Fire in a Neotropical Dry Forest:
Cultural Uses and Ecological Effects

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Abstract

Fires ignited by human activities frequently impact neo-tropical dry forests. While anthropogenic fires are generally considered a destructive disturbance, relatively little is known about their effect on the dry forest plant community and species of conservation concern. In addition, little attention has been paid to the socio-cultural motives that lead to wildfire ignition. This study examines the cultural use of fire and plant community and life history responses to fire in an upland dry forest within the Río Escalante-Chacocente Wildlife Refuge in southwestern Nicaragua. Members of farming communities located within and surrounding the refuge were interviewed about fire practices and the perceived benefits of fire. Fire was described as an essential step for preparing agricultural land and was crucial to many aspects of subsistence farming. The effect of fire was measured in the composition and density of dry forest species in four permanent one hectare forest plots burned by a wildfire and in experimentally burned 15x75 m forest plot. Three years of post-fire monitoring revealed that the impact on vegetation is most significant within the first year post-fire. Diameter was positively correlated with survivorship for woody species, with individuals of > 6 cm dbh suffering less than 20% mortality. Lianas were most negatively affected by fire, suffering high mortality and decreased post-fire recruitment. There was an increase is seedling richness and density post-fire, particularly for overstory tree species. Dry forest species exhibited various responses to fire (sprouting, resistance, post-fire recruitment), but few succumbed to single fire events. Sprouting was the most common response to fire. Three tree species of conservation concern responded positively to fire, showing increased recruitment following fire. Our research demonstrates that fire has complex effects on dry forest, and even in some cases, may serve to enrich the forest. Further research on the ecological role of fire is merited in order to develop a fire policy that meets both ecological and human needs.

INTRODUCTION

Fire is a disturbance factor important for maintaining tropical plant assemblages such as African savannas (Trollope 1984), Neotropical savannas (Kellman 1984), high-elevation *paramo* vegetation (Horn 1993), and bamboo forests (Keeley and Bond 1999). Although fire disturbance is an essential dynamic in many tropical ecosystems, it may have more negative effects in closed-canopy ecosystems, particularly if trends in global climate change and El Niño-Southern Oscillation lengthen the tropical fire season and increase the size and intensity of wildfires (Leighton and Wirawan 1986, Cochrane 2002). Recent research in tropical moist forests has documented the degradation of forests resulting from increasingly frequent fires (Cochrane and Schulz 1999, Cochrane *et al.* 1999, Cochrane 2001). Scientists are concerned that fires are also a serious threat to seasonally tropical dry forests (Janzen 1988, Koonce and González-Cabán 1990, Saha and Howe 2003).

Seasonally tropical dry forests are tree-dominated ecosystems that experience several months of severe and absolute drought on an annual basis (Mooney *et al.* 1995). They are a global conservation priority (Lerdau 1991) because they are often centers of endemism, mammalian diversity and life form diversity (Mares 1992, Gentry 1995, Medina 1995). Dry forests are one of the most human-populated of tropical ecosystems; in large part

Fire is frequently by used by humans in many drought-prone environments (Woodcock and Wells 1994) where physical conditions are often appropriate for fires to spread into nearby forests. Fire is also an important tool for human subsistence and natural resource management throughout many regions of the world, including dry forests (Conklin 1961, Clark and Uhl 1987, Lewis 1994). Nevertheless, many burning activities associated with subsistence can lead to wildfires.

In the dry forest, the majority of wildfires in the dry forest are anthropogenic and therefore not considered a 'natural' disturbance within dry forests (Janzen 1998, Saha and Howe 2003). Nevertheless, ignition by volcano (Goldammer and Seibert 1989 in Cochrane 2003) or lightning (Middleton *et al.* 1997) have both been recently documented in dry forests leading one to question whether fire has actually played a historical role. Regardless of the fire ignition source, fire today is one of the principal disturbance dynamics in the dry forest, thus necessitating a more in-depth understanding of fire in this ecosystem. Although dry forests burn more readily than moist forests, research examining the effects of fire on this ecosystem has been limited (Saha and Howe 2003, Blate and Putz 2003, Kennard and Gholz 2001, Pinard and Huffman 1997). Therefore, data on the effects of fire in a dry forest represent a critical gap in our understanding of this ecosystem.

Patterns of fire disturbance and its effect on the forest are well illustrated in the Central American dry forest (CADF). This forest ecosystem is distributed along the lowland Pacific slopes of Southern Mexico and Central America and also throughout the lowlands of the Yucatan Pensinsula. The Central America tropical dry forest (hereafter CADF) is one of the most threatened ecosystems globally (Janzen 1988) and what little of this forest remains persists in fragments and degraded patches (Sabogal 1992).

Throughout its range, the CADF has been logged for its precious hardwoods and converted to agricultural land or pasture for livestock. Historically, the expansion of cattle ranching was a driving force behind CADF fragmentation (Daubenmire 1972, Toledo 1992) and with ranching came the introduction of non-native, pyrophytic grasses (*i.e. Hyperrania rufa*) (Mueller-Dumbois 1978). Ranchers use fire to maintain this introduced grassland, and a "grass-fire cycle" develops where frequent fires continually exclude woody species from establishment (D'Antonio and Vitousek 1992). In spite of this problem, many CADF patches persist without the presence of these pyrophytic grasses in the forest understory.

Considering the frequent occurrence of fire in CADF and given the debate over the ecological role of fire in this system, we set out to further examine the fire effects in a in CADF; in particular plant community (composition and structure) and plant life history responses to fire We also sought to characterize the cultural use of fire in an upland dry forest within the Río Escalante-Chacocente Wildlife Refuge in southwestern Nicaragua.

The Río Escalante-Chacocente Wildlife Refuge is a critical site for dry forest conservation (Sabogal 1992). Over one thousand local people reside within the refuge boundaries and practice agriculture and hunting for subsistence thereby making it an ideal site for studying the ecological effects of wildfires, because local people use fires throughout subsistence activities and there is little effort to extinguish fires when they spread into nearby forests.

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CHAPTER 1: THE CULTURAL ECOLOGY OF SUBSISTENCE BURNING IN A NICARAGUAN TROPICAL DRY FOREST

INTRODUCTION

Fire is prominent disturbance factor throughout tropical ecosystems. Recent inter-annual climate events such as El Niño-Southern Oscillation (ENSO) have been linked to catastrophic wildfires (Leighton and Wirawan 1986; Cochrane 2002). Trends in global climate change are expected to lengthen the tropical fire season and increase the size and intensity of wildfires (Goldammer and Price 1998). As wildfires become more prevalent, scientists and policymakers have become increasingly interested in determining the cause of such fires. Although most studies point out that they are *anthropogenic*, few have explored in depth the socio-cultural factors associated with these fire ignitions. In this paper, we examine ethnoecology of fire use in *mestizo* communities of Southwestern Nicaragua. We demonstrate that *mestizo* farmers have a complex system of knowledge and beliefs surrounding fire use and they perceive fire as essential to their survival. We also argue that cultural fire use is a key component for understanding the cause of many wildfire events in Nicaragua.

Mestizo burning in Central American tropical dry forest

Our research addresses several gaps in the anthropological literature relating to fire. First, it examines aspects of swidden agriculture neglected in previous studies and does so in a dry tropical region where there has been limited research on the subject. And secondly, our study observes cultural aspects of fire use for a 'non-indigenous' group, while prior research has mainly focused on burning practices among indigenous cultures.

Anthropologists have long been interested in the use of fire within shifting agriculture (see Conklin 1961 for extensive bibliography). Of the five stages of shifting agriculture described by Conklin (1961) – *selecting, cutting, burning, cropping and fallowing* – detailed research has concentrated mainly on the cropping and fallowing stages. Fore example, Dufour (1990) focused on the cropping and fallowing methods employed throughout the Amazonian basin while other authors researching in the same region have focused on the "cutting" stage by quantifying the physical labor required to carry out swidden agriculture (Clark and Uhl 1987). More recent research has described transformations in shifting agricultural systems as population densities have lead to a decrease in fallow periods (Carins and Garrity 1999). While research on cropping and fallowing systems is relatively extensive, aspects related to the "burning phase" of shifting agriculture have been largely ignored. As we will demonstrate in this paper, the burning phase of shifting agriculture can be quite complex and involve an elaborate knowledge system for fuels, weather, and fire behavior.

In addition to overlooking the burning phases of swidden agriculture, studies of shifting agriculture have focused primarily on the humid tropics, while neglecting seasonally dry tropical regions (Lambert 1996). Fire is a preferred subsistence technology within the dry forest zone, because seasonal drought conditions enable easy burning (Lambert 1996, Dixemunde *et al.* 1999, Cochrane 2002). Our study is situated in Central America, where it is estimated that 79% of the population lives within the tropical dry forest ecological zone (Tosi and Voertman in Murphy and Lugo 1995). As expected, seasonally dry portions of this region are burned annually, thereby providing an ideal setting for studying the cultural aspects of fire use.

Many studies have characterized the way in which cultural groups burn intentionally for subsistence. Burning is often conducted with the purpose of changing landscape conditions in order to collect natural resources (e.g. herbs, basket materials), to enhance wildlife habitat, or to create a physical environment more favorable for human habitation. For example, Australian Aborigines burn savannas to create new growth and vegetation patches of various successional stages, thus enhancing habitat for hunted game (Lewis *mestizo* populations and natural resources have demonstrated an in-depth knowledge surrounding biodiversity and resource use (Bentley and Rodriquez 2001, Aguilar and Condit 2001). Our study focuses on fire use and burning practices of a *mestizo* community in Nicaragua. Nicaraguan peasant communities are composed of peoples whose identity and traditions are inextricably linked to an indigenous and colonial past (Romero 1992). Presently, peasant subsistence is based on methods that are both remnants of pre-colonial subsistence (*e.g.* fallow, slash-and-burn, wild honey extraction) and post-colonial modern techniques (*e.g.* mechanization with oxen, hunting with firearms). Knowledge concerning fire use and farming techniques is also a product of this varied history.

Subsistence Burning

Within the anthropological literature, there is not one common term referring to the fires

set for subsistence purposes. Words or phrases that have been commonly used include involve a series of specific objectives. There is a need for a common term that describes the burning practices associated with subsistence and shaped by culture.

In this paper we make use of the term *subsistence burning* to refer to fires employed throughout various aspects of subsistence, where the objectives are related to the production or capture of food and the creation of a home environment. We focus on subsistence burning across *mestizo* households located within a tropical dry forest-agricultural landscape in southwestern Nicaragua.

Our basic research questions include:

1. How does fire enter into subsistence activities within the mestizo household?
2. What is the system of rules and beliefs for the practice of agricultural burns?
3. What are the perceived values of agricultural burning and effects on the surrounding dry forest ecosystem?

STUDY SITE

Our research site is located within a Central American tropical dry forest. Activities such as agriculture, grazing, logging and urbanization have eliminated the majority of dry forest landscapes and what remains persists through a series of small to medium disjunct patches within a densely populated agricultural landscape (Sabogal 1992). Subsistence burning in and around the dry forest is a concern to conservationists because of their potential for creating wildfires (Cochrane 2002, Janzen 1988).

2000), where the dry forest predominates. Our research is centered on communities within and surrounding the Chococente Wildlife Refuge located in the Carazo province of southwestern Nicaragua (Figure 1.). The refuge protects the 'core' of one of the least disturbed tropical dry forests in Central America (Sabogal 1992), thereby making it a conservation priority for Nicaragua (Gillespie 2001).

The Chococente Wildlife Refuge is not solely dedicated to biodiversity protection. While Chococente was declared a reserve by the national government, the park itself is composed of large and small privately owned lands. Large landowners have mostly set aside their land for conservation, while small landowners live within their land parcels and cultivate basic grains. Farming households are interspersed throughout the park and along its edges, with five distinct settlements located within protected area boundaries and thirteen additional communities within the protected area buffer zone. In general, households are built along the banks of rivers where water is more accessible. Households within Chococente are built of wood, often in combination with mud, bricks, or stone around the base of the house. The primary form of subsistence within the communities is farming of grains, the two most important crops being maize and sorghum (98% percent of households cultivate these two crops). Beans are also a principle crop, cultivated by at least 82% of the households. Other crops include rice (5% cultivate), sorghum (17% cultivate) and manioc (10% cultivate). In addition to farming, local people rely heavily on the biodiversity resources within the forest, collecting wild fruits and herbs and hunting wildlife. Residents also fish at estuaries along the coast and illegally collect sea turtle eggs for consumption and sale.

Prior to Spanish colonization, the Nahua-speaking Nicarao people once populated what is today Carazo (Heally 1980). While the people of Chococente identify themselves as having mixed-Spanish ancestry, the strong ties between the Nicaraguan *mestizo* population and their "Indianness" is accepted throughout the Nicaraguan population in general (Fields 1999).

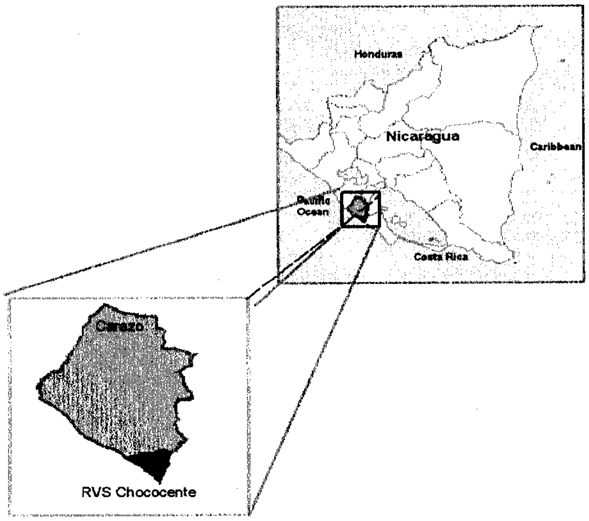

Figure 1. Location map for *Refugio de Vida Silvestre* Chococente, located within the Carazo Department of southwestern Nicaragua.

METHODS

We employed various methods to gather quantitative data and ethnographic information about subsistence burning in Chococente. First, we conducted structured interviews directed towards the female heads of households. Women were selected for structured interviews because they were generally home throughout the day and more willing to reserve were selected on the criteria that they be located within 4 km of reserve

households for structured interviews, a total census was conducted of all households. The 176 households had an average of 6.1 people per household. The households were stratified into three geographic areas and according to number of people per household (Table 1). We then randomly selected 103 households.

Interview questions covered aspects of fire use in and around the home and the frequency

Secondly, we were active in the field for nearly two years gathering ethnographic data. During ecological experiments (refer to Chapter 2), we observed behaviors and attitudes towards fire. Our ethnographic interviews were focused on specific groups of people. For example, we conducted fifteen in-depth interviews with male farmers from a wide range of ages and another six interviews with elderly men and women in the community. These interviews addressed the benefits of burning, decision-making for selecting timing of burns, and techniques for applying fire. We also used participant observation techniques for five separate agricultural burns. During each of these burns, we recorded behaviors with respect to fire and techniques for applying fire on the landscape.

RESULTS

1) Fire in subsistence activities

Fire is prevalent throughout many subsistence activities to the point that the relationships between socio-economic variables and burning activities were statistically insignificant. The lack of variability speaks to the pervasiveness of fire in both agriculture and around the household. We have divided subsistence burning by purpose. A summary of the subsistence activities involving fire is given at the end of this section in Table 2.

Home Maintenance

Women carry out the majority of household activities; therefore they are also the keepers of the fire within the home. Fire is used for cooking in 100% of households, as there is no easy access to either electricity or gas. In 70% of households fire is maintained round the clock because maintaining a fire eliminates the work required to ignite it during the wet season and also saves the cost of matches. Many homes also cook over a traditional Mesoamerican hearth, where a *comal* or cooking dish is balanced over a small fire on three rocks. Of those interviewed, 7% of the homes did not have stoves at all, but relied solely on this traditional hearth.

Fire is used for household activities that generate cash and economic security for women. Nearly half of the households have an adobe oven. While these ovens are often a status symbol because of the work they require to build, they are also used as a tool for acquiring further wealth. 11% of women in the area participate in the local sale of baked goods such as bread and other corn-based goods (e.g. *cositas del horno, tamal dulce*). These women sell the bread 1-2 times per month and earn up to four U.S. dollars profit in sales per sale. We observed that in several households headed by single women, bread sales were the primary activity for acquiring cash needed for basic necessities such as oil, rice and sugar. Women also rely on fire for the elaboration of ceramics. Although less than 10% of local women participate in ceramic-making activities, their work plays an important role in the community because ceramics are used daily in local homes (e.g. ceramic *comales* for making tortillas and *vasijas* for storing water). The firing technique requires that clay objects be buried with hot coals for several days. Knowledge of this traditional technique is taught within families.

Local women say that without fire it would be impossible to achieve a clean home. *Basura* or garbage is considered to be any leaf litter or woody debris that is not of use and is accumulating around the household. This garbage is swept into piles in front of the house and then allowed to burn throughout the day with women and children tending the flames. A simple iron is heated over a stove in order to press clothing for adult family members on special holidays and for community workshops. Finally, mosquito-born illnesses such as malaria and dengue fever are a health risk to families, particularly during the rainy season. Households manage mosquitoes by lighting cow chips or small branches in the house and allowing the fuel to burn on the floor slowly throughout the night.

Hunting

Similar to other cultures throughout the world, local people in Chococente use fire to hunt and collect wild game. Wildlife is a major source of protein, particularly during the dry season months when the harvest of basic grains has ended and food can become somewhat scarce. Respondents in > 64% of households stated that they enter the forest frequently to extract wild game. Fire is primarily used to capture iguanas, a favorite dry season food. Hunting iguanas is so customary that it is referred to as the *cosecha* or harvest, with those who hunt iguanas being called "*garroberos*", derived from the local word for the *Ctenosaura* iguana. Capturing an iguana generally involves a chase where a person or dog pursues the reptile into an opening in a tree or trunk. The hunter then lights a fire at the base of the tree and allows it to burn until the iguana suffocates from captured are sent to markets for cash, 88% of households say they hunt iguanas solely for household consumption, consuming between 1-4 iguanas per season. Although some families admit to consuming more than nine iguanas per season. There was no correlation between the number of household members and the number of iguanas consumed.

Large fires are used by men for hunting deer. Two different methods are employed during the dry season on an annual basis. The first involves lighting a post-agricultural field with medium height brush in an attempt to smoke out the deer. The second involves

burning open areas of land and returning within the week to capture deer that return to feed on resprouting trees and grass damaged by the fire.

One additional resource gathered from the forest through the application of fire is wild honey. Wild honey with the comb is considered an important medicine for birthing women and sick children. Some 44% of households collect wild honey. In recent years, the invasion of Africanized honeybees into forested areas has displaced the native non-stinging bee. Fire is now needed to ward off these aggressive bees while people collect their honey. When a hive is found, a fire is lit at the base of the tree until the smoke has displaced the bees. The local men who specialize in this activity are called the *mieleros*, derived from the root word *miel* or honey. Although honey is generally consumed locally, it has a high market value of up to $8 dollars/liter.

Agriculture

For the local farmers, burning is almost a prerequisite for planting crops. Above 90% percent of respondents stated that they burn annually to prepare their fields, indicating that fire has an integral role in the production of food. The majority of agricultural burns are small in nature since more than 80% of households farm on less than five *manzanas* (*manzana* is a Nicaraguan measurement of area, 1 *manzana* = 0.7 ha, thus 5 *manzanas* = 3.5 ha). Burning is carried out before the first cycle every year. There are generally two crop cycles, the *primera* and *postrera* with the *primera* being planted after the first week of heavy rains and the *postrera* being planted mid-rainy season. During interviews, many farmers expressed concern that there has been a drying trend in the climate over the past 20 years making this first round of cropping nonviable. During particularly dry years (*i.e.* [illegible]

The wide array of subsistence activities in which fire plays a role, attests to its importance within *mestizo* communities. Table 2 illustrates the different forms of subsistence burning and describes how fire is used by both genders across the multiple spheres of daily life: forest, home, and agricultural field.

Table 2. Subsistence activities in which fire plays important role with a description of the activity and its participant.

Activity	Gender	Description	% of population
Cooking	Female	Fires on stoves for all cooking	100
Baking	Female	Baked goods for home & local sale	48
Cleaning yard	Female & Children	Household and yard litter swept into piles and burned	100
Repelling insects	Female & Children	Fuel placed inside home and burned through the night	100
Ceramics	Female	Household ceramics for local sale	<5
Brick/tile making	Male	Bricks fired in underground oven	<10
Hunting	Male	Iguanas smoked out of tree holes and burns open habitat for deer	64
Harvesting honey	Male	Fire placed at base of tree to smoke out aggressive bees	36
Agriculture	Male	Slash cut and dried, then burned prior to planting	90

2) Practicing subsistence burning in agriculture

Mestizo farmers have very specific rules and beliefs with respect to the practice of subsistence burning in agriculture. Knowledge of climate, weather, fuels, and fire behavior all contribute to determining how land is prepared for burning, the frequency with which it is burned, the timing of the burns (season and day) and lighting methods.

Frequency

According to interviews, nearly all farmers burn on a yearly basis. Fallow periods vary between 1and 5 years, with 5 years or more mentioned as the optimal fallow period. Nevertheless, there are many households that have only a small parcel of land, making a fallow period impossible. In these cases, farmers still burn prior to planting, though brush is only cut a few weeks before the burn because fuels are sparsely spread and relatively dry. A few young farmers (<35 years of age) mentioned only burning every second or third year, citing a lack of fuel buildup as a reason for not burning more continuously as there is only "*rastrojo*" or stubble from the previous crop. This may indicate a recent trend in decreased land available for agriculture, given that younger farmers are those who mentioned this issue. Over the past 15 years, the Ministry of Natural Resources (MARENA) has been enforcing rules about not felling mature forest for agricultural land, but previously farmers would have been able to rotate agricultural plots through more densely forested areas without any repercussions. Reduced or eliminated fallow periods may alter the overall impacts that subsistence burning has on soils and the forest.

Preparing for a burn

The majority of men select the part of the field they are going to cultivate according to where there is enough fuel to give a fire "*fuerza*" or strength. A strong fire is one with high flame length (> 1m) creating intense heat. Predicted fire behavior appears to be the most important selective factor, but the availability of land also contributes to decision-making. To prepare for the burn, farmers first cut woody fuels and weeds using machetes and axes for larger trees. The area of land selected for cropping is calculated according to the time required to clear it. Farmers state that 1-2 weeks of physical labor are required to chop one Nicaraguan *manzana*, depending on the size of the "*monte*" or fuels. If fuels are really large, as in the case of a secondary forest with a closed canopy it can require more than two weeks per *manzana*. Considerable planning goes into preparing agricultural land and slashing often occurs up to four months prior to the actual burn. Slashing fuels months in advance allows for plenty of time for large woody debris (1000-hour fuels) to dry thoroughly under the extreme sun and wind of the dry season. Farmers indicate that the dryer the fuels, the better the burn they are able to achieve.

Seasonal timing of the burn

Campesinos emphasize the importance of burning at the seasonally appropriate time to ensure an effective burn. April 25th was the date most frequently mentioned for burning, with most respondents saying that burns should happen anytime from this date forward, but others saying that burns should take place before this date. It is unclear why this particular date is of interest, as there are no local or religious festivities surrounding this date. Independent of the calendar date, there was a general consensus regarding the climate conditions appropriate for burning. Most importantly, burns should take place at the end of the dry season but before the first rains, at a time when the *rumores* or signs of seasonal change begin to manifest themselves. These *rumores* or signs are described as the presence of large rain clouds, decreases in wind, sounds of distant thunder, and an increase in relative humidity. Others say they follow an increase in wildlife activity and the songs of the chacalaca bird (*Ortalis vetula*) to forecast the onset of rains. Table 3 provides examples of local words and phrases specifically describing indicators of the season for burning. By selecting a season when it is still dry but winds have decreased, farmers are able to have dry conditions sufficient for ignition, but with winds calm enough for better control.

Table 3. Local expression and words to describe seasonal changes which indicate appropriate climate conditions for agricultural burns.

Local Expression	Translation or Interpretation
Rumores	the news that the rainy season is coming, generally comes through sounds of thunder, formation of large cumulous clouds
Los señales	indicators regarding what the weather will be like; heat, lack of wind, big clouds
Penacherías de agua	large rain clouds
Nubazones	large dark rain clouds, probably referring to cumulonimbus clouds
Oscuranas	Darkness observed in the sky with increase in clouds
El mar mota el agua	The ocean pushes the water away from itself and in towards land
Arboles llaman la lluvia	The trees call to the clouds
Los calores	Heat described during rainy season when there is less wind and higher humidity, heavy feel to the air
Las calmuras	The period of time when winds decrease and nearly cease, signals rainy season
Época de astillo	The period of time when the weather changes from one season (verano) to the next (invierno).

Specific day and hour to burn

The specific days for burning are selected according to desirable conditions for wind, temperature, relative humidity, and lunar phase. Nearly all farmers agreed that the wind should be calm or slow moving. One common description of the wind movements was that it should be moving "*desde arriba hacia abajo*", likely meaning directly from east to west rather than multiple wind directions or from coastal sea breezes (in Nicaragua *arriba* is east where the sun rises and *abajo* is west where sun sets). Other words used to describe the wind movements included soft, serene, and calm. One farmer said that it should be a '*viento natura*l' or natural wind, which he said meant that the wind would not pull sparks from the fire. Such comments indicate that farmers understand the dynamic interplay between fire behavior and wind.

The temperature and relative humidity is also considered when selecting a time to burn. Many expressed that it is best to burn during the time of day when the "sun begins to cool". We observed the application of this belief for burns that were carried out in the early afternoon when the mid-day heat begins to lessen. Nevertheless, farmers also agreed that the temperature should be hot for a good burn. Their statements made particular reference to the sun's heat and position in the sky as an indicator of the appropriate time, rather than focusing on temperature in the air. They explained that if the saw were not hot, the fire would not burn. Even during the dry season a lower temperature can raise the relative humidity to 90%, greatly inhibiting fire intensity and spread. A minority of respondents said that it is better to burn when it is cool for better control, although it is not clear whether this answer was to appease me, because as one person pointed out, the MARENA says that you should burn in the afternoon.

The actual burns observed were carried out in a range of times between 11:30 a.m. and 3:00 p.m. (see Table 5). Similar to temperature, the majority felt that the air should be dry, although the same people who felt that one should burn during the afternoon felt that the air should be more humid for burning. One farmer provided a good description on how to determine the time of day to burn; "it depends on the fuels, if there are low fuels then you burn early so that the sun with lift them up in the burn, but if there are high fuels you want to burn in the afternoon when it is fresh." This ability to predict fire behavior based on interactions between fuel loads and weather demonstrate the depth of fire knowledge among *mestizo* farmers.

One additional factor considered for the timing of the burn is the lunar phase. Farmers felt that the phase of the moon strongly influences fire behavior and if burns are carried out during the wrong lunar phase the flames will not gather strength and eventually weaken and die. Furthermore, they stated that it is not advisable to carry out burns during the new moon or the early waxing moon because the earth is considered weak, making it difficult for crops to grow and making the crops vulnerable to pests.

Who burns

Although observed burns also had 2 or more participants on the team, the majority of interview respondents stated that just one person is needed to carry out a burn. The small number of people on the burn likely relates to the relatively small size of farms. One respondent related stories from the Sandinista era of the 1980s, where burning teams were very large because members of a cooperative would join together in groups to burn their communal plots. Today, the cooperatives in the area are dissolved and land has been parceled into individual lots.

Burning is exclusively a male activity. When we asked a farmer why women were not allowed to participate, the response was that women would choke and die in the smoke (a noteworthy comment considering the quantity of smoke circulating in the household kitchens). Farmers said women could help in a fire by bringing drinking water to the men in the field, but that the role of the women is in the house. Despite the gender divisions in labor, we observed one burn that was carried out by a single mother and her eldest 14 year old son. Farmers said that it was dangerous for children to participate in the burns; nevertheless during multiple burns I observed there were young children (ages 5-10) participating. The clothing attire for the burns was nothing different from the ordinary day-to-day clothing. Farmers carried out their burns in plastic sandals, explaining that they would not want to ruin a good pair of shoes in the burn.

There are a limited number of tools necessary to carry out a burn. The lighting tool, called a *tizón,* is a thick wood branch with hot embers on the end. The preferred tree species for the *tizón* is the Guasguao (*Acacia centralis* Britton & Rose) because of its reported ability to burn slowly and hot. Younger farmers tend to prefer another lighting tool: a dry corncob speared through the end of a metal roasting stick and soaked in kerosene. During burns, machetes are always kept handy for any need that may arise during the burn, such as cutting a branch that has caught fire on a desirable tree. Farmers sometimes use brush and vines to make provisional brooms that can be used to brush aside flames or fine fuels.

In general, *mestizo* farmers hold very relaxed attitudes towards fire. During nearly all of the burns we observed, men would hoot and holler at one another, particularly when the flames gained in intensity. One farmer carried out the burn while carrying around his transistor radio listening to music. Another says he really enjoys burning because it brings joy to feel the heat of the fire on his ribs. Safety was not an obvious concern, even though farmers seemed to be aware of the risks. They told a story of a local farmer who was engulfed in flames and killed after his rubber boot was stuck in the brush.

Similar to burns carried out for objectives relating to science or ecosystem management, *mestizo* agricultural burns have a culturally accepted system for determining when and how the burn should be conducted. Rather than relying on quantitative measurements for determining the timing for a burn, farmers base their decisions on qualitative measurements and empirical knowledge. When one compares the *mestizo* system with the science-based management system, it is apparent there are many parallels between the two. **Table 4** relays the most common conditions necessary to stay within a fire prescription for both *mestizo* farmers in Nicaragua and resource managers in North America. While this is a simplification of the two systems, it demonstrates that science-based burns rely more heavily on technology than farmers.

Table 4. Factors considered and included in *mestizo* and prescribed burns.

Rx Burning in resource management	Burning for *mestizo* agriculture in Nicaragua
1. Priority: control and safety	1. Priority: speed and efficacy of burn
2. Weather - Moon, not a consideration - Temperature, medium to cool for greater control - Wind, light to moderate - RH, medium	2. Weather - Moon, no burning on new moon - Temperature - hot - Wind, light to moderate speeds - RH, medium, seasonal transition
3. Burn Crew - 6-10 trained and certified adults - Protective Nomex© clothing and helmet - Concern with containing spotting and escape - Stay in the black	3. Burn Crew - 1-3 family members or neighbors, children participate - Normal daily work clothing - Spotting and fire escape acceptable - Rely on speed in lighting fuel and consumption
4. Tools - Drip torch, - Mccloud rakes, Shovel, water packs, etc. - Water truck, hose, mower	4.Tools - *Tizón* of guascuao wood, or corn cob soaked in kerosene, - Broom or stick to guide fire line, - Machete - Drinking water only

How to burn

Farmers explain that burning must start by building *rondas* or fire breaks. The width that they verbally recommended was 2-4 m, depending on the amount of fuels (higher fuels, wider fuel break). Nevertheless, there was a large difference between what farmers recommended for fuel breaks and what was observed in practice. Fire breaks were generally very narrow and even completely absent in one of the burns. Narrow fire breaks likely contributed to the fires spotting and crossing over to nearby forests. Fields, rather than forest, surrounded the one burn in which an escape did not occur. Farmers did not appear to be concerned by the fire entering the forest, although two of the farmers made an effort to contain the forest fires. Nevertheless, when explaining burns, farmers did say that it is important to *apaciguar* or tame the fire so that it does not enter the forest.

Farmers related two different strategies for lighting the fires, but informants were divided on which was the most appropriate method. Many farmers explained that it is important to conduct what is known to fire scientists as a backing fire, where the fire is lit from the downwind side of the burn area and the fire front moves slowly and directly against the wind. Other farmers felt that a heading fire is more efficient because fires are hot and gain strength from moving with the wind. The farmer uses the Tizón for lighting the perimeter of the fire striking the fuels with the flame every two to three meters. What was observed in practice is that ring firing was more commonly used when there were large fuel loads (*i.e.* from a longer fallow period). Table 5. provides a summary of the burns, the width of fuel breaks and the firing techniques employed on each burn.

Table 5. Summary characteristics of the participant observation burns.

	Number of participants	**Date**	**Start time & burn duration**	**Area burned**	**Lighting technique**	**Fire Break**	**Es-cape**
1	2 adults, 1 child	4/24	12:30 p.m. 18 minutes	1.4 ha	Ring firing	.5-1 m	Yes
2	4 adults, 1 child	4/25	1:45 p.m. 15 minutes	2 ha	Backing fire	.5-1 m	Yes
3	4 adults	4/26	2:10 15 minutes	1.8 ha	Pile burning fire	.5 m	No
4	3 adults	4/28	3:15 22 minutes	2.5	Flanking fire	1.5 m	Yes
5	2 adults	4/30	11:30 a.m.	3.5 ha	Heading & flanking fire	none	Yes

During ring firing, the downwind line is ignited, and then the entire perimeter is ignited in a circle. The convection from the fronts draws the fire into the center. Some of the farmers lit spot fires in the middle of these burns in order to facilitate the converging fronts. During these types of burns, strong convective patterns were observed and flame lengths often surpassed 10 m. Figure 2 provides an example of the ring lighting method applied to agricultural plots. The fire portrayed in this figure burned very hot and fast and was considered a success by farmers because fuels were almost entirely consumed. When the final section of the perimeter is lit, the farmer referred to this move as to "atajar" the fire, meaning to cut off the fire or control it.

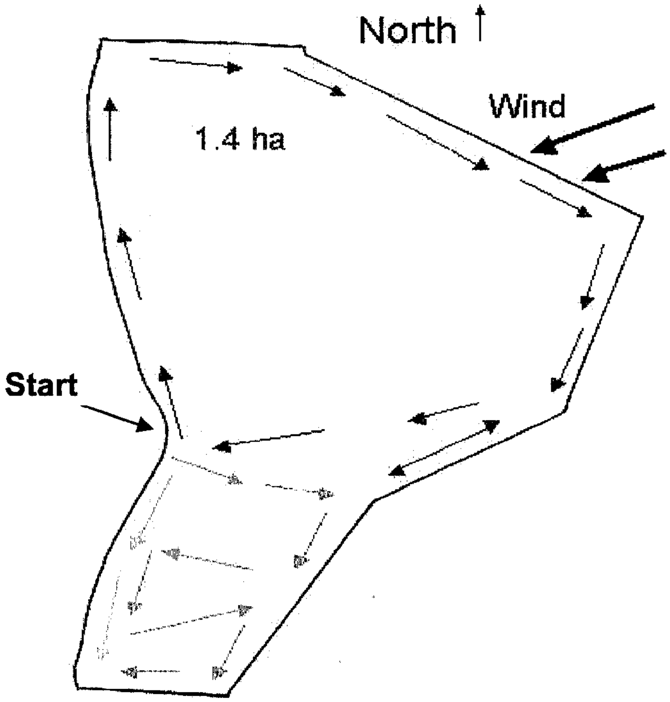

Figure 2. Example of ring firing in agricultural burn. Northern portion of the plot had heavier fuels. Fire was first anchored along the downwind side of the burn area. Farmer proceeded to light fire around perimeter as convection drew outer fire fronts into the center. Smoke column reached 30-50 meters. Burn was on April 24, initiated at 12:30 p.m. and lasted eighteen minutes.

One final consideration during burns is that farmers do not want the fire to cross over into neighboring farms. There is a belief that if ashes from an individual's own burn land on a neighbor's plot, it will diminish the intensity of the neighbor's future fires. Furthermore, the overall effect of this would be to weaken the neighbor's soils and lead to the non-productivity of his land. Farmers say that legally they are bound to compensate their neighbors for any damage to homes or infrastructure a fire might cause. In the years of the Somoza dictatorship, farmers said that if one did not pay for damages, the neighbor could call *la guardia* or civil police, which could lead to a serious predicament.

Farmers use very descriptive language to describe both the action of burning and the fire behavior itself. Not all fires are created equal in their eyes. There are essentially two categories given to fire: fierce and tame. A good fire is one where fire burns intensely and it also know as *fuego bravo*, or fierce fire. Positive words are associated with these types of fire behavior, such as; *fuego bueno* (good fire), *recio* (strong fire), *bravo* and (fierce fire). The flames associated with this type of good burn were also positive and were described as *llamaradas* (large flame) or *la fogalata* (large fire). Hot fires are preferred in agriculture because they leave land clear for planting and are most often associated with [illegible]

Farmers are able to explain the physical relationships enabling fire. In the fire triangle used by fire scientists, there are three major components: radiant heat, air and fuel. While farmers may not use a triangle, they understand the interactions that create fire. They mentioned that fire is part of the air in a way because it feeds off of the air. They also explain that where there is no fuel the fire will not stick or hold. Furthermore, *mestizo* farmers understand that fire behavior can be very erratic and unpredictable under certain weather conditions. They explain that wind is capable of throwing fire great distances and that sparks cannot be trusted because they are *traicionero* (traitorous).

Following burns, farmers wait for the arrival of the rains before they begin planting. Planting generally takes place following the first two to three heavy rainfalls because soils should be at field capacity before planting.

3. Perceived value and effects of fire

The nature of human-fire relationships is characterized by both the utility of fire and the values that local people ascribe to fire. Farmers perceive burning to have multiple benefits for agriculture. During ethnographic interviews, the most frequently mentioned benefit from burning was an improved harvest (Table 6). Farmers make strong statements, such as, by burning they were guaranteeing a successful harvest and without a burn the land would be of no use. Several farmers mentioned and compared specific crop characteristics, pointing out that without a fire, crop leaves are yellowish and with a burn, they are vibrant green. One final explanation of the direct effect of fire on crops was that the plants would *levantar* or grow-up with greater strength where a burn had occurred.

Such statements allude to the belief that fire has a fertilizing affect on the soil. Several farmers stated more directly that fire enriches and gives "strength" to the soil and that the ash that falls on the soil helps the crops to grow. While the biophysical validity to such beliefs has not been tested *en situ*, these beliefs guided the farmer's decision-making process.

Table 6. Beliefs, rank ordered according the frequency mentioned by farmers.

Perceived Benefit	Comments
1. Improves harvest	Guarantees a good crop, where fire does not burn, the garden is no good, *no va a servir*
2. Cleans the soil	Earth is cleaned, easier to work the land, plow does not get caught, avoid labor in clearing
3. Enriches soil/fertilizes	Ash helps milpa grow, *darle fuerza a la tierra*
4. Suppresses weeds	*Quema maldad de hierbas malas,* few weeds grow
5. Kills insect pests	There are less pests, kills the insects that eat the corn

At the time of the burns, farmers expressed their desire to burn in a way that would leave the soil bed clean of vegetation. This cleaning process was another frequently mentioned benefit to burning. If the land is clear of litter then the oxen and plow can pass through with greater ease and there is less risk that the plow will get caught on vegetation. Even those farmers who use a dibble on the hillsides can plant more easily after a hot burn.

This clearing process can also be considered labor saving, as it was suggested that

Another secondary objective is to eliminate or decrease the incidence of pests during the cultivation process. Local people usually consider that fire is important because it kills the small ants or other animals that attack and pull out the planted maize seeds. However, one farmer said that burning actually increases the attacks of pests. Plant pests are also minimized by the burns. As one farmer said, "fire burns the bad out of the bad herbs." After the burns, there are generally larger branches and coals remaining from the fire. Farmers state that any branches or wood left over from the burn is collected for

Presumably, if local people have been carrying out similar subsistence burning practices for generations, they would have had the opportunity to observe the effect of burns on the forest for a long time. Farmer's perspectives on the effect of fire on forests are worth noting because ethnographic interviews demonstrated that farmers have a thorough understanding of forests in other topic areas. For example, during interviews, they were able to explain methods for identifying trees according to their bark and leaf position. They knew the color, shapes and dispersal mechanisms of many of the less abundant tree seeds. They were also able to identify wildlife preferences for food. The in-depth knowledge of the forest is also evidenced by their ability to perceive the relationship between rainfall and forests. They described the process of evapotransipiration by saying "the trees call the water" and "the rain forms due to the freshness of the tree leaves". They can also distinguish between different successional processes. For example they explained how a field left fallow in the middle of a pasture would take 100 years to return to forest, but a field left fallow in the middle of forest it would return to forest within10-20 years.

Given their intimate knowledge of forest dynamics, it is understandable that *campesinos* have beliefs about the effects fire has on the forest. Although farmers did not mention fire as a risk to human safety and infrastructure, many stated that fire poses a risk to the forest. Farmers say that when fires enter a healthy forest, the flames remain close to the forest floor and most of what dies is small herbs. Nevertheless, if the fires gain strength and flame lengths reach the height of a man, the fire is capable of killing wildlife and the entire forest. This type of fire behavior occurs when the forest understory is not *clean.*

Furthermore, after an intense fire of high flame lengths, the forest grows back more dense and is no longer the same. Another concern is that wildfires can burn useful firewood within the forest. Similar to the example of the decreasing wildlife abundances, farmers are primarily concerned with the ecological impacts that directly impact their livelihoods.

We asked farmers what were the effects on the forest of differing fire return intervals. The categorized responses are provided in Figure 3. Nearly all felt that if fire were to enter the forest every fifty years, you would not notice any change. They described it as though there would be a new, reborn forest. Responses for the thirty-year fire return interval were similar to the fifty-year return interval. Farmers said thirty years would provide enough time for the forest to become fresh and cool again and in this time the forest would be recovered. Changes to the forest would be minimal. Within the ten-year fire return interval, there was some disagreement on the severity of the impacts but farmers felt that the forest would not recover and instead would become like a scrub forest with low, dense vegetation and mostly shrub species. If fires were to occur every year, farmers all agreed that there would be no vegetation except a few vines. They mentioned that the ground would be similar to a desert. Perhaps such statements indicate an understanding of the sterilization of soils with repeated fires.

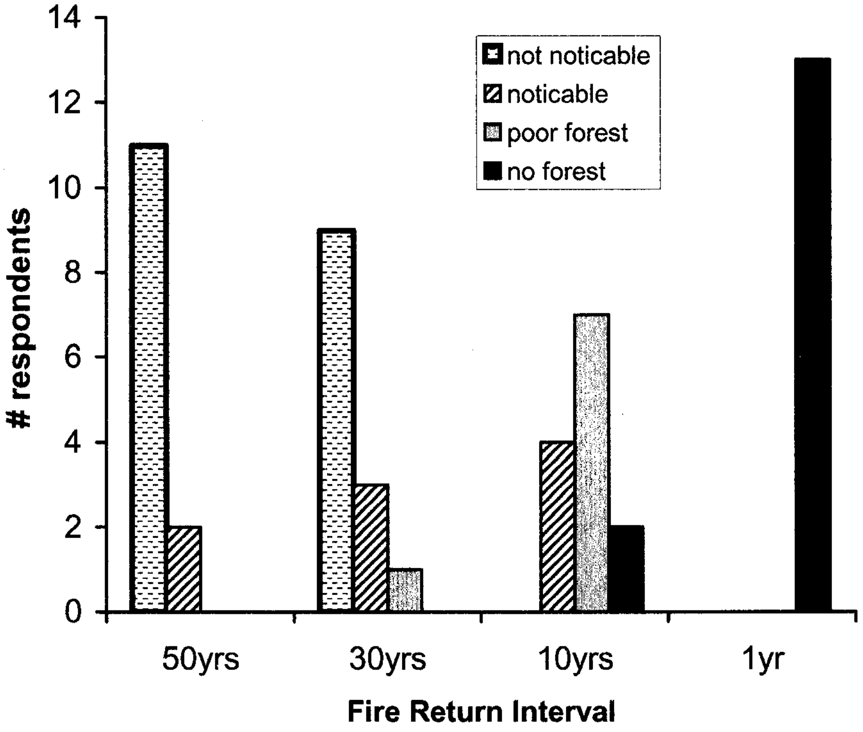

Figure 3. Perceived effect of differing fire return intervals on forest quality.

CONCLUSIONS

Through our research, we have documented the importance of subsistence burning for the mestizo household at the Chococente Wildlife Refuge. Given the cultural and material importance of fire, particularly with respect to agriculture, it is unrealistic to expect that farmers will abandon its use. Nevertheless, it is clear that subsistence burning contributes directly to the incidence of wildfires in the tropical dry forest, even though farmers are aware of the danger that frequent fires pose to forests. Those agencies hoping to reduce wildfire incidences should recommend minor adjustments to burning practices in order to reduce the spread of fire into the forest without impacting the ability for farmers to carry out traditional burning practices. Furthermore, scientists studying the ecological effects of fire on dry forests would benefit by integrating the long-term observations made by *mestizo* farmers into their short term ecological studies.

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CHAPTER 2: FIRE EFFECTS ON A NEOTROPICAL DRY FOREST PLANT COMMUNITY IN SOUTHWESTERN NICARAGUA

INTRODUCTION

Fire is a necessary disturbance for maintaining plant assemblages in ecosystems throughout the world, including areas of the tropics. For example, fires are an important factor in sustaining plant communities such as African savannas (Trollope 1984), high-elevation *paramo* vegetation (Horn 1993), and Neotropical savannas (Kellman 1984). Although fire disturbance is an essential dynamic in many tropical ecosystems, it is tropical moist forests are expected to shift with increased fire frequency (Cochrane and Schulze 1999).

Our research considers the effect of wildfire on seasonally dry tropical forests. These ecosystems experience several months of severe or absolute drought on an annual basis (Mooney *et al.* 1995) and they are important to global conservation because they are centers of endemism (Gentry 1995) and have high levels of mammalian and other life form diversity (Mares 1992; Medina 1995). Dry forests also generally have high human population densities throughout their distribution (Murphy and Lugo 1995) and hence they are experiencing very high rates of habitat loss. Fire is a major disturbance factor within seasonal forests particularly because dry season conditions enable easy burning for those people applying fire as part of their subsistence activities (*i.e.* agriculture and hunting). Fires can easily ignite and spread within an intact dry forest, even after as few as nine rainless days (Blate and Putz 2003).

Although dry forests burn more readily than moist forests, research examining the effects of fire on this ecosystem has been limited to a only a few studies (Saha and Howe 2003, Marod *et al.* 2002, Kennard and Gholz 2001, Pinard and Huffman 1997). Rather than studying the impact of fires on an intact dry forest, most other fire research in dry forests has focused on either 'slash and burn' fires (Kauffman *et al.* 1993; Sampaio *et al.* 1993; Hammond 1995; Miller and Kauffman 1998) or the impact of other tropical disturbances coupled with fire (Snook 1996; Dickinson *et al.* 2001). The limited research considering

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dynamics, particularly when one considers that 42% of intratropical vegetation is dry forest (Mooney et al. 1995; Murphy and Lugo 1986).

Our study focused on the community effects of fire within a Central American dry forest (CADF). CADF is one of the most threatened ecosystems globally (Janzen 1988) and what remains of the forests persists only in fragments and degraded patches (Sabogal 1992) along the lowland Pacific slopes of Southern Mexico and Central America and also throughout the lowlands of the Yucatan Peninsula. Annual rainfall in CADF is less than 2000 mm and is concentrated within a period of approximately 6 months (Murphy and Lugo 1995). During those dry months, northeasterly winds blow across the western leeward slope of the region at high speeds, further drying the vegetation and dead fuels.

Patterns of anthropogenic fire disturbance and its effect on the forest are well illustrated in CADF, in large part because over 79% of Central America's human population lives within the dry forest life zone (Tosi and Voertman in Murphy and Lugo 1995). People living throughout rural Central America apply fire within the forests or along forest margins for shifting agriculture, hunting, and collecting honey. After fires are set, there is little effort to control or extinguish such fires.

Although the impact of fire within CADF is poorly understood, it is generally considered by conservationists to be detrimental to the forest (Janzen 1998 and 2002). This perspective is widely accepted and regional governments have adopted total fire suppression policy as a strategy for dry forest management. Nevertheless, lessons in fire management from North America have demonstrated the need to better understand the ecological role of fire disturbance prior to the adoption of a policy of complete fire suppression. One argument often used against fires in the dry forest is that they are anthropogenic and therefore not part of any 'natural' disturbance regime (Janzen 2002, Saha and Howe 2003). Nevertheless, there is evidence for non-human ignition sources within this ecosystem by either volcanic ignition (personal observation; Goldammer and Seibert 1989 in Cochrane 2003) or lightning (Middleton et al. 1997). Furthermore, humans have long inhabited CADF and recent paleoecological evidence from CADF areas indicate that – during pre-colombian times – fires occurred frequently and were influential in shaping the landscape (Sally Horn, personal communication). If human-ignited fires occurred frequently over millennia, fire would have played a selective role in determining forest community composition.

The historical and present day influence of fire as well as the seasonal nature of the dry forest begs the question whether fires may actually play a role in maintaining this ecosystem. Given the sharp differences in opinion regarding the role of fire in the tropical dry forest and considering the lack of scientific research on which to base fire management decisions, we set out to address the following general questions:

In order to address the first question, we developed a series of null hypotheses regarding the effect of fire on density and diversity of the forest community, which includes the herbaceous understory, lianas and trees. These hypotheses include:

H_o1: Fire has no affect on mortality of overstory trees.

H_o2: Fire has no affect on recruitment of trees, shrubs or lians.

H_o3: Fire has no affect on species diversity.

H_o4: Fire has no affect on forest structure (*i.e.*, increases or decreases in tree, herb, shrub, liana, seedling or herbaceous strata)

If null hypotheses were rejected, we then sought to gauge the longevity of these effects by repeated monitoring for four years after a single burn event. We also analyze shifts in vegetation diversity and structure in view of concerns for biodiversity conservation within the dry forest.

STUDY SITE

The Río Escalante-Chacocente Wildlife Refuge (hereafter Chococente) is located along the Pacific coast of southwestern Nicaragua, Central America (Figure 1.) within the coordinates 11° 30' 33.0" and 11° 35' 28.5" latitude north and 86° 08' 33.7" and 86° 14' 43.1" longitude west. The mean annual temperature is 26°C and mean annual precipitation is 1408 mm (INETER 2001). Rainfall is highly seasonal and is generally

Chococente with lowest and highest recorded annual rainfall between 822 mm and 2113 mm respectively, recorded between the years 1991 to 2000.

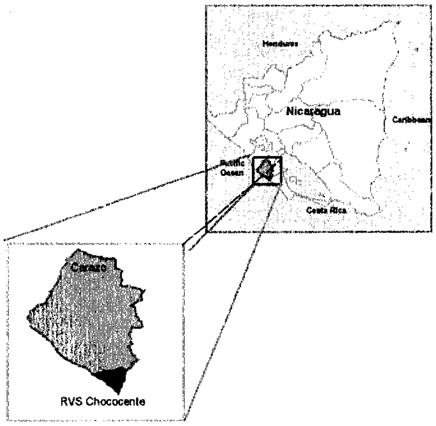


Figure 1. Location of Chococente Wildlife Refuge in Department of Carazo, Nicaragua.

Chococente encompasses 3634 hectares and is located only 80 km from the nation's capital of Managua. Approximately 73.5% of the reserve is forested, including mangrove, upland dry forest, and riparian forests (MARENA 2002). Chococente is a critical site for dry forest conservation because it includes the largest area of dry forest in Nicaragua and represents one of the last remaining old growth dry forests of the region (Sabogal 1992). Conservation management within this protected area is complex because both large and small landholders privately own all the land. Over one thousand local people reside within the reserve boundaries and practice agriculture and hunting for subsistence. The human presence within Chococente makes it an ideal site for studying the ecological impact of wildfire because human fire use of fire in dry season subsistence activities often leads to fire ignitions within the forest.

METHODS

From 1999 to 2001 we monitored the effects of wildfires and experimental burns on the forest community at the Chococente Wildlife Refuge. Below we divide field methods between a experiments and field observations.

Prescribed Burn Experiment

During 1999 we established four, 15x75 plots randomly located and permanently marked. Plots were divided into fifteen, 15x5 meter subplots. Plot locations were selected according to practical considerations including: relative accessibility by road, level topography for better control, and a willingness of the private landowner to participate in prescribed burns. At the end of the rainy season of 1999 (December), we mapped and measured the diameter and height of all woody vegetation greater than 1.5 meters tall, including lianas. We then counted the number of individuals of all woody vegetation less than 1.5 meters height and recorded their species. All woody plants were identified to the species level. We also sampled herbaceous vegetation using the modified Whittaker design (Stohlgren *et al.* 1995). Herbaceous and woody species were sampled and identified at the National Herbarium in Managua, Nicaragua and the Missouri Botanical Gardens.

Immediately prior to experimental burns, fine and course woody debris was measured using Brown transects (Brown 1974) and leaf litter was sampled using 19 m^2 circular plots and subsequently dried and weighed. Leaf litter sample plots were randomly located and arranged in sets of four at random locations within the 75x15 m plot.

During the height of the dry season, when wildfires often occur, we conducted three separate prescribed burns within the plots, leaving one randomly selected control plot unburned. Weather conditions (temperature, relative humidity, wind speed and direction, and fuel moisture) were recorded and burns were carried out within prescription. During the burn, we recorded flame length and speed as well as other indicators of fire behavior. The fires did not burn evenly across the plots and hotspots developed in areas of large woody debris while fires did not burn at all in other areas. Fires were generally absent in areas characterized by *Opuntia sp.* (prickly pear cactus) or where soils were particularly rocky. Local residents helped to carry out burn treatments using a kerosene-soaked branch as a lighting tool. All three experimental burns were low intensity surface fires with a mean char height of 16 cm and an average rate of spread of 0.76 cm/minute. Such fire's are slightly more intense than that observed in moist tropical forests where flame heights of 10 cm creep along the forest floor (Cochrane 2003). One day following the burns, char height was recorded on woody vegetation as a surrogate measurement of fire intensity. Hot spots were identified according to concentrations of visible white ash or if they were burning longer than 24 hours and then marked with flagging for follow-up on post-fire recovery.

Table 1. Methods for measuring forest community responses in natural experiment.

Units	Variables Measured	Timing of Measurements
Four, 15x75 m plots, each divided into fifteen subplots	**Woody Vegetation > 1.5m height:** location, dbh, height, species, char height, mortality and resprouting	4 months prior to burn (year 0). 8, 20, and 33 months after burn (years 1, 2, 3)
Fifteen, 5x15 m subplots within 15x75 m plots	**Woody Vegetation < 1.5 m height:** frequency count, species, from resprout or seed	
Four, Modified Whittaker Plots within 15x75 m plots	**Herbaceous species:** frequency, cover	

For three successive years following the burn, we sampled the post fire vegetation (December of 2000, 2001, 2002) repeating the same sampling methods as those employed prior to the burns for both woody and herbaceous vegetation. Additionally, we followed the revegetation of hot spots for one year. In order to follow up on herbaceous species that increased after fire, we made observations of the most abundant post-fire herbs in paired burned and unburned plots. We sampled random plots along linear transects within areas recently burned, areas of soil disturbance (fire break lines), and areas of no disturbance, estimating the density and cover of the three most abundant herbaceous species following fire.

Natural Observations of Wildfire Effects

The forestry department at the *Universidad Nacional Agraria* (UNA) of Nicaragua established multiple 1 Ha permanent forest monitoring plots in 1992. Each 1 Ha plot was divided into 25, 20x20 m subplots. Within these subplots, trees and shrubs > 10 cm dbh were located and permanently marked and the species, dbh, and height were recorded. UNA resampled these plots annually between 1992-1994. Saplings and seedlings were recorded in 5 randomly selected 20x20 m subplots from the 1 Ha plot. Within theses subplots the species, height, and dbh of regenerating trees and shrubs were recorded using the following methodology: 4-9.9 cm dbh sampled in 20x20m, >1.5 m height and <4.9 cm dbh sampled in nested 10x10 m, and seedlings <1.5 m height sampled in 1x10 m nested transects.

During the drought associated with the 1997-98 El Niño event, Plots A and B of the UNA permanent plots were burned in a wildfire. According to the UNA data, Plot B was also affected by a wildfire in 1994, although the extent of damage is believed to be small. We sampled these two plots during the rainy season of 1999 (1.5 years after the wildfire), Within UNA plots, we carried out further sampling in addition to the protocol established by the university. Intensive sampling of saplings and seedlings was carried out in 2000, 2.5 years post-fire, to compare seedling and sapling densities among burned and unburned subplots, statistically treating burned and unburned areas as paired. We sampled the following size classes: a) <1.5 m height in 10 m^2 transect, b) >1.5 height, in 25 m^2 c) > 4.9 m dbh, < 10 cm dbh in 100 m^2.

There were strong differences between Plots A and B. Plot A has relatively level topography and is located several hundred meters from the coast. Plot A also has a well-developed forest canopy with an understory that is primarily shaded. This plot is difficult to access and there were few signs of human disturbance. Plot B has has steeper topography and is more subject to human disturbance from hunting, cattle grazing, and honey collection.

Analysis

Response variables measured include woody vegetation mortality by size and life form, recruitment by species, resprouting behavior, changes in density and diversity. We used the Shannon-Wiener index throughout as a measure of diversity. Initially, we analyzed treatment effects as an Analysis of Variance (ANOVA), comparing burned and unburned treatment plots. We use a two-way repeated measures ANOVA with Box's Greenhouseinsignificantly different from pre-burn samples. We used Bonferronii multiple comparison tests to assess differences among years and between control and treatment plots.

For the wildfire observations, subplots were treated as replicates, despite the fact that they arose from a single fire event. Although, these represent replicates for assessing the effects of this particular fire, they are pseudoreplicated with respect to the effect of fire in general. Our experimental plots include three separate fires, and are thus more

independent. Nevertheless, we again treat subplots as replicates, and therefore are not able to generalize about the effect of fire. Subplots that were not burned in experimental plot three were considered to be part of a control during analysis. Although we have no

Woody Vegetation

a) Effect of Fire

The most easily observed impact of fire on woody vegetation is through heat-induced mortality. Two potential predictors of mortality are tree size (dbh and height) and fire intensity (char height). We applied a logistic regression test to the relationship between mortality and these two predictors for all trees and shrubs within treatment plots that were burned by the experimental fire. With greater tree size there was an increased likelihood of survivorship, while with increased char height there was a decreased likelihood of survivorship. The overall model is significant and correctly predicts 82% of the responses correctly.

Table 2. Logistic regression for predicting mortality of woody species, Dependent variable 0=dead and 1=survived; Overall model predicts 82% of responses correctly.

Variable	Beta	Standard Error	Chi-Square	Probability Level
DBH	0.1718	4.0675	17.85	.000024
TREE HEIGHT	0.4078	7.6172	28.67	.000000
CHAR HEIGHT	-0.116	8.5264	185.87	.000000

As predicted by the logistic regression, post-fire mortality varied greatly according to size class (Figure 2). We present woody vegetation mortality as a sum of dead and top-killed vegetation using the following formula:

%Mortality = (#dead + # top-kill)/Total Individuals

The highest mortality (74%) was in the smallest size class (0-1.9 cm), while the largest size class experienced as little as 5% mortality. For woody vegetation with a diameter < 6 cm dbh, 21-30% of trees were completely dead. The percentage of dead individuals is halved to 10% in the next larger size class (6-7.9 cm), but only slightly decreases with increasing size in classes 8-9.9 and 10-19.9. Total combined percent mortality was at 12% for both these two highest size classes. The proportion of mortality represented by top-kill decreases with increasing size class. A small portion of the mortality (<2%) was a result of damage from both fire and wind.

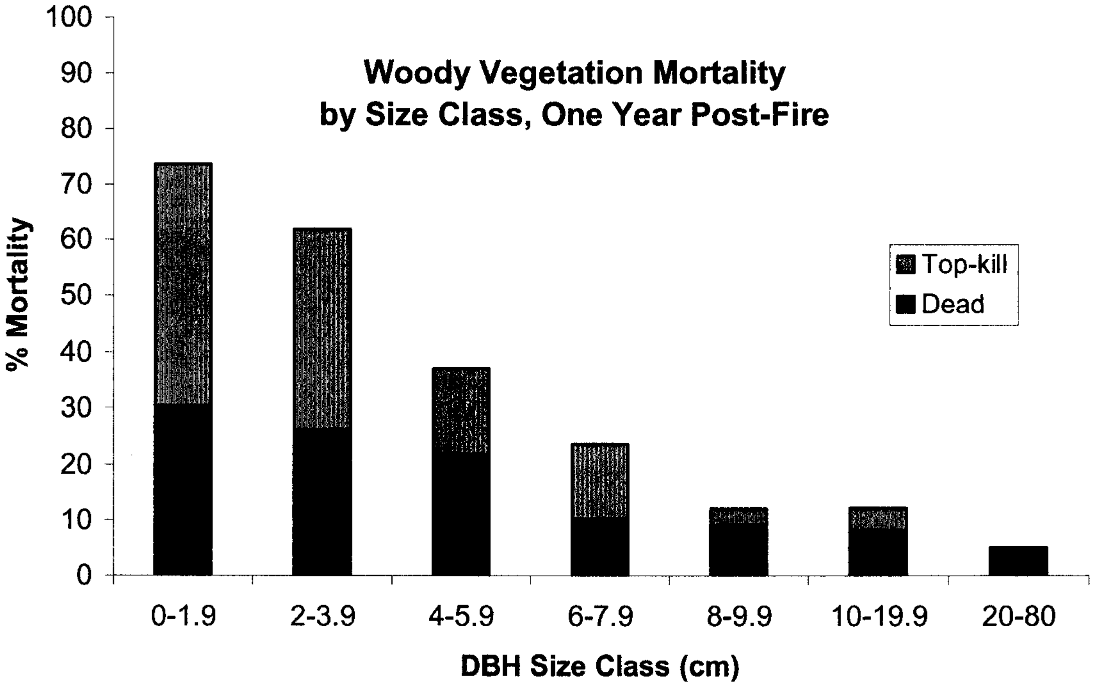


Figure 2. Percent mortality in woody vegetation (trees and shrubs) one year post-fire year. Y-axis = % mortality of total burned trees; X-axis DBH Size class in centimeters. Bars represent total mortality; gray portion is percentage dead and black is percentage top-killed.

Wildfires generally burn with greater intensity than controlled burns because they occur

However, in comparing post-fire woody vegetation >10 cm dbh in permanent plots with pre-fire vegetation (4 years prior to the wildfire), we found percent mortality similar to that observed in the experimental fire (Table 3). We only analyzed plots where there was evidence for 75% or more of the plot burned based on mapping of burned areas and observations of charring.

Table 3. Percent mortality for dbh size classes in experimental burn plots and permanent plots.

	10-19.9 cm dbh	≥ 20 cm dbh
Experimental Burn	12.2%	5%
Wildfire	12.4%	5%

Within the experimental plots, the mortality of woody species varied according to life form. In Figure 3 we separate mortality response between lianas, overstory trees and understory shrubs and trees. In the three smallest size classes, overstory trees consistently have a higher total mortality than shrubs, though trees in these size classes exhibited more resprouting and had a higher proportion of mortality attributed to dieback than shrubs (10-20% higher than shrubs). The proportion of total mortality attributed to death was consistently higher in shrubs than trees in all size classes. Shrubs and understory trees also had higher mortality than trees in higher size classes (> 7 cm dbh). For lianas, there appeared to be no relationship between liana mortality and dbh size class because

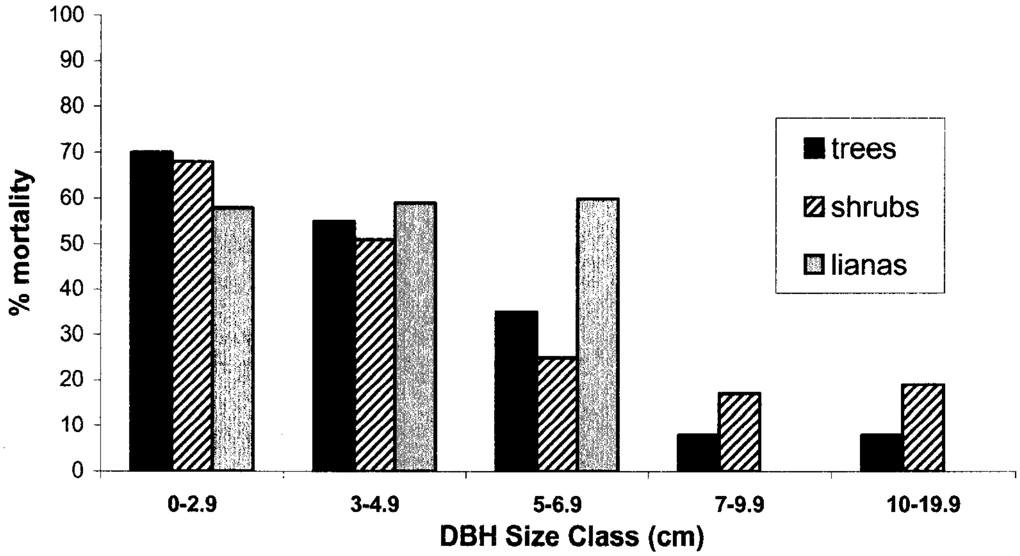


Figure 3. Percent mortality of Axis X – DBH Size Class, Axis Y – %mortality. Black bars represent overstory trees, striped bars represents understory shrubs and trees. Lianas are represented by gray bar.

b) Length of Effect

For all size classes, response to fire was most dramatic 1 year post-fire. For saplings (trees and shrubs <10 cm dbh), we carried out a two-way repeated measure to test the effect of time and fire treatment on stem density. Time, treatment, and the interaction between treatment and time all had a highly significant effect on stem density (P<.00001). Results of a Bonferonni (with control) multiple comparison test demonstrate that stem densities in years 1, 2, and 3 post-fire were significantly different than pre-fire densities (year 0) (Alpha = .05, MSE = 14.60), indicating that the greatest impact of fire in this size class occurs within the first year following fire. Treatment plots were significantly different from controls during all 3 years post-fire (Figure 4). There was a decrease in stem densities over time in both control and treatment plots and year 3 was

(48%) of the sapling mortality the first year post-fire is dieback, but by year three the portion of mortality attributed to die-back fell to just 16%. Changes in the proportion of dieback was primarily due to the death of previously resprouting saplings but also because some saplings marked as die-back were observed with living stems the following year.

treatment alone. Density of trees in treatment plots was significantly less than controls in all three years post-fire. Within controls, there was a significant decrease in stem density between years 1 and 3, presumably due to background mortality.

Observations of saplings in permanent monitoring plots A and B (>1.5 m height and <10 cm dbh), demonstrated that there was a strong and statistically significant decrease over time in the density of stems per hectare. Between 1991 and 1994 there is a significant decrease in stem densities ($P < .01$ for plot A and $P < .05$ for plot B). There was a more gradual decrease in stem densities in plots A and B between 1994 and 1999, even though there was a wildfire in 1998; this change was not statistically significant ($p = .076$ for plot A, $p = .11$ for plot B).

c) Positive or Negative effect

From the perspective of biodiversity conservation, fire effects may be qualified as positive or negative depending on their impacts on ecologically important or threatened plots diversity was not significantly less than pre-fire fire levels until year two post fire diversity (Alpha = .05, MSE = 2.998). However, treatment plot diversity was significantly lower than controls post-fire year 1 and with each successive year.

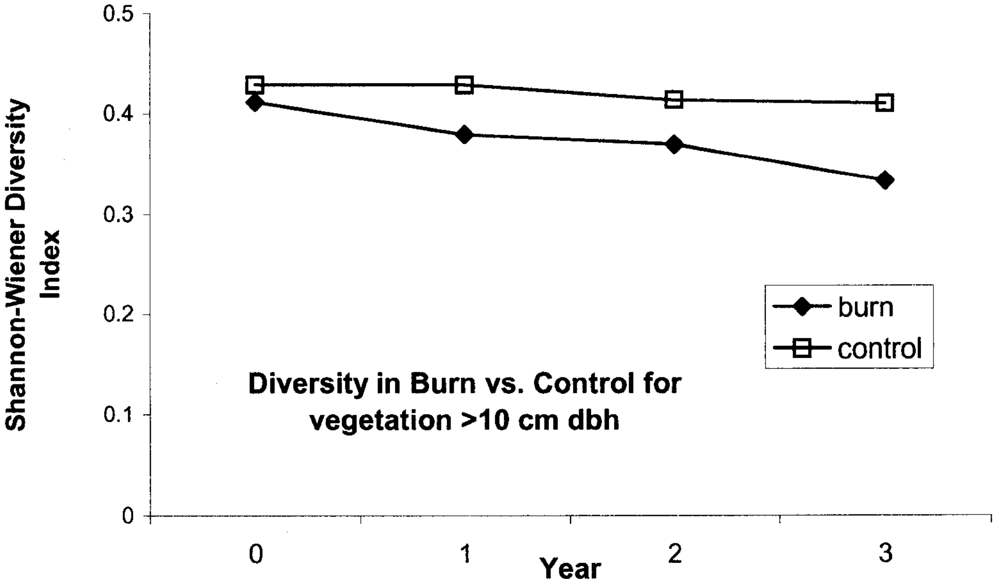


Figure 5. Changes in diversity for trees > 10 cm dbh in experimental burn plots. X-axis Year 0 is pre-fire and 1, 2, 3 are post fire, Y-Axis is Shannon-Wiener Diversity Index

In permanent plots, only slight changes in species diversity were observed over time among trees greater than 10 cm dbh. In plot A there was not a significant decrease between year 1994 and 1999, but 1999 had significantly lower species richness than 1992 (P = .027). For plot B, although there was a slight decrease over time in species richness, the changes between years 1992, 1994, and 1999 were not significant.

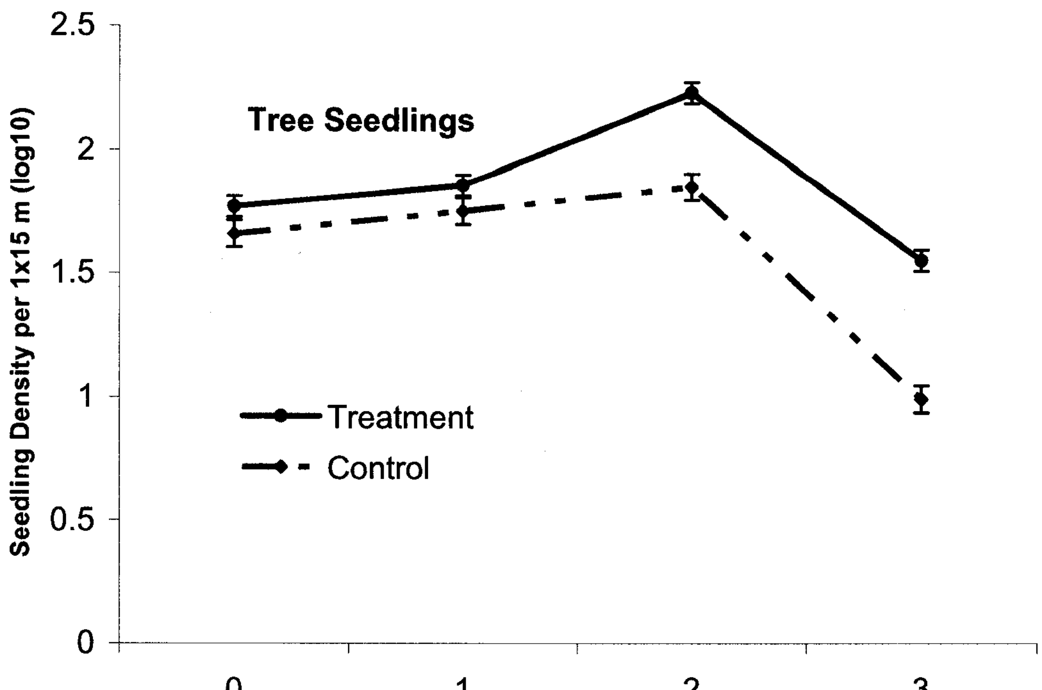
Woody Vegetation Regeneration

a) Effect of fire

Experimental fires had a small but noteworthy effect on seedling densities and richness. There was a slight treatment effect (P=.08) treatment X time interaction (P=.092), and a significant effect of year (P<.0001) on the density of all woody seedlings (including lianas). Multiple comparison tests show no significant difference between the control and treatment plots year one post-fire, but during post-fire year two, seedling densities in treatment plots were significantly higher. By year three, there was again no difference between seedling densities in control versus treatment.

b) Effect of time

By analyzing the different strata of the forest separately we find that burn treatments affect forest components differently. For overstory trees, there was a significant effect of treatment, year, and treatment X year interaction (P< .0001 for all). The density of tree seedlings was significantly higher all three years post-fire (Figure 6). For seedlings of understory shrubs, there was no treatment effect (P=.1), but there was a significant effect of time (P<.0001) and interaction between treatment and time (P<.0001). There were no significant differences in shrub densities until year 3 post-fire where treatment plots had significantly lower shrub seedling densities than pre-fire levels (Figure 7). For lianas, there is a significant effect of treatment and time and treatment interaction (P<.00001), but not for time alone. By year three post-fire, liana densities were significantly lower in treatment plots when compared to controls, despite the fact that liana densities had been higher in controls prior to the fire (Figure 8). In post-fire years one and two, 45% of the seedlings in treatment plots were resprouts; however, by year three, the proportion of seedlings that were resprouts was reduced to 30%. In sum, over time, tree seedling densities became higher in treatment plots, while shrub and liana seedlings are significantly lower densities in treatment plots ($P < .0001$).



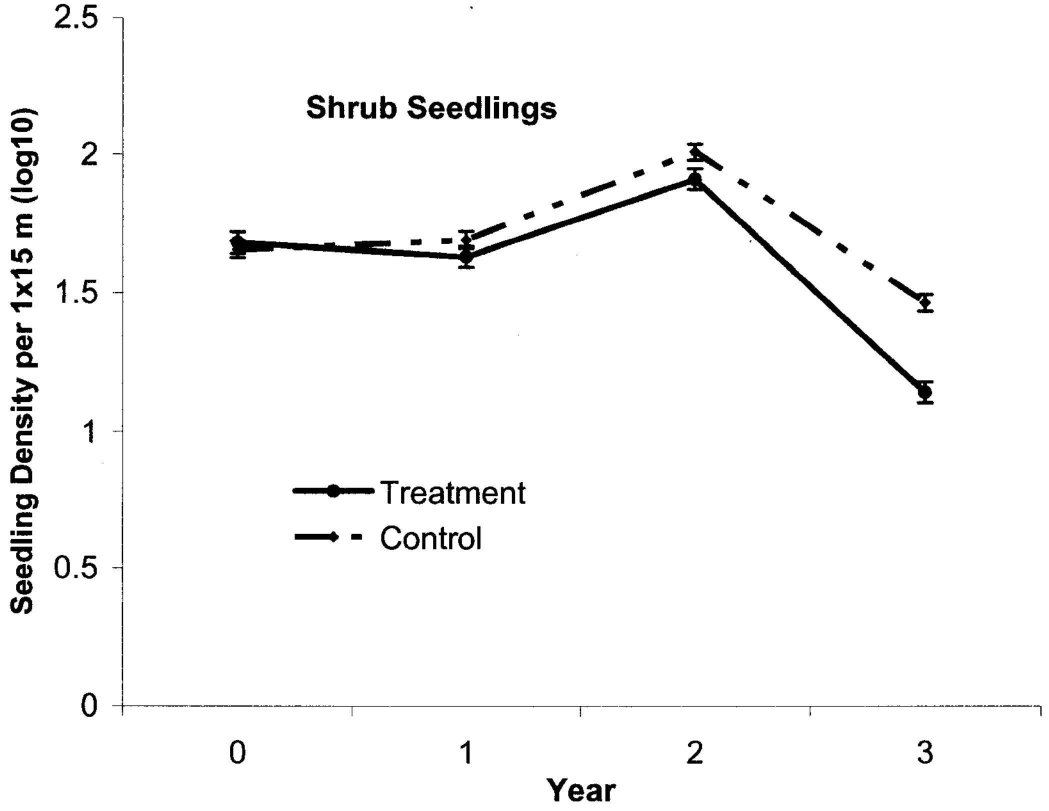


Figure 7. Shrub seedling densities before and after fire treatment. X-Axis – Treatment year 0 is before fire and 1, 2, 3 are post-fire Y Axis – Seedling density per 1x15 m (log10)

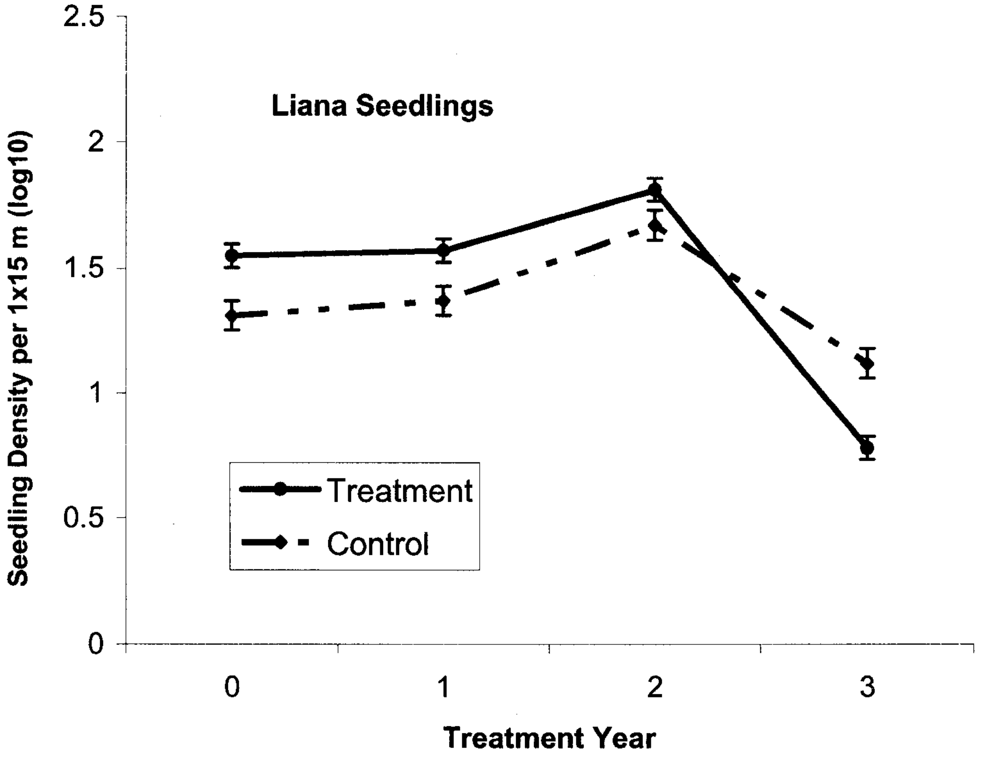


Figure 8. Shrub seedling densities before and after fire treatment. X-Axis – Treatment year 0 is before fire and 1, 2, 3 are post fire Y Axis – Seedling density per 1x15 m (log10)

Changes in seedling density (<1.5 m height) over the 8-yr period are illustrated in Figure 10. The density of seedlings in plot A was consistently less than that of plot B throughout the monitoring period. Seedling densities decreased significantly in both plot A and B between the years of 1992 and 1994. The sharp decrease in seedling densities in plot B in 1999 coincides with a 1994 dry season fire affecting plot B. Sampling was carried out immediately following the fire during the dry season (as opposed to our sampling in the rainy season 1-2 years post-fire). In this burn, 2 of the 5 seedling transects were affected by fire and within these affected plots seedlings densities were very low (0.35/m^2). In 1999, two rainy seasons following the 1998 dry season fire, were the seedling densities in both plots A and B had increased significantly from 1994 levels and had returned to densities similar to those observed in 1992. Repeated measure ANOVA indicates that time has a marginal effect on seedling density (P = .08). Nevertheless, if one excludes data from 1994, there is no significant effect of time on

c) Positive or Negative Effect

Results of a two-way repeated measures analysis demonstrate that both time and burn treatments had a significant effect on seedling richness (P<.00001). Results of the Bonferonni (with control) multiple comparison test demonstrate that seedling richness in years 1, 2, and 3 post-fire were significantly different than pre-fire richness (year 0) (Alpha = .05, MSE = 14.60), thus indicating that the greatest impact of fire in this size class occurs within the first year following fire. Richness in controls remained significantly less than treatment plots all three years post-fire.

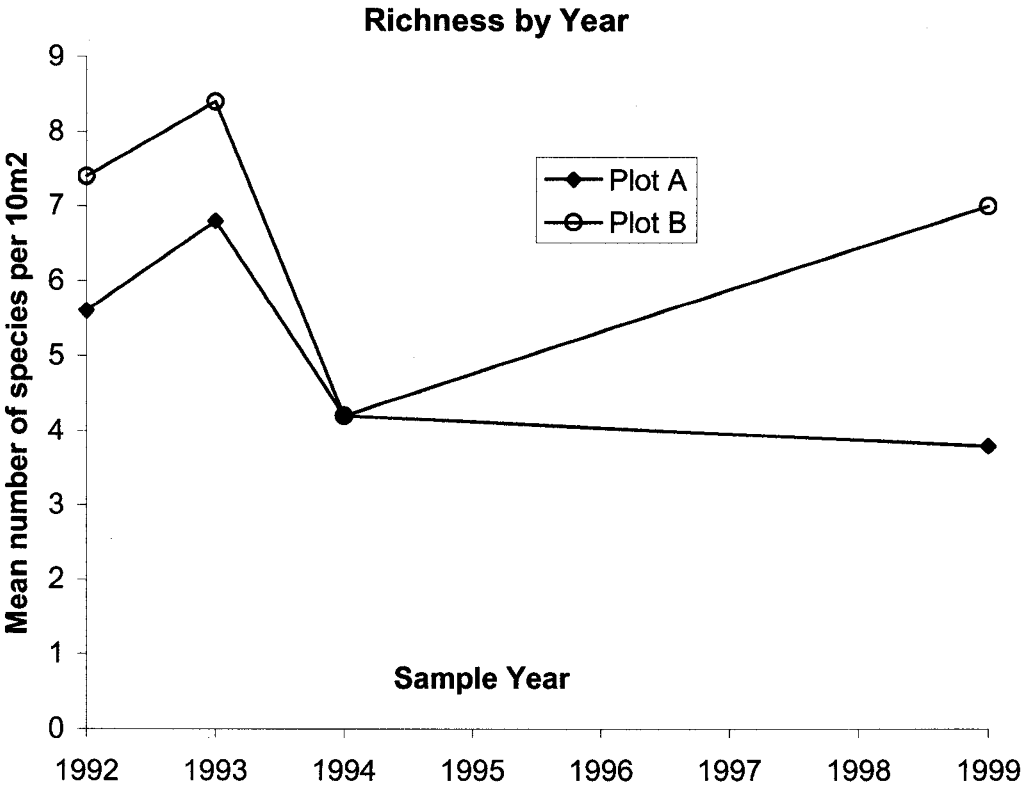


Figure 10. Richness over time in permanently monitored plots. Fire events were in 1998 and 1994 in plot B and only 1998 in plot A. X axis – year, Y axis – mean number of species per $10m^2$

For 1x10 m transects sampled within the permanent plots during the year 2000, t-tests pairing burned vs. unburned transects within Plots A and B showed similar trends. For Plot A, paired transects had significantly higher diversity in burn transects (P=.0002), and significantly higher density (P=.0086). Meanwhile, there was no significant difference among density (P=.86) and diversity in burned versus unburned transects for Plot B (P = .15).

The response of woody species regeneration was positive in hot spots created during the experimental burns. Although, the majority of hotspots were primarily herbaceous, nearly all contained some woody species regeneration and only 4 of a total of 35 hotspots were solely herbaceous plants. Of the woody species, 56% were tree species, 17% were lianas, and 27% were understory trees and shrubs.

Several of the regenerating species were locally rare or internationally endangered. For example, the numbers of Pacific mahogany (*Swietenia humilis*) seedlings increased from 2 individuals to 29 individuals post-fire. *Cordia gerascanthus* increased significantly, while seedlings of its counterpart in moist forests, *C. alliadora,* were almost completely eliminated from one year to the next. Seedlings of the internationally endangered guayacan (*Guaiacum sanctum* L.) was present in pre-fire plots, but its presence was noteworthy within hot spots and throughout burn plots. Guayacan seedling abundance increased four-fold the first year post-fire. A locally rare species, *Rauvolfia tetraphylla L.*, was observed within hotspots and in other locations throughout burn plots. This understory shrub was not observed at all in pre-fire observations, nor was it observed in control plots post-fire. Other tree seedlings only observed following fire, and absent in control plots were of *Zanthoxylum monophyllum* (Lam.) P. Wilson and *Randia cf mon*antha Benth.

The only pioneer tree species that emerged following fire was a species of wild papaya (*Carica papaya*). It was never observed outside of burned areas. In experimental treatment plots there were a total of 6 individuals ranging between 2-4 m tall. Ceiba (*Ceiba pentrandra*) is another tree species that emerged following fire and reached a height of 2-3 m by year 3 post-fire but seedlings of this species were observed outside of

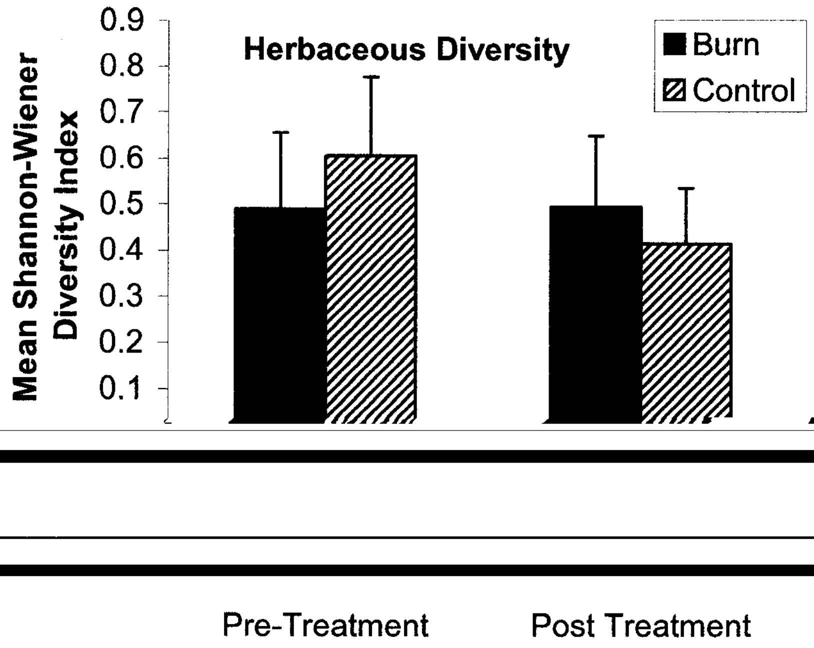


Figure 11. Herbaceous diversity before fire and one year later, post-fire treatment.

Treatment effects on diversity and density of herbs did not extend beyond the first year post-burn. There was no significant treatment effect across time, although there was a significant effect of both time (P<.0001) and the interaction between burn X time (P=.03 for density and P<.01 for diversity). Across time, there were no significant changes in diversity in treatment plots. Nevertheless, there was a significant decrease in herbaceous diversity in the control plot. Similarly, the density of herbaceous plants decreased significantly in the control plot, and density increased in all treatment plots. Increases in density were only significant within plot number two.

Although there were grass species present prior to the burns, their abundance did not increase significantly following burn treatments. There was no presence of exotic grasses either before or after the fire event.

DISCUSSION

Our observations of mortality in woody vegetation are consistent with previous research in the tropics that have shown a strong relationship between mortality and fire intensity and size (Barlow *et al.* 2002; Cochrane and Schulze 1999; and Pinard, M.A. 1997). Although our results demonstrate that fire results in 12% mortality to woody individuals > 10 cm dbh, this level of mortality is far less sever than observed in moist tropical forests (*e.g.* 40-72%, Woods 1989; Kauffman 1991; Holdworth and Uhl 1997; Cochrane and Schulz 1999).

We observed no difference between mortality rates for adult trees in experimental burn plots and wildfire plots. Perhaps percent mortality resulting from wildfire may actually be higher, given that that our results may have included some trees that were not contacted by the fire, even though we only considered areas where fire certainly burned

2002; Woods 1989) and 50-74% in subhumid forest (Pinard *et al* 1999). The observed relationship between size class and resprouting behavior meant that many saplings persisted in the forest through dieback. Resprouting has been established as an important mechanism for persistence (Bond and Midgley 2001).

Our results show high mortality and low recruitment in lianas and thereby contribute to the debate regarding liana response to fire. Conflicting reports have emerged, with some authors reporting increases in lianas following fire (Woods 1989) or low rates of mortality (Pinard *et al.* 1999), while other research reports high liana mortality (Leighton and Wirawan 1986, Holdsworth and Uhl 1997, Cochrane and Schulze 1999). Lianas continued to respond negatively to fire [illegible]

There are certain species that exhibited an immediate response to fire that may be considered a “win” for conservation. For example, wild papaya (*Carica papaya*) was only observed in burn plots. While this species is clearly a rapid colonizer, given its fleshy fruit it likely provides food for wildlife studies. Previous studies comparing the effect of fire on wildlife shows a significant increase in species abundance and diversity of small mammals in burned areas (Fredericksen and Fredericksen 2002). Pacific mahogany (*Sietenia humilis*) – a threatened species of international concern – showed positive recruitment within burn plots. These findings are consistent with Snook (1996), who found positive mahogany recruitment following fire disturbance.

Considering that fire leads to a decrease in forest canopy diversity over time, we would expect that frequent fires would select against trees that are not fire-resistant and, over time, this would lead to an impoverishment of the forest. This is consistent with Saha and Howe (2002), who found that annual burning leads to increased species diversity. Nevertheless, at this time there is no evidence that fires in the dry forest at Chococente are occurring at such a frequency; rather, general observations point to fire return intervals in the forest > 10 years.

This three year study of fire effects is a first for dry forest. One other study in the moist tropics has documented mortality three years post-fire, considering trees > 10 cm dbh (Barlow *et al.* 2003). Similar to our results Barlow *et al.* found that mortality occurring between years one and three was significant, thereby documenting the longer term effects of fire on the overstory. Our results show a 13% decrease between years one and three, while Barlow *et al.* (2003) find a higher decrease closer to 20%. An even greater contrast to their study is that their results show first year mortality at around 60%, while mortality in our study for this size class is only between 5-12%. What is more, we saw many trees that were characterized as top-kill, still alive in post-fire two..

CONCLUSIONS

Although our study provides a first look at the effects of fire on a Central American dry forest, this study does not determine an approximate fire return interval for dry forest maintenance and conservation. Similarly, our research does not consider previous fire regimes or historical disturbances at the site. Similar to other dry forests, it would be difficult to find a dry forest that does not show some persistent effects of past disturbance (Dickinson *et al.* 2001). Other past and present disturbances very common throughout the CADF, such grazing (Stern *et al.*) and firewood collection, should also be evaluated for their detrimental role in dry forests.

The data presented here do not support the contention that total fire suppression is warranted. First, there is no strong evidence of forest degradation with fire. Second, there is an indication that certain species of conservation may depend on periodic fire disturbance in order to maintain their presence within the community.

Though our results do not strongly indicate that fires cause irreversible damage to the forest, we do advocate a more cautious approach to agricultural burning. At the end of this research period, we carried out workshops with local people who had participated in this research to demonstrate ways of containing agricultural burns and preventing their spread into the forest.

Whether ignition is from a natural or human source, fire is currently one of the principal disturbance factors in the dry forests and therefore a more in-depth understanding of its effects is crucial for developing appropriate strategies for dry forest conservation and management.

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CHAPTER 3: LIFE HISTORY RESPONSES TO FIRE IN SELECTED DRY FOREST SPECIES

INTRODUCTION

The Central American dry forest (CADF) has been identified as a global priority for conservation (Janzen 1988a, Lerdau *et al.* 1991). In order to ensure the protection of this ecosystem, it is imperative that the ecological processes regulating it are maintained or restored. Fire is a prominent disturbance throughout CADF (Janzen 2002, Koonce and González-Cabán 1990), occurring at high frequencies and with a low and moderate intensity. Although fire is crucial to maintaining other tropical dry ecosystems such as savannas (Trollope 1984; Kellman 1984), the extent to which fire regulates plant populations of the dry forest is unknown. In this paper we seek to identify and characterize CADF plant responses to fire.

It is widely believed that because fires in CADF are primarily anthropogenic, they are not a part of any 'natural' disturbance regime and are therefore detrimental to the forest. Some scientists go so far as to argue that fire is presently the largest threat to dry forest conservation (Janzen 1988a). Concerns regarding the impacts of wildfires are related primarily to the presence of introduced pyrophytic grasses (i.e. *Hyparrhenia rufa*) in interacting with non-native species to the entire CADF community, particularly because native species' responses to fire have not been thoroughly explored.

Fire's impact on the overall composition of CADF ultimately depends on the life history characteristics of the individual species that compose the forest. Fire-adaptive strategies generally revolve around a plant's ability to survive fire or to regenerate post-fire (Gill 1981; Keeley 1986; Bond and van Wilgen 1996). Surviving fire is often attained through protective features such as thick bark (Uhl and Kauffman 1990, Pinard and Huffman 1997, van Mantgem and Schwartz 2003) or by a plant's ability to produce sprouts that enable both persistence and vegetative recruitment (Bond and Midgely 2001). Species traits known to confer reproductive advantages post-fire enable rapid recolonization or population expansion following fire, these include wind-dispersed seeds (Janzen 1988b), fire-stimulated germination (Sweeney 1956), and serotinous cones with wind dispersal (Gill 1975). Among CADF species sprouting (Snook 1993), wind dispersal (Augspurger 1986, Janzen 1988b, Gentry 1995), and thick bark (Snook 1993) are all traits commonly observed. Absent or reduced buttressing in upland dry forest trees (Smith 1972) is also noteworthy because buttressing is known to increase the vulnerability of tropical trees to fire (Barlow *et al.* 2003). Although the presence of these traits do not necessarily indicate adaptation to fire, the possibility should be explored given the prominent role of have played a role in selecting for a dry forest composition that includes fire-adapted plants.

Bond and van Wilgen (1996) classified fire life histories according to reproduction and survival responses, providing four major factors for classifying fire responses: fire-recruiting species, non-fire-recruiting species, sprouters, non-sprouters. Fire recruiters are species that regenerate after fire from a seed bank and or have an increase in fire stimulated flowering or an increased seed release from serotinous cones. Species that sprout are often considered indicators of high-disturbance environments because they are able to tolerate a variable range of disturbance intervals (Bond and van Wilgen 1996). Sprouters can be categorized as obligate sprouters (genets rarely killed, recruitment consists primarily of resprouting) and facultative sprouters (genet mortality variable, recruitment from both seeds and sprouts) (Keeley and Zedler 1978; Christensen 1985; Keeley 1986). We predict that the majority of sprouters within CADF will be facultative sprouters, either as a result of a frequent and varied disturbance history or as a result of short fire return intervals.

If CADF were composed of species poorly adapted to fire, then one would expect dry forest species to be dominated by fire-sensitive species and we would expect fire to result in changes we would perceived as negative to the structural integrity of the forest (*e.g.* high mortality, low recruitment). In order to explore whether dry forests are vulnerable to fire, we set out to test the following hypotheses for fifteen most abundant dry forest species and for three species of international conservation concern.

H_1 - If species are vulnerable to fire, then they will exhibit both low survivorship and low recruitment

H_2 - If species are adapted to fire, low survivorship species will be accompanied by high recruitment or resprouting

H_3 – If species are resistant to fire then fire will not effect survivorship or recruitment

H_5 - If species are adapted to fire, seedling recruitment will increase markedly following fire

H_6 – If a forest is vulnerable to fire, then there will be an increase in weedy colonizing shrubs and trees and/or non-native species post-fire

METHODS

We established four 15x75 meter plots in an upland dry forest located at the Rio Escalante-Chacocente Wildlife Refuge in Southwestern Nicaragua. Local farmers report that this forest site had not burned for at least 20 yrs. Within each plot we identified all woody species > 1.5 m height, measuring the height and diameter of each individual and mapping its location for continued monitoring. We further divided each plot into fifteen, 5x15 m subplots, conducting species counts for all woody seedlings < 1.5 m height within each subplot. Sampling took place in December at the end of the rainy season. During the dry season following initial sampling we conducted an experimental burn in three of the four plots and left one randomly selected plot as a control. Burns were carried out within prescription and fires were low intensity surface fires. Fires did not consume 100% of the burn plots; therefore, immediately following the fire we recorded char heights on all woody vegetation and mapped the burn. We also marked hot-spots where intense fire was evidenced by white ash and bare clay soil. Hot spot locations were followed during the first year post-fire for observations of revegetation. Following the burn, we repeated pre-fire measurements exactly one, two, and three years from the time

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die-back) and the presence and type of sprouting behavior (basal, root, or stem) during each year post-fire.

ANALYSIS

We evaluated species responses for saplings (<10 cm dbh, >1.5 cm height) by selecting

Appendix II, IUCN endangered C1), and *Swietenia humilis* – Pacific Mahogany (CITES Appendix II, IUCN vulnerable).

RESULTS

We divide our results according to fire effects on 1) common woody species of the understory 2) species of conservation concern.

Common understory vegetation

The effect of fire on understory woody vegetation varied according to species. For the top 15 species of saplings (<10 cm dbh) survivorship was 47%. In contrast, the remaining species had an overall mean survivorship is 57% in the same size class. Table 1 provides a list of understory species and their sprouting behavior. The abundant species represent ten different plant families. Survivorship varied considerably, ranging from 15% to 68%. The three species with highest survival (> 57%) were *Acacia colinsii*, *Casearia corymbosa*, and *Diospyros salicifolia*. The species with the lowest survivorship (35%) were *Randia aculeata*, *Jacquinia nervosa*, and *Semialarium mexicanum*. The shrub species *J. nervosa,* experienced by far the lowest survivorship at15%; however, this same species presented the most vigorous sprouting behavior and was one of the most prominent seedlings in hot spots.

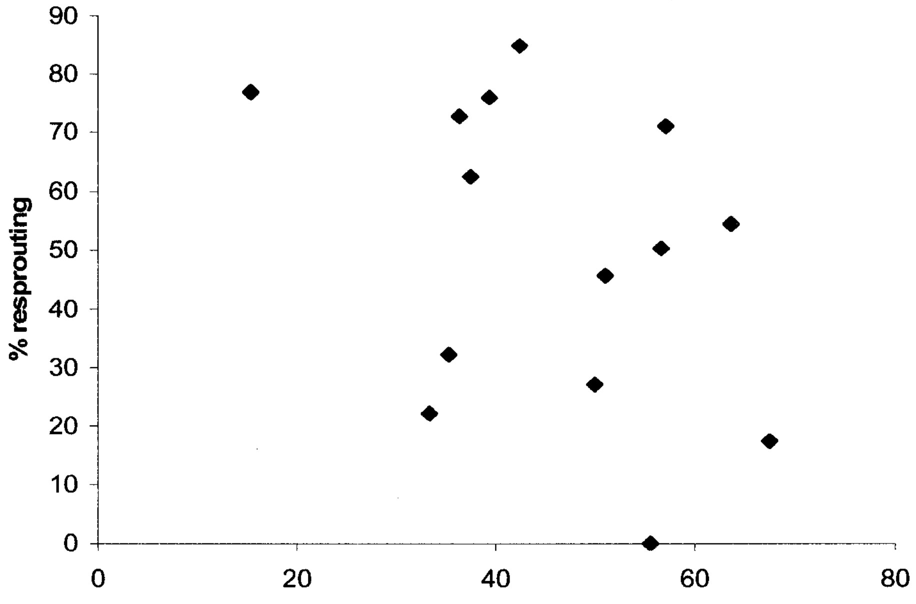
Table 1. Rank order of top fifteen woody species affected by fire (< 10 cm dbh, > 1.5 m height). Indicators of survivorship are percent survivorship, sprouting behavior , and recruitment. Mean change in seedling densities are in relation to control plots. Mean change = (Δ mean treatment plots - Δ mean control plots)/mean prefire density. * = significant treatment effect when analyzed over time with controls.

Species	Percent suvivorship	**Percent sprouting**	**Mean change in seedling densities**	**Mean # sprouts per individual**	**Sprouting Type Observed** **b = basal** **r = root** **s = stem**
Stemmadenia obovata (Hook. & Arn.)	56.64	50.35	-0.15*	5.63	b, r, s
Erythroxylum havanense Jacq.	50	27.17	-0.38	5.44	b, r, s
Erythroxylum sp.	39.39	76	-0.97	10.97	b, r
Acacia collinsii Saff.	67.5	17.5	0.125	4.43	b, r
Randia aculeata L.	35.29	32.35	-0.612*	5.27	b, s
Croton niveus Jacq.	42.42	84.85	0.179	8.46	b, r, s
Casearia tremula (Griseb.) Griseb. ex W. Wright	51.06	45.73	0.6	5.25	b, r
Jacquinia nervosa C. Presl.	15.38	76.92	0.17	3.5	b, r
Trichilia martiana C. DC.	36.36	72.73	-0.39	7.25	b, r
Casearia corymbosa H.B.K	63.64	54.55	-0.95*	3	b
Randia monantha Benth.	55.56	0	-0.75*	--	--
Semialarium mexicanum (Miers)	33.33	22.22	0.329	2	b
Albizia adinocephala (Donn. Sm.)	37.5	62.5	-0.699*	3	b
Diospyros salicifolia Humb. & Bonpl.	57.14	71	1.85*	6.4	b, r
Gyrocarpus americanus Jacq.	50	0	7.2*	--	--

There was no relationship between resprouting behavior and survivorship (Figure 1). Sprouting behavior was observed in all but two species: *Gyrocarpus americanus* and

[redacted]

central stem alive. All sprouting species created basal sprouts, but root sprouts were also observed in nine species and stem sprouting in four species. There was a close relationship between the percent sprouting and the mean number of sprouts per sprouting individual (Figure 2).



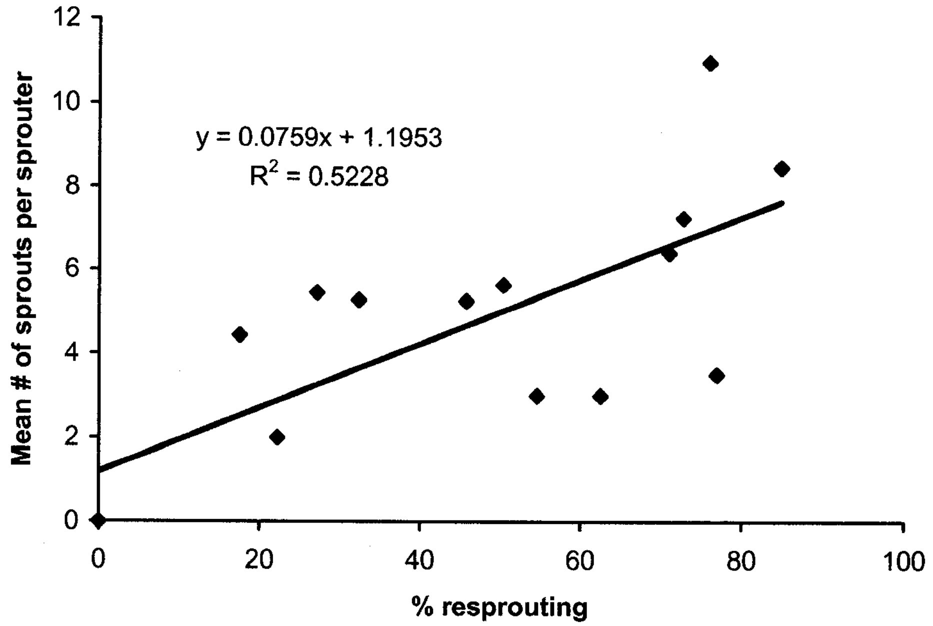


Figure 2. Relationship between portion of population sprouting and the intensity of sprouting behavior. X-axis = % of population of given species sprouting, Y-axis = mean number of sprouts per sprouting individual. The further from zero, the better greater the species' sprouting ability.

Based on our observations of survivorship, recruitment, and sprouting we characterize these species according to their overall fire response. Table 2 provides the description of plant behavior for each of the fire response categories. Only two species of overstory trees, *Gyrocarpus americanus* and *Diospyros salicifolia*, fit the category of recruiters. *G. americanus* is non-sprouting with wind dispersed seeds, while *D. salicifolia* has seeds that are primarily avian dispersed. The six species categorized as resprouting have a

survivorship at or below the mean, yet have vigorous sprouting behavior. Vulnerable species exhibited little or no sprouting behavior and at the same time had negative

Table 2. Fire response categories for dry forest species.

Fire Response Category	Survivorship	Sprouting	Recruiting
Resisters	high	high sprouting	variable recruitment
Vulnerable	low to medium	low sprouting	low recruitment
Recruiters	medium to high	variable	high recruitment
Resprouters	low	high sprouting	low recruitment

Over half of changes in seedling densities were negative for the fifteen species selected for analysis. Meanwhile, nearly all of the seedlings of the 15 species of lowest abundance experienced positive changes in seedling densities. None of the rare trees or most abundant trees in the plots experienced seedling changes that completely eliminated their populations. However, two seedling species (*Bourreira sp.* - Rubiaceae and *Caesalpinia sp.* - Caesalpinaceae) that were rare prior to the burns completely disappeared the first year after fire, though one seedling returned after the first year. Following the fire, there were eighteen new seedling species that were not present during pre-fire sampling. Five of these eighteen did not have adults present within the plots. These results are consistent with the significantly positive increase in seedling diversity observed following burn treatment. (refer to Chapter 2).

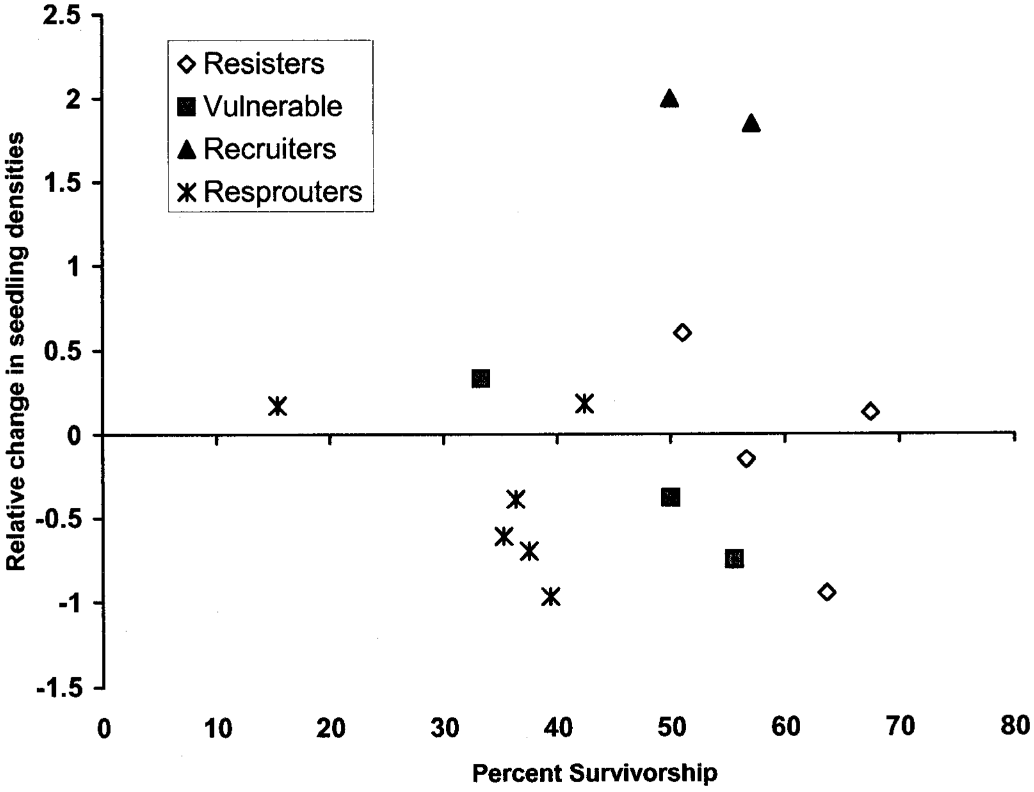


Figure 3. The fifteen most abundant sapling species' response to fire for recruitment and mortality. Survivorship does not include top-killed individuals. X-Axis = percent survivorship one year post fire, Y-Axis = proportional change in mean seedling densities. Fire response categories are provided in legend. Observations of sprouting behavior are used as an additional source for assigned fire response categories.

Species of conservation concern

Seedling densities for all three of the 15 most abundant species increased significantly one year post fire (Figure 4). One-way repeated ANOVA demonstrated a significant effect of fire treatment on seedling densities for *Swietenia humilis* (P = .000278) and *Guajacum sanctum* (P= .0245). There was no significant treatment effect for *P. parviflorum* when compared to the control plot. However, there was a significant increase in *P. parviflorum* seedling densities exactly one year post fire in both control and treatment plots. This result was confounded by the presence of several large adult *P. parviflorum* trees within and between one treatment plot and control plot (seeds are wind dispersed). Adult individuals of *P. parviflorum,* that were burned in treatment plots, exhibited sprouting behavior but did not suffer any mortality.

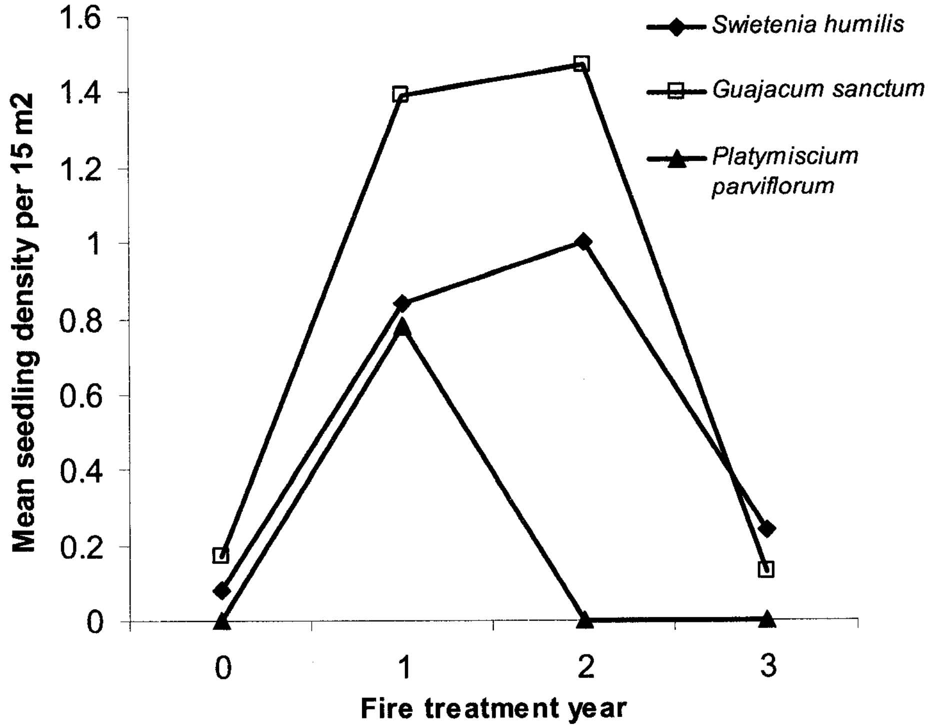


Figure 4. Mean seedling densities for three endangered dry forest species in treatment plots. X-axis = year 0 is pre fire and years 1, 2, and 3 are post successive post-fire years Y-axis = Mean seedling density.

DISCUSSION

Our results do not indicate that this particular dry forest is composed primarily of plants vulnerable to fire. There are positive and negative responders, but the majority of species are not irreversibly impacted. Sprouting was the most widely observed response to fire. Sprouters are favored by frequent and low intensity disturbance regimes (Bond and Midgley 2001), and fire return intervals of < 25 years would favor a sprouting over a seeding strategy (Keeley and Zedler 1978). Our results showed some species surviving the fire yet also putting out new sprouts, thus taking advantage of the opportunity for expansion (Bond and Midgley 1996). One might characterize dry forest sprouters as facultative resprouters, because they sprout following fire, but their expansion is not limited to fire events. A total of 10 out of the fifteen species were root sprouters, argued by some to be a trait indicative of frequent fire return (Saha and Howe 2003). We found that sprouting ability is not necessarily linked to the ability of the main stem to survive fire. If we were to consider die-back as survivorship, then the relationship to sprouting would be easily observed. The species with wide distributions that include moist forest environment were not those categorized as vulnerable, but rather were resprouters. Moist forest species are known to often have vigorous sprouting ability (Kauffman 1991).

Species that lack the ability to sprout are often present within fire-prone vegetation (Bond and van Wilgen 1996).Two of the species considered within this analysis did not demonstrate an ability to sprout. *Randia monantha* had low survivorship and low recruitment, while *Gyrocarpus americanus* have moderate survivorship with significantly increased recruitment. *R. monantha* has a large globulous fruit (7 cm), while *G. americanus* has a one-seeded winged fruit.

The main characteristic of resister species was the ability to withstand fire. Given the small size class of the species in analysis, few if any had exhibited thick bark, however fire-prone vegetation can include species with thin bark (Bond and van Wilgren 1996).

One resister with low sprouting ability was *Acacia colinsii.* We speculate that high survivorship observed in *A. colinsii* may be related to low burn intensities as a result of sparse fuels near the tree base. Ant-shrub mutualism and small leaf size inhibit the accumulation of litter (Janzen 1966). The three species characterized as vulnerable were understory trees or shrubs. *Semialarium mexicanum* (Hippocrateaceae) was considered vulnerable because of low sprouting behavior and high mortality. However, this species has winged seeds, potentially enabling it to recolonize after fire, and perhaps explaining the positive change in recruitment following fire. Another vulnerable species, *Randia monantha,* did not exhibit any sprouting. Despite an increase in seedlings in treatment plots, the overall increase was less than that observed in the controls. *Erythroxylum sp.* was another vulnerable species. It is a very abundant understory shrub, but little is known of its life history as a positive identification was not possible. The most common fire response class was the resprouters. Throughout both moist and dry forests, sprouting is a common feature, perhaps indicating that it should not be used as the sole trait to identify fire adaptation. We cannot infer that species responses post-fire were completely a result of the burn mechanism, because other factors such as interannual variability in rainfall, phenology, and herbivory likely had an effect on recruitment and mortality.

None of the top fifteen species characterized in this study are considered threatened. Nevertheless, they all form part of the native vegetation in the dry forest biome and thereby are important for conservation purposes. Four of the species are described as being part of secondary forest vegetation (Stevens *et al.* 2001), but they are also naturally occurring components of dry forest understory. We described three of these secondary forest species as resprouters and one (*Acacia colinsii*), as a resister. One argument is that the abundance of fire-tolerant species at this particular study site is not evidence of dry forest adaptation to fire; rather, it is evidence that the forest is highly disturbed. There is no doubt that both fire and other human disturbances such as grazing and firewood collection have been intense in recent history (Sabogal 1992; Gillespie 2001); however the dominance of forest species (understory and overstory trees), rather than pioneer species indicates a relatively mature stand. The most abundant woody vegetation under 10 cm dbh (excluding lianas) are understory shrubs and trees which are an important component of dry forests.

Although there was a negative change to many seedling species, no abundant species were devastated by fire's impact and many new species were introduced as a result of the fire. The majority of these new species were relatively rare, including 18 species that were new observations plot post-fire. This increase in seedling richness and abundance (as quantified in Chapter 2), could be considered a positive change for the dry forest.

The introduction of eighteen new seedling species post-fire may be an indication that seeds are stored in the soil. Post-fire, their germination is stimulated by fire, wildlife dispersal (*i.e. Spondias purpurea* L.) or dispersal (i.e. *Cochlospermum vitifolium* (Willd) Spr. in L.). Although many of the newly introduced seedlings may be considered early colonizers (*e.g. Malvaviscus arboreus* Cav.; *Senna pallida* var. *pallida*; *Cordia collococca* L.), at least eight species are overstory trees consistent with a healthy dry forests (*i.e. Pterocarpus rohrii* Vahl; *Lonchocarpus costaricensis* (J. D. Smith); Pittier. *Zanthoxylum sp.*). There were no non-native plants present following the fires.

Species of conservation concern

Regarding fire effects on the three endangered tree species assessed in this study, it is difficult to ascertain that increases in seedling densities is the result of burn treatment effect. Nonetheless, we can conclude that fire did not have an adverse effect on either the few mature and juvenile stems or on seedling densities. One might speculate as to why we observed increases in seedling abundances following fire. First, *S. humilis* has wind-dispersed seeds. Closely related mahogany species are known to disperse up to several hundred meters (Snook 1993). Furthermore, mahogany seedlings require high light environments and bare soil to establish (Wolffsohn 1961 in Snook 1993), therefore they would likely be favored by [illegible]

Martin 1987) and fire scarification may be a mechanism facilitating germination. Nevertheless, fire is not likely the sole means of scarification. In a Costa Rican dry forest, *G. sanctum* populations have reduced regeneration (Jimenez 1999) and fire has been excluded during the past 15 years.

CONCLUSIONS

We observe a whole range of life history strategies with respect to fire. This is similar to other fire-adapted ecosystems where varying strategies likely coexist due to spatial and temporal stochasticity in fire events (Keeley 1986). This study was not able determine the presence of fire adaptation, but we can conclude that populations of three endangered dry forest species are not immediately threatened by a single fire event. As we develop a better understanding of disturbance dynamics in tropical dry forest we will be better able to conserve this unique and threatened ecosystem.

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