

# FIRE EFFECTS ON VEGETATION IN TROPICAL FOREST ECOSYSTEMS ON MOOREA ISLAND, FRENCH POLYNESIA

CARLEA A. WINKLER

*Environmental Science Policy and Management, University of California, Berkeley, California 94720 USA*

*Abstract.* Fire frequency is expected to increase in the tropics over the next few decades as the climate changes and human land use grows. Despite the potential of fire to drastically modify tropical forests, tropical fire ecology has received relatively little attention, especially on islands. In order to learn more about the ecological effects of fire on tropical islands, a paired comparison of three burn sites and adjacent control sites was conducted on the island of Moorea, French Polynesia. In particular, plant community composition, species richness, and the abundance of introduced species were compared between burned and unburned control sites. Results showed significant differences in the plant communities between burn and control sites even at the 22-year-old burn, suggesting that vegetation recovery is a very slow process on Moorea. Species richness was found to be significantly lower at all burn sites, indicating that reduced species richness is also a long-lasting effect of fire. Furthermore, the abundance of modern introduced species was shown to be greater at the youngest burn site compared to its control site, while no significant difference was found at the two older sites. This could suggest that any increase in introduced species after a fire is only temporary. While this study yielded interesting conclusions about fire on Moorea, further research is greatly needed because fire effects are complex and can vary widely depending on different biotic and abiotic factors.

*Key words:* tropical fire ecology; succession; *Dicranopteris linearis*; plant communities; introduced species; Moorea, French Polynesia

## INTRODUCTION

Fire is a natural disturbance in the tropics, yet prior to human settlement it occurred at a very low frequency (Cochrane 2003). In recent times the frequency of fire in tropical forests has increased at a destructive rate due to growing human land use and large-scale slash-and-burn agriculture (Cochrane 2003). This change in the incidence of fire has subjected many tropical ecosystems to fire regimes that they are not evolutionarily adapted to endure, resulting in modified landscapes and altered species compositions (Barlow and Peres 2008).

In order to analyze the effects of fire on vegetation, we must try to understand how succession plays out in different plant communities. Succession is a sequence of changes in an ecosystem following a disturbance (Clements 1916, Begon et al. 1990). Vegetation succession can be broken down into simplified stages; these include primary species that first colonize an opened site, secondary species that later replace primary plants, and lastly a climax community (Dombois 2008). Although this linear model of succession has been critiqued

as too simplistic (e.g., Langston 1995, Glen-Lewin et al. 1992), it can still be useful as a framework for examining the response of plant communities to disturbance.

Plant succession after a burn varies widely between regions, vegetation types, and even microhabitats (Montagnini and Jordan 2005, Syaufina and Ainuddin 2011). While a great deal of research has been done on fire effects in temperate regions (Cochrane 2003), tropical fire ecology has received less attention, especially on islands. It is poorly understood how the impacts of fire on island rainforests will differ from continental forests (Ainsworth and Kauffman 2010). Further studies are crucial because forest fires are likely to become more frequent and severe as human land use increases and the climate changes (Cochrane 2003). This changing disturbance regime will also have an impact on the spread of invasive species (Kriticos et al. 2003), which is of particular concern on islands because of the high numbers of endemic species (Pysek et al. 2008).

Ecological disturbances like fire do not always negatively impact biodiversity (Sousa 1984), however they can also facilitate invasion by increasing available resources and

opening up niches for non-native colonizers (Davis et al. 2000). For example, studies of burn sites on Hawaii have found an increase in introduced species and an elimination of fire-sensitive native species after repeated fires (Ainsworth and Kauffman 2010). Burns can also increase windspeed and decrease moisture availability (Davis et al. 2000), which can create a positive feedback loop for fire (Cochrane 2003). Non-native species themselves can alter disturbance regimes, leading to changes in successional patterns (Ainsworth and Kauffman 2010, Mack and D'Antonio 1998).

The island of Moorea, French Polynesia, presents an unusual case, however, because a previous study showed post-fire dominance by a native species of fern, *Dicranopteris linearis*, rather than introduced species (Koehler 1999). *D. linearis* reproduces asexually and can expand rapidly with indeterminate, branching leaves which shade out other plants (Leung 2001). It is also able to tolerate low mineral levels and has been demonstrated to have allelopathic substances that inhibit the growth of other species (Kato-Noguchi et al. 2012). Studies have shown that *D. linearis* can dominate a burn site for long periods of time before further succession occurs (Russel et al. 1998). It remains to be known what types of plant species replace *D. linearis* after fire on Moorea and whether the new community will be composed of more native or introduced species. Furthermore, Koehler (1999) showed decreased species richness at burn sites, but now that 14 years have passed, species richness may have increased, and plant communities may have returned to their original species composition.

In my study, I aimed to better understand fire effects on Moorea. The study was composed of four main goals. The first was to assess how the plant communities at burn sites compare to unburned sites and to examine how plant communities vary between burn sites of different ages. I hypothesized that plant communities at burn sites are distinct from the plant communities at unburned sites, and that the plant communities would also differ between sites of different ages. Presumably, these varied-age sites would be at different stages of succession.

Second, I asked how species richness compares between burned and unburned sites and between burn sites of different ages. I hypothesized that while fire would initially

decrease species richness due to the dominating effects of *D. linearis* (Koehler 1999), richness would increase after a burn as secondary species establish.

Third, I wanted to determine how fire affects the abundance of non-native plant species. I reasoned that fire would result in a greater abundance of non-native species because of the ability of many introduced species to better withstand disturbance than the native island vegetation (Ainsworth and Kauffman 2010). While *D. linearis* is an exception to this general trend, I hypothesized that most other species at the burn sites would be introduced.

Lastly, I examined how a particular invasive species of legume, *Leucaena leucocephala*, responds to burn conditions. I asked if the condition of the soil, burned or unburned, and the amount of light affect the germination of *L. leucocephala*. I hypothesized that *L. leucocephala* would have a higher germination success rate in burned soil under full sun conditions than in unburned soil under shaded conditions since from preliminary observations it appears to dominate many of the burn sites on the northern side of the island.

## METHODS

This study was conducted on the Island of Moorea, French Polynesia (17°32'19.84"S, 149°49'46.28"W) during the months of October and November 2013. The first component of the study examined two of the burn sites selected in the previous study by Koehler (1999) and one additional site.



FIG. 1. Map of study sites 1, 2, and 3 on Moorea Island. Base map courtesy of the Geospatial Innovation Facility, University of California, Berkeley.

Although the previous study originally

included three burn sites, the 15-year-old site was discarded because it had been developed into a hotel. The remaining two sites burned 18 and 22 years ago, and the new site I chose burned nine years ago. Each site consisted of a burned area and an adjacent control area. The sites were chosen so that all variables other than burn age, including slope angle, aspect, soil type, and hydrological properties, were similar as similar as possible between sites and between each burn area and its corresponding control area (Koehler 1999).

#### *Study sites*

Site 1 is a nine-year-old burn on the top of the Three Coconuts trail on the saddle between Tohlea and Mouaroa at approximately 17°32'49.9"S, 149°50'32.5"W. The burn area is less than 1 Ha, and the fire originated from a small campfire at the top of the ridge (Meyer, pers. com.). The fire traveled westward along the ridge for about 150 m and down a north-facing slope for approximately 50 m. The site receives about 2000 mm of rainfall annually (O.R.S.T.O.M. 1993) and is in direct sunlight throughout the entire day when there are no clouds. At points the slope is as great as 30 degrees. The adjacent control area is located to the west of the burn, and its center point is approximately 17°32'47"S, 149°50'35"W. The control area is very similar to the burn area in terms of hydrological properties, soil type, slope, and aspect, but it receives slightly more shade than the burn area.

Site 2 is an 18-year-old burn also located on the southwest side of the island, just north of Haapiti. The center of the burn is approximately 17°33'10.39"S, 149°52'14.63"W. According to Koehler (1999) the fire originated from a Nono plantation and it traveled up the slope of a west-facing ridge for approximately 1 km. The width of the burn is about 300 m, and the total area of the burn is about four Ha (Koehler 1999). The slope is approximately 25 degrees, and on sunny days the ridge receives direct light for the entire day. The average annual rainfall is about 2100 mm (O.R.S.T.O.M. 1993). The adjacent control area is located to the northeast of the burn with a center point of approximately 17°33'4.09"S, 149°52'3.68"W. Slope, aspect, average rainfall, and soil type are very similar to the burn area.

Site 3 is a 22-year-old burn located on the southwest side of the island, slightly southeast of Haapiti. The center of the burn is approximately 17°33'30.44"S, 149°51'50.48"W.

According to Koehler (1999), the fire originated from a pile of burning waste in a cemetery on the outskirts of Haapiti and traveled along a west-facing ridge for approximately 1.5 km, never exceeding 250 m in width. The total area of the burn is about five Ha, and the slope is approximately 25 degrees along the entire length of the burn (Koehler 1999). The ridge receives direct sunlight for the majority of the day, and the average annual rainfall at the site 2100 mm (O.R.S.T.O.M. 1993). The adjacent control area is located to the southeast of the burn with a center point of approximately 17°33'40.98" S, 149°51'53.15" W. Slope, aspect, average rainfall, and soil type are the same or are very similar to the burn area.

#### *Field Survey*

I used Google Earth (Google 2013) to map out the perimeter of the 18 and 22-year-old burns based on a topographical map of the sites and descriptions included in the Koehler study (1999). The measuring tool was used to draw a line through the center of each burn and control area across their longest dimensions. Five markers were placed equidistant along each line, and the coordinates of these markers were recorded. These coordinates were used as the starting points of the five transects sampled for each burn and control area.

I sampled the vegetation by stretching out a 50 meter transect tape in the upslope direction and recording the plant species present at every four-meter interval along the transect using the line-intercept method. In this method a meter stick is typically placed vertically at the designated intervals, and every plant touching the meter stick, as well as every plant in the canopy directly above it is recorded. However, carrying a meter stick with me was not feasible due to the rough terrain, so I stood with the heels of my feet at each four-meter interval and recorded all of the plants touching my body and every plant directly above my body up to the top of the canopy. Since my body is larger than a meter stick, it is likely that more plants were recorded than would be expected from the traditional method.

The same line-intercept method was used to sample the nine-year-old burn, but the starting points of the transects were chosen while in the field rather than on Google Earth because this site had a significantly smaller area. To determine the starting points, I stood

at the origin point of the fire and walked five meters into the vegetation to the right. The first transect began at this point and stretched perpendicular to the slope away from the origin point of the burn. The second transect continued in the same direction and began five meters from the end of the first transect. This process was repeated for the remaining three transects.

Whenever possible plants were identified in the field, and photographs were taken for later verification. When I was unable to identify the species in the field, I brought samples back to the UC-Berkeley Gump Station to create voucher specimens. I identified some of these plants using descriptions and photographs from the Moorea Digital Flora Project (Murdock 1999) and Whistler (1995). Some plants were identified with help from Dr. Jean Yves Meyer. All voucher specimens were shipped back to UC-Berkeley and have been deposited in the University Herbarium.

Data collected from the line-intercept transects were used to calculate the percent vegetation cover of each plant species at each burn area and control area. To visualize differences in the plant communities between burn sites and control sites and between burn sites of different ages, Non-Metric Multi-Dimensional Scaling Tests (NMDS) were performed and the results were plotted. Additionally, discriminate analysis using the Wilks Lambda statistic were conducted to look for statistically significant differences in the plant communities between burn and control sites, among different controls sites, and among the burn sites. To analyze the effects of fire and age on species richness, a two-way analysis of variance test (ANOVA) was conducted. Lastly, Pearson's chi-square tests were employed to examine differences in the counts of introduced species to native species between each burn site and its control. All tests were conducted in "R" version 3.0.1 (R Core Team 2013), except the discriminate analysis, which was performed in JMP version 11.0 (SAS Institute 2013).

#### *Germination Experiment*

Burned soil was collected from underneath a recently burned pile of vegetation, and unburned soil was collected from a nearby site. Twenty small pots were filled with burned soil and 20 were filled with unburned soil. All of the pots were placed into

two large mesh enclosures behind the Gump Station dormitories. One mesh enclosure had full sunlight conditions, while a covering was placed over the other to create partial shade conditions. Ten pots of each type of soil were placed in full sunlight, and ten pots of each type of soil were placed in partial shade.

Next, eighty seeds were collected from four *L. leucocephala* plants behind the Gump Station and mixed together for randomization. Two seeds were placed into each of the forty pots, and each pot was watered for five seconds every other day for four weeks. The number of seeds that germinated in each group was recorded every other day for four weeks. At the end of the four-week period the total number of seeds from each group that germinated was noted. Seedlings that died within the four-week period were still counted as germination successes in the final total. A generalized linear model with a binomial distribution was performed in the program "R" to look at the effects of soil type and light on the germination success of *L. leucocephala* (R Core Team 2013).

## RESULTS

A combined total of 60 plant species were found within all of the burn and control sites. Fifty-three plants were identified to the species level and seven were distinct, but remained unknown. Fifteen species were ferns, 15 were monocots, and 30 were dicot species. Lichens and mosses were not included in this study.

#### *Community Comparisons*

Site one, the nine-year-old burn, was covered mostly by *Dicranopteris linearis*, *Albizia falcataria*, and *Lantana camara*. The adjacent control area was covered largely by *Hibiscus tiliaceus*, *Miconia calvecens*, *Freycinetia impavida*, *Neonauclea forsteri*, and *Spathodea campanulata*. Only four species overlapped between the burn and control (Fig. 2). Other plant species were present in these areas as well, but they composed less of the percent cover (Fig. 2). Vegetation cover could exceed 100 percent because there were multiple levels of vegetation from the ground to the canopy.

At Site two, the 18-year-old burn, *Dicranopteris linearis*, *Albizia falcataria*, and *Hibiscus tiliaceus* had the highest percent cover. While, its adjacent control site was mostly covered by *Hibiscus tiliaceus*, *Mangifera indica*,

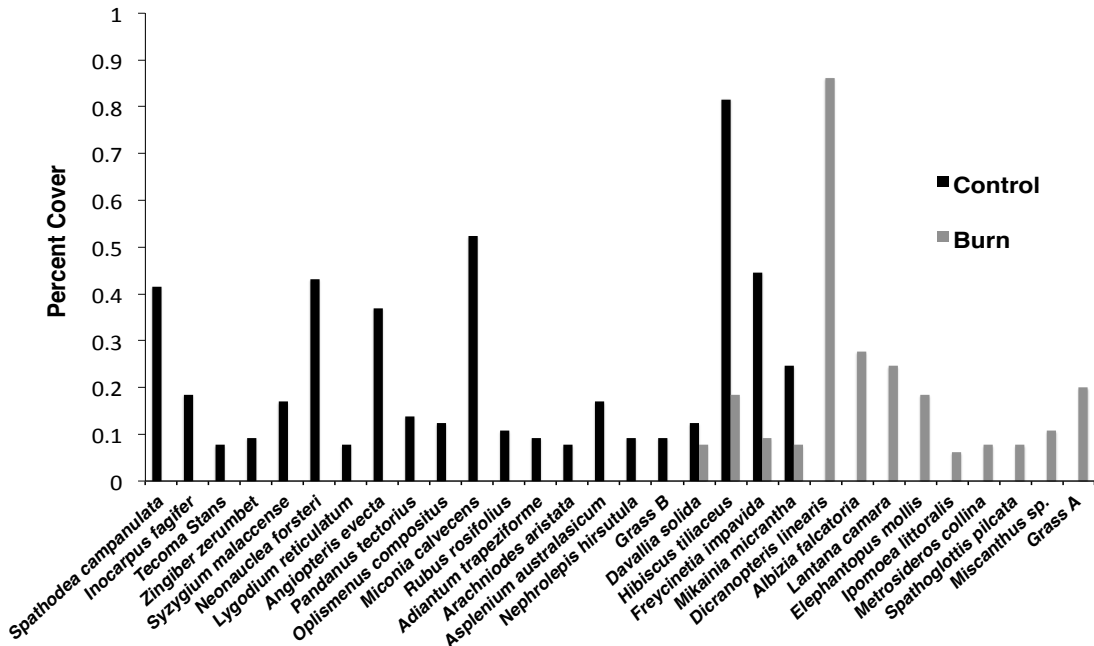


FIG. 2. Average percent cover of each plant species found in burn Site 1, including all species that covered greater than five percent of the total area.

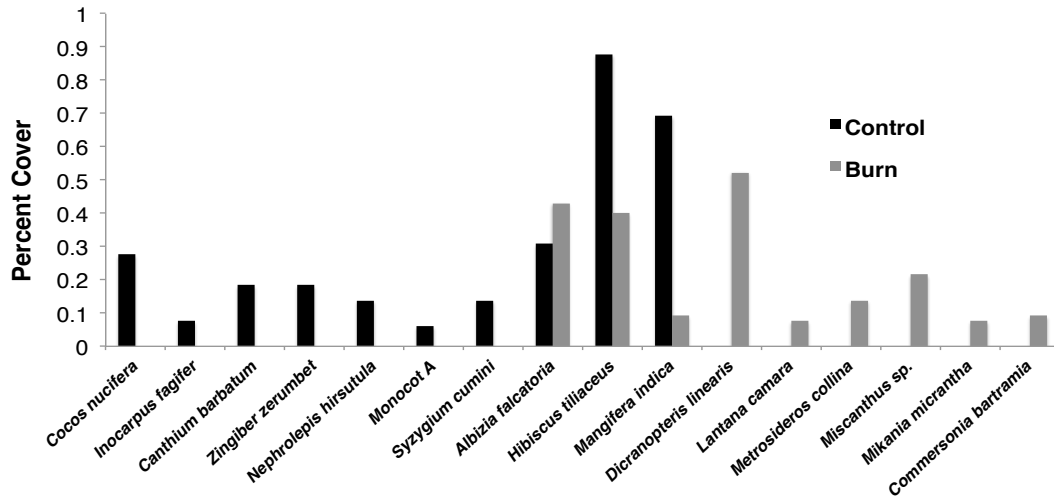


FIG. 3. Average percent cover of each plant species found in burn Site 2, including all species that covered greater than five percent of the total area.

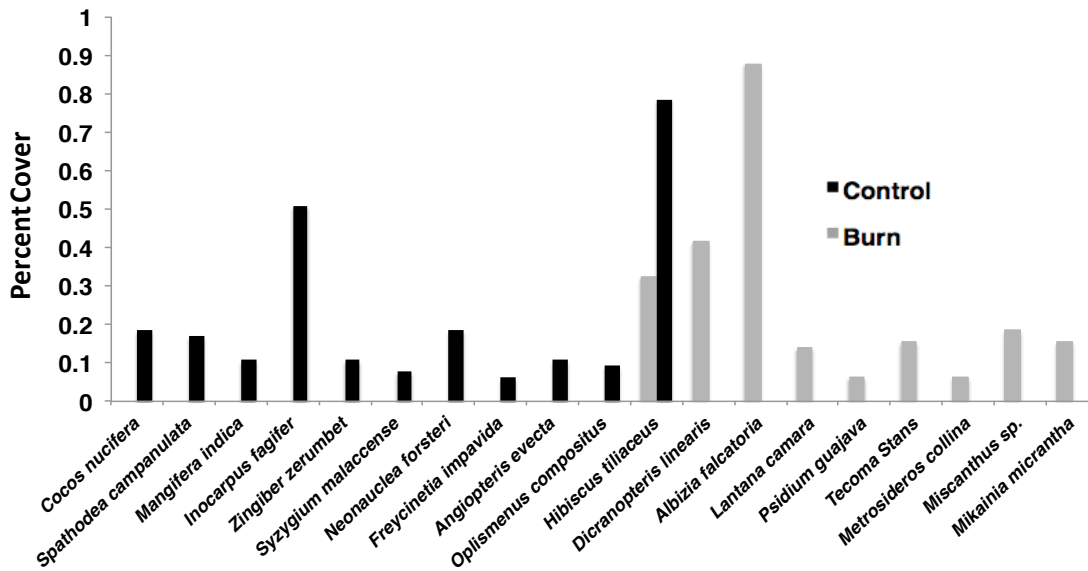


FIG. 4. Average percent cover of each plant species found in burn Site 3, including all species that covered greater than five percent of the total area.

and *Albizia falcataria*. Only three species were present at both the burn and control site. Additional plant species were recorded in these areas as well, but composed less of the vegetation cover (Fig. 3).

Site 3, the 22-year-old burn, was largely covered by *Albizia falcataria*, *Dicranopteris linearis*, and *Hibiscus tiliaceus*. At its adjacent control site *Hibiscus tiliaceus* and *Inocarpus fagifer* had the highest percent cover. Only one species, *Hibiscus tiliaceus*, was shared between the burn and control site. Once again, other species were present but made up less of the vegetation cover (Fig. 4).

A Non-Metric Multidimensional Scaling Test (NMDS) was performed using data for the plant species and their percent cover at each transect. The results of this test were plotted, with each individual point representing a transect (Fig. 5). The points were coded as burned or unburned by color, and as different ages by symbol. There was no overlap in the points for the burn sites and those for the control sites (Fig. 5), indicating strong differences between the plant communities at burns compared to controls. Points for each of the control sites did not overlap either (Fig. 5), showing clear differences in communities between different control sites. The points for the burn sites were mixed together (Fig. 5), indicating that the plant communities at all three burn sites are indistinct from each other.

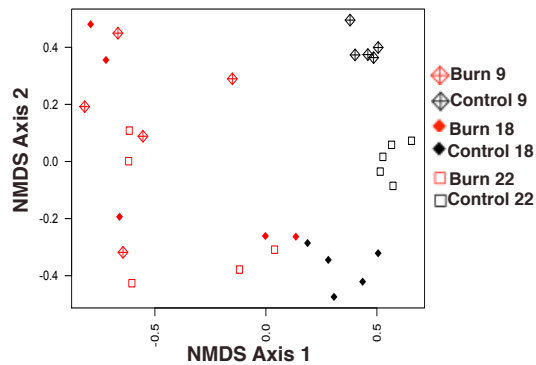


FIG. 5. Plotted results of a Non-Metric Multi-dimensional Scaling Test showing the differences in plant community composition between transects from each site. Points that are close together have a high degree of similarity, while those far apart are more dissimilar.

Discriminate analysis using the Wilks Lambda statistic was conducted to statistically analyze the same data and confirm the results suggested by the NMDS plot. This analysis reported a statistically significant difference in plant communities between burned and unburned sites ( $F=9.3$ ,  $df=17$ ,  $p<0.001$ ), as well as between the different control sites ( $F=18.3$ ,  $df=18$ ,  $p<0.001$ ). The plant communities at burn sites of different ages were not significantly different from each other ( $F=1.9$ ,  $df=16$ ,  $p=0.14$ ).

#### Fire Effects on Species Richness

All of the burn areas had lower mean species richness compared to their control areas (Fig. 6). Species richness also varied at the burn and control areas between different-aged sites (Fig. 6). When comparing the burn areas, the nine-year-old site had the highest species richness with a mean of 10.6 species, and the 22-year-old burn had the lowest species richness with a mean of six species. When comparing the control areas, the nine-year-old site had the highest species richness with a mean of 20 species, and the 22-year-old burn had the lowest species richness with a mean of 8.8 species.

A two-way analysis of variance test (ANOVA) looking at the effect of burn and age on species richness indicated a significant effect of burn on species richness ( $F=24.871$ ,  $df= 1$ ,  $p<0.001$ ) and a significant effect of age on species richness ( $F=42.233$ ,  $df= 1$ ,  $p<0.001$ ). There was also a significant interaction term between burn and age ( $F= 7.007$ ,  $df=1$ ,  $p=0.01$ ).

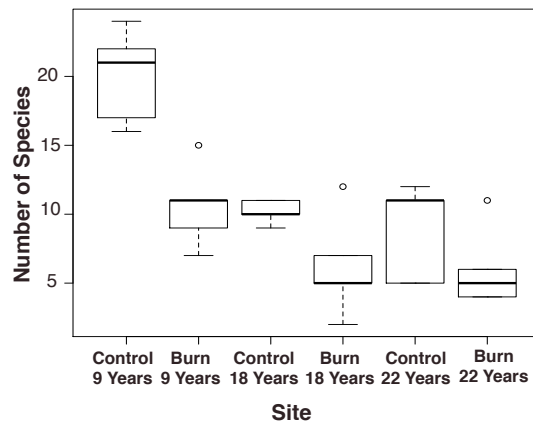


FIG. 6. Species richness at each burn and control area. Mean richness is lower at all burn sites compared to control sites

### Fire Effects on Introduced Species

Plant species were categorized as natives, Polynesian introductions, or modern introductions (Appendix A). For each burn and control area the number of instances that each plant species was recorded was totaled. These totals were then added together for each burn and control area by category. At the nine-year-old site the count of modern introductions compared to native species was significantly higher in the burn area vs. the control (Pearson's chi-square,  $X^2=6.4$ ,  $df=1$ ,  $p=0.01$ ). There was no significant difference in the count of modern introductions compared to native species between the burn and control at the 18-year-old site (Pearson's chi-square,  $X^2=1.9$ ,  $df=1$ ,  $p=0.17$ ) or at the 22-year-old site (Pearson's chi-square,  $X^2=0.69$ ,  $df=1$ ,  $p=0.40$ ).

In order to visualize the differences in plant composition by category between the different sites, counts for each category were converted to percents and graphed (Fig. 7).

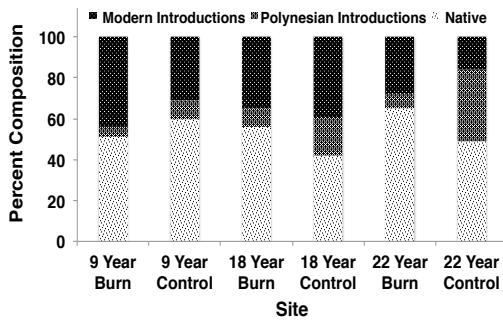


FIG. 7. The vegetation composition of each site broken down into the categories: native, Polynesian introductions, and modern introductions. All sites had the highest percent composition of native species.

### Germination Experiments

Germination was significantly higher in burned v. unburned treatments (GzLM (binomial)  $X^2=9.6747$ ,  $Df=1$ ,  $p < 0.01$ ). There was no significant difference between the light and shade treatments (GzLM (binomial),  $X^2=1e-04$ ,  $Df=1$ ,  $p=0.99$ ). Out of the 20 seeds planted in each treatment group, 40 percent of seeds germinated in the burnt soil and full sunlight conditions; 35 percent of seeds germinated in the burnt soil and partial shade conditions; no seeds germinated in the unburned soil and full sunlight conditions, and five percent of seeds germinated in the

unburned soil and partial shade conditions (Fig. 8).

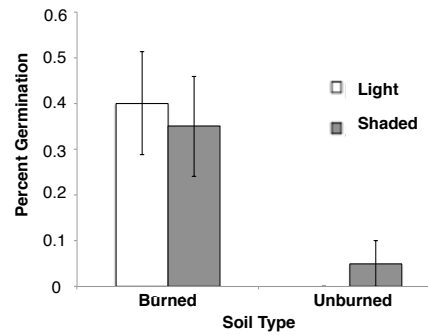


FIG. 8. The average percent of *L. leucocephala* seeds that germinated in each treatment group. Error bars represent one standard error.

### DISCUSSION

#### Community Comparisons

The results of my field survey suggest that fire causes dramatic and long-lasting changes in vegetation composition on Moorea. As I hypothesized, results of the discriminate analysis using the Wilks Lambda statistic and the NMDS plot showed that plant communities at burn sites were distinct from control sites (Fig. 5). It was unexpected, however, that the plant communities at burn sites were not significantly different from each other despite the fact that they ranged from nine to 22 years in age. In contrast, plant communities were significantly different between control sites (Fig. 5). If the control sites are representative of the plant communities at burn sites before fire occurred, then fire appears to homogenize plant communities that originally differed. Furthermore, this homogenization appears to last for up to 22 years and possibly longer.

I had expected burn sites of different ages to be in different stages of succession and therefore distinct from each other. Instead, my findings support Koehler's suggestion that *D. linearis* is greatly slowing succession (Koehler 1999). In fact, the plant communities at the older two burn sites were still largely covered in *D. linearis* like they were in 1999. However, *Albizia falcataria* and *Hibiscus tiliaceus* were also common. This could suggest that over time burn sites will gradually gain woody species and shift away from a fern-dominated landscape. While a study done in Hawaii showed that *D. linearis* can dominate for up to

long periods of time after disturbance (Russell et al. 1998), *D. linearis* dominance for over 22 years seems to be highly unusual.

#### *Fire Effects on Species Richness*

Based on differences in the number of plant species found at burn sites compared to their control sites, it appears that fire negatively impacts species richness on Moorea. The results of a two-way ANOVA also showed that fire is a significant factor in determining species richness, and, as hypothesized, all burn sites had lower species richness than their control sites (Fig. 6). Even after 22 years, site three had a significantly lower number of species than its control site, implying that species richness can be impacted for a remarkably long period of time after fire. These results agree with the Koehler study (1999), which found that species richness decreased after fire.

While it is safe to say that fire decreases species richness on Moorea, it is impossible to conclude from my study how species richness changes over time. An original objective was to look at burn sites of different ages in hopes of understanding how species richness is affected by age since burning. The results of a two-way ANOVA test show that there is a significant effect of age on richness, with richness appearing to decrease at older sites. However, it became apparent that in my study "age" was not only referring to time since burning, but to the different sites in general.

Although an effort was made to choose sites where the only independent variable was age, it was impossible to completely control for other differences between sites, such as elevation. Additionally, the seasonality and severity of the burns were not controlled for, both of which can influence the ecological effects of fire (Newman, pers. com.). These other factors are confounding because they might influence species richness. Moreover, the significant interaction term between burn and "age" indicates that fire interacts with different sites in distinctive ways, and both of these factors combined influence species richness.

#### *Fire Effects on Introduced Species*

On Moorea, fire appears to initially cause a significantly greater abundance of modern-introduced species than would be expected at an unburned site. These results agree with the findings of other studies, which have shown

that fire can facilitate invasion on tropical islands by increasing available resources and opening up niches (Ainsworth and Kauffman 2010, Davis et. al. 2000). However, this difference in the ratio of modern-introduced species to native species was not significant between the 18 and 22-year-old burn areas and their control areas (Fig. 7). The fact that my hypothesis only held true at the nine-year-old site could indicate that the effect of fire on introduced species is only temporary, which has positive implications for vegetation recovery after fire on Moorea.

#### *Germination Experiments*

The observed effects of different treatment types on the germination of *L. leucocephala* provide support for my hypothesis that *L. leucocephala* is more successful at germinating in burned soil vs. unburned soil, but did not show any significant effect of light. For example, the percent germination in both burned treatment groups was significantly higher than the percent germination in both unburned treatments. However, there was no significant difference in germination rate between the full sunlight and partial shade treatments (Fig. 8).

It is possible that *L. leucocephala* seeds are responding to chemicals in the soil after a fire rather than light cues. This phenomenon has been recorded in other plant species that are adapted to fire (Nelson et. al. 2012) but has not been studied in *L. leucocephala*. *L. leucocephala* is an invasive species throughout much of the tropics (Valiente 2010), so these findings could be very significant.

#### *Conclusions*

The results of my study show that on Moorea fire can cause significant changes in plant communities, decreased species richness, and temporarily increased cover of introduced species. Furthermore, these changes can last for up to 22 years and potentially even longer. Changes like these could be especially harmful on small tropical islands because they are more susceptible to invasion, and the plant diversity is already relatively low (Pysek et al. 2008). These results are even more concerning, considering fire frequency is expected to increase in the future as the climate changes and anthropogenic land use grows (Cochrane 2003).

An interesting direction for future research would be to examine how the effects



of fire change depending on geographical and environmental factors such as slope, aspect, elevation, and rainfall. I was unable to obtain fire history records from the fire department; however, if these records were acquired it could be interesting to use G.I.S. mapping to plot fires and look at which vegetation types have established at each burn site and how this correlates to abiotic factors. It could also be informative to set very small controlled fires at different places on Moorea and then record which species colonize the newly burned areas. Permission to do this might be difficult to obtain, but the results could show how early colonizer species vary depending on different geographical and environmental factors.

#### ACKNOWLEDGMENTS

I thank all of the instructors, George Roderick, Brent Mishler, Vince Resh, Jonathon Stillman, and Stephanie Carlson for their guidance and support. I would also like to thank the GSIs Christopher DiVittorio, Julie Hopper, and Lindsey Dougherty for patiently helping me with statistics and for making the class a wonderful experience, as well as my amazing classmates for their assistance in the field. I give special thanks to Erica Newman for sharing her expertise on fire ecology and to Dr. Jean-Yves Meyer for his help with plant identification.

#### LITERATURE CITED

- Ainsworth, A., J. B. Kauffman. 2010. Interactions of fire and nonnative species across an elevation/plant community gradient in Hawaii Volcanoes National Park. *Biotropica* **42**:647-655.
- Barlow, J., C. A. Peres. 2008. Fire mediated dieback and compositional cascade in an Amazonian forest. *Philosophical Transactions of the Royal Society B: Biological Investigations* **363**:1787-1794.
- Begon, M., J.L Harper, and C.R. Townsend. 1990. *Ecology: individuals, populations, and communities*. Blackwell Scientific Publications, Brookline Village, Massachusetts, USA.
- Clements, F. E. 1916. *Plant succession : an analysis of the development of vegetation*. Carnegie Institution of Washington, Washington, USA.
- Cochrane, M.A. 2003. Fire ecology for rainforests. *Nature* **421**: 913-919.
- Davis, M.A., J.P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: A general theory of invisibility. *Journal of Ecology* **88**:528-534
- Dombois, D. M. 2008. Pacific island forests: Successionally impoverished and now threatened to be overgrown by aliens? *Pacific Science* **62**:303-308.
- Glenn-Lewin D. C., R. K. Peet, T. T. Veblen. 1992. *Plant succession : theory and prediction*. Chapman & Hall, New York, New York, USA.
- Google. 2013. Google Earth, Version 7. Retrieved from <http://www.google.com/earth/>
- Kato-Noguchi, H., Y. Saito, and K. Suenaga. 2012. Involvement of allelopathy in the establishment of pure colony of *Dicranopteris linearis*. *Plant Ecology* **213**:1937-1944.
- Koehler, T.B. 1999. Plant recovery on fire scars on Moorea, French Polynesia. *Biology and Geomorphology of Tropical Islands* **8**:71-79.
- Kriticos, D. J., R. W. Sutherst, J. R. Brown, S. W. Adkins, and G. F. Maywald. 2003. Climate change and biotic invasions: a case history of a tropical woody vine. *Biological Invasions* **5**:147-165.
- Langston, N. 1995. *Forest dreams, forest nightmares : the paradox of old growth in the Inland West*. University of Washington Press, Seattle, Washington, USA.
- Leung, T.M. 2001. Ecological growth patterns and distribution of *Dicranopteris linearis* on Moorea, French Polynesia. *Biology and Geomorphology of Tropical Islands* **10**:217-222.
- Mack, M. C., C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology & Evolution* **13**:195-198.
- Montagnini, F., C.F. Jordan. 2005. *Tropical forest ecology the basis for conservation and management*. New York, New York, USA.
- Murdock, A. 1999. Moorea digital flora project. Retrieved from <http://ucjeps.berkeley.edu/moorea/index.html>.
- Nelson, D. C., G. R. Flematti, E. L. Ghiselberti, K. W. Dixon, S. M. Smith. 2012. Regulation of seed germination and seedling growth by chemical signals from burning vegetation. *Annual Review of Plant Biology* **63**: 107-130.

- ORSTOM. 1993. Atlas de la Polynesie Francaise. Paris. Editions de l'ORSTROM 1993.
- Pysek, P., V. Jarosik, P. E. Hulme, J. Pergl, M. Hejda, U. Schaffner, and M. Vila. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology* **18**:1725-1737.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from <http://www.Rproject.org>.
- Russel, A. E., W. Raich, and P. M. Vitousek. 1998. The ecology of the climbing fern, *Dicranopteris linearis* on windward Mauna Loa, Hawaii. *Journal of Ecology* **86**:765-779.
- SAS Institute Inc. 2013. JMP, Version 11. Cary, NC
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15**:353-391.
- Syaufina, L., A. N. Ainuddin. 2011. Impacts of fire on South East Asia tropical forests biodiversity: A review. *Asian Journal of Plant Sciences* **10**:238-244.
- Valiente, C.A. 2010. The invasion ecology of *Leucaena leucocephala* on Moorea, French Polynesia. *Biology and Geomorphology of Tropical Islands* **19**: 65-72.
- Whistler, A.W. 1996. Wayside plants of the islands: A guide to lowland plants of the Pacific Islands. University of Hawaii

APPENDIX A

All plant species recorded at the three sites categorized by their historical presence on Moorea.

Historical Presence	Type of Plant	Species	Reference	
Native	Ferns	<i>Dicranopteris linearis</i>	(Koehler 1999)	
		<i>Asplenium australasicum</i>	(Murdock 1999)	
		<i>Blechnum patersonii</i>	(Murdock 1999)	
		<i>Nephrolepis hirsutula</i>	(Murdock 1999)	
		<i>Arachniodes aristata</i>	(Murdock 1999)	
		<i>Davallia solida</i>	(J. Y. Meyer, pers. com.)	
		<i>Diplazium ellipticum</i>	(Murdock 1999)	
		<i>Lycopodiella cernua</i>	(Murdock 1999)	
		<i>Lygodium reticulatum</i>	(Murdock 1999)	
		<i>Angiopteris evecta</i>	(Murdock 1999)	
		Monocots	<i>Freycinetia impavida</i>	(E. Newman, pers. com.)
			<i>Pandanus tectorius</i>	(J. Y. Meyer, pers. com.)
		Eudicots	<i>Xylosma suaveolens</i>	(J. Y. Meyer, pers. com.)
			<i>Ipomoea littoralis</i>	(E. Newman, pers. com.)
			<i>Ixora moorensis</i>	(J. Y. Meyer, pers. com.)
			<i>Metrosideros collina</i>	(B. Mishler, pers. com.)
			<i>Neonauclea forsteri</i>	(B. Mishler, pers. com.)
			<i>Canthium barbatum</i>	(E. Newman, pers. com.)
			<i>Hibiscus tiliaceus</i>	(B. Mishler, pers. com.)
	<i>Pyllanthus sp.</i>		(J. Y. Meyer, pers. com.)	
	<i>Commersonia bartramia</i>		(J. Y. Meyer, pers. com.)	
	<i>Fagraea berteriana</i>	(E. Newman, pers. com.)		
Polynesian Introduction	Monocots	<i>Zingiber zerumbet</i>	(E. Newman, pers. com.)	
		<i>Miscanthus floridulus</i>	(E. Newman, pers. com.)	
		<i>Dioscorea bulbifera</i>	(E. Newman, pers. com.)	
		<i>Cocos nucifera</i>	(E. Newman, pers. com.)	
		<i>Cordyline fruticosa</i>	(E. Newman, pers. com.)	
		Eudicots	<i>Syzygium malaccense</i>	(Murdock 1999)
			<i>Inocarpus fagifer</i>	(B. Mishler, pers. com.)
Modern Introduction	Ferns	<i>Adiantum trapeziforme</i>	(Murdock 1999)	
		<i>Diplazium proliferum</i>	(Murdock 1999)	
	Monocots	<i>Ananas comosus</i>	(E. Newman, pers. com.)	
		<i>Oplismenus compositus</i>	(J. Bartolome, pers. com.)	
		<i>Spathoglottis plicata</i>	(E. Newman, pers. com.)	
		<i>Melinis repens</i>	(J. Y. Meyer, pers. com.)	
	Eudicots	<i>Lantana camara</i>	(J. Y. Meyer, pers. com.)	
		<i>Albizia falcataria</i>	(B. Mishler, pers. com.)	
		<i>Spathodea campanulata</i>	(B. Mishler, pers. com.)	
		<i>Mikania micrantha</i>	(J. Y. Meyer, pers. com.)	
		<i>Miconia calvecens</i>	(J. Y. Meyer, pers. com.)	
		<i>Stachytarpheta urticifolia</i>	(E. Newman, pers. com.)	
		<i>Psidium guajava</i>	(E. Newman, pers. com.)	
		<i>Tecoma stans</i>	(Whistler 1995)	
		<i>Rubus rosifolius</i>	(Whistler 1995)	
		<i>Elephantopus mollis</i>	(E. Newman, pers. com.)	
		<i>Emilia fosbergii</i>	(E. Newman, pers. com.)	
		<i>Carica papaya</i>	(E. Newman, pers. com.)	
		<i>Merremia peltata</i>	(Murdock, 1999)	
<i>Mangifera indica</i>	(E. Newman, pers. com.)			
<i>Passiflora foetida</i>	(E. Newman, pers. com.)			
	<i>Polyscias scutellaria</i>	(J. Y. Meyer, pers. com.)		

Note: The seven unidentified plant species in my study were not recorded in the table. None of these unidentified species had more than 5% vegetation cover at any site.