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Restoration of dry tropical forests in Central America: A review of pattern and process

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ABSTRACT

Much information on restoration and management exists for wet tropical forests of Central America but comparatively little work has been done in the dry forests of this region. Such information is critical for reforestation efforts that are now occurring throughout Central America. This paper describes processes of degradation due to land use and provides a conceptual framework for the restoration of dry tropical forest. Most of this forest type was initially harvested for timber and then cleared for cattle in the last century (1930–1970). Only 1.7% remains largely restricted to infertile soils and remote areas on the Pacific coastal side of Panama, Costa Rica, Nicaragua and Mexico. These cleared areas are again in a state of transition due to a combination of decreasing land productivity, and land speculation for tourism development. Some farms have been sold to new landowners who are interested in reforesting to increase biodiversity and forest cover. Attempts have therefore been made to reforest by protecting the land from fire and cattle, by supplementing natural regrowth with enrichment planting, or through use of tree plantations. Experimental studies have demonstrated the ability of these lands to grow back to forests because of native species ability to sprout after cutting, and the capacity of remnant trees in field and riparian zones to provide seeds and to moderate edge environment for seed germination and seedling establishment. However, research also shows that on sites with long histories of land clearance, species diversity will remain low with functional groups missing unless some active management occurs. Under-planting with late-successional native tree species can add structure and diversity; enrichment planting with large-fruited shade-intolerant species can initiate new islands of more diverse regeneration beneath their canopies; and plantings of fast-growing, nitrogen-fixing trees that provide light canopy shade can moderate the environment below, promoting regeneration establishment of late-successional species. Plantations are the only option for lands that have lost almost all remnants of native forest, and where soils and vegetation have changed to new states of structure and function. Conversion of pastures to tree plantations that can facilitate natural regeneration beneath them is appropriate when pastures are prone to fire and/or lack immediate seed sources nearby. After the grasses have been shaded out, natural recruitment can slowly occur over a 10–15 years period. Under-planting of shade-tolerant late-successional species can supplement species composition and structure.

1. Introduction

Most experimental studies on forest recovery and secondary succession have been conducted in moist tropical forests in the neotropics (Uhl et al., 1988; Holl, 1998; Nepstad et al., 1990, 1991, 1996; Guevara and Laborde, 1993; Parrotta et al., 1997; Aide, 2000; Holl et al., 2000; Hooper et al., 2002, 2004; Jones et al., 2004; Dupuy and Chazdon, 2008; Norden et al., 2009; Letcher and Chazdon, 2009; Chazdon et al., 2010). Many dry tropical forest studies in Mesoamerica and the Caribbean have focused on dynamics and secondary succession (Lugo, 1986; Murphy and Lugo, 1986b; Sabogal, 1992; Burgos and Maass, 2004; Mizrahi et al., 1997; Gillespie et al., 2000; Quigley and Platt, 2003; Colon, 2006; Duran et al., 2006; Esquivel et al., 2008; Lebrija-Trejos et al., 2008; Sandoval-Perez et al., 2009; Powers et al., 2009) and several papers have reviewed these processes (Mooney et al., 1995; Sanchez-Azofeifa et al., 2005b; Vieira and Scariot, 2006). However, few studies have described the actual processes of degradation of dry tropical forests; and then provided methods for restoration for different circumstances based on experimental work. This paper attempts a review of the processes of degradation and restoration based on the few studies that have been done in Central America. Given the current circumstance of land transformation and change, and an interest in reforestation on the Pacific side of Central America, a

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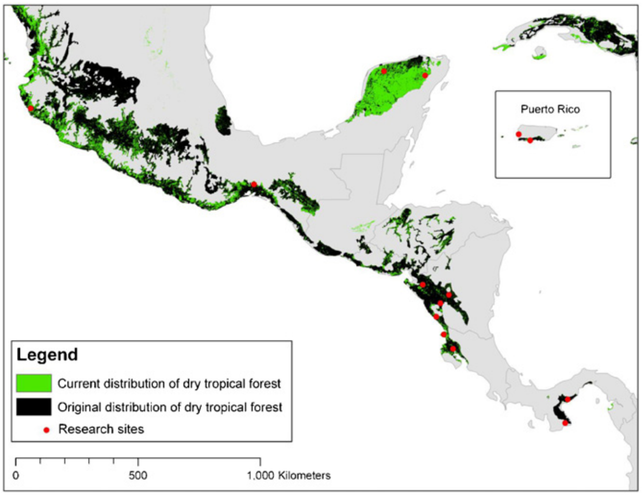

Fig. 1. The original distribution of dry tropical forests was derived from WWF ecoregion dataset (Olson et al., 2001), combining two ecoregions: tropical and subtropical dry broadleaf forests and tropical and subtropical grasslands, savannas, and shrublands. The current distribution was acquired from Miles et al. (2006). For further information, email: spatialanalysis@unep-wcmc.org. They determined this current distribution from the WWF ecoregion data, overlayed with the MODIS (Moderate Resolution Imaging Spectroradiometer) dataset, identifying areas with at least 40% forest cover. Locations of current experimental and observational research in abandoned pastures, plantations, and secondary forests are shown in red.

review of the literature that explores dry tropical forest restoration appears to be timely.

Dry tropical forests were once the most common forest type along the Pacific side of Central America, from Guatemala to Costa Rica, and the southeastern side of the Azuero peninsula in Panama (Sabogal, 1992; Murphy and Lugo, 1995; Sanchez-Azofeifa et al., 2005b) (Fig. 1). Today, 1.7% of the original expanse remains in Central America (Olson et al., 2001; Miles et al., 2006; Calvo-Alvarado et al., 2009) (Fig. 1). The remaining dry forest, reduced to small remnant patches, is considered one of the most threatened tropical ecosystems (Murphy and Lugo, 1986a; Janzen, 1988; Sabogal, 1992; Maass, 1995; Trejo and Dirzo, 2000; Sanchez-Azofeifa et al., 2005a; Vieira and Scariot, 2006). In Mexico, very dry tropical forests are widespread on the Pacific slopes (Becerra, 2005), with 27% still intact (Trejo and Dirzo, 2000). Even though dry tropical forests are less diverse than moist or wet tropical forests (Kalacska et al., 2004), their conservation and restoration[1] is a high priority because they are becoming increasingly rare, have the third highest forest cover loss (Hansen et al., in press), and contain many endemic and economically valuable species (Kalacska et al., 2004; Sanchez-Azofeifa et al., 2005a).

In this paper, we first describe the history of forest clearance and land use. We then describe the ecology of the forest type, its original and current range, species composition and diversity. We then describe the main degradation processes specific to dry tropical forests of Central America. Experimental research on restoration techniques, specifically in Panama and Costa Rica, is then reviewed in order of severity of disturbance impact. Finally, a conceptual model for restoration pathways under different degradation and restoration scenarios that change with social priority (land conservation, ecosystem services or timber and non-timber forest products) is described. This paper does not review the use of native species and dry tropical forests as elements within agroforestry or silvo-pastoral systems which others have reported on (Harvey and Haber, 1999; Harvey et al., 2005; Garen et al., 2009; Hall et al., this issue).

2. Land use history

Understanding the history of disturbance and degradation processes in these systems is essential for successful restoration projects. In many regions, such as on Panama's Azuero peninsula, there are no old growth forests to serve as models for what the forest composition and diversity should be. Determining the historical extent of this forest type is also difficult because many "natural" grasslands could have been forest at one time and are now in a state of arrested succession often mediated by fire (Trejo and Dirzo, 2000; Zanne and Chapman, 2001; Janzen, 2002). Therefore, we must construct our model of a diverse, functionally restored forest, using human-impacted forest fragments, patchy historical records, chronosequence studies of second growth, and experimental planting trials. The historical background of land conversion should also be clearly understood if we are to enable native-species reforestation.

Prior to the arrival of the Europeans, savanna systems were created from dry tropical forest by indigenous peoples, especially along the Pacific coast (Denevan, 1992; Cooke and Ranere, 1992). Some areas were completely deforested except along streams and hilltops (Denevan, 1992; Cooke and Ranere, 1992). Many of these forests were more intensively managed by indigenous peoples compared to moist forests because of the more productive soils for shifting agriculture (Murphy and Lugo, 1986a; Daniels et al., 2008). However, such management regimes were inefficient in clearing land, leaving living vegetation of various kinds (seed sources, vegetative sprouts, roots) and allowing for immediate regeneration after one to two years of cultivation (Parsons et al., 2008).

Pasture conversion for cattle was the main cause of deforestation in Central America after the arrival of the Europeans (Calvo-Alvarado et al., 2009) with tropical dry forests more extensively affected than moist forests (Janzen, 1988; Toledo, 1988; Murphy and Lugo, 1995). Tropical dry forests were popular settlement areas because diseases were rare, land was easier to clear, soil fertility was higher, and a number of high quality timbers occurred within these forests (Murphy and Lugo, 1986a; Ewel, 1999; Calvo-Alvarado et al., 2009). Small-scale deforestation began in the 1500s' with the arrival of the Spaniards and the creation of large haciendas and ranching of European Creole cattle as well as extractive logging of valuable timber (e.g., *Cedrela odorata* L.) on the Pacific side of Costa Rica and Panama (Janzen, 1983; Denevan, 1992; Calvo-Alvarado et al., 2009) (Fig. 2). In the 1800s' landless peasants began to move into these frontier areas to clear land more permanently and raise Criollo cattle on common grazing lands (Heckadon Moreno, 1984; Calvo-Alvarado et al., 2009). In the early 1900s', timber extraction, increased for national and export needs (Calvo-Alvarado et al., 2009). Nicaragua also provided much of this timber from its dry tropical forests (Sabogal, 1992). Expansion of infrastructure support, such as networks of roads into the frontiers, and land policies in the 1930–1940s further encouraged forest clearing for "land improvement" (Harrison, 1991; Calvo-Alvarado et al., 2009).

By the 1940s, a trend towards pasture improvement, which involved planting exotic grasses (e.g., *Hyparrhenia rufa* and raising Zebu cattle breeds, arose, putting further pressure on the land, Heckadon Moreno, 1984; Calvo-Alvarado et al., 2009). Government and international loans for cattle-raising in the 1960s led to a dramatic increase in deforestation in Central America, resulting in the highest rates of deforestation of tropical dry forests in the

[1] For the purposes of this paper we use the word restoration loosely to refer to different modes of reforestation that do not necessarily exactly match, but only approximate historical species compositions and structures prior to land colonization and clearance, and are directed toward today's social values.

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Table 1
Site information is given where research has been conducted on characterizing or restoring altered dry tropical forest ecosystems in Central America, Mexico, and Puerto Rico. Research sites are categorized according to Holdridge's Life Zones (1967).

Research locations in Central America	Status	Mean rainfall (mm)	Mean temp (°C)	Dry months	No. of tree species	Major Genera	Type of research conducted	References
Subtropical very dry forest (500–1000 mm; mean temp < 24 °C)								
Cabo Rojo, Puerto Rico	Abandoned pasture	860					Nurse trees and natural regeneration; Plantations	Santiago-Garcia et al. (2008), Weaver and Schwagerl (2008)
Tuxcacuesco Jalisco, Mexico	Pasture	900	22	6–8			Nurse trees and enrichment planting	Sanchez-Velazquez et al. (2004)
Guanica, Puerto Rico	Protected forest (1919); historically sustainable agriculture	930	24	6	52/ha > 8 cm	*Bucida*, *Coccoloba*, *Pisonia*, *Thouinia*	Soils; characterization; plantations; diversity; succession after pasture abandonment	Lugo (1986), Murphy and Lugo (1986b), Quigley and Platt (2003), Colon (2006)
Tropical very dry forest (500–1000 mm rain; mean temp > 24 °C)								
Chamela, Jalisco, Mexico	Protected forest (1993); historically shifting agriculture	788	24.9	6–8	127/ha > 10 cm	*Bursera*, *Tabebuia*, *Astronium*, *Cordia*	Floristics; land use; succession; floristics; characterization	Quigley and Platt (2003), Burgos and Maass (2004), Duran et al. (2006), Sandoval-Perez et al. (2009)
San Mateo, Jalisco, Mexico	Pasture	679	24.9	6–8			Pasture conversion	Ellingson et al. (2000), Kauffman et al. (2003)
Nizanda, Oaxaca, Mexico	Shifting agriculture	900	26	6–7		*Amphipterygium*, *Apoplanesia*, *Bursera*, *Ceiba*	Succession after shifting agriculture	Lebrija-Trejos et al. (2008)
Motul, Yucatan, Mexico	Abandoned agave plantations (26 years)	800-1000	26.5	9		*Cordia*, *Caesalpinia*, *Acacia*, *Pithecellobium*	Succession after agave cultivation	Mizrahi et al. (1997)
Rio Hato, Panama	Savannah	1000		7			Mixed native species plantations	Wishnie et al. (2007) and Parks et al. (2010)
Tropical dry forest (1000–2000 mm of rain; mean temp > 24 °C)								
OMYK, Yucatan, Mexico	Reserve; milpa agriculture	1200				*Bursera*, *Lysi loma*, *Caesalpinia*	Direct seeding	Bonilla-Moheno and Holl (in press)
Nandaime, Nicaragua	Secondary forest (4, 9, 14 years)	1444	27	5	9 years: 16/.7 ha > 10 cm; 14 years: 21/.7 ha > 10 cm	*Gyrocarpus*, *Tabebuia* *Lonchocarpus* *Caesalpinia*	Chronosquence	Marin et al. (2009)
Chacocente, Nicaragua	Protected wildlife reserve (1983); historically, selectively logged, subsistence agriculture, grazing	1500	26	6	115/12 ha > 10 cm or 54/.1 ha > 2.5 cm	*Gyrocarpus*, *Tabebuia*, *Lysiloma*, *Stemmadenia*	Floristic inventories; diversity; fire and species resistance	Sabogal (1992), Gillespie et al. (2000), Otterstrom and Schwartz (2006)
Rio Grande watershed, Nicaragua	Pasture	1576	24.5			*Guazuma*, *Cassia*, *Tabebuia*, *Albizia*	Characterization, regeneration in pastures	Esquivel et al. (2008)
Santa Rosa, Costa Rica	Protected forest (1971); historically, cattle pasture	1570	25	6	75/.1 ha > 2.5 cm; or 92/.1 ha > 5 cm	*Pachira*, *Calycophyllum*, *Enterolobium*, *Eugenia*	Enrichment plantings, grass removal experiments; diversity; fire exclusion; chronosequence; succession after pasture abandonment	Gerhardt (1993, 1996, 1998), Gerhardt and Hytteborn (1992), Gerhardt and Fredriksson (1995), Gillespie et al. (2000), Janzen (2002), Kalacska et al. (2004), Powers et al. (2009)
Chenadega, Nicaragua	Secondary forest; used for firewood and grazing	1700	27	5	39/6.2 ha > 10 cm	*Guazuma*, *Cordia*, *Bravasia*, *Cassia*	Floristic inventories	Sabogal (1992)
Palo Verde, Costa Rica	Protected forest (1979); historically, cattle pasture	1750	24	5	93/ha > 10 cm or 65/.1 ha > 2.5 cm	*Calycophyllum*, *Astronium*, *Brosimum*, *Spondias*	Floristic inventories; diversity; cattle exclusion experiment; floristics; succession after pasture abandonment;	Janzen (1983), Gillespie et al. (2000), Stern et al. (2002), Quigley and Platt (2003), Powers et al. (2009)
Playa Venado, Azuero peninsula, Panama	Protected forest (1980); historically, selectively logged, burned, and grazed	1700	25	5	28/.16 ha > 10 cm	*Guzuma*, *Cordia*, *Tabebuia*, *Calycophyllum*	Enrichment planting, Native species plantations	Griscom et al. (2005, 2007, 2009), Wishnie et al. (2007), Parks et al. (2010)

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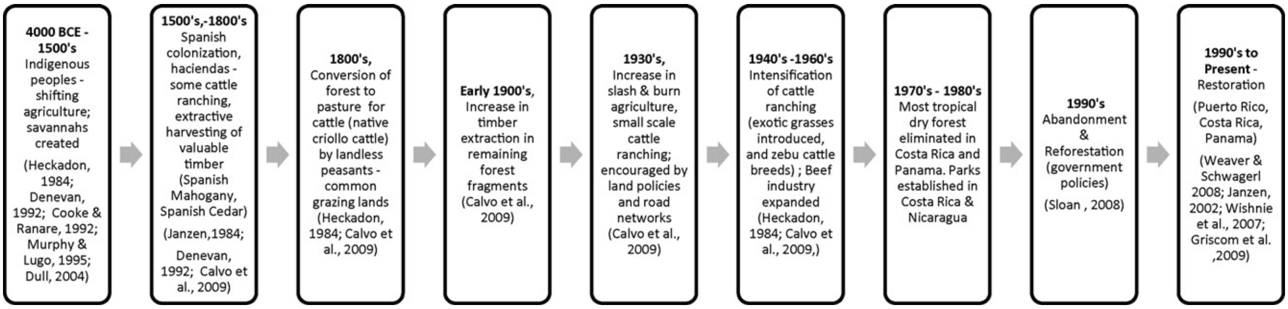

Fig. 2. Timeline of deforestation and degradation within dry tropical forests in Central America (Costa Rica and Panama).

world (Maass, 1995; Arroyo-Mora et al., 2005; Calvo-Alvarado et al., 2009). Most land clearance occurred during this era. As a consequence, few dry tropical forest fragments remain in Panama and Nicaragua (Sabogal, 1992; Griscom et al., 2005) (Fig. 1). The first forest reserve, now the Guanica Biosphere Reserve, was established in 1919 in Puerto Rico's subtropical very dry forest (Murphy and Lugo, 1986b) (Table 1). But for Costa Rica, Nicaragua, and Mexico parks were established much later (1970–1990) to preserve the remaining dry forest fragments (Janzen, 1983; Sabogal, 1992). In 1989, Janzen spear-headed the ecological restoration movement with the creation of Guanacaste National Park in Costa Rica (Holden, 1986; Allen, 1988, 1989; Tenebaum, 1994).

In Central America, pastures remained productive for decades (Murphy and Lugo, 1986a). Today, however, natural recovery and active reforestation are occurring after 30–40 years of deforestation (Sloan, 2008; Calvo-Alvarado et al., 2009; Garen et al., 2009). Pastures throughout Latin America are undergoing abandonment due to changing socio-economic incentives and/or declining productivity (Murphy and Lugo, 1995; Arroyo-Mora et al., 2005; Marin et al., 2009). Falling international beef prices explained land abandonment in Costa Rica (Arroyo-Mora et al., 2005). Forest recovery in Costa Rica (mostly in the Guanacaste province) has been attributed to forest conservation policies (Arroyo-Mora et al., 2005; Calvo-Alvarado et al., 2009). In Panama, reforestation sky-rocketed in the 1990s due to a government tax credit for establishing plantations, 77% of which were monocultures of teak (*Tectona grandis*) (Sloan, 2008). In the 1990s cattle ranches along the Pacific coast began to be sold in Costa Rica and Panama at high prices for tourism development and to foreigners who desired second homes on ocean-front property (Ankersen et al., 2006; Kull et al., 2010).

Today, "conservation gentrification" is occurring as many of these new landowners are interested in protecting and reforesting to increase biodiversity, forest cover, and long-term ecological service value (Ankersen et al., 2006; Kull et al., 2010). In addition, some of the original farmers are interested in obtaining higher levels of agricultural productivity through agroforestry (Garen et al., 2009; Hall et al., this issue). For example, Panamanian farmers on the Azuero are participating in reforestation programs (PRORENA) to improve environmental conditions, and hence agricultural productivity (Garen et al., 2009; Hall et al., this issue).

3. Ecological description of the forest type

Tropical dry forests, originally representing 49% of tropical vegetation in Mesoamerica, are a broad category which includes a range of forest types from grasslands to tall forests (Murphy and Lugo, 1995). There is some discrepancy in the distribution maps within Central America (Murphy and Lugo, 1995; Sanchez-Azofeifa et al., 2005b; Miles et al., 2006) because of this expansive definition. The most recent definition from the TROPI-DRY collaborative research network (http://tropi-dry.eas.ualberta.ca/) defines tropical dry forests as dominated by drought-tolerant deciduous trees (at least 50%), growing in a climate where the mean annual temperature is $\geq 25\,^{\circ}\mathrm{C}$, annual total precipitation ranges between 700 and 2000 mm, and there are three or more dry months of little to no rain (Sanchez-Azofeifa et al., 2005b). The percentage of deciduous trees varies from 50 to 100%, depending on the type of forest and their location along a precipitation gradient (Medina, 2005).

Within dry tropical forests are subcategories, some more loosely defined than others (Table 1). Subtropical dry forests have mean annual temperatures below $24\,^{\circ}\mathrm{C}$ (Holdridge, 1967). Very dry forests receive less than 1000 mm of rain while dry forests receive 1000–2000 mm of rain, as defined by Holdridge (1967). Dry tropical forests are sometimes further subdivided into deciduous, semi-deciduous, or semi-evergreen, referring to the number of deciduous species or stems in the canopy but there are no clear definitions to these terms. Finally, savannahs and thorn woodlands are thought to have at one time been dry tropical forests but have been modified by historical fire and disturbance regimes to new structures and states (Denevan, 1992; Cooke and Ranere, 1992). They are usually included in dry tropical forest distribution maps (Murphy and Lugo, 1986a; Miles et al., 2006).

The original distribution of dry tropical forests in Fig. 1 was derived from WWF ecoregion dataset (Olson et al., 2001), combining two ecoregions: tropical and subtropical dry broadleaf forests and tropical and subtropical grasslands, savannas, and shrublands. This dataset is based off of biogeographic maps rather than biophysical features (e.g., rainfall and temperature) and most likely reflects the distribution of species and communities more accurately (Olson et al., 2001).

Research to date has mostly been to quantitatively describe the composition and structure of largely intact subtropical very dry to dry forests of Puerto Rico and Mexico (Lugo, 1986; Murphy and Lugo, 1986b; Murphy and Lugo, 1987; Mizrahi et al., 1997; Ellingson et al., 2000; Kauffman et al., 2003; Burgos and Maass, 2004; Colon, 2006; Lebrija-Trejos et al., 2008).The two central areas of experimental research on restoration techniques within dry tropical forest ecosystems in Central America are on the Azuero peninsula in Panama and in the Guanacaste province in Costa Rica (Table 1, Fig. 1). On the Azuero peninsula, the dry tropical ecosystem, receives an average of 1700 mm of precipitation, which can fall as low as 1300 mm in droughty years. The dry season is pronounced with 5 months out of the year receiving no rain. Rain begins in late April and ends in late November. The undulating terrain, ranging in elevation from 10 to 100 m, is a mosaic of pastures planted with African grasses *Hyparrhenia rufa* and *Panicum maximum*. Common tree species in the pasture matrix are *Guazuma ulmifolia* and *Cordia alliodora* while the fragments are dominated by *Calycophyllum candidissimum* and *Tabebuia rosea* (Griscom et al., in press) (Table 1).

In the Guanacaste Conservation Area of Costa Rica (Santa Rosa) and in the Tempisque Conservation Area of Costa Rica (Palo Verde),

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the climate is drier than the Azuero, with a 5–6-month dry period and annual rainfall of 1500 mm (Gerhardt, 1993; Powers et al., 2009) (Table 1). *Hyparrhenia rufa* also dominates the abandoned pastures and the land has been grazed with cattle for decades (Gerhardt, 1993; Janzen, 2002). *Calycophyllum candidissimum*, *Spondias mombin*, *Eugenia* spp., *Pachira quinata*, *Enterolobium cyclocarpum*, *Licania* spp., and *Brosimum alicastrum* are commonly found species within secondary forests in these two areas (Janzen, 1983) (Table 1). Common pasture trees are *Byrsonima crassifolia* and *Curatella americana* (Janzen, 1983)

Based on the literature for both subtropical and tropical regions (Table 1), trends in diversity suggest mature, relatively old forests comprise 77–127 species ha^{-1} (Gillespie et al., 2000; Quigley and Platt, 2003) compared to forests used for shifting cultivation which have approximately 30 tree species ha^{-1} (Sabogal, 1992; Griscom et al., in press) (Table 1). Cleared lands that now comprise recovering pastures of 14 years had approximately 21+ tree species ha^{-1} (Marin et al., 2009).

Major lethal disturbances within dry forests include landslides (Velazquez and Gomez-Sal, 2007) and sub-lethal disturbances such as droughts (Ceccon et al., 2006) and hurricanes (Van Bloem et al., 2006). The number of wind dispersed species ranges from 30 to 60% (Vieira and Scariot, 2006) while 57 to 81% of species coppice (Murphy and Lugo, 1986b; Vieira and Scariot, 2006). With modern human impacts and with introduced disturbances of fire and land clearance for pasture, second growth forests present a much higher proportion of wind dispersed (Janzen, 1988; Sabogal, 1992; Powers et al., 2009) and sprouting species (Miller and Kauffman, 1998; McLaren and McDonald, 2003; Griscom et al., 2009).

4. Degradation processes

Understanding the processes of degradation is critical for the development of management recommendations for reforestation (Ashton et al., 2001). The ability of the abandoned land to regenerate will depend on past management and disturbance history. Acute catastrophic events (e.g., land clearance), has a different effect on reforestation compared to the frequency and degree of chronic disturbances (e.g., fires, cattle grazing, selective logging). All these factors will affect sources of natural regeneration and the establishment and growth of woody species (Table 2).

Degradation processes related to different human impacts can therefore be categorized into: (1) acute one-time events; and (2) chronic repeated events. Within each of these categories, degradation processes can be further divided according to: (1) structural changes (e.g. floristics, regeneration mechanisms, successional); and (2) functional changes of the forest and land (e.g. soil fertility, hydrological–infiltration, subsurface flow) (Ashton et al., 2001). Structural changes represent changes in composition because of lack of seed source, or inability to establish (e.g. open conditions, susceptibility to browse) but not because of fundamental changes to the integrity of site. Functional change can be regarded as more severe, altering the actual fertility, hydrology and structure of the soil and hence site productivity, and potentially the ability of native species to adapt to site.

In this paper we have defined different degradation processes in three main sections: (1) acute one-time events (land clearance, introduction of exotic grasses); (2) structural legacies that acute one-time events can leave behind (individual trees, forest fragments) that have lasting effects of native forest ability to regenerate; and (3) chronic events (fire, herbicide application). Chronic events have been subdivided into structural and functional degradation processes.

4.1. Acute one-time events: the nature of land clearance and exotic grass introduction

Land clearance, site preparation, and burning were the major events that shaped the capacity of the forest to recover. The degree of efficiency and intensity of the clearance defines the ability of the land to recover to forest of similar structure and composition as before. In Central America, land was initially cleared for subsistence agriculture as landless peasants expanded into the frontier (Sabogal, 1992; Sloan, 2008; Calvo-Alvarado et al., 2009) (Fig. 2). Surrounding forests were used for firewood (Sabogal, 1992). However, the majority of the forested areas were cleared for pasture with timber extraction as the by-product of deforestation (Calvo-Alvarado et al., 2009). Generally the efficiency of land clearance was controlled by two factors: (i) the fertility of the soil – the greater the fertility the greater the intensity of land clearance to maximize productivity; and (ii) the nature of the topography – the greater the degree of rough terrain the more inefficient the process of land clearance. Hence, sites with rough terrain and lower soil fertility tended to have remnant forest fragments.

The second major event occurred some years later with the introduction of exotic African grasses in the 1940s (Fig. 2). This was done to more easily maintain a productive grassland system for cattle ranching. The persistence of introduced, exotic African grasses after abandonment has created significant barriers to natural succession by preventing germination and out-competing native species for light and soil resources (Nepstad et al., 1996; Cabin et al., 2002; Hooper et al., 2002; Griscom et al., 2009). Some grasses have more of a negative effect than others which depends on their specific growth characteristics. In Nicaragua, natural regeneration was significantly more prolific with *Brachiaria* spp., an erect, bunch-forming plant, than within *Cynodon* spp., which forms a creeping mat (Esquivel et al., 2008). *Hyparrhenia rufa* is the most common pasture grass in Costa Rica and Panama and forms tall, dense monocultures (1–2 m) (Janzen, 2002), decreasing light in the wet season and crushing natural regeneration when it dries in the dry season (Griscom et al., 2009).

Susceptibility to grass competition varies among woody species. For example, small-seeded tropical species (e.g., *Trema micrantha*) are more sensitive to root competition from grasses than large-seeded species (Nepstad et al., 1990; Hooper et al., 2002; Griscom et al., 2009). African grasses have an additional negative, indirect effect on succession by perpetuating fire (Cabin et al., 2002; Janzen, 2002; Lamb et al., 2005; Calvo-Alvarado et al., 2009). Fire-adapted grasses catalyze a positive feedback loop, increasing the frequency and intensity of fire (D'Antonio and Vitousek, 1992), maintaining themselves, and inhibiting change to forest regrowth.

4.2. Structural legacies of acute one-time events: conservation or elimination of regeneration sources

Eradication of trees and their seed dispersers can severely affect abilities of agricultural and ranching landscapes to re-vegetate (Uhl et al., 1988; Holl et al., 2000; Zimmerman et al., 2000; Hooper et al., 2004; Felton et al., 2010). This presents less of an issue in dry tropical forests because of the prevalence of wind dispersal (30–60% are wind dispersed) (Vieira and Scariot, 2006), although there is still the limitation of distance from the parent tree. Wind dispersed seeds will travel up to 250 m into the open pasture from a fragment or isolated tree (Holl, 1999). Wind dispersal is therefore effective as long as networks of trees persist throughout the landscape and seeds can germinate and establish in pasture. Usually, establishment is only possible if nurse trees exist within the pasture to ameliorate microclimate conditions (Uhl et al., 1982; Somarriba, 1988; Guevara et al., 1992; Callaway and Pugnaire, 1999; Hooper et al., 2004; Padilla and Pugnaire, 2006; Santiago-Garcia et al., 2008).

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Table 2
List of tree species that may be appropriate for enrichment planting or plantations in dry tropical regions of Central America. Species are organized by native versus exotic and dispersal mode. Under attributes, growth = fast-growing, nitrogen = nitrogen-fixing, timber = valuable timber, NTFP = non-timber forest product (from www.worldagroforestrycentre.org), animals = fruit for attracting wildlife, nurse = facilitates natural regeneration in the understory, canopy = broad canopy for shade, delayed planting = should be introduced after canopy has been established.

Native, abiotically dispersed	Successional status	Seed dispersal	Evergreen	Resistant to fire	Low susceptibility to browse	Attributes	Plantation or trial species	Reference
Albizia adinocephala (Donn. Sm.) Britton & Rose ex Record	Pioneer	Wind				Nitrogen, Timber	X	Wishnie et al. (2007), Parks et al. (2010), Hall et al. (this issue)
Albizia guachapele, (Kunth) Dugand	Pioneer	Wind				Nitrogen, Timber	X	Wishnie et al. (2007), Parks et al. (2010)
Astronium graveolens, Jacq.	Pioneer	Wind				Timber, Growth	X	Wishnie et al. (2007), Parks et al. (2010), Hall et al. (this issue)
Calycophyllum candidissimum (Vahl) DC	Late-successional	Wind				Growth, Timber	X	Hooper et al. (2002),[a] Kalacska et al. (2004), Wishnie et al. (2007), Parks et al. (2010), Hall et al. (this issue)
Cassia pallida Vahl.	Pioneer	Wind			X			Stern et al. (2002)
Cedrela odorata L.	Pioneer	Wind			X	Growth, Timber	X	Griscom et al. (2005), Parks et al. (2010), Hall et al. (this issue)
Ceiba pentandra (L.) Gaertn.	Late-successional	Wind				Growth, Timber, NTFP	X	Weaver and Schwagerl (2008)
Cochlospermum vitifolium (Willd.) Spreng.	Short-lived, pioneer	Wind		X				Janzen (1983), Hooper et al. (2004)[a]
Colubrina glandulosa Perkins	Pioneer	Explosive						Hall et al. (this issue)
Cordia alliodora, (Ruiz & Pav.) Oken	Long-lived pioneer	Wind		X		Timber, Growth	X	Janzen (1983), Hooper et al. (2004),[a] Wishnie et al. (2007), Parks et al. (2010), Hall et al. (this issue)
Dalbergia retusa Hemsl.	Long-lived pioneer	Wind			X	Nitrogen, Timber	X	Janzen (1983), Stern et al. (2002), Kalacska et al. (2004), Hall et al. (this issue)
Diphysa robinoides, Benth.	Long-lived pioneer	Wind				Nitrogen, Growth	X	Wishnie et al. (2007), Parks et al. (2010)
Gliricidia sepium (Jacq.) Kunth ex Walp.	Long-lived pioneer	Explosive	X	X	X	Nitrogen, Growth, Timber,		Wishnie et al. (2007), Esquivel et al. (2008), Parks et al. (2010), Hall et al. (this issue), van Breugel et al. (this issue)
Hippomane mancinella L.	Pioneer	Water		X				
Hura crepitans L.	Long-lived pioneer	Explosive			X	Timber	X	Hall et al. (this issue), van Breugel et al. (this issue)
Luehea seemannii Triana & Planch	Short-lived, pioneer	Wind					X	Wishnie et al. (2007), Parks et al. (2010), Hall et al. (this issue)
Ochroma pyramidale, (Cav. ex Lam.) Urb.	Short-lived, pioneer	Wind				Growth, Nurse, Timber, NTFP	X	Wishnie et al. (2007), Parks et al. (2010), Hall et al. (this issue), van Breugel et al. (this issue)
Pachira quinata (Jacq.) W.S. Alverson	Mid-successional	Wind				Growth, Timber	X	Wishnie et al. (2007), Kalacska et al. (2004), Parks et al. (2010), Hall et al. (this issue), van Breugel et al. (this issue)
Swietenia macrophylla King	Long-lived Pioneer	Wind				Growth, Timber, Nurse, NTFP	X	Gerhardt (1993), Hall et al. (this issue)
Tabebuia spp.	Long-lived, Pioneer	Wind			X	Growth, Timber	X	Stern et al. (2002), Wishnie et al. (2007), Parks et al. (2010), Hall et al. (this issue), van Breugel et al. (this issue)

Native, biotically dispersed	Successional status	Seed dispersal	Evergreen	Resistant to fire	Low susceptibility to browse	Attributes	Plantation or trial species	Reference
Anacardium excelsum (Kunth) Skeels	Late-Successional	Bat	X			Animals, Timber	X	Janzen et al. (1976), Janzen (1983), Hall et al. (this issue)
Andira inermis (W. Wright) Kunth ex DC.	Late-successional	Bat	X			Nitrogen, Growth, Animals NTFP		Janzen et al. (1976), Zimmerman et al. (2000), Weaver and Schwagerl (2008)
Brosimum alicastrum Sw.	Late-successional	Bat, Bird	X			Animals, Delayed Planting, NTFP, Timber		Janzen (1983), Bonilla and Holl (in press), Hall et al. (this issue)
Byrsonima crassifolia (L.) Kunth	Savannah Colonist	Bird	X			Growth, Animals, NTFP, Timber		Janzen (1983), Hooper et al. (2002),[a] Hall et al. (this issue)
Bursera simaruba (L.) Sarg.	Pioneer	Bird, Monkey				Growth, Animal, Timber, NTFP	X	Janzen (1988), Griscom et al. (2007), Weaver and Schwagerl (2008)
Cecropia spp.	Short-lived Pioneer	Bird, Bat				Animal		Janzen (1983)
Coccoloba spp.	Pioneer	Bird			X	Animal		Kalacska et al. (2004)
Copaifera aromatica Dwyer	Late-successional	Bird, Bat	X			NTFP, Timber		Griscom et al. (2005), Hall et al. (this issue)
Crescentia alata Kunth.	Long-lived Pioneer	Rodent, Ungulate		X		Growth NTFP	X	Janzen (1983), Weaver and Schwagerl (2008)
Curatella americana L.	Pioneer	Bird		X				Janzen (1988), Heckadon Moreno (1984)
Enterolobium cyclocarpum (Jacq.) Griseb	Late-successional	Ungulate, Rodent				Nitrogen, Growth, Timber, Animals, Canopy, NTFP	X	Griscom et al. (2005), Wishnie et al. (2007), Bonilla and Holl (in press), Parks et al. (2010), Hall et al. (this issue)
Erythrina fusca Lour.	Pioneer	Water				Nitrogen, Nurse	X	Wishnie et al. (2007), Parks et al. (2010), Hall et al. (this issue), van Breugel et al. (this issue)
Guazuma ulmifolia Lam.	Pioneer	Bat, Ungulate		X	X	Growth, Animals, Nurse, Canopy	X	Janzen et al. (1976), Wishnie et al. (2007), Esquivel et al. (2008), Weaver and Schwagerl (2008), Parks et al. (2010), Hall et al. (this issue), van Breugel et al. (this issue)
Hymenaea courbaril L.	Late-successional	Rodent, Monkey	X			Growth, Timber, NTFP	X	Gerhardt (1993), Hall et al. (this issue)
Manilkara chicle (Pittier) Gilly	Late-successional	Bat, Monkey	X			Animals, Delayed Planting, NTFP		Gerhardt (1993), Bonilla and Holl (in press), Hall et al. (this issue)
Muntingia calabura L.	Pioneer	Bird, Bat				Animals, Growth, Nurse	X	Jones et al. (2004)[a], Hall et al. (this issue), van Breugel et al. (this issue)
Samanea samen (Jacq.) Merr.	Long-lived Pioneer	Ungulate				Growth, Animals, Nurse, Timber, Nitrogen	X	Janzen (1983), Sabogal (1992), Wishnie et al. (2007), Hall et al. (this issue)
Sciadodendron excelsum Griseb.	Pioneer	Bird				Animals		Kalacska et al. (2004)
Spondias mombin L.	Long-lived Pioneer	Bat, Monkey				Growth, Animals, Nurse, NTFP	X	Janzen (1985), Hooper et al. (2002)[a], Wishnie et al. (2007), Weaver and Schwagerl (2008), Parks et al. (2010), Hall et al. (this issue), van Breugel et al. (this issue)
Sterculia apetala (Jacq.) H. Karst.	Gap-colonist	Rodent, Monkey				Growth, Animals		Hooper et al. (2002)[a], Hall et al. (this issue)
Trema micrantha (L.) Blume	Short-lived Pioneer	Bird				Growth, Nurse	X	Janzen (1983), Hooper et al. (2002)[a], Jones et al. (2004)[a]

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Table 2 (*Continued*)

Exotic Species	Successional status	Seed dispersal	Evergreen	Resistant to fire	Low susceptibility to browse	Attributes	Plantation or trial species	Reference
Acacia mangium Willd.	Pioneer	Wind		X		Nitrogen, Nurse, Timber	X	Otsamo (1999), Wishnie et al. (2007), Hall et al. (this issue), van Breugel et al. (this issue)
Albizia lebbeck (L.) Benth.	Pioneer	Wind		X		Nitrogen, Nurse, Timber	X	Parrotta (1992)
Casuarina equisetifolia L.	Pioneer	Wind	X			Nitrogen, Nurse, Timber, Animals	X	Parrotta (1999)
Eucalyptus robusta Sm.	Pioneer	Wind		X		Nurse, Timber	X	Sabogal (1992), Parrotta (1999)[a]
Gmelina arborea Roxb. ex Sm.	Pioneer	Birds		X		Animals, Nurse, Timber, NTFP	X	Janzen (2002), Hall et al. (this issue)
Leucaena leucocephala (Lam.) de Wit	Pioneer	Wind	X	X	X	Nitrogen, Nurse, Timber, NTFP	X	Sabogal (1992), Parrotta (1999), Santiago-Garcia et al. (2008)
Pinus caribaea Morelet	Pioneer	Wind	X	X		Nurse, Timber, NTFP	X	Lugo et al. (1988), Ashton et al. (1998)[a]
Tectona grandis L.f.	Pioneer	Wind		X		Timber	X	Wishnie et al. (2007), Hall et al. (this issue), van Breugel et al. (this issue)

[a] Information not from dry tropical forests.

Farmers in Central America frequently leave trees for livestock shelter, construction material for buildings and farm implements, edible fruit, firewood and fence posts (Budowski, 1987; Guevara et al., 1986; Harvey and Haber, 1999; Barrance et al., 2003; Leon and Harvey, 2006; Garen et al., 2009; Harvey et al., this issue) or leave riparian fringes or even sizable gallery forests – partly for stream bank stabilization but more frequently because the farmers are unable to control the vigor of riparian vegetation. Trees within riparian zones are also conserved to provide shade and cool water for the cattle (Garen et al., 2009). Farmers also see riparian vegetation as direct competition with cattle for water and consequently, trees are often cut down or girdled (Griscom et al., in press). Farmers might also remove trees that may harm cattle (*Samanea saman*, *Cecropia* spp., *Gliricidia sepium*) (Harvey et al., this issue). Live fences are often created to enclose livestock and to maintain property boundaries. The most commonly chosen species (*Gliricidia sepium, Erythrina* spp.) also fix nitrogen, thereby improving the soils (Harvey et al., 2005). These fences unintentionally serve as important wildlife corridors and habitat within the agricultural landscape (Leon and Harvey, 2006; Harvey et al., 2005). All these practices increase the likelihood of success for establishing a new forest (Guevara et al., 1986; Harvey and Haber, 1999; Estrada et al., 2000; Harvey et al., 2005; Esquivel et al., 2008) (Fig. 3). The number and diversity of trees depends in large part on the ideologies, beliefs, and needs of landowners. This in turn will affect the rate and diversity of forest succession when the land is abandoned.

4.3. *Chronic repeated events: fire, herbicide, and cattle*

4.3.1. *Structural effects*

Fire is an introduced disturbance regime that inhibits woody regeneration and therefore restoration efforts in dry forest ecosystems (Hopkins, 1983; Rundel and Boonpragob, 1995; Zanne and Chapman, 2001; Janzen, 2002; Fensham et al., 2003). Frequent burning also changes species and successional process, as fire-resistant native vegetation (e.g., *G. ulmifolia*, *B. crassifolia*, *Coccoloba* spp.) (Table 2) will survive while fire-intolerant species (e.g. *Sterculia apetala*, *Genipa americana*, *Ceiba pentandra*, *Cecropia* spp.) (Hooper et al., 2002) will be eradicated. Fire-resistant species often have thick bark, larger seeds, and/or prolific root/shoot coppicing (Hooper et al., 2002; Otterstrom and Schwartz, 2006). Consequently, the diversity of the regenerating forest is expected to be lower when fire is a recurring part of the system (Bullock, 1985; Swaine et al., 1990; Medina, 2005; Hooper et al., 2004). In addition to fire, herbicide application is a common practice to eliminate unwanted stump sprouts (e.g., *Psidium guajava*, *Tabebuia* sp., *Casearia arguta*) (Harvey et al., this issue). Annual application of herbicide further destroys the regeneration capacity of the land and increases surface soil erosion.

Lastly, like fire and herbicide, cattle act as a natural selection agent, favoring species that are unpalatable (e.g., *Acacia collinsii*, *Hura crepitans*, *Cedrela odorata*), that they disperse (e.g., *G. ulmifolia*, *E. cyclocarpum*), or that can readily resprout after being damaged by browsing or trampling (e.g., *G. ulmifolia*, *Gliricidia sepium*) (Table 2). In Nicaragua, some of the most dominant species in dry pastures were pioneer species that were dispersed by cattle (*G. ulmifolia*, *Cassia grandis*, *E. cyclocarpum, Leucaena shannonii*) (Esquivel et al., 2008). In Panama, *G. ulmifolia* dominated the pasture landscape because farmers favored it for fodder, it readily sprouts and its seeds are dispersed by cattle (Griscom et al., 2009). For the most part, cattle negatively affect tree seedling growth and survival by trampling and browsing on tree seedlings (Guevara et al., 1986; Guevara and Laborde, 1993; Williams-Linera et al., 1998; Gillespie et al., 2000; Griscom et al., 2005, 2009); thereby reducing diversity and abundance of natural regeneration (see exclusion experiments by Griscom et al., 2009). Likewise, cattle exclusion has been used

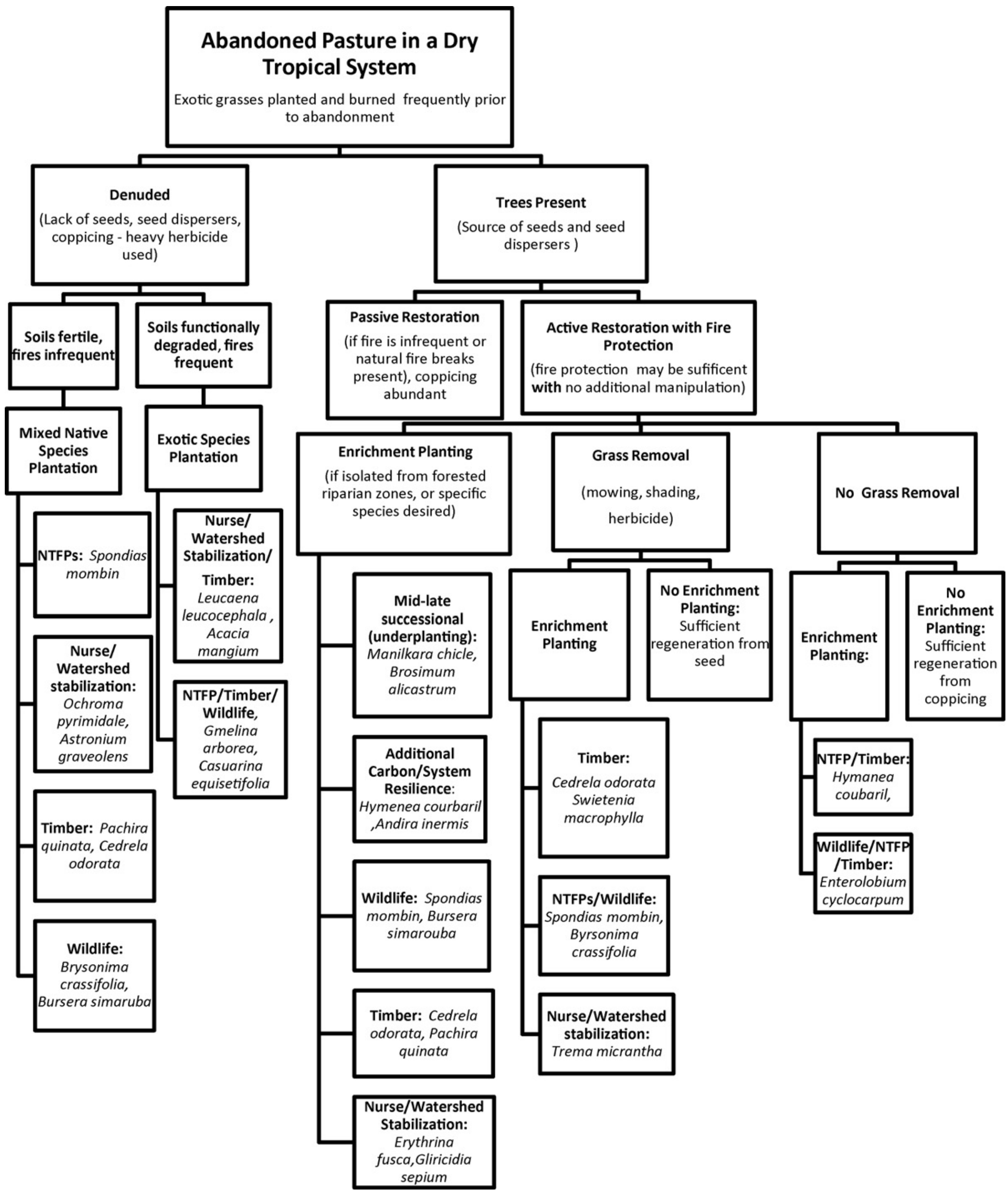

Fig. 3. Restoration pathways of dry tropical forests for different biological and social circumstances. The assumption is that abandoned pastures have been historically grazed by cattle and burned frequently. See Table 2 for rationale of selected tree species.

to restore Hawaii dry tropical forests, if grass can be eliminated as well to avoid fire (Cabin et al., 2002).

4.3.2. Functional effects

The combination of yearly pasture burning, hilly topography, and heavy rainfall, during the wet season, such as on the southern side of the Azuero peninsula, has caused severe top soil erosion and a steady decline in soil fertility (Heckadon Moreno, 1984). Total soil nitrogen can decline by 23–60% (Johnson and Wedin, 1997; Ellingson et al., 2000; Garcia-Oliva et al., 2006; Sandoval-Perez et al., 2009) while soil carbon can decline 18–47% in dry regions of Central America (Johnson and Wedin, 1997; Garcia-Oliva et al., 2006; Sandoval-Perez et al., 2009). The conversion of forest to pasture, grazed for more than 20 years resulted in a loss of 10 Mg ha^{-1} C in moist forest ecosystems of Panama (Neumann-Cosel et al., this issue). However, soil carbon results should be interpreted with caution. Within wet systems, studies have indicated that this change in carbon is only detected at soil depths below 10 cm (Schedlbauer and Kavanagh, 2008). Other studies have found no changes in soil carbon between forest and pasture (Powers and Veldkamp, 2005) or at least not until secondary forests are over 20 years (Neumann-Cosel et al., this issue). Discrepancies in the literature with regards to soil carbon are most likely due to differences in soil type, land-use history and agricultural use between sites (Neumann-Cosel et al., this issue). Soil phosphorus results are mixed. In two studies, no difference in phosphorous levels was detected between forest and pasture (Johnson and Wedin, 1997; Garcia-Oliva et al., 2006) but a third study showed a 60% decline (Sandoval-Perez et al., 2009). The decline in available nutrients (carbon, nitrogen, and potentially phosphorous) can limit the rate, kind and nature of regrowth (Janzen, 2002; Sandoval-Perez et al., 2009).

Decades of cattle grazing have also changed the soil and decreased land productivity (Heckadon Moreno, 1984; Janzen, 1988; Uhl et al., 1988; Sabogal, 1992). Cattle compact the soil, thereby increasing bulk density, reducing infiltration and increasing surface water runoff (Holl, 1999). This in turn reduces subsurface soil water availability (Martinez and Zinck, 2004; Zimmerman et al., 2006; Germer et al., 2010). No data were found on the effect of land conversion in dry tropical forests on soil structure properties but within wet tropical forests converted to pasture, bulk density increased by 27–63% (Neill et al., 1997; Martinez and Zinck, 2004), penetration resistance (MPa) increased by 90% (Martinez and Zinck, 2004), infiltration decreased by 90–94% (Zimmerman et al., 2006; Germer et al., 2010) and soil porosity declined by 20% (Martinez and Zinck, 2004). All such trends would suggest the soils would become more droughty, with greater portions of water moving off the land surface rather than moving more slowly through the soil subsurface; and when rains do come the increased compaction and smaller micropore space make the soils more prone to water logging, and more anoxic (Martinez and Zinck, 2004).

4.4. Summary of degradation processes

Although the degradation processes associated with cattle ranching may be similar between wet and dry tropical forests, the impact of the disturbances and the speed and success of recovery can differ (Vieira and Scariot, 2006). Differences suggest that dry forests are slower to recover, with higher proportions of sprout origin and wind dispersed trees that are fire tolerant (Murphy and Lugo, 1986a; Janzen, 2002; Vieira and Scariot, 2006). Shorter, more unpredictable wet periods and longer, harsher dry seasons, which is sometimes accentuated by excessive drainage from coarse soil, make water limitation an important factor. Limiting water provides for slower growth rates as compared to the wetter forest on the Atlantic side of the region (Wishnie et al., 2007; Quesada et al., 2009; Parks et al., 2010), and may play a role in affecting reproductive capacity as well (Murphy and Lugo, 1986a).

In summary, forest restoration requires a clear understanding of degradation process for successful reforestation to occur under different environmental conditions and social values (Ashton et al., 2001; Garen et al., 2009). The consequence of dry tropical forest degradation is simplification; with tree species remaining that are (1) stump sprouters; (2) inedible to cattle or dispersed by cattle; (3) resistant to fire; (4) tolerant to the desiccating conditions of the pasture environment; (5) wind dispersed; and (6) have some human use and have therefore been selectively kept in the landscape either as isolated trees or live fences.

5. Restoration models

Natural successional processes can be facilitated with minimal intervention (e.g., land protection) or with intensive practices (e.g., site preparation, plantations). Within these two extremes is a range of other restoration techniques, some of which have been experimentally examined within dry tropical forest (Gerhardt, 1993; Janzen, 2002; Griscom et al., 2005, 2009; Wishnie et al., 2007; Parks et al., 2010; Hall et al., this issue; van Breugel et al., this issue).

Five different management techniques are described below in order of investment in terms of cost, time, and maintenance. The five techniques from least investment to most comprise: (1) a hands-off approach (passive restoration) requiring very little input besides minimal protection from logging and cattle grazing; (2) additional protection from fire during the dry season to increase rate and diversity of succession; (3) enrichment planting of native tree species to introduce diversity and/or economic value; (4) removing or controlling grasses to increase survival and growth rate of planted and naturally regenerated seedlings or sprout growth; and lastly (5) an option to uniformly plant exotic or native species tree species because sites have been modified to an extent that few native species can establish or no seed source exists. Selected reforestation options will therefore depend upon history of past management and desired social value.

5.1. Passive restoration

Natural regeneration has a very low maintenance cost and may be the most practical option for the restoration of large areas (Aide, 2000; Hooper et al., 2004). However, this is a risky pathway if thresholds have been crossed, increasing the likelihood of arrested succession (Lamb et al., 2005). Passive restoration has been found to be most effective in the moist tropics if soils are not severely degraded and remnant forests and trees remain in the landscape (Aide, 2000). Four conditions need to be recognized and characterized if passive restoration is to succeed: (1) the presence of legacy trees; (2) the nature and amount of forested riparia; (3) the species composition and diversity of legacy trees and riparia; and (4) the nature of site heterogeneity (aspect, slope, soil type).

5.1.1. Legacy pasture trees are important facilitators of tree regeneration within pastures

Isolated, linear or clustered trees enable seed dispersers to persist in agricultural landscapes by providing habitat and resources that are scarce in the open pasture environment (Guevara et al., 1986; Nepstad et al., 1991; Guevara and Laborde, 1993; Harvey et al., this issue). Bird and bat seed dispersers forage on the fleshy fruited pasture trees (e.g., *B. crassifolia*, *Spondias mombin*, *Eugenia coloradoensis*, *Sciadodendron excelsum*) (Griscom et al., 2007). By foraging on such trees they can facilitate seed dispersal and enlarge patches of animal-dispersed species around isolated pasture trees (Uhl et al., 1981; Guevara and Laborde, 1993; McClanahan and Wolfe, 1993; Nepstad et al., 1996; Slocum and Horvitz, 2000; Janzen, 2002; Griscom et al., 2007). Seed rain has been found to be much greater beneath isolated trees than in the open pasture (Uhl et al., 1981; Willson and Crome, 1989; Guevara and Laborde, 1993; Cardosa da Silva et al., 1996; Nepstad et al., 1996; Slocum and Horvitz, 2000).

Trees also improve microclimate conditions for wind and animal-dispersed species by reducing solar radiation, lowering air and soil temperature, reducing soil water evaporation, and decreasing the risk of fire (Uhl et al., 1982; Somarriba, 1988; Guevara et al., 1992; Callaway and Pugnaire, 1999; Padilla and Pugnaire, 2006; Santiago-Garcia et al., 2008; Hooper et al., 2004). Seedlings display greater growth and survival under nurse trees as long as cattle are excluded (Williams-Linera et al., 1998; Sanchez-Velazquez et al., 2004; Santiago-Garcia et al., 2008). In Puerto Rico, seedlings showed greater performance beneath the canopy of isolated trees of *Leucaena leucocephala* as compared to the open (Santiago-Garcia et al., 2008) while in Mexico, *Brosimum alicastrum* seedlings had higher survival and growth under deciduous pasture trees than in the open (Sanchez-Velazquez et al., 2004).

5.1.2. Forest riparia are critical sources of bird and bat disseminated seed and moderators of edge environments

The presence of forested riparian zones is an even greater resource and predictor of passive restoration success than isolated trees (Griscom et al., 2009). Forested riparian zones facilitate the regeneration of relatively diverse second growth forests after pasture abandonment (Griscom et al., 2009). Studies showed that frugivorous birds and bats visited riparian zones and were the major dispersers of seeds into the adjacent open pasture (Nepstad et al., 1990; Gerhardt and Hytteborn, 1992; Guevara et al., 1992; Aide, 2000; Griscom et al., 2007). Experimental plots associated with forested riparian zones had significantly greater stem density, basal area, and diversity than plots that were away from riparian zones or associated with denuded riparia (Griscom et al., 2009). Riparia also act to moderate climates by acting as windbreaks, and providing increased shade and humidity during the dry season and acting as a fire break (Pettit and Naiman, 2007).

5.1.3. *A diversity of legacy trees provides a diversity of regeneration*

The diversity of species composition of pasture trees, live fences and riparian zones is also important. For example, in Panama, crown morphology and presence of fleshy fruit (or pulpy aril) was found to be an important factor in determining regeneration diversity beneath isolated trees of *E. cyclocarpum,* which have broad canopies and edible fruit (Griscom, 2004); and within mixed native species plantations, with *Inga* spp. recruiting more tree seedlings than six other species (Jones et al., 2004). In contrast, the dominance of certain pasture trees (e.g., *G. ulmifolia* and *Cordia alliodora*, which represented more than half of all inventoried pasture trees) will limit the diversity of regenerating forest (Griscom et al., in press).

5.1.4. *Variation in soil fertility and microclimate influences rates of colonization and growth*

Regeneration is influenced by the nature of the site, in terms of available soil moisture and nutrients, soil compaction, and shade. Regeneration is less diverse, with slower rates of colonization and growth on exposed ridges than on slopes or depressions due to lower soil moisture availability during the dry season, and greater levels of exposure to high radiation regimes (Janzen, 2002; Griscom et al., 2009). Soils on exposed slopes and ridges are also more unstable, with greater levels of erosion and surface runoff (Ashton, 1992), and with lower levels of soil nutrients (Laurance et al., 1999; Cox et al., 2002; Takyu et al., 2002; Wood et al., 2006).

5.2. *Protection from fire and cattle – a human induced disturbance regime*

Removal of cattle can increase susceptibility to fire because fuel loads increase as grass biomass accumulates (Janzen, 2002). The solution in Guanacaste after removing the cattle was to intensively protect the property from fire. This was determined to be the only means of securing natural dry forest regeneration in abandoned pastures (Janzen, 2002). However, using cattle to control fire, rather than creating fire breaks, has been suggested and implemented in Costa Rica as a more economic alternative (Barboza, 1995; Stern et al., 2002) but browse on tree seedlings, lowers species diversity, diminishes structural complexity, and increases future grass competition (Conklin, 1987; Milchunas et al., 1988; Stern et al., 2002; Griscom et al., 2009). Species that are less susceptible to browse will be favored (e.g., *Acacia collinsii*, *Dalbergia retusa*, and *Tabebuia ochracea*), while species that are not will be eliminated (e.g., *Calycophyllum candidissimum*, *P. quinata*) (Stern et al., 2002) (Table 2).

5.3. *Enrichment planting with native tree species – facilitators of succession*

Protection from cattle and fire is not sufficient if there are no sources of propagules for desired tree species. Enrichment planting can serve two purposes. The first purpose is to introduce native tree species when natural regeneration is lacking, poor in diversity, or missing important functional or economic species. Trees that might not colonize the pasture unassisted, such as late-successional, animal-dispersed, evergreen, or valuable timber species, are good candidates for reintroduction (Nepstad et al., 1990; Sabogal, 1992; Holl, 1999; Aide, 2000; Guariguata and Ostertag, 2001; Cole et al., this issue) (Table 2). Some slower growing tree species may need to be reintroduced at a later stage when they are less susceptible to desiccation, (e.g., shade-tolerant, late-successional, evergreen species; *Manilkara chicle*, *Copaifera aromatica*) (Gerhardt, 1993; Janzen, 2002; Griscom et al., 2005). Such trees can be planted as seedlings or sowed directly as seeds (Cole et al., this issue). Bonilla-Moheno and Holl (in press) had success with direct seeding of *Brosimum alicastrum* and more limited success with *Manilkara zapota* in the understory of an 8–15-year-old secondary forest in Mexico, suggesting that direct seeding is appropriate when second growth forest cover has already developed. However, rodent protection may be necessary for some seedlings (e.g., *E. cyclocarpum*). The rodent, *Sigmodon hispidus*, is abundant in pastures and was often found to girdle 2-year-old seedlings in Panama (Griscom et al., 2005, 2007). Protection from land crab herbivory may also be necessary in some coastal areas, as they prey on young tree seedlings (e.g., *E. cyclocarpum*, *P. quinata*) (Lindquist and Carroll, 2004).

The second purpose of enrichment planting is to accelerate succession. Simple plantings of fast-growing, broad but shallow crowned pioneers (e.g. *Gliricidia sepium*, *Muntingia calabura*), will ameliorate the harsh pasture microclimate conditions. Planted seedlings become nurse trees within a short period of time and can have positive effects on soil conditions, the microclimate, and seed dispersal, which may all present barriers to succession (Nepstad et al., 1996; Tucker and Murphy, 1997; Holl et al., 2000; Zimmerman et al., 2000; Cabin et al., 2002; Bandano et al., 2009). Nurse trees can also help protect seedlings from fire (Santiago-Garcia et al., 2008). They facilitate islands of regeneration in a landscape that may be missing or lacking trees.

5.4. *Removal of invasive grasses – reducing competition and susceptibility to fire*

Exotic grasses may need to be removed as they have been shown to represent a major barrier to forest succession in wet and dry tropics (Buschbacher et al., 1988; Guariguata and Ostertag, 2001; Gerhardt and Fredriksson, 1995; Nepstad et al., 1996; Holl, 1998; Hooper et al., 2002; Lamb et al., 2005; Craven et al., 2009). The removal of grass with shading, herbicide, bulldozing or mowing is necessary where their competition with woody regeneration is particularly intense.

In moist tropical systems, the removal of non-native grasses has been found to increase growth rates of planted tree seedlings (Holl, 1998; Hooper et al., 2002; Craven et al., 2009) and increase the diversity of natural regeneration (Holl et al., 2000). Enrichment planting of several animal-dispersed species, which also occur in drier systems, *B. crassifolia* and *Spondias mombin*, was particularly successful in combination with the shading of an impenetrable grass, *Saccharum spontaneum* (Hooper et al., 2002).

In a case study on the Azuero peninsula, planting and natural regeneration response to exotic grass removal in dry tropical forests appeared to be species specific (Griscom et al., 2005, 2009). *Cedrela odorata* performed well with the removal of *Hyparrhenia rufa* and *Panicum maximum* and *Trema micrantha*, a small-seeded, light-demanding tree, regenerated by seed almost exclusively in grass removal plots. However, most natural regeneration of woody species did not benefit from grass removal treatments because of high surface soil temperatures, and desiccating environments and certain large-seeded trees (e.g. *E. cyclocarpum* and *Hymenaea courbaril*) performed best without grass removal (also see Gerhardt, 1993).

5.5. Establishing plantations – changing soil structure and groundstory climate

The most intensive restoration projects are characterized by tree plantations. This involves a greater investment in time and money to start or accelerate succession in severely degraded areas or where sources of natural regeneration have been lost (Lugo, 1992; Parrotta, 1993; Parrotta et al., 1997; Lugo, 1997; Harrington, 1999; Guariguata and Ostertag, 2001; Zanne and Chapman, 2001; Felton et al., 2010).

Lands that would merit planting often have lost core functional attributes of site productivity (soil carbon, nitrogen, infiltration capacity). Such lands have usually been repeatedly burned, overgrazed, planted with exotic grass species, subjected to bulldozing or lost top soil through erosion, and/or devoid of parent tree seed sources (Uhl et al., 1988; Aide and Cavelier, 1994; Felton et al., 2010). If left alone, such lands can remain as a shrubby savanna or grassland in a state of arrested succession (Hopkins, 1983; Olivares and Medina, 1992). In such conditions plantations are a useful management tool to immediately start shading the groundstory, ameliorating soil structure and fertility, reducing the risk of fire and providing an economic return on investment from timber. Within a short amount of time, densely planted trees can promote establishment of secondary succession beneath by providing an immediate habitat for seed dispersers, and providing partial shade protection for young germinants (Lugo, 1992; Parrotta, 1993; Lugo, 1997; Parrotta, 1999; De Souza and Batista, 2004; Jones et al., 2004).

5.5.1. A role for exotic tree plantations

Exotic species plantations are the most traditional approach, involving monocultures or a mix of a few species (Leopold et al., 2001; Wishnie et al., 2007; Parks et al., 2010). The general perception is that exotic plantations produce high quality timber but low levels of plant diversity, and are therefore ineffective in restoration (Lamb et al., 2005). However, experimental treatments have shown that exotic trees can facilitate relay floristics in landscapes that are in a state of arrested succession by serving as a habitat for seed dispersers, shading out competitive grasses, reducing groundstory fires, and ameliorating soil structure and infiltration capacity (Parrotta, 1992, 1999; Ashton et al., 1997, 1998; Shibayama et al., 2006). In cases where sites have changed irrevocably to other vegetative states, use of exotics may be the most realistic and only satisfactory course of action.

Some species will be more effective than others at stimulating succession, depending on canopy characteristics (Table 2). For example, *Leucaena leucocephala* creates a thin canopy with a moderately shaded understory, fixes nitrogen, has readily decomposed leaf litter that provides a nitrogen rich mulch, and suppresses grasses, supporting a diversity of natural regeneration (Parrotta, 1995, 1999; Santiago-Garcia et al., 2008). *Albizia lebbeck*, *Casuarina equisetifolia* and *Eucalyptus robusta* were also successful in supporting natural regeneration beneath their canopies (Parrotta, 1992, 1999). *Casuarina equisetifolia*, a nitrogen fixer that adds high amounts of carbon to the mineral soil, was especially effective in attracting frugivorous bats even though it does not produce fleshy fruits (Parrotta, 1999). *Gmelina arborea* has been the main plantation tree used in the moist forests of Guanacaste because of its ability to effectively shade out the African grasses, reduce susceptibility to fire, and facilitate second growth beneath (Janzen, 2002). *Acacia mangium* was a suitable nurse species in drier, more degraded sites (Norisada et al., 2005; Parks et al., 2010). However, *Acacia magnium*, can become highly invasive on some sites unless it is intermixed with other native species and harvested shortly thereafter (Parks et al., 2010). Plantations of other species, such as *Tectona grandis*, can be more detrimental to recruitment of native vegetation by casting dense shade, facilitating groundstory fires because of their large fire-prone leaves, and/or having an inability to attract seed dispersers (Healey and Gara, 2003).

5.5.2. Use of native species plantations and the value of mixtures

Native species plantations are appropriate in landscapes where barriers are less severe. Plantations have been found to effectively promote regeneration of a diverse suite of species (Butterfield, 1995; Haggar et al., 1997; Leopold et al., 2001; Jones et al., 2004). Species selection is an important part of this process. Primary selection should be based on site suitability which can vary within a site based on aspect, slope position, soil drainage and soil fertility (Parks et al., 2010; van Breugel et al., this issue). Secondary species selection may involve other characteristics such as rarity, timber value or as wildlife food and habitat.

In the dry tropical region of the Azuero, *Gliricidia sepium*, *Erythrina fusca*, *G. ulmifolia*, *Spondias mombin*, *Ochroma pyramidale*, and *P. quinata* had the greatest heights and basal diameter after 2–3 years in open field trials (Wishnie et al., 2007; Parks et al., 2010; van Breugel et al., this issue) (Table 2). *Gliricida sepium* and *Erythrina fusca* had growth and survival that were the same as the exotic species, *Acacia mangium* after 2 years (Wishnie et al., 2007). Three species, *Spondias mombin*, *Ochroma pyramidale*, and *P. quinata* are the most able to increase floristic diversity of a regenerating landscape, assuming the existing presence of *G. ulmifolia* and *Gliricidia sepium*.

Other factors should also be considered when selecting species. As with enrichment planting, some species can promote greater levels of natural regeneration because of their broad canopies and growth habits for perching birds (e.g., *Inga* spp.) (Jones et al., 2004) while other species will attract animals because of fruit (e.g., *Bursera simaruba*, *Muntingia calabura*) (Griscom et al., 2007). Careful consideration should also be given to phenological characteristics. A dominance of deciduous trees may decrease shade and provide increased competition from grasses while too many evergreen species may slow succession (De Souza and Batista, 2004). Mixtures of pioneer and mid- to late-successional species are recommended (Hooper et al., 2002, 2004; De Souza and Batista, 2004; Elliot et al., 2003). Pioneer species will grow quickly, often fix nitrogen, and shade out grasses (Lamb et al., 2005) (for Mesoamercia – *E. cyclocarpum*, *Gliricidia sepium*, *Erythrina fusca*, *G. ulmifolia*, *Ochroma pyramidale*, *P. quinata*); but structure, additional carbon sequestration and habitat quality will be enhanced, by slower growing evergreens (for Mesoamerica – *Copaifera aromatica*, *Hymenaea courbaril*, *Manilkara chicle*) and fruit-producing tree species (for Mesoamerica – *Bursera simaruba*, *B. crassifolia*, *Inga* spp., *Muntingia calabura*, *Spondias mombin*) (Lamb et al., 2005). Income can be increased by incorporating trees that produce timber and non-timber forest products (e.g. *Anacardium excelsum*, *Cedrela odorata*, *Dalbergia retusa*, *Swietenia macrophylla*, *S. humilis*, *Tabebuia* spp.) (Garen et al., 2009; Hall et al., this issue).

6. Conclusions

Restoring dry tropical forests has become a priority as land continues to change in ownership in Central America. Reforesting pastures can preserve biodiversity, restore ecosystem services, and create working landscapes with valuable timber and non-timber forest products. Restoration will be more successful if practitioners have a solid understanding of the degradation processes and their appropriate restoration pathways given the specifics of social and biophysical circumstances (Ashton et al., 2001). Major barriers to regeneration in dry tropical forests are (1) a fire disturbance regime and (2) lack of a diversity of arboreal elements and forested riparian zones in some pastures. Invasive grasses and poor seed dispersal are secondary and indirectly affected by the first two factors. These barriers can be overcome with a variety of restoration techniques (Fig. 3). Exotic species plantations are only recommended on sites where native species would not perform well because of major barriers to growth, such as drought and fire and functional degradation in soil fertility and structure. On the other extreme, passive restoration has very strong potential if seed sources, microenvironmental heterogeneity, and sprout origin regeneration are present. The more trees and forested riparia are conserved, the more likely succession will take place unassisted. The most important management tool is fire protection, especially when there are no natural fire breaks (live fences, riparian zones). Removal of exotic grasses and/or enrichment planting depends on expense and desire for species additions (e.g. habitat value, carbon sequestration, watershed stabilization, income generation). The imbalance in the literature on restoration within dry tropical forests in Central America suggests a need for future experimental studies on the mechanisms underlying the limitations and benefits of different restoration pathways.

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