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SHORT COMMUNICATION

Regeneration beneath a dioecious tree species (*Spondias purpurea*) in a Mexican tropical dry forest

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Abstract: In dioecious plant species different frugivore activity between genders may influence the abundance and richness of the seedling banks underneath their canopies throughout seed removal and dispersal. In the tropical dry forest of Chamela, on the Pacific Coast of Mexico, the role of *S. purpurea* female trees as nucleation sites of regeneration was investigated. The standing density, species richness and dispersal syndrome of woody seedlings (i.e. trees and shrubs, 10–100 cm tall) recruited underneath and outside the canopy of 10 male and 10 female *S. purpurea* trees were recorded in a total of 160 1-m^2 plots. Total density was greater in seedling communities associated with female trees (i.e. underneath and outside their canopies) as compared with male trees (231 vs. 153 seedlings, respectively); whereas overall species richness was greater underneath female canopies. Further, the density of zoochorous species were greater underneath the canopy of *S. purpurea* females (range = 0–5 plants m^{-2}), than elsewhere (outside female canopies, range = 0–3 plants m^{-2}; underneath and outside male canopies, range = 0–2 plants m^{-2}), suggesting a directional dispersal bias towards them. Females of dioecious plant species may act as nucleation sites of initial seedling recruitment in tropical dry forests.

Key Words: dioecy, facilitation, regeneration, *Spondias purpurea*, tropical dry forests

Increased abundance and richness of seedlings and seeds beneath nurse or perching/roosting plants are well-known phenomena in arid and/or semi-arid ecosystems (Callaway & Walker 1997); and for tropical rain forests (Guevara *et al.* 1992). However, indirect facilitative effects in plant communities, including their impacts on diversity and recruitment have not been yet described in detail for tropical dry forest (TDF), limiting our capacity to understand how this forest type regenerates (Chazdon *et al.* 2011). Although resprouting is common in TDF trees (Dunphy *et al.* 2000), early plant life-stages (e.g. seeds and seedlings) are critical to forest regeneration, forest dynamics and for the maintenance of diversity; while seed dispersal is a key factor providing gene flow (Schupp *et al.* 2010).

Dioecious plant species may show between-gender differences in size, growth rates and phenology (Forero-Montaña *et al.* 2010). In tropical forests around 27% of all plant species are dioecious and generally these species possess fleshy fruits which are consumed and dispersed by animals (Ibarra-Manriquez & Oyama 1992). In some dioecious species (e.g. *Myrsine coriacea* and *Juniperus sabina*) females attract more frugivores than males (Begnini & Castellani 2013, Verdú & García-Fayos 2003). Soil conditions under the canopy may also be influenced by tree gender, with higher nutrient concentrations in soils beneath female trees (Rhoades *et al.* 1994).

Several aspects in the life cycle of plants and animals in TDF such as reproduction and phenology, are determined by water-deficit patterns (Mandujano *et al.* 1994). The TDF of Chamela (Pacific Coast of Mexico) is characterized by a pronounced dry season (6–7 mo length). At the end of the dry season a few species produce fruits, including the dioecious tree *Spondias purpurea* (Anacardiaceae; Bullock & Solís-Magallanes 1990). The fleshy fruits of *S. purpurea* are an important source of food and water for many animals under water stress. Massive and prolonged flowering and fruiting periods in *S. purpurea* (≥3 mo)

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provide resources to several animal taxa (i.e. mammals, birds, reptiles and insects) when other plants species do not (Bullock & Solís-Magallanes 1990). This condition may increase animal activity over and beneath the canopy of female trees.

In this study we suggest that *S. purpurea* females could act as nucleation sites of initial regeneration as a result of directed dispersal and by providing highly favourable recruitment sites (*sensu* Schupp *et al.* 2010). We expected that the abundance and richness of woody seedlings (plants 10–100 cm) but especially that of zoochorous species would be greater underneath the canopy of *S. purpurea* females than both beneath the canopy of males and outside the canopy of either gender. The present study could contribute to the understanding of the ecological factors, processes and mechanisms implicated in the regeneration of this tropical system.

The study took place in the Chamela Biological Station (Instituto de Biología, UNAM) within the Chamela–Cuixmala Biosphere Reserve (CCBR). The CCBR comprises a total area of 13 300 ha in the Pacific Coast of Jalisco, Mexico (19°22′–9°35′N, 104°56′–105°03′W). Annual average temperature is 24.7 °C; and precipitation is 740.6 mm (range = 366–1261 mm). In October 2007, along 7 km of forest trails of old-growth TDF we located a total of 20 trees (≥ 5 cm dbh) of *S. purpurea*, 10 females and 10 males. Selected trees were at least 25 m apart and at least 10 m away from the trails (*c.* 1 m wide). The phenology of these trees has been followed consecutively for *c.* 10 y; so the sexual expression of each individual has been accurately determined by analysing the flowers (Calderón-Cortés *et al.* 2011). The most common woody species in the neighbourhood (up to 10 m away) of *S. purpurea* sampled trees were: *Caesalpinia eriostachys*, *Heliocarpus pallidus*, *Cordia alliodora* and *Amphipterygium adstringens.*

Beneath the canopy of each *S. purpurea* tree we positioned four 1-m^2 plots arranged at the four cardinal points using the base of the main trunk as the centre. Parallel to each of the former plots but just outside the canopy perimeter (canopy, *c.* 10 m^2 for both genders), we positioned another four 1-m^2 plots (following Rhoades *et al.* 1994). These plots were located beneath the canopy of neighbouring trees from several other species. To define the area influenced by *S. purpurea* canopy, we projected the canopy area extending down through all foliage levels to the ground. In each plot we recorded all woody individuals (trees and shrubs 10–100 cm tall) in the seedling bank and identified them to the lowest possible taxonomic level. For every species we determined its dispersal syndrome (i.e. biotic or abiotic).

Differences in seedling abundance between gender and position from the canopy were analysed with log-linear models for count data. This analysis was performed for the overall seedling community and for those species dispersed by animals. We specify a Poisson error with a logarithmic link function and corrected for overdispersion as indicated by Crawley (2007). Differences in seedling species richness beneath and outside the canopy of *S. purpurea* trees were assessed by non-parametric methods provided by the EstimateS program (V. 8.2.0). We selected two methods considered as the best estimators of species richness in tropical forest seedling communities (Chazdon *et al.* 1998): (1) ICE, incidence-coverage estimator; and (2) ACE, abundance-based coverage estimator. In all cases we performed EstimateS setting patchiness as 0. For each non-parametric estimator differences in species richness between gender and position were analysed by one-way ANOVA. Data were analysed through generalized linear models using the statistical programme R, V. 2.13.0 (Ripley 2001). Significant differences were set at $P \leq 0.05$.

A total of 384 woody seedlings were found in 160 m^2; 131 seedlings beneath females (range = 2.0–6.0 plants m^{-2}) and 85 beneath males (range = 1.0–5.0 plants m^{-2}); whereas 100 and 68 seedlings were found outside from the canopy of female (range = 1.3–5.3 plants m^{-2}) and male (range = 0.8–3.5 plants m^{-2}) trees, respectively. Total density was significantly greater ($\chi^2 = 6.82$, df = 1, $P < 0.01$) in seedling communities associated to female trees (i.e. beneath and outside) as compared with male trees (231 vs. 153 seedlings, respectively). The abundance of zoochorous species differed significantly between genders ($\chi^2 = 5.94$, df = 1, $P = 0.01$), and in the gender × position interaction term ($\chi^2 = 4.88$, df = 1, $P = 0.03$). Density of zoochorous species declined from beneath *S. purpurea* females (range = 0–5 plants m^{-2}), to outside female canopies (range = 0–3 plants m^{-2}), to underneath and outside male canopies (range = 0–2 plants m^{-2}). Nine zoochorous species were recorded beneath *S. purpurea* female canopies compared with only three species beneath male trees.

Overall, a total of 51 woody species were recorded. There were 29 species beneath and 18 species outside the canopy of females (range, 1–3 and 1–2 species m^{-2}, respectively); while there were 27 species beneath and 22 outside the canopy of male trees (1–2 species m^{-2} and 0–2 species m^{-2}, respectively). No seedling of *S. purpurea* was recorded. The non-parametric estimators showed that: (1) species richness was greater beneath *S. purpurea* females; (2) the lowest species richness was found outside *S. purpurea* female canopies; and (3) for both genders species richness was greater beneath than outside their canopies (S_{obs}, $F_{3,383} = 344$, $P < 0.001$; ICE, $F_{3,383} = 549$, $P < 0.001$; and ACE, $F_{3,383} = 733$, $P < 0.001$; Figure 1).

Our study showed an aggregated spatial pattern of zoochorous species beneath female canopies (anisotropy). These results suggest that this dioecious tree species

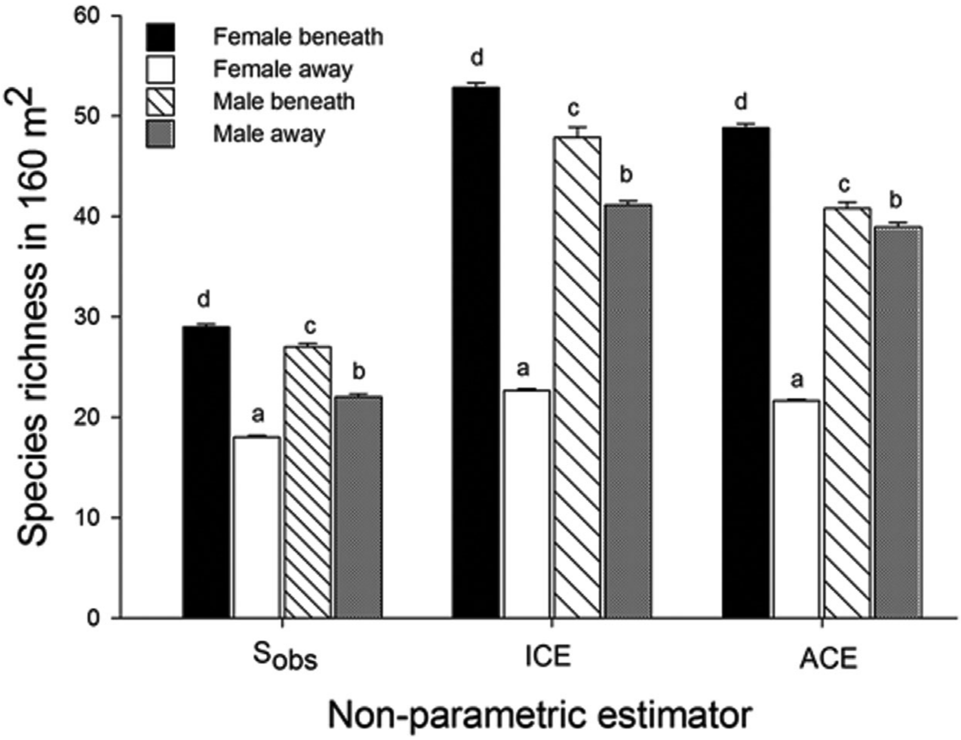

Figure 1. Species richness (mean ± SE) of woody seedlings beneath and outside the canopy of male ($n = 10$) and female ($n = 10$) *Spondias purpurea* trees in the tropical dry forest of the Chamela-Cuiztmala Biosphere Reserve, Mexico. Bars show the observed species richness (S_{obs}) and two non-parametric estimators, where ICE, incidence-based coverage estimator; and ACE, abundance-based coverage estimator. Different letters indicate significant differences at $P < 0.05$. All individuals were trees and shrubs 10–100 cm tall.

attracts frugivorous seed dispersers and has a facilitative effect on TDF regeneration. This is, in the presence of a fruiting *S. purpurea* tree, frugivore activity concentrates there than anywhere (e.g. away from females; Begnini & Castellani 2013). At Chamela apparently, while feeding on *S. purpurea*, animals deposit seeds of other plant species (e.g. *Achatocarpus gracilis*, *Guapira macrocarpa*, *Cephalocereus purpusii* and *Trichilia trifolia*); while *S. purpurea* seeds may be taken and dispersed further away and dropped beneath a conspecific tree or under another species. Seedlings of *S. purpurea* have shown greater survival 10 m away from their parent trees (Mandujano 1992).

Due to its extended fruiting phenology, *S. purpurea* might be one of the few trees being dispersed at some stage, reducing competition for dispersal vectors with other plant species. The lack of conspecific seedlings recorded, suggests that *S. purpurea* propagules were predated and/or dispersed further away. It is likely that *S. purpurea* seeds remain dormant in the soil seed-bank as germination rates of several species in the genus (*S. mombin*, *S. radlkolferi*, *S. purpurea*) are low, suggesting that *Spondias* may need mechanical scarification provided by larger terrestrial frugivores (e.g. peccaries) to release the embryo as shown for other Anacardiaceae (Midgley *et al.* 2012, M. Quesada & J. Benítez-Malvido, pers. obs.).

Females of *S. purpurea* facilitate the regeneration of woody plant species in an environment where seedling recruitment is limited (Janzen 1970). Seedling density found beneath the canopy of *S. purpurea* females almost doubled that reported for undisturbed old-growth TDF in Chamela (average: 3.3 plants m^{-2} vs. 1.8 plants m^{-2}, respectively; Maza-Villalobos *et al.* 2011). Seedling recruitment and survival might be greater beneath the canopy of *S. purpurea* females, not just because of greater seed dispersal but also due to a more favourable and heterogeneous micro-environment underneath (Callaway & Walker 1997). Besides shade provided to seeds and seedlings by the canopy, fruit fall and seed deposition in faeces (e.g. nutrient inputs) and foraging fauna such as chachalaca (*Ortalis poliocephala*), white-tailed deer (*Odocoileus virginianus*) and collared peccary (*Pecari tajacu*) are likely to improve site conditions for seedling establishment (e.g. soil turnover; Feeley 2005, Rhoades *et al.* 1994). In the TDF of Chamela, 24% of the tree species are dioecious (Bullock 1985). Therefore, to elucidate the significance of dioecious trees (e.g. *S. purpurea*) as nucleation sites in the dry tropics, long-term studies on plant demographic processes such as seed predation, germination, seedling competition and growth as well as microclimatic conditions beneath their canopy are needed. This knowledge is relevant to understand how the presence of certain dioecious tree species influences the spatial pattern of other plant species in the dry tropics.

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