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Understanding recruitment failure in tropical tree species: Insights from a tree-ring study

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ABSTRACT

Many tropical tree species have population structures that exhibit strong recruitment failure. While the presence of adult trees indicates that appropriate regeneration conditions occurred in the past, it is often unclear why small individuals are absent. Knowing how, when and where these tree species regenerate provides insights into their life history characteristics. Based on tree age distributions inferences can be made on past forest dynamics and information is obtained that is important for forest management. We used tree-ring analyses to obtain tree ages and reconstruct >200 years of estimated establishment rates in a sparsely regenerating population of *Afzelia xylocarpa* (Fabaceae), a light-demanding and long-lived canopy tree species. We sampled all 85 *Afzelia* trees >5 cm diameter at breast height (dbh) in a 297-ha plot in a seasonal tropical forest in the Huai Kha Khaeng (HKK) Wildlife Sanctuary, western Thailand. The age distribution of the sampled *Afzelia* trees revealed two distinct recruitment peaks centred around 1850 and 1950. The presence of distinct age cohorts provides a strong indication of disturbance-mediated recruitment. Additionally we found three lines of evidence supporting this interpretation. (1) Similarly aged trees were spatially aggregated up to ~500 m, a scale larger than single tree-fall gaps. (2) High juvenile growth rates (5–10 mm dbh year^{-1}) of extant small and large trees indicate that recruitment took place under open conditions. (3) A significant positive correlation between tree age and local canopy height indicates that trees recruited in low-canopy forest patches. Likely causes of these severe canopy disturbances include windstorms and ground fires, which are common in the region. In addition, successful establishment seems to be favoured by wetter climate conditions, as the estimated establishment rate was correlated to the Palmer Drought Severity Index (PDSI). Thus, the co-occurrence of canopy disturbance and favourable climatic conditions may provide a window of opportunity for *Afzelia* establishment. Our results indicate that forest patches with occurrence of large *Afzelia* trees have undergone high-severity canopy disturbance prior to establishment, suggesting that these disturbances have shaped forests at HKK. Tree-ring analyses provide a powerful tool to understanding tropical tree establishment patterns. Rare, high-severity canopy disturbances may play a key role in the regeneration of long-lived tropical canopy tree species with recruitment failure, potentially in interaction with climate variability to determine variation in establishment success over decades or centuries.

1. Introduction

Across the tropics the size distribution of many tree species is characterized by the apparent absence of small trees (Swaine and Whitmore, 1988; Wright et al., 2003). In West Africa, Poorter et al. (1996) described size class distributions for eight large-statured, canopy tree species, of which six did not show the inverse J-shaped distribution expected of a population at equilibrium. In Southeast Asia, Bunyavejchewin et al. (2003) showed that three out of four species in the Dipterocarpaceae family had irregular size distributions, typically lacking individuals in many of the smaller size classes. And in the Brazilian Amazon, Grogan et al. (2008) showed unimodal size distributions for populations of the commercially important mahogany tree (*Swietenia macrophylla*). Although unimodal size distributions may be generated by particular ontogenetic shifts in growth and mortality rates (Bin et al., 2012), they may also be an indication of recruitment limitation (Condit et al., 1998).

This raises questions of how, when and where species with unimodal size distributions regenerate, because without the occasional establishment of new recruits, these populations cannot be viable. Answering these questions is of importance for forest management and tree species conservation. Recruitment

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limitation is thought to be generated by scarcity of parent trees, limited seed availability and small dispersal distances, as well as establishment limitation, which may be coupled to the occurrence of disturbances (Clark et al., 1998; Hubbell et al., 1999; Snook, 1996). In temperate forests, the role of rare and intense disturbances on regeneration of recruitment-limited tree species is well-known. In these forests, tree-ring studies have revealed the presence of discrete age cohorts of light-demanding tree species which were considered a strong indication of recruitment following canopy disturbance (Duncan and Stewart, 1991; Jordan et al., 2008; Splechtna et al., 2005), especially if similarly aged trees are spatially aggregated (Rozas, 2003). Over the past half century, studies on temperate forest dynamics have demonstrated that rare catastrophic disturbances are ubiquitous and shape forest structure and composition by driving tree recruitment patterns (Oliver and Larson 1996).

In tropical forests, the occurrence of intense disturbances is increasingly well documented (Chambers et al., 2013; Whitmore and Burslem, 1998), but the role of intense disturbances in tree recruitment and as a potential mechanism explaining recruitment failure is less well understood. In part this lack of understanding is due to the dominant focus on direct observations at short temporal scales, such as seed trap studies that quantified seed limitation over several years (e.g., Muller-Landau et al., 2008) or censuses showing spatial segregation of seedlings and adult trees (e.g., Gullison et al., 2003). While these studies have been informative, their short temporal scale limits inference of the role of rare events on recruitment of tropical tree species. What is lacking in the study of recruitment limitation of tropical trees is long-term demographic information (Baker et al. 2005). Such a century-long temporal scale is required, because the intensive and large-scale disturbances that are hypothesized to induce successful recruitment in tree species showing absence of small trees, are likely to occur at very low frequency (Chambers et al., 2013).

Tropical dendroecology addresses this knowledge gap by revealing the age structure of populations of non-regenerating tree species (Baker et al., 2005; Rozendaal and Zuidema, 2011). Not only does dendroecology provide data on ages of trees, ring-width measurements also provide information on historical growth rates of trees (Abrams et al., 1997; Druckenbrod et al., 2013). The method can be used to assess whether growth rates of juvenile trees were high, indicative for establishment in disturbed areas with high light conditions (Landis and Peart, 2005; Rozendaal et al., 2010). Moreover, tree establishment after severe canopy disturbance may be inferred from the spatial segregation between mature trees (e.g., in presently closed-canopy forest) and juvenile trees (e.g., in present low-stature forest) (see Oliver and Larson, 1996).

Here we test the hypothesis that episodic recruitment of a tropical tree species with an irregular size distribution is induced by rare, severe canopy disturbance events (Newbery et al., 2004; Poorter et al., 1996; Swaine and Whitmore, 1988). We evaluated the regeneration strategy of the light-demanding and IUCN red-listed tropical tree species *Afzelia xylocarpa* (Kurz) Craib (Fabaceae) in western Thailand, where it is currently poorly regenerating (Baker and Bunyavejchewin, 2006; Baker et al., 2005; Bunyavejchewin et al., 2009). We hypothesize that the present-day population is lacking a regeneration niche because establishment is typically induced by occasional, spatially extensive canopy disturbances that affect several hectares of forest, but may be heterogeneous in intensity (Baker and Bunyavejchewin, 2009; Splechtna et al., 2005; Whitmore and Burslem, 1998). We refer to these events as ‘severe canopy disturbances’.

We used data obtained from tree-ring analyses to address four specific questions. (1) Is there evidence for discrete age cohorts? If *Afzelia* relies on occasional large-scale canopy openings for its regeneration, we expect the age distribution to be strongly clustered. (2) Do age cohorts form spatially discrete patches? If regeneration is induced by severe canopy disturbance, we expect similarly aged trees to be spatially aggregated at a scale larger than that of single treefall gaps. (3) Are growth rates of juvenile trees always high in early stages of growth? High diameter growth rates of juveniles are indicative of trees recruiting in open conditions, and if these are found for both old and young trees, this indicates similar recruitment conditions over time. (4) Is forest structure surrounding current young trees different from the forest structure around old trees? We expect that if recruitment depends on canopy disturbance, then younger trees would be associated with low canopy (building phase) forest and older trees with high canopy (mature phase) forest. We use our findings to discuss the regeneration strategy of the study species and the disturbance history of the study site. We also discuss the potential role of severe canopy disturbance in the regeneration of long-lived tropical canopy tree species in general.

2. Material and methods

2.1. Study area and species

The study area was situated in the Huai Kha Khaeng Wildlife Sanctuary (HKK), Uthai Thani province, western Thailand, around 250 km northwest of Bangkok (15.60 N 99.20 E). HKK is a protected area of global conservation significance. Both HKK and the adjacent Thung Yai-Naresuan Wildlife Sanctuary are International Man and Biosphere Reserves and together form the main core of Thailand’s Western Forest Complex, the largest area of protected forest in continental Southeast Asia. The HKK landscape is characterized by a hilly topography. The climate is monsoonal with a rainy season from May to October and a 4–6 month dry season from November to April (Fig. A.1). Mean annual rainfall is 1473 mm and mean annual temperature is 23.5 °C (Bunyavejchewin et al., 2009). Soils are highly weathered, slightly acidic ultisols and soil textures are sandy loam in the surface and sandy clay-loam in the subsurface horizon (Bunyavejchewin et al., 2009). There is no human influence in HKK, except for the Wildlife Sanctuary infrastructure and as an ignition source for ground fires expanding from agricultural areas around the park (Baker et al., 2008). No logging activities are known to have taken place in our study area. The vegetation in the area is classified as seasonal dry evergreen forest and mixed deciduous forest. A Smithsonian Center for Tropical Forest Science (CTFS) 50-ha forest dynamics plot, installed in 1992, is immediately adjacent to the area we used for our tree-ring study (Fig. 1). Mean density of trees $\geqslant$10 cm dbh in the 50-ha plot is 438 ha^{-1} and mean density of trees $\geqslant$30 cm dbh is 83 ha^{-1} (Bunyavejchewin et al., 2001). Canopy height of the forest is around 30 m, with occasional emergent trees reaching more than 50 m tall. Members of the family Dipterocarpaceae dominate the forest in total basal area; other well-represented families include Annonaceae, Euphorbiaceae and Meliaceae (Bunyavejchewin et al., 2001).

The study species, *Afzelia xylocarpa (*Kurz) Craib (Fabaceae), is known to form annual rings (Baker et al., 2005). The species is classified as light-demanding (So et al., 2010; Sovu et al., 2010) and in HKK the trees are completely leafless for around 1–2 months in the period from December to February (Williams et al., 2008). Due to loss of habitat and overexploitation for its precious wood the species has been classified as endangered on the IUCN Red List (Nghia, 1998). However, in the remote areas of HKK, *Afzelia* is still relatively abundant across the broader landscape. Importantly, though, an earlier survey of the population of *Afzelia* trees in the area revealed an irregular size distribution characterized by many large trees and apparently poor regeneration (Baker et al., 2005). In