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Are species photosynthetic characteristics good predictors of seedling post-hurricane demographic patterns and species spatiotemporal distribution in a hurricane impacted wet montane forest?

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ABSTRACT

In situ measurements of leaf level photosynthetic response to light were collected from seedlings of ten tree species from a tropical montane wet forest, the John Crow Mountains, Jamaica. A model-based recursive partitioning ('mob') algorithm was then used to identify species associations based on their fitted photosynthetic response curves. Leaf area dark respiration (R_D) and light saturated maximum photosynthetic (A_{max}) rates were also used as 'mob' partitioning variables, to identify species associations based on seedling demographic patterns (from June 2007 to May 2010) following a hurricane (Aug. 2007) and the spatiotemporal distribution patterns of stems in 2006 and 2012. R_D and A_{max} rates ranged from 1.14 to 2.02 μmol (CO_2) $m^{-2}s^{-1}$ and 2.97–5.87 μmol (CO_2) $m^{-2}s^{-1}$, respectively, placing the ten species in the range of intermediate shade tolerance. Several parsimonious species 'mob' groups were formed based on 1) interspecific differences among species response curves, 2) variations in post-hurricane seedling demographic trends and 3) R_D rates and species spatiotemporal distribution patterns at aspects that are more or less exposed to hurricanes. The composition of parsimonious groupings based on photosynthetic curves was not concordant with the groups based on demographic trends but was partially concordant with the R_D - species spatiotemporal distribution groups. Our results indicated that the influence of photosynthetic characteristics on demographic traits and species distributions was not straightforward. Rather, there was a complex pattern of interaction between ecophysiological and demographic traits, which determined species successional status, post-hurricane response and ultimately, species distribution at our study site.

1. Introduction

Tropical forests are temporally and spatially heterogeneous (Feng et al., 2004; Comita et al., 2009; Souza et al., 2010; Luke et al., 2014), which can be enhanced by natural disturbances caused by hurricanes that alter biotic and abiotic conditions (especially light) in the forest understory (Comita et al., 2009; Luke et al., 2014). Light is typically the most limited resource in the forest understory and affects species growth as well as their recruitment efficiency (Feng et al., 2004). Changes in light availability influences succession as it impacts the trajectory of species responses in post disturbance environments (Bazzaz and Pickett, 1980; Lugo, 2008). In tropical forests, succession is dynamic and dependent on chance; the successful establishment of a species is dependent on seeds and seedlings occupying suitable sites with adequate resources (Bazzaz and Pickett, 1980).

The response of species to disturbance is determined by their successional status, which is typically described in terms of their shade tolerance. Early successional species are described as shade intolerant, requiring areas with high light (such as canopy gaps) for recruitment and establishment; whereas late successional species can be recruited into both high light or shaded areas (Whitmore, 1989; Feng et al., 2004). Photosynthetic differences among species along a continuum of shade tolerance may be used to predict species response to disturbance (Reich et al., 2003). However, in tropical forests, the successional status of a tree species is not directly related to photosynthetic traits; rather, it is dependent on the probabilistic interaction of ecophysiological, morphological and demographic traits (Davies, 1998). Nonetheless, the photosynthetic characteristics of a species provide a basis from which to analyse species response and successional status. Early successional species are generally described as having high leaf-level light saturated maximum photosynthetic and respiration rates, while showing greater phenotypic and morphological plasticity when compared with late successional species (Davies, 1998; Turner, 2004; Souza et al., 2010). The rapid growth of pioneers and saplings of non-pioneer (but gap-

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benefitting) species in post-hurricane disturbed forests has been attributed to their higher photosynthetic capacity and acclimation to high light environments (e.g. Wen et al., 2008). Consequently, the response of forest species in post-disturbance environments (i.e. successional status) may be related to interspecific variation in species growth rates and other demographic traits (recruitment and mortality) (Davies, 1998; Comita et al., 2009). Leaf-level respiration and both mass- and area-based photosynthetic rates may also be important factors in post disturbance response as they have been shown to be weakly associated with species relative growth rate (RGR) (Reich et al., 2003). However, several studies have failed to find a relationship between both rates (e.g. Dijkstra and Lambers, 1989; Poorter, 1989; Poorter et al., 1990; Dalling et al., 2004). Other leaf-level attributes such as specific leaf area (SLA) may serve as better correlates of leaf-level photosynthesis and plant RGR (Poorter et al., 1990).

In tropical forest environments with frequent disturbance events such as hurricanes, differences in post-disturbance species responses are driven by differences in life history strategies (Comita et al., 2009). Moreover, there may be shared or indirect relationships between demographic and photosynthetic traits of species that have similar life history and successional attributes. The interactions between sets of traits are not easily generalized, but there are trade-offs that are complex and advantageous in some microhabitats (Comita et al., 2009). These trade-offs can influence the response and abundance or distribution of species with different successional attributes in disturbed environments. For example, there may be post-hurricane increases in the abundance of pioneers (e.g. Scatena, 1995; Tanner et al., 2014) and non-pioneer ("usurper") species in hurricane impacted forests (e.g. Bellingham et al., 1995). Similarly, several non-pioneer species that favor post-disturbance environments may also increase their abundance at sites that are more exposed to a single or multiple hurricanes (e.g. Luke et al., 2016a), or there may be shifts in forest species composition due to hurricanes (e.g. Martin et al., 2007). These responses can be explained by a combination of factors such as incongruent species-specific 1) demographic traits (growth, mortality, and recruitment) (Roxburgh et al., 2004), 2) photosynthetic traits (e.g. Wen et al., 2008) and 3) resilience or resistance to hurricanes (e.g. Bellingham et al., 1995). Understanding the trade-offs between plants with different groups of traits (e.g. shade tolerance) is therefore important for predicting species response to disturbance (Comita et al., 2009) and species distribution over the long-term. This is especially important for tropical forests in the Caribbean that are periodically affected by hurricanes, given that the frequency of high intensity hurricanes is expected to increase due to Global Climate Change (Bender et al., 2011; Knutson et al., 2010).

The wet tropical montane forest of the John Crow Mountains, Jamaica, was impacted by three hurricanes in four years: Hurricane Ivan (2004), Dennis (2005) and Dean (2007). Following the most recent hurricane (Dean), seedlings and trees of several species showed varied dynamic and demographic responses and they were shifts in species distribution (Luke et al., 2014, 2016a,b). In this study, we sought to determine if the interspecific photosynthetic characteristics of seedlings of ten species from the John Crow Mountains, Jamaica, could be used to predict seedling post-hurricane demographic and dynamic patterns and species spatiotemporal distribution. Specifically, *in situ* leaf level photosynthetic responses to light from seedlings of selected species were measured using an infra-red gas analyser. This was then used to 1) calculate their light saturated maximum photosynthetic rate (A_{max}) and dark respiration rate (R_D), 2) determine their successional status and 3) to group the species based on their photosynthetic response. We then assessed whether interspecific photosynthetic characteristics/traits were related to post hurricane demographic trends/traits. Finally, we evaluated whether seedling photosynthetic traits could be used to split several species into groups based on similarities in their demographic response (over a period of three years) to disturbance created by the passage of Hurricane Dean in 2007 and based on the topographic parameters (aspect, elevation and slope) that could be used to predict the spatiotemporal distribution of stems in 2006 and 2012.

2. Materials and methods

2.1. Study site

Our study was conducted in the John Crow Mountains (JCM) section of the Blue and John Crow Mountains National Park (18°4′60″N, 76°24′0″W). It is a limestone massif with karst topography, which runs parallel to the eastern coast of Jamaica (Kelly, 1986). It has a maximum altitude of 1143 m asl and annual rainfall ranges from 6150 mm yr^{-1} in Millbank on the forest's western escarpment to 2814–2921 mm yr^{-1} in coastal areas (Kelly, 1986). The high rainfall on the western escarpment is due to orographic uplift. The forests of the John Crow Mountains include a lower montane wet forest, which transitions to an upper montane wet forest with undisturbed broad-leaf forest above 380 m asl. The island of Jamaica and the JCM have been affected by three hurricanes over a period of three years. These hurricanes include Hurricane Ivan (2004), Dennis (2005) and Hurricane Dean on August 2007. Hurricane Dean was a Category 4 hurricane, which passed along the south of the island. The centre of the hurricane was within 35 km of the coastline with wind speeds of up to 125 knots (232 km/h); however, peak winds near the JCM were less than one half this strength (Luke et al., 2016a). Nevertheless, there were both canopy defoliation and tree fall in some plots (Luke et al. 2014, 2016a, 2016b).

2.2. Species and experimental design

The seedlings that were selected represented the most common species found in the JCM. Table 1 lists the species and the number of individuals used in the photosynthetic measurements and modelling. In 2004, 45, 25 × 25 m permanent sample plots (PSPs) were established according to a randomized block design along opposite sides of the JCM (two sites: the north-facing and south-facing slopes). Plots were established across three access ridges at each site and the plots were arranged in blocks at three different elevations on each ridge (between 400 and 500m, 600–700m and 700–800m asl) (see: Luke et al., 2014; Luke et al., 2016a, 2016b). Each block consisted of three PSPs and the distance between each PSP was 20–45m. No blocks were established below 500 m on the south-facing slopes due to a general absence of undisturbed forest below this elevation. Species seedling demographic data (growth, mortality, recruitment) were collected yearly over a three-year period (2007–2010), and were obtained from a previous study that assessed the effects of Hurricane Dean on seedling dynamics (see: Luke et al., 2014). Specifically, seedling demographic data were collected from five randomly selected 5 × 5 m subplots, located within two larger 25 × 25 m plots from each block (30 in total) that were also randomly selected. In addition, all stems ≥ 2 cm DBH within the 45 PSPs were tagged with an aluminium tag in June 2006 and identified using voucher specimens of trees that were compared with herbarium specimens at the University of the West Indies (UWI). Diameter at breast height (DBH; 130 cm above ground) was recorded for each stem (≥ 2 cm DBH) in 2006 and again in 2012.

2.3. Gas exchange measurements

Gas exchange was measured *in situ* over a period of two month (July to August 2015) on the youngest or second youngest fully expanded leaf of at least five individuals for each species selected (total number for each species given in Table 1). Photosynthesis response to increasing light levels (i.e., light response curves) was evaluated using a CI340 handheld infrared gas analyser photosynthesis system with an open system configuration and an artificial light source (CID Bioscience, WA USA). Leaf gas exchange was determined at eight levels of photosynthetically active radiation, PAR (0, 50, 100, 200, 400, 800, 1600 and