



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 *Azelia xylocarpa* (Fabaceae), a light-demanding and long-lived canopy tree species. We sampled all 85 *Azelia* 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 *Azelia* 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 *Azelia* establishment. Our results indicate that forest patches with occurrence of large *Azelia* 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.

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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., Gul-lison 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 *Azelia 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 *Azelia* 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 ≥ 10 cm dbh in the 50-ha plot is 438 ha⁻¹ and mean density of trees ≥ 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, *Azelia 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, *Azelia* is still relatively abundant across the broader landscape. Importantly, though, an earlier survey of the population of *Azelia* trees in the area revealed an irregular size distribution characterized by many large trees and apparently poor regeneration (Baker et al., 2005). In

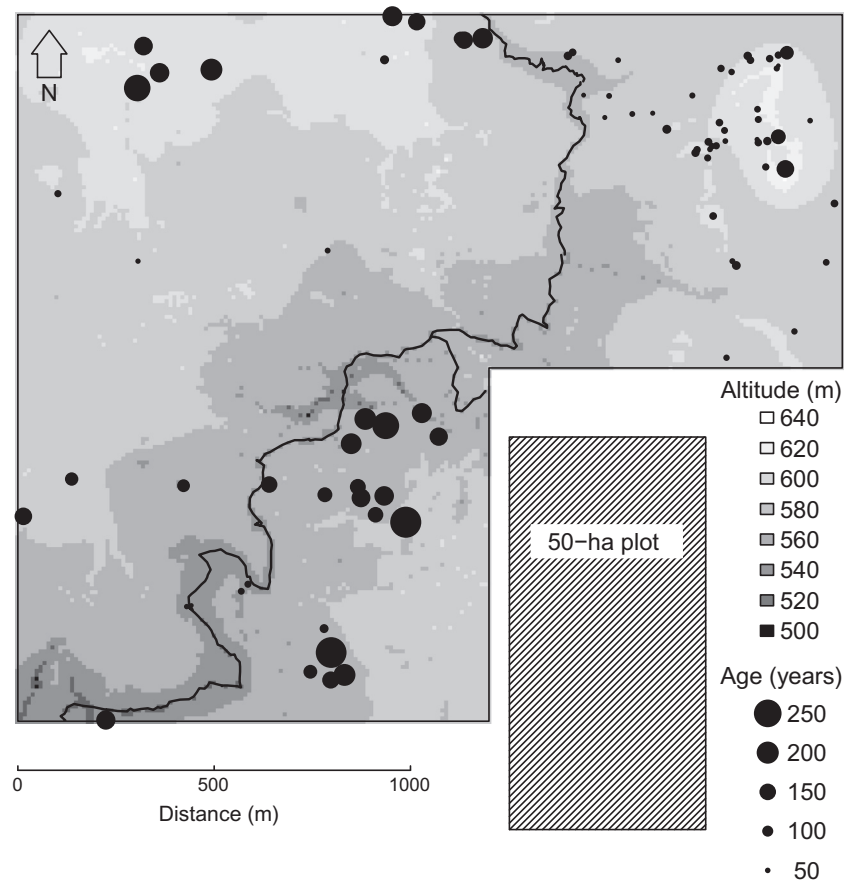


Fig. 1. Topographic map of the study area in the Huai Kha Khaeng Wildlife Sanctuary showing locations of all *Afzelia* sample trees. Dot size is proportional to tree age. The black line indicates the location of a small stream running through the plot. Location of the adjacent 50-ha forest dynamics plot is also shown.

the 50-ha plot small trees are rare, with only 8 individuals ≤ 10 cm dbh, compared to a total of 22 trees with a dbh > 50 cm (Bunyavechewin et al. 2009).

Detailed information on *Afzelia* regeneration under natural conditions, especially the seed dispersal mechanism, is scarce. It has been noticed that the large, aril-covered seeds are attractive to a variety of animals and especially gibbons (LaFrankie, 2010). This is confirmed by our observations during the fruiting season in August 2011 when we found many fresh *Afzelia* seed pods with tooth marks, presumably from primates. Dispersal of similarly shaped seeds of the African congener, *Afzelia quanzensis*, has been found to be facilitated by primates, squirrels and hornbills (Gathua, 2000; Gerhardt and Todd, 2009), species groups that are all abundant at HKK. Seeds of *Afzelia* may therefore be dispersed over considerable distance by animals, in which case seed limitation may not be a limiting factor for recruitment.

2.2. Sampling and measurements

Our 297-ha study site was situated directly northwest of the 50-ha CTFs forest dynamics plot (Fig. 1). Wood samples for tree-ring analysis were collected from 85 individual *Afzelia* trees between December 2010 and December 2011. A total of 5 months was spent to thoroughly search the 297-ha area for all *Afzelia* trees > 5 cm dbh. We used a GPS-tracker (Garmin GPSMAP 60C Sx) to visualize our trails and to verify that the whole area was covered. Characteristic features, such as early branching, a distinctive flakey bark and presence of large superficial roots greatly facilitate the recognition of the species in the field.

The locations of *Afzelia* trees suitable for coring (i.e., no stem deformities or severe stem rot: $< 10\%$ of the individuals encountered were not suitable for coring) were GPS-mapped at ~ 5 m accuracy and the elevation level was recorded. We measured dbh (1.3 m) and diameter at sampling height of each *Afzelia* tree. Height measurements of all sampled *Afzelia* trees and all taller neighboring trees within 10 m of the sample tree were obtained using a digital hypsometer (Nikon Forestry 550).

At a height of approximately 1 m we manually extracted tree cores with 5.15 mm diameter Suunto (Vantaa, Finland) or Haglöl (Långsele, Sweden) increment borers. Thus, in the following 'tree age' refers to the age since reaching coring height. Depending on the diameter of the tree we used borers with lengths varying between 40 and 70 cm. From trees < 40 cm dbh two cores were taken and for all larger individuals we took three cores. Taking multiple cores allowed us to measure rings over at least three complete radii, thereby correcting for radial differences in diameter increment. We only cored trees > 5 cm dbh to minimize damage to the juveniles. Core extraction areas were left untreated (Dujesiefken et al., 1999).

The increment cores were glued to wooden holders and cut perpendicular to the ring boundaries with a large sliding microtome (WSL, Switzerland). Digital images (1600 dpi) of the tree cores were acquired using a high-resolution flatbed scanner (Epson Expression 10,000 XL) and analyzed in the WinDENDRO program for tree-ring analysis (version 2009b; Regent Instruments Canada Inc.). All tree-ring boundaries, defined by marginal parenchyma bands, were marked manually on the screen and measured to the nearest 0.001 mm. Ring-width series were visually crossdated within trees and then among trees (WinDENDRO). During

crossdating the patterns of wide and narrow rings in one tree are matched with those of other trees to improve the dating accuracy of the rings. After crossdating ring-width series were checked for dating errors with the computer program COFECHA (Holmes, 1983). As a quality control for the dating accuracy we aimed to produce a species specific tree-ring chronology, which is a record of ring widths representing the stand level signal. First, ring-width series that correlated poorly with the initial chronology—for example, due to prolonged growth suppressions—were removed from the dataset (Pederson et al., 2004). Second, the raw ring-width data was detrended using a 20-year cubic spline to remove all age related trends. Third, the ring-width data was prewhitened using autoregressive modeling to remove any effect of temporal autocorrelation in growth (dplR; Bunn, 2008). The resulting chronology was cut off when the running expressed population signal (EPS) was <0.85 (Wigley et al., 1984). The EPS is used to assess how well a chronology of a finite number of trees estimates the hypothetical (noise-free) population chronology and can therefore be used to determine the maximum length of the chronology (Wigley et al., 1984).

The pith was not included in many cores, either due to insufficient borer length or because all coring attempts had failed to include the pith of the tree. The pith was not included in the samples taken for ~75% of the trees (64/85 trees), although the missing distance was >3 cm in only 26% of the cases (22/85 trees) (Fig. A.2a). If arcing was visible on the cores the missing distance to the pith was estimated by the degree of arcing in the oldest visible ring, assuming a circular growth pattern (Splechtna et al., 2005). If no arcing was visible on the cores we calculated the missing distance to the pith based on the diameter at sample height measured in the field. The missing distance to the pith was then used to estimate the pith dates by dividing the missing radial distance to the pith by the average width of the five oldest visible rings. Because missing distances to the pith lead to some uncertainty around the age estimates we also used an alternative method to obtain age estimates of trees with no pith. Based on all 21 trees that could be pith-dated we constructed a model of age vs. diameter. This model was then used to obtain an alternative estimate of the missing number of rings to the pith and an alternative age distribution.

2.3. Data analysis

A digital elevation model of the 297-ha plot was created using an inverse distance weighted interpolation (R gstat package; Pebesma, 2004) of ~12,500 individual elevation measurements obtained with the GPS device.

We expected that establishment of new individuals might be related to variability in local climate conditions (Cullen et al., 2001; López et al., 2008; Zimmer and Baker, 2009). Therefore we tested the relation between the estimated establishment distribution and the reconstructed Palmer Drought Severity Index (PDSI) for the summer (June–July–August) monsoon season at the location of our study area using the Monsoon Asia Drought Atlas (MADA) (Cook et al., 2010; Trouet and Van Oldenborgh, 2013). The PDSI is a measure for soil moisture availability, in which a value of 0 indicates normal moisture conditions, while negative values indicate dry and positive values indicate wet conditions. These PDSI values were derived from a network of more than 300 tree-ring chronologies across the part of Asia that is affected by the summer monsoon system. For each decade in 1700–2000 we calculated the estimated establishment rate and the mean PDSI value. As trees that recruited in the distant past have accumulated a higher mortality risk compared to recent recruits, we calculated the estimated number of established trees per decade z for decade y , $z(y)$, assuming an annual mortality rate of 1%. We calculated $z(y)$ as:

$$z(y) = n_y * \left(\frac{100}{99} \right)^{(1990-y)}$$

where n_y is the number of trees that survived until the date of sampling and y is the decade of establishment. A generalized linear model (GLM) with Poisson error structure was used to explain variation in z by decadal mean PDSI values.

We assumed that if trees establish in even-aged patches, that the spatial distribution of tree ages should be non-random, with trees of similar age occurring together (Duncan and Stewart, 1991; Middendorp et al., 2013). This spatial autocorrelation in tree age was calculated using Moran's I coefficient. We used 100 m distance classes and only considered distance classes with more than 15 pairs of neighboring trees. The correlogram was considered globally significant if at least one Moran's I coefficient was significant at a Bonferroni-corrected significance level ($P < 0.05/n$), where n is the number of distance classes in the correlogram (Fortin et al., 1989). Positive Moran's I values indicate that trees over this distance are similarly aged, while negative values indicate dissimilarity in age.

Average growth rates per 10 cm dbh class were calculated for each individual tree to assess the relation between dbh and diameter growth. Growth rates of juvenile trees (<30 cm dbh) were then compared between cohorts. Forest canopy height was estimated by taking the height of the tallest tree within 10 m of the sampled *Afzelia* tree. If no other tree within 10 m from the sampled *Afzelia* tree was taller we estimated forest canopy height as the height of the sample tree. All statistical analyses were performed using the R program for statistical computing, version 2.13.1 (R Development Core Team 2013).

3. Results

Afzelia xylocarpa was found throughout the 297-ha plot, although spatial variation in tree density was considerable. A large proportion of the trees was located in the northeast corner of the plot, directly north of the 50-ha plot (Fig. 1). This forest area was structurally different from the rest of the study area due to the abundance of bamboo clumps of an unidentified species. Patches with older (~150 year) *Afzelia* trees were mainly dominated by large Dipterocarpaceae trees (e.g., *Hopea odorata*, *Vatica harmandiana*).

Based on crossdated ring-width series of 38 trees (38% of the total) we constructed a standardized chronology (Fig. 2). Total chronology length (EPS > 0.85) was 36 years and covered the period between 1976 and 2011 (Table 1). The *Afzelia* chronology was marginally positively correlated ($P < 0.07$, Pearson correlation)

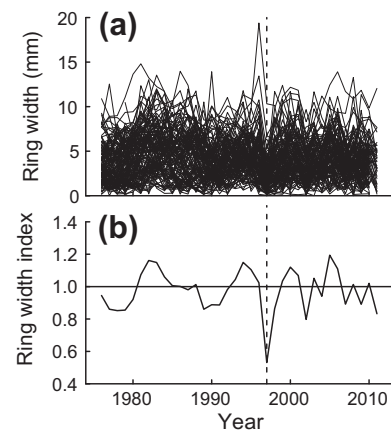


Fig. 2. Ring widths (a) of all *Afzelia* trees that were included in the species-specific chronology (b). The marker year 1997 is indicated by the dashed line.

Table 1Descriptive statistics of the ring-width series used for the chronology of *Afzelia xylocarpa*.

<i>n</i> sampled (trees/radii)	<i>n</i> chronology (trees/radii)	Time span	Years	Rbar.wt ^a	Rbar.bt ^b	EPS ^c
100/341	38/133	1976–2011	36	0.45	0.13	0.90

^a Rbar.wt is the mean of the correlations between series from the same tree.^b Rbar.bt is the mean interseries correlation between all series from different trees.^c EPS is the expressed population signal.

with the annual resolution PDSI values for the location of our study area. The marginally positive correlation between the chronology and PDSI values indicates that years of high growth in *Afzelia* were associated with relatively wet years. This is also supported by the occurrence of a marker year (a year with unusually narrow rings) in 1997 when PDSI values were strongly negative.

The size distribution of all *Afzelia* trees in the 297-ha area did not show an inverse J-shaped distribution. The median dbh of trees in this population was 65.4 cm with a standard deviation of 27.5 cm and a range of 12.4–172.0 cm. A Kolmogorov–Smirnov (KS) test for normality revealed that the diameter distribution for all 85 sampled *Afzelia* trees was not significantly different from a normal distribution ($P = 0.096$, Fig. 3a).

The lack of small-sized individuals in the diameter distribution reflects the absence of recent establishment, only one new *Afzelia* tree had established and survived since 1970 (Fig. 3b). More than 90% of the extant *Afzelia* trees in our study plot established during two periods: around 1850 and around 1950 (Fig. 3b). Of the 52 trees that established in the age cohort between 1930 and 1970, 67% recruited in the 20 years between 1940 and 1960. The 28 trees that established around the 1850s seem to form a second, though less distinct age cohort (1810–1900). The KS test for normality of the age distribution indicated that this distribution was significantly different from a normal distribution ($P < 0.001$). The alternative age distribution, in which age estimates of trees that did not include the pith were based on mean population growth rates, showed very similar results (Fig. A.3). This alternative age distribution was also significantly different from a normal distribution ($P < 0.001$). Because the trees in the 1850s cohort have experienced 100 years of additional mortality risk compared with the 1950s cohort, the estimated number of established trees was probably much higher in that cohort. Indeed, the distribution of estimated establishment rate per decade, z , contained two cohorts of roughly equal size. The 1950s cohort consisted of an estimated 79 trees, vs.

52 extant trees, whereas the 1850s cohort was estimated to have consisted of 117 trees instead of the 28 extant trees (Fig. A.4).

We were interested in the potential role of regional climate variability in explaining decadal variation in estimated establishment rate, z . We therefore related z to the PDSI values for western Thailand (Fig. 3b). We found a significant ($P < 0.001$) positive relationship between 10-year mean PDSI values and estimated establishment rate. For instance, the onset of the second recruitment pulse (~1940), was associated with a period of unusually wet years (annual PDSI > 0) between 1938 and 1956 (Fig. 3b).

The correlogram revealed a significant spatial structure in the distribution of tree ages, with positive Moran's I coefficients at distances < 500 m and negative coefficients at distances > 700 m (Fig. A.5). This reflected a patchy distribution of similarly aged trees at the scale of 0–25 hectares, with trees in the 1950s cohort clumped in a ~25 ha area in the northeast of the plot. Trees belonging to the 1850 cohort are primarily grouped in 3–4 smaller clumps (~5 ha) in the southeast corner and upper northern section of the study area (Fig. 1). The significantly negative values of the Moran's I coefficient at larger distances (750–1500 m) indicated that patches of similarly aged trees were spatially segregated. We found no relationship between sample tree age and elevation suggesting that topography was no causal factor in the observed patchy distribution of ages (Spearman rank correlation, $P > 0.8$).

The growth pattern of *Afzelia* was characterized by a rapid increase in diameter growth just after establishment followed by a decrease over time. Mean diameter growth of juvenile *Afzelia* trees (5–30 cm dbh) was 7.5 ± 4.3 mm year⁻¹ (standard deviation). On average, growth of *Afzelia* reached its maximum of ~10 mm year⁻¹ for trees in the 30–40 cm dbh class and then declined to ~3.0 mm year⁻¹ for the biggest trees (> 80 cm dbh). Variation in growth rates was high (2–20 mm year⁻¹) resulting in variable growth trajectories (Fig. 4a). We found no evidence that trees that established before 1900 had different median growth

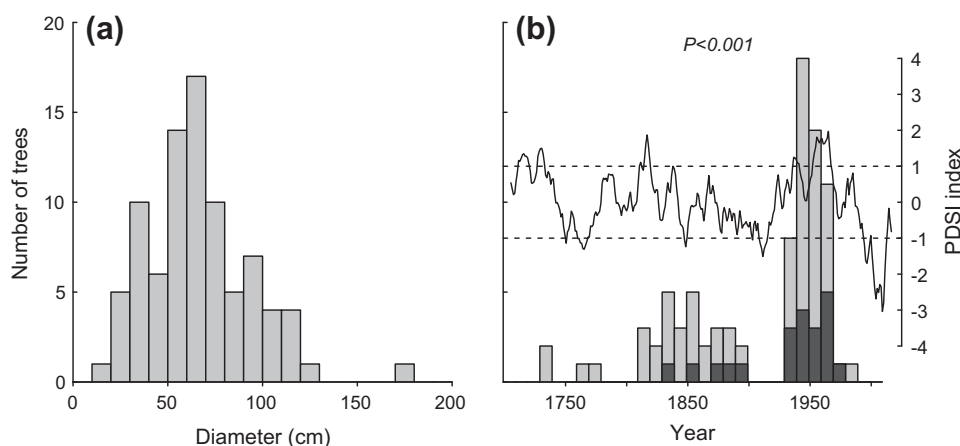


Fig. 3. Diameter distribution in number of individual trees per 10 cm dbh class (a) and age distribution (b) for *Afzelia*. The age distribution is shown as the decadal establishment rate of the extant trees. Dark-grey bars represent ages of those individuals for which the pith was included in at least one of the samples ($n = 21$). Light-grey bars represent those individuals for which the pith was not included in any of the samples ($n = 64$). The black line represents a 10 year running mean of reconstructed Palmer Drought Severity Index (PDSI) values of the regional summer monsoon. Positive PDSI values indicate wet conditions; negative values indicate dry conditions. A generalized linear model (GLM) was used to determine the relation between estimated establishment frequency and mean PDSI values, P -value of the model fit is indicated.

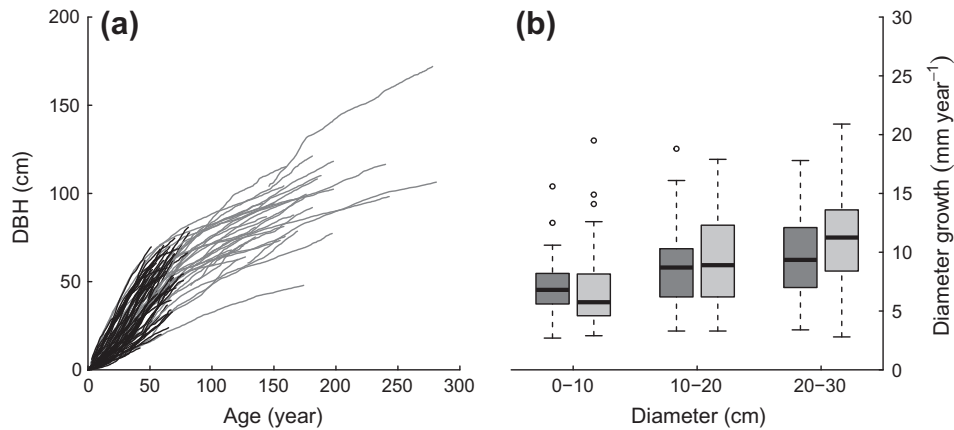


Fig. 4. Growth trajectories of all 85 sample trees (a) and boxplots of diameter growth in three size classes (b). (a) Black lines represent individuals that established after 1900, grey lines represent individuals that established prior to 1900. (b) Boxplots were coloured dark grey for trees that established before 1900 and light grey for trees that established after 1900. No significant differences in growth rates of trees among any of the size classes were present (Wilcoxon rank-sum test, $P > 0.05$).

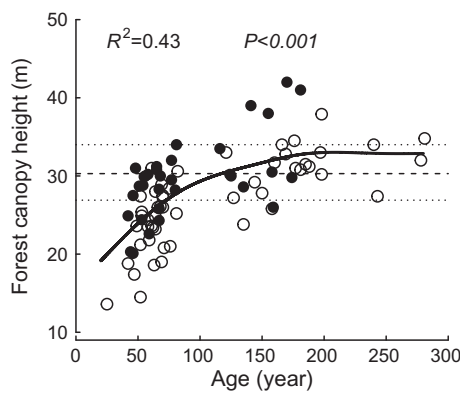


Fig. 5. Relationship between current canopy height and *Afzelia* tree age. Filled circles represent situations in which neighbour trees were taller and open circles represent those situations in which the sampled *Afzelia* tree itself was the tallest tree. The dashed line indicates median canopy height in the study area (30.3 m) and the dotted lines indicate the 25th and 75th percentiles (26.9 m and 34.0 m). The black line represents a fitted generalized additive model (GAM) response curve with a single smoothing parameter, R^2 and P -value of the model fit is indicated.

rates than trees that established in the 20th century. For each size class (0–10, 10–20, 20–30 cm) we compared median growth rates of trees that established before 1900 with trees that established after 1900 (Fig. 4b). We found no significant differences in growth rates of trees among any of the size classes (Wilcoxon rank-sum test, $P > 0.05$).

We expected that younger trees would be associated with more recently disturbed forest and that older trees would be predominantly found in more mature forest. We used estimated canopy height as a proxy for stand development stage (Fig. 5) and found a positive relation between tree age and forest canopy height ($P < 0.001$, generalized additive model (GAM) with one smoothing parameter). Because the estimated canopy height was often the height of the focal individual we performed a second regression in which we only used canopy heights that were based on trees other than the focal tree. This revealed a similarly positive relation between tree age and forest canopy height ($P < 0.001$).

4. Discussion

We hypothesized that the lack of recruitment in *Afzelia* is due to the sporadic occurrence of severe canopy disturbance events.

Based on tree-ring dating we found a bimodal age structure in which similarly aged trees were spatially aggregated, showing evidence of episodic recruitment. The high juvenile growth rates in the past and the present, and the association of young trees with building-phase forest suggest that recruitment peaks were initiated by large canopy openings. This suggests that the process of disturbance-mediated recruitment limitation is not limited to temperate forests and may also play a role in tropical forests.

4.1. Age cohorts

In studies on tree regeneration in temperate forests, the presence of discrete age cohorts in tree populations is considered a strong indication of past severe canopy disturbance (Cullen et al., 2001; Splechna et al., 2005). In our study species we found evidence of two age cohorts. In contrast to most temperate forest studies, in which age cohorts are usually narrow, our age cohorts were rather broad with the oldest one spanning nearly a century. Given that forests in our study area are strongly light-limited and *Afzelia* is a shade-intolerant species (see below), we did not expect to find such broad age cohorts. There are several potential methodological explanations for this pattern. First, counting and measuring growth rings of *Afzelia*, and rings of tropical tree species in general, can be difficult due to the occurrence of missing and false rings (Worbes, 1995). Although growth rings of *Afzelia* are distinctly annual (Baker et al., 2005) and among-tree crossdating was successful, ring identification errors likely occurred and have accumulated towards earlier dates. Second, the majority uncertainty most likely resulted from the missing distance to the pith on cores of ~70% of our sampled trees. For these samples, we estimated the number of missing rings to the pith both by extrapolating growth rates based on the five oldest visible rings and modeling growth rates based on 21 individuals that did include the pith in one of the samples. As the trees in the older cohort were larger, the estimated number of missing rings per tree in the 1850s cohort was higher (median = 12 rings), compared to the estimated number of missing rings per tree in the 1950s cohort (median = 2 rings). Third, the observed age variation may also have resulted from variation in time to reach coring height (~1 m). We estimated that this error would be comparatively small because initial height growth of *Afzelia* juveniles is generally high (So et al., 2010). Although the above factors were almost certainly responsible for part of the age variation in the two cohorts, we cannot rule out the possibility that the broad age cohorts reflect recruitment conditions occurring during a period of several years or decades.

4.2. *Afzelia* regeneration strategy

In general the presence of distinct age cohorts provides a strong indication of disturbance-mediated recruitment. We found three additional lines of evidence which support this interpretation for *Afzelia*. (1) We hypothesized that age cohorts of trees would form spatially discrete patches if recruitment had initiated after severe canopy disturbance (Rozas, 2003; Snook, 1996). Similarly aged trees were indeed aggregated in patches larger than those typically formed by single treefall gaps. This clustering of ages is unlikely under a scenario of for example dispersal limitation (Hubbell et al., 1999), or an association with edaphic factors (e.g., John et al., 2007; Potts et al., 2002), because this only predicts spatial aggregation of individuals of a species, not of individuals of a certain age. (2) We also expected to find high juvenile growth rates indicative of recruitment under very open conditions, similar to those that occur after a severe disturbance. As expected growth rates of juvenile trees (<30 cm dbh) are high, typically 5–10 mm year⁻¹, which is comparable to the shade-intolerant pioneer species *Melia azedarach* (~10 mm year⁻¹) and considerably higher than the 2.4 ± 2.6 mm year⁻¹ mean growth rate for trees <30 cm dbh ($n = \sim 28,000$) in the 50-ha forest dynamics plot (Bunyavejchewin, S., Baker, P.J., unpublished data). (3) Our fourth research question was whether forest structure surrounding current young trees would be different from the forest structure around old trees. We found a significant positive correlation between tree age and canopy height suggesting that *Afzelia* regeneration is associated with younger, more recently disturbed forest patches. In a situation in which this species regenerated in mature forest, where juveniles occur under a canopy of adults, such a canopy-age relation would not have been found. The preference of young *Afzelia* for disturbed forest patches is further supported by studies in which *Afzelia* regeneration was found to be favoured by high light conditions after logging (Kaewkrom et al., 2005; Sovu et al., 2010).

A small share (~10%) of *Afzelia* trees in our study occurred as solitary individuals. These trees tend to be somewhat smaller and younger than the *Afzelia* trees in the surrounding forest, though no clear pattern arises. Young trees that were not in close proximity to other *Afzelia* trees were all in exposed, high-light environments, such as along the stream running through the plot. High light has likely contributed to their establishment success, although increased establishment success may also have resulted from the lower fire risk and intensity in more open vegetation patches. The last observed case of successful establishment of an individual >5 cm dbh occurred around 1987 and was of a solitary individual that recruited in an exposed area along the stream.

4.3. Recruitment success: canopy disturbance and climate stochasticity

The evidence pointed out above suggests that successful establishment of *Afzelia* requires canopy disturbance, but what type of canopy disturbance? In the seasonal tropical forests of continental Southeast Asia the most common types of intense disturbance are wind storms, fires and droughts (Ashton, 1993). All three disturbance types have likely shaped the forest structure of HKK over the past few centuries (Bunyavejchewin et al., 2003) and indications for canopy disturbance in HKK have been found before (Baker et al., 2005; Middendorp et al., 2013). In Thailand heavy winds are mainly associated with the rainy season, resulting in stem breakage and uprooting of large trees (Marod et al., 2004). Windfall would usually result in a diffuse pattern of small and large canopy gaps, increasing understory light levels (D'Amato and Orwig, 2008; Oliver and Larson, 1996). Large amounts of woody debris after windfall may also increase fire susceptibility of the forest in the following dry season. Low-intensity ground fires of anthropogenic

origin occurred nearly every year somewhere within HKK in the past two decades (Baker et al., 2008). Sanctuary wide fires are less common and occur only once every 3–10 years in HKK (Baker et al., 2008). These more widespread fires are possibly associated with intense ENSO events and may increase in intensity after windfall has increased fuel loads (Bunyavejchewin et al., 2009; Wanthongchai et al., 2011). In HKK low-intensity ground fires have been observed to lead to extensive mortality of canopy trees (Baker et al., 2008). But extensive mortality of canopy trees may also be induced by prolonged droughts (Nepstad et al., 2007). So, either canopy damage by a windstorm, ground fire or drought, or a combination of windfall and more intense ground fires may have resulted in an increased openness of the forest canopy around 1850 and 1950. Evidence for the dating of these disturbance events is also consistent with earlier findings from an adjacent study site (Baker et al., 2005).

Our analyses of climate data suggests that disturbance is not the only factor determining *Afzelia* recruitment, as recruitment rates seem to be higher during wetter periods, particularly during the 20th century. Marod et al. (2004) have shown that drought and fire are major bottlenecks for seedling survival in seasonal tropical forests of Southeast Asia. Since 1980 western Thailand has been characterized by strong negative deviations in PDSI values (Cook et al., 2010) and very poor *Afzelia* recruitment in our study area. These droughts may have indirectly hampered recruitment through increased probability of ground fire incidence (Baker et al., 2008). In the first years after germination *Afzelia* seedlings are very prone to ground fires, although they possess the ability to resprout (So et al., 2010). Fire exclusion from the forest area of regenerating trees in the first years might therefore be critical for seedlings to escape the life stage most susceptible to dieback after fire (Grogan et al., 2010). In 1991–1992, 1998 and 2004 ground fires passed through the area of the study site (Baker et al., 2008; Bunyavejchewin et al., 2009) and there is no evidence of recruitment of *Afzelia* during this period.

While we lack direct observation of natural regeneration of *Afzelia*, our results do suggest that severe canopy disturbance followed by relatively wet conditions provide a window of opportunity for successful recruitment of this species (see also Brown and Wu, 2005). Such a wet spell combined with the high light conditions that follows a severe canopy disturbance would allow seedlings to grow rapidly in height and girth, and quickly escape the small size classes susceptible to fire-induced mortality.

4.4. Episodic recruitment in tropical tree species

We have provided evidence that severe canopy disturbance and climate stochasticity may play a key role in the episodic regeneration of a long-lived tropical tree species. Other long-lived, poorly regenerating tropical canopy tree species may possess similar strategies of episodic recruitment (Gullison et al., 2003; Poorter et al., 1996) and their size distribution may obscure an underlying pattern of discrete age cohorts. Such episodic recruitment, in combination with a high observed maximum age, may indicate that a population that appears to lack regeneration is not actually in an “unhealthy” state (Condit et al., 1998). As long as severe disturbances cause occasional wide-spread canopy loss, populations of these tree species will be able to regenerate naturally, thereby sustaining their populations. This observation could have significant implications for the conservation of other IUCN Red List tree species that possess similar life history strategies as *Afzelia*. If regeneration depends on rare disturbance events, possibly in combination with a climate anomaly, it may take decades before protected populations start to regenerate and grow.

Our findings of patchy and episodic recruitment of *Afzelia* provide evidence of severe canopy disturbances at our study site.

The forest patches containing old *Azelia* trees in parts of our study area point to severe canopy disturbances that occurred some 60 and 160 years ago, probably in concert with relatively wet conditions that enhanced seedling survival. The interaction of past disturbances and climatic fluctuations has likely shaped the patchwork mosaic of structurally and floristically distinct forest types that are common in western Thailand (Bunyavejchewin et al., 2001). Such localized, severe disturbance events caused by windfall, ground fire or climate anomalies can be found across the tropics (Ashton, 1993; Burslem et al., 2000; Chave et al., 2008; Foster et al., 1999) and likely shape forest dynamics and tree regeneration (Newbery et al., 2013).

Tree-ring analysis provides a powerful tool for studying regeneration dynamics of tropical tree species with recruitment failure. Annual-ring producing tropical tree species offer the possibility to identify recruitment peaks in the population structure and reconstruct historical growth rates. Using the tree-ring approach we were able to assess a bimodal age structure that would otherwise have been obscured by a unimodal diameter distribution. Our findings provide evidence that severe canopy disturbances and climate stochasticity have played a key role in the regeneration of a long-lived tropical tree species.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.10.016>.

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