THE INVASION ECOLOGY OF *LEUCAENA LEUCOCEPHALA* ON MO`OREA, FRENCH POLYNESIA.

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Abstract. *Leucaena leucocephala* is considered one of the most controversial plants used in agroforestry. Its nitrogen fixing trait, along with other traits, that have labeled it one of the most aggressive invaders in the South Pacific. On Mo`orea, French Polynesia, it is found in large stands and considered a major pest by locals. The aim of this study was to investigated *L. leucocephala* influence on the local environment Mo`orea of and its dispersal potential. The first part of the study consisted of mapping out the current distribution of *L. leucocephala.* The second part consisted of surveying seven sites comparing abiotic conditions, *L. leucocephala* seedlings densities, and plant community structure. The third part was a germination experiment to test the effects of increasing nitrogen levels on the growth and germination of *L. leucocephala* seeds. The distribution of *L. leucocephala* is currently on the northern and eastern coastal regions. Results determined that *L. leucocephala* is negatively influencing the growth of vegetation within its stand. Additionally there is an increase in canopy cover and available nitrogen within the stand. Seedlings were more abundant inside the stand, however, seedlings of taller heights were found outside the stand suggesting possible intraspecific completion within the stand. Supplementary studies should go towards understanding the site requirements for *L. leucocephala* establishment and growth. Further investigation will aid in addressing which areas of Mo`orea may need to be targeted for management.

Key words: Leucaena leucocephala; *agroforestry; nitrogen fixation; plant community structure; French Polynesia; dispersal*

INTRODUCTION

In the past century, science has advanced our understanding of environmental change on a global scale and the corresponding impacts from human activities. Recent studies are shedding light on how human travel and the introduction of exotic species are a major component of global change (Kueffer 1010 and Richardson 2004). In particular, invasive woody plants can completely alter ecosystem dynamics by changing structural diversity, over-story dominance, and light availability (Richardson 1998). Additionally, such changes can make ecosystems more hospitable for other invasive species to establish (Denslow 2004).

Two main reasons for the introduction of exotic tree species are for forestry and agroforestry practices (Richardson 1998). In forestry, woody plants are introduced for timber production, fuel wood, or reforestation. Agroforestry introduces plants that can be used for agricultural purposes, such as shading for crops, or for land restoration, such as erosion control or soil replenishment (Brewbaker 1987, Meyer et al. 2000, and Shelton 2007). Trees are selected based on their ability to grow on marginal landscapes, high seed production, rapid growth rates, low management, and multiple uses of their products (Richardson 1998 and Shelton 2007).

Although agroforestry has been practiced on tropical islands for years, few studies have been conducted on the invasion biology of agroforestry trees and what effect they have on tropical forests (Richardson 2004). Until recently, a dominating theory has been that tropical systems are able to resist invasions due to their high diversity and complete fulfillment of ecological niches (Elton 1958 as mention in Denslow 2003). However, Richardson (2004) mentions that most trees introduced for agroforestry are chosen to withstand harsh environments and have high seed production, and therefore are more likely to out-compete native species. Additionally, a study by Fine (2002), noted that overall, undisturbed tropical forests have had fewer exotic species in comparison to other forest types, but it may not be due to their diversity. Fine illustrates that species invasion depend on many factors such as life history characteristics, human influence and ecosystem conditions. From this, both studies emphasize the importance of investigating agroforestry species prior to being introduced.

Invasive species are particularly damaging to certain ecosystems. Many past studies have shown how island systems are some of the most susceptible and heavily impacted by invasions. Some prevailing theories are that island contain less complex ecosystem which leave them unstable and vulnerable to invasions (Elton 1958 as mentions in Simberloff 1995). Others have hypothesized that island species are unable to compete with mainland introductions that have been exposed to more rigorous pressures (Yoon 1992 as mentions in Simberloff 1995). However, many recent studies are now proposing that island susceptibility depends on a combination of factors. Denslow (2003) argues that it is a combination of plant community interactions and resources utilization that determines the invasibility of an island. Kueffer (2009) suggest that the number of invasives on an island is best predicted by a model including human development, island age, oceanic region and habitat diversity. Although a consensus has not been reached, isolated islands which tend to have endemic species and specialized ecosystems are some of the most valuable hotspots in biodiversity (Meyer et al. 2000). In order to conserve our current natural ecosystems, it is important to understand the life characteristics of invasive species, what processes facilitate their invasion, and what part man takes to assist establishment of these invaders (Fine 2002).

As an example, *Leucaena leucocephala* is considered one of the most controversial plants used in agroforestry that has been introduced to countless island and mainland ecosystems. Its wood products have multiple uses, serving as fodder, fire wood and building timber (Brewbaker 1987 and Shelton 2007). It is a legume, mostly planted for producing natural manure and restoring nutrient levels in soils by nitrogen fixation using rhizobia in their roots (Budelman 1988). However, it is this nitrogen fixing trait, along with other traits, that have labeled it one of the most aggressive invaders in the South Pacific (Meyer 2000, Richardson 2004). *L. leucocephala* was introduced to French Polynesia in 1845 for forage purposes (Meyer et al 2008). Now, on the small island of Mo`orea it is found in large stands and considered a major pest by locals. Due to its small size, isolation and its population's extensive use of land resources, Mo`orea is an ideal site to study the effects of introducing an agroforestry species to an island ecosystem with heavy human influence.

In this study I investigated *L. leucocephala* ecology and dispersal potential. The first part of this study consisted of mapping out the distribution of *L. leucocephala*. Secondly, *L. leucocephala* stands were surveyed to assess abiotic conditions, plant community structure and seedling dispersal. Soil samples were analyzed to assess *L. leucocephala*'s chemical influence on local soils. Finally, a germination experiment was carried out to understand the effect of different nitrogen levels on the germination and growth rates of *L. leucocephala*'s seeds.

METHODS

Study species

Leucaena leucocephala is an early European introduction for the purpose of foraging. This tree grows rapidly and in thick stands blocking sunlight from the understory. It has a high seed production that can establish within the stand (Kuo 2003 and personal observation). The tree flowers and fruits year round, is self-fertilizing and has an early maturity age (once it reaches around 30 cm), allowing its population to increase rapidly even from a small stand (Richardson 2004 and Shelton 2007). Additionally, it can establish a large seed bank due to its long dormancy period (up to 20 years), maintained by its hard seen coat. Finally this tree thrives in disturbed areas, especially those that have been disturbed by fire. This is because saplings can resprout from established shoots or seeds which are heat activated, showing high rates of germination shortly after (Kuo 2003 and Whitesell). In this study a seedling is defined as any *L. leucocephala* plant that is under 30 cm. Any plant above that height will be considered an adult tree.

Study sites

Most *L. leucocephala* stands are found on low areas of hill sides, many of which are on properties of locals. Therefore, seven study sites were chosen for sampling based on availability of transportation and scheduling, and the cooperation of local residents (See Fig. 1)

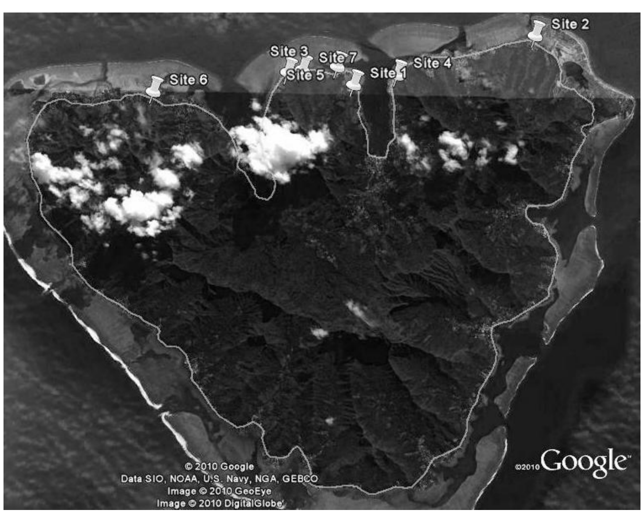

Fig. 1. Location of seven study sites. Image from Google Earth Pro.

Distributional analysis

Using Google Earth Pro., the distribution of *L. leucocephala* was mapped out using polygons to outline stands. For this study, a stand was defined as at least five adult trees, that are no more than three feet apart and whose canopies over lap. On the Google Earth image of Mo'orea, *L. leucocephala* coloration is a dark grey-brown with a feathery texture and flat structure, different from the green coloration and round structure of other plants which allowed most stands to be identified. Exploration of the mapped out sites and visual observations helped verify polygons and identify stands that may not be seen on Google Earth due to clouds or shadows on the image.

Site survey

L. leucocephala seedlings, plant community structure and abiotic condition of sites were measured and compared with data collected from within the stand, the edge of the stand and its surrounding environment, from now refered to as inside, edge and outside areas (see Figure 2). Three quadrats were haphazardly placed within the stand. Two adjacent quadrats were used to compare edge effect by placing one quadrat within the canopy and the other just outside the canopy. Two transects were ran from the edge of the stands, both 1m x 10m, with quadrats being placed at 3m, 6m, and 10m. To avoid bias, one transect was ran North/South and the other East/West. Variables measured included percent bare soil, rock cover, canopy cover, litter and woody debris, non- *L. leucocephala* vegetation, and the number of *L. leucocephala* seedlings present and their heights. Percent bare soil was defined as any soil visible and accessed by sunlight. Canopy cover was measured using a photo camera with the same settings.

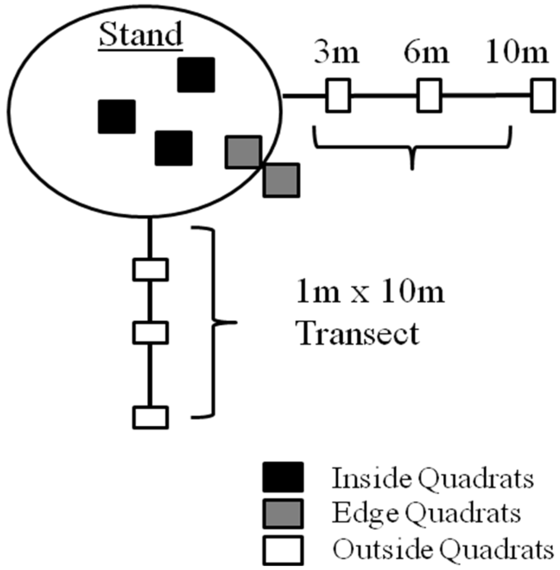

Fig. 2. Locations of the two 1mx10m transects and 1mx1m quadrats placed inside, at the edge and outside a figurative *L. leucocephala* stand.

Soil sampling

For each stand, a representative soil sample was taken within its boundaries, just outside the canopy, and at least five meters from the edge of the canopy serving as the control. Samples were taken 1cm-30cm below the surface from the A horizon where most available nitrogen settles (Kirch, pers. comm). In the lab, soil samples were sieved and mixed with a 1M solution of potassium chloride for 1 hour to extract the nitrogen. Soil extracts were tested using the LaMotte Nitrate Nitrogen Test Kit.

Germination experiment

To test the effects of nitrogen availability on seed germination, seeds were grown in petri dishes watered with three different nitrogen solutions: 0ppm, 3ppm and 10ppm. Each treatment had 5 replicates with twenty seeds placed in each petri dish. Petri dishes were watered twice a day with 5ml of the nitrogen solutions. Seeds were collected from three different stands and checked for viability. To activate, seeds were immersing in hot water (80 ºC) for 3-4 minutes (Whitesell). After, seeds were left soaking in water at room temperature for 12 hours. Petri dishes were kept in trays in the laboratory receiving partial lighting. Seeds were checked every two days to see if any germination occurred. For this experiment, germination is defined as the seeds coat breaking and shoot emerging. Once germinated, seedling was removed. The experiment was conducted in a two week period.

Statistical analysis

Data was analyzed using JMP statistical software, version 7. Plant community structure, abiotic conditions, *L. leucocephala* seedlings, and nitrogen levels were analyzed using the Kruskal-Wallis and Tukey-Kramer test to compared differences within the stand, at the edge and outside the stand Additionally, nitrogen levels and variables describing the abiotic conditions were compared with *L. leucocephala* seedlings, their heights, and the amount of total non- *L. leucocephala* vegetation to test for any correlations using Spearman's Rank. Kruskal-Wallis test was also used to asses is there were any differences in the rate of germination and growth of seedlings between the three treatments.

RESULTS

Distribution

The current distribution of *L. Leucocephala* is illustrated in Figure 3, About 70% of the island was able to be surveyed. Most stands were found along Northern and Eastern coastal regions. *L. Leucocephala* was observed to be on the lower regions of hill sides, behind homes or right along the main road. It was rarely seen on the Western regions which typically were covered in dense vegetation; however, they were still observed along the main road and sometimes on properties on the ocean side of the road. *L. Leucocephala* was also rarely seen when heading toward the interior of the island, even at low elevations.

Fig. 3. Distribution of *Leucaena Leucocephala*. Stands are represented by white polygons.

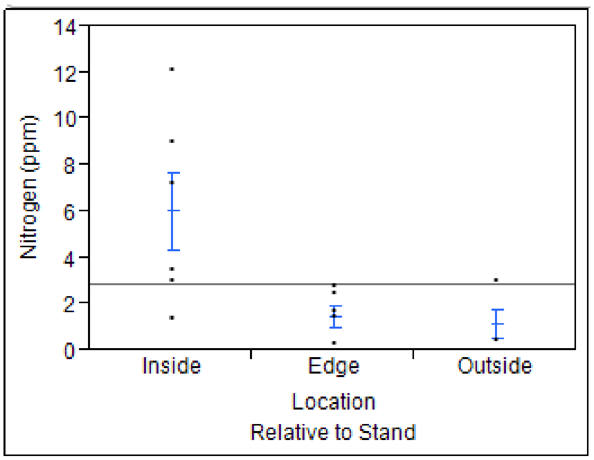

Fig. 4. Nitrogen measurements for soil samples taken inside, at the edge, and outside the stand from six different sites. Nitrogen levels are significantly high inside the stand. Kruskal-Wallis test, $\chi^2 = 7.47$, df=2, p= .024

Site survey

1) Soil Samples

Average nitrogen levels for soil within the stand, at the edge of the canopy and outside the stand from six sites are depicted in Figure 4. There was significantly more nitrogen inside the stand then at the edge or outside the stand. Tukey-Kramer test showed that nitrogen within the stand and outside the stand significantly differed from one another, with inside and outside soils containing an average of 6 ppm and 1.2ppm available nitrogen, respectively, almost a three fold difference.

2) Plant community structure and abiotic conditions

Plant community structure varied across the seven sites, however, using the Kruskal – Wallis test to compare total vegetation between inside, edge and outside the stands showed significant results (Figure 5a). Tukey-Kramer analysis showed that only the vegetation within the stand was significantly less. In addition, canopy cover was significantly higher inside the stand then at the edge and outside the stand (Figure 5b). All other abiotic factors did not show any significant difference between inside, edge and outside the stand.

The decrease in vegetation did not show any strong correlation to any abiotic factor. There were slight but significant negative correlations between the amount of vegetation and canopy cover (Spearman's rank r= -.5, p < .0001). Additionally there were slight but significant negative correlations when comparing total vegetation with a. total litter and b. bare soil (Spearman's rank a. r= -.54, p<.0001 and b. r= -.51, p < .0001).

Seedling dispersal

Number of seedlings and their heights varied between sites as well. Locations of seedlings (inside, edge or outside of stand) was also heavily dependent on site, however, when comparing seedling densities there was significantly more seedlings found inside the stand (Figure 6a).

Comparing seedling size, however, seedling of taller heights were found more outside the stand then inside (Figure 6b). Figure 7 shows the decrease in the number of tall seedlings inside the stand while outside the stand has relatively equal amounts of seedlings of all sizes. Although there are not as many seedlings at the

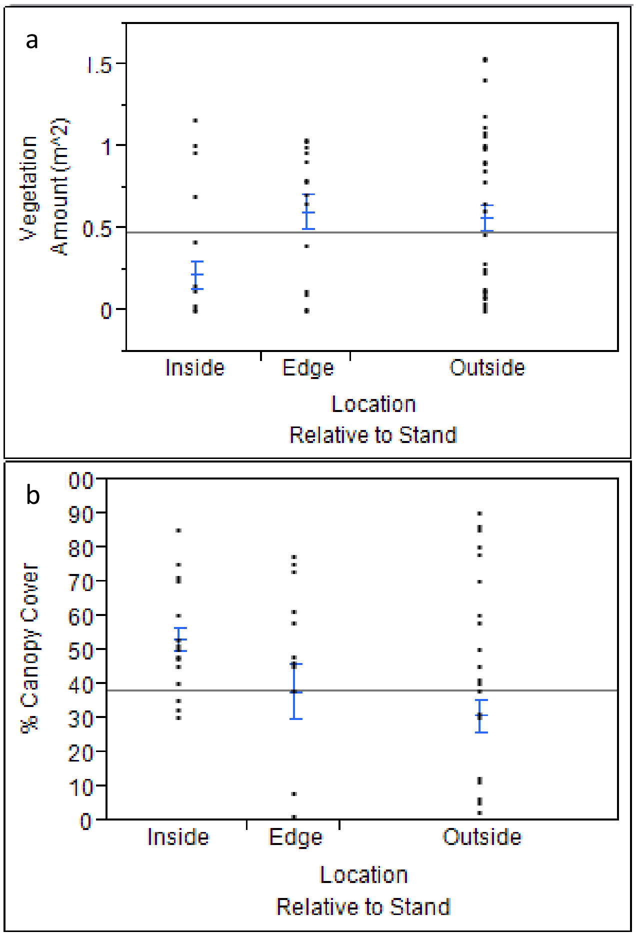

Fig. 5. a)Total non-*L. leucocephala* vegetation (m^2) and b) Canopy cover (%) measured within the stand, at the edge, and outside the stand. Kruskal-Wallis test, a) $\chi^2 = 12.28$, df = 2, p= .0022. b) χ^2=7.72, df = 2, p= .021

edge, it shows a trend similar to the seedlings inside the stand where seedling heights decrease.

When comparing seedling density and their heights to any abiotic factor (such as canopy cover and bare soil) and total vegetation, there seems to be very little correlation. There was a slight but significant correlation between the number of seedlings and the amount of available nitrogen (Spearman's rank, r=.51, p < .0001).

Germination experiment

The germination study gave insignificant results, with increasing nitrogen levels showing

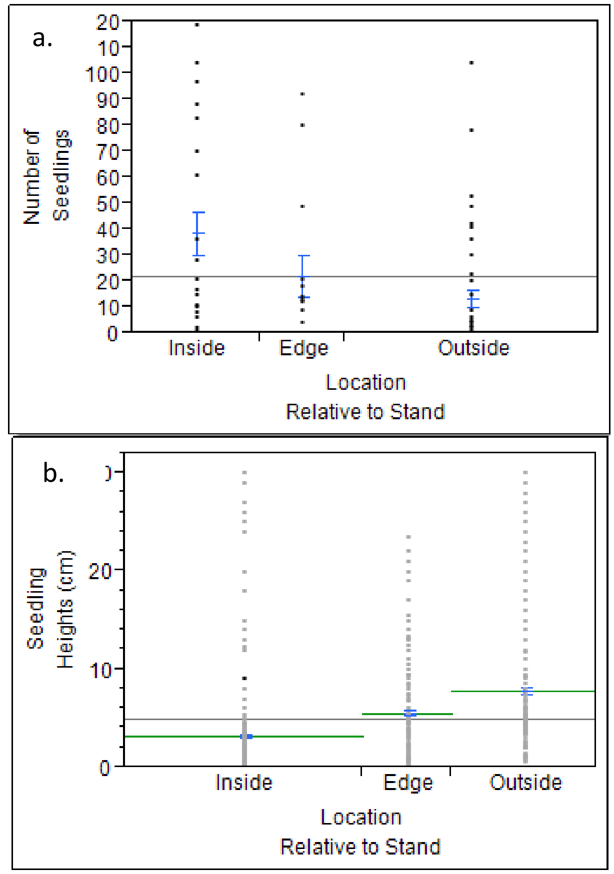

Fig. 6. a) Number of seedlings inside, at the edge, outside the stand. Significantly more seedlings were found inside the stand. b) Seedling heights inside, at the edge and outside the stand. Seedlings outside the stand have a taller average height. Kruskal-Wallis test, a) χ^2 = 13.56, df=2, p= .001. b) χ^2= 357.71, df= 2, p=<.0001

little or no effect on a. the growth or b. the germination rate of *L. leucocephala* seeds (Kruskal-Wallis test, a. χ^2 = 1.05, df=2, p=.59; b. χ^2 = .61, df=2, p=.73)

.DISCUSSION

Distribution

The distribution of *L. leucocephala* seems to be restricted to the outer periphery of the island, in particular the northern and eastern side (Figure 3). Additionally it is frequently found near developed areas like homes and road sides, and rarely found in intact and dense forests. Possible reasons for this type of distribution may have to with different wind, moisture and rain fall patterns along the island. In particular, *L. leucocephala* was usually found in drier areas (personal observation), which in turn could cause a decrease in the density of other vegetation allowing *L. leucocephala* to proliferate once established (Denslow 2003). Furthermore, *L. leucocephala* trees found in gardens and hillsides near homes could be explained by the frequent small fires on locals properties which could possibly activate dormant seeds in the soils. Also, *L. leucocephala* presence on the main road could be due to the fact that it is the most frequently travelled and disturbed road on the island compared to interior roads that are less developed (personal observation). It would be interesting to compare *L. leucocephala* current distribution with past record of fire occurrences and large development projects on Mo`orea. Assessing the types of environments *L. leucocephala* is currently located my help determine which areas may be susceptible to *L. leucocephala* invasion in the future.

Effects on plant community structure and ecological conditions

The results demonstrate that *L. leucocephala* can alter its environment, both chemically and physically (Figure 5 & 6). Chemically, *L. leucocephala* alters the chemical composition of soils by significantly increasing the amount of available nitrogen within its stand. These results correspond with other studies that have shown that litter debris from *L. leucocephala* can release up to 81% its total nitrogen content (Budelmen 1988 and Sandhu et al. 1990). The same studies have shown that nitrogen can be released from its roots and other structural parts. This could largely explain *L. leucocephala* ability to grow on marginal land. Denslow 2003, suggest that islands are more susceptible to invasions when an area has a “high net availability of resources” due to the native flora’s poor ability to utilize these resources. In addition to *L. leucocephala’s* ability to increase its resources in any location, it

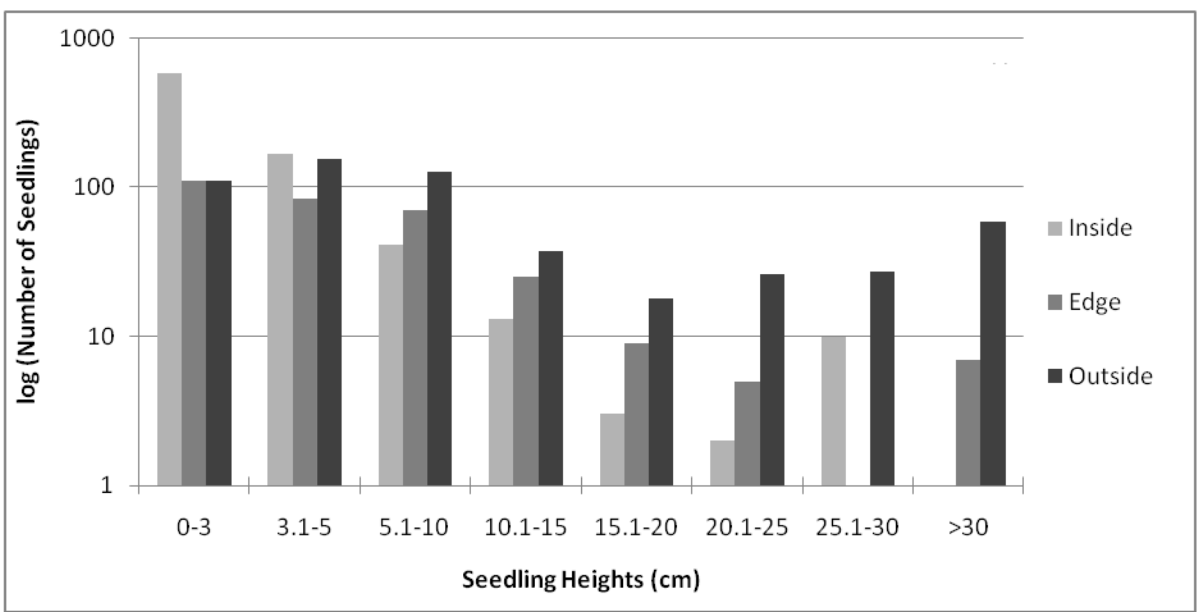

Fig. 7. Number of seedlings of a particular height in each location (inside, edge, outside). Outside the stand seedlings of all sizes are present in relatively equal amounts. Inside the stand there is a dramitic decrease in seedlings of taller heights.

can also settle in areas that have very little vegetation, and hence competition, due to inadequate resources in the area.

The increase in nitrogen levels suggests that *L. leucocephala* can restore soil fertility on Mo`orea, yet, its impacts physically suggest otherwise. Ideally, primary production of vegetation should increase due to the increase in a limiting resource (Parrotta 1999 and Richards 2010). Additionally, locals have been observed using soil from *L. leucocephala* stands as fertilizer for their home gardens and gaining positive results (Ron Falconer, personal interview). However, the dramatic decrease in vegetation and increase in bare soil inside the stand suggest that *L. leucocephala* is somehow hindering the growth of other species. A study by Chou and Kuo (1986) demonstrated that *L. leucocephala* is able to release allelopathic chemicals like mimosine which stunts growth or kills vegetation. Although *L. leucocephala* does alter sun light availability, Chou and Kuo's study also demonstrates that light availability does not have as much influence over vegetation growth compared to the allelopathic effects. Traits such as these could suggest that *L. leucocephala* may not only be invasive but as well as aggressive and harmful to the plant community on Mo`orea.

Dispersal

The dispersal of *L. leucocephala* may be highly influence by its surrounding environment and certain abiotic factors. In particular, canopy cover may influence where *L. leucocephala* can establish. The fact that less *L. leucocephala* seedlings of taller height were found inside stands suggests that some intra-specific competition for resources may be occurring (Figure 7). A likely candidate would be canopy cover since it significantly decreases inside the stand. Additionally, *L. leucocephala* is well established on locations on the island that are less heavily vegetated and that are frequently cleared and disturbed (see above).

These results correspond with a study done by Hata, 2010, that determined that seedlings can not establish in vegetation of taller heights, that seedling taller then 1.3m were positively correlated with distance from parent stand, and that *L. leucocephala* trees found outside the parent stand did not show a relationship with height of the vegetation. From this, Hata suggest that seedlings can not establish within intact canopy because of competition with the established vegetation. (Green et al. 2004 as stated in Hata 2010). Additionally, grown trees are not affected by vegetation height since they are able to access adequate light. This supports the observation that *L. leucocephala* grows well in disturbed and cleared areas. With Mo`orea's increasing population, future protocol and management for *L. leucocephala* should include the close supervision of cleared sites.

Germination Experiment

The germination rate of *L. leucocephala* was not influence by increasing amounts of nitrogen (Figure 4). However, to verify this, future experiments should test with treatments of higher concentrations and compare with naturally occurring nitrogen levels in *L. leucocephala* stands. For now, the data displays that *L. leucocephala* seeds can establish in areas where it has never been established before. In addition, resources may not need to be present for roots development and seed germination.

In order to gain further insight into the requirements for *L. leucocephala* germination, future research should look into sunlight availability and soil temperatures inside and outside the *L. leucocephala* stands. Given that seeds need to be heat activates, it would be interesting to see if soils reach high enough temperatures to active seeds or if they are activated by other means. Additionally, sunlight exposure may be a possible mechanism as to how *L. leucocephala* seedlings reach higher heights outside the parent stand. Future research could compare seedling survival rates inside and outside *L. leucocephala* stands and their corresponding light availability. Further insight into *L. leucocephala* establishment could offer possible protocols for preventing *L.*

leucocephala establishment into areas not of interest.

Implications

L. leucocephala was introduced to French Polynesia for forage purposes over a century ago, and since then it has been labeled as one the 100 most invasive species (Meyer et al 2000). From this study it has already been seen that *L. leucocephala* can negatively impact some of Mo`orea's flora and that it tends to grow near developed sights where there is less established vegetation. In junction with this, Mo'orea's population has had a long history of land manipulation for their establishment, making Mo'orea a dynamic changing landscape in a temporal sense (Theron, Jean Luc and Maryse Noguier, personal interview). Although they have moved to commercial farming, plantations rarely last for more then a few years, moving to new locations after the soil has been depleted of nutrients (Theron, Jean Luc and Maryse Noguier, personal interview). In addition, locals rely mostly on their home gardens for subsistence and constantly disturb their properties by clearing or with small fires (personal observation). Given the characteristics of *L. leucocephala* and the dynamics of the island, Mo`orea's growing population and development may give *L. leucocephala* ideal conditions to spread towards the interior of the island. If *L. leucocephala* is able to spread into higher elevations where more native species are found, it could be a potential threaten Mo`orea's biodiversity and unique ecosystem.

Recent studies have shown that human-introduced species and land manipulation are not recent phenomena, but has been prevalent in past civilization settlements and almost certainly in the far future. Like *L. leucocephala,* species characteristics may make them appealing candidates to be use in agroforestry and other practices. However, known and unknown invasive properties could far out-weigh there benefits if not managed properly. Human facilitated or natural introductions are producing novel interactions and process ubiquitously. Introducing species well equipped to survive and invade into a range of environments could threaten the most valuable hotspots of biodiversity. In addition to studying the introduced species, emphasis should also be placed on understanding the local environment and its ecology. Further knowledge about organisms and ecological processes are just steps towards anticipating future impacts and environmental change.

CONCLUSION

Further study needs to be implemented to shed more light on *L. leucocephala* spread potential and ecology. At the moment only coastal areas seems to be impacted by *L. leucocephala* (Fig. 3). However, it has been observed in higher elevations but only in areas that are frequently cleared and visited. If it spreads it could threaten native species and impact the regeneration of any cleared forest on Mo`orea. *L. leucocephala* was shown to increase canopy cover and nitrogen content in soils where it has established. Furthermore, it negatively impacts the growth of vegetation under its canopy, most likely due to its allelopathic properties.

This study was unable to confidently identify any major factor that facilitates *L. leucocephala* germination and dispersal. However, light availability may be a main contributor to its germination and success outside the parent stand. Additionally, *L. leucocephala* may have some beneficial aspects. Future research could look into the duration of nitrogen and allelopathic chemicals in soils from *L. leucocephala* stands to see its possible uses as a green manure. Additionally, further study should go towards understanding the site requirements for *L. leucocephala* establishment and growth. Further investigation will aid in addressing which areas of Mo`orea may need to be targeted for management.

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