Suppression, release and canopy recruitment in five tree species from a seasonal tropical forest in western Thailand

Patrick J. Baker[*,1] and Sarayudh Bunyavejchewin†

* School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia
† National Parks Wildlife and Plant Conservation Department, Chatuchak, Bangkok 10900, Thailand
(*Accepted 28 February 2006*)

Abstract: We used tree-rings to reconstruct long-term patterns of suppression, release and growth among five sympatric canopy tree species representing the full range of shade tolerance in a seasonal tropical forest in western Thailand. We expected that the frequency and duration of suppression and release events would be positively correlated with shade tolerance. All five species showed evidence of major and moderate growth releases. As expected, *Melia azederach*, an extreme heliophile, had the fewest releases. However, among the other species the number of major releases was consistent across the range of shade tolerance. The most significant difference among the species was the number of moderate releases recorded. There was a general positive correlation between the number of moderate releases and shade tolerance; however, *Chukrasia tabularis*, a relatively shade-intolerant species, had an anomalously high number of moderate releases. The study species also showed considerable variation in canopy accession strategies. The least common canopy accession strategy was establishment in the understorey and growth into the canopy in the absence of any gaps. However, with the exception of *Melia*, all four study species had one or more individuals that successfully reached the canopy using each of the four canopy accession strategies. These results highlight the importance of periodic or episodic bouts of gap formation on canopy tree recruitment and the utility of tree-rings for reconstructing long-term growth patterns in tropical trees.

Key Words: Canopy trees, *Chukrasia tabularis*, gap dynamics, *Melia azederach*, *Neolitsea obtusifolia*, seasonal tropical forest, suppression, Thailand, *Toona ciliata*, tree-rings, *Vitex peduncularis*

INTRODUCTION

Two fundamental facts influence every aspect of tree growth. The first is that trees are sessile organisms and as such cannot move to areas of higher resource availability. The second is that, with the exception of hemi-epiphytes such as figs, new trees establish at ground-level where light is often a scarce resource. Considerable research has focused on the implications of immobility on the population biology of plants and trees in temperate and tropical forests (Condit *et al.* 2000, Connell 1978, Harper 1977, Janzen 1970). Much less attention has focused on the question of how trees reach the canopy from their point of origin on the ground. The strong vertical gradient in light created by the forest canopy presents a major challenge to newly established trees, particularly canopy tree species (Harcombe & Marks 1978).

Current understanding of canopy recruitment patterns is based largely on tree-ring studies in temperate forests that reconstruct historical patterns of diameter growth to identify periods of growth suppression and release (Canham 1985, 1990; Nowacki & Abrams 1997, Rentch *et al.* 2003). These studies have demonstrated that trees grow to the canopy in several different ways. Shade-intolerant tree species typically require the establishment of large gaps that allow them to grow directly into the canopy (e.g. *Liriodendron tulipifera*; Orwig & Abrams 1990). If a shade-intolerant species becomes overtopped, either by neighbouring trees or by lateral extension of crowns adjacent to the gap, growth slows and the probability of mortality increases (e.g. *Quercus rubra*; Rentch *et al.* 2003), unless a subsequent disturbance 'releases' the tree from such competition. In contrast, shade-tolerant tree species are capable of establishing in smaller gaps or in the understorey because they can survive periods of suppression, yet retain the ability to increase growth if ambient light levels increase. Among

shade-tolerant species, however, there is considerable variation in suppression and growth release patterns (Canham 1988). Some shade-tolerant tree species grow slowly in height under suppressed conditions but respond vigorously to even small increases in light availability (e.g. *Fagus grandidentata*; Canham 1985), while others grow more consistently at moderate rates irrespective of light availability (e.g. *Acer saccharum*; Canham 1990).

In tropical forests, it has long been recognized that many canopy tree species require gap formation at some point during their lifetime to successfully grow into the canopy (Wright *et al*. 2003). Most studies of the role of gap dynamics in canopy tree recruitment have focused on the response of seedlings and saplings across a range of light environments from gap centre to shaded understorey (Brokaw 1985, Denslow 1987, Hubbell *et al*. 1999). Few studies have examined the dynamics of saplings and poles to gap formation, although Clark & Clark (2001) have used their long-term dataset from La Selva to show that height growth patterns of poles are strongly influenced by local gap formation. Other studies have used proxy measures such as diameter distributions (Wright *et al*. 2003) or short-term growth patterns (Lieberman *et al*. 1985) to infer the importance of gap dynamics on lifetime success of tree species. However, because most tropical tree species do not form annual growth rings, retrospective studies of forest stand dynamics comparable to those from the temperate zone are rare (although see Grau 2000 for a subtropical example). As such, we have a relatively poor understanding of how individual trees in tropical forests reach the canopy from the seedling or sapling stage or how long-term growth patterns and canopy recruitment are linked to gap dynamics.

In this paper we describe canopy recruitment patterns for five tree species of differing shade tolerance from a seasonal tropical forest in western Thailand. We hypothesized that differences in shade tolerance among our study species would be reflected in patterns of suppression and release in much the same manner that they occur among temperate tree species. Specifically, we expected that the frequency and duration of suppression and release events would be positively correlated with shade tolerance. The five species we examined all form annual growth rings. Thus, we were able to test this hypothesis

by reconstructing the historical growth patterns of individuals using the same dendroecological techniques applied to tree species of temperate zone forests.

METHODS

Study area

The research was conducted at the Huai Kha Khaeng Wildlife Sanctuary (HKK) in Uthai Thani province, west-central Thailand (15°40′N, 99°10′E). The seasonal monsoons are the dominant climatic influence in the study area. Mean July temperature is 27 °C; mean January temperature is 19 °C. Mean annual rainfall at the Kapook Kapiang Ranger Station ($\sim$4 km from the study site) during the period 1983–1993 was 1476 mm ($\pm$113 mm; 1 SD). Mean monthly rainfall for the 6 months from November to April was $<$100 mm during the same period. Elevation within the study site ranges from 525 to 575 m asl. Soils are sandy loams and sandy clay loams and are neutral to slightly acid (pH: 5.2–6.8). In general, soil fertility is considered moderate to high (Lauprasert 1988).

The study was conducted in a contiguous block of seasonal dry evergreen forest (SDEF) several km^2 in extent. SDEF is the most widespread of the seasonal evergreen forest types in continental Thailand, occurring in areas with $>$1200 mm of annual precipitation and 4–6-mo dry seasons (Ashton 1990) and has the highest species richness and the tallest canopy of the forest types occurring at HKK. The tallest trees in SDEF are commonly $>$50 m in height. Important families in SDEF include the Dipterocarpaceae, Annonaceae, Euphorbiaceae and Meliaceae (Bunyavejchewin *et al*. 2001, 2002).

Our study focused on five species that form annual growth rings and are relatively common within the SDEF. The study species represent the full range of canopy tree life histories in the SDEF from the highly shade-intolerant and fast-growing *Melia azederach* to the shade-tolerant, generally slow-growing *Neolitsea obtusifolia*. Table 1 provides a brief description of the sampled trees of each species.

Table 1. General description of study species. The values for maximum dbh were obtained from the 50-ha plot database. Shade tolerance classifications are based on the literature and previous studies at the 50-ha plot (Bunyavejchewin *et al*. 2001, 2002, Troup 1921). Classification of foliar phenology is based on 10 y of phenological data from in and around the 50-ha plot (Bunyavejchewin *et al*., unpubl. data).

| Species	Family	Mean age (y)	Max dbh (cm)	Shade tolerance	Phenology	Number of trees
Melia azederach L.	Meliaceae	33.8	85.3	Very intolerant	Deciduous	14
Toona ciliata M. Roem.	Meliaceae	56.8	76.9	Intolerant	Deciduous	18
Chukrasia tabularis A. Juss.	Meliaceae	62.3	80.4	Intolerant/Intermediate	Evergreen	32
Vitex peduncularis Wall. ex Schauer	Verbenaceae	73.7	68.1	Intermediate	Deciduous	11
Neolitsea obtusifolia Merrill	Lauraceae	77.8	81.9	Tolerant	Evergreen	24
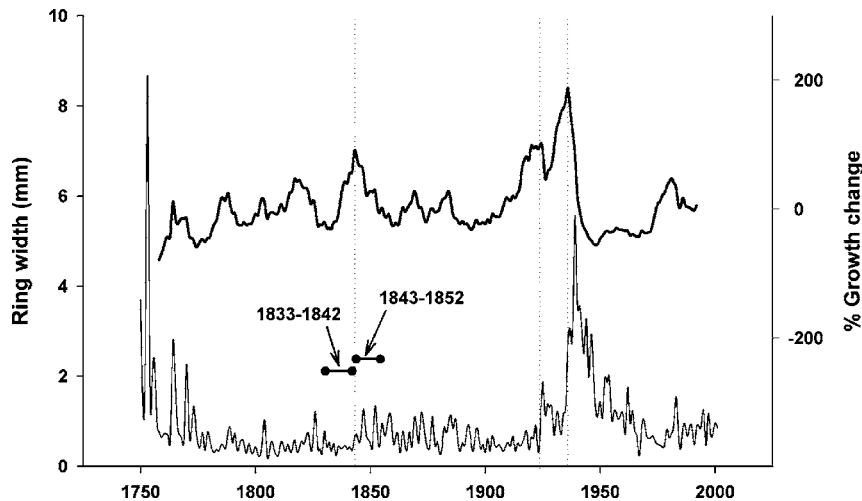
Figure 1. Identifying patterns of suppression and release using radial growth averaging. The lower line represents the raw ring width measurements; the upper line is the calculated per cent growth change values based on the ring width series. Dotted vertical lines represent release years. A moderate release occurred in 1843; major releases occurred in 1924 and 1936. The tree-ring series is from a teak tree (*Tectona grandis*) in southern India.

Sampling and measurements

Sample trees were randomly selected from two large permanent plots located within 500 m of each other at the study site (16 ha and 50 ha; see Baker *et al.* 2005 for plot details). We restricted our sampling to canopy trees, which we define as trees > 20 cm dbh. Analysis of canopy stratification demonstrated that all trees > 20 m tall were in the main canopy stratum (Baker & Wilson 2000, Baker *et al.* 2005). Diameter-height allometries of the study species indicated that most trees > 20 cm dbh were sufficiently tall to be in the main canopy.

Tree cores were obtained with a 40-cm Suunto tree borer. Three cores were taken from each tree at ∼1 m above the ground at different locations approximately equidistant around the stem, although the presence of lianas, buttressing, or pockets of rot sometimes limited the number or location of cores taken. Cores were prepared for analysis by sanding with a series of sandpaper of increasingly fine grit (up to 600) and then buffed with superfine steel wool, if necessary, until a clear, highly polished surface was attained. Cores were then scanned on a high-resolution digital scanner (Epson 1640 SU) at 1200–1600 dpi. Annual growth rings were counted and measured using the tree-ring image analysis software package, WinDendro (Regent Instruments, Inc.). Multiple cores from a tree were measured in sequence and crossdated using the real-time crossdating features of WinDendro. Because missing and false rings are often not consistent around the entire circuit of the tree, this process greatly facilitated the detection of false rings and missing rings, both of which occurred in some of the study species. In addition, by taking multiple cores we were able to ensure that at least one core included or

was within 2 cm of the pith for > 80% of the trees. We excluded any tree for which no core came within 5 cm of the pith as determined by the geometric formula described in Duncan (1989). To further minimize dating errors, we then crossdated all series of a given tree species using the program COFECHA (Holmes 1983). To analyse growth patterns in individual trees, we standardized each tree-ring series by dividing the individual ring width values by the mean ring width value of the series. The standardized series were then averaged to create a mean chronology for each individual tree.

To identify potential growth responses to disturbances and prolonged periods of suppression, per cent growth change (%GC) was calculated for each tree ring series (Abrams *et al.* 1995). For each year of the ring width series, the average radial growth increment of the decade culminating in that year and of the decade following that year was calculated. By using a 10-y moving window we were able to avoid the influence of transient short-term growth fluctuations associated with high frequency climate variation. Per cent growth change was calculated for each year from the formula: $\%GC = [(M_2 - M_1)/M_1] \times 100$, where M_1 is the mean annual diameter growth of the preceding 10-y period (including the current year), and M_2 is the mean annual diameter growth of the subsequent 10-y period (Nowacki & Abrams 1997). For example, the %GC for 1842 is obtained by subtracting the 1833–1842 mean growth rate from the 1843–1852 mean growth rate, dividing by the former, and multiplying by 100 (Figure 1). The %GC was calculated for each year on a core with the exception of those in the first and last decades (for which, by definition, the index cannot be calculated). Periods of suppression and release were identified based on criteria adapted from

Lorimer & Frelich (1989) and Nowacki & Abrams (1997). For all species a 'major' release was defined as a > 100% average growth increase lasting 10 y and a 'moderate' release as a 50–100% average growth increase lasting 10 y.

We used a threshold growth rate approach to determine the proportion of trees for each species that established under suppressed conditions and to calculate the median duration of slow and fast growth periods. Species-specific threshold values were calculated as the 25th and 75th percentile ring widths from all ring width measurements obtained for each species.

We used two classification criteria to determine the canopy recruitment patterns: (1) whether a tree established in a high-light environment (i.e. gap) or not (i.e. understorey) and (2) whether canopy recruitment occurred as a consequence of a major release event (> 100% growth change sustained over 10 y) or not. A tree was considered to have established in a high-light environment if the mean annual growth rate of the first five growth rings was greater than the threshold value for fast growth for the species (i.e. the 75th percentile growth rate based on all measured ring widths of that species). Consequently, each tree was classified into one of four canopy recruitment patterns based on the growth patterns shown in the time series of annual ring widths as follows:

(1) 'Continuous high-light': establishment occurred in a high-light environment such as a treefall gap and the tree never required a growth release to reach the canopy.
(2) 'Gap and release': establishment occurred in a high-light environment, but the tree was subsequently suppressed and required at least one growth release before reaching the canopy.
(3) 'Shade and release': establishment occurred in a low-light environment (i.e. the forest understorey). Eventual canopy recruitment required at least one growth release.
(4) 'Continuous low-light': establishment occurred in a low-light environment, but canopy recruitment did not require growth release associated with gap formation.

For those species that required a major release to recruit to the canopy, we calculated mean residence time of individuals in the understorey prior to final release. We defined understorey residence time as the number of years from establishment to canopy recruitment. We did not include trees that initiated in gaps and that never experienced suppression before canopy recruitment ('continuous high-light') or trees that established in the understorey and did not require a gap to recruit to the canopy ('continuous low-light').
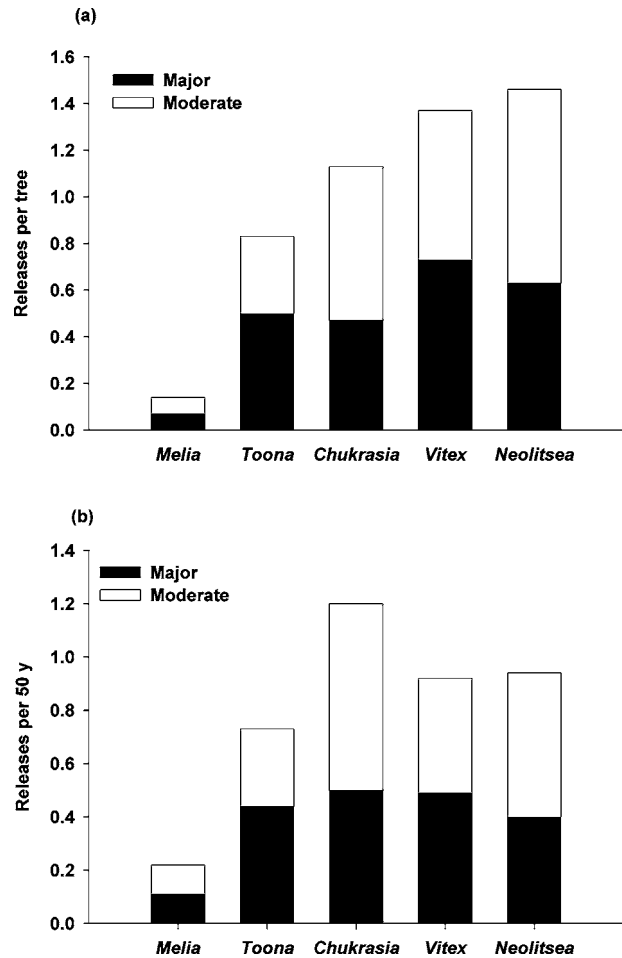

Figure 2. Growth release patterns for five sympatric canopy tree species from western Thailand. Growth releases based on the number of major and moderate releases per tree (a) and the number of major and moderate releases per 50 y (b). The standardized time unit was used to account for differences in mean life span among the study species.

RESULTS

All five study species showed evidence of major and moderate growth releases. However, the number of releases per tree differed significantly among species (Kruskal–Wallis single-factor ANOVA: $H = 27.75$, df = 4, $P \ll 0.001$) and was positively correlated with shade tolerance as hypothesized (Figure 2a). *Melia*, the most shade-intolerant species, had the fewest releases per tree (0.14); whereas *Neolitsea*, the most shade-tolerant species, had the most releases per tree (1.46) – an order of magnitude greater than *Melia*. The other three species were intermediate in their number of releases per tree. Frequency of moderate releases was very closely tied to the observed differences in shade tolerance. Major releases were less so, with *Vitex* having the greatest number of major releases per tree. Three species (*Chukrasia*, *Vitex* and *Neolitsea*) had slightly more moderate releases than major releases. *Toona* had a greater number of major
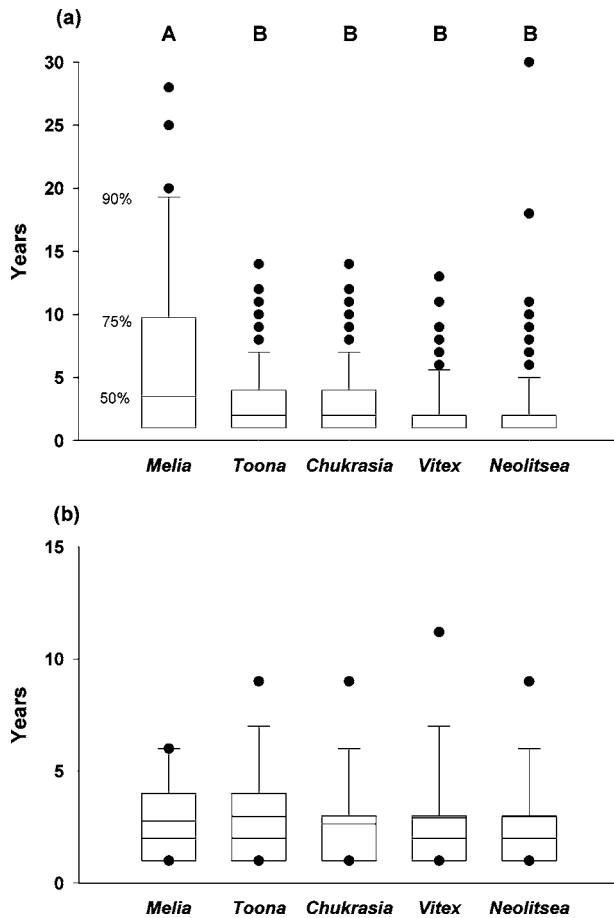
Figure 3. Number of sequential years of slow and fast growth by species. Slow growth years (a) are defined as years in which a tree is growing below a species-specific growth threshold (25th percentile growth rates based on all the tree rings measured for each species). Fast growth years (b) are defined as years in which a tree is growing above a species-specific growth threshold (75th percentile growth rates based on all the tree rings measured for each species). Threshold values for slow and fast growth are given in Table 2. The box and whiskers represent percentiles of the data as follows: the lower and upper box boundaries are 25th and 75th percentiles, respectively; the line in the box is the median value (50th percentile); the upper whisker represents the 90th percentile; and the individual points represent outliers >90th percentile.

Table 2. Species-specific radial growth thresholds $(mm\,y^{-1})$ for identifying periods of low and high growth and maximum number of sequential years with slow or fast growth. Threshold values for fast and slow growth were calculated as the 25th and 75th percentile ring widths, respectively, from all ring width measurements obtained for each species. The longest runs of fast and slow growth are the number of years in which radial growth, as measured by tree-ring widths, was above (fast) or below (slow) the growth rate threshold.

Species	Slow growth threshold	Fast growth threshold	Longest run of slow growth	Longest run of fast growth
Melia azederach	3.40	9.00	28	6
Toona ciliata	1.50	4.69	35	27
Chukrasia tabularis	1.43	3.76	35	16
Vitex penduncularis	1.43	3.31	13	16
Neolitsea obtusifolia	1.14	2.64	30	34

single-factor ANOVA: $H = 14.9$, df $= 4$, $P < 0.005$). In particular, *Chukrasia*, a moderately intolerant species, had significantly more releases in 50 y (1.24) than the much more shade-tolerant species, *Vitex* (0.92) and *Neolitsea* (0.94). The number of major releases per 50 y was lowest for *Melia*, but was very similar among the four other species. The number of moderate releases per 50 y followed the expected pattern relative to shade tolerance, with the exception of *Chukrasia*, which had considerably more moderate releases per unit time than the other species.

The number of consecutive years of slow growth varied significantly among the study species (Kruskal–Wallis non-parametric ANOVA $\chi^2 = 27.9$, $P < 0.001$; Figure 3a). In all five species, periods of slow growth were occasional and relatively brief (range of median values: 1–4 y). Maximum duration of slow growth periods was > 25 y for all of the species with the exception of *Vitex* (max: 13 y) (Table 2). Surprisingly, however, the species with the longest median run of slow-growth years was *Melia*, the most shade-intolerant and fastest-growing of the study species. There was a significant difference between the median length of consecutive years of slow growth of *Melia* when compared to the other species and a general trend of decreasing length of slow growth periods with increasing shade tolerance. A comparison of the proportion of all years in which individuals of each species were growing below the species-specific threshold level showed a similar trend (although *Chukrasia* was somewhat of an outlier in having the highest proportion); that is, the shade-intolerant species spent a greater proportion of their lifetimes growing slowly, relative to their potential growth rates, than the shade-tolerant species (Figure 3a).

A comparison of fast growth among the study species showed no significant differences in length of consecutive years of fast growth (Kruskal–Wallis single-factor ANOVA $H = 3.9$, df $= 4$, $P = 0.436$; Figure 3b). The 90th percentile value for all species was 6 or 7 y of consecutive
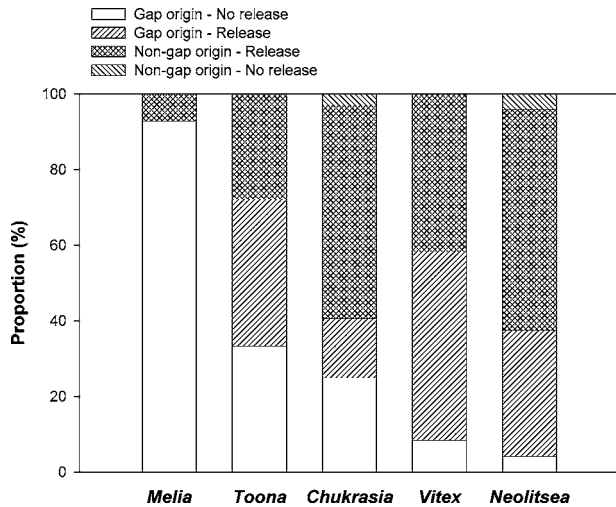
releases than moderate releases and *Melia* was evenly divided between the two.

One shortcoming of simply considering the number of releases per tree is that species-specific differences in mean tree age bias the results. For example, two species with 1.5 releases per tree may reflect very different life history types if one of the tree species has a mean lifespan of 350 y and the other has a mean lifespan of 35 y. To account for this bias and to foster interspecific comparisons, we standardized the results by calculating the mean number of releases that occurred in a 50-y period. While there was still a significant and positive trend between the standardized number of releases and shade tolerance (Figure 2b), the trend was less clear (Kruskal–Wallis

Figure 4. Canopy accession patterns of five sympatric canopy tree species from a seasonal dry evergreen forest in western Thailand. See text for descriptions of each canopy accession pattern.

Table 3. Residence time (mean ± SE and range) in the understorey prior to canopy recruitment. For those species that required a major release to recruit to the canopy, residence time in the understorey is defined as the number of years from establishment to canopy recruitment. We did not include trees that initiated in gaps and that never experienced suppression before canopy recruitment ('continuous high-light') or trees that established in the understorey and did not require a gap to recruit to the canopy ('continuous low-light').

Species	Number of trees	Residence time (y)	Range (y)
Melia azederach	1	7.0	–
Toona ciliata	9	29.1 ± 4.3	13–49
Chukrasia tabularis	14	23.1 ± 2.8	13–54
Vitex peduncularis	8	31.8 ± 8.3	6–66
Neolitsea obtusifolia	13	27.5 ± 4.8	9–65

fast growth. There were few differences in the proportion of years that trees experienced fast growth rates (Figure 3b). With the exception of *Melia*, the study species all grew above species-specific threshold rates during ~40% of their lifetimes. Individuals of *Melia* experienced fast growth during < 20% of their lifetimes.

The five study species varied widely in the relative proportion of individuals reaching the canopy by a given canopy recruitment pattern (Figure 4). The proportion of individuals establishing in high light environments and growing directly to the canopy without being suppressed was highest for *Melia* (~92%) and decreased substantially with increasing shade tolerance. In contrast, trees establishing in low-light conditions and reaching the canopy through release were most common among the shade-tolerant species (~40% of *Vitex* and *Neolitsea* were in this class) and less common among the shade-intolerant species (although, again, *Chukrasia* was somewhat of an exception with 36% of individuals in this class). The proportion of trees establishing in gaps, but requiring a subsequent release event to reach the canopy, did not show a pattern relative to shade tolerance. *Vitex* and *Toona* both had 25–40% of their individuals in this class, *Melia* had none, and *Neolitsea* and *Chukrasia* had relatively few (5–12%). Establishment in the understorey and subsequent growth into the canopy without major release was the least common pattern of canopy accession among the study species, occurring in only 14 trees, primarily *Chukrasia* and *Neolitsea*. It is important to note that 12 of the 14 trees that exhibited this pattern experienced 1–3 moderate releases prior to canopy recruitment. Thus, only 2 of the 99 individuals examined in this study successfully reached the canopy

without the benefit of a canopy gap at some point in their development.

Mean residence time prior to canopy recruitment in a gap varied both within and among species (Table 3). Because all but one of the *Melia* recruited directly from a gap to the canopy without any period of residence in suppressed conditions, we did not include *Melia* in the analyses. The other four species exhibited wide ranges in residence time values. *Vitex* had the largest range with a minimum residence time of 6 y and a maximum of 66 y. However, the mean residence times were not significantly different among species (Kruskal–Wallis single-factor ANOVA $H = 1.06$, df = 3, P = 0.787) and showed no trend associated with relative shade tolerance.

DISCUSSION

Most studies of gap dynamics in tropical forests have focused on processes that occur immediately before or after gap formation, such as seed dispersal into and establishment within gaps (Dalling *et al.* 1998, 2002) and growth patterns of seedlings and saplings within gaps (Brokaw 1985, Brown & Whitmore 1992, Uhl *et al.* 1988). The long-term consequences of gap formation on tree development are poorly understood because of the obvious difficulty of directly observing a complete life cycle of establishment and canopy recruitment of individual trees. Dendroecological studies in tropical forests present an opportunity to assess the role of canopy gaps on long-term growth performance and canopy recruitment dynamics and how individuals of different species take advantage of gaps during their lifetime.

So, how do trees in tropical forests get to the canopy? Across the range of sampled life histories, almost every individual in this study benefited from a gap (reflected in higher radial growth rates) during establishment or subsequent development. Canopy recruitment patterns differed among the species, but most species were capable of reaching the canopy in several ways. Indeed, four of

the five species (*Melia* was the exception) had individuals reach the canopy in all four of the potential canopy recruitment pathways that we evaluated despite widely divergent degrees of shade tolerance. However, some canopy recruitment pathways were more common than others. The least common developmental pathway was that which did not include gaps at any stage of growth. While the importance of gaps to tropical forest dynamics is widely cited (Hartshorn 1978, Whitmore 1978), there is a persistent belief among tropical forest ecologists that individuals of canopy tree species, particularly shade-tolerant species, can establish in the understorey and slowly increase in height until they eventually grow into the canopy without the presence of a nearby opening in the canopy (Clark & Clark 1987, Condit *et al.* 1993, Kelly & Bowler 2002, Poorter *et al.* 2005). Our results suggest that this strategy is extremely rare. Only two of the sampled trees (one *Chukrasia* and one *Neolitsea*) successfully reached the canopy without the direct influence of a major or moderate canopy gap at some point during their growth history. Admittedly, our study was limited to a small number of species. However, the five species that we investigated span the full range of shade tolerance found among the canopy trees in the seasonal dry evergreen forest and should reflect the major trends expected from the larger community. The diversity of canopy recruitment patterns both within and among species may be an important source of interspecific variation that may enable coexistence of tree species, particularly where local disturbance history is relatively heterogeneous (Clark & Clark 2001, Poulson & Platt 1989, Wright *et al.* 2000). Our results suggest that species broadly overlap in the potential patterns of canopy recruitment, but that the relative frequency of individuals following a particular canopy recruitment scenario may differ among species. Further dendroecological studies in other seasonal tropical forests are needed to determine whether this is a broadly consistent feature of tropical forest dynamics or whether it is unique to the HKK study site.

Based on previous studies in temperate zone forests, we expected to find a positive correlation between shade tolerance and patterns of suppression and release (Canham 1989, Orwig & Abrams 1990). For instance, in mixed oak-hardwood forests of the Piedmont Plateau in the eastern US, the shade-tolerant *Nyssa sylvatica* is much more responsive to small disturbances to the forest canopy than the more intolerant *Liriodendron tulipifera* (Orwig & Abrams 1990). Our results showed that for a limited sample of tropical species such trends were not as clear as expected. All of the study species, with the exception of *Melia*, showed a similar number of major releases, similar residence times in the understorey or mid-storey prior to final release, and similar runs of fast and slow growth. What distinguished the species was the ability to respond to small gaps, as evidenced by the number of moderate releases (Figure 2b). In general, the more shade tolerant a species was, the greater the number of moderate releases recorded in the tree-ring time series. *Chukrasia* was the exception in having an anomalously high number of moderate releases given its intermediate to high shade intolerance.

While the results of this study underscore the importance of gaps for canopy recruitment, the nature of gap formation in these forests must be placed in historical context. Studies of gap dynamics typically assume that gap formation is spatially and temporally random (Hubbell *et al.* 1999). At HKK this was not the case. Over the past 150 y the seasonal evergreen forest at our study site has been influenced by disturbances of varying intensities occurring at several spatial and temporal scales (Baker *et al.* 2005). A major catastrophic disturbance destroyed much of the forest in the mid-1800s which led to the establishment of a forest dominated by a single age cohort. Subsequently, several episodes of less intense, but spatially widespread, disturbances have occurred. The dendroecological records show that in the 1890s, 1910s, 1950s and 1970s canopy gaps formed synchronously throughout the forest, possibly due to windstorms or ground fires (Baker *et al.* 2005). These led to the establishment of single-age cohorts of trees scattered throughout the forest. In addition, there have also been low intensity disturbances such as isolated treefall gaps of one or a few trees, typical of the more traditional gap dynamics paradigm. Nonetheless, Baker *et al.* (2005) suggested that at HKK gap dynamics is primarily background 'noise' relative to the much stronger structural and compositional 'signal' of the more intense disturbances.

An unexpected result of the tree-ring analyses was the counter-intuitive patterns of runs of slow and fast years of growth. *Melia*, the fastest growing and most shade intolerant of the study species, had the highest number of sequential slow-growth years, whereas the shade-tolerant *Neolitsea* had the lowest. Most studies of tropical forest growth dynamics show a strong negative correlation between growth rates and shade tolerance (Clark & Clark 1992, Davies 2001). By extension, one would expect that shade-intolerant tree species would have longer runs of fast growth and shorter runs of slow growth than shade-tolerant tree species. Our results differ in this regard because the threshold values for fast and slow growth were established relative to the distribution of growth rates of the given species, not to all species. So, for example, the threshold level for slow growth for *Melia* was 3.40 mm y^{-1} as compared to 1.14 mm y^{-1} for the shade-tolerant *Neolitsea*. We chose to compare growth patterns using species-specific values instead of community-wide averages for two reasons. First, using species-specific thresholds based on empirical data from large samples allows comparison of an individual's annual growth with

the diameter growth potential for that species (Black & Abrams 2003). Second, a community-wide threshold value would be biased towards slow growth given the numerical dominance of small trees in the forest and would provide little information on suppression and release patterns of fast-growing, shade-intolerant species. In this study 53% of the annual growth rings of the *Melia* were narrower than the species-specific threshold size of 3.40 mm, whereas only 27% of the annual growth rings of *Neolitsea* were smaller than its threshold size of 1.14 mm. Both thresholds were determined as the 25th percentile of growth for all annual growth rings measured in the species. The difference appears to be a consequence of the consistent growth pattern of *Melia* in which extremely high initial growth rates are maintained for 10–15 y and then begin a steep decline, with most of the current canopy trees showing very little diameter increment. In contrast, *Neolitsea* had a much more variable growth pattern with some trees having fast initial growth and others with slow initial growth, but with most canopy trees showing relatively high growth rates.

Finally, this study demonstrates the potential for applying dendroecological methods to the study of tropical forest dynamics, particularly in the seasonal tropics, where annual growth rings may be relatively common. Because there are few long-term datasets from tropical forests to develop qualitative or conceptual models of forest dynamics at the scale of decades to centuries, temperate forest models become the default. Tree-ring studies that examine historical dynamics of tropical forests can test whether such models are appropriate and how they will need to be modified to accurately capture the long-term dynamics of tropical forests.

ACKNOWLEDGEMENTS

LITERATURE CITED

ABRAMS, M. D., ORWIG, D. A. & DEMEO, T. E. 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white pine–mixed oak forest in the southern Appalachians, USA. *Journal of Ecology* 83:123–133.

ASHTON, P. S. 1990. Thailand: biodiversity center for the tropics of Indo-Burma. *Journal of the Scientific Society of Thailand* 16:107–116.

BAKER, P. J. & WILSON, J. S. 2000. A quantitative technique for the identification of canopy stratification in tropical and temperate forests. *Forest Ecology and Management* 127:77–86.

BAKER, P. J., BUNYAVEJCHEWIN, S., OLIVER, C. D. & ASHTON, P. S. 2005. Disturbance history and historical stand dynamics of a seasonal tropical forest in western Thailand. *Ecological Monographs* 75:317–343.

BLACK, B. A. & ABRAMS, M. D. 2003. Use of boundary-line growth patterns as a basis for dendroecological release criteria. *Ecological Applications* 13:1733–1749.

BROKAW, N. V. L. 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66:682–687.

BROWN, N. D. & WHITMORE, T. C. 1992. Do dipterocarps seedlings really partition tropical rain-forest gaps? *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 335:369–378.

BUNYAVEJCHEWIN, S., BAKER, P. J., LAFRANKIE, J. V. & ASHTON, P. S. 2001. Stand structure of a seasonal evergreen forest at the Huai Kha Khaeng Wildlife Sanctuary, western Thailand. *Natural History Bulletin of the Siam Society* 49:89–106.

BUNYAVEJCHEWIN, S., BAKER, P. J., LAFRANKIE, J. V. & ASHTON, P. S. 2002. Floristic composition of a seasonal evergreen forest, Huai Kha Khaeng Wildlife Sanctuary, western Thailand. *Natural History Bulletin of the Siam Society* 50:125–134.

CANHAM, C. D. 1985. Suppression and release during canopy recruitment in *Acer saccharum*. *Bulletin of the Torrey Botanical Club* 112:134–145.

CANHAM, C. D. 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology* 69:786–795.

CANHAM, C. D. 1989. Different responses to gaps among shade-tolerant tree species. *Ecology* 70:548–550.

CANHAM, C. D. 1990. Suppression and release during canopy recruitment in *Fagus grandifolia*. *Bulletin of the Torrey Botanical Club* 117:1–7.

CLARK, D. A. & CLARK, D. B. 1987. Population ecology and micro-habitat distribution of *Dipteryx panamensis*, a neotropical rain forest emergent. *Biotropica* 19:236–244.

CLARK, D. A. & CLARK, D. B. 1992. Life history diversity of canopy and emergent trees in a Neotropical rainforest. *Ecological Monographs* 62:315–344.

CLARK, D. A. & CLARK, D. B. 2001. Getting to the canopy: tree height growth in a neotropical rain forest. *Ecology* 82:1460–1472.

CONDIT, R., ASHTON, P. S., BAKER, P. J., BUNYAVEJCHEWIN, S., GUNATILLEKE, S., GUNATILLEKE, N., HUBBELL, S. P., FOSTER, R. B. ITOH, A., LAFRANKIE, J. V., LEE, H. S., LOSOS, E., MANOKORAN, N., SUKUMAR, R. & YAMAKURA, T. 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288:1414–1418.

CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 1993. Identifying fast-growing native trees from the Neotropics using data from a large, permanent census plot. *Forest Ecology and Management* 62:123–143.

CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.

DALLING, J. W., HUBBELL, S. P. & SILVERA, K. 1998. Seed dispersal, seedling establishment, and gap partitioning among tropical pioneer trees. *Journal of Ecology* 86:674–689.

DALLING, J. W., MULLER-LANDAU, H., WRIGHT, S. J. & HUBBELL, S. P. 2002. Role of dispersal in the recruitment limitation of neotropical pioneer species. *Journal of Ecology* 90:714–727.

DAVIES, S. J. 2001. Tree mortality and growth in 11 sympatric *Macaranga* species in Borneo. *Ecology* 82:920–932.

DENSLOW, J. S. 1987. Tropical rain forest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18:431–451.

DUNCAN, R. P. 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycarpus dacryoides*). *New Zealand Natural Sciences* 16:31–37.

GRAU, H. R. 2000. Regeneration of *Cedrela lilloi* (Meliaceae) in northwestern Argentina subtropical montane forests. *Journal of Tropical Ecology* 16:227–242.

HARCOMBE, P. A. & MARKS, P. L. 1978. Tree diameter distributions and replacement processes in southern forests. *Forest Science* 24:153–166.

HARPER, J. L. 1977. *Population biology of plants*. Academic Press. London. 892 pp.

HARTSHORN, G. S. 1978. Tree falls and tropical forest dynamics. Pp. 617–638 in Tomlinson P. B. & Zimmerman M. H. (eds.). *Tropical trees as living systems*. Cambridge University Press, Cambridge.

HOLMES, R. L. 1983. Computer-assisted quality control in tree-ring research. *Tree-ring Bulletin* 39:77–82.

HUBBELL, S. P., FOSTER, R. B., O'BRIEN, S. T., HARMS, K. E., CONDIT, R., WECHSLER, B., WRIGHT, S. J. & DE LAO, S. L. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283:554–557.

JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–528.

KELLY, C. K. & BOWLER, M. G. 2002. Coexistence and relative abundance in tropical trees. *Nature* 417:437–440.

LAUPRASERT, M. 1988. *The creation of a permanent sample plot in dry evergreen forest of Thailand and investigations of a suitable plot size for permanent sample plot programs*. M.Sc. Thesis. International Institute for Aerospace Survey and Earth Sciences (ITC), Netherlands.

LIEBERMAN, D., LIEBERMAN, M., HARTSHORN, G. & PERALTA, R. 1985. Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. *Journal of Tropical Ecology* 1:97–109.

LORIMER, C. G. & FRELICH, L. E. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research* 19:651–663.

NOWACKI, G. J. & ABRAMS, M. D. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs* 67:225–249.

ORWIG, D. A. & ABRAMS, M. D. 1990. Contrasting radial growth and canopy recruitment patterns in *Liriodendron tulipifera* and *Nyssa sylvatica*: gap-obligate versus gap-facultative tree species. *Canadian Journal of Forest Research* 24:2141–2149.

POORTER, L., BONGERS, F., STERCK, F. J. & WOLL, H. 2005. Beyond the regeneration phase: differentiation of height-light trajectories among tropical tree species. *Journal of Ecology* 93:256–267.

POULSON, T. L. & PLATT, W. J. 1989. Gap light regimes influence canopy tree diversity. *Ecology* 70:553–555.

RENTCH, J. S., FAJVAN, M. & HICKS, R. R. 2003. Oak establishment and canopy accession strategies in five old-growth stands in the central hardwoods region. *Forest Ecology and Management* 184:285–297.

TROUP, R. S. 1921. *The silviculture of Indian trees. Volume 1–3*. (First edition) Clarendon Press, Oxford.

UHL, C., CLARK, K., DEZZEO, N. & MAQUIRINO, P. 1988. Vegetation dynamics in Amazonian treefall gaps. *Ecology* 69:751–763.

WHITMORE, T. C. 1978. Gaps in the forest canopy. Pp. 639–655 in Tomlinson, P. B. & Zimmerman, M. H. (eds.). *Tropical trees as living systems*. Cambridge University Press, Cambridge.

WRIGHT, E. F., CANHAM, C. D. & COATES, K. D. 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. *Canadian Journal of Forest Research* 30:1571–1580.

WRIGHT, S. J., MULLER-LANDAU, H. C., CONDIT, R. & HUBBELL, S. P. 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* 84:3174–3185.