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Changes in Patterns of Understory Leaf Phenology and Herbivory following Hurricane Damage[1]

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ABSTRACT

Hurricanes are important disturbance events in many forested ecosystems. They can have strong effects on both forest structure and animal populations, and yet few studies have considered the impacts on plant–animal interactions. Reduction of canopy cover by severe winds increases light availability to understory plants, providing an opportunity for increased growth. An increase in light availability should cause an increase in annual production of leaves and a more even production throughout the year (*i.e.*, less seasonality in production). This change will affect the availability of food resources to folivorous insects that feed primarily on young leaves; outbreaks of these insects could nullify the temporary advantage of increased understory light levels. On 21 September 1998, Hurricane Georges struck Puerto Rico, providing an excellent opportunity to determine the effect of the hurricane on leaf production and herbivory in the forest understory by comparing post-hurricane data with data obtained from a previous study conducted at the same site. Eight species were analyzed at El Verde Field Station, a wet forest site in eastern Puerto Rico. For the eight species combined, there was an increase in number of leaves produced after the hurricane and a more even seasonal pattern of leaf production, as predicted. Levels of herbivory were much lower (2.03%) after the hurricane compared with pre hurricane conditions (16.05%), indicating that increased light availability to understory plants was not offset by increased herbivory. Lower levels of herbivory were possibly due to herbivore satiation, changes in leaf chemistry, changes in herbivore populations, changes in herbivore predator populations, or a combination of two or more of these factors.

RESUMEN

Los huracanes son perturbaciones importantes en muchos ecosistemas forestales. Estos pueden tener fuertes efectos en la estructura de los bosques y en las poblaciones de animales, sin embargo pocos estudios han considerado su impacto en las interacciones planta–animal. La reducción de la cobertura del dosel, dada por fuertes vientos, aumenta la disponibilidad de luz para las plantas del sotobosque, dando una oportunidad de crecimiento para éstas. Un aumento en la disponibilidad de luz, podría causar un aumento en la producción anual de hojas al igual que una producción más continua a través del año. Este cambio afectaría la disponibilidad de alimento para insectos folívoros, que se alimentan principalmente de hojas jóvenes. Si el aumento en recursos se traduce en un gran aumento en las poblacionales de folívoros, esto podría anular la ventaja temporal dada por incrementos en niveles de luz. En 21 septiembre de 1998, el Huracán Georges azotó Puerto Rico, dando una oportunidad excelente para determinar el efecto de un huracán en la producción de hojas y herbivoría en el sotobosque, por medio de comparaciones con datos obtenidos antes del huracán. Ocho especies se analizaron en la Estación Biológica del Verde, en la parte Este de Puerto Rico. Para las ocho especies combinadas hubo un aumento en producción de hojas después del huracán, y un patrón de producción uniforme a lo largo del año. Los niveles de herbivoría fueron mucho menores (2.03%) después del huracán, comparados con las condiciones pre huracán (16.05%), indicando que el aumento en la disponibilidad de luz para las plantas del sotobosque no fue afectada por aumentos de herbivoría. Los bajos niveles de herbivoría pudieron darse posiblemente porque los herbívoros fueron saciados, cambios en la química de las hojas, cambios en las poblaciones de herbívoros, cambios en las poblaciones de depredadores de herbívoros o por la combinación de dos o más de estos factores.

Key words: *folivory; Hurricane Georges; leaf flushing; Puerto Rico; tropics.*

The structure and dynamics of ecological systems are controlled by productivity (“bottom-up control”), predation (“top-down control”), or some combination of both (Menge 1992, Power 1992). The effects of disturbance on ecosystems can be viewed in terms of their impacts on these controlling factors. Thus, for example, interactions between plants and herbivores can be considered in terms of the impact of disturbance on plant productivity relative to changes in herbivore and predator populations. Large and severe windstorms associated with hurricanes dominate the disturbance

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regime in many tropical and temperate regions (Brokaw & Walker 1991; Walker *et al.* 1992; Carlton & Bazzaz 1998a,b; Chinea 1999; Platt *et al.* 2000). Structurally, the most evident effect of a hurricane in a forest is the opening of the canopy due to great loss of leaves and branches and damage to tree boles (Brokaw & Grear 1991, Zimmerman *et al.* 1994, Vandermeer *et al.* 1996). As a result, there is a significant increase of light availability in the forest understory (Fernández & Fetcher 1991; Carlton & Bazzaz 1998a, b). To the degree that understory plants survive the immediate impacts of the storm, the increased light availability will represent a window of opportunity for increased growth and reproduction (Carlton & Bazzaz 1998a, b; Battaglia *et al.* 1999). Although higher light will stimulate growth, the net result will depend in part on the impact of the herbivore community.

Many types of herbivores prefer the young leaves of woody species because of their physical and nutritional characteristics (Coley 1983, Crawley 1983, Coley & Barone 1996). Therefore, all else being equal, increased production of new leaves in a forest understory following canopy disturbance should lead to an increase in herbivore populations and levels of herbivory. In most forests, production of new leaves is highly seasonal and is apparently controlled by increases in light availability and changes in cloud cover or day length (van Schaik *et al.* 1993; Wright & van Schaik 1994; Coley & Barone 1996; Barone 1998; Angulo-Sandoval & Aide 2000a, b; Williams-Linera 2003; *cf.* Reich 1994). If changes in understory light availability promote not only increased production of new leaves but also year-round production of new leaves, then herbivore populations may be expected to increase to the point that increased herbivory outweighs the advantage of increased light availability in the understory. High levels of herbivory, as observed in Puerto Rico following Hurricane Hugo (1989) by Torres (1992), may close the "window of opportunity" for understory plants offered by storm damage to the canopy; however, Torres' (1992) observations were limited to herbaceous and early successional plant species and it is not clear that these results can be extended to understory, woody plants.

Few studies have examined the effect of hurricanes on herbivory (Torres 1992, Schowalter 1994, 1995, Koptur *et al.* 2002) and no study has described the effect of these disturbances on plant–herbivore interactions at the community level for the woody understory plants. Angulo-Sandoval and Aide (2000b) described patterns of leaf production and herbivory in the understory of a wet forest site in Puerto Rico between 1994 and 1996, prior to Hurricane Georges (1998). This provided a unique opportunity to determine clearly the impact of a hurricane on plant–herbivore interactions at the community level. This study repeated the design of Angulo-Sandoval and Aide (2000b) at the same site and with the same species, following Hurricane Georges. We addressed the following questions: (1) Does hurricane damage to the forest canopy promote an overall increase in understory leaf production?; (2) How does canopy opening affect the seasonality of leaf production in the understory?; and (3) How are levels of herbivory affected by increased light availability?

METHODS

Study site.—The study was conducted at the El Verde Field Station (350 m elev.) in the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico (18° 20′N, 65° 49 W; detailed information on the study site is in Angulo-Sandoval & Aide 2000b). Evapotranspiration is lower than precipitation throughout the year (Waide & Reagan 1996) and for that reason it can be considered an aseasonal forest. Mean monthly temperatures range between 21 and 25°C (Brown *et al.* 1983). On 21 September 1998, Hurricane Georges with sustained winds of 110 mph traveled the length of Puerto Rico, affecting the entire island. The most recent storm of similar magnitude was Hurricane Hugo in September 1989. Both hurricanes had severe effects on forest structure in the LEF due to extensive leaf stripping, branch breakage, and tree snapping and uprooting (Walker 1991, Basnet *et al.* 1992, Zimmerman *et al.* 1994). These changes in forest structure affected understory plants and different animal populations, with changes in herbivore community composition (Torres 1992, Schowalter 1994, 1995) and increased numbers of predators in the understory (Reagan 1991, Woolbright 1991, Pfeiffer 1996). To determine the effect of Hurricane Georges on plant–herbivore interactions, we studied patterns of leaf production and levels of herbivory from January to December 1998. We compared data with those obtained by Angulo-Sandoval and Aide (2000b) in the same forest location and for the same species.

Study species.—Two shrubs, *Palicourea riparia* (Rubiaceae) and *Piper glabrescens* (Piperaceae), and juveniles of six tree species, *Casearia arborea* (Flacourtiaceae), *Dacryodes excelsa* (Burseraceae), *Guarea guidonia* (Meliaceae), *Manilkara bidentata* (Sapotaceae), *Sloanea berteriana* (Elaeocarpaceae), and *Tabebuia heterophylla* (Bignoneaceae), were studied. Leaf phenology and leaf damage were measured on 20 adult individuals (1–2 m tall) of *Pa. riparia* and *Pi. glabrescens* and 20 juveniles (1–2 m tall) of the remaining species. Plants were haphazardly located in the understory along *ca* 5 km of trails. Data were obtained during 12 months for all species except *Pa. riparia* (10 mo).

LEAF PHENOLOGY AND LEAF DAMAGE CENSUSES.—The study was conducted from January to December 1999. To determine leaf production, all new leaves were counted each month, and up to ten leaves per plant were randomly chosen and marked with plastic telephone wire to estimate herbivore damage (per leaf). One month later, when leaves were fully expanded, a plastic grid was used to estimate leaf area to the nearest 1.0 cm^2 and damage to the nearest 0.1 cm^2.

ANALYSIS.—For each individual, the monthly proportion of annual leaf production was calculated. To estimate the annual pattern of leaf production for each species, average leaf production for the 20 individuals was calculated every month. In addition, patterns of monthly leaf production for the eight species combined were calculated by averaging the monthly means of each species. Pre-hurricane and post-hurricane patterns of leaf phenology for each species and for the eight species combined were compared using the Kolmogorov–Smirnov test (Ott 1993). Average leaf production per individual per year for pre-hurricane and post-hurricane conditions was calculated. Pre- and post-hurricane leaf production were compared using a paired *t*-test on log transformed data. Herbivory was calculated based on total leaf area produced before and after the hurricane. For each leaf, total area and removed area were measured. Percent herbivory data were calculated based on total leaf area of each species produced during a particular month or year. The same calculations were performed on the pre-hurricane data. Monthly and annual herbivory was calculated for each species and for all species combined. Herbivory data were log transformed prior to analysis (the standard arcsine square root transformation did not normalize the data). Monthly pre-hurricane and post-hurricane levels of herbivory for all species were compared using a two-way ANOVA (factors used were species and before vs. after hurricane).

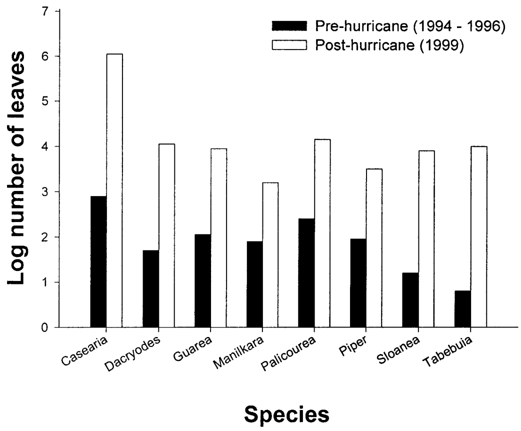

FIGURE 1. Total annual leaf production for 20 individuals of eight species. Pre-hurricane data are the averages of two years (1994–1996), and post-hurricane data are for one year (1999–2000).

RESULTS

LEAF PRODUCTION.—The amount and pattern of leaf production changed dramatically following Hurricane Georges (Figs. 1–3). Total leaf production increased dramatically after the hurricane (t = 4.11, $P \ll 0.01$; Fig. 1), increasing from 2 to 12 times, depending on the species measured (Fig. 1). Hurricane Georges also significantly affected the seasonal pattern of leaf production (Kolmogorov–Smirnov = 0.23; P = 0.01; Fig. 2). At the community level (8 spp. combined), there was a strong peak in leaf production during May and June prior to the hurricane (Fig. 2). After the hurricane, leaf production was more continuous, and there were minor peaks in January and during June–August. At the level of the individual species, the pattern of leaf production in seven of eight species was significantly changed from strongly or moderated synchronous to more continuous with no peak in leaf production during May or June (Kolmogorov–Smirnov > 0.43, $P \ll 0.01$; Fig. 3). The pattern of leaf production in *C. arborea*, a species that normally has continuous leaf production, was not changed by the hurricane (Kolmogorov–Smirnov = 0.15; P = 0.2; Fig. 3).

LEAF DAMAGE.—The majority of leaf damage was done by chewing insects, with the exception of *M. bidentata*, for which the main herbivore was a leaf miner (Angulo-Sandoval & Aide 2000a, b). Levels of leaf damage for all species combined were much lower after the hurricane (2.03%) than before

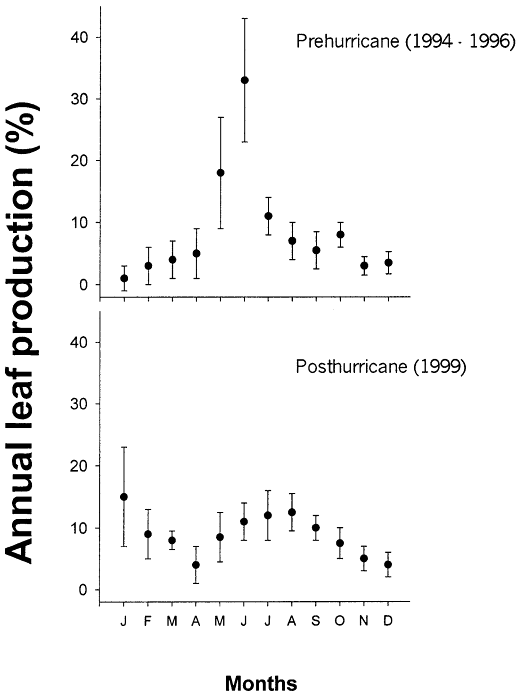

FIGURE 2. Patterns of annual leaf production for eight species combined. Pre-hurricane data were obtained by Angulo-Sandoval and Aide (2000 b) between November 1994 and October 1996. Monthly averages and standard deviations are shown for comparison.

(16.05%; Fig. 4 and Table 1). Significant differences were observed for herbivory before and after the hurricane ($F = 17.1$, $P \ll 0.01$) and differences due to species were significant overall (two-way ANOVA, $F = 27.65$, $P < 0.01$). Among species, pre-hurricane leaf damage ranged from 3.08 percent for *D. excelsa* to 32.43 percent for *M. bidentata* (Table 1). Post-hurricane damage ranged from 0.63 percent for *P. glabrecens* to 8.06 percent for *G. guidonia* (Table 1). After the hurricane, leaf damage was 1.2–30 times lower than before the hurricane for six of the eight species (Table 1). Pre- and post-hurricane levels of herbivory were not different for *G. guidonia* and *D. excelsa*, two species with low pre-hurricane levels of herbivory.

DISCUSSION

Hurricanes defoliate canopy trees, break branches, and snap and uproot trees. During Hurricane Hugo (1989), most of the damage occurred to large trees in the LEF (Zimmerman *et al.* 1994). This resulted in a decrease in canopy height from 21.1 to 9.3 m (Brokaw & Grear 1991, Walker 1991), a large input of leaves and branches into the understory (Lodge *et al.* 1991), and an increase in understory light availability (Fernández & Fetcher 1991). Following the hurricane, the canopy structure changed continuously due to refoliation and branch regrowth (Walker 1991, Zimmerman *et al.* 1994, Schowalter & Ganio 1999) and the establishment of pioneers (Fernández & Fetcher 1991). Although many species can recover rapidly, the average levels of light availability in the LEF ten months after Hurricane Hugo were similar to values previously observed for large treefall gaps (Fernández & Fetcher 1991). Thus, light availability one year after the hurricane was still much greater than before the hurricane.

Similar to Hurricane Hugo, Hurricane Georges opened the forest canopy, increasing the light levels in the understory and causing a dramatic increase in leaf production by the study plants. In addition, the seasonality of leaf production shifted dramatically. Prior to the hurricane, the community produced the majority of the leaves in a synchronous flush during May and June. Following the hurricane, the community pattern switched to a much more continuous pattern, presumably due to the continuous high levels of light availability throughout the year. Other studies have demonstrated the positive effects of canopy disturbance on growth of shrubs (Williams-Linera 2003) and juvenile woody plants (Aide & Zimmerman 1990, Hubbell & Foster 1990).

The increase in leaf production and the continuous availability of young leaves in the forest understory were expected to cause an increase in both herbivore populations and levels of herbivory (Aide 1991, 1993). Our results did not support this prediction. Post-hurricane levels of leaf damage were significantly lower than pre-hurricane levels. Torres (1992) observed outbreaks of insect folivores along forest edges, but in this study, there was no evidence of increases in herbivore populations or levels of herbivory within the forest understory.

Although we did not collect data to distinguish among possible explanations for decreased levels of herbivory following Hurricane Georges, four non-mutually exclusive explanations include (1) herbivore satiation, (2) a decrease in herbivore populations due to direct effects of the hurricane, (3) changes in plant leaf chemistry, or (4) an increase in populations of herbivore predators. As a guide to further research, we discuss these four possibilities.

Low levels of herbivory may be explained by herbivore satiation (Aide 1993), but this hypothesis

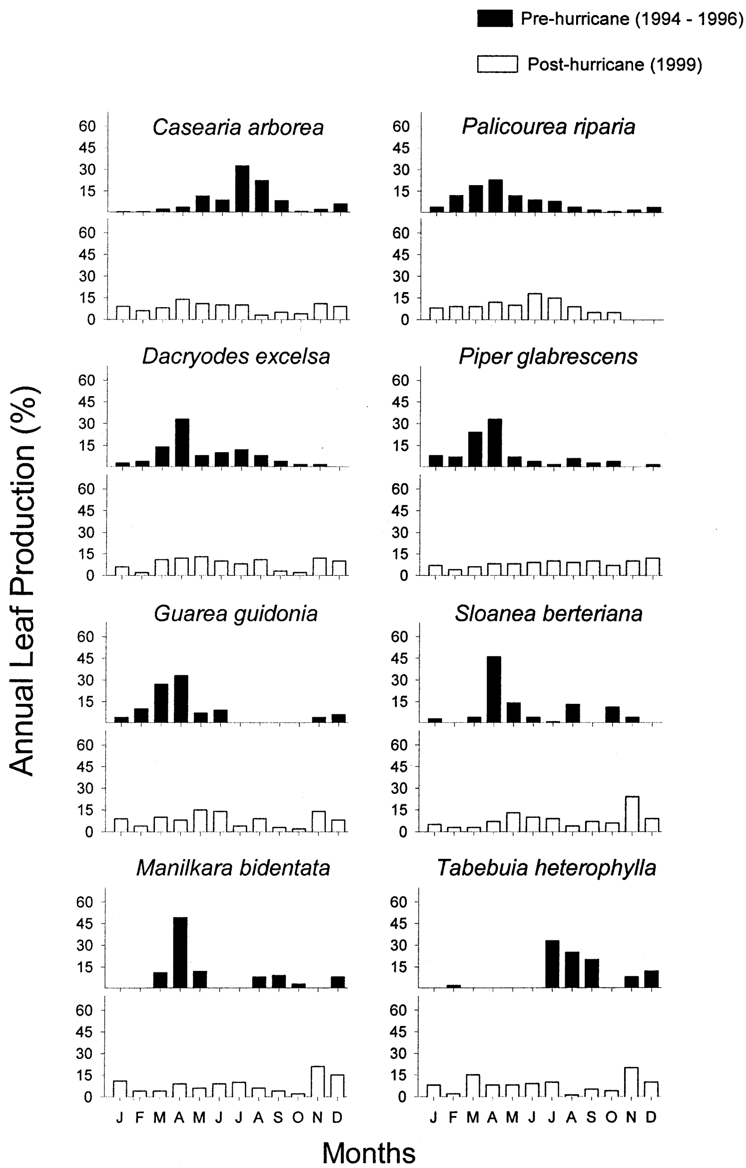

FIGURE 3. Annual leaf production for eight common species in LEF. No data was collected for *Palicourea riparia* in January and February 1999.

argues that satiation should be most obvious during peaks of leaf production. A major effect of the increase in light availability was to change the leaf production phenology from synchronous to more continuous. Following the satiation hypothesis, this should have resulted in higher levels of herbivory rather than the lower levels that were observed.

The direct effects of the hurricane may have reduced herbivore populations by causing local extinction or by eliminating critical resources. In Florida, many common herbivores and seed predators disappeared for more than seven months after Hurricane Andrew (Pascarella 1998, Koptur *et al.* 2002). Other studies have shown a diversity of responses by insects to hurricanes, with some groups increasing and others decreasing (Torres 1992; Schowalter 1994, 1995; Garrison & Willig 1996; Schowalter & Ganio 1999; Barberena-Arias & Aide 2002). Without data on specific herbivore species, it is difficult to determine if this was the

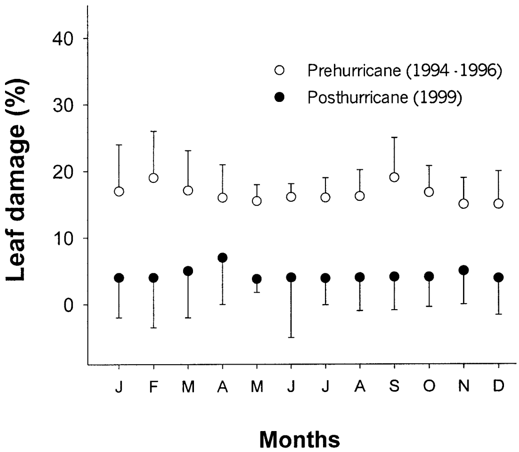

FIGURE 4. Mean monthly leaf damage before and after Hurricane Georges for the eight species combined. Errors bars represent standard deviation.

major reason for lower levels of herbivory in our study.

Another possibility is that there were important changes in leaf chemistry following the hurricane and that these changes resulted in greater defenses and less herbivore damage. Hurricanes could indirectly affect leaf chemistry by increasing light availability in the understory plants, resulting in a greater allocation of resources for carbon-based defenses (Hunter & Fokner 1999). Unfortunately, we did not perform any chemical analysis to determine if there was a correlation between increased production of carbon-based defenses and lower levels of herbivory.

The reduction in herbivores and herbivory may be explained by an increase in populations of herbivore predators following the hurricane. After Hurricane Hugo, the abundance of web-building spiders in LEF increased by more than 100 percent in the understory (Pfeiffer 1996). In the LEF, as on other islands, amphibian and reptiles are important insect predators (Dial & Roughgarden 1995). Amphibian populations, including *Eleutherodactylus coqui*, the most common species, increased following Hurricane Hugo (Woolbright 1991, Stewart & Woolbright 1996). Although the increase in amphibian populations was less pronounced following Hurricane Georges (L. Woolbright, pers. comm.), given their high abundance, a small increase could have helped to reduce herbivore populations. There was also an increase in the abundance of *Anolis* lizards in the understory due to a vertical shift of canopy species into the understory (Klawinski, pers. comm.), as occurred after Hurricane Hugo (Reagan 1991). These changes in the abundance and distribution of predators following the hurricane may be the most important factor influencing the decline of herbivory in the understory.

This study supports the idea that canopy disturbances (*e.g.*, hurricanes and droughts) in tropical forest can be beneficial for understory plants, mainly due to an increase in light availability. This can result in increased growth and reproduction for shrub species and increased growth for juveniles of canopy species. This effect will be even greater if these changes are associated with a reduction in herbivory, as has been observed in this study. Although we have not determined the cause for lower herbivory damage, we believe that it is likely to be an increase in predation on herbivores due to the changes in forest structure, which increased the abundance and diversity of predators in the understory, perhaps in combination with changes in leaf chemistry and herbivore satiation.

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TABLE 1. *Percent leaf damage (±SD) for each species before (1994–1996) and after (1999) Hurricane Georges.*

Species	Leaf damage (%) before Hurricane Georges	Leaf damage (%) after Hurricane Georges
Casearia arborea	14.61 ± 9.2	1.76 ± 4.7
Dacryodes excelsa	3.08 ± 5.1	1.87 ± 1.8
Guarea guidonia	14.26 ± 10.9	8.06 ± 6.5
Manilkara bidentata	32.43 ± 29.6	2.13 ± 4.2
Palicourea riparia	15.42 ± 21.2	2.87 ± 3.6
Piper glabrescens	12.12 ± 21.3	0.63 ± 3.9
Sloanea berteriana	14.70 ± 17.6	2.00 ± 4.6
Tabebuia heterophylla	8.91 ± 7.6	1.79 ± 1.9
Community	16.05 ± 11.2	2.03 ± 3.6

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