



# Tamm Review: Large-scale infrequent disturbances and their role in regenerating shade-intolerant tree species in Mesoamerican rainforests: Implications for sustainable forest management



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## ABSTRACT

Forest management of tropical lowland and hill wet evergreen forests traditionally assumes that succession, species composition, and forest structure are largely driven by small, frequent disturbances. More recent ecological studies, archaeological findings, palynology and climate records demonstrate that tropical rainforests in general are not only subject to treefall disturbances but also to large-scale, infrequent disturbances driven by both past ancient and more recent human land use, and by natural forces of climate and geology. This paper reviews the case for the presence and extent of large-scale infrequent disturbances in Mesoamerica. We then use this knowledge to understand effects shaping species composition and structure. We evaluate current silvicultural regeneration systems for forest management based on the gap dynamics paradigm and propose potential alternative and complementary regeneration methods for forests and tree species that are driven by large-scale disturbances. We propose that the shade-intolerant timber species observed today are in large part a reflection of legacies of human land use and historical large-scale disturbances. Such species require larger, more dramatic disturbance regimes to regenerate and to attain the canopy in future managed forests. We suggest that such conditions are not provided for by current silvicultural systems within the region that require multiple entries to the stand every 15–30 years and should be coupled with liberation thinnings to promote shade-tolerant, commercially valuable timber species. Alternative silvicultural systems, such as shelterwoods and seed-tree methods of regeneration and management, purposefully promote the regeneration of valuable, shade-intolerant timber species. We propose applications for reserve design, and the management of non-timber forest products in conjunction with timber products to complement such activities. These systems differ in their goals, species promoted (shade-tolerant vs. -intolerant) and the ecological assumptions driving their operations. We conclude that shelterwoods and seed-tree systems are more appropriate to manage forests rich in shade-intolerant timber species. Such methods need to be included in the suite of silvicultural options available to managers of tropical wet evergreen forests in Mesoamerica.

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## 1. Introduction

Philosophical approaches toward the management of tropical lowland and hill wet evergreen forests have traditionally relied on the assumption that succession, species composition, and forest structure is driven by gap dynamics. Much of this work was done toward the later part of the last century at a time when tropical forests were first being logged extensively for their timber (for example see gap dynamics work in Whitmore and Burnham, 1975; Hartshorn, 1978; Hartshorn, 1980; Brokaw, 1982; Brokaw, 1985; Brokaw, 1987; Denslow, 1980; Denslow, 1987; Whitmore, 1984; Brandani et al., 1988; Nuñez-Farfán and Dirzo, 1988; Hartshorn, 1989; Denslow et al., 1998). These ideas evolved from early ecological understandings of old-growth in temperate moist forests of Western Europe and North America (Clements, 1916; Sernander, 1936; Watt, 1947; Barden, 1980, 1981; Runkle, 1981).

The main driver of wet tropical forest dynamics in Mesoamerica (i.e. the geographical and cultural region from Mexico through to Panama) was thought to be single- and multiple-tree fall gaps driven by autogenic disturbance. Research on gap dynamics of neotropical rain forests is largely based on work carried out in Costa Rica and Panama from 1970 to 1990 (Hartshorn, 1980; Brokaw, 1982; Brokaw, 1985; Brokaw, 1987; Denslow, 1980; Denslow, 1987; Brandani et al., 1988; Nuñez-Farfán and Dirzo, 1988; Hartshorn, 1989; Denslow et al., 1998; Guariguata and Pinard, 1998).

Archaeological findings and climate records demonstrate that tropical rainforests are also subject to large-scale infrequent disturbances (LIDs) (Oliver, 1981; Attiwill, 1994; Dale et al., 1998; Foster et al., 1998; Sugden, 1992; Turner et al., 1997; Turner et al., 1998; Whitmore and Burslem, 1998; Burslem and Whitmore, 1999; Fredericksen and Putz, 2003; Mascorro et al., 2016). Examples of LIDs affecting tropical forests include hurricanes (Lugo et al., 1983; Basnet et al., 1992; Attiwill, 1994; Lugo and Scatena, 1996; Foster et al., 1998; Whitmore and Burslem, 1998; Chazdon 2003); convective windstorms (Ediriweera et al., 2008); severe droughts (Condit et al., 1995; Potts, 2003; Engelbrecht et al., 2007); fires (Kauffman, 1991; Cochran et al., 1999; Urquhart, 2008); floods (Gullison et al., 1996; Foster et al., 1998); volcanic eruptions; and landslides following periods of heavy rains or seismic activity (Garwood et al., 1979; Guariguata, 1990; Foster et al., 1998; Sigl et al., 2015). In addition, evidence suggests that human influence from ancient permanent agricultural systems, swidden cultivation, and the management of fallow

fields played an important role in the origin of many rain forests (Deevey et al., 1979; Gómez-Pompa, 1987; Leyden, 1987; Denevan, 1992; Bush and Colinvaux, 1994; Peters, 2000; Cooke, 2005; Nichols, 2015).

In the case of certain kinds of disturbances such as hurricanes, floods, fires, earthquakes, permanent agricultural systems, and volcanic activity, the forces exerted may change the landscape dramatically (Garwood et al., 1979; Lugo and Scatena, 1996; Everham and Browkaw, 1996; Turner et al., 1997; Foster et al., 1998; Michener and Hauber, 1998). Milder events such as droughts, groundstory fires, swidden cultivation and winds, although capable of rearranging vegetation are not generally catastrophic (Attiwill, 1994; Condit et al., 1995; Everham and Brokaw, 1996; Lugo and Scatena, 1996; Chazdon, 2003; Baker et al. 2008). Both kinds of events are a major episodic component of the disturbance regime complimenting the continuous smaller single- and multiple-tree fall disturbances that were thought to be the main driver of species composition and structure.

A large body of scientific inquiry has led a paradigm shift away from considering tropical forests as stable tree communities. Tropical forest ecologists increasingly recognize the dynamic nature of forests and the influence of large-scale episodic disturbances occurring over long intervals of time (Oliver, 1981; Brandani et al., 1988; Sprugel, 1991; Brown and Whitmore, 1992; Attiwill, 1994; Lugo and Scatena, 1996; Clark, 1996; Whitmore and Burslem, 1998; Dale et al., 1998; Foster et al., 1998; Turner et al., 1997; Turner et al., 1998; Chazdon, 2003; Fredericksen and Putz, 2003; Baker et al., 2005). Current tropical forest management paradigms, however, do not reflect the state-of-the-art ecological understanding of tropical forest dynamics.

In this paper we review the case for the presence and extent of LIDs in Mesoamerican wet evergreen rainforest. We then use this knowledge to understand the successional forces shaping species composition and structure. We evaluate current silvicultural regeneration methods for forest management and propose potential alternative and complementary regeneration methods for forests and tree species adapted to LIDs. The paper is organized into four sections comprising: (1) a description of the physical environment defining rainforests in Mesoamerica; (2) a review of the evidence that supports the role LIDs play in Mesoamerican rain forests (both human-induced and natural); (3) a review of current methods of forest management and logging (i.e. based on minimum felling diameter); and lastly (4) a case for the inclusion and application of shelterwoods and seed-tree systems for regenerat-

ing and releasing shade-intolerant timber species in Mesoamerica. We propose that the shade-intolerant timber species that we observe today are in large part a reflection of historical large-scale disturbances. As such, these species require larger, more dramatic disturbance regimes to regenerate and ascend to the canopy in managed forests; conditions not provided for by current silvicultural systems.

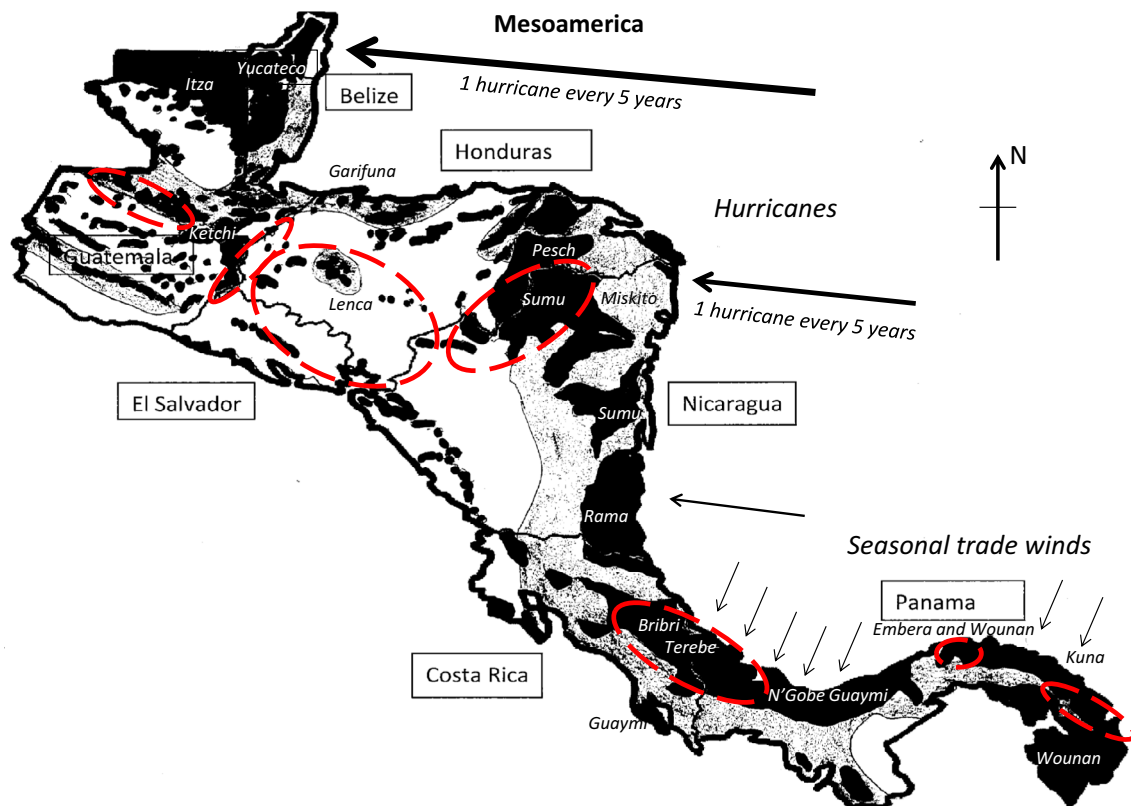
## 2. Physical description of the Mesoamerican lowland and hill rainforests

The lowland, wet forests of Mesoamerica, hereafter referred to simply as rainforests, receive more than 2000 mm of rainfall annually and present a mean annual temperature greater than 24 °C (Holdridge, 1947). These rainforests are multistoried and present a discontinuous canopy with emergent trees reaching heights greater than 45 m (Richards, 1952; Lamprecht, 1989). Differences in rainfall amount and distribution with latitude or altitude have profound effects on the ecology of the forest (Holdridge, 1967; Coen, 1991; Montagnini, 2006).

Approximately 78 million hectares (78,000 km<sup>2</sup>) of Mesoamerica remains in tropical wet evergreen forest cover, representing ~30% of the total region (Guatemala 53%, Belize 62%, Costa Rica 52%, El Salvador 27%, Honduras 56%, Nicaragua 53%, Panama 48%, and Mexico 34%) (Giri and Jenkins, 2005). The majority of Mesoamerican rainforest is distributed along the Atlantic coast, beginning at the eastern side of the Yucatán Peninsula and the Petén. For Mexico this chiefly comprises Calakmul biosphere reserve on the southern border. In Guatemala, this includes: the

Maya Biosphere Reserve, the Tikal National Park, the Sierra del Candor National Park to the West, and the Laguna del Tigre National Park to the Northwest. Large tracts of continuous rainforest remain at the Honduran/Nicaraguan Mosquitia with the Honduran Rio Platano Biosphere Reserve that extends into Nicaragua as the Bosawas Biosphere Reserve. Southwards from Nicaragua the rainforest extends into Costa Rica where it occurs along the Atlantic coast and across the main mountain ranges until the Panamanian border. In Panama, the rainforest extends along the Misquito Gulf to Colon and finally into the Panamanian Darien until the Colombian border. On the Pacific slopes, the largest tract of rainforest is found in the Osa Peninsula in Costa Rica and continues into Panama ending at the western coast of Los Santos (Fig. 1).

Geologically, the Mesoamerican isthmus was formed from a volcanic arc where the Cocos plate (Pacific side) was being subducted beneath the Caribbean Plate. The arc eventually formed a continuous land bridge connecting North and South America (Coates and Obando, 1996). This process has been ongoing for 15 million years, although the final closure of the isthmus did not occur in a single event (Coates and Obando, 1996). Soil properties vary enormously across the isthmus and with it forest composition and structure (Holdridge, 1967). The two most important geologic formations of the rainforest region are: (1) the limestone formations in the Guatemalan Petén; and (2) the Atlantic coastal uplands and lowlands (USDA, 1975; Mata, 1991). In general, soils underlying tropical rainforests are highly leached, acidic and nutrient poor. In Mesoamerica, however, the young geology coupled with nutrient rich volcanic rock makes the soils relatively rich in nutrients but highly erodible, as compared to other tropical rainforests (Ashton, 2004). The ultisols and oxisols occur on the steeper



**Fig. 1.** Central America (Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama) and the remaining forests within the region (black). The gray shading defines the wet zone (>2000 mm per year) and therefore the wet tropical forest regions within Central America. The dashed red lines depict landslide and flood prone mountainous areas. The arrows depict strong winds that strengthen in frequency and intensity with increase in latitude from Panama (strong frontal storms and seasonal winds) to Belize/Yucatan (intense category  $\geq 4$  hurricanes once every ten years). Data from various sources including – Global Climate Risk Index, Germanwatch, Bonn, Germany; Office of Foreign Disaster Assistance, USAID; National Geographic, 1992, Coexistence of indigenous peoples and the natural environment in Central America.

upland topography of the central mountains. The limestone of the outer lying coastal shelf (e.g. the Yucatan), comprises extremely variable calcareous mollisols ranging from very deep and fertile to extremely skeletal and droughty (Isphording, 1975). The floodplains of the larger valleys and coastal plains are comprised of nutrient rich entisols formed from alluvium.

### 3. The case for episodic disturbances in the Mesoamerican rainforests

Many authors have emphasized the need to acknowledge large-scale infrequent disturbances (LID's – first coined by Turner et al., 1998) as an important factor shaping the development of tropical forests (Oliver, 1981; Attiwill, 1994; Lugo and Scatena, 1996; Whitmore and Burslem, 1998; Dale et al., 1998; Foster et al., 1998; Turner et al., 1997; Turner et al., 1998; Chazdon, 2003; Fredericksen and Putz, 2003; Chazdon et al., 2007; Stanturf et al., 2007; Lugo, 2008; Griscom and Ashton, 2011). LID's promote the establishment or release of shade-intolerant timber species that at maturity make up the emergent and main canopy of many forests, but are incapable of thriving under a closed-canopy (Aubréville, 1938; Richards, 1952; Canham, 1989; Poorter et al., 1996; van Gernerden et al., 2003) (Table 1). LID's can be defined as canopy-leveling disturbances at or larger than the scale of a stand (e.g. stand replacing) within a forested landscape. They comprise two major types: Those that are driven by climate, and those that are anthropogenic. These LIDs are sufficient to initiate stand-scale regeneration but do not necessarily destroy every canopy tree, rather in many instances the result is patchy with large gaps and interspersed intact canopy groups and single surviving stems.

#### 3.1. Evidence of climate-related large-scale infrequent disturbances in Mesoamerican

Large-scale infrequent disturbances form an integral part of a disturbance regime (i.e. type, magnitude and frequency of events) that drive and shape the dynamic of a forest (Table 2).

##### 3.1.1. Landslides

Landslides are the most severe LID. Removing the topsoil and vegetation completely, they are often associated with volcanic or tectonic activity, or as mudslides from rain soaked unstable soils on steep slopes. Landslides occur mostly in very steep, erodible soils of the Cordillera Central running down the spine of Mesoamerica, but also affect lowland hill forests following earthquakes (Garwood et al., 1979; Guariguata, 1990). During a one hundred-year interval in Panama, landslides destroyed 2–3% of the forest cover (Garwood et al., 1979). This is likely an under representative estimate compared to the rest of Central America because Panama, as a physiographic region, is a narrow isthmus with relatively flat terrain and a mountain range that peaks at the border with Costa Rica (Weyl, 1980). Tree recruitment patterns vary within landslide gaps. One study in Puerto Rico, found mineral soil and exposed bedrock colonized by primarily by light-demanding ferns in the upper zone of a landslide, whereas the lower zone accumulated top soil and organic matter allowing for the germination of shade-intolerant tree species and the release of the buried seed bank. The same study reported regrowth following landslides in 300–600 m<sup>2</sup> gaps took 52 years to restore to pre-landslides conditions (Guariguata 1990).

##### 3.1.2. Flooding and erosion

Floods and river activity are important disturbance events on the slopes of steeply dissected mountains, the bottomlands of valleys, and the lower lying floodplains of the Atlantic coast. Effects

vary with topographic position, intensity of the event, and the permanence of the water (i.e. swamp forests versus riparian forests). In upland slope forests, water erodes and dissects steep valleys annually following heavy rains. Floristic associations forming along these waterways are dominated by fast-growing (e.g. *Cecropia* spp.), often nitrogen fixing, pioneers (e.g. *Alnus* spp.). The soil seed bank is an important seed source for annual herbs and grasses, whereas dispersal by water is relatively more important for canopy tree species and can determine episodes of recruitment on new eroded cut banks or fresh deposits after flooding (Petit and Froend, 2001).

On the larger floodplains of the lowlands and coastal plains, large events often follow a supra-annual periodicity; forests can remain in a constant state of succession as river systems move back and forth across the floodplain (Chazdon, 2003). For example, in the larger river basins at the foothills of the Peruvian Andes, Terborgh and Petren (1991) estimate that it takes 300 years for species composition to return to pre-flooding conditions. The river systems are not as large or as dramatic in Mesoamerica but smaller floodplains at the base of the Cordillera Central play an important role in shaping the successional development of the Atlantic rainforest.

##### 3.1.3. Hurricanes

Hurricanes in the Mesoamerican tropics are commonplace and destroy wide ranges of forest areas (Ackerman et al., 1991; Sugden, 1992; Vandermeer et al., 2000). Hurricanes occur more frequently and with more force within latitudinal belts between 10° and 20° north; predominantly on the Atlantic coasts of Nicaragua, Honduras, Guatemala, Belize and the Yucatan of Mexico (Boose et al., 1994; Everham and Brokaw, 1996; Whitmore and Burslem, 1998). Studies of Hurricane damage to forests have been done on the Yucatán Peninsula of Mexico and Belize (Lynch 1991; Mascorro et al., 2016), the Antilles (Lugo et al., 1983; Walker, 1991; Tanner et al., 1991; Bellingham et al., 1992), and on the Atlantic coasts of Nicaragua, Honduras and Guatemala (Boucher, 1990; Boucher et al., 1990; Acosta, 2000). In addition, several reviews of the nature of hurricane damage to forest systems have been completed (Sousa, 1984; Walker, 1991; Attiwill, 1994; Boose et al., 1994; Foster and Boose, 1992; Everham and Brokaw, 1996; Lugo and Scatena, 1996).

The most comprehensive studies of forest succession post hurricane have been done by Lugo et al. (1983) for the 1979 Hurricane David in Dominica; Bellingham et al. (1992) for the 1988 Hurricane Gilbert in the Blue Mountains, Jamaica; Walker (1991), among many others, for the 1989 Hurricane Hugo in the Luquillo Experimental Forest of Puerto Rico; Boucher et al. (1990), Yih et al. (1991), and Vandermeer et al. (1995) for the 1988 Hurricane Joan which devastated the Atlantic coastal forests in Nicaragua; and lastly, Acosta (1998) for the 1974 Hurricane Fifi in Honduras. All of these hurricanes are considered stand-replacing, meaning that large areas of forest, greater than several hundred acres (and usually thousands), are affected, and considerable damage to the canopy occurs, allowing a new forest-scale cohort to develop. Although these disturbances are patchy and vary in degree of severity with all or some of the canopy being destroyed, they transcend the scale of a stand for the forest type in question.

On islands in the Caribbean hurricane belt, the return interval for stand-replacing hurricanes is 10–60 years (Waide, 1991). In Puerto Rico, extensive blowdowns occur every 15–33 years; and forest-leveling hurricanes strike the island every 50–150 years (Boose et al., 2004). Scatena and Larsen (1991) estimate a return interval of 30–60 years for category 4 hurricanes in Puerto Rico. The category 5 Hurricane David destroyed some 250,000 ha of rainforest in Dominica in 1979 (Lugo et al., 1983).



**Table 1**

A list of timber species and their growth and reproductive characteristics for Mesoamerica. Source information for the construction of the table comprise: Condit et al. (2011), Roman et al. (2012) and Hall and Ashton (2016).

Species	Family	DBH <sup>1</sup> at maturity	MAI (cm/yr)	Growth	Shade tolerance	Successional stage of dominance	Recalcitrant	Dispersal vector	Capability to resprout	Specific weight (g/cm <sup>3</sup> )	Role in system	Applicable regeneration method (s)
<i>Anacardium excelsum</i>	Anacardiaceae	250	●	Moderate	Intolerant	Mid-Late	High	Birds, primates, bats	Low	0.42	Leader	Shelterwood
<i>Jacaranda copaia</i>	Bignoniaceae	●	2.0	Fast	Intolerant	Early	Low	Wind	●	●	Leader	Seed Tree/Patch Selection
<i>Tabebuia guayacan</i>	Bignoniaceae	125	●	Moderate	Intolerant	Early-Mid	Moderate	Wind	●	0.86	Leader	Seed Tree
<i>Ceiba pentandra</i>	Bombacaceae	200	3.0	Fast	Intolerant	Mid	High	Wind	Moderate	0.25	Leader	Seed Tree/Patch Selection
<i>Ochroma pyramidale</i>	Bombacaceae	80	5.3	Very Fast	Intolerant	Early	Moderate	Wind	None	0.2	Leader	Seed Tree/Patch Selection
<i>Cordia alliodora</i>	Boraginaceae	100	2.0	Fast	Intolerant	Early	High	Wind	Low	0.42	Leader	Seed Tree/Patch Selection
<i>Calophyllum brasiliense</i>	Clusiaceae	150	1.6	Moderate	Shade tolerant	Mid-Late	Moderate	Birds, bats, mammals	Low	0.46	Companion	Shelterwood/Selection
<i>Terminalia amazonia</i>	Combretaceae	70	2.1	Moderate	Shade intermediate	Mid-Late	Moderate	Wind	●	0.6	Leader	Shelterwood
<i>Terminalia oblonga</i>	Combretaceae	●	●	Fast	Intolerant	Mid-Late	Moderate	Wind	●	0.65	Leader	Shelterwood
<i>Hura crepitans</i>	Euphorbiaceae	100	●	Fast	Intolerant	Early-Mid	Moderate	Explosive, water	Moderate	0.33	Leader	Shelterwood
<i>Hyeronima alcheornoides</i>	Euphorbiaceae	187	1.7	Moderate	Shade intermediate	Mid-Late	Low	Mammals, birds	High	0.6	Leader	Shelterwood
<i>Andira inermis</i>	Fabaceae	150	0.2	Moderate	Shade intermediate	Mid	High	Bats, mammals	Low	0.77	Companion	Shelterwood/Selection
<i>Copaifera aromatica</i>	Fabaceae	90	●	Slow	Shade intermediate	Mid-Late	Low	Birds, mammals	Low	0.5	Companion	Shelterwood/Selection
<i>Dalbergia retusa</i>	Fabaceae	●	●	Slow	Shade intermediate	Mid-Late	Low	Water, mammals	High	0.72	Companion	Shelterwood/Selection
<i>Dialium guianensis</i>	Fabaceae	●	●	Moderate	Intolerant	Mid	Moderate	Birds	Low	0.86	Companion	Shelterwood
<i>Dipteryx panamensis</i>	Fabaceae	●	0.8	Fast	Intolerant	Late	Low	Bats, Mammals	Low	0.79	Leader	Seed Tree/Patch Selection
<i>Enterolobium cyclocarpum</i>	Fabaceae	150	1.8	Fast	Intolerant	Early-Mid	High	Mammals, cows, horses	High	0.39	Leader	Seed Tree
<i>Hymenaea courbaril</i>	Fabaceae	100	0.9	Moderate	Shade intermediate	Early-Mid	Low	Mammals, bats, rodents	Moderate	0.72	Leader	Seed Tree/Shelterwood
<i>Hymenolobium mesoamericanum</i>	Fabaceae	156	0.3	Slow	Intolerant	Mid-Late	High	Wind	●	0.6	Companion	Shelterwood
<i>Myroxylon balsamum</i>	Fabaceae	100	●	Moderate	Shade tolerant	Mid-Late	Low	Wind	●	0.72	Companion	Seed Tree
<i>Ormosia coccinea</i>	Fabaceae	●	●	Moderate	Intolerant	Mid	Moderate	Mammals, birds	●	●	Companion	Shelterwood
<i>Parkia pendula</i>	Fabaceae	●	●	Slow	Intolerant	Mid	High	Birds, primates	●	●	Leader	Seed Tree
<i>Pentaclethra macroloba</i>	Fabaceae	130	0.3	Fast	Shade tolerant	Late	High	Explosive	Low	0.6	Leader	Shelterwood/Selection
<i>Platymiscium pinnatum</i>	Fabaceae	●	●	Moderate	Intolerant	Late	Moderate	Wind	●	0.66	Companion	Shelterwood
<i>Prioria copaifera</i>	Fabaceae	100	●	Moderate	Shade tolerant	Late	High	Water, mammals	●	0.39	Leader	Shelterwood/Selection
<i>Schizolobium parahyba</i>	Fabaceae	●	●	Fast	Intolerant	Early	Low	Wind	●	●	Leader	Seed Tree/Patch Selection
<i>Vatairea lundellii</i>	Fabaceae	●	●	Moderate	Shade intermediate	Mid-Late	High	Wind	●	0.66	Companion	Shelterwood
<i>Humiriastrum diguense</i>	Humiriaceae	75	●	Moderate	Shade intermediate	Mid-Late	Low	Mammals	●	0.6	Companion	Shelterwood
<i>Vantanea barbourii</i>	Humiriaceae	150	●	Moderate	Shade intermediate	Mid-Late	High	Mammals	●	0.6	Companion	Shelterwood
<i>Lecythis ampla</i>	Lecythidaceae	161	●	Moderate	Intolerant	Late	Moderate	Bats, primates, rodents	Low	0.81	Companion	Shelterwood
<i>Carapa guianensis</i>	Meliaceae	●	●	Fast	Intolerant	Early-Mid	Moderate	Rodents, mammals, water	Low	0.46	Leader	Shelterwood/Seed Tree
<i>Cedrela odorata</i>	Meliaceae	180	1.5	Very fast	Intolerant	Early	Moderate	Wind	Low	0.39	Companion	Seed Tree
<i>Swietenia macrophylla</i>	Meliaceae	200	2.5	Moderate	Shade intermediate	Mid	High	Wind	Moderate	0.46	Leader	Seed Tree
<i>Brosimum alicastrum</i>	Moraceae	●	●	Moderate	Shade	Early-Mid	High	Mammals, birds	●	●	Leader	Shelterwood/Selection

Table 1 (continued)

Species	Family	DBH <sup>1</sup> at maturity (cm)	MAI (cm/yr)	Growth	Shade tolerance	Successional stage of dominance	Recalcitrant	Dispersal vector	Capability to resprout	Specific weight (g/cm <sup>3</sup> )	Role in system	Applicable regeneration method (s)
<i>Virola koshnyi</i>	Myristicaceae	150	2.1	Moderate	intermediate	Early-Mid	High	Mammals, birds, fish	●	0.39	Leader	Shelterwood
<i>Minquartia guianensis</i>	Olacaceae	82	0.2	Very Slow	Shade tolerant	Late	High	Mammals, birds	●	0.75	Companion	Shelterwood/Selection
<i>Podocarpus guatemalensis</i>	Podocarpaceae	●	●	Moderate	Shade	Early-Mid	Low	Birds and water	●	0.55	Leader	Seed Tree
<i>Manilkara zapota</i>	Sapotaceae	●	●	Slow	intermediate	Mid	High	Bats, birds, mammals	●	●	Leader	Shelterwood/Selection
<i>Sideroxylon capiri</i>	Sapotaceae	120	●	Moderate	Shade	Mid	Moderate	Primates, birds	●	0.66	Leader	Seed Tree
<i>Qualea paraensis</i>	Vochysiaceae	100	●	Moderate	intermediate	Mid	Medium	Wind	●	0.46	Leader	Seed Tree
<i>Vochysia ferruginea</i>	Vochysiaceae	80	2.2	High	Intolerant	Early-Mid	High	Wind	●	0.37	Leader	Seed Tree
<i>Vochysia guatemalensis</i>	Vochysiaceae	100	2.3	High	Intolerant	Early-Mid	High	Wind	●	0.35	Leader	Seed Tree

<sup>1</sup> Diameter at breast height (1.3 m above ground level), in centimeters.

For Mesoamerica, hurricanes (categories 4–5) that are able to dramatically modify structure through forest leveling occur on average about every 100 years (Boucher, 1992). In 1989 Hurricane Hugo cleared 500,000 ha of forest in Atlantic Nicaragua (Boucher, 1990). Urquhart (2008) found evidence of an extremely severe hurricane that hit the Atlantic coast of Nicaragua in 3340 years BP. Similarly, in Belize, McCloskey and Keller (2009) found evidence of an important hurricane event in 1500 CE. Further, they identified two periods of high hurricane incidence approximately 4500 and 2500 years BP (McCloskey and Keller, 2009). Less devastating hurricane events (categories 1–3) occur more frequently; for example on average the Belizean coast is hit by hurricanes once every decade (McCloskey and Keller, 2009). However, in the northern Yucatan hurricanes can occur almost every year, where they were responsible for 26% of all land cover change between 2005 and 2010 (Mascorro et al. 2016).

Damage from wind is largely determined by biotic factors (*i.e.* forest structure, composition and successional stage) and by their interaction with abiotic factors such as geomorphology and soil moisture (Ackerman et al., 1991; Everham and Brokaw, 1996). Interactions among these factors results in complex patterns of disturbance in forested landscapes (Boose et al., 1994; Lugo and Scatena, 1996). Surprisingly, studies have shown that hurricane damage correlates poorly with topographical features but it can be very site specific. Tree size, crown architecture and species are in part determined by aspect and exposure (Walker, 1991). Because species composition and stature of the forest can change, hurricane damage is not necessarily directly related to topographic relief and exposure. Therefore, similar topographies with different compositions or structures may not present the same pattern of damage.

Everham and Brokaw (1996) classified post-hurricane vegetation responses as: (1) regrowth; (2) recruitment; (3) release; and (4) repression. Regrowth is the most dominant response type (*i.e.*, 85% of all cases analyzed,  $n=27$ ), mainly by re-sprouting (Everham and Brokaw, 1996). For example, Boucher et al. (1990) observed that 75% of all downed trees re-sprouted within a year after Hurricane Joan in Nicaragua. Also, surviving trees may rapidly increase in growth as reported for *Manilkara bidentata* after Hurricane Hugo in Puerto Rico (You and Petty, 1991); or in general for many species (Walker, 1991).

Recruitment is generally low, but increases with increasing severity of damage to the original vegetation (Everham and Brokaw, 1996). Other disturbances seem to be important, in conjunction with hurricanes, to promote recruitment of shade-intolerant species. For example, fire following hurricanes is believed to help establish *Swietenia macrophylla* (Snook, 1996); but recruitment can also be constrained by deep litter layers (*i.e.* a consequence of tree defoliation during the hurricane) (Whigham et al., 1991; Yih et al., 1991).

Release follows canopy-replacing hurricanes where the understory remains fairly protected or where there is plentiful advanced regeneration (Smith et al., 1997). This mode of regeneration is recognized as important for the recovery of post-hurricane forests (Lugo and Scatena, 1996). However, advanced regeneration may be suppressed if the species composing the stand are capable of re-sprouting vigorously. Suppression may also occur if vines and other smothering plants quickly colonize available growing-space (Everham and Brokaw, 1996) or mechanical damage from falling material destroys advanced regeneration and limits seedling establishment (Shiels et al. 2010).

### 3.2. Evidence of pre-Columbian human influence on the Mesoamerican rainforests

Evidence of human inhabitation in Mesoamerica is widespread. At least 28.4 million indigenous inhabitants lived in large settle-

**Table 2**  
Studies of natural disturbance in Mesoamerica listed by disturbance regime and type, and accompanied by descriptions of their variation in relation to topography, hydrology and climate.

Disturbance	Type <sup>1</sup>	Topographic and biotic relationship <sup>2</sup>	Associations to other disturbances <sup>3</sup>	References
Hurricanes	Exogenous	Damage predictable at landscape level, but determined by forest structure, composition and successional stage at fine scales. Canopy species susceptible to hurricanes, regeneration is sheltered and released afterwards if undamaged	Directly causes strong winds and may trigger localized flooding and landslides. Large-scale fires have been reported to follow extreme events in Mesoamerica	Ackerman et al. (1991), Walker (1991), Boose et al. (1994), Everham and Brokaw (1996), Lugo and Scatena (1996), Turner et al. (1997), Foster et al. (1998), and Urquhart (2008)
Landslides	Exogenous	Frequent on the Mesoamerican Cordillera Central on steep topography, although they may occur on flatter areas during earthquakes. Completely denudes the top soil and often exposes the bedrock. Root systems are mostly destroyed	Associated to volcanic activity, earthquakes and triggered by heavy rains and windstorms	Garwood et al. (1979), Guariguata (1990), and Turner et al. (1997)
Flooding and erosion	Exogenous	Variable spatial damage. Along waterways in riparian forests, on steep topography and on floodplains in lowland forests. Physically damages understory vegetation and inundates root systems in general impeding aeration. In upland forests erosion dissects steep valleys promoting fast-growing and nitrogen-fixing trees species associations	More severe during ENSO <sup>4</sup> -years. Causes periodic debris flow and is triggered by heavy rainstorms frequently linked to hurricanes or other forms of tropical storms	Turner et al. (1997), Foster et al. (1998), Petit and Froend (2001), and Chazdon (2003)
Fire	Endogenous and exogenous	Fire is more frequently associated with human inhabitation. Intensity is determined by available fuel, weather conditions and continuity of forests. Ridges may act as firebreaks and there is less fire damage on downwind slopes. Stand – replacing crown fires causes extensive heat and burning. Generally, if fires are too severe and intense topography is less relevant to the event	More severe and frequent during ENSO years and droughty conditions. Hurricanes may precede large-scale fires due to the increase in fuel availability and drier and hotter micro-climates. Volcanic activity and landslides may trigger fires	Attiwill (1994), Turner et al. (1997), Foster et al. (1998), Cochrane (2003), Urquhart (2008), e.g. Williams and Bradstock (2009)
Droughts	Endogenous and exogenous	More severe on drier steep to moderate topography such as ridges, upland forests and mid-slopes. Floodplains and bottomlands are less vulnerable to damage. Damage is selective and vulnerable species are especially affected. Drought-tolerant species may survive and/or improve growth altering species composition	More severe and frequent during ENSO years and years with low rainfall	Condit et al. (1995), Potts (2003), and Engelbrecht et al. (2007)
Convictional windstorms	Exogenous	Damage coastal forests and foothills of inland mountains. Blowdowns hit Northeastern aspects as they come inland from the ocean and strike in the direction of predominant NE winds. Successional stage and stand density determines extent and severity of damage. Over stocked stands are more susceptible to damage as well as tall trees with large crowns	Supra-annual and annual climate fluctuations that influence air masses movements can create ideal conditions for massive wind blowdowns, e.g., ENSO years	Nelson et al. (1994) and Whitmore and Burslem (1998)
Volcanic activity	Exogenous	Along the Cordillera Central on the foothill forests in proximity to volcanoes. Damage is determined by direction of blast and topography	Volcanic activity causes fires at varying scales, intense heat, lava and debris flows, deposition of toxic chemicals, and explosive blasts	Foster et al. (1998)

<sup>1</sup> Turner et al. (1997) described LIDs as being caused by exogenous: “synoptic weather conditions” or endogenous “fuel availability” disturbances.

<sup>2</sup> LIDs interact with landscapes, their configuration and features. Different topographies may induce certain types of disturbances, while also determining their severity on forest ecosystems.

<sup>3</sup> LIDs may be associated with or trigger other LIDs at different spatial scales.

<sup>4</sup> El Niño–Southern Oscillation.

ments prior to the Spanish arrival in 1492 (Denevan, 1992; Bush and Colinvaux, 1994). Charcoal remains, archeological evidence, and palynology studies within the Mesoamerican region all suggest extensive human influence throughout the region (Bush et al., 1992; Horn and Sanford, 1992; Bush and Colinvaux, 1994; Piperno and Fritz, 1994; Kennedy and Horn, 2008; Nichols, 2015). Pre-Columbian civilizations transformed the landscape most dramatically in the more seasonal areas of the Yucatan, but swidden practices were common on the less fertile oxisols of the large rainforest regions of the Atlantic coast, while terracing and drained-field agriculture and the cultivation of desirable plants were practiced widely throughout the region but restricted to

more fertile soils (entisols). These practices gave rise to many of the forest communities we see today (Denevan, 1970; Gómez-Pompa, 1987; Denevan, 1992; Bush and Colinvaux, 1994; Northrop and Horn, 1996; Peters, 2000; Van Gemerden et al., 2003; Cooke, 2005; Neff et al., 2006).

### 3.2.1. Seasonal rainforest of the Maya region

In northern Mesoamerica, pre-Columbian inhabitants managed the native vegetation upon their arrival approximately 11,000 years B.P., and started transporting and cultivating plants 9000–7000 B.P. (Cooke, 2005). Furthermore, palynology studies suggest these forests were largely cleared near the most populated

settlements (Deevey et al., 1979). In the Guatemalan Petén, 2600 years of Mayan occupation had an enormous influence on the local rain forest, most notably through agriculture (Rue, 1987), but also through conversion into savannas (Leyden 1987) and regular clearing on a rotation of between 15 and 30 years under the sophisticated “milpa” system (Gómez-Pompa, 1987; Peters, 2000). Evidence in the pollen record indicates that pre-Columbian residents in the Veracruz area, in Mexico, intensively worked the rainforests during a period of agriculture intensification from 2600 to 1600 years B.P. (Goman and Byrne, 1998).

Other agricultural practices also played an important role in the domestication of the landscape. For example, evidence of the cultivation of useful tree species are observable where tree gardens were established or older forests were enriched (Peters, 2000). The almost pure stands of *Brosimum alicastrum* (Moraceae) in the Mayan lowlands are evidence of the purposeful perpetuation of these stands (Gómez-Pompa, 1987). Additionally, many valuable timber species were cultivated such as *Cordia dodecandra*, *Diospyros digna*, *Leucaena* spp., *Manilkara zapota*, *Spondias* spp., and *Pouteria* spp., which now dominate the canopy in many rainforests in Mexico and Guatemala (Gómez-Pompa, 1987) (Table 1).

Fallow field management was an important indigenous silvicultural practice (Peters, 2000). This included planting, transplanting, protection of valued species, and plant breeding (Denevan, 1992). Other practices common to Maya silviculture were the conservation of forest patches, the maintenance of soils and nutrient cycling, the selection of useful trees in fallow fields and forests, enrichment plantings, terracing and drained-field agriculture (Gómez-Pompa, 1987; Denevan 1992; Montagnini, 2006). In the Huastec territory of Northeastern Mexico, forest regrowth followed the abandonment of home gardens, managed fallow fields, managed forests and mono-specific plantations (Alcorn, 1981). Thus, natural forests merged with managed agricultural and forestry systems favoring the emergence of compositions optimized for species with ethnobotanical value (Alcorn, 1981).

### 3.2.2. Rain forest of the Atlantic coast and hill region

The region encompassing the wetter and less fertile soils of the southern Atlantic coastal regions of Mesoamerica (Nicaragua, Costa Rica and Panama), was thought for many years to be “pristine,” but has more recently been recognized to have been intensively cultivated, at least in parts, by humans for over 4000 years (Bush et al., 1992; Bush and Colinvaux, 1994; Cooke, 2005). The rainforests currently standing are in fact a historical legacy of fragmentation and agricultural land-use dating to hundreds of years ago (Bush and Colinvaux, 1994).

Forest management intensity diminished with the arrival and establishment of the Spaniards and with the decimation of indigenous populations (Mann, 2006). However, prior to colonization evidence exists of human disturbance and its effects on forest dynamics (Denevan, 1992). For instance, traces of carbon and maize pollen together with archeological findings discovered in the La Selva rainforests in Costa Rica suggest large-scale fire caused by lightning and/or humans inhabiting alluvial terraces 3000 years B.P. (Kennedy and Horn, 2008). Furthermore, the pollen record indicates that these floodplain forests were cleared for agriculture and subsequently abandoned ~400 years B.P. (Kennedy and Horn, 2008). Many indigenous groups used these practices in Nicaragua, Costa Rica and Panama (Montagnini, 2006). To this day indigenous peoples such as the Bri Bri, Ngobe, Terebe and Bugle (Atlantic coastal regions of western Panama and southeastern Costa Rica); Embera, Wounan and Kuna (Darién and eastern Panama); and Miskito, Sumo and Garifuna (Atlantic Miskito coasts of Nicaragua, Guatemala and Belize) practice swidden agriculture similar to the Mayan systems but with much longer return intervals, and with the use of less intensive techniques. These systems were based

on a transition from corn and beans (or more recently upland rice), to banana, and then following forest regeneration, selected fruit (*Malpighia* spp., *Spondias* spp., *Pouteria* spp.) and timber trees (*Anacardium excelsum*, *Cordia alliodora*) were tended as even-aged patches (Table 1). Depending upon the fertility of the soil such patches are revisited for clearance and cultivation after forest regrowth between 30 and 60 years.

## 4. Selective logging in the context of the selection regeneration method

Selective logging is currently the chief method for timber harvesting in Mesoamerica (FAO, 2008). Using silvicultural principles for establishing natural regeneration and based on the gap dynamics paradigm, selective logging can be considered a corrupted form of the selection regeneration method employing minimum diameters as the criterion for tree felling (Broun, 1912; Troup, 1928; Bauer, 1964; Lamprecht, 1989; Smith et al., 1997). The system thrives because it is easily implemented in the field, is suited to relatively unskilled personnel across broad forest areas (Troup, 1921; Wadsworth, 1981; Wadsworth, 1987) and is popularly recognized as less destructive (Webb, 1997; Fredericksen and Putz, 2003). In the tropics selective logging might have formally originated in the 1770 s in Java where Dutch foresters applied a 35 cm minimum felling diameter for managing teak plantations (Dawkins and Philip, 1998), but it was re-kindled for hill Mixed Dipterocarp Forests of post-independence southeast Asia (1950–1975) based upon the selective logging practices of the 1940s and 50s in forests of temperate North America and northern Europe and the ideas about gap dynamics at that time (Reyes, 1968; Bauer, 1964; Burgess, 1975; Appanah, 1998).

Other regeneration methods have been tested in the tropics, for example shelterwoods were implemented in Western Africa (Foggier, 1960; Dawkins 1961), Southeast Asia (Wyatt-Smith, 1963; Ashton and Peters, 1999; Ashton, 2003) and the Neotropics (Beard, 1946; Lamprecht, 1989). However, adverse administrative, political and social circumstances deterred their use at larger scales (Ashton and Peters, 1999).

For the last thirty years selective logging has been widely applied to forests throughout Asia, Africa and Latin America based on 50–60 cm minimum felling diameters and cutting cycles between 15 and 35 years (Hall et al., 2003; Sist et al., 2003; Putz et al., 2008a, 2008b). Without doubt selective logging remains prevalent as the most popular forest management system in use in Mesoamerica and throughout tropical rainforest more generally.

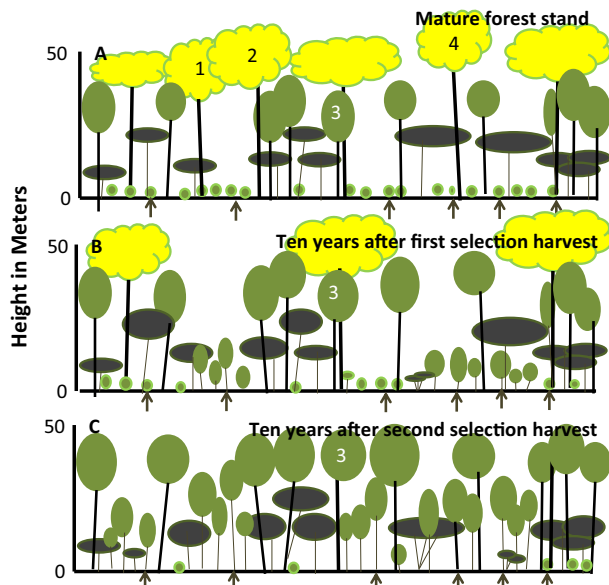
### 4.1. The selection regeneration method

The single-tree selection system extracts single canopy trees creating small gaps of varying sizes (80–250 m<sup>2</sup>) at frequent intervals (Fig. 2a). At the stand level, purposeful gap creation provides enough growing space for one or just a few trees to attain the canopy. Overall, the collection of cohorts growing in these gaps reflects an all-aged forest (Smith et al., 1997).

Selection systems may have canopy trees removed across the stand forming openings arranged as irregular patches (2500 to 5000 m<sup>2</sup>), or smaller openings where groups of canopy trees are taken out together (300–500 m<sup>2</sup>). Patch or group selection systems mimic larger multiple-windthrows and are suitable for regenerating shade-intolerant species if advance regeneration of the desired canopy trees exist or if the gap is large enough for seeds to germinate (Fredericksen and Putz, 2003).

Trees can also be removed in strips to create linear openings. These linear openings create more edge effect but their orientation can moderate or accentuate radiation, moisture and wind effects





**Fig. 2a.** A mature forest stand dominated in the canopy by long-lived light-demanding canopy tree species. The stand is to be regenerated by the single-tree selection method on a cutting cycle of 30 years. Profile A depicts the stylized and simplified condition of a mature stand, prior to regeneration treatment (e.g. year 0). Trees in the canopy and emergent stratum are the long-lived light-demanding trees (represented by yellow puffy-shaped crowns). Late-successional shade-tolerant canopy trees are represented by green vertically oval shapes; and subcanopy and understory tree species have dark gray horizontally spreading shapes. The numbered trees are those long-lived canopy trees that in a selection system would be the first trees to be cut because they are the largest. The arrows point to advance regeneration of the late-successional shade-tolerant canopy that is released when the large trees are removed. Profile B depicts the stand structure and composition 10 years after the first cutting of a selection harvest (e.g. year 10) that removes some of the largest long-lived light-demanding canopy trees (1, 2, 4) to create canopy openings. At ten years the young stand is dominated by advance regeneration that was present before the openings were created and that has now been released. Pioneers and long-lived light-demanding species have failed to regenerate because of shade or loss of parent tree seed source. Profile C depicts the stand structure and composition 10 years after the second entry in a selection harvest (e.g. year 40) that removes the next largest trees to create more canopy openings. This removes the last remaining largest long-lived light demanding canopy tree species. The stand is now dominated by advance regeneration of two released cohorts of late-successional shade-tolerant trees by prior harvests. Subcanopy and understory tree species that were cut to create the openings during the harvests have sprouted back vegetatively.

and mitigate potential susceptibility to soil erosion (Smith et al., 1997). Strips may be enlarged at the regenerating edge adjacent the mature canopy at each entry in the cutting cycle, allowing strip systems to be used in circumstances where steep slopes are prone to erosion or where stands are adjacent to riparian floodplains.

Strip, group, and single-tree selection normally clear less forest area, providing for greater amounts of side and canopy shade and favoring shade-tolerant species; whereas patch selection systems favor the establishment and release of more shade intolerant canopy timber species (Smith et al., 1997). At each entry these variants of the selection regeneration method require thinning (dominant thinning) and release (liberation release treatments) treatments fostering the growth of desirable species (see Smith et al., 1997 for silvicultural terminology).

Usually selective logging of tropical forests employs a modified version of single-tree selection whereby no liberation from smaller strata or dominant thinning to larger strata is applied (Hall et al., 2003; Putz et al., 2008a, 2008b). Initially, small gaps release advance regeneration and sprout growth of shade tolerant species (often subcanopy tree species) which outcompete seeds of germinating shade-intolerant trees. Later, much of the gap growing space is replaced by surrounding canopy and subcanopy tree in-



**Fig. 2b.** A mature forest stand dominated in the canopy by long-lived light-demanding canopy tree species that is regenerated by the shelterwood method. Profile A depicts the same stylized and simplified condition of a mature stand, prior to regeneration treatment as the example for the single-tree selection harvests (see above (a)). The numbered trees are those long-lived canopy trees that remain after treatment to serve as a seed source and to grow further. The arrows point to advance regeneration of the late-successional shade-tolerant canopy that is released in future shelterwood treatments. Profile B depicts the stand structure and composition 10 years after a shelterwood harvest that has removed all but a few canopy trees (1, 2, 4) judiciously left behind as a seed source for the long-lived light-demanding canopy trees (some are subsequently removed later after successfully establishing the new stand). At ten years the young stand is dominated in the canopy by very fast-growing light-demanding pioneers that came in immediately after the harvest from seed rain. These trees are depicted by open horizontal green oval lines and open vertical ovals. The advance regeneration present before treatment has been released and grows more slowly beneath the pioneers, the understory and subcanopy trees that were cut during the shelterwood harvest are sprouting back. The regeneration of long-lived light-demanding canopy trees established with the pioneers in the high light conditions and open soils immediately after the shelterwood harvest. The seed of the long-lived light-demanding tree species came from nearby parent trees left behind after the shelterwood harvest. Profile C depicts an essentially even-aged, mixed-stratified stand after 30 years of growth and development, with a single older reserve (1) left after the original cutting. No major intrusions have been done other than to harvest the early successional non-timber forest products. The pioneers have either been harvested or died from being over-topped by the current canopy of long-lived light-demanding canopy trees and subcanopy slower-growing late-successional trees that were released originally as advance regeneration. Sub-canopy and understory trees of the same age that are largely of vegetative origin, fill out the strata.

growth. In many cases, even shade-tolerant regeneration may not establish. In these circumstances shade-intolerant trees rarely survive to maturity (Ashton, 2003).

#### 4.2. Efficacy of the selection regeneration method

Selection systems were originally designed to manage shade-tolerant mono-specific, all-aged, small acreage stands in temperate forests (Troup, 1928). In these systems the forest dynamic is highly predictable and easily tracked, as for example the shade-tolerant *Picea abies* (Norway spruce) forests in northern Europe (Fries et al., 1997; Lundqvist, 2003). Conversely, the science of tropical forest dynamics and particularly the autecology of most tropical tree species remains poorly understood (Norden et al. 2015).

In many tropical regions, tree-level all-aged management can be an important practice through selection systems but under very different circumstances. For example ancient indigenous silviculture of tree gardens and managed fallow systems that have been intensively managed have been well described specifically for Mesoamerica (Gómez-Pompa, 1987; Peters, 2000) but also more

generally (Gómez-Pompa and Kaus, 1992; Salafky, 1994; DeJong, 1996; Marjokorpi and Ruokalainen, 2003). In Mesoamerica, Indigenous silviculture (e.g. Maya) worked within a diversity of economic and social systems (multiple values) justifying intensive all-aged silvicultural practices in small areas. The French even termed the system *jardinage* (“gardening”) a name owed to the regular care needed to implement these systems (Broun, 1912; Troup, 1928).

For many shade-tolerant trees in relatively species poor temperate and boreal forests, selection systems can be implemented at an economically efficient scale that does not dramatically compromise tree diversity. In diverse tropical forests, with weak and less diverse timber markets, unstable land tenure, and weak environmental regulation, this irremediably promotes maximizing economic returns in the short run and minimizing costs that simplify the selection regeneration method (Putz et al., 2000, 2008). This is accomplished by implementing a minimum-felling diameter without regard to changes in forest growth and the characteristics of individual species. Instead selective logging applies a broad scale prescription across a variety of floristic associations, sites, stocking and age class distributions (Figs. 2b and 3). In temperate forests this has often been termed high-grading, particularly if little regard is given for the regeneration of the timber species being harvested and the long term stability of the mixture (Nyland, 2002). Tropical silviculture is limited by the costly inputs of accessing a slow growing resource comprised of just a few high value timber trees (Wadsworth, 1981; Hartshorn, 1989).

Regardless of the forest type, selection systems should require intensive management practices in small stand-specific areas, applied to site-specific floristics with an in-depth knowledge of the species composing the stand (Brandis, 1907; Troup, 1921). Very early in the history of tropical forestry, Dietrich Brandis (1907) stated that, “correctly identifying the species is the first step toward the systematic treatment of forests”. At present this foundational knowledge is largely lacking from timber-oriented management systems (Biscaia de Lacerda and Nimmo, 2010). However, work in Costa Rica (Clark and Clark, 1987; Clark et al., 1998; Clark et al., 1999) Panama (Engelbrecht et al., 2007), and the region as a whole demonstrate shifts in floristic associations along topographic, and edaphic gradients within tropical forests, particularly as stands age (van der Sande et al. 2016). These studies highlight the importance of developing silvicultural systems that are site-specific, stand-based, and related to the autecology of the species present (Ashton, 2003; Ashton and Hall, 2011).

Considerable work, again in Costa Rica and Panama, demonstrates differential growth and mortality rates within mixed species stands (Lieberman et al., 1985; Condit et al., 1995; Bloor and Grubb, 2003). Because species grow at different rates and mature at different times, applying selection systems in diverse floristic associations can be troublesome (Ashton and Peters, 1999; Ashton and Hall, 2011). Managing the numerous pollination and dispersal interactions within the complex forest structures of high-species-diversity tropical forests requires both skill and ecological knowledge (Fredericksen, 1998). The lack of baseline information has largely restrained tropical forest silviculture from evolving more rapidly.

#### 4.3. Understanding the selective in selective logging

Troup (1921) stated that, “selection systems are the most difficult of all silvicultural systems to apply correctly”. In theory, selective logging should incorporate treatments intended to release existing cohorts (e.g. liberation release and dominant thinning) at the same time as the final harvest of the large timber trees (treatments intending to promote establishment of a new cohort (e.g. creating openings of sufficient size to open up new growing space at the groundstory) into one operation (Smith et al., 1997). How-

ever, in practical application tree selection is almost always based on the industry needs rather than on regeneration requirements of future cohorts (Dawkins and Philip, 1998). This is why priority is mostly assigned to the size of tree harvested rather than the type of regeneration to purposefully establish (Zamorano-Elgueta et al., 2014). Selectively logged forests are therefore often depleted of their largest seed-producing trees. The problem is further complicated by the focus on a small subset of commercially viable species (Fredericksen and Licona, 2000). Capability to establish new regeneration in gaps after harvest is therefore lost (Hutchinson, 1987; Fredericksen, 1998). For this reason selective logging in rainforests often fails to regenerate vigorous cohorts of the desired species, especially when the valued timber species are shade-intolerant (Peña-Claros et al., 2008).

For a forest type with a canopy of long-lived shade intolerants, an irreversible structural impoverishment follows from several cutting cycles (Fredericksen, 1998). The emergent and canopy trees are removed (i.e. selected for their value and size) and a subcanopy size-class of more shade-tolerant tree species that are below the minimum felling diameter usurps the canopy growing space (Hall et al., 2003). Furthermore, a compositional homogenization of strata occurs as shade-tolerant sub canopy trees are favored by low light in single-tree gaps (Wadsworth, 1987; Peña-Claros et al., 2008). The long-term stability of the mixture is thus compromised. These widely observed effects provide a parsimonious explanation for the shifts in species composition and structure observed in old growth forests throughout the region (van der Sande et al. 2016).

Appropriate silviculture purposefully increases the concentration of valuable and desired species in the stand while limiting the prevalence of undesired species (Peters, 2000). Selective logging as currently practiced extracts valuable timber species but the gap area surrounding the selected tree(s) is seldom arranged to regenerate the species removed, but rather, scaled to reduce the residual impact of the harvesting process. The silvicultural deficiencies of selective logging are therefore three-fold: (1) it removes the seed-bearing trees prior to securing regeneration (i.e. only advanced regeneration and sprout growth is favored) (Wadsworth, 1987; Ashton, 2003; Ashton and Hall, 2011); (2) potentially removes successful genotypes for seed production, growth and competition (Degen et al., 2006; Sebben et al., 2008); and (3) it fails to create the light environment sufficient to allow shade-intolerant trees to establish or to be released to form a new developing cohort (Ashton and Hall, 2011).

#### 4.4. Selective logging as a practice in Mesoamerica

When compared to its Amazonian, African and South-East Asian analogs, the Mesoamerican rainforests have little reported research on post-logging forest regeneration. Original work in Mesoamerica was in Belize (Lamb, 1947; Lamb, 1966). But more recently silvicultural research has focused on Costa Rica (1960-ongoing) through the Tropical Agricultural Research and Higher Education Center (CATIE). Budowski's (1960) work on succession initiated the trend toward documenting and testing experimental silviculture treatments in Costa Rica (Hutchinson, 1987; Finegan and Camacho, 1999; Finegan et al., 1999).

Selective logging is the chief silvicultural method used in Mesoamerica for the extraction of large timber trees (FAO, 2008). One example is the management of the Atlantic coastal forest of Costa Rica, dominated by *Pentaclethra macroloba* (Fabaceae) (Sitoe et al., 2001). This shade-tolerant timber tree vigorously colonizes any available gap area after selective logging, often outcompeting more commercially valuable species such as the shade-intolerant *Carapa guianensis* (Webb, 1998; Finegan et al., 1999). Due to its abundance and even distribution among size classes,

sustainable production of *P. maculoba* appears compatible with the application of minimum felling diameters. Similarly, regeneration of shade-tolerant *Mortoniendron vestitum* (Malvaceae) was prevalent in gaps after selective logging in Honduras (Kukkonen et al., 2003).

In forest stands dominated by *Peltogyne purpurea* (Caesalpinaceae) and *Caryocar costaricense* (Caryocaceae) on the Osa Peninsula of Pacific side Costa Rica, densities of smaller trees of these species actually decreased 15 years after selective logging (Lobo et al., 2007). If harvests continue every 15 years without liberation and thinning treatments (Hutchinson, 1987), a reduction in reproductive individuals is likely (Lobo et al., 2007). Although data are limited, in cases where species are especially shade-intolerant, even the addition of post-harvest liberation and thinning treatments may not provide sufficient light to establish a new cohort (Finegan et al., 1999).

Selection systems do sustain shade-tolerant *Mora excelsa*, and associates, *Ocotea* spp., and *Peltogyne venosa* in a similar forest type and timber species in Suriname using the CELOS system (De Graaf, 1986). In this system, careful tending of commercial crop trees by removing vegetative competition through liberation treatments is important at each entry. Thinning and liberation treatments accompany selection harvests removing 20–40 m<sup>3</sup> ha<sup>-1</sup> of merchantable timber at 20–30 year intervals. In addition to maintaining species diversity, the CELOS system has a higher financial return than a less intensive 100-year return interval with little silvicultural input (De Graaf et al., 2003).

Though, species like *Pentaclethra maculoba* have an autecology compatible with selection systems there are many examples of more shade-intolerant species where “selective logging” has proven incompatible. One example is *Swietenia macrophylla* (mahogany, Meliaceae), especially in the Maya Region (Mexico, Belize and Guatemala) and in the rainforests of the Atlantic coast and hill region in Nicaragua and Panama (CITES, 2003; Manzanero and Pinelo, 2004; Cámara-Cabral and Snook, 2005; Snook, 2005; FAO, 2008). To this point, mahogany has largely driven forest investment in this region (Dawkins and Phillips, 1998). Since World War II, minimum felling diameters coupled with 12- to 15-year cutting cycles have been used to exploit mahogany in Belize and elsewhere in Mesoamerica, originally based upon Lamb (1947). This method has been unsuccessful in regenerating mahogany and other species have had to be marketed (e.g. *Mora* spp., *Virola* spp., *Cedrela* spp.) (Negreiros-Castillo et al., 2003; Dawkins and Philip, 1998).

Another shade-intolerant Meliaceae, *Carapa guianensis*, is also extensively harvested in Costa Rica and Nicaragua. In the Atlantic coastal forest of Nicaragua selective harvests at a 70 cm DBH limit of *Carapa guianensis* (Meliaceae) trees removed 6.3 trees ha<sup>-1</sup> yielding a merchantable volume of 45.8 m<sup>3</sup> ha<sup>-1</sup>, and reducing stand basal area by 20%, with 18% residual damage (Webb, 1998). No evidence was recorded of successful regeneration and growth.

When larger gaps are created whereby groups or patches of trees are removed, coupled with site preparation techniques and/or thinning and liberation practices, selective logging may promote the regeneration of shade-intolerant trees (e.g. in southeastern Mexico; Dickinson et al., 2000). Current studies indicate more directed disturbances than those created by diameter-limit cutting are required for most timber trees in Mesoamerica, however this needs further investigation and testing (Table 1). This is an important point that cannot be over-emphasized and implies that although selection systems are not incompatible with more shade intolerant trees and forest types, canopy opening size should often be much larger (group- to patch-sized) and that more intensive site treatments to the groundstory may be warranted. The problem is that with selective logging this kind of silviculture is almost never properly implemented.

## 5. Alternative regeneration methods for shade-intolerant timber species

Though selective logging with diameter limit cutting is the norm throughout the tropics, there are alternative methods to regenerate forests. The main distinction separating selection systems (of which selective logging is a variant) and other methods is that other methods plan for and establish regeneration separately from post establishment treatments (thinnings, liberation). For example, in shelterwood and seed tree systems, regeneration is secured first by purposefully opening growing space and creating the appropriate environment (moisture and shade conditions) for germination and establishment of seedlings from nearby seed trees, while also releasing existing advance regeneration. The final removal of the parent tree overstory is then planned only after the regeneration is established and the composition and structure of the emerging cohort inventoried and assessed. Then over the course of development, the new stand is tended through release treatments and subsequent thinning as the trees mature (Fig. 2b). It is not until the end of the rotation nears that the stand is again purposefully regenerated (see Smith et al., 1997).

### 5.1. Shelterwood and seed tree regeneration methods

Shelterwood and seed tree systems focus on rotations rather than cutting cycles. In these systems, young stands are given considerable time (40+ years) to develop after regeneration before any entry is made; later thinnings accelerate stand growth by purposefully directing resources to the most desirable individuals (Smith et al., 1997). When the stand attains maturity, it is again regenerated all at once. By carefully delineating the landscape into a stand-scale mosaic, the forest is managed to sustain a continuous supply of timber that is constrained by other values (e.g. open space recreation, biodiversity conservation, surface water supply) (Fig. 3). Stands are delineated based on differences in floristics and age class distribution, which are largely guided by changes in topography, soil fertility and historical disturbance. Stands are then allocated to protection (e.g. ecological reserves, riparian and wetland reserves) or production (timber and non-timber forest products). Those stands allocated to production are managed in such a way as to insure all phases of forest development (initiation, stem exclusion, understory re-initiation, old growth; after Oliver and Larson, 1996) are apportioned across the forest equally. Such planning promotes better integration of incompatible values, yields higher economic efficiencies, and facilitates easier monitoring of growth, yield, and forest condition (Ashton, 2003; Ashton and Hall, 2011).

Shelterwoods can be best applied to manage for shade-intermediate and shade-intolerant heavy-seeded tree species (Fig. 2b). However, they can also be modified to fit any shade-tolerance level depending upon the amount of residual overstory permanently left after successful regeneration and growth release (Lamprecht, 1989). The flexibility of the shelterwood system allows foresters to create very open stands in which trees are purely left as a seed source (i.e. seed-tree systems) or partial shade or darker canopy environments ideal for heavy-seeded shade-intermediate and shade-tolerant species reliant on advance regeneration (shelterwoods) (Ashton and Peters, 1999).

Shelterwoods (and to a lesser degree seed tree systems) can often include individual or groups of trees (e.g. reserves) that are left after canopy parent tree removal and satisfactory establishment of the new stand (Smith et al., 1997; Ashton and Hall, 2011). Preserving part of the original forest structure and composition; i) accommodates changes in future markets; ii) sustains a future forest structure and composition fostering seed dispersers



and pollinators; and iii) maintains an element of the tree species composition that is not the main focus of the new stand (Smith et al., 1997). Additionally, different site preparation techniques can be incorporated (e.g. burning, soil scarification) to promote particular disturbance dependent species. The more severe site treatments tend to be associated with the more open spaced canopies (i.e. seed trees methods). Shelterwoods often require little manipulation of the understory or the ground unless clonal herbaceous (i.e. Marantaceae, Zingiberaceae) or woody plants (i.e. Arecaceae) have completely occupied growing space purposefully reserved for establishment of advance regeneration (Fredericksen and Putz, 2003).

Financially, Ashton and Peters (1999) recommended that shelterwood and seed tree methods be practiced in forests with merchantable volumes of shade intolerant timber trees equal to or greater than  $40 \text{ m}^3 \text{ ha}^{-1}$  and where markets are diverse enough to accommodate many timber species. Shelterwood and seed tree methods are most effective for forests dominated by shade-intermediate and shade-intolerant timber species that regenerate well together, and are usually associated with large historical LIDs (e.g. hurricanes, swidden cultivation).

Systems designed to mimic precisely this process were implemented at a large scale by British foresters in 1940s and 50s in the African tropics (i.e. “tropical shelterwoods”; Lamprecht, 1989) but have been put into practice in Southeast Asia for at least two centuries (Troup, 1921; Wyatt-Smith, 1963; Ashton and Peters, 1999; Ashton, 2003). Shelterwoods were also adapted for the Mora forests in Trinidad (Beard, 1946). Shelterwoods consist of a series of canopy and subcanopy removal treatments inducing natural regeneration of shade-intolerant trees species adapted to canopy-replacing LIDs. The resulting even-aged mixtures of tree species can be highly diverse (Ashton, 1992; Smith et al., 1997); but will develop following an initial floristics model whereby all tree species are represented at the first stage of succession (Egler, 1954; Oliver and Larson, 1996). Subsequently, vertical stratification based on different species growth rates occurs allowing the most shade-intolerant faster-growing species to attain the canopy (Ashton, 1992; Ashton and Hall, 2011).

## 5.2. Applying shelterwood and seed tree methods in Mesoamerican rainforests

Mesoamerican rainforests are currently being managed using selective logging (FAO, 2008), with harvesting conducted at short intervals regulated by minimum felling diameters (Fredericksen, 1998). By extracting a smaller portion of the merchantable volume at each entry the forest structure is assumed to be relatively better preserved. However, multiple-entries for harvesting (every 15–30 years; Dekker and De Graaf, 2003) cause considerable and repeated damage, leaving questions as to whether selection systems really protect intact forest structure in the long term when compared to other silvicultural systems (Dawkins, 1961). Selective logging assumes the regeneration of desirable species by simply allowing forest gaps to re-vegetate from preexisting advanced regeneration without subsequent injury from surrounding impacts to the forest made later in time – an assumption that is largely erroneous (Fredericksen, 1998).

Shelterwood and seed tree systems purposefully focus on securing regeneration of desired timber species under a protected seed-bearing canopy while taking into account particular species regeneration requirements. These attributes make them an attractive alternative to selection systems (and selective logging). Both regeneration methods therefore do not purport to slavishly imitate nature's small gap processes and dynamics over time but reflect more episodic, infrequent, and larger disturbances (Ashton and Peters, 1999; Ashton, 2003). Many timber tree distributions in

Mesoamerica are clearly associated with differences in soil fertility and soil moisture (Clark and Clark, 1987; Clark et al., 1998; Clark et al., 1999; Engelbrecht et al., 2007). Many shade-intolerant timber species also originate from large-scale disturbances to regenerate. In both circumstances timber trees are therefore patchily distributed across the forest landscape. Treatments should therefore conform to the stand-scale distribution patterns of the timber trees within the forest.

Given the changes in our ecological understanding of forest dynamics, over this past thirty years, we suggest shelterwood and seed tree systems be developed to complement selection methods and to match our better understanding of forest dynamics. With new methods we can manage for a greater variety of forest stand structures and compositions particularly for shade-intermediate and -intolerant species. A growing body of circumstantial evidence supports the implementation of shelterwood and seed-tree regeneration methods, however, further experimental research is needed to confirm the utility of these methods under field conditions.

To date, as far as we are aware, just one case study tests the shelterwood regeneration method on a 29.3-hectare property with a *Pentaclethra macroloba*-dominated rainforest in Costa Rica. The shelterwood was conducted by removing all non-merchantable >10 cm DBH subcanopy trees to promote shade-intolerant regeneration establishment beneath. In the experiment, the shelterwood treatment presented less mortality to regeneration after harvesting when compared to a selection system with liberation, with recruitment higher than the mortality of the residual overstory trees from dieback and shock from sudden over-exposure to full sun (Finegan and Camacho, 1999).

Examples where shelterwoods and seed tree methods should be applied are diverse. We propose that shelterwoods are applicable to floristic associations that have originated from LIDs (Fig. 3). Shelterwood and seed tree design should vary in residual overstory retention according to the shade tolerance, mode of seed dispersal and germination requirements of the target timber species. For Mesoamerica, we define three general groups of timber species: (i) long-lived heavy-seeded trees often associated with flooded low-lying areas; (ii) long-lived wind-dispersed trees on windy and/or fire-prone sites; and (iii) short to medium-lived wind-dispersed trees that are shade intolerant and are associated with second-growth after pasture abandonment. Silvicultural differences between all three groups depend upon a need for coupling shelterwood or seed tree regeneration method with different site-preparation techniques, a variety of patterns and ways of retaining overstory reserves, and the spacing of seed trees. What follows are a series of suggestions for appropriate stand and topographic conditions that need to be experimentally tested.

### 5.2.1. Flooded and riparian forests

Many canopy timber species with heavy seeds or large fruits are often associated with low-lying alluvium flood plains, swamps or where riparia are extensive (Standley and Steyermark, 1958; Pennington and Sarukhán, 1968; Zamora, 2000; Jiménez et al., 2002; Flores, 2003; Barwick, 2004; Pérez, 2008). These forests are predominantly located on the more seasonal, wetter, Atlantic coastal side of Mesoamerica, especially in Honduras, Nicaragua and Costa Rica (Holdridge, 1947; Holdridge, 1967). These sites are regularly inundated with floodwater and prone to small-to-large-scale windthrow primarily from seasonal convectional windstorms (Boucher et al., 1994; Acosta, 2000). Flooding (Salo et al., 1986) or occasional droughts (Schleuning et al., 2008) in these forests can sometimes inhibit clonal development of herbaceous understories (i.e. Heliconiaceae, Marantaceae, Bromeliaceae and Pteridophyta); in other forest types, which are perhaps more regularly flooded, vegetative and clonal understories (e.g. bamboo,



palms) can be more dominant. Clonal understories of flooded forests have been reported elsewhere in the neotropics (e.g. Peruvian Amazon – Griscom et al., 2007). Advance regeneration of large-seeded canopy timber trees can establish in the understory and grow beyond the flood level in one season because of the sizeable parental endowment in the seed (Richards, 1996; Dalling, 2002). This advance regeneration is normally released after a windstorm as a single-aged cohort (Boucher, 1990; Ashton, 1992; Oliver and Larson, 1996; Baker et al., 2005), but no research in Mesoamerica has been done to demonstrate this.

These species and sites are probably suited to the development of shelterwoods and need to be experimentally tested. Shade-intolerant timber trees that are restricted to flooded riparia (*Anacardium excelsum*, *Andira inermis*, *Dipteryx panamensis*, *Hura crepitans*) (Clark et al., 1992; Jimenez et al., 2002) or flooded swamp systems (*Carapa guianensis*, *Pachira aquatica*, *Pterocarpus officinalis*) (Clark et al., 1999; Jimenez et al., 2002) could be regenerated using shelterwood treatments that remove the entire subcanopy leaving parent tree canopy spacing that is relatively uniform. After securing advance regeneration the canopy can be partially or entirely removed and spaced. Retaining a parent tree overstory may not be necessary if advance regeneration is well established prior to harvest. Under these circumstances, no preparatory treatments is necessary to secure establishment of advance regeneration and instead the subcanopy and canopy can be removed in a single cutting (i.e., one-cut shelterwood). Such systems are commonly used to regenerate temperate heavy-seeded shade-intolerant species such as hickory and oak (Hannah, 1988), especially in the large floodplains of the U.S. Gulf (Oliver et al., 2005). Reserves left for structure, habitat, and greater species diversity should be grouped together to reduce the shading effect of the canopy edge on the release of the young shade-intolerant stand below. For example shade-tolerant species within shelterwoods for riparia and lowland forest (e.g. *Calophyllum brasiliense*, *Copaifera camibar*, *Hyeronima alchorneoides*, *Hymenaea courbaril*, *Prioria copaifera*, *Virola* spp.) (Clark and Clark, 1992; Clark and Clark, 1999; Clark et al. 1999; Flores, 2002), and flooded swamps (e.g. *Pentaclethra maculobola*) (Clark, 1994) can be retained either in groups or singly as subcanopy trees, with a tighter spacing of parent trees in the overstory. Caution must be used in regulating the amount of retained overstory because dense canopies readily dampen the rapid growth of shade-intolerants, preferentially favoring more shade-tolerant species over the longer term.

### 5.2.2. Upland forests in the hurricane belt

Wind-dispersed long-lived timber species often dominate upland sites where large-scale wind damage interacts with fire. The Mesoamerican rain forests most prone to wind and fire exhibit strong seasonality and susceptibility to hurricanes. This includes the hurricane belt of Mexico's Yucatan Peninsula, parts of the Guatemalan Petén, and Belize, and the drier Pacific side of Panama. Fire is also more frequent in this region because anthropogenic ignitions of post hurricane debris is prevalent during the dry months (Uruqhart, 2008), and is often associated with nearby agriculture and settlements. Fire has a long historical legacy in this forest as well dating to ancient swidden and agricultural systems (e.g. Maya region: Peters, 2000).

Fire-prone conditions are created when hurricanes and strong windstorms cause multiple and widespread windthrow and snap-offs across the forest (Lugo et al., 1983; Everham and Brokaw, 1996; Turner et al., 1997). When the slash and debris caused by these wind storms is exposed to full sun, it rapidly dries leaving conditions a tinderbox ready for fire. Ground-story fires clear the understory and stand-replacing fires burn forest areas, scarify, and expose the mineral soil. Post-disturbance regeneration is dominated by shade-intolerant mast-fruiting, and/or wind-

dispersed canopy timber trees that can withstand winds and endure fire through deep rooted stems with thickened fire-enduring bark (Snook, 1996; Barlow et al., 2003; Rocha et al., 2006; Baker et al., 2008; Negreros-Castillo and Mize, 2008).

To emulate such events, methods can use nearby parent tree seed sources in tandem with site treatments that eradicate ground-story competition, and in some cases prescribed fire or mechanical scarification (Snook, 1996, 2003; Negreros-Castillo et al., 2003; Snook et al., 2005; Toledo-Sotillo and Snook, 2005). In these treatments subcanopy and understory trees are removed and the spacing among parent trees is wide; reserves are minimized avoiding excessive edge effect on newly established shade-intolerant regeneration. Indeed, experimental evidence from these forests suggests pairing relatively large (.5 ha) gaps with site treatments like burning and machine clearing, floristic composition can return to pre-harvest levels in approximately 5 years (Valdez-Hernandez et al., 2014).

Wind-dispersed timber species compatible with seed tree methods on upland, well-drained acidic soils are *Albizia* spp., *Tabebuia* spp., *Terminalia* spp., and *Vochysia* spp. (Jiménez et al., 2002; Flores, 2003; Barwick, 2004). Seed tree methods for *Luehea seemannii*, *Swietenia macrophylla*, and *Cedrela* spp., are usually associated with rich soils along ephemeral streambeds (Snook, 1996; Jiménez et al., 2002; Flores, 2003; Snook 2003; Barwick, 2004; Grogan et al., 2005; Snook et al., 2005; Negreros-Castillo and Mize, 2008). On nutrient rich soils, such systems also mimic swidden cultivation as reported for forests in Panama, Costa Rica, Nicaragua, Guatemala, Honduras and Mexico (Binford and Leyden, 1987; Rue, 1987; Piperno and Pearsall, 1998; García-Montiel, 2002; Montagnini, 2007). Existing stands of *S. macrophylla* in the Maya territory in Quintana Roo, Mexico, where swidden agriculture was practiced, is evidence of this (Whitmore and Burslem, 1998). In almost all cases the site specific distributions of these timber trees mandate that stands are restricted to relatively small patches embedded within the forest. Patches should be managed sequentially to insure continuous sustainable harvests over the long term.

Other more site generalist and light-seeded timber species such as *Cordia* spp., *Jacaranda copaia*, *Ceiba pentandra*, *Ochroma pyramidale*, and *Schyzolobium parahyba* are suited to soil scarification (Dalling et al., 1997; Fredericksen and Pariona, 2002; Fredericksen and Putz, 2003) and will be voluntary co-associates requiring little attention because of their more effective wind, bird, or bat dispersal from distant parent trees (Fig. 3, Fredericksen, 1998).

To include more shade-tolerant species (e.g. *Manilkara* spp., *Brosimum alicastrum*) on these sites the regeneration method may require a more moderate approach. It could reflect a hybrid between shelterwood and seed tree where some of the subcanopy is preserved, more overstory shelter and seed source of shade-tolerants left, and site treatments to the groundstory (prescribed burning and scarification) restricted to certain areas within the stand to allow some shade tolerant advance regeneration to survive.

Lastly, conifer types within the rain forest region of Mesoamerica are suited to site specific shelterwood or seed tree systems given their masting habits and need for mineral soil for best germination. For instance native forests of Caribbean pine (*Pinus caribaea*) are drought adapted and fire-enduring (Parsons, 1955; Myers and Rodríguez-Trejo, 2009). Such forests are restricted to infertile, sandy coastal ridges on the Atlantic side of northern Mesoamerica (Belize, Guatemala, Honduras, Nicaragua) where groundstory fires can be common (Parsons, 1955; Myers and van Lear, 1998; Myers and Rodríguez-Trejo, 2009). Seed-tree systems with groundstory burns and mechanical scarification are likely ideal regeneration methods for these forests.

By contrast *Podocarpus* stands within high elevation cloud forests occur in ever-wet climates with thick organic soil surface hori-

zons. *Podocarpus* spp. are relatively shade-tolerant and require a nearby seed source, along with exposed mineral soil to establish adequate stocking of advance regeneration (Teketay, 2011). In this case, shelterwood regeneration methods that retain more canopy trees could be paired with localized site scarification.

### 5.2.3. Second growth forests originating on old field pastures

The original study of old field succession in Mesoamerica was by Budowski (1960) who first described the composition changes over time. Many more recent studies document these patterns and processes in more detail (e.g. Chazdon et al., 2007; Holl, 2007). This process can be slow, with in-growth and seedling establishment of shade-tolerant slow-growing timber tree species still occurring beneath 16–18 year old pioneers (Guariguata et al., 1997). Most studies demonstrate the ability of regeneration to colonize old fields in the wet regions of Mesoamerica (Guariguata and Ostertag, 2001; Norden et al., 2009). The strength and composition of the re-growth is dependent upon nearby seed sources and the nature of prior agricultural land use (Guariguata and Ostertag, 2001; Norden et al., 2009). Forest re-growth is also dependent on many interacting site specific conditions, making exact predictions of the nature of secondary forest composition and structure unpredictable (Guariguata and Ostertag, 2001); however, overall these forests are generally resilient in species re-assembly (Norden et al., 2009). Unfortunately, most studies have only investigated the earliest stages of secondary succession. Little work has been done on mature second growth stands because so few are now present (Finegan, 1996).

Researchers at CATIE have suggested the use of shelterwoods for secondary forests of old field origin (Finegan, 1992; Finegan and Camacho, 1999). Such forests are dominated by fast-growing shade-intolerant species such as *Ceiba pentandra*, *Cordia alliodora*, *Laetia procera*, *Ochroma pyramidale*, *Rollinia* spp., *Schyzolobium parahyba*, *Simarouba amara*, *Spondias mombin*, *Stryphnodendron microstachyum*, *Tabebuia rosea*, *Vernonia trifusculosa*, *Vochysia ferruginea*, and *V. guatemalensis* (Finegan, 1992; Louman et al., 2001).

Depending on shade-tolerance and dispersal mode, shelterwoods on old field pastures may protect and release existing advanced regeneration or promote shade-intolerant regeneration through subcanopy and canopy removals. When wind-dispersed timber trees form the canopy, seed tree methods may be employed to establish regeneration (e.g. Finegan and Sabogal, 1988). For example, a seed tree method could be used to regenerate a 25-year old *Vochysia ferruginea* forest stand in Atlantic Costa Rica ( $161.9 \text{ m}^3 \text{ ha}^{-1}$ ; 953 trees  $\text{ha}^{-1}$  >5 cm DBH) (Fernández, unpublished data). However, if sufficiently more shade-tolerant advance regeneration (e.g. *Hyeronima alchorneoides*) is present a new, even-aged, cohort can be released by cutting all parent trees in one operation (i.e., one cut shelterwood). But if there is not sufficient advance regeneration present and there is a profuse cover of shrubs in the understory (e.g. *Vismia macrophylla*, *Henrietta fascicularis*, *Psychotria* spp.), site preparation needs to remove the understory through cutting to provide sufficient growing space for regeneration establishment before canopy removal. Experimental studies need to be done to test these suggestions but such treatments are commonly applied to second growth mixed-broadleaf forests in moist temperate realms (Smith et al., 1997).

## 5.3. Landscape and diversity considerations

### 5.3.1. Reserve stands and reserve trees within managed forest landscapes

One of the main criticisms of the use of shelterwoods and seed tree regeneration methods for tropical forests is that they simplify species composition and homogenize structure. However, shelterwood and seed tree systems should not be broadly applied across

widely varying topography (as are selection systems in many instances), but rather, are planned within a stand-scale mosaic across a landscape (Fig. 3). Stands that are allocated as reserves of different sizes and shapes are designed to protect an element of mature forest structure and composition across a managed forest landscape (Smith et al., 1997; Miller et al., 2006). Stands that are reserves are purposefully used to protect rare, threatened or potentially valuable species accentuating the structural complexity of adjacent managed stands (Ashton and Hall, 2011). In this sense, reserves create habitat for wildlife and foster seed dispersal (Bierregaard et al., 1992; MacArthur and Wilson, 2001; Norden et al., 2009). Many tropical timber species rely on animals to disperse their seeds (Dalling, 2002; Jimenez et al., 2002); particularly heavy-seeded tree species that are dispersed by large birds, large rodents, deer, tapirs and peccaries (Levey et al., 2002).

Individual or groups of trees (reserve trees e.g. snags, den trees, keystone fruit trees) left within stands managed under shelterwood and seed tree systems are also termed “reserves” (Figs. 2b and 3). They too are important structures that support nesting and foraging for animals; though commonly used in temperate silvicultural systems, only recently has research been directed to purposefully incorporating them into tropical forest management (Ashton and Hall, 2011). Den trees such as old hemi-epiphytic *Ficus* spp. create ideal habitat for wildlife (Richards, 1996). In temperate regions, snags, den and certain fruit trees are often purposefully kept after successful regeneration of a new cohort in shelterwoods to provide critical habitat for wildlife and seed dispersal agents (i.e. especially birds) (Gibbs et al., 1993). Recent research shows that snag density varies considerably among tropical forest sites, but in general snags in tropical forests are much larger than in their temperate analogs (Gibbs et al., 1993; DeWalt et al., 2003). Group and individual tree reserves may also be kept to preserve part of the original forest structure and age class distribution, retain slow growing late-successional species (i.e. *Minquartia guianensis*, *Dialium guianensis*) and promote important future seed sources for wildlife such as *Ficus* spp., *Virola* spp., and a variety of palms (Arecaceae) (Levey et al., 2002). Silviculturally, choosing reserve trees and their arrangement will vary according to the objectives of each shelterwood/seed tree. For example, on the Atlantic side of the Nicaragua–Costa Rica border, large individuals of *Dipteryx panamensis* should be kept to protect the nesting sites of the great green macaw (*Ara ambiguus*) (Hanson et al., 2006). Larger reserves may serve to keep patches of rare tree species such as *Ticodendron incognitum* in southern Pacific Costa Rica (Fernández, unpublished data).

### 5.3.2. Non-timber forest products

In Mesoamerica, the large-scale cultivation of NTFPs in combination with timber products dates back to the agricultural systems practiced by the Mayans, especially through swidden systems (i.e. intensively managed old field re-growth) (Gómez-Pompa, 1987; Peters, 2000). Guariguata et al. (2009, 2010) recently reviewed the compatibility of producing timber and NTFPs in the under existing conditions in tropics. Despite the lack of research in the region, we believe NTFP production to be compatible with shelterwood and seed tree timber regeneration systems (Guariguata et al., 2010). Work done by Chazdon and Coe (2001) in second growth supports this contention finding higher diversity of ethnobotanical uses than selectively logged and mature forests. Integration of NTFPs may also provide for enhanced financial returns. For example, results from a financial analysis in Asia revealed that long-term timber harvesting can be compatibly coupled with annual NTFP production, and that one-cut and uniform shelterwood systems were much more profitable than selective logging because of this. Net present values for the production of timber in combination with enrichment plantings of cardamom (*Elletaria ensal*), rattan

**Table 3**

A list of indigenous non-timber forest products (NTFPs) by species and family, stage of stand development at maturity, shade tolerance, use and the part of the plant utilized. These species can be compatibly grown through a successional sequence of stand developmental stages through shelterwood and seed tree regeneration methods for timber trees. Shade tolerance rankings – VSI–very shade-intolerant; SI–shade-intolerant; ST–shade tolerant; VST–very shade-tolerant. Stage of stand development after [Oliver and Larson \(1996\)](#) – SI–stand initiation; SE–stem exclusion; UR–understory re-initiation; OG–old growth. Source data: Modified from [Ocampo \(1994\)](#).

Species	Family (common name)	Growth habit	Shade tolerance	Use	Plant part used
<b>Stand initiation<sup>1</sup></b>					
<i>Aechmea magdalenae</i>	Bromeliaceae (pita plant)	Bromeliad (monocot)	SI	Fiber – basketry	Leaf
<i>Ageratum conyzoides</i>	Asteraceae (goatweed)	Pioneer herb	VSI	Biocide	Leaf
<i>Bixa orellana</i>	Bixaceae (achiote)	Early pioneer tree	SI	Food dye	Seed
<i>Bromelia pinguin</i>	Bromeliaceae (piñuela)	Bromeliad (monocot)	SI	Food, fiber	Fruit, leaf
<i>Capsicum annuum</i>	Solanaceae (chilli pepper)	Very early pioneer shrub	VSI	Spice	Fruit
<i>Carica papaya</i>	Caricaceae (papaya)	Early pioneer shrub	VSI	Food	Fruit
<i>Cecropia</i> spp.	Moraceae	Early pioneer tree	SI	Fiber	Bark
<i>Croton draco</i>	Euphorbiaceae (draconis palm)	Early pioneer shrub	SI	Resin	Bark
<i>Dysphania ambrosioides</i>	Amaranthaceae (Mexican tea)	Pioneer herb	VSI	Biocide	Leaf
<i>Eryngum foetidum</i>	Apiaceae (cilantro)	Pioneer herb	VSI	Seasoning, medicinal	Leaf
<i>Fevillea cordifolia</i>	Cucurbitaceae (javello)	Pioneer vine	VSI	Oil, medicinal	Seed
<i>Gyneryum saggittatum</i>	Poaceae (wild cane)	Grass (monocot)	SI	Roofing, construction	Stem
<i>Heliconia mariae</i>	Heliconiaceae (heliconia)	Shrub (monocot)	SI	Food, ornamental	Shoot
<i>Hypolepis</i> spp.	Dennstaedtiaceae	Fern	SI	Food	Leaf
<i>Indigofera</i> spp.	Fabiaceae	Herb	SI	Medicinal	Leaf
<i>Lippia alba</i>	Verbenaceae (bushy lippie)	Very early pioneer shrub	VSI	Oil, seasoning	Leaves
<i>L. graveolens</i>	“ (Mexican oregano)	Very early pioneer shrub	VSI	Seasoning, oil	Leaves
<i>Malvaviscus arboreous</i>	Malvaceae	Very early pioneer shrub	SI	Fiber, ornamental	Bark, flowers
<i>Momordica charantia</i>	Cucurbitaceae (bitter melon)	Pioneer vine	VSI	Medicinal	Whole plant
<i>Neurolaena lobata</i>	Asteraceae (jackass bitters)	Pioneer herb	VSI	Medicinal	Leaf
<i>Ocimum</i> spp.	Lamiaceae (basil)	Pioneer herb	VSI	Food, oil, medicinal	Leaf
<i>Petiveria alliacea</i>	Phytolaccaceae (Guinea henweed)	Pioneer shrub	VSI	Medicinal	Whole plant
<i>Phytolacca rivinoides</i>	Phytolaccaceae	Scandent shrub	SI	Medicinal	Stem
<i>Quassia amara</i>	Simaroubaceae (amargo, bitterwood)	Pioneer shrub	SI	Medicinal, biocide	Wood
<i>Renealmia aromatica</i>	Zingiberaceae	Shrub (monocot)	SI	Food	Fruit
<i>Ruta graveolens</i>	Rutaceae (common rue)	Pioneer herb	VSI	Medicinal, seasoning	Leaf
<i>Satureja viminea</i>	Lamiaceae (Jamaican mint)	Pioneer herb	VSI	Oil	Leaf
<i>Tagetes erecta</i>	Asteraceae (marigold)	Pioneer herb	VSI	Biocide	Whole plant
<b>Stem exclusion<sup>2</sup></b>					
<i>Acrocomia vinifera</i>	Arecaceae (grugru palm)	Palm tree (monocot)	SI	Food	Nut, fruit
<i>Apeiba</i> spp.	Malvaceae	Pioneer tree	SI	Resin	Seeds
<i>Attalea rostrata</i>	Arecaceae	Palm tree (monocot)	SI	Roofing, construction	Leaf
<i>Chusquea simplicifolia</i>	Poaceae (South American bamboo)	Bamboo (monocot)	SI	Fiber	Stem
<i>Desmoncus</i> spp.	Arecaceae	Climbing palm (monocot)	ST	Fiber	Stem
<i>Genipa americana</i>	Rubiaceae (genip)	Pioneer tree	ST	Food	Fruit
<i>Gliricidia sepium</i>	Fabiaceae	Pioneer tree	SI	Biocide	Leaf
<i>Haematoxylum</i> spp.	Fabiaceae (bloodwood)	Tree	ST	Dye	Wood
<i>Heliocarpus appendiculatus</i> (jonote)	Malvaceae	Pioneer tree	SI	Bark	Wood
<i>Lonchocarpus</i> spp.	Leguminosae	Tree	SI	Biocide	Leaf
<i>Mammea Americana</i>	Calophyllaceae (mammee apple)	Tree	ST	Food, biocide	Fruit, seed
<i>Mucuna andreana</i>	Fabiaceae	Climbing shrub	SI	Dye	Seed
<i>Pachira aquatica</i>	Malvaceae (Malabar chestnut)	Pioneer tree	SI	Ornamental, food	Whole plant, seed
<i>Serjania</i> spp.	Sapindaceae	Vine	SI	Biocide	Leaf
<i>Simarouba amara</i>	Simaroubaceae	Pioneer tree	SI	Medicinal	Bark
<b>Understory re-initiation<sup>3</sup></b>					
<i>Amphilophium paniculatum</i>	Bignoniaceae	Scandent understory vine	SI	Fiber, ornamental	Stem, whole plant
<i>Annona muricata</i>	Annonaceae (soursop)	Understory tree	ST	Food, biocide	Fruit, seed
<i>A. reticulata</i>	“ (custard apple)	Understory tree	ST	Food, biocide	Fruit, seed
<i>Anthurium scandens</i>	Araceae	Understory herb (monocot)	ST	Fiber	Root
<i>Arrabidaea chica</i>	Bignoniaceae (cricket vine)	Scandent understory vine	SI	Dye, medicinal	Leaf
<i>Asplundia</i> spp.	Cyclanthaceae (jungle drum)	Palm shrub (monocot)	ST	Ornamental	Whole plant
<i>Asterogyne maritima</i>	Arecaceae	Palm tree (monocot)	ST	Roofing, construction	Leaf
<i>Bactris gasipaes</i>	Arecaceae (peach palm)	Palm tree (monocot)	SI	Food	Fruit, young leaf shoot
<i>Brosimum utile</i>	Moraceae	Canopy tree	ST	Fiber	Bark
<i>Calathea insignis</i>	Maranthaceae (rattlesnake plant)	Understory herb (monocot)	ST	Ornamental	Whole plant
<i>Calyptrogyne</i> spp.	Arecaceae	Palm tree (monocot)	ST	Roofing, construction	Leaf
<i>Carapichea ipecacuanha</i>	Rubiaceae	Understory shrub	ST	Medicinal	Root
<i>Carludovica drudei</i>	Cyclanthaceae	Palm shrub (monocot)	SI	Fiber	Stem, leaf
<i>C. palmata</i>	“(toquilla)	Palm shrub (monocot)	ST	Food, fiber,	Shoot, stem, leaf,

Table 3 (continued)

Species	Family (common name)	Growth habit	Shade tolerance	Use	Plant part used
<i>Chamaedorea costaricana</i>	Arecaceae (bamboo palm)	Palm tree (monocot)	SI	ornamental	flower
<i>Cydistia diversifolia</i>	Bignoniaceae	Vine	ST	Ornamental	Whole plant
<i>Enterlobium</i> spp.	Fabiaceae (Guanacaste)	Canopy emergent tree	SI	Fiber	Stem
<i>Euterpe precatoria</i>	Arecaceae (acai, palmitche)	Palm tree (monocot)	ST	Resin	Bark
<i>Geonoma congesta</i>	Arecaceae	Palm tree (monocot)	ST	Food	Fruit, shoot
				Dye, roofing, construction	Leaf
<i>G. cuneata</i>	"	Palm tree (monocot)	ST	Roofing, construction	Leaf
<i>Heteropsis oblongifolia</i>	Araceae	Understory vine (monocot)	ST	Fiber	Root
<i>Iriartea deltoidea</i>	Arecaceae (bombona)	Palm tree (monocot)	ST	Food	Shoot
<i>Licania platypus</i>	Chrysobalanaceae	Understory tree	ST	Food	Fruit
<i>Peperomia</i> spp.	Piperaceae	Herb, shrub	ST	Ornamental	Stem
<i>Pimenta guatemalensis</i>	Myrtaceae (allspice)	Understory shrub	ST	Food, spice	Seed
<i>Pithecoctenium echinatum</i>	Bignoniaceae (monkey-comb)	Scandent understory vine	ST	Fiber	Stem
<i>Protium</i> spp.	Burseraceae	Sub-canopy tree	ST	Resin	Bark
<i>Ryania speciosa</i>	Salicaceae	Understory tree	SI	Biocide	Wood
<i>Smilax</i> spp.	Smilacaceae (greenbriar)	Understory vine	ST	Medicinal, fiber	Root, stem
<i>Socratea exorrhiza</i>	Arecaceae (walking palm)	Palm tree (monocot)	ST	Construction	Stem
<i>Theobroma bicolor</i>	Malvaceae (jaguar tree)	Understory tree	ST	Resin	Bark
<i>T. simiarum</i>	"	Understory tree	ST	Food	Fruit
<i>Trattinickia aspera</i>	Burseraceae	Understory tree	SI	Food	Fruit
<i>Welfia georgii</i>	Arecaceae	Palm tree (monocot)	ST	Food, construction	Shoot, stem
<b>Old growth<sup>4</sup></b>					
<i>Calthea micans</i>	Marantaceae	Understory herb (monocot)	VST	Ornamental	Whole plant
<i>Cattleya dowiana</i>	Orchidaceae (Guraia de Turrialba)	Epiphytic orchid	ST	Ornamental	Flower
<i>Cyclanthus bipartitus</i>	Cyclanthaceae	Understory palm (monocot)	VST	Medicinal	Leaves
<i>Hymenaea courbaril</i>	Fabaceae (stinktoe)	Late-succesional canopy tree	ST	Resin	Bark
<i>Philodendron rigidifolius</i>	Araceae	Hemi-epiphytic climber (monocot)	VST	Fiber	Root
<i>Pleurotus</i> spp.	Pleurotaceae (oyster mushrooms)	Saprotrophic mushrooms	VST	Food	Whole mushroom
<i>Reinhardtia gracilis</i>	Arecaceae	Understory palm shrub	VST	Ornamental	Seed
<i>R. simplex</i>	"	"	VST	"	"
<i>Synechanthus</i> spp.	Arecaceae	Understory palm shrub	VST	Ornamental	Seed
<i>Zamia skinneri</i>	Zamiaceae	Understory cycad shrub	VST	Ornamental	Whole plant

<sup>1</sup> **Stand initiation** – Very open conditions where the canopy of woody regenerating plants has not closed and is suitable initially (years 1–5) for very early successional herbs and then shrubs and later very fast growing early successional woody pioneers that are the first to create conditions of canopy closure (years 6–10).

<sup>2</sup> **Stem exclusion** – closed canopied conditions with extreme competition and crown self-thinning among woody pioneers that make conditions appropriate for early successional vines and climbers that require dense stem support from fast-growing columnar and narrowly-crowned trees.

<sup>3</sup> **Understory re-initiation** – closed canopied conditions whereby the stature and the self-thinning of the forest as amplified stratification and vertical structure and has promoted the re-establishment of herbs and woody regeneration of canopy trees in the understory. Many NTFP's that are understory monocots (e.g. palms and aroids) and shade-tolerant shrubs and sub-canopy trees are suited to these conditions as well as long-lived shade intolerant trees that have attained the canopy.

<sup>4</sup> **Old-growth** – comprises openings and a broken canopy with patchy, dead and dying large trees and young regenerating shade-tolerant late successional trees with a noticeable absence of pioneers and shade-intolerant shrubs and herbs because the openings are small. NTFP's that represent this stage of stand development comprise the decay dependent mushrooms, slow growing very shade-tolerant understory herbs, epiphytes and shrubs, and late-successional shade-tolerant subcanopy and canopy trees.

(*Calamus zeylanicus*) and fish tail palm (*Caryota urens*) that preserved the land in forest was comparable to the alternative agricultural use – monocrop tea cultivation (Ashton et al., 2001).

Similar possibilities exist for Mesoamerica, if commercially important NTFPs can be managed in timber production systems following a compatible successional sequence (Table 3). For example, many commercially valuable NTFPs such as herbs (*Ocimum* spp., *Eryngium foetidum*), monocots (*Heliconia* spp.), shrubs (*Lippia* spp., *Quassia amara*) and trees (*Cecropia* spp., *Bixa orellana*) may be grown to harvest during the stand initiation phase.

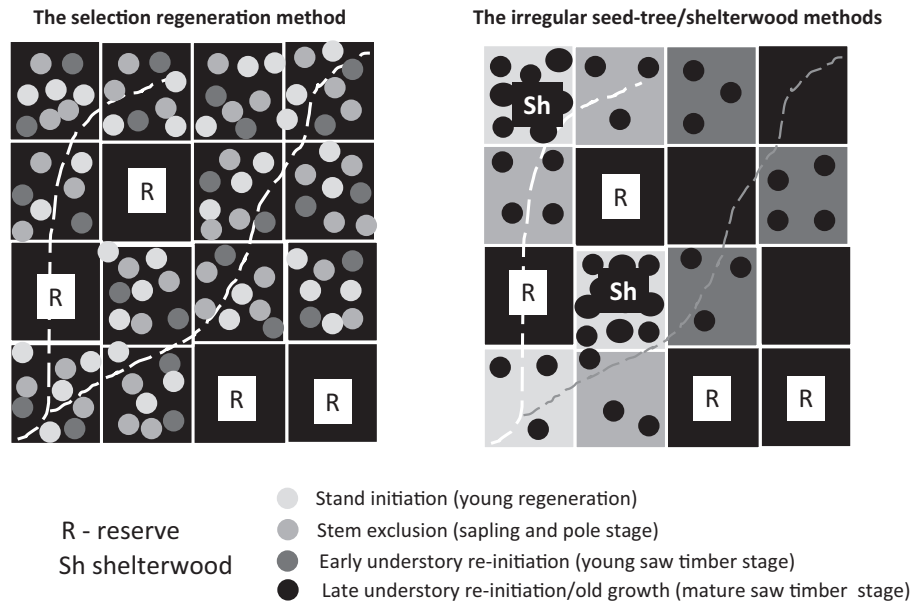
During stem exclusion, several timber trees also yield commercially valuable NTFPs, such as *Gliricidia sepium*, *Lonchocarpus* spp., *Pachira aquatica* and *Simarouba amara* (Table 3). Seed tree systems may favor more shade-intolerant herbs and shrubs, while shelterwoods may be used to manage shade-tolerant shrubs (*Pimenta* spp., *Peperomia* spp.) and trees (*Theobroma* spp., *Garcinia* spp.). The problem with NTFP cultivation is that the forester must accept the window of time when the particular NTFP being managed is successional compatible to harvest and must refrain from fighting succession as the forest continues to develop. Hence, the forester must manage for a continuously changing successional compatible series of NTFP's rather than just one. To insure contin-

uous yields of each and every NTFP desired within shelterwoods and seed tree systems means that the whole forest needs to comprise stands of different stages of development. In the end this makes for a more biologically and socially resilient forest to both changes in markets and human values and the vagaries of climate and natural disturbance (see Fig. 3).

### 5.3.3. Operational considerations

There have been many reviews regarding the improvement of felling and harvesting practices irrespective of the silviculture used (Putz et al., 2000, 2008); but little attention has been given to differences in the nature of operations among silvicultural systems. The biggest advantage in cost and operations is that shelterwoods and seed tree systems utilize a skid trail and road system only toward the end of the rotation. This leaves a large period of time from initiation to understory re-initiation during which time vehicular access is closed (Fig. 3), potentially controlling illegal use, erosion, and the suite of other detrimental secondary effects following open roads. This effect is bolstered, by the fact that shelterwood harvests focus logging impacts on a smaller area, requiring fewer roads to harvest the same volume of wood. With selection systems, by contrast, timber harvests are on a shortened





**Fig. 3.** A stylized depiction of a tropical forest landscape under two scenarios of silvicultural management: 1. Selection methods of regeneration; and 2. Irregular seed-tree or shelterwood methods of regeneration. The squares represent 16 stands of which four have been identified as reserves (R) where no timber cutting is done (protected areas). Under the selection method all stands have been logged at periodic intervals (cutting cycle) to create, in this case, four developmental age classes within the openings – regenerating (stand initiation), sapling/pole (stem exclusion), young saw timber (early understory re-initiation), and mature saw timber (late understory re-initiation/old growth). Under the irregular shelterwood/seed-tree methods the reserves (older age-class trees left behind as a source of seed and shade – depicted by dark circles) can be seen within stands representing the three younger developmental age-classes (stand initiation, stem exclusion, early understory re-initiation) that regenerated uniformly across each stand in prior years. For comparison these stand-level age classes were created at approximately the same time as the stand entries under the selection system. For stands in the young regeneration stage that were regenerated through the shelterwood method more trees were held initially for shade and some removed later (depicted as Sh). In the landscape managed under selection each stand would have a permanent set of skid trails (not illustrated) for extracting timber to roads (depicted by the dashed white lines) that would be permanently maintained. In the landscape managed under seed-tree/shelterwoods skid trails within each stand would only be utilized during the stand initiation stage and then “put to bed”. The road system would be only used where stands are being regenerated. In other areas the road can be closed down.

cutting cycle, and wood is harvested over a larger area meaning road systems are larger and need to be maintained and open more continuously (Laurance et al. 2009). Such continued access promotes illegal hunting, fragmentation, and continuous intrusion and damage from felling and extraction to parts of the stand that were regenerated in the prior harvest entry, driving landscape-scale degradation (Dykstra and Heinrich, 1992; Ashton and Hall, 2011; Clark and Covey 2012) (see Fig. 3). However, contrary arguments can be made whereby if forests under shelterwood management are not carefully policed, selection systems maybe more appropriate given a stronger permanence of infrastructure and people over the whole forest area. Further given numerous factors such as different land tenures (i.e. private land management, community forest ownership, government concession), market forces and their access, road access and infrastructure, and nature of personnel and their organization make illegal access for logging and hunting highly location-specific.

One caveat in the comparison of shelterwood and seed tree systems with the application of selection systems across forests is how they are classified through remote sensing and for purposes of monitoring. When applying these technologies care should be taken to classify patches of regenerating forest so as not to conflate forest management with deforestation in remote monitoring protocols.

## 6. Implications for forest management

Today's selective logging systems may appear to be a logical approach to managing the diverse forests of Mesoamerica. However, in practice, we believe the widespread use of this system degrades forest growing stock by gradually removing valuable, shade-intolerant timber species composing the emergent stratum

of the forest (Fredericksen, 1998; Sist et al., 2003; Fienkedly and Siehe, 2004; Degen et al. 2006; Sebben et al. 2008). We believe the time span at which LIDs occur and the constant focus on the frequently occurring perturbation of gap dynamics has promoted a perspective that disregards LIDs and the connection to practical silvicultural implementation where appropriate.

Historically, we have developed the tools for achieving sustainable tropical forest management but have failed to use them properly (Dawkins and Philip, 1998). Operations that reduce and minimize the impact of the logging to the site by improving harvesting technology and with careful planning by itself cannot guarantee sustainability (Putz et al., 2008a, 2008b). A “silvicultural intensification” has been proposed to promote the regeneration of more shade-intolerant timber species (Putz and Fredericksen, 2004). Here, we provide a framework for intensification and diversification of methods for obtaining tropical forest regeneration based on the autecology of the Mesoamerican forest association and site type. Foresters and policy makers should apply the full range of regeneration methods available, tailoring treatments to the forest type, ecology of the tree species involved, and the whole suite of site-specific factors. The development of these systems will require a generation of new experiments testing the application of seed-tree and shelterwood systems in the Mesoamerican region, but the continued reliance on the routine application of a single harvesting method ignores the differences in origin and dynamic among complex forest stands and endangers the sustainability of the region's forests.

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## References

- Ackerman, J.D., Walker, L.R., Scatena, F.N., Wunderle, J., 1991. Ecological effects of hurricanes. *Bull. Ecol. Soc. Am.* 72, 178–180.
- Acosta, L.E., 1998. Análisis de la composición florística y estructura para la vegetación del piso basal de la zona protectora La Cangreja Mastatal de Puriscal. Informe de Práctica de Especialidad. Instituto Tecnológico de Costa Rica, Cartago, Costa Rica, p. 69.
- Acosta, L.E., 2000. Regeneración de especies arbóreas en bosque manejados un año y medio de después del Huracán Mitch, en la costa norte de Honduras. CATIE, Turrialba.
- Alcorn, J.B., 1981. Huastec noncrop resource management: implications for prehistoric rain forest management. *Hum. Ecol.* 9, 395–417.
- Appanah, S., 1998. Ch. 8, Management of natural forests. In: Appanah, S., Turnbull, J. M. (Eds.), A review of Dipterocarps taxonomy, ecology and silviculture. Center for International Forestry Research, Jakarta, pp. 133–150.
- Ashton, P.M.S., 1992. Establishment and early growth of advance regeneration of canopy trees in moist mixed-species broadleaf forest. In: Kelly, M.D., Larson, B. C., Oliver, C.D., (Eds.), *The Ecology and Silviculture of Mixed-Species Forests*. Kluwer Academic Publ., Dordrecht, pp. 101–125.
- Ashton, M.S., 2003. The silviculture of dipterocarp forests in the Asian wet tropics. *For. Chron.* 79, 263–267.
- Ashton, P.M.S., Peters, C., 1999. Even-aged silviculture in mixed moist tropical forests with special reference to Asia: lessons learned and myths perpetuated. *J. Forest.* 97, 14–19.
- Ashton, M.S., Hall, J.S., 2011. The ecology, silviculture and use of tropical wet forests with special emphasis on timber rich types. In: Gunter, S., Weber, M., Stimm, B., Mosandl, R. (Eds.), *Silviculture in the Tropics*. Springer Verlag, New York, pp. 145–192.
- Ashton, P.M.S., Gunatilleke, C.V.S., Singhakumara, B.M.P., Gunatilleke, I.A.U.N., 2001. Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. *For. Ecol. Manage.* 154, 409–430.
- Ashton, P.S., 2004. Soils in the tropics. In: Losos, E.C., Leigh, J., Giles, E. (Eds.), *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network*. University of Chicago Press, Chicago, pp. 56–68.
- Attiwill, P.M., 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. *For. Ecol. Manage.* 63, 247–300.
- Aubréville, A., 1938. La forêt coloniale: les forêts de l'Afrique occidentale Française. Société d'éditions Géographiques, Maritimes et Coloniales 9, 1–245.
- Baker, P.J., Bunyavejchewin, S., Oliver, C.D., Ashton, P.S., 2005. Disturbance history and historical stand dynamics of a seasonal tropical forest in Western Thailand. *Ecol. Monogr.* 75, 317–343.
- Baker, P.J., Bunyavejchewin, S., Robinson, A.P., 2008. The impacts of large-scale, low-intensity fires on the forests of continental South-east Asia. *Int. J. Wildl. Fire* 17, 782–792.
- Barden, L.S., 1980. Tree replacement in a cove hardwood forest of the southern Appalachians. *Oikos* (1), 16–19.
- Barden, L.S., 1981. Forest development in canopy gaps of a diverse hardwood forest of the southern Appalachian Mountains. *Oikos*, 205–209.
- Barlow, J., Lagan, B.O., Peres, C.A., 2003. Morphological correlates of fire-induced tree mortality in a central Amazonian forest. *J. Trop. Ecol.* 19, 291–299.
- Barwick, M., 2004. *Tropical and Subtropical Trees: An Encyclopedia*. Timber Press, Portland, Oregon, USA, p. 484.
- Basnet, K., Likens, G.E., Scatena, F.N., Lugo, A.E., 1992. Hurricane Hugo: damage to a tropical rain forest in Puerto Rico. *J. Trop. Ecol.* 8, 47–55.
- Bauer, G.N., 1964. *The Ecological Basis of Rainforest Management*. Ministry of Conservation, New South Wales.
- Beard, J.S., 1946. The Mora forests of Trinidad, British West Indies. *J. Ecol.* 33, 173–192.
- Bellingham, P.J., Kapos, V., Varty, N., Healey, J.R., Tanner, E.V.J., Kelly, D.L., Dalling, W., Burns, L.S., Lee, D., Sidrak, G., 1992. Hurricanes need not cause high mortality: the effects of Hurricane Gilbert on forests in Jamaica. *J. Trop. Ecol.* 8, 217–223.
- Bierregaard, R.O., Lovejoy, T.E., Kapos, V., dos Santos, A.A., Hutchings, R.W., 1992. The biological dynamics of tropical rainforest fragments. *Bioscience* 42, 859–866.
- Binford, M.W., Leyden, B., 1987. Ecosystems, paleoecology and human disturbance in subtropical and tropical America. *Quatern. Sci. Rev.* 6, 115–128.
- Biscaia de Lacerda, A.E., Nimmo, E.R., 2010. Can we really manage tropical forests without knowing the species within? Getting back to the basics of forest management through taxonomy. *For. Ecol. Manage.* 259, 995–1002.
- Bloor, J.M., Grubb, P.J., 2003. Growth and mortality in high and low light: Trends among 15 shade-tolerant tropical rain forest tree species. *J. Ecol.* 91, 77–85.
- Boose, E.R., Foster, D.R., Fluet, F.M., 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecol. Monogr.* 64, 370–400.
- Boose, E.R., Serrano, M.I., Foster, D.R., 2004. Landscape and regional impacts of hurricanes in Puerto Rico. *Ecol. Monogr.* 74, 335–352.
- Boucher, D.H., 1990. Growing back after hurricanes. *Bioscience* 40, 163–166.
- Boucher, D.H., 1992. ¿En la costa un huracán cada siglo? *Wani* 12, 32–34.
- Boucher, D.H., Vandermeer, J.H., Yih, K., Zamora, N., 1990. Contrasting hurricane damage in tropical rain forest and pine forest. *Ecology* 71, 2022–2024.
- Boucher, D.H., Vandermeer, J.H., Mallona, M.A., Zamora, N., Perfecto, I., 1994. Resistance and resilience in a directly regenerating rainforest: Nicaraguan trees of the Vochysiaceae after Hurricane Joan. *For. Ecol. Manage.* 68, 127–136.
- Brandani, A., Hartshorn, G.S., Orrians, G.H., 1988. Internal heterogeneity of gaps and species richness in Costa Rican tropical wet Forest. *J. Trop. Ecol.* 4, 99–119.
- Brandis, D., 1907. *An Account of Trees, Shrubs, Woody Climbers, Bamboos and Palms Indigenous or Commonly Cultivated in the British Indian Empire*. Constable and Company Limited, London.
- Brokaw, N.V.L., 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14, 158–160.
- Brokaw, N.V.L., 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66, 682–687.
- Brokaw, N.V.L., 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. *J. Ecol.* 75, 9–19.
- Broun, A.F., 1912. *Silviculture in the Tropics*. MacMillan, London.
- Brown, N.D., Whitmore, T.C., 1992. Do Dipterocarp seedlings really partition tropical rain forest gaps? *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 4, 369–378.
- Burgess, P.F., 1975. *Silviculture in the Hill Forests of the Malay Peninsula*. Malaysian Forest Department Research Pamphlet 66, Kuala Lumpur, Malaysia.
- Burslem, D.F.R.P., Whitmore, T.C., 1999. Species diversity, susceptibility to disturbance and tree population dynamics in tropical rain forest. *J. Veg. Sci.* 10, 767–776.
- Bush, M., Piperno, D.R., Colinvaux, P.A., De Oliveira, P.E., Krissek, L.A., Miller, M.C., Rowe, W.E., 1992. A 14,300-yr paleoecological profile of a lowland tropical lake in Panama. *Ecol. Monogr.* 62, 251–275.
- Bush, M.B., Colinvaux, P.A., 1994. Tropical forest disturbance: paleoecological records from Darien, Panama. *Ecology* 75, 1761–1768.
- Cámara-Cabrales, L., Snook, L.K., 2005. Producción de semillas de caoba en México: Patrones de variación e implicaciones para la sostenibilidad. *Recursos Naturales y Ambiente (Costa Rica)* 44, 9–18.
- Canham, C.D., 1989. Different responses to gaps among shade-tolerant tree species. *Ecology* 70, 548–550.
- Chazdon, R., 2003. Tropical forest recovery: legacies of human impact and natural disturbances. *Perspect. Plant Ecol., Evol. Systemat.* 6, 51–71.
- Chazdon, R.L., Coe, F.G., 2001. Ethnobotany of woody species in second-growth, old-growth, and selectively logged forests of Northeast Costa Rica. *Conserv. Biol.* 13, 1312–1322.
- Chazdon, R.L., Letcher, S.G., van Breugel, M., Martínez-Ramos, M., Bongers, F., Finegan, B., 2007. Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philos. Trans. R. Soc. B* 362, 273–289.
- CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora), 2003. *The Sustainable Management of Swietenia macrophylla*. Second meeting of the Bigleaf Mahogany Working Group. Belem, BR.
- Clark, D.A., 1994. Plant demography. In: McDade, L. et al. (Eds.), *La Selva: Ecology and Natural History of a Neotropical Rainforest*. University of Chicago Press, Chicago, USA, pp. 90–105.
- Clark, D.B., 1996. Abolishing virginity. *J. Trop. Ecol.* 12, 735–739.
- Clark, D.B., Clark, D.A., 1987. Population ecology and microhabitat distribution of *Dipteryx panamensis* a neotropical rainforest emergent tree. *Biotropica* 19, 236–244.
- Clark, D.A., Clark, D.B., 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecol. Monogr.* 62, 315–344.
- Clark, D.B., Clark, D.A., 1999. Assessing the growth of tropical rain forest trees: issues for modeling and management. *Ecol. Appl.* 9, 981–997.
- Clark, D.B., Clark, D.A., Read, J.M., 1998. Edaphic variation and the mesoscale distribution of tree species in a Neotropical rain forest. *J. Ecol.* 86, 101–112.
- Clark, D.B., Palmer, M.W., Clark, D.A., 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology* 80, 2662–2675.
- Clark, J.B., Covey, K.R., 2012. Tree species richness and the logging of natural forests: a meta-analysis. *For. Ecol. Manage.* 276, 146–153.
- Clements, F.E., 1916. *Plant succession: an analysis of the development of vegetation* (No. 242). Carnegie Institution of Washington.
- Coates, A.G., Obando, J.A., 1996. The geologic evolution of the Central American Isthmus. In: Jackson, J.B.C., Budd, A.F., Coates, A.G. (Eds.), *Evolution and Environment in Tropical America*. The University of Chicago Press, Chicago, pp. 21–56.
- Cochrane, M.A., Alencar, A., Shulze, M.D., Souza, C.M., Nepstad, D., Lefevre, P., Davidson, E.A., 1999. Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science* 284, 1832–1835.
- Cochrane, M.A., 2003. Fire science for rainforests. *Nature* 421 (6926), 913–919.
- Coen, E., 1991. Climate. In: Janzen, D.H. (Ed.), *Natural History of Costa Rica*. Editorial de la Universidad de Costa Rica, San José, pp. 35–47.
- Condit, R., Hubbell, S.P., Foster, R.B., 1995. Mortality rates of 205 neotropical tree species and the responses to a severe drought. *Ecol. Monogr.* 65, 419–439.
- Condit, R., Perez, R., Daguerre, N., 2011. *Trees of Panama and Costa Rica*. Princeton Field Guides. Princeton University Press, Princeton, NJ.
- Cooke, R., 2005. Prehistory of native Americans on the Central American land bridge: colonization, dispersal, and divergence. *J. Archaeol. Res.* 13, 129–187.
- Dale, V.H., Lugo, A.E., MacMahon, J.A., Pickett, S.T.A., 1998. Ecosystem management in the context of large, infrequent disturbances. *Ecosystems* 1, 546–557.
- Dalling, J.W., 2002. Ecología de semillas. In: Guariguata, M.R., Kattan, G. (Eds.), *Ecología y Conservación de Bosques Neotropicales*. Editorial Tecnológica de Costa Rica, Cartago, Costa Rica, pp. 345–375.

- Dalling, J.W., Swaine, M.D., Garwood, N.C., 1997. Soil seed bank community dynamics in seasonally moist lowland tropical forest, Panama. *J. Trop. Ecol.* 13, 659–680.
- Dawkins, H.C., 1961. New methods of improving stand composition in tropical forests. *Caribb. For.* 22, 12–20.
- Dawkins, H.C., Philip, M.S., 1998. Tropical Moist Forest Silviculture and Management: A History of Success and Failure. CAB International, Wallingford.
- De Graaf, N.R., 1986. A silvicultural system for natural regeneration of tropical rain forest in Suriname. PhD thesis. Agricultural University Wageningen, pp. 250.
- De Graaf, N.R., Filius, A.M., Huesca Santos, A.R., 2003. Financial analysis of sustained forest management for timber: perspectives for application of the CELOS management system in the Brazilian Amazon. *For. Ecol. Manage.* 177, 287–299.
- Devee, E.S., Rice, D.S., Rice, P.M., Vaughn, H.H., Brenner, M.M.S., 1979. Mayan urbanism: impact on a tropical karst environment. *Science* 206, 298–306.
- Degen, B., Blanc, L., Caron, H., Maggia, L., Kremer, L., Gourlet-Fleury, S., 2006. Impact of selective logging on genetic composition and demographic structure of four tropical tree species. *Biol. Cons.* 131, 386–401.
- DeJong, W., 1996. Swidden-fallow agroforestry in Amazonia: diversity at close distance. *Agrofor. Syst.* 34, 277–290.
- Dekker, M., De Graaf, N.R., 2003. Pioneer and climax tree regeneration following selective logging with silviculture in Suriname. *For. Ecol. Manage.* 172, 183–190.
- Denevan, W.M., 1970. Aboriginal drained-field cultivation in the Americas. *Science* 169, 647–654.
- Denevan, W.M., 1992. The pristine myth: the landscape of the Americas in 1492. *Annu. Assoc. Am. Geogr.* 82, 369–385.
- Denslow, J.S., 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46, 18–21.
- Denslow, J.S., 1987. Tropical rainforest gaps and tree species diversity. *Annu. Rev. Ecol. Syst.* 18, 431–451.
- Denslow, J.S., Ellison, A.M., Sanford, R.E., 1998. Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *J. Ecol.* 86, 597–609.
- DeWalt, S.J., Maliakal, S.K., Denslow, J.S., 2003. Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife. *For. Ecol. Manage.* 182, 139–151.
- Dickinson, M.B., Whigham, D.F., Hermann, S.M., 2000. Tree regeneration, felling, and natural treefall disturbance in a semideciduous tropical forest in Mexico. *For. Ecol. Manage.* 134, 137–151.
- Dykstra, D.P., Heinrich, P., 1992. Sustaining tropical forests through environmentally sound harvesting practices. *Unasylva* 43, 9–15.
- Ediriweera, S., Singhakumara, B.M.P., Ashton, M.S., 2008. Variation in light, soil nutrition and soil moisture in relation to forest structure within a Sri Lankan rain forest landscape. *For. Ecol. Manage.* 256, 1339–1349.
- Egler, F.E., 1954. Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. *Vegetatio* 4, 412–417.
- Engelbrecht, B.M., Comita, L., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L., Hubbell, S.P., 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Science* 447, 80–81.
- Everham, E.M., Brokaw, N.V.L., 1996. Forest damage and recovery from catastrophic wind. *Bot. Rev.* 62, 113–185.
- FAO, 2008. Planificación e Implementación del Manejo Forestal a Nivel Operacional en Centro América. Documento de Trabajo sobre Ordenación Forestal FM/34, Servicio de Desarrollo de Recursos Forestales, Dirección de Ordenación Forestal, FAO, Roma.
- Finegan, B., 1992. El potencial de manejo de los bosques húmedos secundarios neotropicales de las tierras bajas. CATIE, Turrialba, p. 28.
- Finegan, B., 1996. Pattern and process in neotropical secondary rain forests: the first 100 years of succession. *Trends Ecol. Evol.* 11, 119–124.
- Finegan, B., Sabogal, C., 1988. El desarrollo de sistemas de producción sostenible en bosques tropicales húmedos de bajura: un estudio de caso en Costa Rica. *El Chasqui* 17, 3–24.
- Finegan, B., Camacho, M., 1999. Stand dynamics in a logged and silviculturally treated Costa Rican rain forest. 1988. *For. Ecol. Manage.* 121, 177–189.
- Finegan, B., Camacho, M., Zamora, N., 1999. Diameter increment patterns among 106 tree species in a logged and silviculturally treated Costa Rican rain forest. *For. Ecol. Manage.* 121, 159–217.
- Finkeldey, R., Ziehe, M., 2004. Genetic implications of silvicultural regimes. *For. Ecol. Manage.* 197, 231–244.
- Flores, E., 2003. Árboles del Trópico Húmedo. Editorial Tecnológica de Costa Rica, Cartago, Costa Rica, p. 922.
- Flores, E.M., 2002. Hyeronima alchorneoides Allemao. In: Vozzo, J.A. (Ed.), Tropical Tree Seed Manual. Agricultural Handbook 721. Washington: Forest Service, United States Department of Agriculture, pp. 514–517.
- Foggier, A., 1960. Natural regeneration in the humid tropical forest. *Caribb. For.* 21, 73–81.
- Foster, D.R., Boose, E.R., 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. *J. Ecol.* 80, 78–98.
- Foster, D.R., Knight, D.F., Franklin, J.F., 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* 1, 497–510.
- Fredericksen, T.S., 1998. Limitaciones del aprovechamiento selectivo de baja intensidad para el manejo forestal sostenible en el trópico. BOLFOR, Santa Cruz.
- Fredericksen, T.S., Licona, J.C., 2000. Invasion of non-commercial tree species after selection logging in a Bolivian tropical forest. *J. Sustain. For.* 11, 113–123.
- Fredericksen, T.S., Pariona, W., 2002. Effect of skidder disturbance on commercial tree regeneration in logging gaps in a Bolivian forest. *For. Ecol. Manage.* 171, 223–230.
- Fredericksen, T.S., Putz, F.E., 2003. Silvicultural intensification for tropical forest conservation. *Biodivers. Conserv.* 12, 1445–1453.
- Fries, C., Johansson, O., Pettersson, B., Simonsson, P., 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. *For. Ecol. Manage.* 94, 89–103.
- García-Montiel, 2002. El legado de la actividad humana en los bosques neotropicales contemporáneos. In: Guariguata, M.R., Kattan, G.H. (Eds.), Ecología y Conservación de Bosques Neotropicales. Editorial Tecnológica de Costa Rica, Cartago, Costa Rica, p. 690.
- Garwood, N.C., Janos, D.P., Brokaw, N., 1979. Earthquake-caused landslides: a major disturbance to tropical forests. *Science* 205, 997–999.
- Gibbs, J.P., Hunter, M.L., Melvin, S.M., 1993. Snag availability and communities of cavity nesting birds in tropical versus temperate forests. *Biotropica* 25, 236–241.
- Giri, C., Jenkins, C., 2005. Land cover mapping of Greater Mesoamerica using MODIS data. *Can. J. For. Res.* 31, 274–282.
- Goman, M., Byrne, R., 1998. A 5000-year record of agriculture and tropical forest clearance in the Tuxtla, Veracruz, Mexico. *Holocene* 8, 83–89.
- Gómez-Pompa, A., 1987. On maya silviculture. *Mexican Stud.* 3, 2–24.
- Gómez-Pompa, A., Kaus, A., 1992. Taming the wilderness myth. *Bioscience* 42, 271–277.
- Griscom, H.P., Ashton, M.S., 2011. Restoration of dry tropical forests in Central America: a review of pattern and process. *For. Ecol. Manage.* 261, 1564–1579.
- Griscom, B.W., Daly, D., Ashton, P.M.S., 2007. Comparative floristics of lowland terra firme forests with and without dominance by aborescent bamboo (*Guadua* spp.) in southwestern Amazonia. *Bull. Torrey Bot. Soc.* 85, 101–115.
- Grogan, J., Landis, R.M., Ashton, P.M.S., Galvão, J., 2005. Growth response by big-leaf mahogany (*Swietenia macrophylla*) advance seedling regeneration to overhead canopy release in southeast Pará, Brazil. *For. Ecol. Manage.* 204, 399–412.
- Guariguata, M.R., 1990. Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. *J. Ecol.* 78, 814–832.
- Guariguata, M.R., Pinard, M.A., 1998. Ecological knowledge of regeneration from seed in neotropical forest trees: implications for natural forest management. *For. Ecol. Manage.* 112, 87–99.
- Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest sucesión: changes in structural and functional characteristics. *For. Ecol. Manage.* 148, 185–206.
- Guariguata, M.R., Chazdon, R.L., Denslow, J.S., Anderson, L., 1997. Structure and floristics of secondary and old growth forest stands in lowland Costa Rica. *Plant Ecol.* 132, 107–120.
- Guariguata, M.R., Fernández, C.G., Nasi, R., Sheil, D., Jáuregui, C.H., Cronkleton, P., Ndoye, O., Ingram, V., 2009. Hacia un manejo múltiple en bosques tropicales: Consideraciones sobre la compatibilidad del manejo de madera y productos forestales no maderables. CIFOR, Bogor, Indonesia.
- Guariguata, M.R., García-Fernández, C., Sheil, D., Nasi, R., Herrero-Jauregui, C., Cronkleton, P., Ingram, V., 2010. Compatibility of timber and non-timber forest product management in natural tropical forests: perspectives, challenges, and opportunities. *For. Ecol. Manage.* 259, 237–245.
- Gullison, R.E., Panfil, S.N., Strouse, J.J., Hubbell, S.P., 1996. Ecology and management of mahogany (*Swietenia macrophylla* King) in Chimanes Forest, Bed, Bolivia. *Bot. J. Linn. Soc.* 122, 9–34.
- Hall, J.S., Ashton, M.S., 2016. A Native Species Planting Guide for Reforestation in Central America. Smithsonian Tropical Research Institute, Panama, p. 178.
- Hall, J.S., Harris, D.J., Medjibe, V., Ashton, P.M.S., 2003. The effects of selective logging on forest structure and tree species composition in a Central African forest: implications for management of conservation areas. *For. Ecol. Manage.* 183, 249–264.
- Hannah, P.R., 1988. The shelterwood method in northeastern forest types: a literature review. *North. J. Appl. For.* 5, 70–77.
- Hanson, T., Brunsfeld, S., Finegan, B., 2006. Variation in seedling density and seed predation indicators for the emergent tree *Dipteryx panamensis* in continuous and fragmented rain forest. *Biotropica* 38, 770–774.
- Hartshorn, G.S., 1978. Tree falls and tropical forest dynamics. In: Tomlinson, P.B., Zimmerman M. (Eds.), Tropical Trees as Living Systems. Cambridge University Press, Cambridge, UK, pp. 617–638.
- Hartshorn, G.S., 1980. Neotropical forest dynamics. *Biotropica* 12, 23–30.
- Hartshorn, G.S., 1989. Application of gap theory to tropical forest management: Natural regeneration on strip clear-cuts in the Peruvian Amazon. *Ecology* 70, 567–576.
- Holdridge, L.R., 1947. Determination of world plant formations from simple climatic data. *Science* 105, 367–368.
- Holdridge, L.R., 1967. Life Zone Ecology. Tropical Science Center, San José.
- Holl, K.D., 2007. Old field vegetation succession in the Neotropics. In: Cramer, V., Hobbs, R.J. (Eds.), Old Fields: Dynamics and Restoration of Abandoned Farmland. Island Press, Washington DC, USA, pp. 93–118.
- Horn, S.P., Sanford, R.L., 1992. Holocene fires in Costa Rica. *Biotropica* 24, 354–361.
- Hutchinson, I.D., 1987. Improvement thinning in natural tropical forest: aspects and institutionalization. In: Mergen, F., Vincent, J.R. (Eds.), Natural Management of Tropical Moist Forests. Yale University, New Haven, pp. 113–133.
- Isphording, W.C., 1975. The physical geology of Yucatan. *Trans. Gulf Coast Assoc. Geol. Soc.* 25, 231–262.
- Jiménez, Q., Rojas, F.E., Rojas, V., Rodríguez, S., Feeney, C., 2002. Timber Trees of Costa Rica: Ecology and Silviculture. INBio, Heredia, Costa Rica, p. 361.
- Kauffman, B.J., 1991. Survival by sprouting following fire in tropical forests of the Eastern Amazon. *Biotropica* 23, 219–224.
- Kennedy, L.M., Horn, S.P., 2008. A late Holocene pollen and charcoal record from La Selva biological station, Costa Rica. *Biotropica* 40, 11–19.



- Lamb, A.F.A., 1947. The influence of modern trends in timber utilization on silviculture policy in British Honduras. Paper presented to the Empire Forestry Conference, Canada.
- Lamb, F.H., 1966. Mahogany in Tropical America: Its Ecology and Management. University of Michigan Press, p. 220.
- Lamprecht, H., 1989. Silviculture in the Tropics: Tropical Forest Ecosystems and Their Tree Species: Possibilities and Methods for Their Long-Term Utilization. Paul Parey Verlag, Eschborn.
- Laurance, W.F., Goosem, M., Laurance, S.G.W., 2009. Impacts of roads and linear clearings on tropical forests. *Trends Ecol. Evol.* 24, 659–669.
- Levey, D.J., Silva, W.R., Galetti, M. (Eds.), 2002. Seed Dispersal and Frugivory: Ecology, Evolution, and Conservation. CAB.
- Leyden, B.W., 1987. Man and climate in the Maya lowlands. *Quatern. Res.* 28, 407–414.
- Lieberman, D., Lieberman, M., Hartshorn, G., Peralta, R., 1985. Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. *J. Trop. Ecol.* 1, 97–109.
- Lobo, J., Barrantes, G., Castillo, M., Quesada, R., Maldonado, T., Fuchs, E.J., Solis, S., Quesada, M., 2007. Effects of selective logging on the abundance, regeneration and short-term survival of *Caryocar costarricense* (Caryocaraceae) and *Peltogyne purpurea* (Caesalpinaceae), two endemic timber species of southern Central America. *For. Ecol. Manage.* 245, 88–95.
- Louman, B., 2001. Sistemas silviculturales. In: Louman, B., Quirós, D., Nilsson, M. (Eds.), *Silvicultura de bosques latifoliares húmedos con énfasis en América Central*. CATIE, Turrialba, pp. 81–127.
- Lugo, A.E., 2008. Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecol.* 33, 368–398.
- Lugo, A.E., Scatena, F.N., 1996. Background and catastrophic tree mortality in tropical moist, wet and rain forests. *Biotropica* 28, 585–599.
- Lugo, A.E., Applefield, M., Pool, D.J., McDonald, R.B., 1983. The impact of Hurricane David on the forests of Dominica. *Can. J. For. Res.* 13, 201–211.
- Lundqvist, L., 2003. Some notes on the regeneration of Norway spruce on six permanent plots managed with single-tree selection. *For. Ecol. Manage.* 46, 49–57.
- Lynch, J.F., 1991. Effects of Hurricane Gilbert on birds in a dry tropical forest in the Yucatan peninsula. *Biotropica* 23, 488–496.
- MacArthur, R., Wilson, E.O., 2001. *Island Biogeography Theory*. Princeton University Press, Chicago, USA.
- Mann, C.C., 2006. 1491: New Revelations of the Americas Before Columbus. Vintage Books, New York.
- Manzanero, M., Pinelo, G., 2004. Plan Silvicultural en Unidades de Manejo Forestal: Reserva de la Biosfera Maya, Petén, Guatemala. Serie Técnica # 3.WWF Centroamérica. 49 p.
- Marjokorpi, A., Ruokalainen, K., 2003. The role of traditional forest gardens in the conservation of tree species in West Kalimantan, Indonesia. *Biodivers. Conserv.* 12, 799–822.
- Mata, R., 1991. Los órdenes de suelos en Costa Rica. In: Vahrson, W.-G., Alfaro, M., Palacios, G. (Eds.), *Taller de Erosión de Suelos*. Universidad Nacional, Heredia, pp. 28–32.
- McCloskey, T.A., Keller, G., 2009. 5000 year sedimentary record of hurricane strikes on the central coast of Belize. *Quatern. Int.* 1–2, 53–68.
- Michener, W.K., Hauber, R.A., 1998. Flooding: natural and managed disturbances. *Bioscience* 48, 677–680.
- Miller, G.W., Kochenderfer, J.N., Fekedulgen, D.B., 2006. Influence of individual reserve trees on nearby reproduction in two-aged Appalachian hardwood stands. *For. Ecol. Manage.* 224, 241–251.
- Mascorro, V.S., Coops, N.C., Kurz, W.A., Olguín, M., 2016. Attributing changes in land cover using independent disturbance datasets: a case study of the Yucatan Peninsula, Mexico. *Reg. Environ. Change* 16, 213–228.
- Montagnini, F., 2006. Homegardens of mesoamerica: biodiversity, food security, and nutrient management. In: Kumar, B.M., Nair, P.K.R. (Eds.), *Tropical Homegardens: A Time-Tested Example of Sustainable Agroforestry*. Springer, Dordrecht, pp. 61–84.
- Myers, R.K., van Lear, D.H., 1998. Hurricane-fire interactions in the coastal forests of the south: a review and hypothesis. *For. Ecol. Manage.* 103, 265–276.
- Myers, R.L., Rodríguez-Trejo, D.A., 2009. Fire in tropical pine ecosystems. In: Cochrane, M.A. (Ed.), *Tropical Fire Ecology*. Springer, pp. 557–605.
- Neff, H., Pearsall, D.M., Jones, J.G., Arroyo, B., Collins, S.K., Freidel, D.E., 2006. Early Maya adaptive patterns: mid-late Holocene paleoenvironmental evidence from Pacific Guatemala. *Lat. Am. Antiquity* 17, 287–315.
- Negreros-castillo, P., Mize, C.W., 2008. Regeneration of mahogany and Spanish cedar in gaps created by railroad tie extraction in Quintana Roo, Mexico. *For. Ecol. Manage.* 255, 308–312.
- Negreros-castillo, P., Snook, L.K., Mize, C.W., 2003. Regenerating mahogany (*Swietenia macrophylla*) from seed in Quintana Roo, Mexico: the effects of sowing method and clearing treatment. *For. Ecol. Manage.* 183, 351–362.
- Nelson, B.V., Kapos, V., Adams, J.B., Oliveira, W.J., Braun, O.P.G., 1994. Forest disturbance by large blowdowns in the Brazilian Amazon. *Ecology* 75, 853–858.
- Nichols, D.L., 2015. Intensive agriculture and early complex societies of the basin of Mexico: the formative period. *Anc. Mesoam.* 26, 407–421.
- Norden, N., Chazdon, R.L., Chao, A., Jiang, Y.-H., Vilchez-Alvaredo, B., 2009. Resilience of tropical rain forests: tree community reassembly in secondary forests. *Ecol. Lett.* 12, 385–394.
- Norden, N., Angarita, H.A., Bongers, F., Martínez-Ramos, M., Granzow-de la Cerda, I., van Breugel, M., Lebrija-Trejos, E., Meave, J.A., Vandermeer, J., Williamson, G.B., Finegan, B., Mesquita, R., Chazdon, R.L., 2015. Successional dynamics in Neotropical forests are as uncertain as they are predictable. *Proc. Natl. Acad. Sci.* 112, 8013–8018.
- Northrop, L.A., Horn, S.P., 1996. Pre-Columbian agriculture and forest disturbance in Costa Rica: palaeoecological evidence from two lowland rainforest lakes. *Holocene* 6, 289–299.
- Núñez-Farfán, J., Dirzo, R., 1988. Within-gap heterogeneity and seedling performance in a Mexican tropical forest. *Oikos* 51, 274–284.
- Nyland, R.D., 2002. *Silviculture: Concepts and Applications*. Waveland Press, Long Grove, IL, p. 682.
- Ocampo, R.A., 1994. Situación Actual de los Productos no Maderables del Bosque en Costa Rica. Doc. Trab. 7. Proyecto Conservación para el Desarrollo Sostenible en América Central (Proyecto Olofo). CATIE, Turrialba.
- Oliver, C.D., 1981. Forest development in North America following major disturbances. *For. Ecol. Manage.* 3, 153–168.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*. J. Wiley & Sons, New York.
- Oliver, C.D., Burkhardt, E.C., Skojac, D.A., 2005. The increasing scarcity of red oaks in Mississippi River floodplain forests: influence of the residual overstory. *For. Ecol. Manage.* 210, 393–414.
- Parsons, J.J., 1955. The Miskito Pine Savanna of Nicaragua and Honduras. *Ann. Assoc. Am. Geogr.* 45, 36–63.
- Peña-Claros, M., Fredericksen, T.S., Alarcón, A., Blate, G.M., Choque, U., Leño, C., Licóna, J.C., Mostacedo, B., Pariona, W., Villegas, Z., Putz, F.E., 2008. Beyond reduced-impact logging: silvicultural treatments to increase growth rates of tropical trees. *For. Ecol. Manage.* 256, 1458–1467.
- Pennington, T.D., Sarukhan, J., 1968. *Árboles Tropicales de México*. FAO, Rome, Italy, p. 413.
- Pérez, R., 2008. Árboles de los bosques del Canal de Panamá. Burica Press, Ciudad de Panamá, Panamá, p. 465.
- Peters, C.M., 2000. Precolumbian silviculture and indigenous management of neotropical forests. In: Lentz, D.L. (Ed.), *Imperfect Balance: Landscape Transformations in the Precolumbian Americas*. Columbia University Press, New York, pp. 203–224.
- Petit, N.E., Froend, R.H., 2001. Variability in flood disturbance and the impacts on riparian tree recruitment in two contrasting river systems. *Wetland Ecol. Manage.* 9, 13–25.
- Piperno, D.R., Fritz, G.J., 1994. On the emergence of agriculture in the New World. *Curr. Anthropol.* 35, 637–643.
- Piperno, D.R., Pearsall, D.M., 1998. *The Origins of Agriculture in the Lowland Neotropics*. Academic Press, USA.
- Poorter, L., Bongers, F., van Rompaey, R.S.A.R., de Klerk, M., 1996. Regeneration of canopy tree species at five sites in West African moist forest. *For. Ecol. Manage.* 84, 61–69.
- Potts, M.D., 2003. Drought in a Bornean everwet rain forest. *J. Ecol.* 91, 467–474.
- Putz, F.E., Fredericksen, T.S., 2004. Silvicultural intensification for tropical forest conservation: a response to Sist and Brown. *Biodivers. Conserv.* 13, 2387–2390.
- Putz, F.E., Sist, P., Dykstra, D., 2008a. Reduced-impact logging: challenges and opportunities. *For. Ecol. Manage.* 256, 1427–1433.
- Putz, F.E., Dykstra, D.P., Heinrich, P., 2000. Why poor logging practices persist in the tropics. *Conserv. Biol.* 14, 951–956.
- Putz, F.E., Sist, P., Fredericksen, T., Dykstra, D., 2008b. Reduced-impact logging: challenges and opportunities. *For. Ecol. Manage.* 256, 1427–1433.
- Reyes, M.R., 1968. Selective logging: a must tool for continuous production of Philippine mahogany in the Philippines. *Philipp. For.* 2, 14–21.
- Richards, P.W., 1952. *The Tropical Rain Forest: An Ecological Study*. Cambridge University Press, Cambridge, UK.
- Richards, P.W., 1996. *The Tropical Rain Forest: An Ecological Study*. With contributions by R.P.D. Walsh, I.C. Baillie, and P. Greig-Smith. second ed., Cambridge University Press, Cambridge, UK.
- Rocha, O.J., Vilchez, B., Araya, A.L., 2006. A mast fruiting episode of the tropical tree *Peltogyne purpurea* (Caesalpinaceae) in the Osa Peninsula, Costa Rica. *Int. J. Trop. Biol.* 54, 1151–1155.
- Roman, F., De Leon, R., Deago, J., Sautu, A., Hall, J.S., 2012. Guía para la Propagación de 120 Especies de Árboles Nativos de Panamá y el Neotrópico. Environmental Leadership and Training Initiative, Yale University, New Haven, p. 162.
- Rue, D.J., 1987. Early agriculture and early postclassic Maya occupation in western Honduras. *Nature* 336, 285–286.
- Runkle, J.R., 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62 (4), 1041–1051.
- Salafsky, N., 1994. Forest gardens in the Gunung Palung region of West Kalimantan, Indonesia: defining a locally-developed, market-oriented agroforestry system. *Agrofor. Syst.* 28, 237–268.
- Salo, J., Kallio, R., Häkkinen, I., Niemelä, P., Puhakka, M., Coley, P.D., 1986. River dynamics and the diversity of Amazon lowland forest. *Nature* 322, 254–258.
- Scatena, F.N., Larsen, M.C., 1991. Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropica* 23, 317–323.
- Schleuning, M., Huamán, V., Matthies, D., 2008. Flooding and canopy dynamics shape the demography of a clonal Amazon understory herb. *J. Ecol.* 96, 1045–1055.
- Sebben, A.M., Degen, B., Azevedo, V.C.R., Silva, M.B., de Lacerda, A.E.B., Ciampi, A.Y., Kanashiro, M., Carneiro, F.D.S., Thompson, I., Loveless, M.D., 2008. Modeling the long-term impacts of selective logging on genetic diversity and demographic structure of four tropical tree species in the Amazon forest. *For. Ecol. Manage.* 254, 335–349.
- Sernander, R., 1936. Granskär och Fiby urskog [The primitive forests of Granskär Fiby]. *Acta Phytogeographica Suecica* 8, 1–232 (in Swedish with English summary).



- Shiels, A.B., Zimmerman, J.K., García-Montiel, D.C., Jonckheere, I., Holm, J., Horton, D., Brokaw, N., 2010. Plant responses to simulated hurricane impacts in a subtropical wet forest, Puerto Rico. *J. Ecol.* 98, 659–673.
- Sigl, M., Winstrop, M., McConnell, J.R., Welten, K.C., Plunkett, G., Ludlow, F., Buntgen, U., Caffee, M., Chellman, N., Dahl-Jensen, D., Fischer, H., Kipfstuhl, S., Kostick, C., Maselli, O.J., Mekhaldi, F., Mulvaney, R., Muscheler, R., Pasteris, D.R., Pilcher, J.R., Salzer, M., Schupbach, S., Steffensen, J.P., Vinther, B.M., Woodruff, T. E., 2015. Timing and climate forcing of volcanic eruptions for the past 2500 years. *Nature* 523, 543–549.
- Sist, P., Fimbel, R., Sheil, D., Nasi, R., Chevallier, M.-H., 2003. Towards sustainable management of mixed dipterocarp forests of South-east Asia: moving beyond minimum diameter cutting limits. *Environ. Conserv.* 30, 364–374.
- Sitoe, A., Finegan, B., Franc, A., 2001. Gavilán: un modelo para simulación del crecimiento, rendimiento y cambios florísticos de los bosques centroamericanos dominados por *Pentaclethra macroloba*. *Rev. For. Cen.* 34, 19–22.
- Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1997. *The Practice of Silviculture: Applied Forest Ecology*. J. Wiley and Sons, New York.
- Snook, L.K., 1996. Catastrophic disturbance, logging and the ecology of mahogany (*Swietenia macrophylla* King): grounds for listing a major tropical timber species in CITES. *Bot. J. Linn. Soc.* 122, 35–46.
- Snook, L.K., 2003. Regeneration, growth and sustainability of mahogany in Mexico's Yucatan forests. In: Lugo, A., Figueroa-Colón, J., Alayón, M. (Eds.), *Big-leaf Mahogany: Ecology, Genetics and Management*, Ecological Studies, vol. 159, pp. 169–192.
- Snook, L.K., 2005. Aprovechamiento sostenido de caoba en la Selva Maya de México: de la Conservación Fortuita al manejo sostenible. *Recursos Naturales y Ambiente* 44, 9–18.
- Snook, L.K., Cámara-Cabrales, L., Kelty, M.J., 2005. Six years of fruit production by mahogany trees (*Swietenia macrophylla* King): patterns of variation and implications for sustainability. *For. Ecol. Manage.* 206, 221–223.
- Sousa, W.P., 1984. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* 15, 353–391.
- Sprugel, D.G., 1991. Disturbance, equilibrium, and environmental variability: what is 'natural' vegetation in a changing environment? *Biol. Cons.* 58, 1–18.
- Standley, P.C., Steyermark, J.A., 1958. *Flora of Guatemala*. Chicago Natural History Museum Press, Chicago, USA.
- Stanturf, J.A., Goodrick, S.L., Outcalt, K.W., 2007. Disturbance and coastal forests: a strategic approach to forest management in hurricane impact zones. *For. Ecol. Manage.* 250, 119–135.
- Sugden, A.M., 1992. Hurricanes in tropical forests. *Tree* 7, 146–147.
- Tanner, E.V.J., Kapos, V., Healey, J.R., 1991. Hurricane effects on forest ecosystems in the Caribbean. *Biotropica* 23, 513–521.
- Teketay, D., 2011. Natural regeneration and management of *Podocarpus falcatus* (Thunb.) Mirb. in the Afromontane Forests of Ethiopia. In: Günter, S., Weber, M., Stimm, B., Mosandl, R. (Eds.), *Silviculture in the Tropics*, Springer verlag, pp. 325–338.
- Terborgh, J., Petren, K., 1991. Development of habitat structure through succession in an Amazonian floodplain forest. In: Bell, S.S., McCoy, E.D., Mushinsky, H.R. (Eds.), *Habitat Structure. Population and Community Biology*, vol. 8, Springer, Netherlands, 28–46 pp.
- Troup, R.S., 1921. *The Silviculture of Indian Trees*. Clarendon Press, Oxford.
- Troup, R.S., 1928. *Silvicultural Systems*. Oxford University Press, Oxford.
- Turner, M.G., Dale, V.H., Everham, E.H., 1997. Fires, hurricanes, and volcanoes: comparing large disturbances. *Bioscience* 47, 758–768.
- Turner, M.G., Baker, W.L., Peterson, C.J., Peet, R.K., 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* 1, 511–523.
- Urquhart, G.R., 2008. Paleoeological record of hurricane disturbance and forest regeneration in Nicaragua. *Quatern. Int.* 195, 88–97.
- USDA, 1975. *Soil Conservation Survey-USDA Soil Taxonomy: A Basic System of Classification for Making and Interpreting Soil Surveys*. US Government Printing Office, Washington DC.
- van Gernerden, B.S., Olff, H., Parren, M.P.E., Bongers, F., 2003. The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. *J. Biogeogr.* 30, 1381–1390.
- Valdez-Hernández, M., Sánchez, O., Islebe, G.A., Snook, L.K., Negreros-Castillo, P., 2014. Recovery and early succession after experimental disturbance in a seasonally dry tropical forest in Mexico. *For. Ecol. Manage.* 334, 331–343.
- van der Sande, M.T., Arets, E.J.M.M., Peña-Claros, M., de Avila, A.L., Roopsind, A., Mazzei, L., Ascarrunz, N., Finegan, B., Alarcón, A., Cáceres-Siani, Y., Licona, J.C., Ruschel, A., Toledo, M., Poorter, L., 2016. Old-growth Neotropical forests are shifting in species and trait composition. *Ecol. Monogr.* 86, 228–243.
- Vandermeer, J., Granzow de la Cerda, I., Boucher, D., Perfecto, I., Ruiz, J., 2000. Hurricane disturbance and tropical tree species diversity. *Science* 290, 788–791.
- Vandermeer, J., Mallona, M.A., Boucher, D.H., Yih, K., Perfecto, I., 1995. Three years of ingrowth following catastrophic hurricane damage on the Caribbean coast of Nicaragua: evidence in support of the direct regeneration hypothesis. *J. Trop. Ecol.* 11, 465–471.
- Wadsworth, F.H., 1981. Management of forest lands in the humid tropics under sound ecological principles. In: Mergen, F. (Ed.), *Natural Management of Tropical Moist Forests*, International Symposium on Tropical Forest Utilization and Conservation. Yale University, New Haven.
- Wadsworth, F.H., 1987. Applicability of Asian and African silviculture systems to naturally regenerated forests of the neotropics. In: Mergen, F., Vincent, J.R. (Eds.), *Natural Management of Tropical Moist Forests*. Yale University, New Haven, pp. 94–111.
- Waide, R.B., 1991. Summary of the response of animal populations to hurricanes in the Caribbean. *Biotropica* 23, 508–512.
- Walker, L.R., 1991. Tree damage and recovery from hurricane Hugo in Luquillo experimental forest, Puerto Rico. *Biotropica* 23, 379–385.
- Watt, A.S., 1947. Pattern and process in the plant community. *J. Ecol.* 35, 1–22.
- Webb, E.L., 1997. Canopy removal and residual stand damage during controlled selective logging in lowland swamp forest of northeast Costa Rica. *For. Ecol. Manage.* 95, 117–129.
- Webb, E.L., 1998. Gap-phase regeneration in selectively logged lowland swamp forest, northeastern Costa Rica. *J. Trop. Ecol.* 14, 247–260.
- Weyl, R., 1980. *Geology of Central America*. Gebrüder Borntraeger, p. 371.
- Whigham, D.F., Olmsted, I., Cano, E.C., Harmon, M.E., 1991. The impact of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatan Peninsula. *Biotropica* 23, 434–441.
- Whitmore, T.C., Burnham, C.P., 1975. *Tropical Rain Forests of the Far East*. Clarendon Press.
- Whitmore, T.C., 1984. *Tropical Rain Forests of the Far East*. Oxford University Press, Oxford.
- Whitmore, T.C., Burslem, D.F.R.P., 1998. Major disturbances in tropical forests. In: Newbery, D.M., Prins, H.H.T., Brown, N.D. (Eds.), *Dynamics of tropical communities: the 37th symposium of the British Ecological Society*, Cambridge University, 1996, Cambridge, pp. 549–565.
- Williams, R.J., Bradstock, R.A., 2009. Large fires and their ecological consequences: introduction to the special issue. *Int. J. Wildl. Fire* 17 (6), 685–687.
- Wyatt-Smith, J., 1963. *Manual of Malayan silviculture for inland forests*. Malay Forest Records No. 23.
- Yih, K., Boucher, D.H., Vandermeer, J.H., Zamora, N., 1991. Recovery of the rain forest of Southeastern Nicaragua after destruction by hurricane Joan. *Biotropica* 23, 106–113.
- You, C., Petty, W.H., 1991. Effects of Hurricane Hugo on *Manilkara bidentata*, a primary tree species in the Luquillo Experimental Forest of Puerto Rico. *Biotropica* 23, 400–406.
- Zamora, N., 2000. *Árboles de la Mosquitia Hondureña: descripción de 150 especies*. CATIE, Turrialba, Costa Rica, p. 314.
- Zamorano-Elgueta, C., Cayuela, L., Rey-Benayas, J. María, Donoso, P.J., Geneletti, D., Hobbs, R.J., 2014. The differential influences of human-induced disturbances on tree regeneration community: a landscape approach. *Ecosphere* 5, art90.