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Understanding hurricane resistance and resilience in tropical dry forest trees: A functional traits approach

Horacio Paz*, Flor Vega-Ramos, Felipe Arreola-Villa

Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Antigua Carretera a Pátzcuaro No. 8701. Col., San José de la Huerta, CP 58190 Morelia, Michoacán, Mexico

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ABSTRACT

Understanding hurricane resistance and resilience in tree species is a challenge to the management and conservation of coastal tropical forests. Tree responses to hurricanes partly depend on species attributes related to architecture and resource use strategy; however, few studies have used multiple traits to identify the role of functional trade-offs in tree resistance and resilience. In this study, we apply a functional traits approach to explore how characteristics involved in tree shape, size and function influence the type and severity of damage by hurricane winds, and examine the potential for recovery by re-sprouting. We tested the hypothesis that traits involved in the fast-slow trade-off mediate tree responses to hurricanes. Eighteen months after the passing of a category 2 hurricane, we assessed the damage types found in 993 trees of dbh > 10 cm, from 36 dominant tree species in a tropical dry forest on the Mexican Pacific coast that was impacted by the event, and measured five functional traits related to species size, architecture and resource acquisition strategy. In addition, the sectional area recovered by re-sprouting in main tree trunks or branches was measured in 16 species. The results indicated that several traits could serve as good indicators of resistance and resilience. Maximum height, wood density and specific leaf area correlated positively with severe damage (together accounting for up to 47% of the variance in uprooting). In turn, re-sprouting recovery was positively associated with maximum height and specific leaf area but negatively with wood density and slenderness (together informing *ca.* 50% of the variance). We found evidence that the fast-slow continuum of resource use strategies can mediate the capacity of trees to resist and recover following hurricane winds; however, contrary to expectation, the consequences of the fast-slow syndrome for the response to hurricanes seem to vary with the axis of plant strategies considered. Our results challenge the notion that dense-wooded trees of the tropical dry forest should resist hurricanes better, and suggest that these climatic events may actually favor light-wooded, wide-stemmed trees.

1. Introduction

Hurricanes are a major cause of damage to vegetation along the tropical and subtropical coasts of the world (Lugo, 2000). Understanding the drivers of damage severity and the rate of vegetation recovery is at the core of research into ecosystem resistance and resilience against major disturbances (Gunderson, 2000; Ostertag et al., 2005). Since hurricane regimes of higher intensity are expected with the projected future warming of the ocean and air (Walsh et al., 2016), accurate prediction of the resistance and recovery of tree species following these events may enhance our abilities to manage vegetation and model ecosystem responses in the face of climate change. In addition to the wind intensity, the severity of the physical damage to the vegetation depends strongly on the topography, rain, soils and location of the forest in relation to the wind forces (Tanner et al., 1991; Boose et al., 1994 among others). However, several studies suggest that vegetation properties such as stature, structure and composition also affect levels of damage (Brokaw and Walker, 1991; Gresham et al., 1991; Everham and Brokaw, 1996; Peterson, 2004; Kupfer et al., 2008). In fact, extensive surveys have indicated that tree species are damaged to different degrees by hurricanes and that the extent of the damage may depend on species traits (Francis and Gillespie, 1993; Ostertag et al., 2005). Trees of high stature or those with extended crowns are expected to present the greatest damage because, when trees are subjected to lateral wind forces, such structural traits act to increase the tension transmitted to the pole or roots (Curtis, 1943; Frangi and Lugo, 1991; Francis and Gillespie, 1993). Slender trees (those with thin trunks in relation to their height or crown width) are expected to suffer more damage, since they experience high tension on a relatively weak pole (King, 1986; Niklas, 1992). Wood density can potentially affect the

* Corresponding author.
E-mail address: hpaz@cieco.unam.mx (H. Paz).

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severity of damage in two ways, since this trait is positively associated to pole and branch stiffness and thus resistance to trunk breakage, but also negatively related to the flexibility of these structures and thus to the capacity of the tree for avoiding root fracture (Asner and Goldstein, 1997). Evidence from extensive hurricane damage surveys in the Americas has amply documented the vulnerability of tall species (Everham and Brokaw, 1996; Francis and Gillespie, 1993; Peterson, 2000, among others). However, there has been little research on other traits such as tree slenderness, crown dimension, leaf traits or other components of tree shape (Zimmerman et al., 1994; Bellingham et al., 1995; Curran et al., 2008a; Webb et al., 2014). Moreover, only a few studies have explored the effects of wood density, yielding equivocal evidence in terms of tree vulnerability, and suggesting that this trait may affect not only the severity, but also the type of damage (Putz et al., 1983; Walker, 1991; Zimmerman et al., 1994; Curran et al., 2008a; Webb et al., 2014). Zimmerman et al. (1994) concluded that generalizations on the effects of tree shape on resistance to hurricanes are difficult to make, partly because different components of a complex architecture play a role (see also Peterson, 2004; Ostertag et al., 2005; Xi and Peet, 2011; Webb et al., 2014). In this context, analysis of wind damage as a function of both single traits and integrative descriptors of tree shape may be valuable.

One of the main mechanisms of vegetation recovery following hurricane damage is regrowth of the surviving trees. Many studies indicate wide interspecific variation in the capacity for subsequent re-sprouting (Everham and Brokaw, 1996 and references therein); however, few have analyzed this response in relation to species traits (Bellingham et al., 1994; Zimmerman et al., 1994; Everham and Brokaw, 1996; Curran et al., 2008b). Capacity for re-sprouting after physical damage is expected to increase with fast growth and developmental rates (Putz et al., 1983), as well as with the amount of carbohydrate reserves in the trunks or roots (Poorter et al., 2010). However, previous studies do not clearly support this: some suggest that fast growing trees re-sprout more vigorously after hurricanes (Putz et al., 1983; Putz and Brokaw, 1989), while others report the opposite (Zimmerman et al., 1994).

It has been suggested that species growth strategies along the fast-slow continuum may determine the manner in which trees respond to hurricanes (Ostertag et al., 2005; Curran et al., 2008b; Webb et al., 2014). In particular, because of their high stature and low wood density, fast-growing resource acquisitive species are expected to experience more damage, but re-sprout more vigorously, while high wood density, slow-growing species are expected to suffer less damage but re-sprout more slowly (Curran et al., 2008b); i.e., the fast-slow continuum of plant strategies may impose a trade-off on the response to hurricanes, producing different ways to deal equally with the impact of severe winds. Despite of its potential implications for predicting species and ecosystem responses to hurricanes, to our knowledge, only a few studies have addressed this question through analysis of the effects of single traits (Curran et al., 2008b; Webb et al., 2014). One question that remains open is to what extent suites of coordinated species-specific traits determine both the risk of suffering damage and the ability to recover growth following the impact of hurricane winds. Such a task demands a mechanistic approach, where tree responses to hurricanes can be inferred based on general principles in their coordination of mechanical, architectural and physiological traits, and the derivation of clear indicators of such responses.

In this study, we adopt a functional traits approach (*sensu* Diaz et al., 2004; McGill et al., 2006; Reich, 2014) to address the following specific questions: (i) how do single functional traits affect damage type and recovery in trees after hurricanes? (ii) How are functional traits coordinated and how do the resulting functional strategies affect tree responses to hurricanes? (iii) Which suite of traits can be used as the best predictor of severe damage and recovery? In order to answer these questions, we gathered information pertaining to tree damage and functional traits in 993 trees (of 36 species) and recovery in 191 trees (of 16 species), following the landing of a category 2 hurricane in a tropical dry forest (TDF) region of the Mexican Pacific coast subject to infrequent hurricanes. This is the third study to explore how functional traits mediate resistance *vs*. resilience to hurricane damage in trees and the first to examine the consequences of trait spectra or the coordinated variation of multiple traits.

2. Methods

2.1. Study area and hurricane Jova

The Chamela-Cuixmala reserve is located on the Mexican Pacific coast and comprises an old-growth TDF of canopy height 7–15 m (Rzedowski, 2006). This forest is developed on a hilly landscape of elevations 50–250 m asl (Martínez-Yrizar et al., this issue). The climatic regime is characterized by a mean annual temperature of 24.9 C ± 8 °C and mean annual precipitation of 795 mm (366–1329 mm). There is marked seasonality, with 87% of the precipitation occurring from June to October (Maass et al., this issue). On October 2011, the category 2 (Saffir-Simpson scale) Hurricane Jova impacted the study area, with wind speeds ranging 150–180 km/h (Parker et al., this issue) and a total precipitation of 233 mm over a three-day period. This event caused soil saturation and elevated runoff, as well as considerable damage mainly to large trees.

2.2. Assessment of tree damage and re-sprouting

Since we aim to understand what traits make trees more resistant and more capable of recovery after damage, we sampled the most damaged areas in the forest in order to maximize the number of large (dbh > 10 cm) trees that had been damaged by wind, as well as the number of species in our analysis. For this, 12 sites were selected, each comprising ten 10 m × 10 m plots, in heavily damaged areas (those in which many large trees presented loss of main branches, or were uprooted, leaning, or snapped) all located on hilltops (100–150 m asl) and separated by a distance of 150–800 m from each other. Within each 100 m^2 plot, all trees with dbh > 10 cm were tagged, identified and damage type determined as follows: no apparent damage (NOD); defoliation and loss of small tertiary branches (DEF); loss of main branches -those of diameter > 20% of the dbh-(LMB); leaning trees (LEA); snapped trees (SNA); uprooted fallen trees (UPR). These categories were exclusive; each individual was assigned only to the most severe category of damage exhibited. In these same plots, we evaluated the re-sprouting potential of each species following damage. For this, we selected the trees that presented a broken main trunk or principal branches up to 3 m in height, and counted the number of sprouts growing around the damaged area. At this proximity, the sprouts were clearly differentiated from extant branches, since the former typically develop in dense packs right below the point where the trunk or branch was broken, and normally present greenish and smooth bark.

Each sprout was visually assigned to three size categories based on basal diameter: < 1 cm; 1–3 cm and > 3 cm. The recovery capacity per species was then calculated as the percentage of stem sectional area recovered, by taking the ratio: sum of basal area of all sprouts over the basal area of the main trunk or principal branch at the point at which it was broken. This index was zero when no sprouts were present, and increased with the number and cross-sectional area of the sprouts developed. Tree damage and re-sprouting potential following damage were both evaluated per species, 18 months after the impact of the hurricane. This particular time was chosen in order to avoid the rapid rush of ephemeral sprouts (of rapid production and short longevity observed in other tropical dry forests immediately after the hurricane (Paz, pers. comm.) and also to take advantage of the beginning of the rainy season, when the flushing of first leaves facilitated species identification and provided excellent visibility of the tree dimensions and damage.

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