DISTURBANCE HISTORY AND HISTORICAL STAND DYNAMICS OF A SEASONAL TROPICAL FOREST IN WESTERN THAILAND

PATRICK J. BAKER,[1,2,6] SARAYUDH BUNYAVEJCHEWIN,[3] CHADWICK D. OLIVER,[1,4,7] AND PETER S. ASHTON[5]

[1]*College of Forest Resources, University of Washington, Seattle, Washington 98195 USA*
[2]*Institute of Pacific Islands Forestry, USDA Forest Service, Hilo, Hawaii 96720 USA*
[3]*Royal Forest Department, Chatuchak, Bangkok 10900, Thailand*
[4]*Yale School of Forestry and Environmental Studies, New Haven, Connecticut 06511 USA*
[5]*Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138 USA*

Abstract. Disturbances influence forest dynamics across a range of spatial and temporal scales. In tropical forests most studies have focused on disturbances occurring at small spatial and temporal scales (i.e., gap dynamics). This is primarily due to the difficulty of reconstructing long-term disturbance histories of forests in which most tree species lack annual growth rings. Consequently, the role of past disturbances in tropical forests is poorly understood. We used a combination of direct and indirect methods to reconstruct the historical disturbance regime and stand development patterns in mature and regenerating seasonal dry evergreen forest (SDEF) in the Huai Kha Khaeng Wildlife Sanctuary in western Thailand. Direct estimates of long-term establishment and growth patterns were obtained from 12 tree species that form annual growth rings as a consequence of the region's strong intra-annual rainfall seasonality. Indirect estimates of establishment patterns were obtained from analyses of stand structure and individual tree architecture and application of age-estimation models to 10 dominant canopy-tree species using demographic data from a large-scale, permanent forest-dynamics plot.

The combination of direct and indirect methodologies revealed a complex disturbance history in the seasonal evergreen forest over the past 250 years. In the mid-1800s, 200–300 ha of forest were destroyed by a catastrophic disturbance, which led to the synchronous establishment of many of the trees that presently dominate the forest canopy. Since then widespread disturbances of variable intensity have occurred at least three times (1910s, 1940s, and 1960s). These disturbances created discrete temporal pulses of establishment in small to large gaps in the forest matrix across several square kilometers. Background mortality and gap formation were evident in every decade since 1790, but these varied in intensity and frequency.

The SDEF retains a distinct structural and floristic legacy from the catastrophic disturbance of the mid-1800s. The single-age cohort that established after the disturbance has developed a complex three-dimensional structure as a consequence of differences in interspecific growth patterns of the canopy-tree species and subsequent disturbances of moderate and low intensity. While no single methodological approach provided a complete picture of the disturbance history and stand development patterns of the seasonal evergreen forest, taken together they offered new insights into the long-term dynamics of a primary tropical forest. In particular, the study highlighted the role of disturbance at multiple spatial and temporal scales and varying intensities in determining the structure and composition of a complex, species-rich tropical forest and raises important questions about the role of rare, catastrophic events on tropical forest dynamics.

Key words: age estimation; catastrophic events and tropical forest regeneration; dendroecology; disturbance history; Hopea odorata; *Huai Kha Khaeng Wildlife Sanctuary, Thailand; stand-development patterns; tree architecture; tropical forest dynamics.*

INTRODUCTION

In the temperate zone, understanding of forest stand dynamics has advanced rapidly in recent decades due in large part to dendroecological studies that reconstruct historical patterns of recruitment, growth, and mortality from annual growth rings (e.g., Henry and Swan 1974, Swetnam and Lynch 1993, Foster et al. 1996). These studies have demonstrated the ubiquity of disturbances at multiple spatial and temporal scales, ranging from frequent, small-scale canopy gaps created by the death of individual trees (Runkle 1982) to rare catastrophic disturbances, such as fires and windstorms, that may destroy hundreds of square kilometers of forest (Lorimer 1977, Romme 1982).

In the tropics the long-term influence of disturbances on forest dynamics is little understood. While small-scale disturbances created by a single tree or small group of trees falling have been widely observed and studied in tropical forests (Hartshorn 1978, Whitmore 1978, Denslow 1987), the impact of infrequent catastrophic disturbances has only recently been documented (e.g., Zimmerman et al. 1994) and their long-term impact not at all. The low frequency of catastrophic disturbances limits opportunities for direct observation, although recent examples exist (e.g., Vandermeer et al. 2001), and the lack of annual growth rings in most tropical tree species hampers development of proxy records that provide indirect evidence of past disturbances. Nonetheless, the body of anecdotal evidence for catastrophic disturbances in the tropics has become substantial, even for the most aseasonal forests (see Whitmore and Burslem [1998] for an extensive review).

Disturbances play an important role in determining the structure and functioning of ecosystems (Oliver 1981, Paine and Levin 1981, Pickett and White 1985). They directly affect community and population dynamics by altering resource availability (Denslow et al. 1998), by causing mortality and providing opportunities for recruitment (Canham and Marks 1985), and by influencing the relative competitive status of individuals (Sousa 1984). Disturbances may also be important in maintaining species diversity, particularly in species-rich ecosystems such as tropical forests (Connell 1978, Huston 1979, Glitzenstein et al. 1986), by providing occasional periods favorable to recruitment for long-lived organisms such as certain tree species (Warner and Chesson 1985).

A central challenge in ecology is identifying the relevant scale at which processes such as disturbances occur (Levin 1992). Ecological and silvicultural research in temperate-zone forests has addressed a wide range of temporal and spatial scales using a variety of methodological approaches (e.g., pollen and charcoal stratigraphy, tree-ring analyses, stand chronosequences, permanent census plots). In contrast, research in tropical forests has primarily examined short-term dynamics (i.e., years to decades) using large-scale permanent plot studies (e.g., Condit 1995) or long-term dynamics (i.e., centuries to millennia) through paleoecological studies (e.g., Bush and Colinvaux 1994). There remains a major gap in our understanding of dynamics at the intermediate scale (i.e., decades to centuries) in tropical forests (Ashton 1981, Bormann and Berlyn 1981). For long-lived organisms such as trees, this may be the relevant time-scale for evaluating mechanisms of coexistence. Catastrophic disturbances that occur once every several hundred years in a given area of tropical forest may, as in temperate forests (e.g., Duncan 1992), be critical to long-term maintenance of species diversity.

Despite the widely held belief that tropical tree species do not form annual growth rings, the presence of annual rings in some tropical tree species has been documented since the late 1800s (e.g., Gamble 1920, Pearson and Brown 1932, Worbes 2002). In recent decades paleoclimatologists and dendrochronologists have begun to use tree-ring records from tropical forests to reconstruct multi-century proxy records of interannual variation in temperature and rainfall. Recent examples include tree-ring chronologies for *Pterocarpus angolensis* (Stahle et al. 1999, Fichtler et al. 2004), *Burkea africana* (Fichtler et al. 2004), *Tectona grandis* (Jacoby and D'Arrigo 1990, Bhattacharya et al. 1992, Pumijumnong et al. 1995), *Toona ciliata* (Bhattacharya et al. 1992; Heinrich and Banks, *in press*), *Piranhea trifoliata* (Schongart et al. 2004), *Capparis indica* (Enquist and Leffler 2001), *Genipa americana* (Enquist and Leffler 2001), and several tropical species of *Pinus* (Segura and Snook 1992, Savage 1994, Buckley et al. 1995). Fundamental data on tree age and growth rate have also been obtained from tropical tree-ring studies, particularly in Neotropical forests (e.g., Worbes 1989, 1999, Worbes et al. 1992, Dezzeo et al. 2003, Fichtler et al. 2003). Only a few studies (e.g., van Groenendal et al. 1996, Worbes et al. 2003) have used tree rings to investigate long-term community dynamics of tropical forests, and these have been limited to secondary forests. However, even in those tropical forests in which some tree species have annual growth rings, most species do not. Several other approaches are available for obtaining tree ages to reconstruct historical stand-development patterns in tropical forests (see Martínez-Ramos and Alvarez-Buylla [1998] for a recent review). These include techniques such as radiocarbon dating and mortality- and growth-based estimation procedures. Indirect evidence of historical development patterns can, in some cases, be obtained from data on stand structure and floristic composition (e.g., Debski et al. 2000). To date, however, these methods have not been applied, either alone or in combination, to reconstruct community-level dynamics in tropical forests.

In this study we describe the historical development patterns of a species-rich tropical forest in western Thailand. The seasonal dry evergreen forest (SDEF) in the Huai Kha Khaeng Wildlife Sanctuary is an ideal system for addressing questions of historical stand development because a number of the canopy-tree species have annual growth rings that can be used for dendroecological analyses and because a long-term, large-scale forest-dynamics plot provides valuable demographic data for understanding the life-history traits of many of the tree species (Bunyavejchewin et al. 2001, 2002). The underlying question that motivated this research was: How did a stand of species-rich SDEF develop and change over time to reach its current condition? In particular, we focused on the question of whether the dynamics of the seasonal dry evergreen

forest have been relatively uniform in recent decades and centuries or, rather, whether they have been characterized by episodic fluctuations in recruitment and growth induced by exogenous disturbances. To do so, we used three complementary methodological approaches: (1) a detailed description of stand structure, (2) a reconstruction of stand age structure using diameter-based age estimation models, and (3) dendroecological analyses using annual growth rings. The rationale for this combination of methodologies is as follows. First, the current structure of a stand provides a fixed reference point for the study of historical forest dynamics, in that any realistic stand-development pathway must ultimately lead to the current stand structure within the constraints imposed by the life-history traits of the tree species that occur there. Second, the estimated age distributions provide a temporal context to stand development for species without tree rings, allowing interspecific comparisons of age distributions among dominant tree species. Third, dendroecological reconstruction of the age distributions of tree species provides direct empirical evidence for spatial and temporal patterns of establishment and growth of some species, and a means of calibrating indirect methods, permitting dynamics at the stand and landscape scale to be inferred over decades and centuries.

METHODS

Study area

This study was conducted at the Huai Kha Khaeng Wildlife Sanctuary (HKK) in Uthai Thani province, west-central Thailand (15°40′ N, 99°10′ E). HKK is dominated by a mosaic of three forest types: seasonal dry evergreen forest (SDEF), mixed deciduous forest, and deciduous dipterocarp forest. SDEF has the highest species richness and the tallest canopy of these forest types. Less than one-third of the canopy species in the SDEF are deciduous. Important families in SDEF include the Dipterocarpaceae, Annonaceae, Euphorbiaceae, and Meliaceae (Bunyavejchewin et al. 2002). The climate is monsoonal; mean annual rainfall is ~1500 mm with a six-month dry season (November–April) in which mean monthly rainfall is <100 mm. Some years have sporadic rainfall during the dry season, while others have little or no rain during the entire dry season. Mean July temperature is 27°C; mean January temperature is 19°C. Soils are highly weathered ultisols with neutral to slightly acid pH and moderate fertility (Lauprasert 1988).

Four study sites within a contiguous block of SDEF several square kilometers in extent were used for the study (Appendix A). Three of the study sites were located in mature forest; the fourth study site was located at an area of relatively young forest within the matrix of mature forest. (We use the term ''mature'' to refer to SDEF in which the forest canopy has reached maximum height and gap formation has led to the estab-

lishment of younger trees and greater spatial heterogeneity of forest structure. In contrast, we use ''young'' to refer to forest in which the canopy trees have reached <50% of their maximum height and no new trees have established nor gaps formed, creating a relatively homogenous stand structure.) Two of the study sites are permanent forest-dynamics plots. One, a 50-ha plot, includes all trees ≥1 cm in diameter at breast height (dbh) and was censused in 1994 and 1999 (Bunyavejchewin et al. 1999). The other, a 16-ha plot located several hundred meters east of the 50-ha plot, includes all trees ≥10 cm dbh (on 9 ha) and ≥15 cm dbh (on 7 ha) and was censused in 1987 and the 9-ha section was recensused in 1999. The third study site (Young *Hopea*) was located ~1.5 km east of the 50-ha plot in the only regenerating stand of SDEF of which we are aware. The fourth study site (Huai Gading) was located ~1 km southwest of the 50-ha plot and was dominated by large individuals of *Afzelia*.

Species selection

We selected two sets of tree species for this study (Table 1). The first set of species ($N = 10$) was selected from the 50-ha plot for detailed demographic study and indirect estimation of population age structures. The 10 species were subjectively chosen to represent the dominant canopy-tree species in the evergreen forest. All of the selected species were important components of the 50-ha plot in terms of frequency or basal area. The second set of species was used for dendroecological analyses. We included 12 species with reliable annual growth rings (Baker 2001); however, most analyses were based on 6 tree species with particularly clear annual rings. Two species, *Chukrasia tabularis* and *Neolitsea obtusifolia*, were common to both the demographic and dendroecological studies. For brevity, generic names are used when referring to study species. Taxonomy and nomenclature follow Bunyavejchewin et al. (1999).

The focus of the study was on the historical dynamics of the canopy trees. An analysis of stratification patterns showed that all individuals >20 m tall were included in the canopy stratum of the forest and height–dbh allometries for each of the study species showed that most trees >20 cm dbh were also at least 20 m tall (data not shown). Therefore, for this study, canopy individuals were defined as those trees >20 cm dbh.

Study design: stand structure

Diameter distributions.—To provide a quantitative basis for comparison of population size structures, Weibull functions were fit to species- and quadrat-based diameter distributions. Diameter distributions were evaluated for species with >100 individuals, the 50-ha plot as a whole, and representative 1-ha subsamples within the plot. A Weibull probability density function was fit to each diameter distribution using a maximum-likelihood algorithm (Cohen 1965, Bailey and Dell

TABLE 1. Total frequency (*N*) and basal area (BA) of each of the study species from the 1994 census in the 50-ha permanent forest-dynamics plot in seasonal dry temperate forest (Huai Kha Khaeng Wildlife Sanctuary, west-central Thailand).

Species	Family	Total *N*	Total BA (m²)	Used in study?† Age estimation	Used in study?† Tree rings
Hopea odorata	Dipterocarpaceae	330	169.13	yes	
Saccopetalum lineatum	Annonaceae	1 833	129.26	yes	
Polyalthia viridis	Annonaceae	6 069	84.69	yes	
Tetrameles nudiflora	Datiscaceae	1 626	61.39	yes	
Neolitsea obtusifolia	Lauraceae	1 172	48.31	yes	yes
Alphonsea ventricosa	Annonaceae	1 225	43.76	yes	
Garcinia hombroniana	Clusiaceae	1 630	35.71	yes	
Litsea cambodiana	Lauraceae	360	35.35	yes	
Acer oblongum	Aceraceae	618	24.36		yes
Afzelia xylocarpa	Leguminosae	41	22.45		yes
Chukrasia tabularis	Meliaceae	204	8.97	yes	yes
Melia azederach	Meliaceae	189	8.76		yes
Vitex peduncularis	Verbenaceae	177	6.93		yes
Mangifera sp.	Anacardiaceae	81	6.15		yes
Macaranga siamensis	Euphorbiaceae	708	5.53	yes	
Toona ciliata	Meliaceae	14	2.81		yes
Cassia fistula	Leguminosae	116	2.66		yes
Michelia champaca	Magnoliaceae	17	1.11		yes
Ulmus lancifolia	Ulmaceae	14	0.94		yes
Gmelina arborea	Verbenaceae	15	0.35		yes
Total		16 439	698.62		
Percentage of 50-ha plot total		20.25	45.87		

† Species used in the age estimation/architecture studies or the dendroecological studies.

1973). The Weibull distribution can take a wide variety of shapes as determined by the shape parameter, *c*. When $c < 1$, the function is a steeply descending, monotonic function; when $c = 1$ it is a negative exponential distribution. For values of $c > 1$, the function is unimodal; when $1 < c < 3.6$ the distribution has a positive skew, when $c = 3.6$ it is approximately normal, and when $c > 3.6$ the distribution has a negative skew. One-tailed 95% confidence intervals for *c* were calculated for each species following Cohen (1965) to test whether $c > 1$. Compound diameter distributions, which have steeply descending curves in the smallest size classes followed by broad peaks in the larger size classes (usually >10–15 cm dbh) (Lorimer and Krug 1983), are not well described by the Weibull or other simple density functions. However, for the Weibull distribution they typically have $c < 1$ because of the large number of individuals in the smallest size class(es). All diameter distributions were classified as "compound" or "not compound" based on visual examination of the histograms.

Profile diagrams.—Profile diagrams were made in three of the study areas using standard protocols (Richards 1996) to provide a qualitative description of forest structure and a quantitative analysis of canopy stratification patterns. Two transects were placed in the 50-ha plot; one transect was placed in the 16-ha plot, and one transect was placed in the young *Hopea* stand. For each profile diagram a belt transect of 10 × 60 m was established in which all trees >5 m tall were mapped to plot coordinates, identified by species, and measured for dbh, height (*H*) and height to base of live crown (H_{BLC}). Heights were measured with a clinometer from a position in which a clear view of the treetop was available and the measured angle was ~45° (Romesburg and Mohai 1990). Vertical stratification was analyzed for each profile-diagram transect using a quantitative algorithm (Baker and Wilson 2000). The algorithm sorts the transect trees by *H* and H_{BLC}, respectively, and compares the height of each tree, in descending order of height, to a moving average of H_{BLC}. If the difference between a tree height and the moving average of H_{BLC} is greater than a predefined overlap constant, a new stratum is considered to begin and the moving average of H_{BLC} is reset to the H_{BLC} of the first tree in the new stratum. The overlap constant (k_o) was set to 1.5 m following Baker and Wilson (2000). The algorithm identifies the number of strata that exist in a stand and the stratum in which each tree occurs.

Architectural analysis.—Individual tree form can provide important information on historical growing conditions and can be particularly informative when comparing species with similar growth patterns (Lutz and McComb 1935, Kohyama 1980). Two approaches were used to characterize individual tree architecture. The first classified trees into four groups based on two readily observable architectural features (Torquebiau 1986): (1) the height of a tree relative to the height of the forest canopy; and (2) the height of the morpho-

logical inversion point of a tree relative to the total height of the tree. The ''morphological inversion point'' is the height of the lowest fork along the main stem of the tree (Hallé et al. 1978). It is a significant architectural feature of a tree because it indicates the point at which the tree began to develop its crown through ''reiterated'' architectural units and denotes the ontogenetic shift from sapling to mature tree (Hallé et al. 1978). The second architectural classification describes the general character of the main stem of the tree. Each tree was classified as straight or sinuous in the upper and lower halves of the bole and was assigned to one of four possible categories: entirely straight (Str), entirely sinuous (Sin), upper stem sinuous and lower stem straight (USin), and lower stem sinuous and upper stem straight (LSin). Trees that had grossly deformed stems (Def) or broken tops (BT) were described as such and were not included in the four sinuosity categories. Study trees were randomly selected from the 50-ha plot and the 16-ha plot databases.

Architecture and growth of Hopea *saplings and poles.*—Hopea odorata is the dominant structural element of the seasonal dry evergreen forest (SDEF) in our study area. The population of *Hopea* is dominated by massive (>75 cm dbh, >50 m tall) trees with straight, branch- and knot-free boles that rise into the upper reaches of the canopy, a common feature of dipterocarps in the forests of Southeast Asia (Ashton 1964, Whitmore 1985). However, regeneration of *Hopea* is scant and casual observation suggested that most *Hopea* in the smallest size classes are unlikely to survive and grow into the canopy. To determine the character and potential of the putative regeneration of *Hopea*, we surveyed every individual of *Hopea* <30 cm dbh ($N = 47$ trees) on the 50-ha plot in July 1998. For each tree, diameter at breast height and height were measured. In addition, a relative estimate of exposure to direct and indirect sunlight was assessed by assigning a crown illumination (CI) index to each tree on a scale of 1 (low) to 5 (high) following Clark and Clark (1992). To determine the growth potential of the *Hopea* recruits, the architecture of saplings and poles was qualitatively assessed for the: (1) tree stem, detailing the location of all crooks, forks, and obvious defects, as well as a general indication of overall sinuosity of the bole; and (2) tree crown, describing the terminal shoot as straight, flat topped, broken, or exhibiting localized mortality (i.e., terminal dieback). Diameter growth rates (1994–1998) of the *Hopea* recruits were compared between groups (e.g., suppressed/non-suppressed, deformed/non-deformed) using a one-way ANOVA.

Study design: age-estimation models

We used two approaches to indirectly estimate tree age based on tree size and growth rate. The methods differ in their assumptions about how trees grow to the canopy and, as such, are sensitive to interspecific dif-

ferences in shade tolerance. We provide here a brief description of each approach. For a detailed discussion of the models, their rationales, and their relative advantages see Baker (2003). We used the age estimates in two ways. First, we compared the age structure of individual species to determine if there were common periods of synchronous establishment. Second, we combined the estimated ages of trees from all the study species to create a community-level age structure, which we compared among the different age-estimation approaches to identify the range of potential stand-age structures.

Crown-class model.—For the crown-class model, tree age is estimated by dividing the dbh of a tree of given crown class (=CI) by the mean growth rate of trees of the same crown class. For example, if a 15-cm-dbh tree was suppressed (i.e., CI = 1) and the mean diameter growth rate of conspecific suppressed trees was 1 mm/yr, then the estimated age of the tree would be 150 yr. If the tree was co-dominant (i.e., CI = 4) and the mean growth rate of conspecific co-dominant trees was 5 mm/yr, then the estimated age of the tree would be 30 yr. The crown-class model assumes that an individual has received the same relative crown illumination over its entire life. As such, it is best suited for estimating the age of shade-intolerant trees, which are less likely to shift crown classes through suppression (and survive), than shade-tolerant trees. To obtain mean diameter growth rates by CI for this study, we measured diameter and scored CI for ~60 trees per species across the entire range of size classes (>1 cm dbh) within the 50-ha plot. Diameter growth was calculated as the annualized increment over the 1994–1998 measurement period.

PAI-regression model.—We used a modified version of the periodic annual increment (PAI) method developed by Condit et al. (1993), which uses instantaneous relative growth rate regressed on dbh, to calculate lifetime age-size relationships for each of the study species using data from the 1999 recensus of the 50-ha plot. The PAI-regression model assumes that the current canopy trees established and grew under the same conditions as trees that are presently establishing in the forest. While this may be true for shade-tolerant species that can survive in the low-light environment of the understory and subcanopy of the forest, many shade-intolerant species cannot survive under such conditions. Consequently, the PAI-regression model provides better age estimates for shade-tolerant tree species (Baker 2003).

Mixed model.—Given the differences in estimation accuracy of the crown-class and PAI-regression methods relative to shade tolerance, we used a third approach for estimating stand-level age structure based on species' relative shade tolerance. Each of the study species was assigned to a shade-tolerance category based on relative length of the live crown. This measure has been used by foresters and forest ecologists as a

reasonable approximation of relative shade tolerance (Graham 1954, Lorimer 1983) and provided reasonable estimates for the HKK (Huai Kha Khaeng Wildlife Sanctuary) study species (Baker 2001). Ages were then estimated for individuals of the shade-intolerant and mid-tolerant species using the crown-class method and for individuals of shade-tolerant species using the PAI-regression method. Stand-level age structures were then compared with those obtained from the crown-class and PAI-regression approaches.

Sample trees for age estimation.—Sample trees were taken from 42 circular 1250-m^2 plots established for a separate study of *Hopea* growth. The dbh and CI were recorded for all individuals of the 10 study species in each plot. The data for each species were divided into 10-cm-dbh classes. Where there were <5 individuals in a given species–dbh class combination, additional trees were selected at random from the 50-ha plot database. Tree age was estimated using both the crown-class and PAI-regression approaches described above. ''Age'' was defined as the length of time during which a tree has been >1.3 m tall (i.e., the sampling height for dbh). No attempt was made to account for the number of years required to reach 1.3 m because data were not available to do so and the highly variable rates of height growth among seedlings and saplings in the complex light environment of the understory would introduce an age error of unknown magnitude.

Testing age estimates.—Two species, *Chukrasia* and *Neolitsea*, have annual growth rings that provide independent age data to evaluate the accuracy of the age-estimation methods. *Chukrasia* and *Neolitsea* differ in their life-history traits. While both species are capable of reaching the upper canopy, *Neolitsea* is more shade tolerant and can endure in low-light conditions for extended periods, whereas *Chukrasia* is shade intolerant and rarely found in the low-light conditions of the forest understory. Based on validation results for tree species in the southeastern United States (Baker 2003), we expected the crown-class method to provide better age estimates for *Chukrasia* and the PAI-regression method to better predict the ages of *Neolitsea*.

Study design: tree-ring analyses

The annual nature of growth-ring formation was determined for 51 tree species in the SDEF by a cambial wounding experiment (Wolter 1968, Shiokura 1989). In 1987 several thousand trees were tagged and identified in the 16-ha plot. Tags were attached to the tree with aluminum nails. When a nail is driven sufficiently deep into a live tree, it wounds the cambium and creates a permanent, datable scar that is recorded in the xylem (Shiokura 1989). In August 1998 we removed a section of wood around the nail for 1–5 individuals of each species. The wood sections were then bisected along the horizontal plane passing through the nail using a handsaw with an extremely fine (0.5 mm) kerf. One section was then sanded (150 to 600 grit sand paper

series) until the wood anatomy was readily distinguishable under 10× magnification. In wood samples that had recognizable rings, the rings between the nail scar and the cambium were counted. Because the wood samples were collected in August 1998, individuals with annual growth-ring formation should have had 11 rings distal to the nail scar. Of the 51 species, 18 species (36%) had annual growth rings (Baker 2001). Our analyses included 12 of these species, although the majority of the dendroecological work was based on 6 tree species (*Afzelia*, *Chukrassia*, *Melia*, *Neolitsea*, *Toona*, and *Vitex*) with particularly clear annual rings.

Sampling methods for the dendroecological analyses varied by plot depending on the relative abundance of species with annual growth rings. In the 50-ha plot individuals were selected at random from the plot database. In the 16-ha plot individuals were randomly selected from the northeastern 9 ha of the plot. Trees on the remaining 7-ha subset were generally excluded because of poor tagging practices and inconsistent species identification during the initial census. In the young *Hopea* stand a series of parallel transects was established in an area of ~2 ha and cores were taken from all individuals of the study species. In the Huai Gading site cores were taken from six individuals, primarily large *Afzelia*. As previously mentioned, sampling was generally limited to trees >20 cm dbh because the historical dynamics of the canopy trees were the focus of the study; however, in some instances smaller trees were cored and analyzed. Since it was not possible to obtain suitable cores from every tree because of mortality, rot, stem deformities (e.g., fluting and buttressing), and the presence of strangling figs, several individuals from each species were also chosen opportunistically during field sampling.

Tree cores were obtained with a 40-cm Suunto (Vantaa, Finland) tree borer. Two to four cores were taken at 1 m height on each tree at different locations approximately equidistant around the stem. Every effort was made to include the pith in at least one core from each tree. While this was not always possible, most cores either included the pith or passed within 2 cm of the pith. *Afzelia* was unique because of its great size (all individuals of *Afzelia*, except those at the young *Hopea* stand, were >100 cm dbh). Nonetheless, all *Afzelia* cores, including those that did not pass within a few cm of the pith, were used in the analyses because they provided the longest ring-width series and thus offered insights into patterns of growth and release over the past 250 or more years.

Cores were prepared using standard techniques to obtain a clear, highly polished surface. Prepared cores were scanned on a high-resolution digital scanner (Epson 1640 SU [Epson America, Long Beach, California, USA]) at 1200–1600 dpi (dots per inch). Annual growth rings were counted and measured using the WinDendro tree-ring image analysis software (Version 6.4a, Regent Instruments [Sainte-Foy, Quebec, Cana-

TABLE 2. Decision rules for classifying growth releases when multiple ring-width series from the same tree were available.

Release type	Definition
Extreme	>100% GC sustained for at least 10 yr in ≥2 ring-width series
Major	>100% GC sustained for at least 10 yr in 1 ring-width series
Moderate	50–99% GC sustained for at least 10 yr in ≥2 ring-width series
Minor	50–99% GC sustained for at least 10 yr in 1 ring-width series

Notes: Percentage growth change (% GC) was calculated for each tree-ring series according to the formula % GC = [$(M_2 - M_1)/M_1$] × 100, where M_1 is the mean annual diameter growth of the preceding 10-yr period (including the current year) and M_2 is the mean annual diameter growth of the subsequent 10-yr period. Each tree was cored 3–4 times. A release may have occurred in only one of the ring series taken from the tree, or it may have occurred in 2, 3, or all 4 of the ring series.

da]). Multiple cores from a tree were measured in sequence and cross dated using the real-time cross-dating features of WinDendro. This process greatly facilitated the detection of false rings and missing rings. In addition, ring-width series were cross dated using the program COFECHA (Holmes 1983). When the pith was not included in the core, Duncan's (1989) geometric model was used to calculate the missing distance to the pith for all species (Appendix B).

To identify establishment patterns, tree ages were grouped by plot and by species. Establishment was defined as the time at which an individual tree reached 1 m in height (i.e., the coring height). Early growing conditions were inferred from the growth rates of the five earliest rings in the core. As part of a study on short-term dynamics of the SDEF, diameter-increment data were obtained for trees in the 50-ha plot across the full range of crown classes. Analytical functions to differentiate suppressed trees (CI < 3) and non-suppressed trees (CI ≥ 3) on the basis of mean annual diameter increment (measured over a 5-yr period) were developed for *Chukrasia*, *Melia*, *Neolitsea*, and *Toona*. Sufficient data were not available for the other study species. Based on the mean ring width of the first five annual growth rings and the discriminant functions, each cored tree was classified as having established as suppressed or non-suppressed.

To identify potential growth responses to disturbances and prolonged periods of suppression, percentage growth change (%GC) was calculated for each tree-ring series (Abrams et al. 1995). Percentage growth change was calculated for each year from the formula: %GC = [$(M_2 - M_1)/M_1$] × 100, where M_1 is the mean annual diameter growth of the preceding 10-yr period (including the current year), and M_2 is the mean annual diameter growth of the subsequent 10-yr period (Nowacki and Abrams 1997). Periods of suppression and release were identified based on criteria adapted from Lorimer and Frelich (1989) and Nowacki and Abrams (1997). For all species a "major release" in a tree-ring series was defined as a >100% growth increase lasting 10 yr and a "moderate release" as a >50% growth increase lasting 10 yr. Decision rules for classifying

releases from multiple cores within the same tree were developed and applied to all trees (Table 2).

We used regression analyses to assess the relationship between age and dbh. Small sample sizes for some study species and lack of establishment dates for most *Afzelia* restricted analyses to the five species with >10 individuals (*Chukrasia*, *Melia*, *Neolitsea*, *Toona*, and *Vitex*).

RESULTS

Stand structure

Diameter distributions.—At the community level, diameter distributions were negative exponential, both for individual 1-ha quadrats within the 50-ha plot and for the 50-ha plot as a whole (Weibull c = 0.895; P < 0.001 that c > 1.0). Species' diameter distributions varied widely in shape. Of the 73 species with >100 individuals on the 50-ha plot, the Weibull shape parameter (c) ranged from 0.66 to 4.09 (mean =1.31, SE = 0.086; Fig. 1). The 73 species accounted for 93.9% of the trees on the 50-ha plot. The species-specific diameter distributions could be divided into three general groups: negative exponential, positively skewed unimodal, and compound. Of these three, the positively skewed unimodal distribution was the most common (N = 40 species, 54.8% of species), followed by the compound (N = 20, 27.4%) and negative exponential (N = 13, 17.8%). Forty-eight species (65.8%) had values for the Weibull c parameter significantly >1 (one-tailed test, α = 95%). Of the 25 species with c not significantly >1, 15 species had compound diameter distributions. Only 10 (13.7%) species had diameter distributions best described by a negative exponential function. *Hopea* had the highest c value (4.09) of any species in the plot and was the only species with a diameter distribution that was approximately normally distributed with a slight negative skew (Fig. 2). Of the other nine species considered in detail in this study, only *Litsea cambodiana* had a diameter distribution that was also distinctly unimodal (Weibull c = 2.91). Five of the study species (*Alphonsea*, *Chukrasia*, *Garcinia*, *Saccopetalum*, and *Tetrameles*) had compound diameter distributions with distinct secondary peaks in
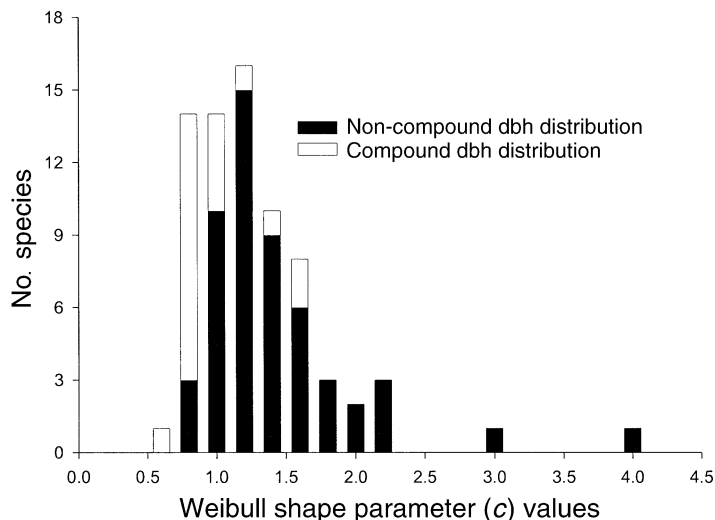
FIG. 1. Distribution of Weibull shape parameter (*c*) for all 73 species with *N* > 100 individuals. Compound diameter distributions are bimodal distributions with a large number of stems in the smallest size classes and a broad peak in the large size classes (see *Results: Stand structure* for details). Diameter distributions for the two species with extreme Weibull *c* (i.e., shape parameter) values, *Litsea cambodiana* (*c* = 2.91) and *Hopea odorata* (*c* = 4.09), are shown in Fig. 2.

the larger size classes (Fig. 2). Diameter distributions of two species (*Neolitsea* and *Polyalthia*) significantly departed from negative exponential by being overrepresented in the larger size classes. Of the 10 dominant species examined in this study, only *Macaranga*, a large-leaved, gap-dependent pioneer species, had a negative exponential diameter distribution.

Profile diagrams.—The 50-ha and 16-ha plots showed similar patterns of stratification, species distribution, and relative species dominance in the profile-diagram transects (Appendix C). Each transect had two strata, an overstory and a mid-story (the numbers of individuals and species in each stratum are shown in Appendix Table C1). *Hopea* were the tallest trees in each transect. Below the *Hopea* several species, including *Alphonsea*, *Garcinia*, *Neolitsea*, and *Saccopetalum*, routinely occurred. The upper crowns of the taller individuals of these species overlapped with the lower portions of the crowns of the *Hopea*. Consequently, *Hopea* did not constitute a separate ''emergent'' stratum. The lower stratum of the transects contained *Baccaurea ramiflora*, *Dimocarpus longans*, *Orophea polycarpa*, *Phoebe tavoyana*, *Polyalthia viridis*, *Memecylon* spp., and suppressed individuals of shade-tolerant canopy species such as *Garcinia* and *Saccopetalum*. *Hopea* did not occur in the lower stratum. The 16-ha and 50-ha plot transects differed only in the relatively deep upper stratum of the 16-ha plot transect. In the 50-ha plot, the lower limits of the upper strata were 16 m and 20 m, while the lower limit of the upper stratum in the 16-ha plot profile-diagram transect was 10 m. The stratification algorithm output for the 16-ha transect showed that 50% of the trees in the upper stratum had crowns just tall enough to overlap with the *Hopea* in the upper portion of the profile, effectively reducing the lower boundary of the upper stratum. In general, however, the patterns of total height, number of strata, and species composition described in the pro-

file diagram from the 16-ha plot were nearly identical to those from the 50-ha plot.

The pattern of stratification in the young *Hopea* stand was remarkably similar to that of the older *Hopea* stands, but on a reduced vertical scale (Appendix C). As in the profile diagrams from the 16-ha and 50-ha plots, the canopy was composed of two strata and dominated by *Hopea*. *Garcinia* and *Saccopetalum* were common in the upper stratum, although, based on general stem and crown physiognomy, several *Garcinia* appeared to be relict trees. The lower stratum was dominated by *Garcinia*, but, like the other transects, contained *Baccaurea*, *Dimocarpus*, and *Phoebe*. *Hopea* did not occur in the lower stratum. The sole difference between the young and mature forest transects was the total height of the canopy: at the young *Hopea* stand, the patterns of stratification and species distribution within the vertical profile of the forest were compressed into 25 m, whereas in the mature forest transects, they occurred over a ≥50 m vertical gradient.

Individual tree architecture.—Architectural assessments of 509 individuals from the 10 study species provided indirect evidence of the historical development patterns of individual trees. Given the range of variation in life-history traits exhibited by the study species, remarkably little variation was found in the architecture of the trees, either within or among species. Although all architectural categories were represented (with the exception of trees that were 1L *and* LS), the architectural categories were not equally distributed among species (Tables 3 and 4). For the inversion point index (Table 3), >80% of the trees were classified as 2H (i.e., taller than the mid-height of the canopy and with a fork in the uppermost portion of the stem). Species with >10 sampled individuals had from 64% (*Garcinia*) to 100% (*Tetrameles*) of trees classified as 2H. Only 14 trees were classified as 1H or 1L. The sinuosity index also showed an unequal distribu-
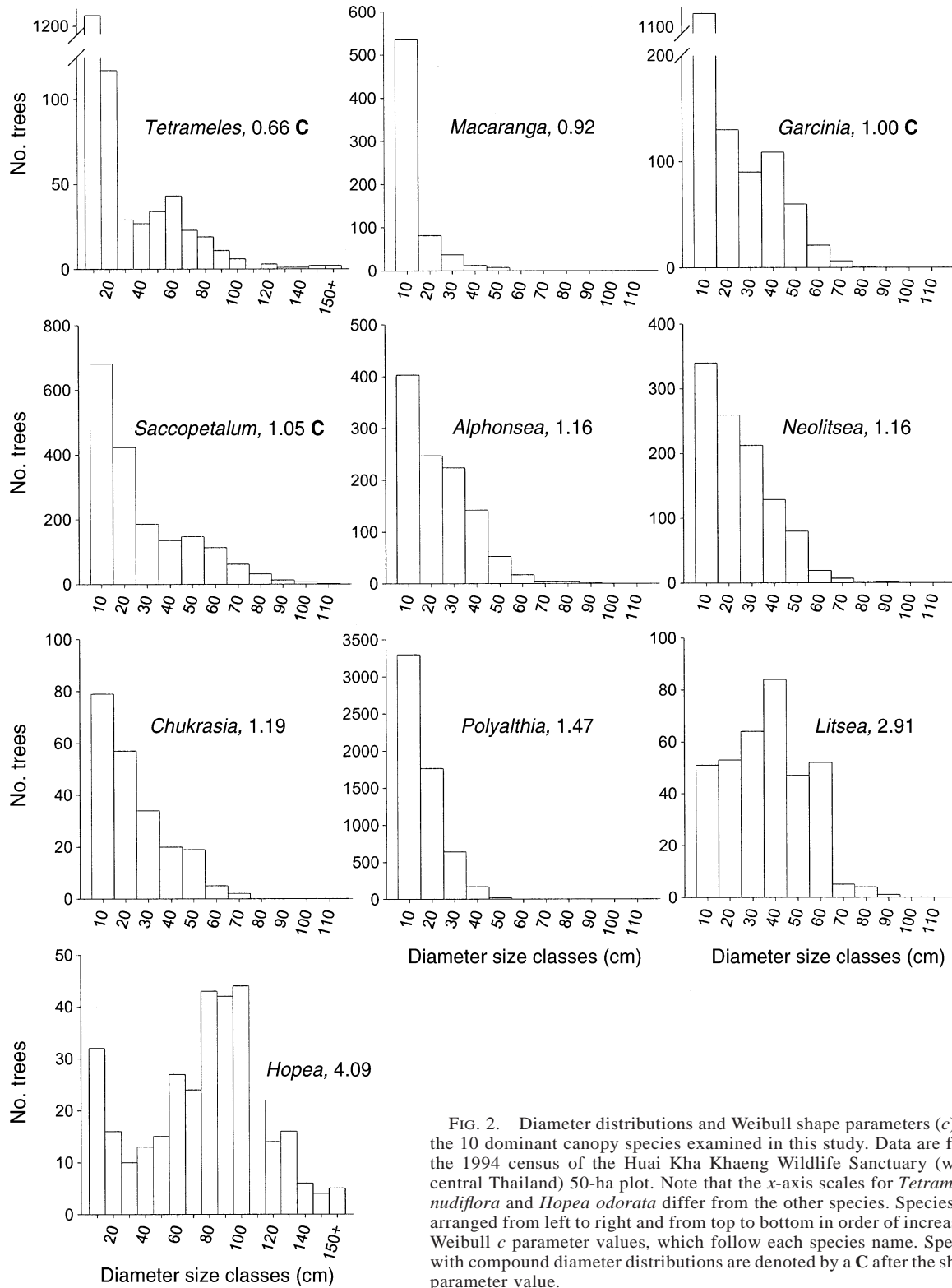
FIG. 2. Diameter distributions and Weibull shape parameters (*c*) for the 10 dominant canopy species examined in this study. Data are from the 1994 census of the Huai Kha Khaeng Wildlife Sanctuary (west-central Thailand) 50-ha plot. Note that the *x*-axis scales for *Tetrameles nudiflora* and *Hopea odorata* differ from the other species. Species are arranged from left to right and from top to bottom in order of increasing Weibull *c* parameter values, which follow each species name. Species with compound diameter distributions are denoted by a **C** after the shape parameter value.

TABLE 3. The number (and percentage) of individuals of each species in architectural categories based on the relative height of the tree within the forest canopy and the relative height of the inversion point (sensu Hallé et al. 1978) within the individual tree (Torquebiau 1986).

Species	Stand categories†				Total no. individuals	χ^2	P‡
	1H	1L	2H	2L			
Hopea	4 (2.8)	0	104 (73.3)	34	142	195.7	<0.0001
Saccopetalum	0	1 (0.8)	119 (90.8)	11 (8.4)	131	305.1	<0.0001
Polyalthia	0	0	52 (98.1)	1 (1.9)	53	151.2	<0.0001
Litsea	0	0	36 (80.0)	9 (20.0)	45	77.4	<0.0001
Neolitsea	3 (7.5)	1 (2.5)	29 (72.5)	7 (17.5)	40	50.0	<0.0001
Garcinia	1 (2.6)	3 (7.7)	25 (64.1)	10	39	36.4	<0.0001
Alphonsea	0	0	30 (83.3)	6 (16.7)	36	68.0	<0.0001
Chukrasia	0	0	11 (91.7)	1 (8.3)	12	28.7	<0.0001
Tetrameles	0	0	7 (100.0)	0	7	21.0	0.0001
Macaranga	1	0	2 (50.0)	1 (25.0)	4	2.0	0.57
Total	9 (1.8)	5 (1.0)	415 (81.5)	80	509	895.6	<0.0001

† Architectural categories are: 1H, tree height <50% of mean stand height and inversion point in upper half of the tree; 1L, tree height <50% of mean stand height and inversion point in lower half of the tree; 2H, tree height >50% of mean stand height and inversion point in upper half of the tree; 2L, tree height >50% of mean stand height and inversion point in lower half of the tree.

‡ P values refer to significance levels from comparisons among architectural categories within each species and all species combined using chi-square tests.

tion of trees among measurement categories (Table 4); 56.6% of the trees were classified as straight (Str), and 31.2% had straight lower stems and sinuous upper stems (USin). Relatively few trees had completely sinuous stems (Sin) or sinuous lower stems with straight upper stems (LSin). Most species followed this general pattern. The exceptions were *Litsea* and *Chukrasia*, which had relatively high proportions of trees with sinuous upper stems (77.8% and 75%, respectively). The three species from the Annonaceae (*Saccopetalum*, *Polyalthia*, and *Alphonsea*) had more straight stems than expected—most likely the consequence of the excurrent growth form characteristic of the Annonaceae (Hallé et al. 1978). Finally, only seven trees were classified as grossly deformed, of which six were *Garcinia*.

Architecture and growth of Hopea *saplings and poles.*—Close examination of the small *Hopea* illustrated the distinction between the regeneration and can-

opy populations in the 50-ha plot (Appendix D). Fifty-one *Hopea* <30 cm dbh were recorded in the original plot census (1994); these represent 15.6% of the total *Hopea* population in the plot. Forty-seven individuals were still alive in 1998 when the fieldwork was conducted. The majority of small *Hopea* were severely suppressed and showed no potential to become canopy trees. Of the 47 trees examined, 42 trees received no direct sunlight ($CI < 3$) and none had fully exposed crowns ($CI = 5$). Mean annual growth of suppressed trees was significantly less than that of non-suppressed trees (Table 5). Qualitative assessment of stem form showed that 44 of the 47 individuals had sinuous stems with either significant forks, crooks, lean, or general sinuosity (Table 5). Only three trees had relatively straight, defect-free boles. Crown assessment showed that 18 of the 47 individuals had flat-topped crowns, 11 trees had either broken terminal shoots or terminal

TABLE 4. The number (and percentage) of individuals of each species in architectural categories based on the sinuousity or lack thereof in the upper and lower half of each tree's bole.

Species	Architectural categories†						Total no. individuals	χ^2	P
	LSin	Sin	USin	Str	BT	Def			
Hopea	6 (4.2)	13 (9.2)	48 (33.8)	75 (52.8)	0	0	142	87.1	<0.0001
Saccopetalum	2 (1.5)	4 (3.0)	31 (23.7)	94 (71.8)	0	0	131	168.8	<0.0001
Polyalthia	2 (3.8)	5 (9.4)	9 (17.0)	37 (69.8)	0	0	53	58.6	<0.0001
Litsea	0	5 (11.1)	35 (77.8)	5 (11.1)	0	0	45	68.3	<0.0001
Neolitsea	0	6 (15.0)	11 (27.5)	21 (52.5)	2 (5.0)	0	40	24.9	<0.0001
Garcinia	0	0	10 (25.6)	23 (59.0)	0	6 (15.4)	39	43.2	<0.0001
Alphonsea	3 (8.3)	1 (2.8)	3 (8.3)	28 (77.8)	0	1 (2.8)	36	56.8	<0.0001
Chukrasia	1 (8.3)	2 (16.7)	9 (75.0)	0	0	0	12	16.7	0.0008
Tetrameles	0	0	2 (28.6)	5 (71.4)	0	0	7	9.6	0.023
Macaranga	0	2 (50.0)	1 (25.0)	0	1	0	4	3.7	0.29
Total	14 (2.8)	38 (7.4)	159 (31.2)	288 (56.6)	3 (0.6)	7 (1.4)	509	381.7	<0.0001

† Architectural categories are: LSin, sinuous lower half, straight upper half; Sin, upper and lower sections sinuous; USin, sinuous upper half, straight lower half; Str, neither half sinuous (i.e., straight bole); BT, broken top; Def, grossly deformed.

‡ P values refer to significance levels from comparisons among architectural categories (excluding BT and Def) within each species and all species combined using chi-square tests.

TABLE 5. Median diameter growth rates and sample size (N) for two two-class comparisons describing the architecture and future recruitment potential of *Hopea* trees <30 cm dbh in the 50-ha plot in seasonal dry evergreen forest at HKK in 1998.

Class	Growth rate (mm/yr)	N
Recruitment to canopy†		
Suppressed trees	0.9	42
Non-suppressed trees	4.9	5
Architecture‡		
Crown deformed	1.13	35
Crown not deformed	2.30	12

Note: Significance levels are based on comparisons using a Kruskal-Wallace ANOVA: for suppressed vs. non-suppressed trees, $P < 0.001$; for deformed vs. non-deformed crown, $P = 0.082$.

† Suppressed individuals had a crown-illumination index (CI) < 3; non-suppressed individuals had CI > 3.

‡ Trees were tallied as deformed if the central stem was severely forked, twisted, or broken.

shoot dieback, 3 trees were covered in vines, and 3 trees had candelabra forks (i.e., multiple terminal shoots). Only 12 of the 47 trees did not have significant crown deformities. Mean diameter growth of trees with crown deformities was lower but not significantly different than for trees without deformities (Table 8). Those small *Hopea* that did have well-exposed crowns had high growth rates and straight boles.

Age estimation

Stand-scale estimated age distributions.—Two distinct patterns were evident in the crown-class estimated age distributions of the dominant canopy-tree species from the SDEF (seasonal dry evergreen forest). The most shade-intolerant species (*Macaranga*, *Tetrameles*, and *Chukrasia*) had relatively young, unimodal age distributions with the mode <80 yr old (Fig. 3). Of these three species, only two individuals of *Chukrasia* were >100 yr old. Six species (*Alphonsea*, *Garcinia*, *Litsea*, *Neolitsea*, *Saccopetalum*, *Polyalthia*) had unimodal age distributions with peaks 100–180 yr BP (BP = before present [1998]) (Fig. 3). *Hopea* had a broader and older estimated age distribution than the other species. While the oldest estimated age for *Hopea* was 376 yr, few individuals were >310 yr old; the modal age class was 230 yr.

Age estimates from the periodic-annual-increment (PAI) regression method were generally similar in form, although greater in magnitude, to those obtained from the crown-class approach (Fig. 3). The estimated age distributions could be separated into the same species groups as those described for the crown-class approach. Among the shade-intolerant species, *Macaranga* had the same estimated age distribution for both the PAI regression and crown-class methods. In the case of *Chukrasia*, the form of the distribution changed

slightly, and the mode increased ~20 yr. *Tetrameles* exhibited the most pronounced difference, shifting from a unimodal distribution with a modal age class of 50 yr (crown-class method) to a bimodal distribution with peaks in the 70 and 150 yr age classes (PAI-regression method). *Litsea*, *Neolitsea*, *Saccopetalum*, and *Polyalthia* had unimodal age distributions, with the peaks between 150 and 210 yr, as did *Garcinia* and *Alphonsea* (Fig. 3).

While the PAI-regression age estimates for *Hopea* were unimodally distributed, they were unique among the study species in their great age. The modal age class was 340 yr and the maximum estimated age was 857 yr. However, the great ages for *Hopea* were due to the asymptotic form of the predicted growth-trajectory curve, which led to unrealistic exponential increases in age estimates among the largest trees.

When all of the study species were considered together, two distinct age cohorts emerged (Fig. 4). The shade-intolerant species formed a young age cohort that established in the latter half of the 20th century and the rest of the species formed a distinct unimodal age distribution with a peak in the mid-1800s. Mean and median ages for the older age cohort were 146 yr (SD = 73.3) and 136 yr for the crown-class method, 199 yr (SD = 115.7) and 172 yr for the PAI-regression method, and 156 yr (SD = 75.3) and 154 yr for the mixed method (Fig. 4). Strong peaks occurred 100–160 yr BP for the crown-class age estimates, 140–200 yr BP for the PAI-regression age estimates, and 120–180 yr BP for the mixed method. The crown-class age estimates also showed a vague secondary peak 230 yr BP composed mostly of *Hopea*. The estimated age distribution obtained by PAI-regression had a long tail with low frequencies in age classes >250 yr. All trees with estimated ages >320 yr were *Hopea*.

Assessing the accuracy of age estimates for Chukrasia *and* Neolitsea.—Estimated ages and tree-ring ages for individuals of *Chukrasia* and *Neolitsea* were relatively similar. As expected, the crown-class age-estimation method generated more accurate age estimates for the more intolerant *Chukrasia* (Fig. 5). The mean of the absolute errors (abs[estimated age − tree-ring age]) was 15 yr (SD = 13.65, N = 25 trees) for the crown-class method, compared to 35 yr (SD = 24.11) for the PAI-regression method. The crown-class method showed no bias towards over- or underestimation (mean of the raw errors = +1 yr), whereas the PAI regression had a strong tendency to overestimate the ages (mean of the raw errors = +33 yr).

Contrary to expectation the crown-class method also provided better age estimates for the shade-tolerant *Neolitsea* (Fig. 5). The mean of the absolute errors was 23 yr (SD = 20.82, N = 24 trees) for the crown-class method, compared to 53 yr (SD = 22.50) for the PAI-regression method. Because both methods overestimated nearly every tree age for *Neolitsea*, the means of the absolute and raw errors were almost identical.
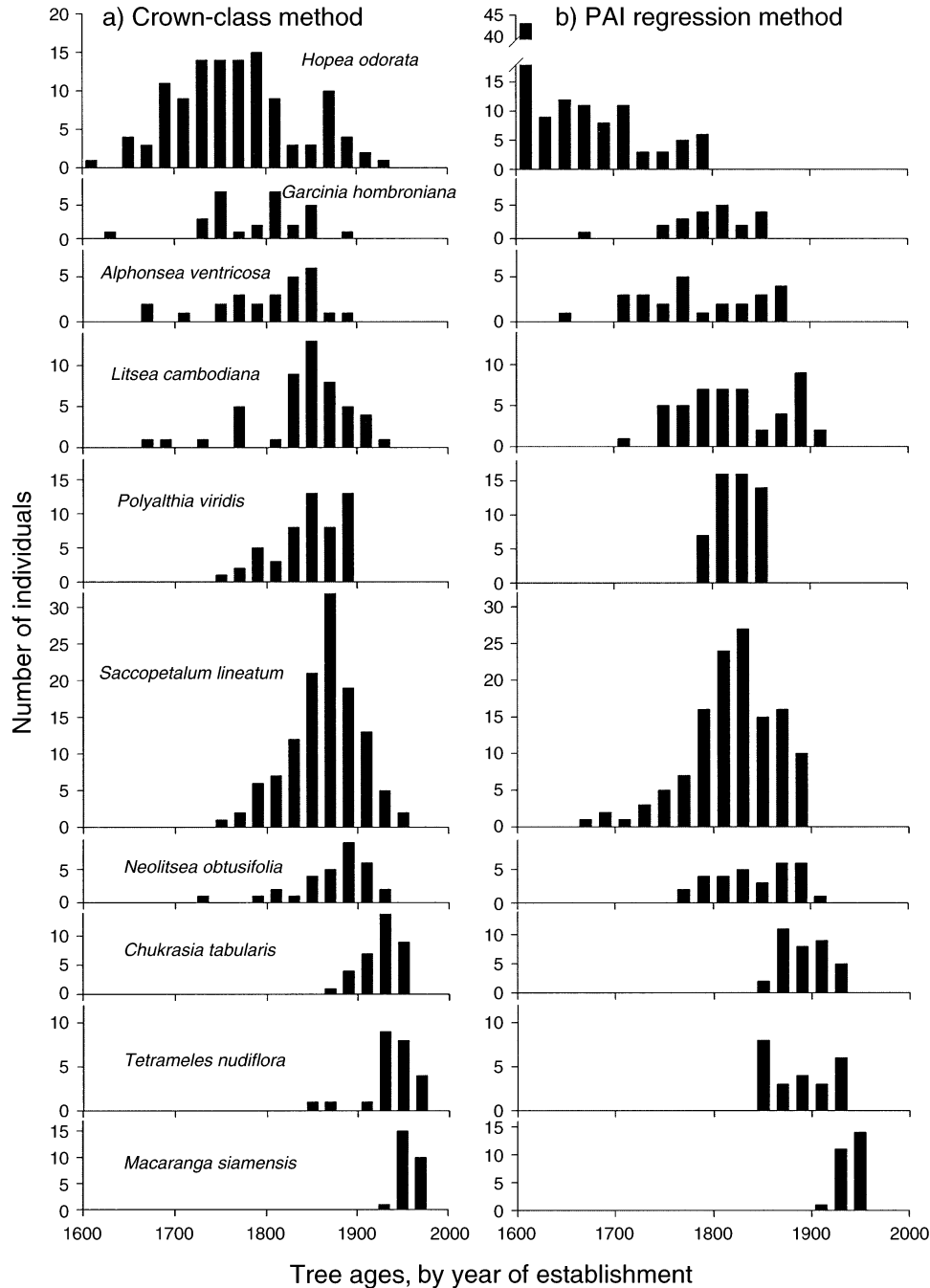
FIG. 3. Estimated age distributions for individuals >20 cm dbh for each of the 10 study species using (a) the crown-class and (b) the periodic annual increment (PAI) regression methods. See *Methods: Study design: age-estimation models* for descriptions of each age-estimation method.

For the crown-class method, the mean error was strongly influenced by five intermediate and suppressed trees for which the ages were overestimated by 50–65 yr. Recalculating the ages for those trees using the co-dominant crown-class growth rate (0.448 mm/yr) decreased the mean of the absolute errors to 13 yr.

Tree-ring analyses

Stand age structure (50-ha plot).—Forty-nine trees from six species were cored in the 50-ha plot. Most samples (86%) were obtained from the northern half of the plot. The age distribution was irregular, with two minor peaks of recruitment in the 1920s and the 1940s–

FIG. 4. Pooled estimated age distributions for individuals >20 cm dbh of 10 study species from the seasonal dry evergreen forest using the (a) crown-class method, (b) PAI-regression method, and (c) mixed method. See *Methods: Study design: age-estimation models* for descriptions of each age-estimation method. Open bars are estimated ages of the three highly shade-intolerant species (*Chukrasia*, *Macaranga*, and *Tetrameles*). Solid bars are estimated ages for all other study species.

less frequent and more irregular in temporal distribution. Peaks in major and extreme releases occurred in the mid-1800s, the 1940s, and 1970s. Growth releases in the 1920s and 1940s coincide with peaks in establishment dates, suggesting that disturbances of sufficient intensity to permit successful establishment of new recruits and to promote growth of surviving trees must have occurred at least twice in the past century. Four of the nine *Afzelia* had major growth releases between 1831 and 1845 and one had a moderate release in 1841. Several *Afzelia* had substantially higher growth rates (>2× the mean growth rate) during the period 1835–1875 (Fig. 8). Only two *Afzelia* showed no growth increases in the early 1800s.

Data on early growth rates for *Chukrasia*, *Melia*, *Neolitsea*, and *Toona* were consistent with expectations based on relative shade tolerance (Table 6). Among the shade-intolerant species, most *Toona* and all *Melia* established in non-suppressed conditions, while 50% of the *Chukrasia* had growth rates indicating suppressed conditions during establishment. Only shade-tolerant *Neolitsea* had a majority of individuals establish under suppressed conditions. There was no evidence among any of the species of increased frequency of high early growth rates during the two periods of peak establishment.

Stand age structure (16-ha plot).—Sixty-four trees of 11 species were cored in the 16-ha plot. Five species (*Chukrasia*, *Neolitsea*, *Vitex*, *Melia*, and *Toona*) accounted for >85% of the trees. The age distribution was roughly bimodal, with peaks in the 1910s and 1940s (Fig. 6). The oldest tree was a *Neolitsea* that established ca. 1888. *Vitex*, *Neolitsea*, and the less com-

1950s (Fig. 6). *Chukrasia*, *Melia*, and *Toona* recruited exclusively during the past 100 yr. Species varied in their relative rates of establishment on the 50-ha plot during the past century. *Neolitsea* dominated the age peak in the 1920s, whereas *Toona* and *Chukrasia* dominated the 1940s and 1950s. *Melia* was the only species that established after 1960. Of the three species (*Chukrasia*, *Neolitsea*, and *Toona*) that established throughout the past century, none established in every decade. With the exception of one *Neolitsea* that was 129 yr old and a *Mangifera* that was 154 yr old, only *Afzelia* established prior to 1890. The oldest *Afzelia* dated to 257 yr BP, but the cores did not reach the pith. None of the *Afzelia* were <135 yr old, although, based on estimates of distance to pith and mean growth rates of the oldest tree rings, at least two *Afzelia* appear to have established during 1810–1830.

At the 50-ha plot growth releases occurred in every decade between 1790 and 1980. Minor and moderate releases occurred throughout this period but varied in frequency among decades (Fig. 7). Peaks in moderate releases were evident in the early 1800s, the 1860s, 1920s, and 1960s. Major and extreme releases were
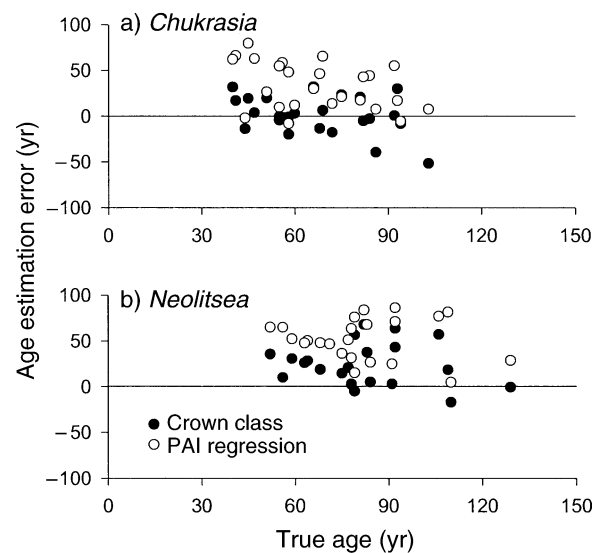

FIG. 5. Age-estimation errors for *Chukrasia* and *Neolitsea*. Ages were estimated using the crown-class and PAI-regression methods (see *Methods: Study design: age-estimation models* for details) and validated against ages derived from annual growth rings.
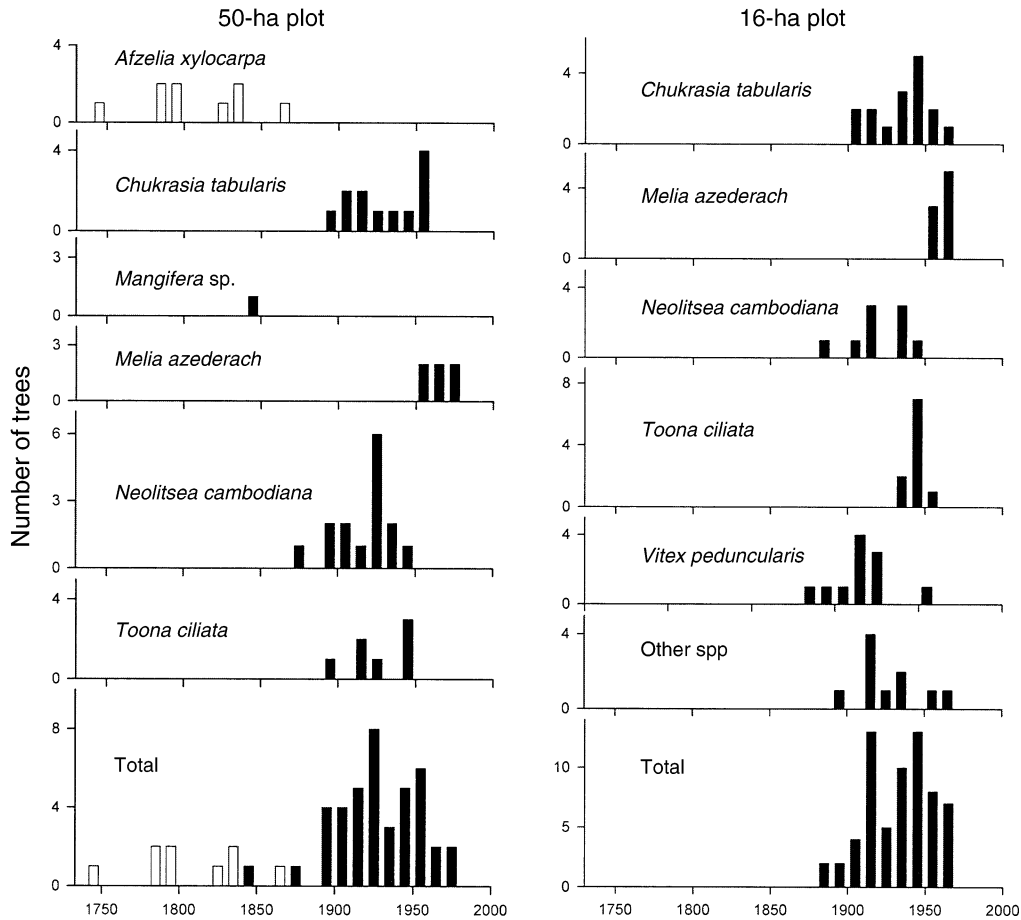
FIG. 6. Age distribution of trees from the 50-ha plot and 16-ha plot; all *y*-axes are number of trees. Open bars are minimum establishment dates for *Afzelia* with incomplete cores; the dates represent the year on or before which the tree must have established. The values on the abscissa represent the first year of each decade.

mon species *Acer, Cassia, Mangifera,* and *Ulmus* dominated the 1910 establishment peak. With the exception of *Cassia,* all of these species are relatively shade tolerant. In contrast, the peak in the 1940s consisted primarily of *Toona* and *Chukrasia,* both of which are relatively shade intolerant.

Establishment patterns varied among species. *Melia* and *Toona* had relatively brief periods of recruitment. Every individual of *Melia* established between 1950 and 1970 and 80% of the *Toona* established during a single 10-yr period (1939–1948). In contrast, *Chukrasia* and *Neolitsea* showed a pattern of relatively uniform establishment over an extended period. Individuals of *Chukrasia* established in every decade between 1900 and 1960, with no decade having more than 25% of the total number of sampled trees. Similarly, individuals of *Neolitsea* established in five of the eight decades between 1880 and 1960. *Vitex* was intermediate in its establishment pattern. While *Vitex* established in six of the eight decades between 1880 and 1960, there was an obvious peak in establishment in the 1910s and 1920s. The less common species (*Acer,*

Cassia, Gmelina, Mangifera, and *Michelia*) had too few individuals (1–2 trees per species) to assess their establishment patterns as individual species; however, as a group, most of their establishment occurred in the 1910s and 1920s (68%) and the 1950s and 1960s (25%).

At the 16-ha plot growth releases occurred in every decade beginning in the 1920s (Fig. 9). A large peak in growth releases occurred in the 1960s and 1970s. The total number of releases was greater in the 1970s ($N = 26$ trees), but there were more major and extreme releases in the 1960s ($N = 10$ trees). A smaller peak in growth releases occurred in the 1940s and comprised mostly minor releases. The peak in establishment of *Melia,* a highly shade-intolerant tree species, was synchronous with the peak in releases of the 1960s, implying the occurrence of a locally intense disturbance that created a high-light environment suitable for recruitment of the most shade-intolerant pioneer species. Interspecific differences in early growth patterns in the 16-ha plot were similar to those in the 50-ha plot (Table 6) for *Melia* and *Toona,* but differed for *Chukrasia* and
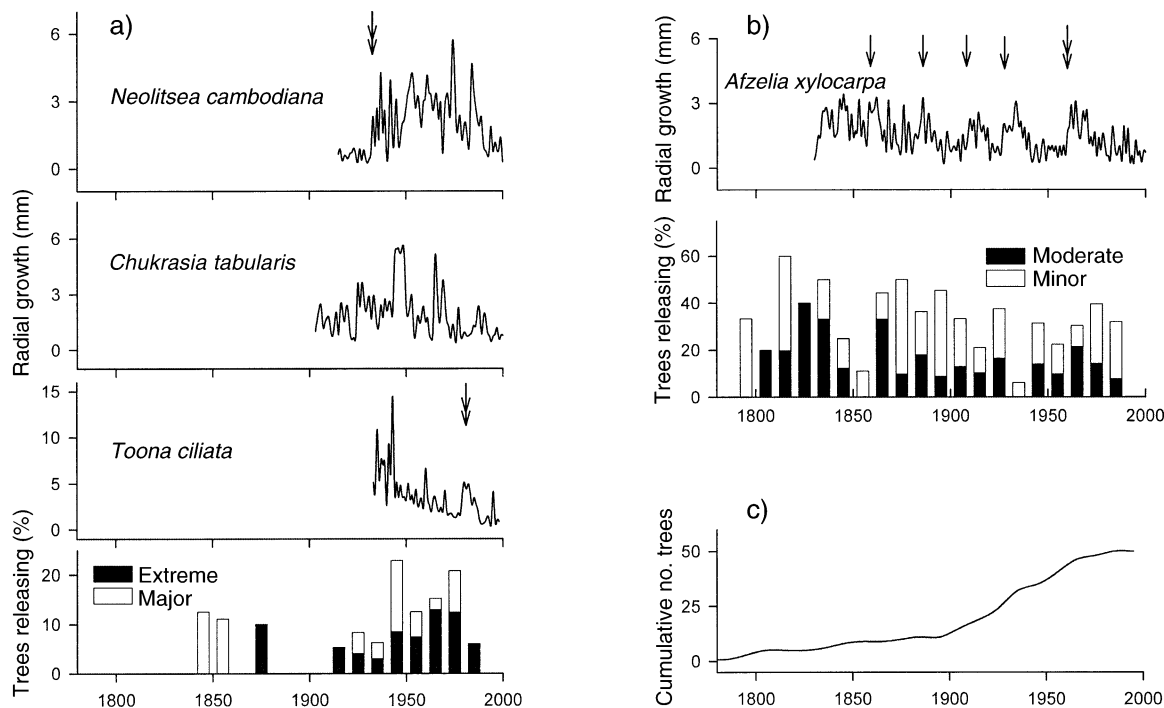
FIG. 7. Growth-release patterns and examples of growth releases from the 50-ha plot: (a) major and extreme releases; (b) minor and moderate releases; (c) sample size of tree cores over time. See Table 2 for definitions of the release types. For the individual ring-width series, major releases (>100% GC sustained over 10 yr) are indicated on the ring-width series with double arrows, and moderate releases (50–99% GC sustained over 10 yr) are indicated with single arrows. Growth releases are presented as the percentage of the trees releasing to account for temporal trends in the number of ring-width series available for analysis.

Neolitsea. A larger proportion of the *Chukrasia* in the 16-ha plot were growing under low-light conditions during establishment than in the 50-ha plot; conversely, the proportion of *Neolitsea* growing under low-light conditions was smaller in the 16-ha plot than in the 50-ha plot.

Stand age structure (young Hopea *stand).*—Fifteen trees were cored at the young *Hopea* stand, nine of which were *Afzelia*. Twelve of the 15 trees established between 1940 and 1952 (Fig. 10). Of the three older trees, two were relict *Afzelia* that established prior to the 1860s and the one was a *Cassia* that established in 1891. The age distribution indicates the occurrence of a severe disturbance in the late 1940s that destroyed most, but not all, of the canopy trees in the stand. No trees established after 1955, although this is in part a consequence of the minimum sampling size of the trees. Relatively few growth releases were found in the tree-ring series from the young *Hopea* stand—primarily because of the stand's young age (Fig. 10). Most of the observed growth releases occurred in the 1960s and 1970s. A single minor growth release occurred in one of the relict *Afzelia* during the 1870s. The three older *Afzelia* showed no evidence of release during the period of peak establishment in the 1940s. Early growth rates were variable. Early growth rates for *Afzelia* were not particularly high; mean annual radial increment for all

individuals establishing in the 1940s was 2.8 mm. However, mean annual radial increment of the young *Afzelia* averaged over the 50–60 yr of their lives was extremely high (>5 mm mean annual radial increment in 5 of 7 trees) for a heavy hardwood species such as *Afzelia*.

Stand age structure (Huai Gading stand).—Only six trees were sampled at the Huai Gading stand (five *Afzelia* and one *Chukrasia*). Because cores from two *Afzelia* and the *Chukrasia* were within 5 cm of the pith, it was possible to estimate their establishment dates. All three trees appear to have established between 1840 and 1880 (Fig. 11). The remaining trees all established prior to 1840. Growth releases occurred in 11 of the 15 decades between 1850 and 1990. Peaks in growth release occurred in the 1900s, 1930s, and 1960s (Fig. 11). Major or extreme releases occurred in each of these decades, as well as in the 1970s and 1980s. Early radial growth rates were >3.5 mm/yr in four of the five *Afzelia*. One *Afzelia* had early radial growth rates >10 mm/yr. The early growth rate of the sole *Chukrasia* was >3 mm/yr, implying that it was not suppressed during establishment. While the results from the Huai Gading stand do not provide a detailed description of the development patterns of the stand because of the small sample size, they are consistent with the results from the other sample sites and suggest that the disturbance patterns
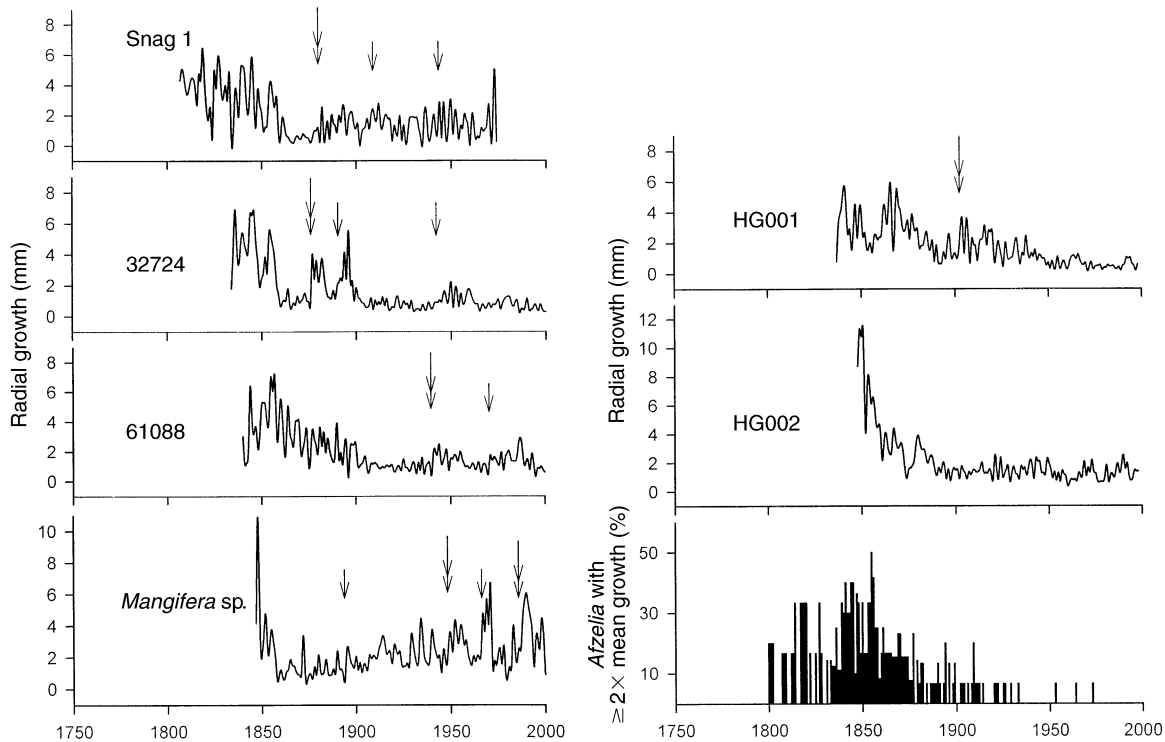
FIG. 8. Radial growth patterns for long-lived trees in the study plots showing evidence of increased growth rates during the mid-1800s. All ring-width series are from *Afzelia* with the exception of one *Mangifera* (63906) that established in 1848. The histogram shows the percentage of *Afzelia* in each year that had growth rates that were ≥2 times greater than the mean annual radial increment for the ring-width series. The format is as in Fig. 7.

evident in the tree-ring records were occurring across a broad spatial scale.

Age–size relationships.—Tree age and dbh were not significantly correlated when all trees were analyzed together. Among the five species with >10 individuals, only *Neolitsea* and *Toona* had significant relationships between age and dbh (Appendix E). However, the relationship between size and age was not particularly strong (as evidenced by low r^2 values) in either species.

TABLE 6. Relative number of trees establishing under high-light conditions in the 16-ha and 50-ha plots based on tree-ring analyses.

| Species† | 16-ha plot | | 50-ha plot | |
	N	High light (%)	N	High light (%)
Chukrasia	16	18.8	12	50.0
Melia	8	87.5	6	100.0
Neolitsea	9	55.6	15	26.7
Toona	10	60.0	7	85.7
Total	43	48.8	40	55.0

Notes: Trees were considered to be growing in high-light conditions based on the mean width of the innermost five tree rings and species-specific growth-rate thresholds obtained from demographic data from the 50-ha plot. See *Methods: Study design: tree-ring analyses* for details.

† *Toona* and *Melia* are shade-intolerant species, *Neolitsea* is shade tolerant, and *Chukrasia* is moderately shade intolerant.

In addition, the regression for *Toona* was heavily influenced by one outlying point, which, if excluded, led to a nonsignificant result. None of the other species, *Chukrasia*, *Melia* or *Vitex*, showed a correlation between age and dbh.

DISCUSSION

Disentangling the complex histories and dynamics of species-rich tropical forests presents a major challenge. The lack of annual growth rings in most tree species necessitates the development and validation of alternative methods of reconstructing historical stand dynamics. Reconstructing the disturbance history of the seasonal dry evergreen forest (SDEF) required multiple methodological approaches. While no approach provided a complete picture of the historical stand development patterns, together the different methodologies offered a relatively detailed history of the forest. Furthermore, by using different techniques we were able to qualitatively assess the consistency of the results. Data from tree rings, indirect age estimates, and measures of stand structure demonstrate that over the past 250 years stand-development patterns in the species-rich SDEF have been influenced by disturbances across a range of spatial and temporal scales. While non-catastrophic disturbances have contributed to the present heterogeneity of the forest, the SDEF retains a
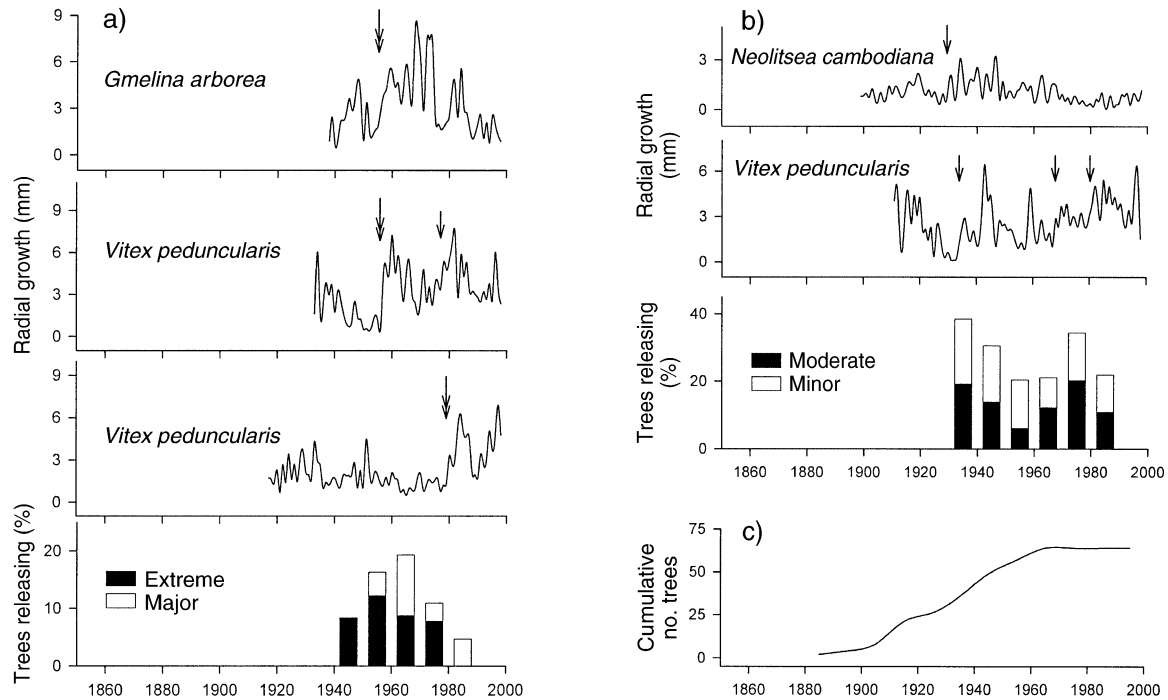
FIG. 9. Growth-release patterns and examples of releases from the 16-ha plot: (a) major and extreme releases; (b) minor and moderate releases; (c) sample size of tree cores over time. See Table 2 for definitions of the release types and Fig. 7 for individual tree-ring series format.

distinct structural and floristic legacy from a catastrophic disturbance that occurred nearly two centuries ago, initiating a single-age cohort stand that over time has developed a complex three-dimensional structure created by differences in interspecific growth patterns and subsequent disturbances of moderate and low intensity.

Here we synthesize our results and consider the influence of disturbances at different spatial and temporal scales on the historical stand development patterns of the SDEF at Huai Kha Khaeng Wildlife Sanctuary (HKK) in west-central Thailand (Fig. 12). We then discuss several caveats regarding our methodological approaches and their impact on the historical reconstruction. Finally, we consider the implications of these results for understanding tropical forest dynamics.

Disturbances and forest dynamics of the SDEF

Intense, large-scale disturbance.—Previous analysis of floristic and structural data from the 50-ha plot has suggested the occurrence of a catastrophic disturbance in the past (Bunyavejchewin et al. 2001, 2002). For example, the 50-ha plot contains several long-lived secondary forest species, such as *Ailanthus triphysa*, *Toona ciliata*, *Anthocephalis cadamba*, and *Ficus* spp., with small populations dominated by extremely large (>60 cm dbh) canopy trees and having little or no regeneration (Bunyavejchewin et al. 2001). All of these species require high-light conditions to establish, implying that sometime in the past there was a brief op-

portunity for recruitment created by one or more intense disturbances. However, the floristic and structural data from the 50-ha plot do not provide insight into the timing or spatial extent of such disturbances or sufficient resolution to recreate the history of other, less intense, disturbances that may have occurred. In the present study we used several other methodological approaches to address these issues. The results were remarkably consistent. All of the methodological approaches that we used to reconstruct the historical stand-development patterns in the SDEF suggested the occurrence of a catastrophic disturbance that impacted all of our study sites, i.e., several hundreds of hectares, and initiated a single-age cohort of trees that now, nearly two centuries later, continues to dominate the structure and composition of the forest canopy.

The legacy of this disturbance is evident in the structure of the forest and the architecture of the trees. First, size distributions for the common canopy species are all irregular, unimodal or compound, suggesting that recruitment, growth, and mortality have not been continuous through time. The most notable example was *Hopea odorata*, a long-lived, shade-intolerant dipterocarp (Smitinand et al. 1980) that is the dominant structural feature of a large contiguous block (~250 ha) of SDEF in the study area. In the 50-ha plot the dbh distribution of *Hopea* was approximately normal, which for shade-intolerant tree species is characteristic of a single age cohort (Lorimer and Krug 1983). Debski et al. (2000) described a similar pattern in subtropical rain
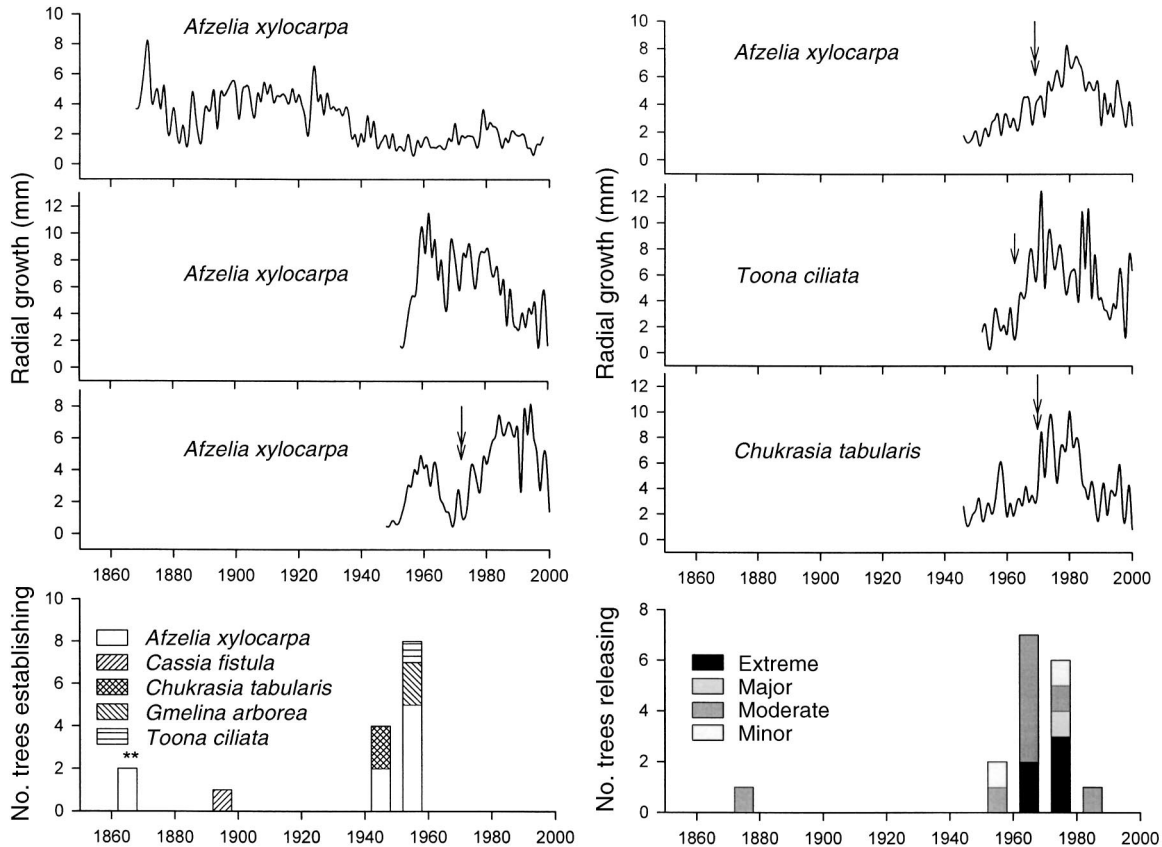
FIG. 10. Establishment and release patterns at the young *Hopea* stand with examples of ring-width series from selected individuals. The lower left panel shows establishment patterns at the young *Hopea* stand. Ages of the two oldest *Afzelia* (denoted by **) are minimum ages from incomplete cores. The lower right panel shows growth-release patterns from the stand. The upper six panels are examples of tree-ring series from the young *Hopea* stand. See Fig. 7 for individual tree-ring series format.

forest in southeast Queensland, Australia, where *Sloanea woollsii* dominated stand basal area and had a normal diameter distribution with a mean diameter of ~70 cm dbh. They concluded that the study site had been subject to a rare, intense disturbance—most likely a cyclone—a century or more earlier, which had set the developmental pathway of the stand (Debski et al. 2000).

Second, despite the diverse taxa examined and their range of life histories and growth habits, the dominant canopy tree species in the SDEF were remarkably uniform in their general architecture. Most individuals had straight, unbranched lower stems and straight or sinuous upper stems. The implication is that many trees in the SDEF established and grew under similar environmental conditions, namely high light and crowding by neighbors of similar height. Stem sinuosity reflects the influence of several factors, including repeated suppression, terminal leader mortality, and genetic factors (Hallé et al. 1978, Spicer et al. 2000, Clark and Clark 2001). Trees stems that have both straight and sinuous lengths imply a change in growing conditions (Meadows et al. 1984). Trees that have never

experienced severe suppression, overtopping, or physical damage, or that have a strongly excurrent growth form resistant to such effects, tend to develop straight stems. The large *Hopea* that dominate the canopy provide good examples of the former, while *Saccopetalum*, *Polyalthia*, and *Alphonsea*, all members of the Annonaceae, are examples of the latter. In contrast, trees with straight lower stems and sinuous upper stems suggest a period of free growth followed by suppression or physical damage to the terminal leader (Trimble 1968, Kohyama 1980, Meadows et al. 1984, Clark and Clark 2001). Such conditions occur in single- or multi-cohort, mixed-species stands where interspecific differences in height growth rate and maximum height lead to stratification within the stand (Oliver 1978). Similar patterns may also emerge in trees establishing in small canopy gaps where initial high-light conditions and stem densities within the gap lead to straight stems during early development, but subsequent gap closure through branch extension (Trimble and Tryon 1966) precipitates an architectural shift from orthotropic to plagiotropic leaf display (Hallé et al. 1978). Given that most of the study species (excluding the three most
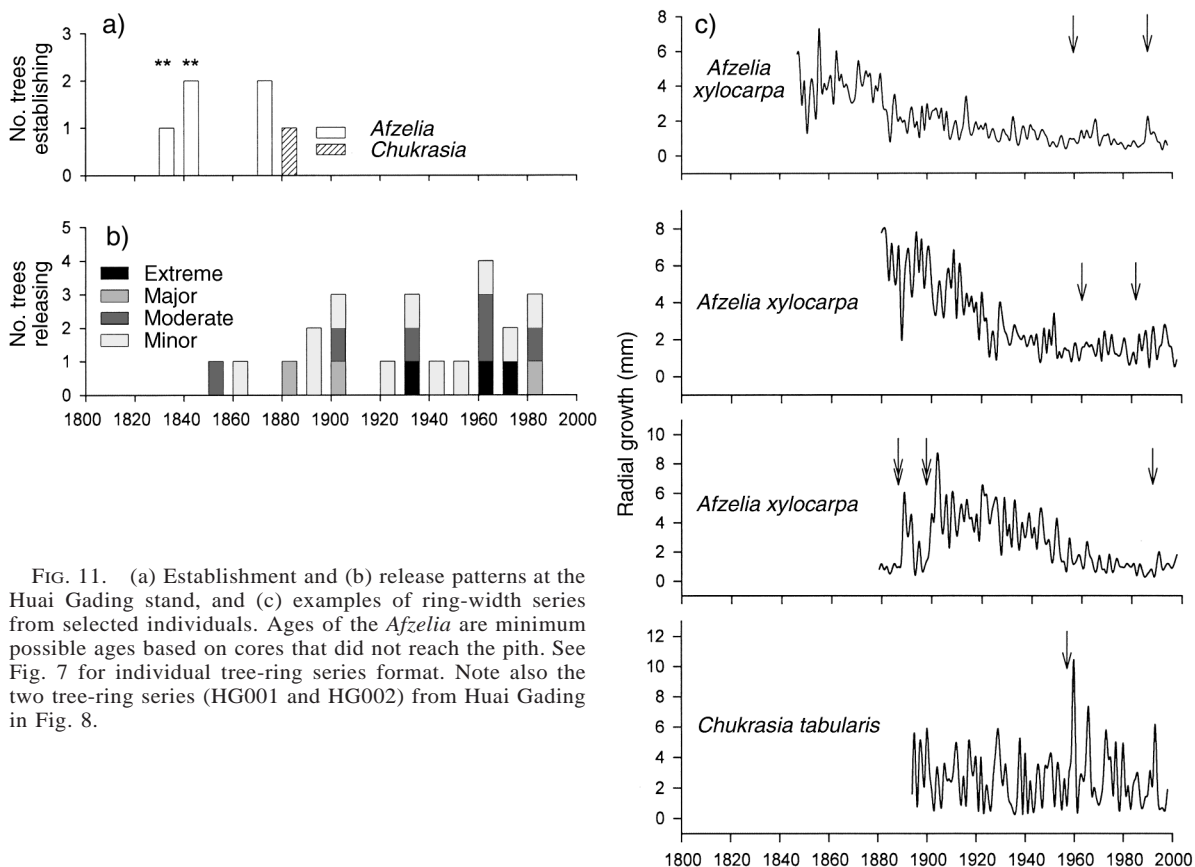
FIG. 11. (a) Establishment and (b) release patterns at the Huai Gading stand, and (c) examples of ring-width series from selected individuals. Ages of the *Afzelia* are minimum possible ages based on cores that did not reach the pith. See Fig. 7 for individual tree-ring series format. Note also the two tree-ring series (HG001 and HG002) from Huai Gading in Fig. 8.

shade-intolerant species) had irregular diameter distributions with obvious peaks in the larger size classes (e.g., *Hopea*, *Litsea*, *Garcinia*, *Saccopetalum*) and distinct peaks in their estimated age distributions, the gap-development explanation would require the near-synchronous establishment of many gaps in the study area—that is, a major catastrophic event—as the principal engine of stand reestablishment. However, less intense disturbances that have occurred since the catastrophic disturbance of the mid-1800s have provided subsequent gap-establishment opportunities and contributed to the wide range of diameters found in most species.

Third, data on the architecture and growth of *Hopea* regeneration clearly show that *Hopea* cannot successfully establish in the environmental conditions created by the current forest structure. Few studies have examined the crown form of saplings and poles in temperate or tropical forests. Trimble (1968) demonstrated that the terminal leaders of saplings of *Acer saccharum* in uneven-aged forests in the eastern United States lose epinastic control under low-light conditions and become "flat-topped"; upon exposure to high-light conditions following thinning, a lateral leader asserted dominance leading to the formation of a crook in the stem, and repeated partial harvests led to the devel-

opment of multiple crooks. Clark and Clark (1991, 2001) have shown that many of the understory trees in a Costa Rican rain forest suffer broken or deformed terminal shoots as a consequence of dieback, falling debris, and insect attacks. In the SDEF the straight boles and lack of crooks and other deformities among most canopy *Hopea* and the ubiquity of flat-topped, damaged, or multiple-leadered individuals among *Hopea* saplings implies that the older trees established under very different environmental conditions than those that currently occur. This, in combination with the fact that *Hopea* seeds have no dormancy, are susceptible to drought-induced mortality (Baker 1997), cannot successfully establish on thick leaf litter, and have high mortality and poor growth in low light (Raja Barizan 1996), strongly suggests that *Hopea* cannot establish under the canopy of other trees. Indeed, the only site in which vigorous regenerating *Hopea* occur is the young *Hopea* stand, which initiated after an intense disturbance destroyed ~3 ha of mature forest. Forty years after that disturbance the relative vertical structure of the young and mature forests is nearly identical: straight-boled, large-crowned *Hopea* overtop a predictable assemblage of shade-tolerant canopy species such as *Saccopetalum* and *Garcinia*, which overtop extremely shade-tolerant understory species such as
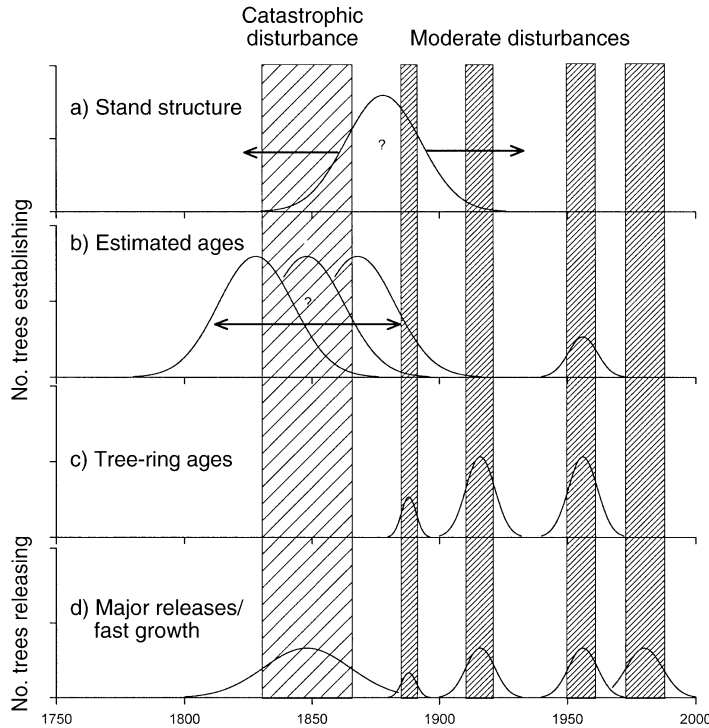
Fig. 12. Schematic summary of the disturbance history of the seasonal dry evergreen forest at HKK based on the methodologies used in this study. (a) The stand structure data suggested a single age cohort of canopy trees, but did not indicate the timing of the initiating disturbance (as indicated by the question mark and arrows). (b) Estimated age distributions indicated that a single age cohort of the dominant canopy species established in the 1800s, although each age-estimation technique provided a slightly different peak during that period. Indirect age estimates also showed a peak in the most shade-intolerant species in the mid-1900s. Tree-ring data indicated peaks in (c) recruitment and (d) growth in the 1910–1920s and 1940–1950s, as well as a minor episode of recruitment and release in the late 1800s and increased growth releases in the 1970s. Among the long-lived *Afzelia*, exceptionally high growth rates occurred in the mid-1800s. Together these different lines of evidence point to a catastrophic, stand-replacing disturbance occurring in the mid-1800s, followed by a series of moderate-intensity disturbances during the 20th century.

Baccaurea, *Dimocarpus*, and *Phoebe*. Pioneer species have disappeared. The only difference, as illustrated in the profile diagrams, is the total height of the forest.

While structural and architectural data can be used to infer the *relative* age of trees in a community (e.g., whether a given tree is older, younger, or approximately the same age as a neighboring tree), they offer no guidance to the *absolute* age of the trees. Age estimates from stem diameter, we found from verification with tree-ring data in two species, provide a reasonable estimate of tree age. In the SDEF, estimated age distributions indicated that most individuals of the seven tolerant and mid-tolerant canopy species had established 100–250 yr before present, with most individuals having established during a short period in the mid-1800s. Thus, small canopy trees of shade-tolerant species and large canopy trees of shade-intolerant species may be the same age, but historical differences in growth rates and light availability within the forest have led to differences in stem size (Oliver 1980, Palik and Pregitzer 1991). The estimated age distribution of *Hopea* suggests that most canopy individuals established 200–250 yr ago, ~100 yr before most of the other canopy tree species. However, because the current diameter growth rates of *Hopea* may be significantly lower than historical growth rates because of the large size of the trees, their ages may be overestimated. Adjusting the *Hopea* growth rates to be more consistent with those at the young *Hopea* stand would make the estimated age distribution of the *Hopea* almost identical to the other canopy species (P. J. Baker, *unpub-*

lished data). Alternatively, *Hopea* may have established following an earlier catastrophic disturbance (as suggested by the distribution of estimated ages), while many of the other main canopy species established following a subsequent disturbance event in the mid-1800s. However, this scenario would require that the second disturbance was intense enough to provide regeneration opportunities for all of the other canopy species several of which are relatively shade intolerant, but without killing any of the *Hopea* and *Afzelia*. We believe that this is a less parsimonious explanation than the occurrence of a single intense disturbance, particularly given the evidence from the young *Hopea* stand where *Hopea*, *Afzelia*, and most of the other main canopy species clearly established synchronously after an intense disturbance in ~1950.

Tree-ring series provide the most accurate means of dating past disturbances. In many cases analysis of tree-ring series can identify the precise year in which a disturbance occurred (e.g., Oliver and Stephens 1977, Clark 1990, Swetnam and Lynch 1993). For the SDEF data, however, most of the amenable study species did not reach great age, limiting dendroecological insights into the catastrophic disturbance. Only *Afzelia* had individuals >160 yr old; however, of those, ~50% of those at the 50-ha plot and Huai Gading showed substantially higher growth (>2× the mean growth rate) from 1835 to 1875. Few *Afzelia* showed such high growth rates before or after this period. In addition, a *Mangifera* and several small *Afzelia* (65–75 cm dbh) appear to have established with high growth rates dur-

ing the early to mid-1800s. These results are consistent with the indirectly estimated age distributions of the dominant canopy species and further support the hypothesis that an intense disturbance destroyed a large swath of forest during this period.

An obvious question is what type of disturbance could have had such a profound impact on the structure and dynamics of the SDEF? Despite limited documentation of large-scale disturbances in the forests of Southeast Asia, the most likely answer is wind. Destructive windstorms generated by convective downdrafts or cyclones have severely impacted large areas of tropical forests elsewhere (e.g., Boucher 1990, Nelson et al. 1994). Thailand is in the cyclone belt of Southeast Asia. During the past century major cyclones have impacted neighboring Myanmar repeatedly (14 of the 25 worst natural disasters in Myanmar from 1901 to 2000 were windstorms associated with cyclones [ADRC 2003]). Destructive cyclones hit Thailand in 1952 and 1962 (ADRC 2003). In addition, intense local windstorms are known to occur in the region. In 1928 and 1931, tornadoes or line squalls flattened strips of forest several square kilometers in extent in an area of Myanmar ~60 km east of HKK (Anonymous 1929, 1932). Within HKK an area of ~30 ha was knocked over by windstorms in 1987 (T. Prayurisiddhi, *personal communication*).

Catastrophic drought is another potential disturbance agent. Recent observations in tropical forests suggest that severe droughts may have substantial impacts on tree mortality, particularly among canopy species (Condit et al. 1995, Potts 2003). In Thailand several severe droughts have occurred in recent decades (ADRC 2003); however, there are few long-term rainfall records for continental Thailand. Tree-ring proxy records for rainfall are limited to a 110-yr teak chronology from Northern Thailand (~300 km from HKK; Pumijumnong et al. 1995) and several ~160 yr chronologies for *Pinus khesiya* and *P. merkusii* from east-central and northern Thailand (230–400 km from HKK; Buckley et al. 1995). The teak chronology is too short to provide insights into potential climate anomalies in the mid-1800s and the *Pinus* chronologies, which date to the 1840s, suggest that growing conditions were slightly above average between 1840 and 1860, with no evidence of particularly severe years or long-term drying trends. There is the possibility that above-average rainfall in the 1840s could have favored establishment of evergreen forest species over deciduous forest species following a major disturbance. However, the areas in which the tree-ring chronologies were developed are hundreds of kilometers from HKK and experience significantly different climatic regimes and, therefore, may not provide a good representation of past climate at HKK. Despite the lack of good historical climate data, catastrophic drought seems unlikely to account for the mid-1800s stand-replacing disturbance at the SDEF, primarily because the seasonal evergreen forest that initiated at that time occurs in a discrete patch of ~250 ha. There are no obvious topographic or edaphic factors that would make this patch of forest more susceptible than adjacent sites to a catastrophic drought (Baker 1997).

Fire has been part of the forest ecosystems of continental Southeast Asia for at least 10 000 yr (Stott 1988). Fires have burned through the 50-ha plot three times in the past decade; however, the recent fires were very low intensity and typically had flame lengths <10 cm (P. J. Baker, *personal observation*). Recent fire frequency may be somewhat higher than in the past due to recent establishment of a permanent agrarian population on the forest fringe. In the past, less frequent fires may have permitted a build-up of litter and dense ladder fuels (e.g., tall grasses, shrubs, treelets) leading to rarer, but more intense, fires. Nonetheless, in the event of a catastrophic, stand-replacing fire, a layer of residual charcoal in the soil would be expected. Such charcoal layers have been found in tropical forests in Central and South America (Saldarriaga and West 1986, Horn and Sanford 1992) and central Africa (Hart et al. 1996). No such evidence has been found in either soil pits or extensive soil core sampling in the vicinity of the 50-ha plot and neighboring areas (P. J. Baker, *personal observation*). Thus, it seems unlikely that a catastrophic fire would have led to the initiation of the present cohort of canopy trees.

Humans are also potential disturbance agents in these forests. People have lived in continental Southeast Asia for thousands of years and have had a profound impact on the forests (Wyatt 1984). However, the lack of anthropological or archaeological evidence from the study area makes it difficult to assess the potential for intense, large-scale human-induced disturbances in recent centuries. Historical mass movements of clashing Thai and Burmese armies in the region during the late 1500s and the 1760s and 1780s have been well documented (Wyatt 1984). The armies are known to have cleared areas of forest for timber and temporary rice cultivation; however, the main routes of the warring armies were to the south (Three Pagodas Pass, Kanchanaburi Province) and north (Mae Sot, Tak Province) of HKK (Wyatt 1984).

Non-catastrophic disturbance at varying scales.— Disturbances of moderate intensity in the period following the stand-initiating catastrophic disturbance of the mid-1800s were evident in the stand-structure data, estimated age distributions, and tree-ring records from the SDEF. Such disturbances have not occurred uniformly in space or time in the SDEF over the past two centuries. Instead, temporally discrete but spatially widespread disturbances have generated pulses of gap formation across the study area. Tree-ring data provided evidence of establishment and growth release in the late 1870s in all four study sites. The oldest individuals of *Chukrasia*, *Michelia*, *Neolitsea*, *Toona*, and *Vitex* all established within 15 years. In the 1910–1920s, one or

more disturbances led to the diffuse establishment of individuals in both the 16-ha and 50-ha plots, but not in the young *Hopea* or Huai Gading plots. Recruitment of *Neolitsea*, *Vitex*, and *Chukrasia* during that period suggests that the disturbance(s) created small- to moderate-sized gaps in the forest canopy, albeit over an area of several square kilometers. In the late 1940s or early 1950s another extensive disturbance of variable intensity occurred in the SDEF. Increased establishment of the gap species *Toona* and *Chukrasia* in the 16-ha and 50-ha plots suggests that the disturbance was of intermediate intensity and affected the canopy principally through the creation of moderate- to large-sized gaps. However, the synchronous establishment of an even-aged cohort of *Afzelia*, *Hopea*, and other common SDEF tree species in a contiguous area of ~3 ha at the young *Hopea* stand suggests that the disturbance was more intense in some places than others. Finally, a major peak in growth releases occurred in the late 1960s and early 1970s across all of the plots, implying another widespread disturbance of moderate intensity. Establishment during this period was dominated by the fast-growing, shade-intolerant *Melia*; however, the lack of other tree species establishing at that time may be a consequence of our minimum sampling diameter. Indirect age estimates for the shade-intolerant species, *Chukrasia*, *Macaranga*, and *Tetrameles*, were consistent with the dendroecological evidence, showing a sharp recruitment peak for individuals scattered throughout the 16- and 50-ha plots during the period 1950–1970.

Windstorms, fire, and drought are the most likely types of disturbance to have created these patterns. Studies in temperate and tropical forests have documented similar patterns of widespread non-catastrophic disturbance created by windstorms (Runkle 1982, Proctor et al. 2001). The timing of the 1952 and 1962 cyclones that struck Thailand is consistent with the initiation of the young *Hopea* stand in the early 1950s and the high frequency of growth releases in the mid-1960s. In 1998 fires burned across much of the HKK landscape (Giri and Shrestha 2000). Most of the fire-induced mortality was in the smallest size classes, but occasionally a large tree with a basal wound from a previous fire or piles of sloughed bark around its base would be killed and toppled, creating a moderate- to large-sized gap in the canopy (P. J. Baker, *unpublished data*). Such fires could generate the broad-scale non-catastrophic disturbances of moderate intensity that appear to have occurred in the SDEF repeatedly during the past century. Climate anomalies, such as severe droughts, may also have led to the observed pattern of discrete periods of widespread but diffuse mortality among the study sites. The teak tree-ring chronology indicates periods of reduced wet-season rainfall in the 1920s and 1960s (Pumijumnong et al. 1995), consistent with periods of disturbance at the 50-ha and 16-ha plot. In contrast, years of increased rainfall may also influ-

ence forest dynamics. Following the intense disturbance in the early 1950s at the young *Hopea* stand, there were a series of extremely wet years (Nakhon Sawan Meteorological Station, *unpublished rainfall data* for 1950–1996), which may have contributed to the successful establishment of SDEF species at the site.

Background mortality.—In addition to the stand-initiating catastrophic disturbance and subsequent widespread disturbances of variable intensity, background mortality in the SDEF has generated low-intensity disturbances in the form of treefall gaps throughout the past two centuries. Senescence, competition, and insect or pathogen attacks may lead to the occasional death of individual trees or small groups of trees that create gaps in the forest canopy. Mortality and subsequent canopy gap formation are endogenous to the forest and the developmental stage of the stand and are distinct from disturbances caused by exogenous factors such as wind, drought, or fire (Lugo and Scatena 1996). Demographic data from the HKK 50-ha plot demonstrated this pattern of small-scale mortality and the presence of canopy gaps throughout the forest. For example, the negative exponential or compound diameter distributions and highly aggregated spatial patterns of extreme heliophiles, such as *Macaranga* and *Tetrameles*, attest to perennial formation of canopy gaps within the SDEF (Bunyavejchewin et al. 2002). In addition, the tree-ring data show relatively consistent low levels of growth release over the past century across the study area. In any given decade, ~5% (range: 1–9%) of the sampled trees showed evidence of a major growth release indicative of gap formation. Assuming that growth releases determined from tree rings represent a reasonable measure of gap formation across the study area, then these results are consistent with other studies that have evaluated gap-formation rates in temperate and tropical forests. For instance, in temperate old-growth forests, decadal gap-formation rates have been estimated to range from ~5 to 7% (Runkle 1982, Lorimer and Frelich 1989, Zeigler 2002) for various forest types. In tropical forests, studies have documented somewhat higher gap-formation rates, ranging from ~7 to 12% per decade (Lang and Knight 1983, Brokaw 1985, Lugo and Scatena 1996), but still within the observed range of values for HKK during the past century.

Assessing the methods: some caveats

Given the inherent limitations of tree-ring studies in tropical forests, several important caveats to the present study are necessary. First, relatively few of the species that occur in the SDEF have annual rings. We sampled 51 relatively common canopy species out of a total of 250 species in the 50-ha plot. Of these, 18 species (36%) had annual growth rings (Baker 2001). However, 90% of the ring-width series used in the present study came from six species with particularly high-quality

annual rings. While these species span the entire range of life-history traits among canopy trees at HKK—from extremely shade intolerant (*Melia*) to shade tolerant (*Neolitsea*)—as well as a wide range of abundance, most species with annual growth rings were relatively shade intolerant. Consequently, our tree-ring data should be particularly informative about gap dynamics over the past several decades or century, but less clear about dynamics from previous centuries (since most individuals of the shade-intolerant species were not particularly old).

Second, the purpose of the study was to reconstruct the historical dynamics of the forest canopy. As such, sampling was generally limited to trees >20 cm dbh. A considerable fraction of the tree flora in the SDEF is restricted to the understory or midstory of the forest, rarely exceeding the minimum sampling diameter for this study. These species contribute to the structural and floristic diversity of the SDEF and typically have markedly different growth and reproductive patterns than the canopy species. None that we have sampled possess annual growth rings and because all are suppressed and subject to highly variable temporal patterns of illumination, age estimates are unreliable. Consequently, we have no data on the timing of recruitment or growth of small-statured species relative to the canopy species.

Finally, missing and false rings in the tree-ring series introduce errors in the dating process. While every effort was made to minimize such errors through visual and statistical crossdating, it is unreasonable to imagine that in tree species with such complex wood anatomy occasional errors in identifying false or missing rings would not occur. However, the synchronous occurrence among several species of peaks in establishment and growth releases, both spatially and temporally, suggested that the tree-ring series were relatively accurate. An alternative possibility is that dating errors were consistently biased, not random; however, given the number of species, the range of life-history traits, and the large sample sizes of establishment and release dates, such consistently biased errors seem unlikely.

Despite multiple sources of data on historical details of stand dynamics in the SDEF, some important questions remain unresolved. For example, What type of forest dominated the study area prior to the intense disturbance of the early 1800s? Was it SDEF, or something more akin to the mixed deciduous forest that is widespread across the landscape at HKK? Bunyavejchewin et al. (2004) suggested that the presence of scattered individuals of deciduous forest species, such as *Shorea siamensis*, *Terminalia bellerica*, *Dipterocarpus obtusifolius*, *Pterocarpus macrocarpus*, and *Afzelia*, that have large, low branches typical of relict trees, may be indicative of a forest prior to the catastrophic disturbance in which deciduous forest species were more common. However, the presence of evergreen forest species, such as *Duabanga grandiflora* and *Gar-*

cinia hombroniana, with similar architecture suggests that evergreen forest species were also present prior to the stand-replacing disturbance; and the limited seed-dispersal distances of most species implies the presence of a local seed source or survival of advance regeneration from a forest in which SDEF species were widespread. In the absence of more detailed data, however, descriptions of the earlier history of the forest remain speculative.

Implications of reconstructing historical stand dynamics of tropical forests

Over the past several decades evidence of catastrophic disturbances in tropical forests has accumulated through direct observation and anecdotal information (Whitmore and Burslem 1998). The current paradigm of tropical forest dynamics, which stresses the importance of small-scale disturbances and gap dynamics, requires revision to account for the influence of larger, more intense disturbances (e.g., Oliver and Larson 1996). However, because catastrophic disturbances are infrequent and often occur in remote areas, long-term observations of tropical forest dynamics following such disturbances are exceedingly rare. As a consequence, few examples exist from which to generalize a conceptual model of tropical forest dynamics inclusive of catastrophic disturbance. While the present study provides only one example of the effects of catastrophic disturbance on subsequent stand-development patterns, it is consistent with observed patterns in temperate forests (e.g., Oliver 1981, Franklin et al. 2002) and recently disturbed tropical forests (e.g., Vandermeer et al. 2001). Our study is also consistent with the results of Worbes et al. (2003), the only other dendroecological study to describe stand-development patterns of tropical forest. They showed that in a secondary semi-deciduous tropical forest in Cameroon the majority of individuals established synchronously 60–70 yr earlier, but that differences in growth rate and shade tolerance led to a distinct pattern of vertical stratification, despite the similarity in ages of the main canopy and understory trees.

Where a catastrophic disturbance kills a large proportion of the trees in the forest, the abrupt increase in resource availability allows a massive pulse of recruitment from the soil seed bank (where it exists, mainly in the seasonal tropics and among pioneer species) as well as from vegetative propagation. Few disturbances, however, eliminate all of the living aboveground biomass; most leave a complex mosaic of standing live and dead trees, alone and in clumps, above a matrix of fallen trees, branches, and leaves, exposed mineral soil, and surviving seedlings and saplings (Foster et al. 1998). These structural legacies of disturbances create heterogeneous microsite conditions for establishment of new seedlings and growth of surviving advance regeneration (Carlton and Bazzaz 1998). Subsequent development of the forest depends on the spa-

tial arrangement of the regeneration with respect to resource availability and inter- and intraspecific competitors, as well as the availability of seeds and seedlings. As the stand develops, differences in life-history traits among species and differences in the availability of resources among individuals will determine the outcome of competitive interactions as well as the structure and composition of the forest. In particular, differences in shade tolerance, growth rate, and maximum height will lead to stratification of trees' crowns in the forest canopy, creating the heterogeneous vertical structure typical of many tropical forests (Ashton and Peters 1999). Subsequent disturbances of lesser intensity will further increase the heterogeneity and complexity of the three-dimensional structure of the forest (Paine et al. 1998).

The predictability of post-disturbance stand development (i.e., succession) depends on the relative balance of stochastic and determinate factors and their possible interactions (Webb et al. 1972, Denslow 1985). Some factors, such as the autecology of the tree species, are relatively determinate (i.e., trees will respond in approximately the same manner given the same growing conditions); others, such as the distribution of seeds and seedlings and resources following a disturbance, are not. In tropical forests, where the number of species is high and range of life-history traits is broad, small-scale heterogeneity in post-disturbance microsite conditions and resource availability combined with considerable variation in neighborhood species composition greatly limit our ability to anticipate future stand composition and structure. Integrating these sources of variation over a complex disturbance regime may provide an effective means for a diverse assemblage of tree species to coexist. Further studies examining the historical stand-development patterns and disturbance regimes of tropical forests at the scale of decades to centuries are needed to test the generality of these processes.

Literature Cited

Abrams, M. D., D. A. Orwig, and T. E. Demeo. 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.

ADRC [Asian Disaster Reduction Center]. 2003. Natural disasters in Thailand/Burma. Asian Disaster Reduction Center, Kobe, Japan.

Anonymous. 1929, 1932. Annual reports on working plans and silviculture in Burma. Superintendent of Government Printing and Stationary, Rangoon, Burma.

Ashton, M. S., and C. M. Peters. 1999. Even-aged silviculture in tropical rain forests of Asia. Journal of Forestry **97**:14–19.

Ashton, P. S. 1964. Ecological studies in the mixed dipterocarp forests of Brunei State. Oxford Forestry Memoirs Number 25. Clarendon Press, Oxford, UK.

Ashton, P. S. 1981. The need for information regarding tree age and growth in tropical forests. Pages 3–6 *in* F. H. Bormann and G. P. Berlyn, editors. Age and growth rates of tropical trees: new directions for research. Bulletin Number 94. School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut, USA.

Bailey, R. L., and T. R. Dell. 1973. Quantifying diameter distributions with the Weibull function. Forest Science **19**:97–104.

Baker, P. J. 1997. Seedling establishment and growth across forest types in an evergreen/deciduous forest mosaic in western Thailand. Natural History Bulletin of the Siam Society **45**:17–41.

Baker, P. J. 2001. Age structure and stand dynamics of a seasonal tropical forest in western Thailand. Dissertation. University of Washington, Seattle, Washington, USA.

Baker, P. J. 2003. Tree age estimation for the tropics: a test from the southern Appalachians. Ecological Applications **13**:1718–1732.

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

Bhattacharyya, A., R. R. Yadav, H. P. Borgaonkar, and G. P. Pant. 1992. Growth-ring analysis of Indian tropical trees: dendroclimatic potential. Current Science **62**:736–741.

Bormann, F. H., and G. P. Berlyn, editors. 1981. Age and growth rates of tropical trees: new directions for research. Bulletin Number 94. School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut, USA.

Boucher, D. 1990. Growing back after hurricanes. BioScience **40**:163–166.

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

Buckley, B. M., M. Barbetti, M. Watanasak, R. D'Arrigo, S. Boonchirdchoo, and S. Sarutanon. 1995. Dendrochronological investigations in Thailand. IAWA Journal **16**:393–409.

Bunyavejchewin, S., P. J. Baker, J. V. LaFrankie, and P. S. Ashton. 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., P. J. Baker, J. V. LaFrankie, and P. S. Ashton. 2002. Floristic structure of seasonal dry evergreen forest at Huai Kha Khaeng Wildlife Sanctuary, western Thailand. Natural History Bulletin of the Siam Society **50**:125–134.

Bunyavejchewin, S., P. J. Baker, J. V. LaFrankie, and P. S. Ashton. 2004. Structure, history, and rarity in a seasonal evergreen forest in western Thailand. Pages 145–158 in E. C. Losos and E. G. Leigh, editors. Forest diversity and dynamism: findings from a network of large-scale tropical forest plots. University of Chicago Press, Chicago, Illinois, USA.

Bunyavejchewin, S., J. V. LaFrankie, and P. S. Ashton. 1999. The 50-ha forest research plot at Huai Kha Khaeng Wildlife Sanctuary, Thailand: methods, maps, and diameter tables. Smithsonian Tropical Research Institute, Balboa, Panama.

Bush, M. B., and P. A. Colinvaux. 1994. Tropical forest disturbance: paleoecological records from Darien, Panama. Ecology 75:1761–1768.

Canham, C. D., and P. L. Marks. 1985. The response of woody plants to disturbance: patterns of establishment and growth. Pages 197–216 in S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbances and patch dynamics. Academic Press, New York, New York, USA.

Carlton, G. C., and F. Bazzaz. 1998. Resource congruence and forest regeneration following an experimental hurricane blowdown. Ecology 79:1305–1319.

Clark, D. A., and D. B. Clark. 1991. The impact of physical damage on canopy tree regeneration in tropical rain forest. Journal of Ecology 79:447–457.

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

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

Clark, J. S. 1990. Fire and climate change during the last 750 yr in northwestern Minnesota. Ecological Monographs 60:135–159.

Cohen, A. C. 1965. Maximum likelihood estimation in the Weibull distribution based on complete and on censored samples. Technometrics 7:579–588.

Condit, R. 1995. Research in large, long-term tropical forest plots. Trends in Ecology and Evolution 10:18–22.

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

Condit, R., S. P. Hubbell, and R. B. Foster. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. Ecological Monographs 65:419–439.

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

Debski, I., D. F. R. P. Burslem, and D. Lamb. 2000. Ecological processes maintaining differential tree species distributions in an Australian subtropical rain forest: implications for models of species coexistence. Journal of Tropical Ecology 16:387–415.

Denslow, J. S. 1985. Disturbance-mediated coexistence of species. Pages 307–323 in S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbances and patch dynamics. Academic Press, New York, New York, USA.

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. Annual Review of Ecology and Systematics 18:431–451.

Denslow, J. S., A. E. Ellison, and R. E. Sanford. 1998. Treefall gap size effects on above- and below-ground processes in tropical wet forests. Journal of Ecology 86:597–606.

Dezzeo, N., M. Worbes, I. Ishii, and R. Herrera. 2003. Annual tree rings revealed by radiocarbon dating in seasonally flooded forest of the Mapire River, a tributary of the lower Orinoco River, Venezuela. Plant Ecology 168:165–175.

Duncan, R. P. 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycar-*

pus dacrydioides). New Zealand Natural Sciences 16:31–37.

Duncan, R. P. 1992. Flood disturbance and the coexistence of species in a lowland podocarp forest, South Westland, New Zealand. Journal of Ecology 81:403–416.

Enquist, B. J., and A. J. Leffler. 2001. Long-term tree ring chronologies from sympatric tropical dry forest trees: individualistic responses to climatic variation. Journal of Tropical Ecology 17:41–60.

Fichtler, E., D. A. Clark, and M. Worbes. 2003. Age and long-term growth of trees in an old-growth tropical rain forest, based on analyses of tree rings and ^{14}C. Biotropica 35:306–317.

Fichtler, E., V. Trouet, H. Beekman, P. Coppin, and M. Worbes. 2004. Climatic signals in tree rings of *Burkea africana* and *Pterocarpus angolensis* from semiarid forests in Namibia. Trees 18:442–451.

Foster, D. R., D. H. Knight, and J. F. Franklin. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. Ecosystems 1:497–510.

Foster, D. R., D. A. Orwig, and J. S. McLachlan. 1996. Ecological and conservation insights from reconstructive studies of temperate old-growth forests. Trends in Ecology and Evolution 11:419–424.

Franklin, J. F., et al. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155:399–423.

Gamble, J. S. 1920. A manual of Indian timbers. Second edition. Sampson, Low, Marston & Company, London, UK.

Giri, C., and S. Shrestha. 2000. Forest fire mapping in Huay Kha Khaeng Wildlife Sanctuary, Thailand. International Journal of Remote Sensing 21:2023–2030.

Glitzenstein, J. S., P. A. Harcombe, and D. R. Streng. 1986. Disturbance, succession, and maintenance of species diversity in an east Texas forest. Ecological Monographs 56:243–258.

Graham, S. A. 1954. Scoring tolerance of forest trees. Michigan Forestry 4:1–2.

Hallé, F., R. A. A. Oldeman, and P. B. Tomlinson. 1978. Tropical trees and forests: an architectural analysis. Springer-Verlag, New York, New York, USA.

Hart, T. B., J. A. Hart, R. Dechamps, M. Fournier, and M. Ataholo. 1996. Changes in forest composition over the last 4000 years in the Ituri basin, Zaire. Pages 545–563 in L. J. G. van der Maesen, X. M. Van der Burgt, and J. M. Van Medenbach de Rooy, editors. The biodiversity of African plants. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Hartshorn, G. S. 1978. Tree falls and tropical forest dynamics. Pages 617–638 in P. B. Tomlinson and M. H. Zimmerman, editors. Tropical trees as living systems. Cambridge University Press, London, UK.

Heinrich, I., and J. C. G. Banks. *In press*. Dendroclimatological potential of the Australian red cedar. Australian Journal of Botany.

Henry, J. D., and J. M. A. Swan. 1974. Reconstructing forest history from live and dead plant material: an approach to the study of forest succession in southwest New Hampshire. Ecology 55:772–783.

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

Horn, S. P., and R. L. Sanford. 1992. Holocene fires in Costa Rica. Biotropica 24:354–361.

Huston, M. 1979. A general hypothesis of species diversity. American Naturalist 113:81–101.

Jacoby, G., and R. D'Arrigo. 1990. Teak (*Tectona grandis* L. f.), a tropical species of large-scale dendroclimatic potential. Dendrochronologia 8:83–98.

Kohyama, T. 1980. Growth pattern of *Abies mariesii* saplings under conditions of open-growth and suppression. Botanical Magazine (Tokyo) **93**:13–24.

Lang, G. E., and D. H. Knight. 1983. Tree growth, mortality, recruitment, and canopy gap formation during a 10-yr period in a tropical moist forest. Ecology **64**:1075–1080.

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. Thesis. International Institute for Aerospace Survey and Earth Sciences, Enschede, The Netherlands.

Levin, S. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943–1967.

Lorimer, C. G. 1977. Pre-settlement forest and natural disturbance cycle of northeastern Maine. Ecology **58**:139–148.

Lorimer, C. G. 1983. A test of the accuracy of shade-tolerance classification based on physiognomic and reproductive traits. Canadian Journal of Botany **16**:1595–1598.

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

Lorimer, C. G., and A. G. Krug. 1983. Diameter distributions in even-aged stands of shade-tolerant and midtolerant tree species. American Midland Naturalist **109**:331–345.

Lugo, A. E., and F. N. Scatena. 1996. Background and catastrophic tree mortality in tropical moist, wet and rain forests. Biotropica **28**:585–599.

Lutz, H. J., and A. L. McComb. 1935. Origin of white pine in virgin forest stands of northwestern Pennsylvania as indicated by stem and basal branch features. Ecology **16**:252–256.

Martinez-Ramos, M., and E. R. Alvarez-Buylla. 1998. How old are tropical rain forest trees? Trends in Plant Science **3**:400–405.

Meadows, J. S., J. D. Hodges, E. C. Burkhardt, and R. L. Johnson. 1984. Response of sugarberry to release treatments. Pages 220–226 *in* E. Shoulders, editor. Third Biennial Southern Silvicultural Research Conference. General Technical Report SO–54. USDA Forest Services, Southern Research Station, Asheville, North Carolina, USA.

Nelson, B. W., V. Kapos, J. B. Adams, W. J. Oliveira, O. P. G. Braun, and I. L. do Anural. 1994. Forest disturbance by large blowdowns in the Brazilian Amazon. Ecology **75**:853–858.

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

Oliver, C. D. 1978. The development of northern red oak in mixed stands in central New England. Bulletin Number 91. School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut, USA.

Oliver, C. D. 1980. Even-age development of mixed-species stands. Journal of Forestry **78**:201–203.

Oliver, C. D. 1981. Forest development in North America following major disturbances. Forest Ecology and Management **3**:153–168.

Oliver, C. D., and E. P. Stephens. 1977. Reconstruction of a mixed-species forest in central New England. Ecology **58**:562–572.

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs **51**:145–178.

Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems **1**:535–545.

Palik, B. J., and K. S. Pregitzer. 1991. The relative influence of establishment time and height-growth rates on species vertical stratification during secondary forest succession. Canadian Journal of Forest Research **21**:1481–1490.

Pearson, R. S., and H. P. Brown. 1932. Commercial timbers of India: their distribution, supplies, anatomical structure, physical and mechanical properties and uses. Government of India, Central Publication Branch, Calcutta, India.

Pickett, S. T. A., and P. S. White, editors. 1985. The ecology of natural disturbances and patch dynamics. Academic Press, New York, New York, USA.

Potts, M. D. 2003. Drought in a Bornean everwet rain forest. Journal of Ecology **91**:467–474.

Proctor, J., F. Q. Brearley, H. Dunlop, K. Proctor, Supramono, and D. Taylor. 2001. Local wind damage in Barito Ulu, central Kalimantan: a rare but essential event in a lowland dipterocarp forest? Journal of Tropical Ecology **17**:473–475.

Pumijumnong, N., D. Eckstein, and U. Sass. 1995. Tree-ring research on *Tectona grandis* in Northern Thailand. IAWA Journal **16**:385–392.

Raja Barizan, R. J. 1996. Growth and survival of planted seedlings of *Hopea odorata* under different light conditions and fertilizer levels in logged-over forests. Pages 180–188 *in* S. Appanah and K. C. Khou, editors. Proceedings of the Fifth Round-Table Conference on Dipterocarps. Forest Research Institute of Malaysia, Kuala Lumpur, Malaysia.

Richards, P. W. 1996. The tropical rain forest. Cambridge University Press, Cambridge, UK.

Romesburg, H. C., and P. Mohai. 1990. Improving the precision of tree height estimates. Canadian Journal of Forest Research **20**:1246–1250.

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs **52**:199–221.

Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology **63**:1533–1546.

Salldarriaga, J. G., and D. C. West. 1986. Holocene fires in the northern Amazon basin. Quaternary Research **26**:358–366.

Savage, M. 1994. Land-use change and the structural dynamics of *Pinus kesiya* in a hill evergreen forest in northern Thailand. Mountain Research and Development **14**:245–250.

Schongart, J., W. J. Junk, M. T. F. Piedade, J. M. Ayres, A. Huttermann, and M. Worbes. 2004. Teleconnection between tree growth in the Amazonian floodplains and El Niño-Southern Oscillation effect. Global Change Biology **10**:683–692.

Segura, G., and L. C. Snook. 1992. Stand dynamics and regeneration patterns of a pinyon pine forest in east central Mexico. Forest Ecology and Management **47**:175–194.

Shiokura, T. 1989. A method to measure radial increment in tropical trees. IAWA Bulletin **10**:147–154.

Smitinand, T., T. Santisuk, and C. Phengklai. 1980. The manual of Dipterocarpaceae of mainland Southeast Asia. Royal Forest Department Herbarium, Bangkok, Thailand.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics **15**:353–391.

Spicer, R., B. L. Gartner, and R. L. Darbyshire. 2000. Sinuous stem growth in a Douglas-fir (*Pseudotsuga menziesii*) plantation: growth patterns and wood quality effects. Canadian Journal of Forest Research **30**:761–768.

Stahle, D. W., P. T. Mushove, M. K. Cleaveland, F. Foig, and G. A. Haynes. 1999. Management implications of annual growth rings in *Pterocarpus angolensis*. Forest Ecology and Management **124**:217–229.

Stott, P. A. 1988. The forest as phoenix: towards a bioge-ography of fire in mainland southeast Asia. Geographical Journal **145**:337–350.

Swetnam, T. W., and A. M. Lynch. 1993. Multicentury, re-gional-scale patterns of western spruce budworm out-breaks. Ecological Monographs **63**:399–424.

Torquebiau, E. F. 1986. Mosaic patterns in dipterocarp forest in Indonesia, and their implications for practical forestry. Journal of Tropical Ecology **2**:301–325.

Trimble, G. R. 1968. Form recovery by understory sugar maple under uneven-aged management. USDA Forest Ser-vice Research Note NE-89.

Trimble, G. R., and E. H. Tryon. 1966. Crown encroachment into openings cut in Appalachian hardwood stands. Journal of Forestry **64**:104–108.

Vandermeer, J. H., D. H. Boucher, I. G. de la Cerda, and I. Perfecto. 2001. Growth and development of the thinning canopy in a post-hurricane tropical rain forest in Nicaragua. Forest Ecology and Management **148**:221–242.

van Groenendael, J. M., S. H. Bullock, and L. A. Perez-Jimenez. 1996. Aspects of the population biology of the gregarious tree *Cordia eleagnoides* in a Mexican tropical deciduous forest. Journal of Tropical Ecology **12**:11–24.

Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. American Naturalist **125**:768–787.

Webb, L. J., J. G. Tracey, and W. T. Williams. 1972. Regen-eration and pattern in the subtropical rain forest. Journal of Ecology **60**:675–696.

Whitmore, T. C. 1978. Gaps in the forest canopy. Pages 639–655 *in* P. B. Tomlinson and M. H. Zimmerman, editors. Tropical trees as living systems. Cambridge University Press, London, UK.

Whitmore, T. C. 1985. Tropical rain forests of the Far East. Second edition. Clarendon Press, Oxford, UK.

Whitmore, T. C., and D. F. R. P. Burslem. 1998. Major dis-turbances and tropical rainforests. Pages 549–565 *in* D. M. Newbery, N. D. Brown, and H. H. T. Prins, editors. Pop-ulation and community dynamics in the tropics. Blackwell Scientific Press, Oxford, UK.

Wolter, K. E. 1968. A new method for marking xylem growth. Forest Science **14**:102–104.

Worbes, M. 1989. Growth rings, increment, and age of trees in inundation forest, savannas, and a mountain forest in the Neotropics. IAWA Journal **10**:109–122.

Worbes, M. 1999. Annual growth rings, rainfall-dependent growth, and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. Journal of Ecology **87**:391–403.

Worbes, M. 2002. One hundred years of tree-ring research in the tropics—a brief history and an outlook to future challenges. Dendrochronologia **20**:217–231.

Worbes, M., H. Klinge, J. D. Revilla, and C. Martius. 1992. On the dynamics, floristic subdivision, and geographical distribution of varzea forests in Central Amazonia. Journal of Vegetation Science **3**:553–564.

Worbes, M., R. Staschel, A. Roloff, and W. J. Junk. 2003. Tree ring analysis reveals age structure, dynamics and wood production of a natural forest stand in Cameroon. Forest Ecology and Management **173**:105–123.

Wyatt, D. K. 1984. Thailand: a short history. Yale University Press, New Haven, Connecticut, USA.

Ziegler, S. S. 2002. Disturbance regimes of hemlock-domi-nated, old-growth forests in northern New York, USA. Ca-nadian Journal of Forest Research **32**:2106–2115.

Zimmerman, J. K., E. M. Everham, R. B. Waide, D. J. Lodge, C. M. Taylor, and N. V. L. Brokaw. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. Journal of Ecology **82**:911–922.

APPENDIX A

A map showing the location of the study plots at the Huai Kha Khaeng Wildlife Sanctuary in west-central Thailand is available in ESA's *Electronic Data Archive*: *Ecological Archives* M075-012-A1.

APPENDIX B

A description and evaluation of Duncan's (1989) method estimating the distance to the pith from an incomplete core are available in ESA's *Electronic Data Archive*: *Ecological Archives* M075-012-A2.

APPENDIX C

Profile diagrams and stratification patterns from the seasonal dry evergreen forest at Huai Kha Khaeng Wildlife Sanctuary (HKK), west-central Thailand, are available in ESA's *Electronic Data Archive*: *Ecological Archives* M075-012-A3.

APPENDIX D

A figure illustrating stem architecture of *Hopea* seedlings and seedlings from the 50-ha plot is available in ESA's *Electronic Data Archive*: *Ecological Archives* M075-012-A4.

APPENDIX E

A table summarizing results of age–tree-size regression analyses for selected study species from the seasonal dry evergreen forest is available in ESA's *Electronic Data Archive*: *Ecological Archives* M075-012-A5.