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Wind effects and regeneration in broadleaf and pine stands after hurricane Felix (2007) in Northern Nicaragua

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ABSTRACT

Large-scale wind disturbances shape forest structure and composition and leave long lasting legacies. Adequate understanding of the role of disturbances in tropical stand dynamics is necessary to guide management efforts. In this study, we used field data to characterize the effects of a major hurricane in broadleaf and pine stands in Northern Nicaragua. First, we described tree and stand attributes associated with observed structural effects: branch loss, snapping and uprooting. Secondly, to assess the potential influence of hurricane Felix on stand composition, we characterized two key life-history traits: regeneration through resprouting and shade tolerance. Findings indicated that tree attributes such as diameter at breast height (dbh) and height to diameter ratio (hdr), were strongly associated with the type and magnitude of wind effects. All trees >70 cm dbh exhibited visible effects and trees taller than 14 m were more likely to be uprooted (7.3% vs. 0.8% of total). Results confirmed that Felix caused significant structural effects in broadleaf stands and mild effects in pine stands. Abundant post-hurricane resprouting was observed in both shade-tolerant and shade-intolerant species but was absent in pines. Among canopy trees we found eleven shade-intolerant species that exhibited abundant resprouting. These species could become dominant in the next decade. Our findings illustrate the role of wind disturbances on tropical stand dynamics at different spatial and temporal scales.

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1. Introduction

Disturbance events and competitive interactions among trees drive forest dynamics (Sousa, 1984; Foster et al., 1998; West et al., 2009; Turner, 2010). Disturbances change the physical environment, reallocate resources, and create biological legacies that influence ecosystem processes (Norberg, 1988; Foster and Boose, 1992; Pacala et al., 1993; Kulakowski and Veblen, 2003; Boose et al., 2004). Disturbances may also be important in maintaining species diversity, particularly in species-rich tropical ecosystems (Huston, 1979; Warner and Chesson, 1985; Denslow, 1995; Granzow-de la Cerda et al., 1997). Although the factors that determine forest susceptibility to wind disturbances have been characterized in temperate ecosystems, they have received limited attention in tropical forests (e.g., Foster and Boose, 1992; Boucher et al., 1990; Lugo and Scatena, 1996). Specifically, it is not well understood how tree-and-stand attributes influence susceptibility to wind and subsequent stand dynamics (Lugo, 2002).

A few general relationships between wind effects and tree-and-stand attributes have been identified. First, some studies have found a positive relationship between increasing tree height and increased uprooting (Everham and Brokaw, 1996). Second, stand susceptibility to wind is linked to the height to diameter ratio (hdr) of dominant trees. This ratio depends on light availability and stand density: trees growing in full sunlight tend to have lower values, while trees growing in shaded conditions – e.g., in dense stands-tend to have greater values (Mitchell, 1995). For this reason foresters use it as a quantitative indicator to guide thinning operations (Wilson and Oliver, 2000).

The importance of forest type (i.e., broadleaf vs. pine) on the severity of wind effects has been examined in numerous locations with different results (Everham and Brokaw, 1996). Although conifers are sometimes more susceptible than angiosperms, given the greater diversity in wood density and tree architecture of the

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latter, wind effects seem to be more dependent on stand characteristics such as tree density and canopy height, rather than species' traits (Boucher et al., 1990; Mitchell, 1998).

By snapping and uprooting trees differentially, windstorms also shape stand structure (Zimmerman et al., 1994; Vandermeer et al., 2000). For example, in Puerto Rico windstorms occur every decade and thus favor the development of dense and homogenous stands with low regeneration and high competition (Boose et al., 2004; Van Bloem et al., 2007). In contrast, in Nicaragua, windstorms occur approximately once every century and create space for the establishment of surviving and new seedlings (Vandermeer et al., 2001).

Most studies of tropical forest dynamics have focused on short-term and small-scale disturbances, i.e., gap dynamics (Hubbell, 1979; Denslow, 1987; Denslow et al., 1998; Condit et al., 2004), in part because of the difficulties in determining tree age using growth rings and identifying sterile individuals (Rejmanek and Brewer, 2001; Chambers et al., 2013). Consequently, the role of infrequent hurricanes in shaping forest composition and diversity is less understood (Nelson et al., 1994; Zimmerman et al., 1994; Baker et al., 2005). By opening space over large areas (>1000 km^2), hurricanes create landscape heterogeneity, change the ecological space available to organisms and favor tree recruitment (Huston, 1979; Denslow, 1995; Negrón-Juárez et al., 2010). For example, Vandermeer et al. (2000) documented an increase in tree species richness after the passage of hurricane Joan in 1988, which was attributed to the growth of the seedling bank coupled with resprouting of affected trees. Their 10-year data series indicated that following geographically large disturbances (~5000 km^2), dispersal limitations prevented pioneer species (e.g., *Cecropia* spp.; *Ochroma* spp.) from rapidly colonizing available space, in contrast to small gaps (~0.5 km^2). Lastly, studies in Puerto Rico have showed that hurricanes can also shape the composition of the seedling layer (Comita et al., 2010).

It has been proposed that tree response to wind disturbances depends on three main life-history traits: resprouting capacity, dispersal ability and shade tolerance (Canham et al., 1990; Oliver and Larson, 1996; Montagnini and Jordan, 2005). While post-hurricane resprouting and dispersal ability have been characterized in some Caribbean forests (Boucher and Mallona, 1997; Van Bloem et al., 2005), it is unknown if tropical canopies are dominated by shade tolerant or shade intolerant species, or a combination of the two. This information is important to understand historical stand dynamics and develop adequate management strategies (see Baker et al., 2005). By compiling empirical data from numerous studies, Gunter et al. (2011) defined three shade classes: tolerant, intolerant, and partially intolerant, which were used in this study to classify canopy species.

The landfall of hurricane Felix provided us with the opportunity to characterize the factors that control wind effects and regeneration, specifically: (i) how do tree and stand attributes determine the type and magnitude of wind effects; (ii) what is the relationship between forest type (broadleaf vs. pine) and wind effects; (iii) which canopy tree species resprout following wind disturbances; and (iv) what is the proportion of canopy species that are shade tolerant. By using field data to characterize wind effects at the stand scale, this study complements previous efforts that used aerial surveys and satellite imagery to characterize wind effects at the landscape scale (Inafor, 2007; Rossi et al., 2013).

1.1. Study area

The Autonomous Region of the Northern Caribbean of Nicaragua (hereafter RACN) comprises 32,000 km^2 and hosts a population of ~315,000 (Nicaraguan Census Bureau – INIDE, 2005). Average annual temperature is 25 °C and annual rainfall 2500 mm, with a marked dry season from February to early May. The RACN harbors 1.4 million hectares of forest (43% of Nicaragua's forests), which include the Bosawás UNESCO's Biosphere Reserve (Inafor, 2009). Two forest ecosystems cover most the region: dense, closed tropical broadleaf forests located towards the interior and pine savannas on coastal areas.

Broadleaf (hardwood) forests are found mostly in crumb-structured humic clays in areas of undulating topography (Parsons, 1955). For centuries these forests have attracted foreign logging companies in search of mahogany (*Switenia macrophylla*) and Spanish cedar (*Cedrela odorata*) which were selectively harvested along rivers and roads. Yet, up until hurricane Felix' impact, a significant portion of these forests remained inaccessible and poorly studied. Presently, numerous valuable timber species can be found in broadleaf stands, including *Calophyllum brasiliense*, *Carapa guianensis*, *Dialium guianense*, *Guaiacum sanctum*, *Hyeronima alchorneoides*, *Hymenaea courbaril* and *Terminalia amazonia* (Smith, 2003; Inafor, 2009). Over the last three decades, land-use practices consisted on selective logging and fuelwood collection, although a large portion of the forests of the region remains unmanaged (Salazar, 2005; Diaz, F. personal communication, 2010). Because of the high density and moisture, these broadleaf stands rarely burn (Inafor, 2009).

Pine savannas dominated by *Pinus caribaea* comprise approximately 10,000 km2 along the Atlantic coast of Nicaragua. The soils of the pine savannas are mostly composed of nutrient poor sands, highly weathered quartz-gravels and clays in poorly drained areas (Parsons, 1955; Myers et al., 2006). This ecosystem harbors numerous herbaceous species and depends on recurrent fires that create adequate conditions for pine regeneration and prevent hardwood establishment (O'Brien et al., 2008; Ratnam et al., 2011; Hoffmann et al., 2012). Due to the abundance and accessibility of pines across the coastal plains of the region, logging and fuelwood collection have been common for over a century (Castilleja, 1993; McSweeney, 2004). In addition, near communities, pine stands are often burned to promote grass growth for cattle and deer (Alvarado, 2010).

On 4 September 2007, hurricane Felix made landfall near the community of Awastara in Northern Nicaragua (14°18′44.07″N, 8 3°12′12.04″W), as a Saffir-Simpson category five hurricane (NOAA, 2013). The cyclone travelled across the region and became a low pressure system over northern Honduras early on September 5th (Brennan et al., 2009; Fig. 1). Felix caused substantial damage to infrastructure in coastal communities and affected more than 3000 km^2 of broadleaf and pine stands. Estimates based on aerial surveys and satellite imagery suggest that one million m^3 of tropical hardwoods were blown down by this hurricane (Inafor, 2007).

Weather records indicate that no major storms had affected Northern Nicaragua since the late 1890s (Beven et al., 2008; Kar, 2010; NOAA, 2013). Similarly, historical data indicates that although numerous tropical storms regularly pass over Northern Nicaragua, most Atlantic hurricanes have not made landfall in this region (NOAA, 2016). Taken together, historical and weather records suggest that broadleaf stands located in the center of the RACN had remained undisturbed for at least a hundred years before Felix's impact.

2. Methods

2.1. Data collection

Four field sites were defined using land cover maps based on proximity to the hurricane path and availability of large forest patches of broadleaf and pine stands to allow for comparisons

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