states.

Plant communities may not revert to pre-disturbance conditions if certain thresholds have been passed (Lugo 1988; Aronson et al. 1993). These thresholds of irreversibility mark the point where a system cannot naturally return to its previous state and human assistance is required. Under a classic succession approach, human intervention would accelerate natural processes leading to the desired end state. As the science of restoration ecology has progressed, through field experience, experimentation and scientific discussion, the diverse array of factors that inhibit, halt or alter the natural fluctuations of communities have also been recognized. Disturbance itself can result in communities that sustain themselves without intensive inputs, but do not resemble the pre-disturbance community (George et al. 1992; Allen-Diaz and Bartolome 1998). The goal of restoration should be to restore the temporal and spatial diversity inherent in intact ecosystems.

The concepts of alternative steady states, thresholds of irreversibility and discontinuous transitions have stimulated development of state and transition models to assist in understanding the dynamic nature of communities (Westoby et al. 1989). State-transition models are based on the assumption that multiple stable states exist in any community and communities are rarely in equilibrium. Transitions can occur from one state to another in the presence of natural events or management actions. Transient states exist, as most changes are not sudden, however, they are not included in models. In many community restoration projects, there are multiple current states or levels of disturbance as well as end states.

Management activities focused on directing succession can affect a plant community's composition and structure. Mowing or fire can favour the growth of perennial species at the detriment of annuals; the use of herbicides to control weeds can prevent germination of native species (Berger 1993) or stimulate recruitment of invasive species (Breton and Klinger 1994). Unique combinations of management activities and environmental conditions could result in one of many possible states.

The number of possible states is dependent upon the community. Current models for forests likely underestimate the number of states due to a lack of sufficient scientific knowledge and tend to define them based on management criteria. The value of state-transition models for conservation management is not reduced by the lack of a scientific basis, in contrast too much dependence on theory would render the models complex and beyond the scope of most management systems. State-transition models and classical succession models are, therefore, based on species composition and abundance and assume these conspicuous ecosystem components are a direct result of a specific set of soil, geomorphic and climatic attributes. States, while they are not truly stable, do maintain the species composition and structure that define each state for a long period of time within the context of a human lifetime.

State-transition models can guide decision-making processes by identifying the array of possible outcomes given each current state and identify the conditions required to make the transition. Laylock (1991) suggests the use of state-transition models increases the feasibility of management programs and reduces false expectations. Undesirable states can be identified, as well as the activities that facilitate transition to these states, and a pro-active approach taken to prevent their occurrence (Westoby et al. 1989; Whalley 1994). The categorization of opportunities and hazards in community restoration will assist in allocating limited resources to feasible projects.

The use of a state-transition model can assist in the development of a restoration framework for the Scalesia forest on the island of Santa Cruz, Galapagos. Forest dominated by the endemic tree, *Scalesia pedunculata* Hook fil. was cleared for elephant grass (*Pennisetum purpureum* Schum.) pasture. In some areas, elephant grass is encroaching on remnant forest, and local disturbances, often caused by human and domestic animal access, allow for the spread and establishment of elephant grass within its interior. Elephant grass is an aggressive perennial that effectively prevents regeneration of the Scalesia forest by shading out seedlings with a dense vegetative mat. Anthropogenic and natural disturbance also have a significant influence on the forest community.

The purpose of a restoration framework for the Scalesia forest is to ensure that the restoration goal is attained with as little effort and few resources as required. The restoration goal is to put the disturbed community on a trajectory towards the species diversity, abundance and structure of the chosen reference sites. In the short-term, this is measured by high density and richness of native and endemic species and low density and richness of alien species. Given limited resources, decisions will have to be made regarding where and when to focus efforts. It is not sufficient to simply determine the least costly option; each infestation has a unique set of conditions and the least costly option for one set of conditions, may not be for another set. A state-transition model can provide the basis for discussing the opportunities for, and obstacles to, restoration of the Scalesia forest on Santa Cruz.

5.1.1 Research Objective

The objective of this paper is to develop a framework to assist in determining where and when proven management and restoration activities should be applied. This framework includes development of a state-transition model, prioritization of sites based on conservation value, level of disturbance, and management effort and cost, and an examination of the restoration project within the context of Scalesia forest community dynamics and the socio-economic climate of Santa Cruz.

5.2 Methods

5.2.1 Model Development

A state-transition model was developed for the Scalesia forest community located on the island of Santa Cruz. *S. pedunculata* forest exists on four islands in Galapagos (Table 5.1) and this model may apply to these communities, though differences in soils, climate, land use and management may alter outcomes.

To define states and transitions within the Scalesia forest, it was necessary to have an understanding of the dynamic nature of the forest community to examine the causes behind the persistence and expansion of elephant grass, and to understand the effects of existing land use and future management on the forest. Information was gained through literature review, discussion with Charles Darwin Research Station (CDRS) staff, researchers and Santa Cruz residents, and personal observations between 1997 and 2000.

Three assumptions were made:

1. The Scalesia community in undisturbed areas on the north side of Santa Cruz was representative of the community species diversity, composition and structure for the past 200 years. Direct human impacts on this community have been minimal and only within the past 50 years.
2. If elephant grass pasture was left unmanaged it would not be reinvaded by native species. Some studies have suggested that with time reinvasion does occur in some systems, however, this is only on sites where the persistent grass does not form a dense vegetative mat, and invaders are often not native to the surrounding community (e.g., Aide et al. 2000). Elephant grass has persisted for over 30 years in these abandoned pastures with no observations of invasion by native species.
3. Domesticated animals are the only predators of elephant grass. Feral pigs may be present but would not graze elephant grass. Feral goats may also be present and could graze elephant grass though their numbers and thus impact would be low. No insect in Galapagos has been found to depend on elephant grass, though in Africa some fungi have parasitized the grass (Duke 1993).

5.2.2 Prioritization of States and Sites

Generally, areas of high conservation value and low disturbance are given priority for restoration (Hobbs and Humphries 1995; Van Haveren et al. 1997). Within the context of the Galapagos, areas of high conservation value would be considered those with high occurrence of endemic and/or rare species, overall high species diversity and absence of alien species. These areas require less effort and therefore lower cost to restore as native seed sources, if not vegetation islands, still exist. Invasive alien species are the primary disturbance factor in the Galapagos, as land clearing is uncommon. Restoration of areas surrounding high conservation forest should be considered urgently, as they will impact the success of adjacent efforts.

Based on other successful experiences with invasive species management and effective restoration, the following three areas, in order of priority, should be the focus of a Scalesia forest restoration program on Santa Cruz: 1) areas of high conservation value and low disturbance, 2) areas adjacent to areas of high conservation value regardless of disturbance level, and 3) areas of moderate conservation value, and low disturbance.

5.2.3 Determination of Management Effort and Cost and Land Use

Twelve treatment combinations aimed at controlling elephant grass and accelerating the restoration of native Scalesia forest were tested in 1999. The combinations were composed of four management treatments: one-time cutting, repeated cutting, one-time herbicide application and repeated herbicide application, and three revegetation treatments: natural recovery, use of hand-collected seed and use of a donor soil seed bank. The effectiveness of each treatment was evaluated by measuring parameters such as elephant grass canopy and basal cover, and height as well as the density of native and alien recruitment. Treatments were then ranked according to a reduction in elephant grass cover and height and increase in native recruitment. The cost of each treatment over the year study period was calculated based on detailed records of expenditures and labour requirements kept from March 1999 to March 2000. Cost-effectiveness of treatments was then assessed qualitatively.

From January to December 1999, regular visits were made to the region of the Scalesia forest zone on Santa Cruz, by Los Pichachos and El Puntundo. Trips were made by foot, following the main paths to these two locations and then secondary paths to study sites. All observations of National Park use, including date, type of activity and number of people and animals were recorded. Indirect observations such as audio identification of hunters or signs of trail use and fruit collection by items left behind were also recorded. During visits, the presence of alien species was also recorded along the trails in particular noting flowering and fruiting periods, and expanded distribution. There were month long gaps in visits during May and September.

5.3 The Restoration Framework

5.3.1 The State-Transition Model

5.3.1.1 Factors Influencing Elephant Grass Expansion

Four factors were identified as influencing the persistence and expansion of elephant grass in the highlands of Santa Cruz. The first factor is the Galapagos climate. The climate is semi-arid subtropical. Due to the islands' location at the crossways of the Humboldt (Peru) and Gulf currents, they experience regular El Ninos. During an El Nino, ocean temperatures dramatically increase, leading to high precipitation and cool air temperatures. This phenomenon is cyclic in nature with minor events every 5 to 7 years, and major events every 15 years. Years following an El Nino are often marked by drought. Elephant grass flourishes under extreme wet and dry conditions, and range expansion within the Scalesia forest, was noted during the drought years following the major 1982-1983 El Nino and in 1999 (personal observation). The Scalesia forest zone is located on each island at mid to high elevations in regions of moderate to high rainfall and with deep fertile soils that are favoured by elephant grass.

Second, the dynamics of *Scalesia* stands must be understood. In the years following El Nino, the Scalesia forest community experiences stand-level dieback (Hamann 1979; Itow 1995; Shimizu 1997). Although every El Nino does not trigger such an event, the extreme ones may. The strong winds and rains may weaken the tall, spindly, shallow rooted *Scalesia* trees, and in the following drought years, trees die back. Once a few trees fall to the ground, the disturbance generally causes other trees to fall, through direct collision and increased wind exposure. *Scalesia* regeneration does not occur until the canopy is opened. Elephant grass is also a shade-intolerant species and benefits from these canopy openings.

Third, local forest disturbance due to the open access policy within the Galapagos National Park (GNP) must be considered. Although the GNP has restricted access to a number of islands, access on the island of Santa Cruz is open. Official trails do not exist except to Cerro Croker but numerous unofficial trails can be found throughout the Scalesia forest zone on the north side. Local residents access this region of the national park for fruit collection, hunting, recreation and animal grazing (Table 5.2). In 1959, agriculture was removed from this region, though regulations were not strictly enforced until the late 1960s and early 1970s. Elephant grass pastures remain, but have not been grazed for over 30 years. Impacts of this open access policy include trail creation, trail widening, soil disturbance, cutting of vegetation, species introduction and the dispersal of introduced seed to new areas via clothing, footwear and animals. Elephant grass seed has bristles, which facilitate attachment to dispersal vectors as they brush by plants.

Fourth, grazing management practices on Santa Cruz may impact the persistence of elephant grass. If overgrazed, elephant grass tillering is encouraged over leaf formation and the resultant woody stems are of poor forage value. Overgrazing also reduces seed production, increases soil disturbance and the establishment of non-forage native and non-native species particularly ferns and opportunistic species. Once overgrazed, a pasture may require replanting of the species to establish the previous cover in a short period of time and avoid weed control. Most pastures in Galapagos are poorly managed, as rotation does not occur. Elephant grass has also flourished along roadsides where it is not grazed.

5.3.1.2 The Model

S1 is Scalesia forest of high conservation value (Figure 5.1). These are areas of forest that have had little access by humans in the past or present, and support the full suite of native plant and animal species. On the south side of the island, few such areas exist, but there is remnant forest on the north side, particularly towards Los Gemelos. Without anthropogenic disturbance, the stand of Scalesia trees will naturally dieback (T1) and regenerate (T2) every 10 to15 years. Following dieback (S2), the density of mature *Scalesia* trees will be lower, *Scalesia* regeneration high and understory species abundant. Alien species are still not present. As access and trails increase within the Galapagos National Park, alien species will be introduced (T3), or populations of alien species will expand their range into these areas of high conservation value. Scalesia forest may also be cleared to create elephant grass pasture (T4).

S3 is Scalesia forest of moderate to high conservation value. A number of alien plant species are present, though in low to moderate abundance. Feral pigs and goats may also be a concern. The full suite of native species, however, is still present. With time, the abundance of alien species will increase and new introductions may occur. Eventually, the forest will experience natural dieback (T1). The result will be Scalesia forest with numerous small to large gaps and alien species present (S4). These canopy gaps will provide opportunities for further forest invasion, including by elephant grass. Expansion will occur by seed from neighbouring pastures or vegetative spread. With the initiation of an invasive species management program at S3 or S4, but with continued open access to the forest, the transition from S3 to S4 and back (T5) could continue indefinitely.

Without a management program, aggressive alien species will take advantage of the increase in light and expand exponentially (T5). Most alien species are opportunistic, flourish in full sun and are more effective competitors for limited resources than natives. Elephant grass is the only alien species currently present that forms a dense vegetative mat to effectively compete with understory vegetation. *Passiflora* spp., the second most abundant alien group, relies on tree canopies to spread. Scalesia forest now becomes dominated by elephant grass (S5). *Scalesia* snags are present, as are some native shrub and fern species. Native shrubs and ferns may be able to survive for some period of time under an elephant grass canopy (personal observation). Eventually, however, elephant grass will outcompete all native species and *Scalesia* snags will collapse and decompose (T6). The result, assuming the absence of grazers and natural fire, will be a stable elephant grass community (S9). In the absence of elephant grass, invasive tree species such as red quinine and guava will eventually dominate the forest (S6). The native understorey species may survive, however, *Scalesia* will be locally extirpated.

Under moderate to heavy grazing (T7), elephant grass will dominate the community; however, opportunistic native and alien species will also establish and a high proportion of bare ground exists. Native ferns, ubiquitous weeds and some invasive species will be common components of this community (S7) (personal observation). If light grazing and/or management techniques to control elephant grass are implemented, the native community may have the opportunity to re-establish (T8). As *Scalesia* dies off so will *Passiflora* spp. and management efforts should be less intensive; seeding may, however, be required for *Scalesia*. If fire, not grazing, occurred or was prescribed, the community would likely regenerate to the S6 state fairly quickly, depending on the fire's intensity.

5.3.2 Prioritization of States and Sites

Shimizu (1997) explicitly called for a three tier approach to conserving the Scalesia forest by keeping natural conditions (preventing further invasion), eliminating introduced plants and animals and restoring Scalesia forest in disturbed areas. The state-transition model assists in identifying where and when to most effectively direct resources, as states can be prioritized and transitions developed to avoid further deterioration of the forest. Prioritization of sites requires a balance of costs with long-term forest community sustainability. Cost and community sustainability will be influenced by conservation value, effort required for effective management and restoration, and type of competing land uses (Hiebert 1997).

5.3.2.1. Conservation value

High quality habitat is generally easier and less costly to restore than an already degraded site. Based on conventional prioritization strategies, areas containing states S1 to S4 would be the focus of restoration efforts in the initial program. S1 and S2 would be considered of high conservation value and S3 and S4 of moderate conservation value. Once these states were identified in the field, the extent of disturbance could then be evaluated. High disturbance sites may be considered for restoration only if they are adjacent to high conservation value sites, or if they are the last remnants of a community. In the Galapagos, this may be true on San Cristobal or Santiago, but on other islands low to moderate disturbance sites exist.

An appropriate strategy would be to work outward from core, high conservation value habitat within Galapagos National Park. If dispersal of invasive species to restored sites is a concern (e.g. if initial restoration sites are downwind of non-native seed sources) it would be most cost-effective to remove these seed sources, through control and restoration, even if sites are of lower conservation value than others. The differentiation between core natural areas and adjacent buffer zones was recognized in the IUCN Biosphere Reserve program (Borrini-Feyerabend 2000). Core areas were denoted by high conservation value and few competing landuses. Buffer zones encircle the core areas to be protected. As long as areas adjacent to protected areas are being negatively impacted, the long-term stability of protected areas is reduced. Buffer zones recognize that the feasibility of eliminating human use and presence in large natural areas is low, but by focussing on sustainable resource use with each subsequent buffer, the core areas may be protected (Reichard 1997).

5.3.2.2. Management Effort

The greater the richness of alien species, the greater the effort required to restore a site. A number of cultivated species exist within the forest, including avocado (*Persea americana*), banana (*Musa* spp.) and coffee (*Coffea arabica*). Although not invasive at this time, advantage should be taken of their ease of removal. Many introduced vines and trees, however, are difficult to control. Two *Passiflora* vines and four trees *Cestrum auriculatum, Cinchona pubescens, Psidium guajava and Cedrela odorata*, are invasive and present in moderate to high densities. These tree species sucker when cut and some sucker following herbicide application. Vines such as *Passiflora* spp. have numerous stems high in the tree canopy; not only are they difficult to reach, but the likelihood of successfully killing all stems at one time is low, thus repeated management is necessary. The fruits of *Solanum quitensis* and *Canna edulis,* which are non-woody shrubs, can be removed and/or plants hand pulled.

This research has shown that effective management will require repeated efforts; one-time efforts to remove alien species are not effective, particularly once species are well established. Elephant grass seed is most likely dispersed short distances by humans and animals, and awaits disturbance to establish. Once established, elephant grass expands its range vegetatively from edges of pasture into forest. Successful vegetative reproduction relies on an aggressive root system that is increasingly difficult to manage with time. Small infestations have repeatedly been cited as appropriate targets for more effective use of management resources (Moody and Mack 1988; Hobbs and Humphries 1995).

Time since initial disturbance also increases the management effort required. Whether the initial disturbance was land clearing, or small disturbances over a period of time, as the abundance of native species decline, seed sources for recruitment are reduced. As invaded area increases, short-distance dispersed native species, which number many in the Scalesia forest, are at a disadvantage. The persistence of native shrubs in early invasion stages occurs due to their capability for vegetative reproduction. Once grass is suppressed, this can facilitate rapid revegetation. The ability to rely on the relict seed bank and dispersal from neighbouring areas not only reduces short-term costs, accelerates restoration and reduces invasion potential, but likely increases the genetic diversity and resilience of the community. In turn, long-term management effort and costs are significantly reduced.

5.3.2.3. Management Costs

Besides the direct costs of elephant grass removal and seeding, management costs must include costs to manage other invasive species already present in the Scalesia forest. Management of these species is integral to successful forest restoration and may include efforts to eradicate the remaining feral animals, as well as invasive plants (Hobbs and Humphries 1995; Randall 1996). Management costs are directly impacted by management effort. The greater the number and abundance of alien species present, the greater the effort to manage invasive species, and the greater the cost.

The least expensive option to manage elephant grass may not be the most suitable. Short-term goals, such as the importance of reducing elephant grass seed sources given the presence of human disturbance in the forest, may only be achieved using methods that are not cost-effective in the long-term. However, unless these short-term objectives are quickly met, long-term costs will continue to increase. Management and restoration methods have been tested (See Chapters 2. to 4.) and associated costs calculated (Table 5.3). Effectiveness of elephant grass control methods was directly related to cost. One-time control efforts, whether manual or herbicide, were the least expensive to implement and the least effective. Repeated cutting or herbicide application efforts were similar in cost; however, the effectiveness of herbicides significantly outweighed that of repeated cutting. Labour requirements were higher for manual cutting, however the cost of herbicide and application equipment made herbicide methods more expensive. In the past, CDRS has received donations of herbicide and equipment from manufacturers, and this may assist in offsetting costs in future restoration programs. While other herbicides are available in North America, there are none less expensive and changes in national licensing of pesticides would be required for application in the Galapagos.

Initial research on restoration techniques found natural recovery was the least expensive restoration option, but it may not achieve desired restoration objectives. The relict seed bank is dominated by opportunistic species, which are common colonizers in tropical regions, and native seed dispersal appears to be limited. Hand-collecting seed increased the abundance of those species seeded, but otherwise was similar to natural recovery, though was more expensive. The use of a donor soil seed bank increased recruitment density, however species composition was also similar to other treatments. Any seeding method would benefit from further experimentation; the increased cost would be balanced by future restoration success. A large-scale seeding program would also benefit from the purchase of specific seed collection and application equipment.

5.3.2.4. Disturbance

Disturbance within the Scalesia forest results from both anthropogenic and natural events. The greatest disturbances in the Scalesia forest on the north side of Santa Cruz are currently regular human access, and stand level dieback following El Nino events.

There are three communities on Santa Cruz: Puerto Ayora, Bellavista and Santa Rosa. Access to the GNP is obtained through Bellavista and occasionally Santa Rosa, while

Puerto Ayora, a coastal community, supports the majority of the island's population. The trip from Bellavista to Cerro Croker, the highest point of the island, is 1 to 2 hours by horse or foot. The restoration sites for this study were approximately another half an hour beyond this point. Observations and discussion with residents indicate that few residents, particularly families, enter the park zone for recreation (Table 5.2). Park entry by residents is mainly for fruit collection, timber extraction or hunting. While the latter two activities result in the removal of alien species (e.g., quinine, and feral pigs and goats), the former creates greater dependence on various alien species. Tourist operators occasionally bring individuals by horse to the lookouts of Media Luna and Cerro Croker (Espinosa 1998). The activities of park guards and researchers comprise a large portion of park entries, and these visits are often to remote and sensitive areas. The intensity and frequency of entry is not extreme; however, in the presence of an abundance of alien species, even slight disturbances may create opportunities for plant invasions.

Free range grazing occurred within GNP in early 1999 due to drought. The main trail from the park border to Media Luna doubled in width during 1999, as a result of access by people and horses, and precipitation in the highlands. The extent of elephant grass along the trail also expanded. The majority of trail use is between the park border and Cerro Croker, and few enter the Scalesia zone on the north side of the island. Access in this region is limited to fruit collection (avocado, banana, passion fruit and naranjia were planted in the 1960s) hunting, and grazing of cattle. Interference with restoration sites, intentional and unintentional, were noted during active hunting months, although they were rare. Activity adjacent to the Scalesia zone also directly threatens the forest, as satellite populations of alien species act as staging areas, waiting for natural and anthropogenic forest disturbance to facilitate expansion.

5.3.3 Opportunities and Obstacles for Restoration

5.3.3.1 A Community Dynamics Perspective

In the absence of human intervention and/or severe natural disturbance, states S1 and S9 can persist in perpetuity. However, no community is in complete isolation and natural events in the islands are unpredictable. For example, in the past, volcanic eruptions had a significant impact on vegetation development in the Galapagos. As the population of

Galapagos continues to expand exponentially, human influences are inevitable and the threat of a shift from S1 to a higher state increases. Monitoring and management of disturbance levels in the Scalesia forest of the GNP could assist in the maintenance of the forest's current composition, structure and function. To move from S9 to a lower state intensive inputs are required to remove elephant grass and facilitate restoration of the pre-disturbance community. Manual cutting, or burning if current policy changes, and repeated herbicide application to regrowth may successfully control elephant grass. Even with intensive seeding, however, a long time period would be required to achieve objectives.

Restoration efforts, including management of elephant grass, will place the forest community on a trajectory towards any one of the states from S1 to S5. Although S1 is most desirable, a satisfactory goal would be between S1 and S4. Over time, the site being restored will pass through many transition states resulting, from unique combinations of management and restoration activities, and natural events. Every successive El Nino will also forward the transition of forest dominated by *Scalesia* to forest dominated by alien species, unless intensive management is undertaken. Once at S3 or S4, these states could be maintained through management of invasive species and disturbance levels. Particular focus on management following stand dieback events would be required to remove seedlings of invasive species and facilitate Scalesia regeneration. Invasive species management at this time would be less labour intensive than once plants were established.

One-time manual cutting or herbicide application in the presence of an elephant grass seed source will return the forest community to state S9. Repeated manual cutting would create a community similar to one with grazing (S8), though the result of follow-up activities cannot be predicted. Repeated herbicide applications without seeding would put the community on a trajectory towards S3 to S5, however, the timeframe may be extremely long. S7 sites may require less effort and fewer resources to restore than S5 or S6 sites. The effort and cost required to restore S5 sites will depend on the alien species present. Successful methods to control the dominant invasive trees do not exist or are disruptive; disturbance would only encourage a transition from S7 to S5 and not beyond. As the plant community develops, the risk of off-target effects from herbicide use will increase. More selective application methods will have to considered, thereby increasing the time required to implement repeated efforts. Communities such as S1 and S2 can be maintained with intensive management. If management is coupled with restricted park access, the introduction and establishment of alien species, and therefore the effort required to maintain sites, would be reduced. Access to protected areas is continually cited as a factor in the expansion of alien species (Macdonald 1990; Cronk and Fuller 1995; Reichard 1997).

If elephant grass was removed, follow-up control activities carried out for a period of time, and no adjacent alien seed sources (assuming limited park access continued) were present to re-establish the site, natural recovery could occur. The greater the abundance of native species prior to initiating restoration efforts, for example at states S5 or S7, the greater the feasibility of natural recovery. Obtaining a community composition and structure, however, similar to S1 would require quite some time if it could ever be achieved. The rare and uncommon species, as well as the abundance of epiphytes in the Scalesia forest would require at least 30 years, or two *Scalesia* life cycles, depending on dispersal and establishment requirements. Natural invasion would be site dependent, due to the extreme variability in seed banks and the dependence on site area and position for successful seed dispersal.

With seeding, or with small sites, particularly downwind from remnant forest, the timeframe for transition to states S1 to S4 is shortened and woody species would reduce elephant grass regeneration. Even for small areas, supplementary seeding of *Scalesia* and other fast growing woody species may be worthwhile to speed the process and to reduce follow-up management efforts. Little is known about seed ecology of native species, thus research would need to be incorporated into a seeding program, whether hand-collecting seed or relying on a donor soil seed bank.

5.3.3.2 A Socio-Economic Perspective

The Need for Restoration

Restoration objectives were developed based on the management goals of the GNP and CDRS. Whenever objectives are developed by one or few groups there is the risk of overlooking the needs and desires of those not directly involved. The interests of the Galapagos community were informally solicited and the GNP and CDRS have a long history as part of this community, therefore, it is believed that there is support for a large-scale restoration project within the GNP on Santa Cruz. Outside of the national park but within the Scalesia forest, private landowners have expressed interest in obtaining Scalesia seedlings in order to reforest their own lands. A significant portion of the ranch lands are not grazed or maintained. The Scalesia forest is one of the dominant vegetation types on Santa Cruz and the most well known. The tree is the symbol of conservation in the Galapagos Islands, through its use by a local educational and conservation group as well as the CDRS. Residents are also proud that so many international visitors come each year to the beautiful islands where they live.

Objection to restoration would come from those whose daily activities would be impacted by such a project, including those who collect fruit, extract timber, hunt or graze cattle within the GNP. The number of individuals would not number more than 50 of the island's total population of 10,000. Fruit collection and grazing occur seasonally, while timber extraction and hunting are year round activities. While fruit collection may supplement a family's income, the price for the most common species passion fruit and naranjia is low and they are widely available in cultivated areas of the island. It is estimated that this would provide not more than 8% of an average family's yearly income. The impacts of fruit collection, besides the soil and vegetation disturbance that occurs along trails and in forest, include peels and cores containing seeds that are randomly discarded by collectors.

Timber extraction and hunting, on the other hand, are lucrative activities and can be beneficial components of park management. The main species being extracted for timber, *Cinchona pubescens* and *Cedrela odorata*, are undesirable and extraction would contribute to the goal of eradication within the park. Sanctioned timber extraction could be maintained under an organized system of removal to reduce frequent trips into the park zone. Approved removal methods would assist in reducing soil disturbance and park staff could follow-up to control regrowth from suckers. Removal would allow GNPS to put resources towards other species, or towards more intensive follow-up control, while allowing residents to earn income. The hunting of feral animals is one of the most destructive of the current land uses, as hunters cover large, remote areas in search of prey and rely on horses and dogs. Few feral animals, however, remain today making the destructive nature of the pursuit outweigh the benefit of removal. It may be appropriate to limit feral animal control to GNPS park guards, or contracted hunters, when required.

The CDRS Education Department develops and presents children's programs on a wide variety of environmental issues relevant to the conservation of the Galapagos Islands. Adult education, however, is limited. Grassroot programs need to target adults particularly those in rural communities that are most likely to enter the park zone. Workshops regularly held in conjunction with the GNPS, CDRS and local officials to elucidate the issues of concern and possible solutions regarding invasive plant species, park access and potential restoration efforts are recommended. In return, these institutions need to provide the community with data on the impact of invasive species, evidence of range expansion and causes, and the ability to provide a consistent approach to infestations and landuse issues as they occur.

For example, in 1999, an agreement to permit grazing was drawn up between a few wealthy landowners and the GNPS; however, grazing was not permitted to all residents. If this were to be a feasible option, grazing rights would need to be extended to all ranchers. This would not be recommended, as cattle grazing resulted in invasive alien species establishing in faeces throughout the forest as well as soil disturbance and vegetation trampling. Cattle accessed large and remote areas. Acceptance of a grazing agreement would also mean acceptance of higher density and richness of alien species, according to the model. Restrictions to park access by domestic animals (i.e. horses, cattle, mules) would require changes in the regular operations of the GNPS as well as residents. Routine inspections by park guards could be made by foot as sites are accessible within a few hours walk. A ground level survey of the park could assist in early detection of new populations of alien species, which could be removed immediately. Horses are required for transport of equipment and resources during special park operations (e.g., construction or extensive management and restoration projects).

The GNPS may face pressure to allow tourism to expand within the park zones on Santa Cruz. Although current levels of land based tourism are low in the Cerro Croker region this could change given the history of political uncertainty in the islands. Large scale land-based tourism would not be economical on the island of Santa Cruz. The average

Galapagos tourist is greater than 50 years of age, with reduced mobility and generally an interest in the fauna rather than the flora of the islands (pers. obs.). The few tourists who choose to visit the highlands are young, and interested in more adventurous activities such as hiking. While large and frequent groups of tourists are not desirable from a conservation standpoint, small-scale targeted ecotourism is beneficial and can be highly lucrative given the current international demand. Restoration of abandoned pastures, particularly the larger ones, would increase the aesthetics and therefore tourism value of the island, as the pastures can clearly be seen from the island's main viewpoint Cerro Croker.

Availability of Resources

Funding for invasive species management and restoration remains the greatest limitation to program implementation and maintenance. Park entry permits could be required for activities other than recreation. Fees, however, would not be feasible in GNP due to small scale of operations, although they have been suggested in other protected areas to mitigate disturbance. Fees could be applicable to large-scale tourism operations, if this were ever to develop, or international research efforts. While some form of permitting and fees does exist for research and tourism, the monies are not directed to invasive species programs including education rather they are absorbed by administration. Continued collaboration and partnerships with outside research, conservation and development organizations should be the short-term focus to initiate a restoration strategy for the Scalesia forest zone on Santa Cruz.

Methods tested were those most readily available in Galapagos. More cost-effective methods may exist and could be tested in the future, but methods that will provide adequate to good results are required immediately. Through a partnership with the manufacturer of Roundup, the GNP is almost guaranteed a supply of herbicide in the future. Many men work casually as labourers on Santa Cruz to supplement wages earned in seasonal work, and are willing to work for the GNP/CDRS. It would be advantageous to hire and train a semi-permanent or seasonal crew for invasive species management. Consistency in the labour force would reduce the time required, increase the quality of work and foster a sense of pride among members in the work completed.

Reduction in Forest Disturbance

Reducing disturbance on the north side of Santa Cruz (north of Cerro Croker and current tourist routes) may provide a chance for Scalesia forest to recover following invasive species management. Humans are a component of the Galapagos ecosystem and therefore cannot be wholly removed, but through education and community outreach the impacts of their actions can be minimized. In the long-term, the abundance of the introduced species that residents depend on will be reduced by management efforts whether by GNP staff or with the assistance of residents. While activities may not cease, knowledge of how to leave a lighter footprint on the land will hopefully remain.

The development of a collaborative education, tourism and conservation program at Media Luna and Cerro Croker may foster an understanding of the need for conservation management among the greater Galapagos community. Although, encouraging access could be seen as a hindrance to conservation initiatives, organized or self-directed access may provide opportunities to increase the success of restoration programs. Santa Cruz residents are proud Galapagenos, though are largely unaware of the uniqueness of the islands from a scientific viewpoint and of the detrimental impact their activities could have on the environment. Educational programs, including signage along the main trails, could emphasize the problem of alien plant species, identify species that are prevalent and clearly indicate those activities that facilitate their establishment and spread. At the same time, the need to maintain and enhance native communities can be addressed.

Once a community understanding is fostered, the potential for volunteer programs to actively assist with the management of invasive plant species grows, reducing maintenance effort and costs. Volunteer work days have been organized by the CDRS with success and are frequented by school groups as well as community members. Although access to remote areas remains an issue of concern, management in more accessible and high profile areas immediately bordering the national park, could assist in reducing propagule sources of a number of alien species and initiate creation of a buffer zone around the GNP.

5.4 Recommendations

The researchers of this study recommend the following actions as part of a restoration framework for the Scalesia forest on the island of Santa Cruz.

1. Identify sites of high conservation value (no aliens) and work outwards from these core areas with restoration efforts. In the absence of areas free from invasion, identify areas with few scattered individuals and/or small patches of a single invasive species.
2. Target areas surrounding high conservation value sites, starting with those immediately adjacent, and in states still containing the full suite and relative abundance of native species, but also some alien species (S3 or S4).
3. If areas adjacent or surrounding core areas are already dominated by alien species (S5 to S7) focus efforts on controlling seed sources, then work on restoration plans. If *Passiflora* spp. or invasive tree species are the main concern, then feasibility will be low; if alien forbs and non-suckering shrubs or trees are present, these sites should be targeted.
4. Work on connecting areas of high conservation value through restoration efforts in intervening areas.
5. Monitor restoration sites at least twice a year (wet and dry seasons) to eliminate new infestations as soon as possible.
6. Re-evaluate site prioritizations each year to identify hazards to successful restoration of core and adjacent areas.
7. Develop and enforce consistent access regulations with residents, tourists, researchers and park staff. Work with communities to address park access issues and develop education and outreach programs.
8. Act now: small satellite populations of alien species are the greatest threat to remnant forest but are easier to control, and have the greatest potential for successful restoration. More effective methods to control elephant grass and restore Scalesia forest may exist, but trials can be conducted simultaneously with active management programs.

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Table 5.1. Estimates of the pre-settlement and current area of the Humid Zone on the four islands where *Scalesia pedunculata* forest is present, Galapagos 1999. The Humid Zone is comprised of *S. pedunculata* forest and a fern/sedge zone on the islands of Santa Cruz and San Cristobal.

Island	Pre-settlement	Current
Santa Cruz	118 km^2	28 km^2
San Cristobal	84 km^2	6 km^2
Floreana	-	not available
Santiago	-	$\leq$ 0.1 km^2

Table 5.2. Access to the highlands of Santa Cruz near Cerro Croker, Galapagos National Park, January to December 1999. Based on personal observations during regular trips to this area.

Landuse	Occurrences (individuals)	Month(s)
Community Activities		
Recreation/Fruit collection*	6 (10)	June to August
Hunting*	10 (33)	July to October
Tourism*	2 (8)	July, November
Timber Extraction*	3 (9)	July to September
Grazing domestic animals	20 (n/a)	January to March
Camping	3 (10)	July and August
CDRS Activities		
Research**	3 (6)	March, July, August
Photographers	2 (3)	March, August
GNPS Activities		
Construction*	15 (2-3)	June and July
Petrel conservation	20 (1)	June and July
Quinine management	30 (20)	November and December
Study Activities		
Research set-up	15 (4)	February and March
Restoration	15 (2)	February and March
Elephant grass management	30 (2)	February to December
Monitoring	40 (2)	February to December

* Horses, and dogs in the case of hunting, often employed.

** Excluding research for this study. See Study Activities.

Table 5.3. Cost ha^{-1} (Cdn.$) of treatments to manage elephant grass and restore native Scalesia forest in abandoned pasture, Santa Cruz, Galapagos, 1999. Effectiveness rank is based on experimental trials to reduce elephant grass canopy cover, basal cover and height and allow native recruitment.

	Labour*	Equipment	Total	Effectiveness Rank**
One-time manual cutting	$555.00	$2.00	$557.00	4
Repeated cutting	$1095.00	$2.00	$1097.00	2
One-time herbicide application	$600.00	$178.40	$778.40	3
Repeated herbicide application	$780.00	$296.00	$1150.40	1
Natural recovery	$90.00	$2.00	$92.00	2
Hand-collected seed	$360.00	$7.00	$367.00	2
Donor soil seedbank	$240.00	$23.75	$263.75	2

* $15.00 per labourer per day

** 1 = good to 4 = poor

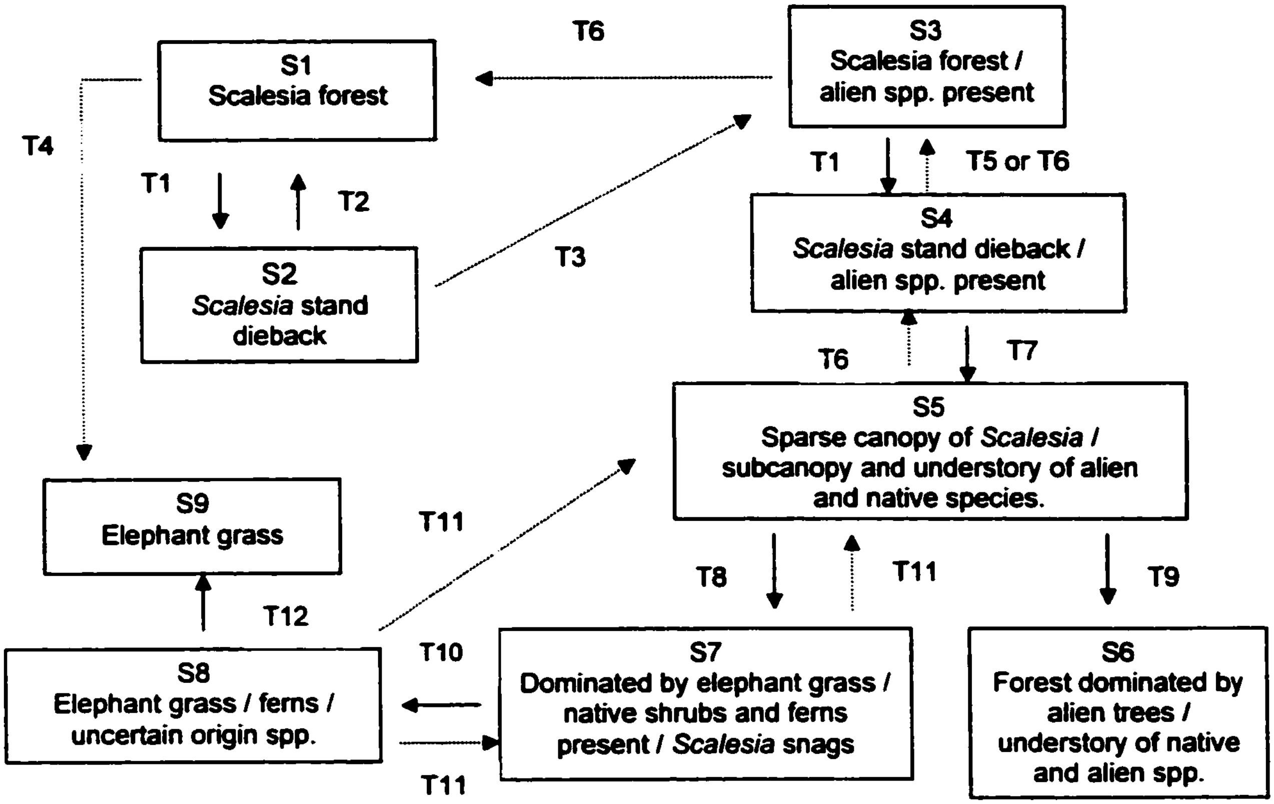

Figure 5.1. State-transition model for the Scalesia forest within Galapagos National Park, Santa Cruz. Lines and arrows indicated transitions between states; dotted lines indicate those that require human intervention. Key to states (S) and transitions (T):

S1 - Forest without presence of alien species.
S2 - Forest following stand dieback.
S3 - Forest with low abundance of alien species other than elephant grass.
S4 - Forest with numerous canopy gaps and low to moderate abundance of alien species including elephant grass.
S5 - Low-density of *Scalesia* and a subcanopy/understory of alien and native species.
S6 - Forest dominated by alien trees.
S7 - Forest invaded by elephant grass; *Scalesia* snags present and some native shrubs and ferns in low abundance.
S8 - Elephant grass dominated, native and alien species present, moderate amount of bare ground.
S9 - Elephant grass community, no other species present.
T1 - El Nino resulting in stand dieback.
T2 - *Scalesia* regeneration.
T3 - Open access to forest by humans and domestic animals and/or presence of alien seed sources.
T4 - Forest clearing for pasture.
T5 - Open access to forest, and management of alien plants and animals.
T6 - Restricted access to forest, management of alien plants and animals, and time.
T7 - No management of alien plants and animals, and open access to forest.
T8 - Moderate to high density of elephant grass in adjacent areas, and stand dieback.
T9 - No elephant grass in adjacent areas, alien tree species present, with/without open access.
T10 - Grazing permitted, no other management of alien plants and animals.
T11 - Cut grass and repeated herbicide application to regrowth plus seeding.
T12 - Prescribed burn, cutting only or no management.

APPENDIX A – STUDY SITE INFORMATION

Table A.1. Soil analysis from the three study sites, Scalesia forest zone, Santa Cruz, Galapagos. Samples were collected, following a heavy rainfall, from each site on January 30^{th}, 2000 and composited. Analyses conducted by Agrobiolab, Quito, Ecuador.

	Site A		Site B		Site C	
	0-10 cm	10-20 cm	0-10 cm	10-20 cm	0-10 cm	10-20 cm
% sand	84	78	84	90	80	78
% clay	10	12	8	4	10	10
% loam	6	10	8	6	10	12
texture	sandy loam	loamy sand	sandy loam	sand	loamy sand	loamy sand
pH	5.8	6.1	6.2	6.3	5.8	5.8
organic matter	31.95	10.22	26.92	16.14	25.80	13.19
% moisture	53	46	58	49	55	55
NH_4 (ppm)	103.0	102.0	144.0	106.0	163.0	122.0
NO_3 (ppm)	12.0	9.0	13.0	10.0	14.0	10.0
P (ppm)	19.0	6.0	21.0	3.0	9.0	5.0
K (Meq)	0.55	0.21	0.79	0.18	0.30	0.21
CEC (Meq)	0.55	0.21	0.79	0.18	0.31	0.21

Table A.2. Common plant species of the Scalesia forest, Santa Cruz, Galapagos.

Species[1,2,3]	Common name[3]	Family
Scalesia pedunculata	tree scalesia	Asteraceae
Psidium galapageium	Galapagos guava	Myrtaceae
Pisonia floribunda	Galapagos pisonia	Nyctaginaceae
Zanthoxylem fagara	cat's claw	Rutaceae
Chiocoacca alba	milkberry	Rubiaceae
Tournefortia rufo-sericea	rough-haired tournefortia	Boraginaceae
Pyschotria rufipes	white wild coffeee	Rubiaceae
Darwiniothamnus tenuifolius	thin-leafed Darwin's shrub	Asteraceae
Darwiniothamnus lancifolius	lance-leafed Darwin's shrub	Asteraceae
Passiflora colinvauxii	Colinvaux's passion fruit	Passifloraceae
Ionopsis utriculariodes	ionopsis	Orchidaceae
Borreria laevis	smooth borreria	Rubiaceae
Justicia galapagana	Galapagos justica	Acanthaceae
Tillandsia insularis	Galapagos tillandsia	Bromeliaceae
Epidendrum spicatum	buttonhole orchid	Orchidaceae
Peperomia galapagensis	Galapagos peperomia	Piperaceae
Phoradendron henslovii	Galapagos mistletoe	Viscaceae
Lycopodium spp.	clubmoss	Lycopodiaceae
Adiantum spp.	maidenhair ferns	Adiantaceae
Polypodium spp.	polypody ferns	Polypodiaceae
Doryopteris spp.	hand ferns	Sinopteridaceae
Asplenium spp.	spleenwort ferns	Aspleniaceae

Sources: [1] Wiggins and Porter 1971 [2] Jackson 1993 [3] McMullen 1999.

Table A.3. Study site characteristics, Scalesia forest zone, Santa Cruz, Galapagos.

	Site A	Site B	Site C
GPS Co-ordinates	S 00°38'02.8", W 090°19'54.4"	S 00°38'08.2", W 090°19'38.4"	S 00°38'07.0", W 090°19'38.7"
Elevation	700 m a.s.l.	750 m a.s.l.	750 m a.s.l.
Cover	100%	100%	100%
Mean height	275 cm	272 cm	224 cm
Site dimensions	6 x 5 array of plots	3 x 10 array of plots	3 X 10 array of plots
Average plot area	101 m^2	107 m^2	94 m^2
Mean distance to forest (N,E,S,W)	77 m, 10 m, 54 m, 19 m	25 m, 125 m, 78 m, 88 m	35 m, 60 m, infinite, 65 m
Aspect	340° NNW	330° NNW	230° NNE
Mean slope	NS +5.5% / EW +1.5%	NS +3.5% / EW +6%	NS +6% / EW +29%
Soil texture	sandy loam / loamy sand	sandy loam / sand	loamy sand

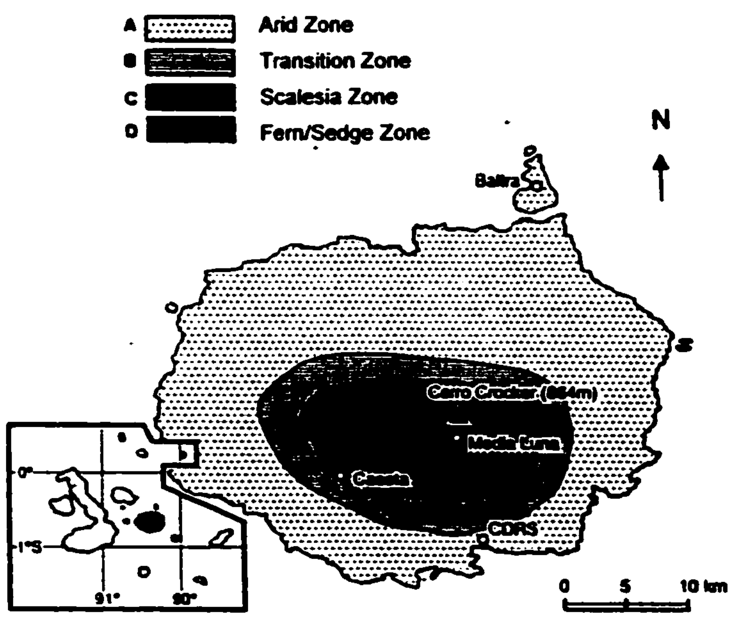

Figure A.1. Vegetation zones on the island of Santa Cruz, Galapagos. The Scalesia Forest and Fern/Sedge zones collectively comprise the Humid Zone. Inset figure of Santa Cruz (in black) within the context of the main Galapagos islands. Adapted from Itow 1992.

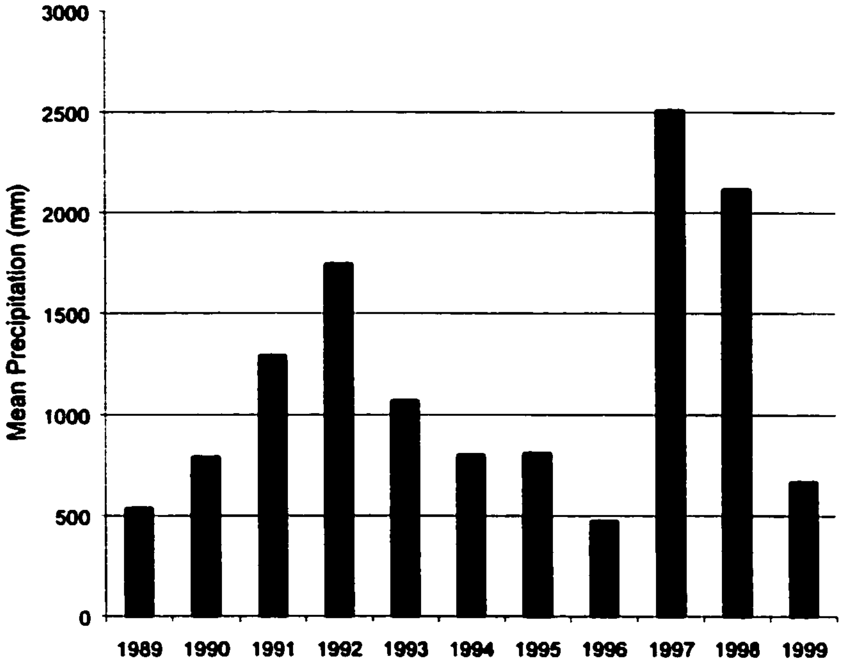

Figure A.2. Mean annual precipitation, Bellavista weather station (194 m a.s.l.), Santa Cruz, Galapagos, 1989-1999.

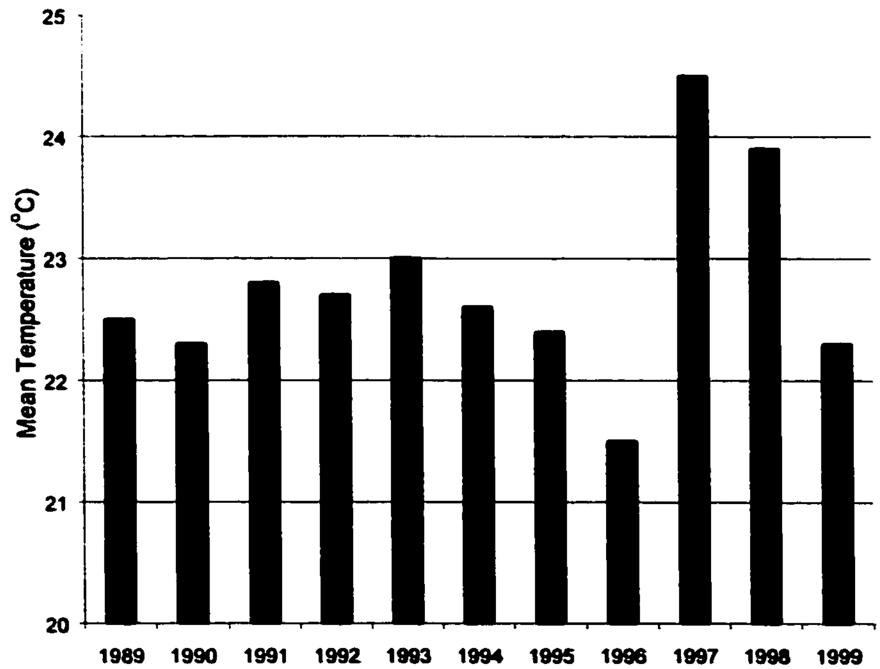

Figure A.3. Mean annual temperature, Bellavista weather station (194 m a.s.l.), Santa Cruz, Galapagos, 1989-1999.

Sources:

Itow, S. 1992. Altitudinal change in plant endemism, species turnover and diversity on Isla Santa Cruz, the Galapagos Islands. Pacific Science 46(2):251-268.

Jackson, M.H. 1993. Galapagos: a natural history. University of Calgary Press. Calgary, Alberta. 315 pp.

McMullen, C.K. 1999. Flowering plants of the Galapagos. Comstock Publishing Associates. London, England. 370 pp.

Wiggins, I. and D.M. Porter. 1971. Flora of the Galapagos Islands. Stanford University Press. Stanford, California.

Table B.1. Schedule and resource requirements for manual management treatments to control elephant grass in the Scalesia forest, Santa Cruz, Galapagos. M treatments were completed at the first cutting date.

Date	Days since last follow-up	Mean labour hours / 100 m^2
March 12th	n/a	2.50
June 9-12th	90	1.00
August 14th-15th	63	0.75
October 8th-9th	54	0.75
November 16-17th	39	0.50
December 7-8th	21	0.50

Table B.2. Schedule and resource requirements to complete herbicide management treatments to control elephant grass in the Scalesia forest, Santa Cruz, Galapagos. H treatments were completed at the first spraying date.

Date	Days since last follow-up	Mean labour hours / 100 m^2	Mean litres of 2% Roundup solution / 100 m^2
March 12th (cut)	n/a	2.50	n/a
March 24th	12	0.25	6.66
June 9-12th (cut)	78	1.00	n/a
June 30th	21	0.25	3.89
August 14-15th	45	0.28	4.00
October 8th	55	0.23	2.92
December 7th	60	0.15	1.00

Table B.3. Monitoring dates and vegetation measurements between March 1999 and March 2000, Scalesia forest, Santa Cruz, Galapagos.

Dates	Canopy Cover	Basal Cover	Height	Recruitment Density
March 22-23rd, 1999	X		X	X
April 27-29th, 1999	X	X	X	X
May 28-29th, 1999	X		X	
June 8-9th, 1999	X	X	X	X
July 1-2nd, 1999	X	X	X	X
July 21-22nd, 1999	X	X	X	X
August 16-17th, 1999	X	X	X	X
September 10-11th, 1999	X	X	X	X
September 29-30th, 1999	X	X	X	X
October 22-23rd, 1999	X	X	X	X
November 11-12th, 1999	X	X	X	X
December 9-10th, 1999	X	X	X	X
January 5-6th, 2000	X		X	
February, 2000				
March, 2000				
March 29-30th, 2000				X

Table B.4. Vegetation cover classes corresponding to assigned canopy cover values.

Assigned Value	Cover Range
1	< 1%
2	1-5%
3	6-25%
4	26-50%
5	51-75%
6	76-95%
7	>95%

Source: Elzinga et al. 1998.

Table B.5. Correlation analysis for elephant grass reproductive variables in the Scalesia forest, Santa Cruz, Galapagos.

Variables	Pearson's Correlation Coefficient
No. of seeds and no. of florets	-0.03
No. of seeds and no. of inflorescences	-0.14
No. of seeds and length of inflorescences	-0.15
No. of florets and no. of inflorescences	0.87*
No. of florets and length of inflorescences	0.35**
No. of inflorescences and length of inflorescences	0.30

* Correlation is significant at the p ≥ 0.01 level.
** Correlation is significant at the p ≥ 0.05 level.

Table B.6. One-way ANOVA tables for elephant grass reproductive attributes at three study sites in the Scalesia forest, Santa Cruz, Galapagos.

Source	Sum of Squares	Degrees of Freedom	Mean Square	F-statistic	P-value
Seed Production					
Between groups	645.85	2	322.93	0.35	0.71
Within groups	27786.27	30	926.21		
Total	28432.13	32			
Floret Production					
Between groups	523592.14	2	261796.07	4.13	0.03
Within groups	2091884.70	33	63390.45		
Total	2615476.84	35			
Inflorescence Production					
Between groups	4.38	2	2.19	3.22	0.05
Within groups	22.44	33	0.68		
Total	26.82	35			
Inflorescence Length					
Between groups	57.36	2	28.68	1.18	0.32
Within groups	800.16	33	24.27		
Total	858.16	35			

Table B.7. Friedman Test for differences in mean rank between management treatments to control elephant grass, Scalesia forest, Santa Cruz, Galapagos. Kendall's coefficient indicates the similarity in ranking between the three study sites, 0 = no similarity 1 = identical.

	Canopy Cover[1]	Height[2]	Recruitment Density[3]	Live Basal Cover[2]	Dead Basal Cover[2]
Chi-square	11.30	12.00	10.37	11.47	7.93
(p-value)	(0.02)	(0.02)	(0.04)	(0.02)	(0.09)
Kendall's Coefficient of Concordance	0.94	1.00	0.86	0.96	0.66

[1] Analysis on data collected 10 months following initial treatment.
[2] Analysis on data collected 9 months following initial treatment.
[3] Analysis on data collected 12 months following initial treatment.

Table B.8. Spearman's correlation coefficients for all measured variables 1, 3, 6 and 9 months following initial treatments to control elephant grass in March 1999, Scalesia forest zone, Santa Cruz, Galapagos.

Variables	1 mo.	3 mo.	6 mo.	9 mo.
Canopy Cover, Height	0.51*	0.42*	0.52*	0.97*
Canopy Cover, Live Basal Cover	0.84*	0.76*	0.74*	0.77*
Canopy Cover, Dead Basal Cover	-0.54*	-0.46*	-0.28	-0.40*
Canopy Cover, Recruitment Density	-0.94	-0.30	-0.41**	-0.62*
Height, Live Basal Cover	0.38**	0.28	0.38**	0.77*
Height, Dead Basal Cover	-0.43*	-0.32*	-0.01	-0.40**
Height, Recruitment Density	-0.61	-0.09	-0.10	-0.60*
Recruitment Density, Live Basal Cover	-0.14	-0.40**	-0.49*	-0.65*
Recruitment Density, Dead Basal Cover	-0.15	0.24	0.30	0.40**
Live Basal Cover, Dead Basal Cover	-0.57*	-0.63*	-0.57**	-0.63*

* Correlation is significant at the $p \geq 0.01$ level.
** Correlation is significant at the $p \geq 0.05$ level.

Sources:

Elzinga, C.L., D.W. Slazer and J.W. Willoughby. 1998. Measuring and monitoring plant populations. U.S. Department of Interior, Bureau of Land Management and Nature Conservancy. BLM Technical Report 1730-1. Denver, Colorado. 477 pp.

APPENDIX C – RESTORATION TREATMENTS

Table C.1. Calculated seeding rates and criteria per 100 m^2 for three species collected in the Scalesia forest adjacent to study sites, Santa Cruz, Galapagos.

Species	Seeding Rate	Expected Density	Estimated Seed Viability	Estimated Seedling Recruitment	Density in Forest	Total Seed Collected	Seed Weight per 100
Scalesia pedunculata	21,440	21 trees	10%	1%	21 trees	>514,560	0.075 g
Tournefortia rufo-sericea	104	n/a	n/a	n/a	12% cover	832	9.000 g
Paspalum conjugatum	1,600	10% cover	50%	75%	10% cover	>38,400	0.090 g

Table C.2. ANOVA table for differences in soil seed bank between management and restoration treatment combinations, Scalesia zone, Santa Cruz, Galapagos.

	Chi-square	Degrees of Freedom	P-value
Total Density	3.68	11	0.98
Total Species Richness	6.26	11	0.86

Table C.3. Friedman Test for differences in mean rank recruitment by plant group between twelve treatment combinations, 4 management treatments to control elephant grass and 3 treatments to enhance restoration of the Scalesia forest, Santa Cruz, Galapagos. Kendall's coefficient indicates the similarity in ranking between the three study sites, 0 = no similarity, 1 = identical.

	Total	Native	Endemic	Uncertain Origin	Alien
Chi-square (p-value)	28.16 (0.01)	29.60 (0.00)	23.36 (0.03)	26.25 (0.01)	23.86 (0.02)
Kendall's Coefficient of Concordance	0.78	0.82	0.65	0.73	0.66

Table C.4. P-values for two-way ANOVAs between three restoration treatments, natural recovery, use of hand-collected seed and use of a donor soil seed bank, one year following four treatments to control elephant grass in the Scalesia forest, Santa Cruz, Galapagos.

	Density					Species Richness				
Control Method	Native	Endemic	Uncertain	Alien	Total	Native	Endemic	Uncertain	Alien	Total
Manual	0.11	0.11	0.39	0.39	0.24	0.39	0.11	0.29	0.39	0.44
Repeated Cutting	0.05*	0.49	0.05*	0.34	0.06**	0.09**	0.49	0.20	0.39	0.12
Herbicide	0.39	0.13	0.24	0.61	0.24	0.30	0.06**	0.19	0.19	0.14
Repeated Herbicide Application	0.06**	0.05*	0.12	0.13	0.04*	0.12	0.06**	0.09**	0.05*	0.12

* Significant at the p $\geq$0.05 level when compared to control treatment
** Significant at the p $\geq$ 0.10 level when compared to control treatment

Table C.5. Correlation analysis among germinable seed density in soil seed bank and aboveground recruitment by plant group, Scalesia forest, Santa Cruz, Galapagos.

	Density		Species Richness	
	Pearson's Coefficient	P-value	Pearson's Coefficient	P-value
Native	-0.12	0.47	-0.06	0.72
Endemic	0.12	0.46	0.15	0.37
Uncertain Origin	-0.05	0.77	0.22	0.19
Alien	-0.10	0.54	-0.16	0.34
Total	-0.18	0.28	0.10	0.53

Table C.6. Germination rates of species native to the Scalesia forest and seeded in the study, Santa Cruz, Galapagos. In controls, seed was placed directly in petri dish lined with moist paper towel.

Species	Date Collected	Date Treated	Treatment[1]	Sample Size	No. Germinated	% of Sample Germinated
Scalesia	18-Jan	22-Jan	H	226	33	15
Scalesia	18-Jan	22-Jan	RT	226	34	15
Scalesia	26-Jan	3-Feb	H	418	20	5
Scalesia	26-Jan	3-Feb	RT	418	10	2
Scalesia	08-Feb	12-Feb	H	89	34	38
Scalesia	08-Feb	12-Feb	RT	89	29	33
Scalesia	08-Feb	16-Feb	H	193	6	3
Scalesia	08-Feb	16-Feb	RT	193	4	1
Scalesia	23-Mar	1-Apr	H	100	25	25
Scalesia	23-Mar	1-Apr	RT	100	27	27
Scalesia	23-Mar	1-Apr	B	50	5	10
Scalesia	23-Mar	1-Apr	B	50	4	8
Scalesia	23-Mar	1-Jul	RT	200	83	42
Scalesia	23-Mar	1-Jul	H	200	12	12
Scalesia	14-Mar	1-Jul	RT	198	94	48
Scalesia	14-Mar	1-Jul	H	200	20	10
Scalesia	14-Mar	1-Jul	C	197	97	39
Scalesia	23-Mar	1-Jul	B	100	10	20
Scalesia	23-Mar	1-Jul	B	100	28	56
Tournefortia	21-Feb	1-Mar	RT	50	0	0
Tournefortia	21-Feb	1-Mar	H	50	0	0
Tournefortia	21-Feb	1-Mar	C	50	0	0
Paspalum	12-Feb	17-Feb	C	27	2	7
Paspalum	12-Feb	17-Feb	C	30	17	57
Paspalum	12-Feb	17-Feb	C	30	26	87

[1] RT = room temperature, H = hot, C= control, B= burial

Table. C.7. ANOVA table for difference in density of woody species between restoration treatments, Scalesia zone, Santa Cruz, Galapagos. Seeded species *Scalesia* and *Tournefortia* were excluded from analysis.

Source	Sum of Squares	Degrees of Freedom	Mean Sum of Squares	F statistic	P-value
Between	2.66	3	0.89	0.249	0.861
Within	124.65	35	3.56		
Total	127.31	38			

Table C.8. ANOVA table for difference in elephant grass canopy cover between restoration treatments, Scalesia zone, Santa Cruz, Galapagos.

Source	Sum of Squares	Degrees of Freedom	Mean Sum of Squares	F statistic	P-value
Between	5500.342	3	1833.447	1.315	0.285
Within	48808.682	35	1394.534		
Total	54309.025	38			

Table C.9. Scalesia forest plant species and mean abundances m^{-2} in reference plots during the 1999 wet season, Santa Cruz, Galapagos.

Species	Mean Cover*	Habit	Origin
Cordia leucophlyctis	9	subcanopy tree	E
Croton scouleri	1	subcanopy tree	E
Jaegaria gracilis	T	forb	E
Passiflora colinvauxii	9	vine	E
Pilea baurii	T	forb	E
Psidium galapageium	3	tree	E
Psychotria rufipes	21	shrub	E
Scalesia pedunculata	85	tree	E
Tournefortia rufosericea	15	shrub	E
Adiantum macrophyllum	1	fern	N
Alternanthera halmifolia	T	forb	N
Asplenium spp.	4	fern	N
Asplenium auritum	T	fern	N
Asplenium cristatum	T	fern	N
Blechum browneii	8	forb	N
Blechnum occidentale var. *puberulum*	11	fern	N
Chiococca alba	14	subcanopy tree	N
Commelina diffusa	3	forb	N
Ctenitis pleiosoros	6	fern	N
Doryopteris pedata var. *palmata*	2	fern	N
Galium galapagense	1	forb	N
Ipomoea triloba	2	vine	N
Polypodium lanceolatum	T	fern	N
Polypodium phyllitidis	T	fern	N
Pteridium aquilinum	4	fern	N
Thelypteris spp.	T	fern	N
Zanthoxylem fagara	10	subcanopy tree	N
Ageratum conyzoides	5	forb	U
Borreria laevis	16	forb	U
Hyptis rhomboidea	1	forb	U
Ichnanthus nemorosus	22	grass	U
Paspalum conjugatum	28	grass	U
Salvia occidentalis	1	forb	U
Sida rhombifolia	3	shrub	U
Cedrela odorata	1	tree	A
Cestrum auriculatum	1	tree	A
Passiflora edulis	4	vine	A
Passiflora quadrangularis	4	vine	A
Psidium guajava	T	tree	A

* T indicates a cover less than 1%.