Annual growth rings in dry tropical forest trees

by

Bonnie Hayden

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ABSTRACT

Annual growth rings in dry tropical forest trees

Bonnie Hayden

Tropical dry forests are one of the most diverse ecosystems on earth. Despite their ecological, commercial and cultural importance, however, we still know little about their population dynamics. In this thesis I focus on dendrochronological problems and possibilities in the dry tropical biome. I begin with an exhaustive compilation of all the tropical tree species that have been shown to produce annual growth rings, for this I include both wet and dry tropical forests. I follow with a study that was conducted in a tropical dry forest in western Mexico to determine the periodicity of radial wood formation in six drought-deciduous tree species. It is suggested that the intense drought that is prevalent in this climate type induces the cessation of cambial activity in these trees; and thus annual ring formation may be assumed for non-riverine drought-deciduous tree species. A third chapter details an experimental study of the effect of rare dry season rains on leafless tree species. In particular, I examined the relationship between one-time water receipt and (1) the degree of bud burst (and, for one species, flowering), and (2) the formation of a false ring. Also, I used long-term records at a nearby meteorological station to determine the frequency of a rain event exceeding a particular intensity. Finally, I end with a broad review of dry tropical forest ecology, the biome known to be most conducive to the formation of annual growth rings in tropical trees.

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Table of Contents

Chapter 1: Tropical dendrochronology: a review and compilation of research on growth rings in tropical trees.

Chapter 2: Annual growth rings in 6 tropical dry forest tree species in Mexico

Chapter 3: The effect of dry season precipitation on annual ring formation and leaf phenology in a seasonally dry tropical forest

Appendix A: Tropical Dry Forests: Structure, Distribution and Dynamics

List of figures

List of tables

Introduction

Dendrochronology, or using growth rings to determine a tree's age, has made valuable contributions to our understanding of forest dynamics and yield potential in the higher latitudes for over a century. However, it has rarely been used in the tropics despite the fact that information on the population dynamics of tropical trees would be invaluable to the forest industry, conservationists, and local landowners in these areas (Stahle et al 1999; Worbes 1999). A prerequisite for obtaining information on population dynamics would be to know the periodicity of a tree's growth rings; that is, whether they are truly annual. There is clearly a lack of research on growth ring periodicity in tropical trees and studies such as this one are imminent to the development of a better understanding of tropical forests.

Growth ring formation requires sharp variation in a tree's cambial activity. Cambial activity in temperate trees is widely known to be influenced by the seasons (Philipson et al 1971). Induced largely by an increase in temperature in early spring, the cambium of temperate trees becomes active and wood formation begins. The cessation of wood growth in the autumn occurs when temperature subsequently declines (Philipson et al 1971). The wood produced at the end of the growing season in one year will be morphologically distinct from that produced at the beginning of the next year, and thus determination of tree age in temperate trees is generally straight-forward.

Much like temperate trees, the cambium of tropical trees can go through a period of inactivity while growing conditions are unfavorable and become active again once favorable growing conditions return (Worbes 2002). This transition between active and inactive cambium, caused by variation in growing conditions, will show up as growth zones in the wood. One of the most influential environmental factors affecting cambial activity in tropical trees is water availability (Alvim 1964). Water availability becomes especially important in the growth of trees in tropical areas that undergo a severe drought or inundation (Worbes 2002). What is required for strictly annual rings, however, is that there be only one sustained period of unfavorable growing conditions each year.

Clearly a single long period of drought would be a potentially conducive environment for annual ring formation in tropical trees. Tropical precipitation patterns at low latitudes vary from ever-wet to seasonally dry, and this can cause variation in tree growth periodicity (Breitsprecher and Bethel 1990). Growth rings may be formed annually, biannually, or irregularly in tropical trees, with a small group designated as continuously growing and without growth rings (Tomlinson and Longman 1981). The majority of trees, however, when badly stressed by drought, will not grow continuously but will go through periods of inactivity characterized by leaf loss and cambial dormancy (Breitsprecher and Bethel 1990, Philipson et al 1971). Trees may have a genetically fixed schedule of cambial activity that works within the constraints imposed by the environment, allowing for periodic growth even in areas with almost constant favorable growing conditions (Philipson et al. 1971, Jacoby 1989).

There is significant variation in growth ring structure in tropical wood in many species. The growth rings produced by tropical trees (whether formed, for example, annually due to seasonal flooding, or biannually due to two dry seasons on an annual basis, or irregularly), may be defined in several ways. Tropical growth rings may be distinct (ring boundary is defined by an abrupt structural change in wood anatomy between any two rings) or indistinct (boundaries may be defined by a gradual structural change in wood anatomy, usually visible only when magnified) (Wheeler et al 1989). Whether distinct or indistinct, the growth rings of tropical trees can then be defined according to one (or more) of several anatomical features (as reviewed in Coster 1927 and Worbes 1985).

The chapters of this thesis will address the issue of growth rings in tropical trees from several different perspectives. The first chapter brings the current state of tropical dendrochronology into perspective. This chapter reviews the difficulties associated with tropical tree ring research and, more importantly, provides a compilation of every tropical species known to produce annual growth rings. Further, for each species, I list the wood anatomy type; geographic region; whether or not it is deciduous; and the method used to determine if the species' rings are annual. In Chapter 2, I test a simple hypothesis: any deciduous tree species in the dry tropical forest will have annual rings. I examine trees of known age from six species to test this hypothesis. Chapter 3 looks at the effect of dry season rainfall on wood growth. Here, I describe an irrigation experiment where tropical trees were irrigated during the dry season to determine (1) the degree of leaf extension and flowering to a gradient of water receipt; and (2) whether or not a false ring was formed in response to this simulated (rare) dry-season rainfall. If false rings are sufficiently common in the tropics due to episodic dry season rains, then dendrochronology there will be far more complicated than we imagined. A review of seasonally dry tropical forests, already accepted for publication and presented in this format (email: spring 2008), is included as an appendix and will introduce the region of the tropics where most dendrochronological studies have taken place. This review however is hardly limited to dendrochronology, focusing more generally on plant population dynamics.

Chapter 1: Tropical dendrochronology: a review and compilation of research on growth rings in tropical trees

1.1 Introduction

Unlike mid-latitude forests where stand reconstructions permit fine detailing of the community dynamics of woody plant populations (Oliver and Stephens 1977), the little we know about tropical community processes, such as succession, has been rooted in other methods. These include age estimations based on extrapolated diameter growth rates (Baker 2003), age projections based on tree size (Leiberman et al 1985), repeated measurements from permanent plots (Brienen 2005), and wood chemistry studies (Swain et al 1981). But as Baker et al (2005) have shown, at least for their drought-deciduous forest in Thailand, that many of the species had detectable annual rings and thus a stand reconstruction could be used to delineate the temporal changes in population abundances and growth rates.

Several factors contribute to the paucity of growth ring studies in the tropics. An early hindrance to dendrochronological work had simply been the long-held belief that tropical trees exhibit continuous growth due to an aseasonal climate (Leiberman 1985, Whitmore 1990, Worbes 2002, Jacoby 1989). The marked seasonality of large areas of the tropics has now become so well-recognized, however, that perhaps this handicap to research in ageing has been permanently lifted.

Other challenges associated with tropical dendrochronology include the anatomy of the wood itself. Unlike conifers and many northern hardwoods, a large fraction of tropical species possess indistinct growth rings, making the identification of ring boundaries difficult (Jacoby 1989). In addition to indistinct growth rings, there can be variability in wood anatomy both within and between tree species (Jacoby 1989). Different species growing on the same site may show very different features in their growth rings (e.g. Dunisch et al 2002). Perhaps more difficult to contend with is the fact that two trees from the *same* species may show different anatomical structures in the wood that delineates a growth boundary (Jacoby 1989, Fahn 1981, Worbes 1989).

In addition to wood anatomy, there are other characteristics common to tropical wood that make ring delineation difficult. The high wood density of many species prevents the use of increment corers for sampling rings (Jacoby 1989, Gourlay 1995). Obtaining a sufficient sample size may also be difficult with tropical species, given the economic, cultural, and conservation value of these trees (Jacoby 1989). Likewise, sample size problems within a stand can arise simply because so many of the species are necessarily rare in a highly-diverse forest.

Despite these challenges, the number of investigations in tropical dendrochronology continues to increase. In general, it is accepted that tropical areas that undergo a severe drought or inundation for part of the year are the most likely to support tree growth that follows a rhythmic (probably annual) cycle and that annual growth periodicity is possible even in areas classified as ever-wet (Worbes 2002). The positive relationship between total precipitation and ring width has also been generally accepted as a truism for many tree species in the tropics (Worbes 2002).

In response to this recent surge of interest, I have assembled here the first comprehensive list of tropical tree species that have been proven to form annual growth rings. The list includes information on tree taxonomy, leaf habit (deciduous, semi-deciduous, or evergreen) and study location. Also included are the methods used in determining the periodicity of the growth rings, as well as the wood anatomy type.

To the best of my knowledge there have been previously only two dendrochronological compilations of tree species that have included tropical species. One, published by Grissino-Mayer (1993), is a list of almost 600 tree species that have been studied by dendrochronologists, but it consists largely of temperate species. Another, more recent list, was developed by Worbes (2002) and it includes over 100 South American tree species that have been examined. Unfortunately, this list does not address the crucial issue of whether or not these species do indeed possess annual rings. The list offered here is not only more recent, but focuses on all tropical trees regardless of region or economic importance. Further, it includes all species known to possess annual rings. Finally, the current effort is the first to provide detailed information about the tree species so as to ascertain whether the likelihood of annual ring production is a function of leaf habit, taxonomy, or wood anatomy.

In addition to information on tree species known to produce annual growth rings, the list will be compared with two inclusive lists of tropical tree species to ascertain whether species with annual rings tend to be found clustered preferentially in certain families.

1.2 Methods

To the best of my knowledge, I have included every published citation on tropical tree species where an attempt was made to determine whether rings were annual. Shrubs and lianas have been excluded. I also include those species whose rings have been proven *not* to be annual. Due to the surprisingly low number of species in this category, they are not included in the subsequent analysis. Of the species forming annual growth rings, some appear on the list more than once. In these cases, each entry on the list is considered separately as there was usually a difference in wood anatomy and/or methodology reported in each study.

Characteristics of interest for this compilation were taxonomy (family, genus, species); study location, including country and forest type (seasonally dry, seasonally inundated, and wet, which includes moist, humid and ever-wet forests); leaf habit (deciduous, semi-deciduous, or evergreen); the method used to determine ring periodicity (divided into 14 different methods); and finally the wood anatomy type (divided into 10 anatomic types).

The 14 methods included in Appendix 1 are loosely divided among three groups: primary methods (1-5), each of which can be used independently to prove the periodicity of a tree's growth rings; secondary methods (6-10), which are generally used in combination with, or following the use of a primary method; and a final group of methods (11-14) that are used to physically study the rings. These methods are briefly explained here, with their corresponding number from Appendix 1 in brackets.

Radiocarbon dating (1) is based on the known rate of radioactive decay of Carbon-14 contained in organic material. This rate of decay can be detected for particular tree rings and the number of rings between dated rings counted (Worbes 1989). Cambial wounding (2) is a method in which a datable scar in the wood is formed by removing a small portion (usually a few cm^2) of bark, to a depth sufficient to include the cambium. At some time after the initial incision is made, the tree is cut and the timing of ring production ascertained (Worbes 1995). Fire scars or pointer years (3) are similar to cambial wounding but are produced naturally by the tree due to some exogenous disturbance such as the fall of a nearby bole (Worbes 1995). Collecting samples from trees of known age (4) can be used to compare the number of growth rings to the age of the tree (Worbes 1995, Mariaux 1981). Dendrometers (5) follow a tree's radial growth by providing a constant monitoring of cambial activity (Worbes 1995). Crossdating (6), ring width analysis (7), shoot analysis (8), and comparison of wood anatomy with phenology (9) and climate (10) may be employed in combination with, or following the use of a primary method, generally to reinforce a study's findings of ring periodicity. The methods that are pertinent only to the viewing of the growth rings include whether increment cores (11) and/or stem disks (12) were used, microscopic analysis (13) of ring boundaries, and the staining of wood (14) to enhance the visibility of wood anatomy.

The ring wood anatomy column includes 10 possible growth ring characteristics. They are described here with the letter corresponding to Appendix 1 following in brackets. The visibility of growth rings is identified as either distinct (A) (in which there is a sudden and clear change in wood anatomy between one ring and the next, often visible to the naked eye) or indistinct (B) (in which there is a more subtle change in wood anatomy between two rings and the identification of a ring boundary often requires the use of a microscope) (Wheeler et al. 1989). The ring boundaries are further divided into vessel porosity categories. This is often a factor in determining the distinctness of growth rings and is a description of vessel size within one growth ring. Ring porous wood (C) implies that there is an abrupt change in vessel size between the wood at the beginning of the growth ring and the later-formed wood. At the other end of the spectrum is diffuse (D) porous wood in which the vessels within a ring appear the same size throughout. The intermediate stage is known as semi-ring porous (E) (Wheeler et al. 1989). Finally, the ring boundaries are often also defined by some wood characteristic that delineates one growth ring from the next (e.g. a parenchyma band (either terminal, marginal, or in patterns) (F), change in fiber density or formation (G), bands of parenchyma and fibers (H), change in vessel density (I), or changes in color, pores, rays, or crystal chains (J). It should be noted that each of these characteristics of ring wood anatomy can overlap (e.g. distinctness is a reflection of both porosity and boundary characteristics) but they appear individually in the results section as it is useful to know each attribute separately.

The information included in my list is reported from each study when provided; where nothing about the methodology, wood anatomy, leaf habit, etc was mentioned in a paper, then it was classified as “unknown” in the tables.

To make comparisons between the tree species in Appendix 1 and tropical trees more generally, two lists were used that served as admittedly partial inventories of tropical tree species (Reyes et al. 1992, Condit et al. 2002). The lists are limited in their inclusiveness. The list by Reyes et al (1992), although covering all of tropical Africa, Asia and the Americas, is biased toward commercially-valuable tree species. Condit et al (2002), while inclusive of all trees within a region, includes trees from only three Neotropical locations. I will compare the number of tree families represented on each list as well as the number of families that contain species that produce annual rings. With these lists, I will be able to reach preliminary conclusions regarding the likelihood of tropical trees producing annual growth rings.

1.3 Results

Based on the 43 citations I found, over 240 tree species growing in the tropics have now been proven to form annual growth rings (Appendix 1). These species were found among 52 families (Table 1). The Fabaceae had the highest proportion of species on the list (59 species, 24%) followed by the Meliaceae (28 species, 11%). The remaining 50 families on the list were represented by 12 (5%), or fewer, species.

There were also 7 tree species (Appendix 2) reported *not* to produce annual growth rings (of these, 2 reported no growth zones, 3 reported more than one growth ring per year and the problems with the remaining 2 species were not elaborated upon).

A significantly higher number of tree species producing annual growth rings have been reported in seasonally dry tropical forests (73% of all studies reporting forest type) than in either wet forests or seasonally inundated forest types (both with 14% of the species, excluding the unknown category) (Figure 1; Chi-square test omitting the "unknown" category; $P<<0.05$). Correspondingly, of the studies reporting leaf phenology (and therefore excluding the unknown category), the most frequent leaf habit was deciduous (51%), with semi-deciduous the second most frequent (33%) and the evergreen leaf habit displayed by 16% of the species (Figure 2; Chi-square test omitting the "unknown" category; $P<<0.05$).

In general, more than one lab or field method was used in each publication to study the annual nature of growth rings. The frequencies of the methods are shown in Figures 3, 4, and 5. Cambial wounding and radiocarbon dating were employed more often than any other method (Figure 3) and tree species were frequently crossdated

(Figure 4). One can see that stem disks were used more often than increment cores (Figure 5).

Although many of the studies did not report wood anatomy, there was generally more than one characteristic reported per species that defined the ring boundary. It was apparent that there were more distinct (79%) than indistinct growth ring boundaries reported for the tree species on the list (Figure 6). The most common vessel porosity reported in these trees was semi-ring porous (Figure 7). The two most frequently reported ring boundary characteristics were parenchyma bands (terminal, marginal or in patterns) and a change in fiber density or formation (Figure 8).

Although tropical dendrochronological studies have been taking place throughout the 20th century, more than 90% of all tropical tree ring studies have been conducted in the last 20 years (Figure 9).

Approximately 15% of the 622 genera that are on the wood density inventory list of trees for tropical forests in Asia, Africa, and the Americas are included in Appendix 1 (Reyes et. al. 1992). Likewise, 16% of the 319 tree-containing genera at Barro Colorado Island in Panama (Condit et. al. 2002) were on my list.

1.4 Discussion

Appendix 1 includes over 240 tree species from tropical locations worldwide. The trees varied in leaf phenology from evergreen to semi deciduous to obligate deciduous. They grew in all manner of tropical locations, including rainforests, mangroves, and arid ecosystems. But clearly, this list was biased toward dry tropical forests (80% of the records where the forest type is given) and the trees typical of such a region (93% of the given data are for deciduous and semi-deciduous habits).

Why should this be? There are two speculative possibilities, neither of which I can discount. The first is that winter-deciduous species are more likely to have distinct rings, and investigators are, quite reasonably, more willing to attempt to prove rings are annual when they are initially seen to be distinct. This same speculative bias toward more promising candidates may be the reason so few species (less than 3% of all examined species) are reported to lack annual rings. A second possibility is that the investigative bias is toward deciduousness, and this trait is far more common in seasonally dry areas.

Despite the common argument (Jacoby 1989, Shiokura 1989, Gourlay 1995) that the density of tropical wood is so great as to, in many cases, preclude coring, coring is a common method for physically extracting the wood for subsequent examination. We have no reason to think that coring (as a percentage of field exercises) is more or less common than in the tropics.

There are many comparative analyses that cannot be done with the list provided here, and this is because we have no large comprehensive compilations of tropical tree species in relation to particular traits. Thus, for example, if there were a list of species (or even of genera) providing the global or regional frequency distribution of porosity types, one could ask if species with annual rings tend to be unusually rich in, say, ring-porous anatomies. Likewise, if there were a list of tree species per family in the tropics, one could test to see if, for example, the Fabaceae and Meliaceae were significantly over-represented in the present survey. But no such list exits either globally or regionally.

Many species in Appendix 1 have been studied in more than one location. This allows us to observe the occurrence of annual growth rings in two (or more) locations of a single genus and/or species. For example, the growth rings of *Cedrela spp.* have been investigated in five locations including India, Africa, and various sites in South America (Chowdhury 1930, Villalba et. al. 1985, Boninsegna et. al. 1989, Detienne 1989, Dunisch et. al. 2002, Worbes 1999, Brienen & Zuidema 2005). These areas host a range of growing conditions including moist forest in Bolivia and seasonally dry forest in Venezuela. Despite the difference in climate, this genus produces annual growth rings in all five study locations. Indeed, of all the genera in Appendix 1 that have been studied in at least two locations, 68% show annual growth rings in more than one country. This may allow researchers to connect patterns of growth within a genus between locations.

Of the four species that have been studied in more than one location, *C. odorata, S. macrophylla, S. amara,* and *V. cymosa,* all have been proven to produce annual growth rings in both a wet and dry ecosystem. Additionally, *Toona ciliata,* a species that has been proven to produce annual growth rings in Thailand (Baker 2005) has also shown promising results for dendrochronological work in both Australia (Heinrich and Banks 2006) and India (Bhattacharya et al 1992). While it is perhaps premature to draw conclusions regarding the periodicity of growth rings in a species studied in one area and not another (Jacoby 1989, Fahn 1981), one would like to assert the same freedom as in the mid-latitudes where we assume that a particular species has annual rings wherever one might find it.

According to the two inventories I used, about 15% of tropical tree genera have been proven to produce growth rings with an annual periodicity. This agreement is probably spurious. One inventory is biased toward commercially valuable species (our knowledge of the species in my list is too incomplete to narrow it for a serious comparison), while the other is three selected Neotropical regions.

As the number of studies included in Appendix 1 illustrates, however, there have been remarkable advances in recent decades in tropical dendrochronology. Working towards a more comprehensive approach to tropical dendrochronology remains the goal of many researchers and will allow for much progress in tropical forestry, climatology, and ecology with specific applications in forest conservation and management (Jacoby 1989), climate reconstructions (Trouet et al. 2001), historical stand dynamics (Baker 2005), and predicting timber yields (Brienen 2005). In particular, our understanding of tropical forest ecology will develop far more rapidly once we are assured that certain species (no matter where an individual tree is found) produce annual rings. It would be especially useful to have generalizations grounded in certain traits (e.g. deciduousness or porosity type), as we then might make useful assumptions about congeners.

Table 1: The distribution of tree species having annual rings by family. Two families (Fabaceae and Meliaceae) contain over 35% of the species, the remaining tree species are distributed among 50 families.

Family	Number
Aceraceae	2
Anacardiaceae	3
Annonaceae	4
Aquifoliacaea	1
Araucariaceae	2
Bignoniaceae	11
Bombacaceae	9
Boraginaceae	6
Burseraceae	7
Capparidaceae	2
Caryocaraceae	1
Clusiaceae	1
Combretaceae	6
Connaraceae	1
Cupressaceae	3
Cyrillaceae	1
Dilleniaceae	1
Dipterocarpaceae	1
Ebenaceae	3
Euphorbiaceae	3
Fabaceae	59
Flacourtiaceae	4
Goupiaceae	1
Hugoniaceae	1
Juglandaceae	1
Lauraceae	6
Lecythidaceae	2
Lythraceae	1
Magnoliaceae	3
Malvaceae	1
Meliaceae	28
Moraceae	5
Myricaceae	1
Myristicaceae	2
Myrtaceae	3
Nothofagaceae	1
Olacaceae	1
Oleaceae	1
Pinaceae	6
Rhizophoraceae	2
Rhamnaceae	1
Rutaceae	1
Rubiaceae	2
Salicaceae	1
Sapindaceae	1
Sapotaceae	8
Simaroubaceae	2
Sterculiaceae	12
Tiliaceae	2
Ulmaceae	5
Verbenaceae	12
Vochysiaceae	1

Figure 1: Distribution of tropical tree species with annual rings by forest type.

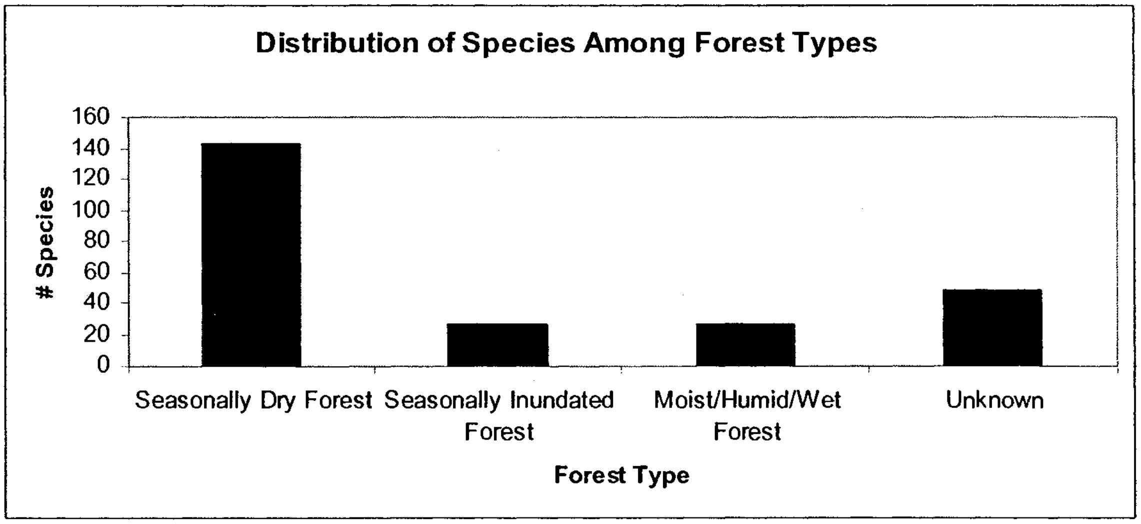


Figure 2: Frequency of tropical tree species that form annual rings in each leaf category, evergreen, semi-deciduous, deciduous, and unknown.

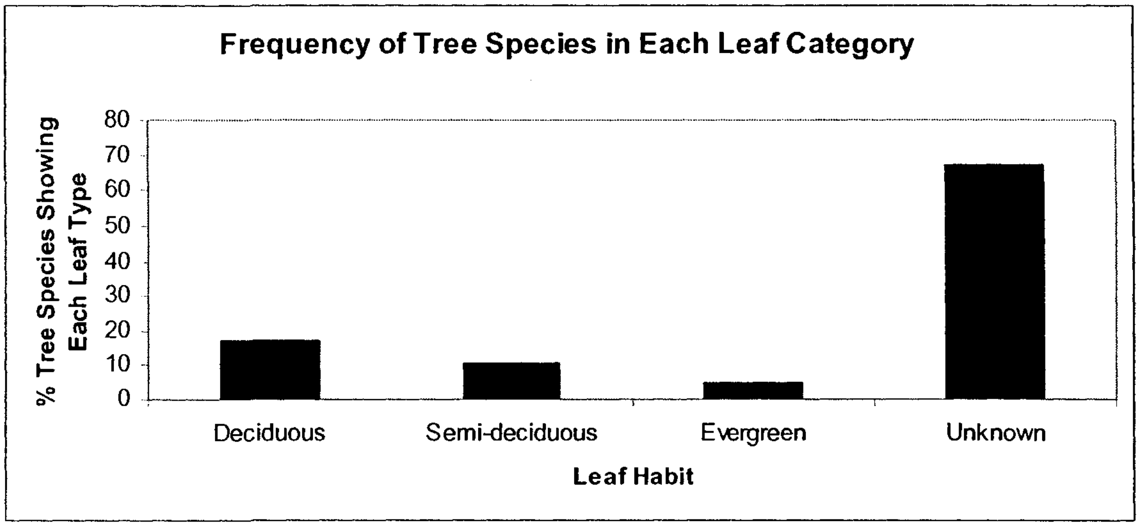


Figure 3: The primary methods used to determine the periodicity of growth rings in tropical trees and the number of times each method was used.

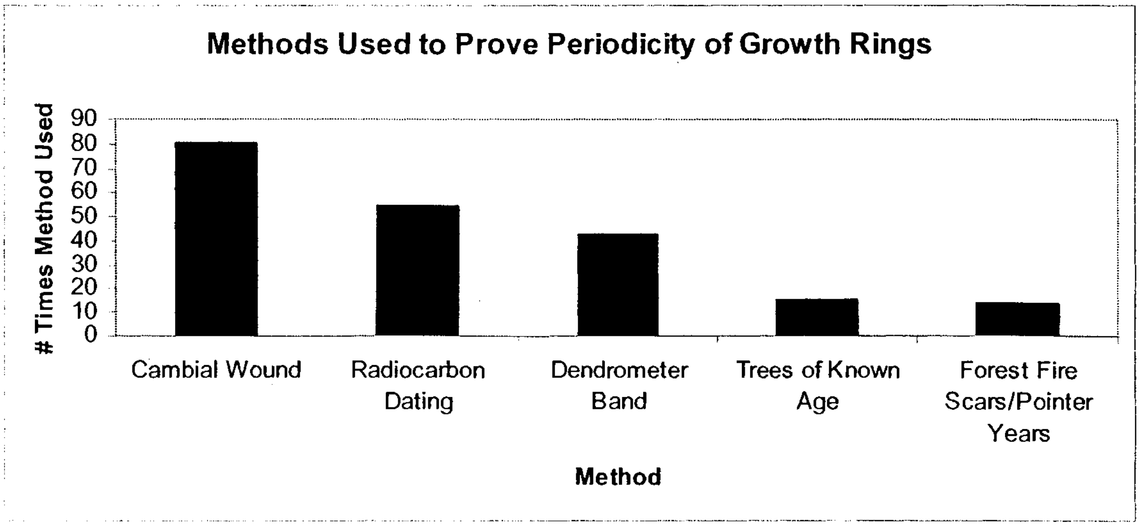


Figure 4: Secondary methods used to determine periodicity of growth rings in tropical trees. Generally these methods are used in combination with another method.

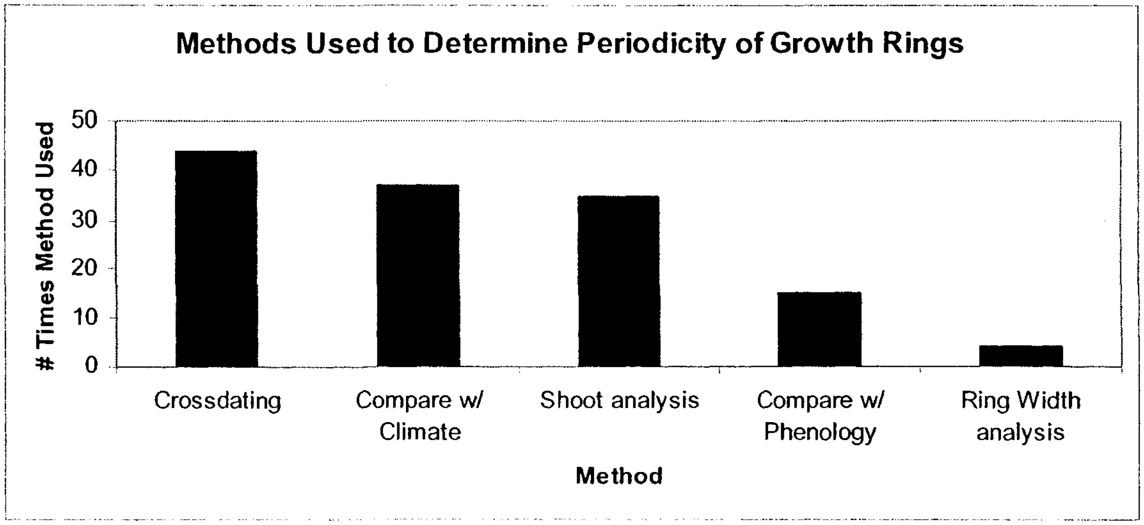


Figure 5: Methods used to examine growth rings in tropical trees.

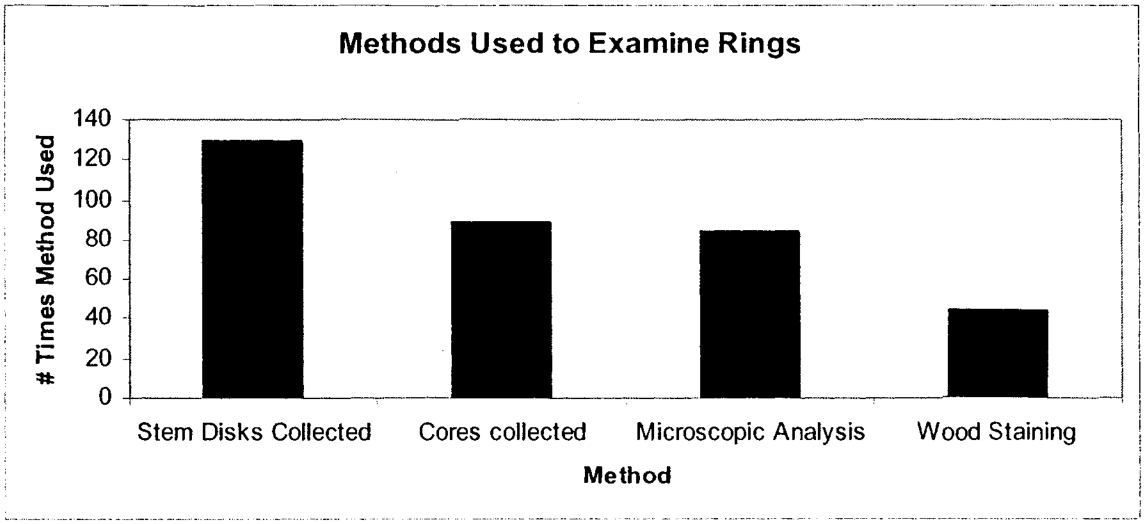


Figure 6: Number of tropical tree species exhibiting either distinct or indistinct growth ring boundaries.

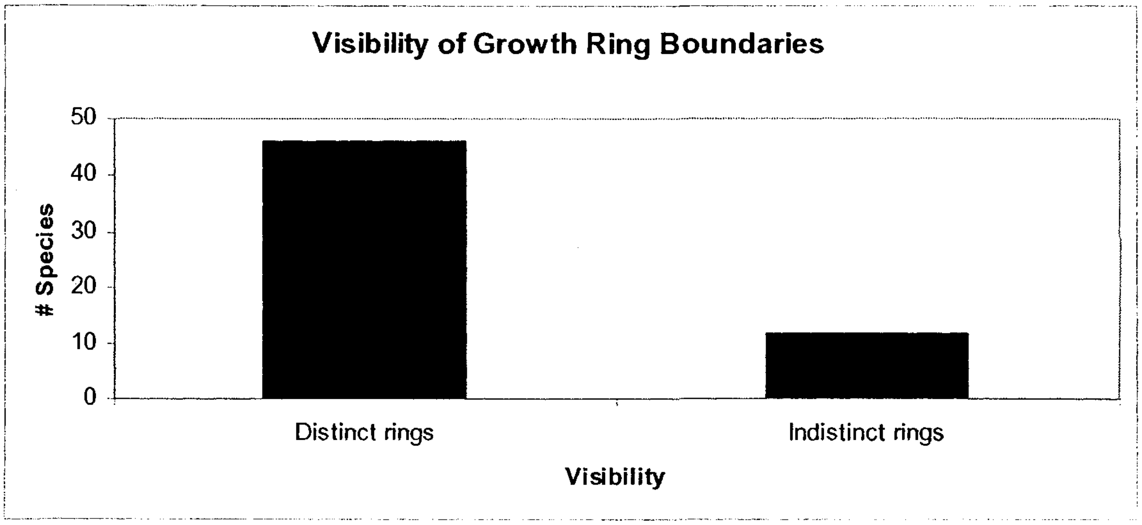


Figure 7: Number of tropical tree species in each category of wood porosity type.

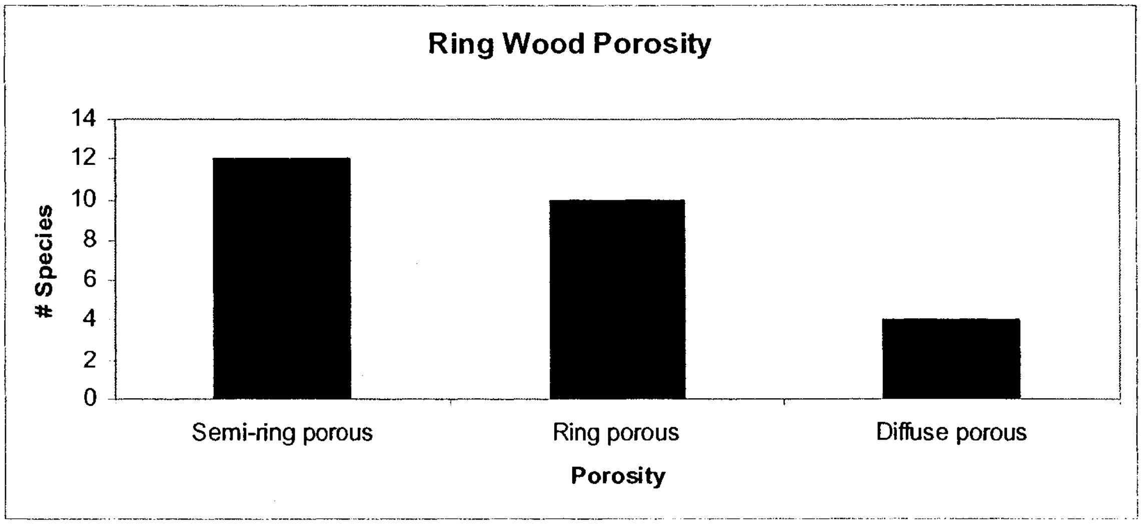


Figure 8: Number of tropical tree species exhibiting each annual growth ring boundary characteristic.

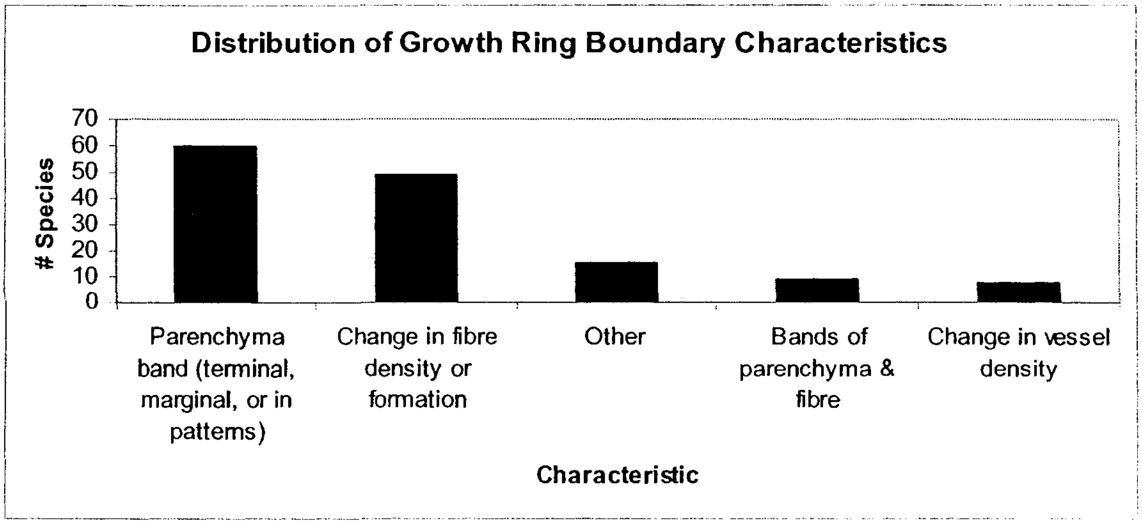
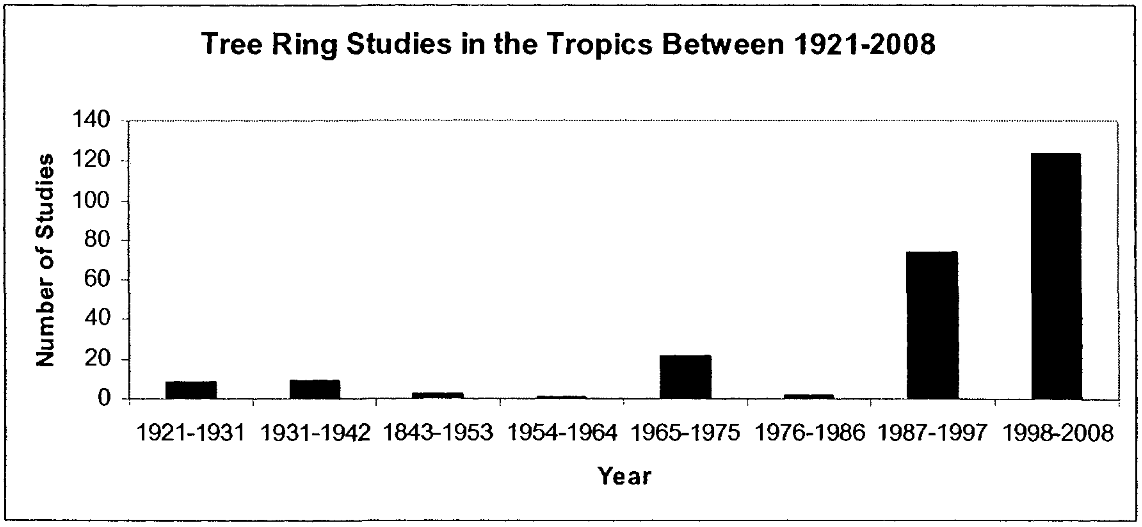


Figure 9: Distribution of tree ring studies in the tropics since the beginning of the 20th century.



Appendix 1: Tropical tree species that are known to produce annual growth rings. For details of the lab or field methods and the wood anatomy categories, see methods section of the text.

Family	**Tree Species**	**Leaf Habit**	**Location**	**Method Used**	**Ring Wood Anatomy**	**Authors**	**Year of Publication**
Aceraceae	*Acer rubrum*	Deciduous	Subtropical S. Florida	2, 3		Tomlinson & Craighead	1972
Aceraceae	*Acer oblongum*		W. Central Thailand, Seasonally dry			Baker et al	2005
Anacardiaceae	*Mangifera sp.*		W. Central Thailand, Seasonally dry			Baker et al	2005
Anacardiaceae	*Tapirira cf. guianensis*		Venezuela,	1	A	Worbes & Junk	1989
Anacardiaceae	*Astronium fraxinifolium*		Brazil, semi-deciduous forest dry winter	8, 14,	G	de Mattos et al	1999
Annonaceae	*Annona spraguei*		Central Panama		D	Devall et al	1995
Annonaceae	*Pseudoxandra polyphleba*		Manaus, Brazil. Central Amazon inundation forest	1, 12		Worbes & Junk	1989
Annonaceae	*Monodora tenuifolia*		Nigeria, Lowland Rainforest	9, 10, 11, 14		Amobi	1973
Annonaceae	*Polyalthia suaveolens*	Semi-deciduous	W. Africa, Cameroon, Dry season	1, 6, 11, 12, 13	A	Worbes et al	2003

Aquifoliacaea	*Ilex inundata*		Manaus, Brazil. Central Amazon inundation forest	1, 12		Worbes & Junk	1989
Araucariaceae	*Araucaria angustifolia*		Brazil	1, 12, 13	A,I	Lisi et al	2001
Araucariaceae	*Agathis moorei*		New caledonia	2, 5, 12	G	Detienne	1989
Bignoniaceae	*Jacaranda copaia*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Bignoniaceae	*Jacaranda cuspidifolia*		Brazil, semi-decid forest, dry season	8, 14,	F, G	de Mattos et al	1999
Bignoniaceae	*Tabebuia barbata*		Manaus, Brazil, Central Amazon, inundation forest	1, 2, 11, 12, 13		Worbes	1989
Bignoniaceae	*Tabebuia doneell-smithii*	Deciduous	W. Mexico, Seasonally dry	4, 9, 11, 12, 13	B, F, I	Hayden et al	2008
Bignoniaceae	*Tabebuia donnell-smithii*	Semi-deciduous	Colima, Mexico, Seasonally dry	2, 11, 13	G	Lopez et al	2006
Bignoniaceae	*Tabebuia aurea*		Brazil, semi-deciduous forest, dry season	8, 14	F, G	de Mattos et al	1999
Bignoniaceae	*Tabebuia heptaphylla*		Brazil, semi-deciduous forest, dry season	8, 14	E, F	de Mattos et al	1999
Bignoniaceae	*Tabebuia impetiginosa*		Brazil, semi-deciduous forest, dry season	8, 14	E, F	de Mattos et al	1999

Bignoniaceae	*Tabebuia ochracea*		Brazil, semi-deciduous forest, dry season	8, 14	F, G	de Mattos et al	1999
Bignoniaceae	*Tabebuia rosea*	Deciduous	W. Mexico, Seasonally dry	4, 9, 11, 12, 13	B, H	Hayden et al	2008
Bignoniaceae	*Tabebuia rosea-alba*		Brazil, semi-deciduous forest, dry season	8, 14	F, G	de Mattos et al	1999
Bombacaceae	*Bombax malabaricum*		India			Chowdhury	1930-40
Bombacaceae	*Bombax buonopozense*		Nigeria, Lowland Rainforest	9, 10,11, 14		Amobi	1973
Bonbacaceae	*Ceiba pentandra*	Deciduous	W. Mexico, Seasonally dry	4, 9, 11, 12, 13	B, G, I	Hayden et al	2008
Bombacaceae	*Ceiba pentandra*				A	Mariaux	1969-1977
Bombacaceae	*Pseudobombax septenatum*	Deciduous	Central Panama		D	Devall et al	1995
Bombacaceae	*Pseudobombax munguba*		Manaus, Brazil. Central Amazon inundation forest	1, 12		Worbes & Junk	1989
Bombacaceae	*Pseudobombax marginatum*		Brazil, semi-deciduous forest, dry season	8, 14	G	de Mattos et al	1999
Bombacaceae	*Bombacopsis quinata*	Deciduous	Caparo, Venezuela, Seasonally dry	2, 5, 10, 11, 12, 13	B	Worbes	1999
Bombacaceae	*Chorisia speciosa*		Argentina, Amazon pluvial forest	13		Boninsegna et al	1989

Boraginaceae	*Cordia glabrata*		Brazil, semi-deciduous forest, dry season	8, 14	F, G	de Mattos et al	1999
Boraginaceae	*Cordia alliodora*		Central Panama		D	Devall et al	1995
Boraginaceae	*Cordia alliodora*		Costa Rica	4		Tschinkel	1966
Boraginaceae	*Cordia apurensis*	Evergreen	Caparo, Venezuela, Seasonally dry	2, 5, 10, 11, 12, 13	B	Worbes	1999
Boraginaceae	*Cordia eleagnoides*	Semi-deciduous	Colima, Mexico, Seasonally dry	2,11,13	F, I	Lopez et al	2006
Boraginaceae	*Cordia trichotoma*		Argentina, Amazon pluvial forest	13	C, G	Boninsegna et al	1989
Burseraceae	*Bursera instabilis*	Deciduous	W. Mexico, Seasonally dry	4, 9, 11, 12, 13	B, G	Hayden et al	2008
Burseraceae	*Bursera simbaruba*	Deciduous	Subtropical South Florida	2, 3		Tomlinson & Craighead	1972
Burseraceae	*Bursera simbaruba*	Semi-deciduous	Colima, Mexico, Seasonally dry	2, 11, 13	G	Lopez et al	2006
Burseraceae	*Aucoumea klaineana*		Africa, Congo, Savannah-forest mosaic, dry season	6, 12, 13		Belingard et al	1996
Burseraceae	*Aucoumea klaineana*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Burseraceae	*Canarium schweinfurthii*		Africa-Guinean-Congolese OR French Guiana both	2, 5, 12	G	Detienne	1989

			w/ dry season				
Burseraceae	*Protium heptaphyllum*		Brazil, semi-deciduous forest, dry season	8, 14	F, G	de Mattos et al	1999
Capparidaceae	*Crataeva benthamii*		Manaus ,Brazil, C. Amazon, inundation forest	1, 2, 11, 12, 13		Worbes	1989
Capparidaceae	*Capparis indica*	Evergreen	Guanacaste, Costa Rica, Seasonally dry	6, 11,13		Enquist, Leffler	2001
Caryocaraceae	*Caryocar glabrum*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	J	Detienne	1989
Clusiaceae	*Symphonia globulifera*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	F	Detienne	1989
Combretaceae	*Terminalia argentea*		Brazil, semi-deciduous forest, dry season	8, 14	H	de Mattos et al	1999
Combretaceae	*Terminalia tomemtosa*		India			Chowdhury	1930-40
Combretaceae	*Terminalia ivorensis*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Combretaceae	*Terminalia superba*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Combretaceae	*Terminalia guianensis*	Evergreen	Caparo, Venezuela, Seasonally dry	2, 5, 10, 11, 12, 13	A	Worbes	1999

Combretaceae	*Anongeissus leiocarpus*	Semi-deciduous	W Africa, forest/savanna dry season	6, 10, 11, 12, 13	A, I	Schongart et al	2006
Connaraceae	*Rourea sp*		Manaus, Brazil. Central Amazon inundation forest	1, 12		Worbes & Junk	1989
Cupressaceae	*Fitzroya cupressoides*		Chile, wet	6, 10, 11		Devall et al	1998
Cupressaceae	*Fitzroya cupressoides*		Argentina humid forest	6, 11		Boninsegna et al	1985
Cupressaceae	*Taxodum distichum*	Deciduous	Subtropical South Florida	2, 3		Tomlinson & Craighead	1972
Cyrillaceae	*Cyrilla racemiflora L.*	Evergreen	Puerto Rico, dry season	9, 11	C	Drew	1998
Dilleniaceae	*Dillenia indica*	Semi-deciduous	Subtropical Wet forest, India	9, 10, 13, 14	B, G	Venugopal, et al	2007
Dipterocarpaceae	*Hopea odorata*	Evergreen	E. Thailand Dry evergreen forest	2, 10, 13, 14	D, F, G	Nobuchi et al	1995
Ebenaceae	*Diospyros virginiana*	Deciduous	Subtropical South Florida	2, 3		Tomlinson & Craighead	1972
Ebenaceae	*Diosporous abyssinica*	Evergreen	W Africa, forest/savanna, dry season.	6, 10, 11, 12, 13	A, H	Schongart et al	2006
Ebenaceae	*D. Crassiflora*	Semi-deciduous	W. Africa, Cameroon, Dry season	1, 6, 11, 12, 13	A	Worbes et al	2003
Euphorbiaceae	*Piranhea trifoliata*		Manaus, Brazil, Central Amazon, inundation	1, 2, 11, 12, 13		Worbes	1989

			forest				
Euphorbiaceae	*Sapium styllare*	Deciduous	Caparo, Venezuela, Seasonally dry	2, 5, 10, 11, 12, 13	B	Worbes	1999
Euphorbiaceae	*Ricinodendron heudelotii*		Nigeria, Lowland Rainforest	9, 10 , 11, 14		Amobi	1973
Fabaceae	*Acacia tortilis*		Africa, Rift Valley, Sparse woodland,dry season	4, 10, 11, 12	F, J	Eshete et al	1999
Fabaceae	*Acacia senegal*		Africa, Rift Valley, Sparse woodland , dry season	4, 10, 11, 12	F, J	Eshete et al	1999
Fabaceae	*Acacia seyal*		Africa, Rift Valley, Sparse woodland , dry season	4, 10, 11, 12	F, J	Eshete et al	1999
Fabaceae	*Acacia etbaica*		Africa, Rift Valley, Sparse woodland , dry season	4, 10, 11, 12	F, J	Eshete et al	1999
Fabaceae	*Acacia catechu*		India			Chowdhury	1930-40
Fabaceae	*Acosmium nitens*	Deciduous	Venezuela, Dry tropical forest with seasonal flooding	7, 12	F	Dezzeo, et al	2003
Fabaceae	*Afzelia xylocarpo*		W. Central Thailand, Seasonally dry			Baker et al	2005
Fabaceae	*Afzelia sp*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	F	Detienne	1989

Fabaceae	*Afzelia africana*	Semi-deciduous	W Africa, forest/savanna , dry season.	6, 10, 11, 12, 13	A, F	Schongart et al	2006
Fabaceae	*Albizia lebbek*		India			Chowdhury	1930-40
Fabaceae	*Albizia niopioides*		Brazil, semi-decid forest, dry season	8, 14	E, G	de Mattos et al	1999
Fabaceae	*Anadenanthera colubrina*		Brazil, semi-decid forest, dry season	8, 14	F, J	de Mattos et al	1999
Fabaceae	*Andira coriacea*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	F	Detienne	1989
Fabaceae	*Andira cuyabensis*		Brazil, semi-decid forest, dry season	8, 14	E, F	de Mattos et al	1999
Fabaceae	*Amburana cearensis*	Obligate Deciduous	Bolivia, lowland moist forest, dry season	6, 12, 13	I, J	Brienen, Zuidema	2005
Fabaceae	*Balizia elegans*	Deciduous	Costa Rica lowland wet forest	1, 12, 13	A	Fitchler et al	2003

Fabaceae	*Bowdichia virgilioidea*		Brazil, semi-decid forest, dry season	8, 14	E, F	de Mattos et al	1999
Fabaceae	*Brachystegia spiciformis Benth*		East Africa, Miombo woodland, Seasonally dry	6, 10	A, F	Trouet et al	2006
Fabaceae	*Burkea africana*	Deciduous	Namibia, Africa, Seasonally dry Semi-arid forest	6, 10, 12, 13	A, F	Fichtler et al	2004
Fabaceae	*Campsiandra laurifolia*	Maintains leaves throughout flood	Venezuela Dry tropical forest with seasonal flooding	1, 7, 12	F	Dezzeo et al	2003
Fabaceae	*Cassia fistula*		W. Central Thailand, Seasonally dry			Baker et al	2005
Fabaceae	*Cassis fistula*		East Java	11		Coster	1927
Fabaceae	*Cedrelinga catenaeformis*	Semi-deciduous	Bolivia, lowland moist forest, dry season	6, 12, 13	J	Brienen, Zuidema	2005
Fabaceae	*Dalbergia sisoo*		India			Chowdhury	1930-40
Fabaceae	*Daniellia ogea*		Nigeria, Lowland Rainforest	10, 9, 11, 14		Amobi	1973

Fabaceae	*Daniellia oliveri*	Semi-deciduous	W Africa, forest/savanna, dry season.	6, 10, 11, 12, 13	A, F	Schongart et al	2006
Fabaceae	*Dicorynia guianensis*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 3, 12	F	Detienne	1989
Fabaceae	*Dipterix alata*		Brazil, semi-deciduous forest, dry season	8, 14	E, H	de Mattos et al	1999
Fabaceae	*Dipteryx panamensis*	Deciduous	Costa Rica lowland wet forest	1, 12, 13	A, C, F	Fitchler et al	2003
Fabaceae	*Hymenea stigonocarpa*		Brazil, semi-deciduous forest, dry season	8, 14	F	de Mattos et al	1999
Fabaceae	*Hymenolobium mesoamericanum*	Deciduous	Costa Rica lowland wet forest	1, 12, 13	A, F	Fitchler et al	2003
Fabaceae	*Inga uruguensis*		Brazil, semi-deciduous forest, dry season	8, 14	G	de Mattos et al	1999
Fabaceae	*Isoberlinia tomentosa (Harms)*	Deciduous	East Africa, Miombo woodland, Seasonally dry	6, 10	F	Trouet et al	2001

Fabaceae	*Isoberlinia doka*	Semi-deciduous	W Africa, forest/savanna dry season.	6, 10, 11, 12, 13	A, F	Schongart et al	2006
Fabaceae	*Macrolobium acaciaefolium*		Manaus, Brazil, Central Amazon, Inundation forest	1, 2, 11, 12, 13		Worbes	1989
Fabaceae	*Mouriri elliptica*		Brazil, semi-deciduous forest, dry season	8, 14	F, J	de Mattos et al	1999
Fabaceae	*Parapiptadenia rigida*		Argentina, Amazon pluvial forest	13	F	Boninsegna et al	1989
Fabaceae	*Parkia sp.*		Brazil	1, 12, 13	A, H	Lisi et al	2001
Fabaceae	*Parkia auriculata*		Manaus, Brazil. Central Amazon inundation forest	1, 12		Worbes & Junk	1989
Fabaceae	*Pithecellobium inaequale*		Manaus, Brazil, Central Amazon, Inundation forest	1, 2, 11, 12, 13		Worbes	1989
Fabaceae	*Poecilanthe amazonica*		Manaus, Brazil, Central Amazon, Inundation forest	1, 2, 11, 12, 13		Worbes	1989
Fabaceae	*Prioria copaifera*		Costa Rica	2	F	Mckenzie	1972

Fabaceae	*Peltogyne cf. heterohylla*	Semi-deciduous	Bolivia, lowland moist forest, dry season	1	F	Brienen, Zuidema	2005
Fabaceae	*Prosopis flexuosa DC*		Chile, Argentina, Seasonal climate	6, 12, 13	C, F	Villalba et al	1989
Fabaceae	*Pterocarpus angolensis*		Tanzania	4		Bryant	1968
Fabaceae	*Pterocarpus angolensis*	Deciduous	Africa Miombo woodland/dry tropical forest	6, 9, 10, 11, 12, 13	C, F, J	Stahle, et al.	1999
Fabaceae	*Pterocarpus angolensis*	Deciduous	Namibia, Africa, Seasonally dry, Semi-arid forest	6, 10, 12, 13	A, C, F	Fichtler et al	2004
Fabaceae	*Pterocarpus indicus*		East Java	11		Coster	1927
Fabaceae	*Pterocarpus erinaceus*	Deciduous	W Africa, forest/savanna, dry season.	6, 10, 11, 12, 13	A, I	Schongart et al	2006
Fabaceae	*Pterocarpus vernalis*	Deciduous	Caparo, Venezuela, Seasonally dry	2, 5, 10, 11, 12, 13	A	Worbes	1999
Fabaceae	*Pterocarpus soyauxii*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	F	Detienne	1989
Fabaceae	*Pterogyne nitens*		Brazil, semi-deciduous forest, dry season	8, 14	E, H	de Mattos et al	1999

Fabaceae	*Sclerolobium aureum*		Brazil, semi-deciduous forest, dry season	8, 14	H, G	de Mattos et al	1999
Fabaceae	*Stryphnodendron obovatum*		Brazil, semi-deciduous forest, dry season	8, 14	G	de Mattos et al	1999
Fabaceae	*Swartzia laevicapa*		Manaus, Brazil. Central Amazon inundation forest	1, 12		Worbes & Junk	1989
Fabaceae	*Swartzia polyphylla*		Manaus, Brazil, Central Amazon, inundation forest	1, 2, 11, 12, 13		Worbes	1989
Fabaceae	*Tachigali vasquezii*	Semi-deciduous	Bolivia, lowland moist forest, dry season	6, 12, 13	J	Brienen, Zuidema	2005
Fabaceae	*Tachigalia sp.*		Manaus, Brazil, Central Amazon, inundation forest	1, 2, 11, 12, 13		Worbes	1989
Fabaceae	*Vatairea macrocarpa*		Brazil, semi-deciduous forest, dry season	8, 14	G	de Mattos et al	1999
Flacourtiaceae	*Homalium tomemtusum*		East Java	11		Coster	1927
Flacourtiaceae	*Laetia suaveolens*		Manaus, Brazil, Central Amazon, inundation forest	1, 2, 11, 12, 13		Worbes	1989
Flacourtiaceae	*Casearia decandra*		Brazil, semi-deciduous forest, dry season	8, 14	E, G	de Mattos et al	1999
Flacourtiaceae	*Casearia sylvestris*		Brazil, semi-deciduous forest, dry season	8, 14	G	de Mattos et al	1999

Goupiaceae	*Goupia glabra*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Hugoniaceae	*Roucheria sp.*		Manaus, Brazil, Central Amazon, inundation forest	1, 2, 11, 12, 13		Worbes	1989
Juglandaceae	*Juglans australis*		Bolivia and Argentina	11	A, G	Villalba et al	1985
Lauraceae	*Persea borbonia*		Subtropical South Florida	2, 3		Tomlinson & Craighead	1972
Lauraceae	*Ocotea rubra*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Lauraceae	*Ocotea suaveolens*		Brazil, semi-deciduous forest, dry season	8, 14	G	de Mattos et al	1999
Lauraceae	*Ocotea sp.*		Manaus, Brazil, Central Amazon, inundation forest	1, 2, 11, 12, 13		Worbes	1989
Lauraceae	*Ocotea sp. II*		Manaus, Brazil, Central Amazon, inundation forest	1, 2, 11, 12, 13		Worbes	1989
Lauraceae	*Neolitsea obtusifolia*		W. Central Thailand, Seasonally dry			Baker et al	2005
Lecythidaceae	*Eschweilera sp.*		Manaus, Brazil, Central Amazon, inundation forest	1, 2, 12, 13, 14		Worbes	1989
Lecythidaceae	*Bertholletia excelsa*	Deciduous	Bolivia, lowland moist forest, dry season	4, 13, 14	H	Brienen, Zuidema	2005

Lythraceae	*Lagerstroemia speciosa*		East Java	11		Coster	1927
Magnoliaceae	*Michelia champaca*		India			Chowdhury	1930-40
Magnoliaceae	*Michelia champaca*		W. Central Thailand, Seasonally dry			Baker et al	2005
Magnoliaceae	*Magnolia virginiana*		Subtropical South Florida	2, 3		Tomlinson & Craighead	1972
Malvaceae	*Hildegardia barteri*	Deciduous	Nigeria, Lowland Rainforest	5, 9, 11, 14		Amobi	1973
Meliaceae	*Toona ciliata*		W. Central Thailand, Seasonally dry			Baker et al	2005
Meliaceae	*Toonia sureni*		East Java	11		Coster	1927
Meliaceae	*Melia azederach*		W. Central Thailand, Seasonally dry			Baker et al	2005
Meliaceae	*Melia azedarach*		East Java	11		Coster	1927
Meliaceae	*Cedrela toona*		India			Chowdhury	1930-40
Meliaceae	*Cedrela angustifolia*		Bolivia and Argentina	11	A, C	Villalba et al	1985
Meliaceae	*Cedrela fissilis*		Argentina, Amazon pluvial forest		C, F	Boninsegna et al	1989

Meliaceae	*Cedrela odorata*	Deciduous	W. Mexico, Seasonally dry	4, 9, 11, 12, 13	A, E, F	Hayden et al	2008
Meliaceae	*Cedrela odorata*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	A, E, F	Detienne	1989
Meliaceae	*Cedrela odorata*		Central Amazon, drier period	2, 4, 5, 6, 11, 12		Dunisch et al	2002
Meliaceae	*Cedrela odorata*	Deciduous	Caparo, Venezuela, Seasonally dry	2, 5, 10,11, 12, 13	A	Worbes	1999
Meliaceae	*Cedrela odorata*	Deciduous	Bolivia, lowland moist forest, dry season	6, 12, 13	A, F	Brienen, Zuidema	2005
Meliaceae	*Swietenia macrophylla*		Central Amazon, drier period	2, 4, 5, 6,,11, 12		Dunisch et al	2002
Meliaceae	*Sweitenia macrophylla*	Deciduous	Caparo, Venezuela, Seasonally dry	2, 5, 11, 12, 13	A	Worbes	1999
Meliaceae	*Swietenia mahagoni*	Deciduous	Subtropical South Florida	2, 3		Tomlinson & Craighead	1972
Meliaceae	*E. cylindricum*	Semi-deciduous	W. Africa, Cameroon, seasonall dry	1, 6, 11, 12, 13	A	Worbes et al	2003
Meliaceae	*Chukrasia tabularis*		W. Central Thailand, Seasonally dry			Baker et al	2005
Meliaceae	*Trichilia singularis*		Manaus, Brazil, Central Amazon, inundation forest	1, 2, 11, 12, 13		Worbes	1989

Meliaceae	*Trichilia elegans*		Brazil, semi-deciduous forest dry season	8, 14	F, J	de Mattos et al	1999
Meliaceae	*Khaya anthotheca*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Meliaceae	*Khaya ivorensis*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Meliaceae	*Lovoa trichilioides*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Meliaceae	*Entandrophragma angolense*		Ghana		F	Hummel	1946
Meliaceae	*Entandrophragma angolense*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	F	Detienne	1989
Meliaceae	*Entandrophragma candollei*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	F	Detienne	1989
Meliaceae	*Entandrophragma cylindricum*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	F	Detienne	1989
Meliaceae	*Entandrophragma utile*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	F	Detienne	1989
Meliaceae	*Guarea cedrata*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	F	Detienne	1989

Moraceae	*Chlorophora excelsa*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Moraceae	*T. madagascariense*	Semi-deciduous	W. Africa, Cameroon, seasonally dry	1, 6, 11, 12, 13	A	Worbes et al	2003
Moraceae	*Morus rubra*	Deciduous	Subtropical South Florida	2, 3		Tomlinson & Craighead	1972
Moraceae	*Sorocea duckei*		Manaus Brazil Amazon inundation forest	1, 12		Worbes & Junk	1989
Moraceae	*Bosqueia angolensis*	Evergreen	Nigeria, Lowland Rainforest	9, 10, 11, 14		Amobi	1973
Myricaceae	*Myrica cerifera*		Subtropical South Florida	2, 3		Tomlinson & Craighead	1972
Myristicaceae	*C. preussii*	Semi-deciduous	W. Africa, Cameroon, seasonally dry	1, 6, 11, 12, 13	A	Worbes et al	2003
Myristicaceae	*Virola melinonii*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Myrtaceae	*Psidium ovatifolium*	Maintains leaves thru flood	Venezuela, Dry tropical forest with seasonal flooding	7, 12	F	Dezzeo et al	2003
Myrtaceae	*Psidium acutangulum*		Manaus, Brazil, Central Amazon, inundation forest	1, 2, 11, 12, 13		Worbes	1989

Myrtaceae	*Myrciaria amazonica*		Manaus, Brazil, Central Amazon, inundation forest	1, 2, 11, 12, 13		Worbes	1989
Nothofagaceae	*Nothofagus nitida*		Chile, wet forest	6, 10, 11		Devall et al	1998
Olacaceae	*Minquartia guianensis*	Evergreen	Costa Rica lowland wet forest	1, 12, 13	B, C	Fitchler et al	2003
Oleaceae	*Fraxinus caorliniana*	Deciduous	Subtropical South Florida	2, 3		Tomlinson, & Craighead	1972
Pinaceae	*Pinus kesiya*		Thailand seasonally dry	6, 10, 11, 12, 13		Buckley et al	1995
Pinaceae	*Pinus merkusii*		Thailand seasonally dry	6, 10, 11, 12, 13		Buckley et al	1995
Pinaceae	*Pinus longifolia*		India			Chowdhury	1930-40
Pinaceae	*Pinus elliottii*		Subtropical South Florida	2, 3		Tomlinson & Craighead	1972

Pinaceae	*Pinus occidentalis*		Dominican Republic, Cordillera central	6, 10, 11, 12	A	Speer et al	2004
Pinaceae	*Pinus caribaea*	Evergreen	Caparo, Venezuela, Seasonally dry	2, 5, 10, 11, 12, 13	A	Worbes	1999
Rhizophoraceae	*Rhizophora mangle*		North Brazil	1		Menezes et al	2003
Rhizophoraceae	*Rhizophora mucronata*		Kenya, coastal region, seasonal rainfall	2, 4, 10, 12	B, I	VerHeyden at al	2004
Rhamnaceae	*Rhamnidium elaeocarpum*		Brazil, semi-deciduous forest, dry season	8, 14	F, G	de Mattos et al	1999
Rutaceae	*Fagara hassleriana*		Brazil, semi-deciduous forest, dry season	8, 14	F, G, J	de Mattos et al	1999
Rubiaceae	*Mitragyna ciliata*	Semi-deciduous	W. Africa, Cameroon, seasonally dry	1, 6, 11, 12, 13	A	Worbes et al	2003
Rubiaceae	*Genipa americana*	Deciduous	Guanacaste, Costa Rica, Seasonally dry	6, 11, 13		Enquist, Leffler	2001
Salicaceae	*Salix caroliniana*	Deciduous	Subtropical South Florida	2, 3		Tomlinson & Craighead	1972

Sapindaceae	*Dilodendron bipinnatum*		Brazil, semi-deciduous forest, dry season	8, 14	G	de Mattos et al	1999
Sapotaceae	*Pouteria ramiflora*		Brazil, semi-deciduous forest, dry season	8, 14	G	de Mattos et al	1999
Sapotaceae	*Pouteria orinocoensis*	Maintains leaves throughout flood	Venezuela Dry tropical forest with seasonal flooding	1, 7, 12	F	Dezzeo et al	2003
Sapotaceae	*Elaeoluma glabrescens*		Manaus, Brazil. Central Amazon inundation forest	1, 12		Worbes & Junk	1989
Sapotaceae	*Labatia glomerata*		Manaus, Brazil. Central Amazon inundation forest	1, 12		Worbes & Junk	1989
Sapotaceae	*Aningeria robusta*	Semi-deciduous	W. Africa, Cameroon, seasonally dry	1, 6, 11, 12, 13	A	Worbes et al	2003
Sapotaceae	*G. perpulchra*	Semi-deciduous	W. Africa, Cameroon, seasonally dry	1, 6, 11, 12, 13	A	Worbes et al	2003
Sapotaceae	*Neoxythece elegans*		Manaus, Brazil, Central Amazon, inundation forest	1, 2, 11, 12, 13		Worbes	1989
Sapotaceae	*Teighemella heckelii*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	F	Detienne	1989

Simaroubaceae	*Simarouba amara*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Simaroubaceae	*Simarouba amara*	Evergreen	Costa Rica lowland wet forest	1, 12, 13	B, F	Fitchler et al	2003
Sterculiaceae	*Triplochiton sp*		Nigeria	4		Onochie	1947
Sterculiaceae	*Triplochiton sp*		Nigeria			Onochie	1947
Sterculiaceae	*Triplochiton sp*		Nigeria	14	F	Lowe	1961
Sterculiaceae	*Triplochiton scleroxylon*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Sterculiaceae	*E. oblonga*	Semi-deciduous	W. Africa, Cameroon, seasonally dry	1, 6, 11, 12, 13	A	Worbes et al	2003
Sterculiaceae	*T. scleroxylon*	Semi-deciduous	W. Africa, Cameroon, seasonally dry	1, 6, 11, 12, 13	A	Worbes et al	2003

Sterculiaceae	*Pterygota sp.*	Semi-deciduous	W. Africa, Cameroon, seasonally dry	1, 6, 11, 12, 13	A	Worbes et al	2003
Sterculiaceae	*N. papaverifera*	Semi-deciduous	W. Africa, Cameroon, seasonally dry	1, 6, 11, 12, 13	A	Worbes et al	2003
Sterculiaceae	*S. rhinopetala*	Semi-deciduous	W. Africa, Cameroon, seasonally dry	1, 6, 11, 12, 13	A	Worbes et al	2003
Sterculiaceae	*Sterculia apetala*		Brazil, semi-deciduous forest, dry season	8, 14	G, J	de Mattos et al	1999
Sterculiaceae	*Mansonia altissima*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Sterculiaceae	*Tarrietia utilis*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Tiliaceae	*Mollia sp.*		Manaus, Brazil, Central Amazon, inundation forest	1, 2, 11, 12, 13		Worbes	1989
Tiliaceae	*Luehea paniculata*		Brazil, semi-deciduous forest, dry season	8, 14	G, J	de Mattos et al	1999
Ulmaceae	*Celtis laevigata*	Deciduous	Subtropical South Florida	2, 3		Tomlinson & Craighead	1972
Ulmaceae	*Celtis adolfi-frederici*	Semi-deciduous	W. Africa, Cameroon, seasonally dry	1, 6, 11, 12, 13	A	Worbes et al	2003

Ulmaceae	*C. zenkeri*	Semi-deciduous	W. Africa, Cameroon, seasonally dry	1, 6, 11, 12, 13	A	Worbes et al	2003
Ulmaceae	*Ulmaceae I.*	Semi-deciduous	W. Africa, Cameroon, seasonally dry	1, 6, 11, 12, 13	A	Worbes et al	2003
Ulmaceae	*Ulmus lancifolia*		W. Central Thailand, Seasonally dry			Baker et al	2005
Verbenaceae	*Tectona grandis*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	A, E, F	Detienne	1989
Verbenaceae	*Tectona grandis*	Deciduous	Caparo, Venezuela, Seasonally dry	2, 5, 10, 11, 12, 13	A	Worbes	1999
Verbenaceae	*Tectona grandis*		India			Chowdhury	1930-40
Verbenaceae	*Tectona grandis*		East Java	11		Coster	1927
Verbenaceae	*Peronema canescens*		East Java	11		Coster	1927
Verbenaceae	*Citharexylum fructicosum*		Subtropical South Florida	2, 3		Tomlinson & Craighead	1972
Verbenaceae	*Vitex cymosa*		Brazil, semi-deciduous forest, dry season	8, 14	C	de Mattos et al	1999
Verbenaceae	*Vitex cymosa*		Manaus, Brazil, Central Amazon, inundation forest	1, 2, 11, 12, 13		Worbes	1989
Verbenaceae	*Vitex peduncularis*		W. Central Thailand, Seasonally dry			Baker et al	2005

Verbenaceae	*Gmelina arborea*	Deciduous	W. Mexico, Seasonally dry	4, 9, 11, 12, 13	B, E, J	Hayden et al	2008
Verbenaceae	*Gmelina arborea*		W. Central Thailand, Seasonally dry			Baker et al	2005
Verbenaceae	*Triplochiton scleroxylon*		Africa-Guinean-Congolese OR French Guiana both w/ dry season	2, 5, 12	G	Detienne	1989
Vochysiaceae	*Qualea grandiflora*		Brazil, semi-deciduous forest, dry season	8, 14	H	de Mattos et al	1999

Appendix 2: Tropical tree species known *not* to produce annual growth rings. For explanation of methods column, see methods section in text.

Family	**Tree Species**	**Leaf Habit**	**Location**	**Method Used**	**Ring Wood Anatomy**	**Authors**	**Year of Publi-cation**
Dipterocarpaceae	*Shorea leprosula*	Evergreen	W. Malaysia Humid, weakly seasonal	2	No growth zones	Sass et al.	1995
Dipterocarpaceae	*Dryobalanops sumatrensis*	Evergreen	W. Malaysia Humid, weakly seasonal	2	No growth zones	Sass et al.	1995
Fagaceae	*Quercus copyensis*		Costa Rica Wet forest	1	>1 growth zone on an annual basis	Worbes and Junk	1989
Fagaceae	*Quercus costaricensis*		Costa Rica Wet forest	1	>1 growth zone on an annual basis	Worbes and Junk	1989
Meliaceae	*Carapa guianensis*		Central Amazon	2, 4, 5, 6, 11, 12	>1 growth zone on an annual basis	Dunisch et al	2002
Rhizophoraceae	*Bruguiera gymnorrhiza*		Micronesia	5, 10		Krauss et al.	2006
Sonneratiaceae	*Sonneratia alba*		Micronesia	5, 10		Krauss et al.	2006

Chapter 2: Annual growth rings in 6 tropical dry forest tree species in Mexico

2.1 Introduction

The periodicity of growth ring production in many tropical tree species is not known. This is due, in part, to the formation of indistinct rings by some tree species as well as the general lack of research into growth ring formation in tropical trees (Jacoby 1989). While annual growth rings can provide invaluable information regarding the plant population and community dynamics of tropical forests (e.g Baker 2005, Brienen 2005), few studies have attempted to address this. Indeed, the prevailing assumption during the last three decades has been that this approach to tropical forest dynamics was unreliable; in turn, this assumed unreliability was perhaps the driving argument for why very large permanent plots (e.g. Barro Colorado Island in Panama) were considered to be the best way to understand dynamics. This tacit cry for patience perhaps reflects a misunderstanding of how common annual rings may be in tropical species.

For annual growth rings to occur in tropical trees there must be a period of cambial dormancy, or near-dormancy, only once per year. In turn, this cessation of radial growth creates an identifiable change in wood anatomy (Worbes 1995). A decline or cessation of cambial activity is possible in some tree species that experience a dry season of at least two months during which less than 50 mm precipitation will fall (Worbes 1995). A decrease in precipitation for months at a time leaves many trees severely desiccated (Borchert 1994), and results in a water deficit for the essential growth processes of cell development and elongation (Kramer 1964). Cambial activity, more specifically the development of cambial initials into xylem tissue (Kramer 1964), will be necessarily reduced during the dry season due to the sensitivity of cell growth to water stress (Borchert 1994c). With this process halted, there is no potential for radial wood growth during the driest part of the year.

Seasonally dry tropical forests have a drought season that is sufficiently severe and prolonged that one suspects annual rings to be normal rather than exceptional for non-riverine drought-deciduous species. This phenological cycle indicates that physiological changes must take place within the tree during times of drought and may serve as a first indication of cambial dormancy for some trees (Tomlinson and Longman 1981, Jacoby 1989, Worbes 1995). Indeed, cambial activity in some tropical trees has been positively correlated with bud break and leaf emergence (Amobi 1973, Reich and Borchert 1984), possibly due to an increase in photosynthesis and/or the establishment of nutrient or hormone gradients (Alvim 1964). Leaf flushing induces cambial activity in deciduous trees growing in a dry tropical forest; the cambial development does not cease until the soil water deficit cues leaf abscission (Alvim 1964, Reich and Borchert 1984).

With little or no water available, essentially all non-riverine drought-deciduous species growing in dry tropical forests should be regarded as promising candidates for an annual radial growth cycle. At one extreme within this climate category, the dry tropical forest along the Pacific coast of Mexico endures a five to seven month drought interrupted typically by only a few low-intensity rainfall events (Bullock 1986). Aside from deep gullies and river margins, almost all tree species lose their leaves during the first half of this interval (Bullock and Solis-Magallanes 1990)

The objective of this study is to determine whether or not the growth rings of six drought deciduous tree species, chosen more or less randomly from within this region in western Mexico, were indeed both distinct and annual by examining the rings of trees of known age. Knowing nothing more than that all six species are typically deciduous, I hypothesized that all would show an estimated age equal to the known age.

2.2 Methods

This study was conducted on the Pacific coast of Mexico in the state of Jalisco during the dry season of 2007. The trees used in this study were originally planted on private land covered in a mixture of other plantation tree species as well as naturally-grown forest approximately 8 km from the Chamela Biology Station (19° 30'N, 105° 03'W). The vegetation is part of the seasonally dry tropical forest ecosystem (Bullock 1986), receiving an average of 763 mm of annual rainfall (Figure 10). The rainfall is distinctly seasonal; over 80% falling between the months of June and November (Bullock 1986). Mean annual temperature is 25°C with little fluctuation throughout the year (Figure 10). Our sites, within 3 km of the coast, had a maximum altitude less than 150 m asl. The soils were derived from well-eroded pyroclastic and rhyolitic.

All trees sampled for this study had been planted as one-year old seedlings on private land by the same individual. I worked only with individual trees whose age the landowner felt certain about. The species selected for this study were *Bursera instabilis, Cedrela odorata, Ceiba pentandra, Gmelina arborea, Tabebuia donnell-smithii,* and *Tabebuia rosea.* These species were leafless (or almost completely so) at the time of sampling. Sample trees were located on dry upland sites, well away from rivers, and all were deciduous when they were sampled, mid-way through the drought season. Trees ranged in diameter from 7 to 71 cm at 1.37 m (breast height) above the ground.

Trees were either felled or cored (Table 2). Stem disks were taken from a representative of each study species as close to the ground as possible, while cores were taken approximately 20 cm above the ground from other individuals. One core was taken from each tree. Sample size for each species ranged from one to five. These sample sizes reflected the limits of the owner's confidence in his ages, as well as my discrimination against individuals with sharply curving boles, low-level rot, or incipient buttressing roots.

Disks and cores were allowed to air dry, mounted on wooden blocks, and sanded using progressively finer sandpaper (80-150 grit size). Transverse sections were examined macroscopically as well as microscopically using a stereo microscope. Rings were counted along 4 radii on disks.

2.3 Results

Sample trees varied in age from 4 to 26 years old. The growth rings were annual; all observed ages were within 1 year of the predicted age (Table 2, Figure 11). The rings of each tree species varied in distinctness, with some species producing rings clearly demarcated both macro- and microscopically, and others producing rings that were quite indistinct with only subtle changes in wood anatomy delineating the ring boundary (Table 3). In all cases, the wood within a growth ring had some visible change in anatomy (e.g. low to high vessel frequency) that was repeated for each ring and that permitted the differentiation of annual rings. The wood anatomy characteristics for each species were as follows.

Bursera instabilis had the most indistinct growth rings in the study. There was, however, a recognizable change in fiber density between the earlywood and latewood zones, with the denser latewood denoted macroscopically by a slightly darker coloration in the wood.

At the other extreme, *Cedrela odorata* had the most distinct growth rings of the six species studied. The rings of this species were delineated by a band of marginal parenchyma (recognizable both macro-and microscopically). The size arrangement of vessels in *Cedrela* (semi-ring porous with larger diameter vessels in the earlywood and smaller in the latewood) also contributed to the ease of recognition.

Ceiba pentandra, a ubiquitous species on the Pacific coast of Mexico, showed a dense band of fibres at the ring boundary as well as a change in vessel frequency between the earlywood and latewood. *Gmelina arborea*, an Asian native recently introduced to Mexico, showed visible growth zones at the macroscopic level. Upon closer analysis with a microscope, these growth zones possessed a semi-ring porous structure, with a change in vessel size from larger to smaller in the earlywood and latewood, respectively.

Tabebuia donnell-smithii produced a characteristic band of marginal parenchyma between growth zones and had a change in vessel frequency between earlywood and latewood. The congener, *T. rosea*, produced growth zones that were more difficult to discern than *T. donnell-smithii.* This species showed alternating bands of parenchyma and fiber that were somewhat indistinct. Nonetheless, fiber bands were closer together and darker in color at the growth ring boundary.

2.4 Discussion

All the individuals examined here created approximately one ring per year. At the time they were chosen for this study, I did not know if these six species possessed distinct rings, or if previous studies had shown that they produced annual rings. I knew only that they were drought-deciduous, and hypothesized that necessarily then they would have annual rings. These results support the hypothesis that drought-deciduous trees species growing in a seasonally dry tropical climate type can be expected to produce annual growth rings.

Cessation of radial wood production and the subsequent formation of annual growth rings in the sampled trees was caused by the dramatic soil water deficit typical of dry seasons in this climate type. These trees grew in an area where the rainfall is distinctly seasonal (Figure 12). Rainfall quantity has been shown to be influential in tropical tree growth in several studies (Brienen & Zuidema 2005, Enquist & Leffler 2001, Worbes 1999). Through the use of dendrometer bands, researchers have determined that cambial activity was greatly influenced by precipitation patterns in tropical dry forests in that it slowed considerably or ceased completely during the dry season in many species (Detienne 1989, Worbes 1999). Several studies have confirmed that cambial activity in many tropical tree species decreased markedly or stopped during the dry season, being active during the wet season only (Vetter and Botosso 1989, Detienne 1989, Villalba and Boninsegna 1989, Worbes 1999, Amobi 1973). Indeed, in tropical areas that experience two annual dry seasons, two growth rings were produced in some tree species (Jacoby 1989). In a dry tropical forest in Costa Rica, leaf phenology that was clearly seasonal was noted as a key factor in the formation of annual growth rings in some tree species (Borchert 1999).

The one-year difference in age and number of growth rings in some of the tree species may be attributed to one of several causes. An intra-annual growth band, caused by an abnormal change in growing conditions within a growing season (e.g. a period of drought within a normally wet month) will appear as a growth ring in some instances (Stokes and Smiley 1968). Another possible cause of the discrepancy would be error in predicting the actual age of the tree (the memory of the landowner may have been less than perfect). A one year difference in age and number of growth rings is considered a minor discrepancy and the growth rings can still be considered annual in nature (Flinn et al. 1994, Gourlay 1995, Eshete and Stahl 1999, VerHeyden et al 2004).

Using trees of known age (i.e. plantations) to carry out research into the growth periodicity of tropical trees is a frequent and reliable method in dendrochronology (Dunisch 2002, Verheyden 2004, Eshete and Stahl 1999, Gourlay 1995, Worbes 1995, Flinn et al 1994). Many of the species investigated in this study have been proven to produce annual growth rings in other areas of the tropics (Tomlinson & Craighead 1972, Lopez et al 2006, Detienne 1989, Worbes 1999, Brienen & Zuidema 2005, Dunisch et al 2002, Baker et al 2005, De Mattos et al 1999).

I tentatively conclude that deciduous trees in any seasonally dry tropical forest characterized by a single prolonged drought will reliably exhibit annual rings. That is, it can be assumed that, as in the higher latitudes, dendroclimatological studies and stand reconstructions in tropical dry forests can proceed without first having to demonstrate that the rings of the species of interest are annual. Thus, our understanding of tropical forest dynamics need not be limited to permanent plots.

Figure 10: Annual rainfall and temperature distribution at Chamela (Jalisco) based on monthly averages from 1996-2006. Data courtesy of La Estacion Biologica de Chamela.

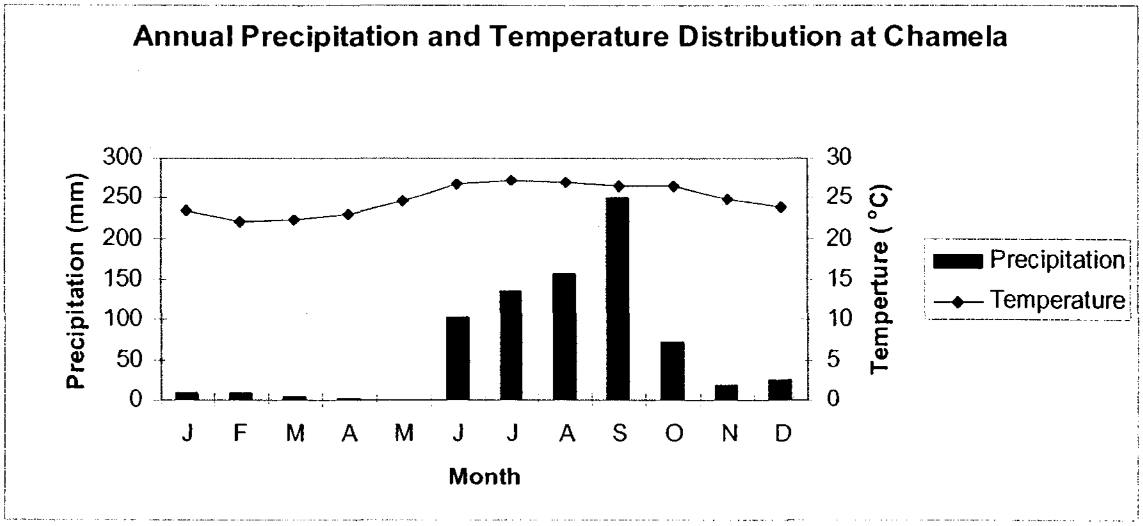


Figure 11: Relationship between measured age and predicted age of the six study species.

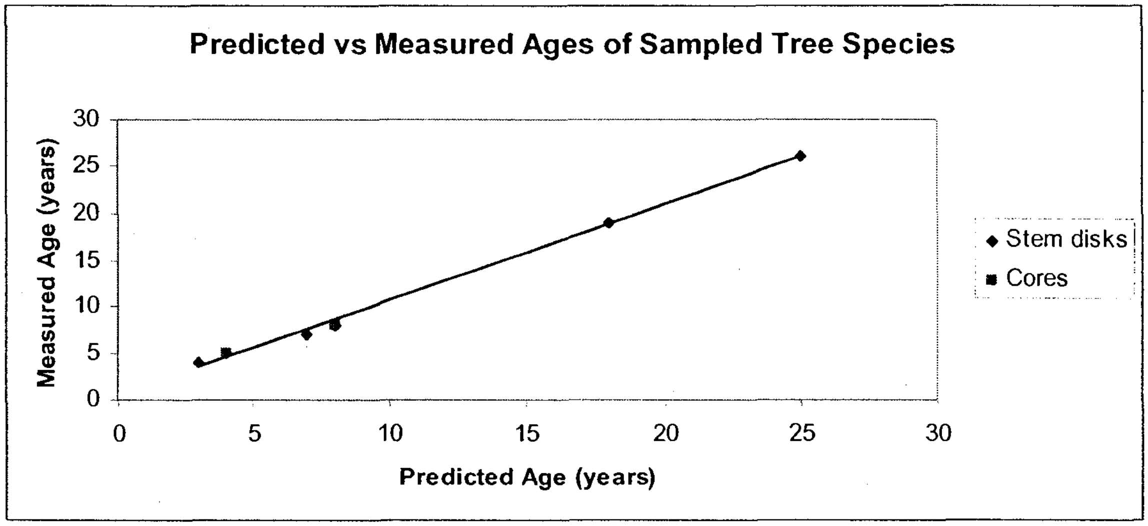


Table 2: Predicted versus measured ages obtained from ring counts applied to stem disks and core samples.

Species	**Known Age**	**Measured age**	**Sample Type**
Bursera instabilis	7	7	Stem disk
Cedrela odorata	8	8	Stem disk
C. odorata	8	8	Core
C. odorata	8	8	Core
C. odorata	8	8	Core
C. odorata	8	8	Core
Ceiba pentandra	25	26	Stem disk
Gmelina arborea	4	5	Stem disk
G. arborea	4	5	Core
G. arborea	4	5	Core
G. arborea	4	5	Core
G. arborea	4	5	Core
Tabebuia donnell-smithii	18	19	Stem disk
Tabebuia rosea	3	4	Stem disk

Table 3: Tree species investigated and corresponding anatomy of growth rings.

TREE	**RING WOOD ANATOMY**
Bursera instabilis	Indistinct rings. Change in fiber density between earlywood and latewood
Cedrela odorata	Distinct rings. Semi-ring porous (vessels smaller in latewood), Marginal parenchyma.
Ceiba pentandra	Indistinct rings. Dense band of fibres at ring boundary and change in vessel frequency between earlywood and latewood
Gmelina arborea	Indistinct rings. Semi-ring porous (few, large vessels in earlywood gradually change to more numerous, smaller-sized vessels in latewood). Light-colored earlywood and darker latewood.
Tabebuia donnell-smithii	Indistinct rings. Marginal parenchyma band, change in vessel frequency between earlywood and latewood.
Tabebuia rosea	Indistinct rings. Alternating bands of fiber and parenchyma, with higher density of fibers at ring boundary.

Chapter 3: The effect of dry season precipitation on annual ring formation and leaf phenology in a seasonally dry tropical forest

3.1 Introduction

Trees in seasonally dry tropical forests possess several functional traits that permit them to endure severe water stress for 5 to 7 months of the year (Borchert 1994a). Trees on parched soils (middle and upper slopes) typically respond to the extended drought by abscising leaves (Borchert 1994a). Occasionally, however, these seasonally dry forests experience a rainfall during the dry season, and the precipitation can be sufficient to cause bud break and leaf expansion in many tree species (Bullock and Solis-Maganalles 1990).

While it has been argued that the minimal amount of rain required for drought deciduous trees to flush a cohort of leaves during the dry season is between 40-50 mm during one event (or perhaps a few temporally-close events) (Daubenmire 1972, Bullock and Solis-Maganalles 1990, Myers et al 1998), the phenological response to sudden water availability will not be "all-or-nothing". Although the relationship has not been studied, one expects a positive correlation between water receipt and some quantitative tree response such as proportion of buds burst or leaf area index. Irrigation experiments could delineate this response but have so far been limited to extremely large amounts (Borchert 1994b Wright and Cornejo 1990). This coupling of the tree response to varying irrigation amounts in a leafless forest stand in western Mexico represents my first objective.

Invariably, leaves flushed by an ephemeral event subsequently desiccate as the soil rapidly dries (Borchert 1994b). One speculates that the newly-flushed leaves are functioning for too brief a period to offset their carbon costs. A second objective of this study is to determine if the trees in the irrigated stands suffered diminished growth during the subsequent wet season as a result of this net energetic loss. That is, I hypothesize that subsequent wet-season growth will be inversely proportional to water receipt during the previous irrigation experiment.

A third objective involves the effect of dry season rainfall and the subsequent flushing of leaves on radial wood formation; this subject has not been well studied (Bullock 1997, Heinrich and Banks 2006). It is known that the prolonged drought characterizing seasonally dry forests leads to a cessation in cambial activity, at least for the drought-deciduous species (Lopez et al 2006, Baker et al 2005, Worbes 1999, Buckley et al 1995, Worbes and Junk 1989). Clearly, our ability to use the rings of tropical tree species for stand reconstructions (e.g. Baker et al 2005) or climate response studies (e.g. Enquist and Leffler 2001) will be hampered if false rings due to dry season rain events are common. Thus, for the irrigated stands, I will also look at the formation of rings as a function of watering intensity.

My final objective is to use long-term records from the nearby Chamela research station to determine the probability of a dry season storm sufficient to cause a particular level of bud burst or ring formation.

3.2 Materials and Methods

This study was conducted on the Pacific coast of Mexico in the state of Jalisco during the dry seasons of 2007 and 2008. The study area was located on private land in an early stage of re-growth (most stems were about 15-20 years old) located approximately 4 km south of the Estacion Biologia de Chamela (19° 30'N, 105° 03'W) and 1 km from the ocean. The stand, dominated by small-stemmed trees (20-80mm DBH) with an average height of 5.6m, was located about 70 m above sea level on steeply-sloping ground. The soil had little organic matter aside from the thick layer of recently-fallen leaves, and was derived from pyroclastic deposits (a mix of stones and volcanic ash). The annual average precipitation received in this area is 763 mm (Figure 12), with over 80% falling between the months of June and November (Bullock 1986). The mean annual temperature is 25°C with little fluctuation throughout the year (Figure 12).

On a steep slope, four irrigation plots (each measuring 25 m^2), with a minimum of 8 meters between the edges of any two plots were used. The control plot, also $25m^2$, was located 15 m uphill from the nearest irrigation plot. All trees located within the plots were included in the study. There were between five and fourteen trees included in the study from each plot, with an average of 3 individuals per species per plot (Table 4). The tree species found in the plots were *Cordia alliodora,* a *Piptadenia sp*., an *Acacia sp, Mimosa arenaria,* a *Platimicium sp., Heliocarpus pallidus*, and a *Caesearia* sp. The only species used in the statistical analyses were *Cordia alliodora* and *Piptadenia sp.* as they were the only ones found on almost every plot.

In the dry season of 2007, all trees used in the study were marked by cambial wounding (2 cm^2 of bark was removed to a depth sufficient to include the cambium) at breast height (1.37 m). Tree diameter (DBH) was measured near the wound and the point of measurement marked with paint prior to irrigation.

Water was distributed across the plots so that every m^2 of the plot received approximately the same amount of water. Plots were irrigated, one each day, from March 11th to March 14th in 2007 and received an amount of water varying from 0 (the control) to 200 mm (Table 4).

The degree of subsurface seepage of water into the soil outside of plots was determined using two $1m^2$ test blocks well off to the side of the irrigation plots. Water amounting to the highest irrigation intensity (200 mm) was applied to each $1m^2$. Soil was then dug out of this test area to gauge the extent of subsurface flow on the steep slope.

The leaf and flowering responses of the trees were monitored daily for 40 days following irrigation. The leaf response, an amalgam of number of leaf buds opened, and leaf size, was quantified on a scale of 0-3, with 0=no response; 1=weak response with only a few, underdeveloped leaves appearing; 2=moderate response where 20-80% of buds were opened, but many leaves were not full size; and 3=full response with essentially all buds opened and leaves full size. Only *Piptadenia* flowered following irrigation; for this species the flowering response was quantified dichotomously as: 0=no response; 1=a range from partial response (a few flowers developing) to complete flowering (inflorescences fully-developed and covering >75% of the crown).

Trees were measured for changes in stem diameter (using calipers) at the same time each day (between 0700 and 0800 hrs) to avoid the effects of diurnal fluctuations in stem water content. In January, 2008, a random selection of *Cordia alliodora* and *Piptadenia sp.* trees within each plot were cut down. A stem disk was taken at the point of cambial wounding. Stem disks were prepared by sanding using progressively finer sand paper (80-150 grit size). Tree rings were examined using a stereo microscope. Xylem was examined from the scar tissue to the bark and compared with previous growth rings for any abnormalities that may have been caused by irrigation (i.e. any visible indication of cambial activation due to irrigation, and, if so, were there two growth rings for the year).

Weather records for the past 30 years were obtained from the meteorological station at La Estacion Biologia de Chamela, located 4 km from the stand, to determine the frequency with which substantial rainfall events occur during the dry season in this area.

Spearman rank correlation was used to compare irrigation intensity with two different responses: leaf extension, and relative growth rate (RGR). RGR was calculated as $RGR = (\ln W_2 - \ln W_1) / (t_2 - t_1)$; where W_1 and W_2 are tree diameters (DBH) at times t_1 and t_2. .

3.3 Results

Cordia alliodora and *Piptadenia sp.* comprised 81% of the trees (Table 4). All leaves and flowers produced in response to watering were completely desiccated by the end of the study period (40 days after irrigation). No rain fell during this interval. No fruit developed from flowers.

There was no surface flow during the application of water. In the two excavated 1 m^2 areas outside the irrigated plots, the 200 mm intensity of water application caused very little subsurface flow, with water extending only about 20 cm downslope (and about 20 cm in depth) in a cone-like shape from the downslope edge of the 1 m^2 area. There was essentially no lateral subsurface movement of water.

All irrigated plots showed some leaf response (Figure 13). The weakest response occurred in the plot receiving the lowest amount of water, with strength of the response increasing as irrigation rate increased. For all individuals lumped regardless of species, there was a significantly positive relationship between the ordinal growth response measure and the irrigation intensity (Spearman rank correlation corrected for ties; $P<0.01$; $n=43$). *Cordia alliodora* and *Piptadenia sp.* comprised 81% of all the trees. For these two species separately, the Spearman rank correlation was even more significant than when all species are aggregated ($P< 0.001$; $n=25$ or 10, respectively).

Flower production in response to irrigation occurred only for *Piptadenia* and only at the 200 mm watering intensity (Figure 14). At this intensity, two of the five *Piptadenia* trees were fully in flower (fully developed inflorescences across the entire crown), another two showed a weak flowering response (few inflorescences; many of them only partially developed), and one tree showed no response at all.

The scar tissue produced due to wounding of the cambium served as a point of reference for wood growth since irrigation (Figure 15). All individuals of all species produced exactly one growth ring following cambial wounding. That is, no intensity of irrigation yielded a false growth ring. (Examples for *Cordia alliodora* and *Piptadenia* sp., are shown in Figure 16a, b.)

There was no significant relationship between the subsequent relative growth rate (RGR for DBH increase) of these trees at the end of the 2007 rainy season and either irrigation intensity or leaf response. Likewise, performing the correlation separately for the species *Cordia alliodora* and *Piptadenia sp.* yielded insignificant results (Spearman rank correlation corrected for ties; P>0.4 in all cases).

Meteorological records for the study area were examined for a 31-year period (Figure 17). In only 4 years were there rainfall events in the dry season exceeding 75 mm. A very serious precipitation event (177 mm), rivaling our most intense irrigation quantity, occurred only once in 31 years.

3.4 Discussion

All trees, regardless of species, flushed more leaves as the water receipt increased. (For *Piptadenia*, flowering also increased with irrigation intensity although the sample size was quite small.) All the leaves and flowers were desiccated within a few weeks following the watering episode. The two most common species, *Cordia alliodora* and *Piptadenia*, normally initiate leaf abscission in October or November, and subsequently flush new leaves soon after the first rains of the wet season in June (Borchert 1994c; Bullock and Solis-Magallanes 1990), and this is quite typical of the non-riverine species in western Mexico.

Some flushing response to rare precipitation events appears to be normal for dry tropical forest species (Bullock and Solis-Magallanes 1990, Bullock 1986; Myers et al. 1998; Borchert 1994b). (This generalization is not valid, however, for the wet tropics where heavy applications of water by Wright and Cornejo (1990) led to leaf emergence in only 4 of 29 species.) Based on natural dry season rainfall events, it has been argued that the minimal amount of precipitation required for drought deciduous trees to flush at least some leaves is between 40-50 mm (Daubenmire 1972, Bullock and Solis-Maganalles 1990, Myers et al 1998). Our trees on this slope were more resistant to flushing; at 50 mm half the trees showed no response at all. At the other extreme, with 200 mm of water, essentially all trees showed a very strong response. Likewise, Borchert (1994b) applied 200-280 mm in Costa Rica and obtained full leaf emergence from a number of tree species.

For *Cordia alliodora* or *Piptadenia*, no false ring developed in response to any intensity of irrigation. Indeed, there was no detectable alteration in the wood anatomy of the 2007 ring for any individual. One argument would be that cambial activity occurred, but then ceased as the leaves wilted. Somehow, then, the initial 2007 dry season ring graded seamlessly into the subsequent ring developed during the 2007 wet season. This seems an unlikely explanation because both species have rings that are characterized by marked changes in wood anatomy in the autumn as the soil deficit increases. It is most probable that no reactivation of the cambium occurred at all despite the rehydration; perhaps there was simply too little time.

Judging from the 31 year record at Chamela, dry season rain storm exceeding 75 mm (and therefore causing on average a moderate degree of flushing among most trees) would occur about once each 8 years. A full canopy of newly-emerged leaves would require on the order of 200 mm, and this should occur only a few times per century. While it might be useful to fit a longer record to a probability distribution such as the Gumbel distribution, nonetheless it is clear from this study that, at least in western Mexico, an extreme response should only occur a few times during the lifetime of a tree. This rarity, coupled with the lack of a false ring response, means that both community dynamics studies (via stand reconstructions; e.g. Baker 2005) and dendroclimatological studies can proceed without worrying about any confounding effect of extreme dry season precipitation events.

Bullock (1997) found no effect of dry season rainfall on the amount of radial growth of two western Mexico tree species over the course of a decade, but this could merely have been because any effect was swamped by other factors such as inter-annual differences in rainy season total precipitation. The results presented here are more compelling evidence for the lack of a negative effect from extreme dry season events because all the trees will experience the same rainy season water receipt. We conclude that the net loss suffered by these trees during even extreme events (200 mm) must be sufficiently small that we can detect no effect on subsequent growth. Perhaps a large amount of photosynthesis occurred during the few weeks that elapsed between water receipt and subsequent desiccation.

Drought deciduous trees that produce growth rings in this area are most likely dormant throughout the dry season, with an influx of moisture at this time of year having no apparent affect on wood growth. Drought deciduous trees require an influx of water to reactivate the cambium; however, this requirement must be coupled with some other mechanism (e.g. auxin gradient) that will initiate radial growth.

Figure 12: Annual precipitation and temperature distribution at Chamela.

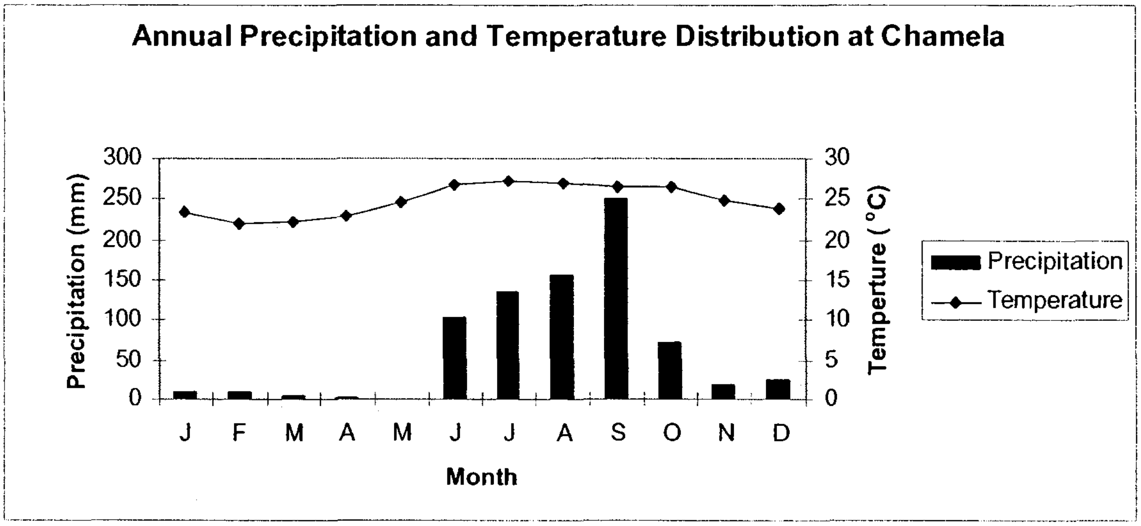


Figure 13: The leaf response to irrigation (scaled as 0 to 3 where 0=no response, 1=weak response, 2=moderate response and 3=full response: see text) as a function of water receipt.

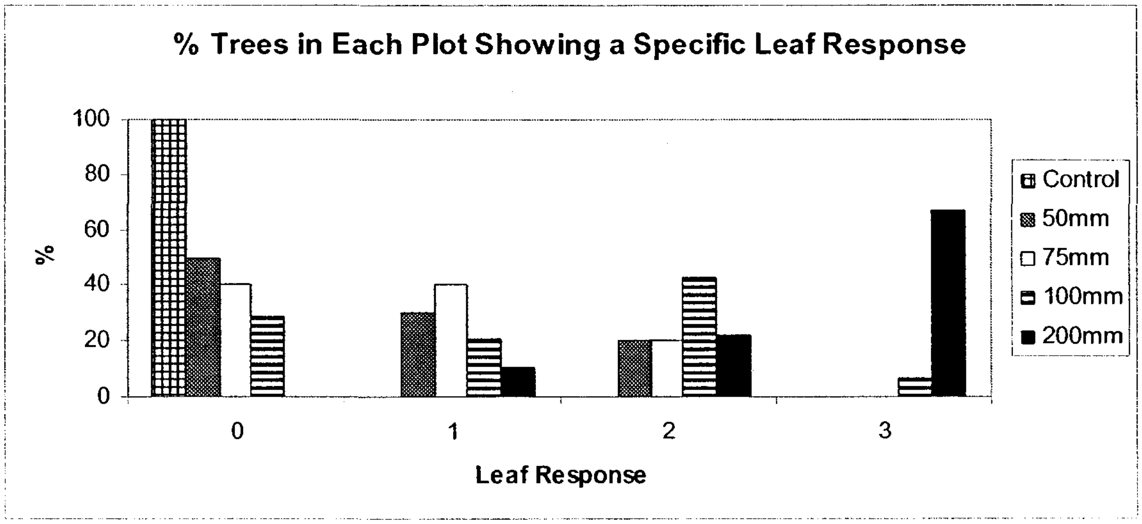


Figure 14: Flowers of *Piptadenia* produced in response to irrigation.

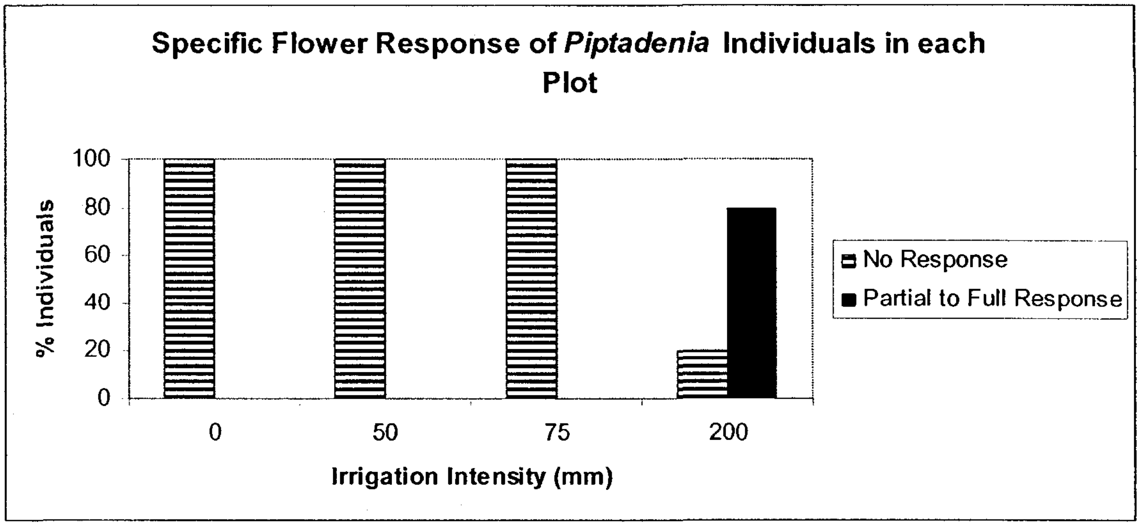


Figure 15: Scar tissue produced due to cambial wounding (arrow). The scar tissue acted as a reference point to monitor wood growth following irrigation. Any wood produced between the scar tissue and the bark was investigated for changes in anatomy and size of increment following irrigation.

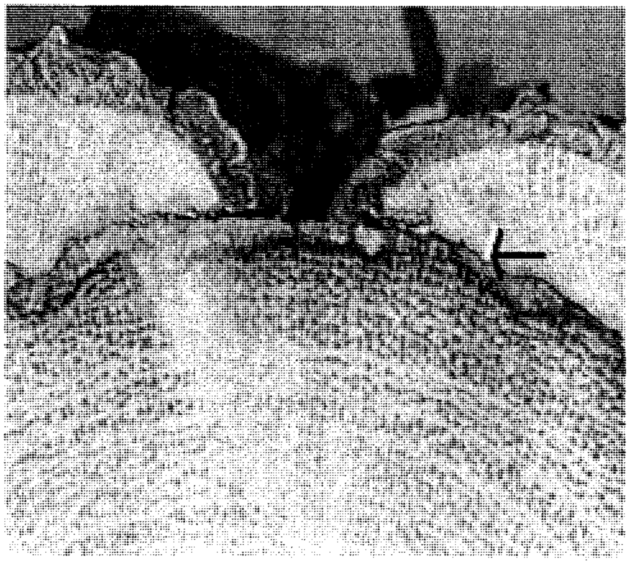
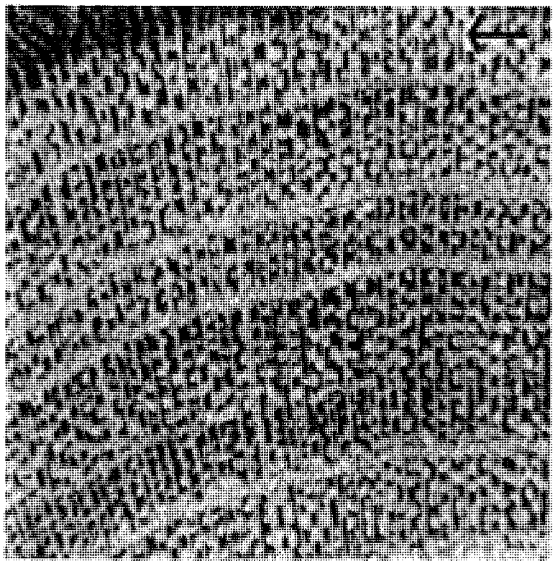
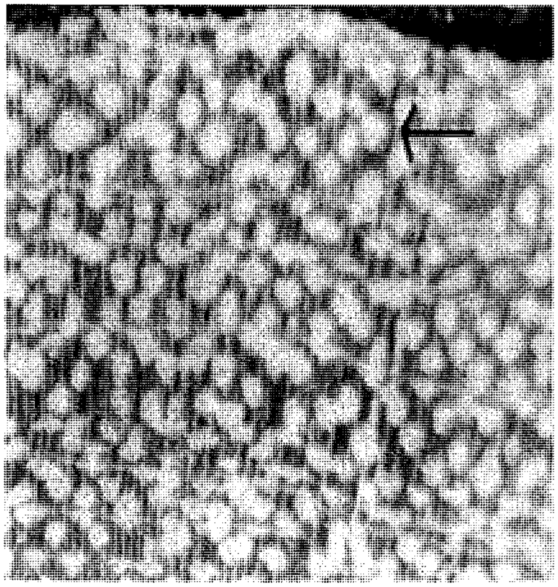


Figure 16: Cross sections of *Cordia alliodora* (a) and *Piptadenia sp.* (b) showing the lack of change in wood anatomy of the final growth ring (arrow) following irrigation.



a.



b.

Figure 17: Dry season rainfall at Chamela from 1977-2007.

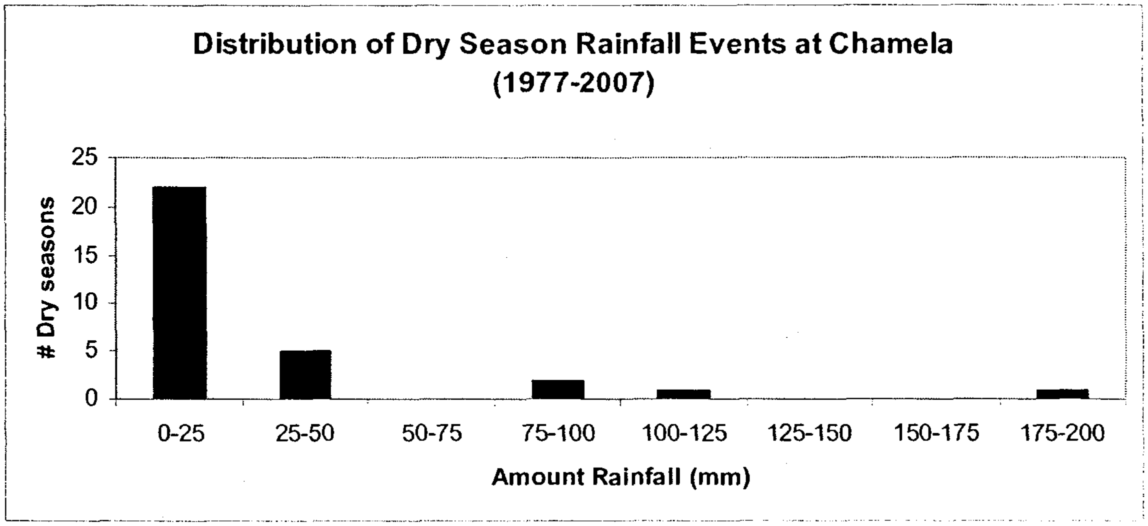


Table 4: The simulated rainfall amount, irrigation rate, tree species, and number of trees in each plot. The number of trees for each species is given in parentheses.

	Control 0 mm	**50 mm**	**75 mm**	**100 mm**	**200 mm**
Irrigation rate (L/m^2)	0	28	42	56	113
Tree species	*Cordia alliodora* (5)	*Cordia alliodora* (4)	*Cordia alliodora* (3)	*Cordia alliodora* (11)	*Cordia alliodora* (3)
	Piptadenia sp. (2)	*Piptadenia sp.* (2)	*Piptadenia sp.* (1)	*Platimicium sp.* (1)	*Piptadenia sp.* (5)
		Mimosa arenaria (1)	*Platimicium sp.* (1)	*Heliocarpus pallidus* (1)	*Acacia sp.* (1)
		Platimicium sp. (1)		*Caesearia sp.* (1)	
Total # trees/plot	7	8	5	14	9

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The following review (Appendix A) has been accepted for publication:

Hayden, B. and D. Greene (*in press*) 2008. Tropical Dry Forest Structure, Distribution, and Dynamics in *Encyclopedia of Life Support Systems*, UNESCO.

Appendix A:

TROPICAL DRY FOREST STRUCTURE, DISTRIBUTION, AND DYNAMICS

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Keywords
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Summary

Dry tropical forests are perhaps the most extensive vegetation type in the tropics, originally covering more than 40% of the tropical landmass. They are characterized by a prolonged and severe drought for several months and rainy, humid conditions for the remainder of the year. Plants within this forest type include deciduous and evergreen trees that have specialized water-retention traits such as stem-succulence to help tolerate the stress of the prolonged dry season. Except along rivers, trees are short with broad

crowns; the closed-canopy forest has few layers. Leaf fall, flowering, and dry-fruit production usually peak during the dry season. Vegetative growth is highest in the wet season, with some flowering and fleshy-fruit production also occurring then. The growth-limiting dry season means that one can often use tree growth rings to study the population dynamics of these forests. Germination is confined to the early wet season to ensure adequate water throughout the first growth stages. Diversity is high, and endemism is pronounced. Globally, dry forest has been altered to a great extent and only a small portion of the original forest remains. Human population density is greater in this ecosystem than in other tropical systems due to the more clement climate and more fertile soils. The largest threats to dry tropical forest include anthropogenic fire, livestock grazing, and the low proportion that has been conserved.

A.1. Introduction

A.1.1. Distribution and Climate

While all tropical forests tend to have at least one period in the year with lowered water availability, tropical dry forests (TDFs) are the subset where the dry season is both prolonged and severe. More generally, they can be defined as areas within the tropics where there is a drought (<30 mm of rain per month for at least four months) during the low sun period, and a rainy season of several months duration when the sun is highest in the sky and there is more than 100mm of monthly rain. The fact that the drought is in the period of minimum evapotranspiration permits a forest rather than shrub-dominated vegetation, as occurs more poleward in Mediterranean climates. Annual precipitation is in the range of 400-1700 mm. Further, a TDF is defined as having a continuous cover of trees; thus, we exclude savannas as they are too open. It is estimated that about 1 million km^2 of TDF remains today with about half of that in South America (Figure 1). Other regions with substantial areas of TDF include India and Southeast Asia, Australia, the Caribbean and Central America, and two parallel belts in Africa.

Broadly, there are two mechanisms for the development of a tropical climate regime characterized by drought in the low sun season and rain in the high sun season. On the west side of continents, the subtropical high pressure system will dominate during the low sun season bringing dry subsiding air, clear skies, and stable conditions. During the high sun season this high pressure shifts more poleward and is frequently replaced by the **Inter-tropical Convergence Zone** which is associated with convective storms. A second mechanism, more typical of the east sides of continents, is a monsoonal regime whereby winter conditions are dominated by cool, dry air drawn from a source area deep within continental interiors. In summer the flow is reversed, and now moist, warm air (the monsoon) flows in from tropical oceanic source areas. Regionally, the presence of mountains can complicate these mechanisms by inducing orographic precipitation and rain shadows.

A.1.2. Overview of Dry Forest Structure and Origin

The most distinctive characteristic of TDF is the loss of leaves by the majority of trees during the long dry season with its characteristically low relative humidity. This is especially common away from valley bottoms. In consequence, there is a pulse of biological activity concentrated in the wet season (in much the same way as activity is limited to the period when soils are thawed in the vegetation of higher latitudes). TDFs are quite different from either wet tropical forests or mid-latitude forests, and should not be regarded as transitional between those vegetation types. For one thing, the trees are only about half the size (measured as diameter or height), and heavily draped with lianas. The characteristic shape of these trees is different from mid-latitude and wet tropical forests: the crown being quite wide relative to the height. The canopy height is less homogenous, and, as one discovers when trying to walk through TDF, there is a well-developed understory of shrubs.

The origins of this vegetation type are unclear. Two reasons for the lack of knowledge are that (1) the great majority of the tree species are animal-pollinated, and therefore there is a paucity of pollen grains in lake sediments to permit delineation of past plant assemblages. Second, it is hard to discern a TDF community using macrofossils (e.g. fossilized leaves); these will be preferentially preserved in wet sites, but the characteristic genera of TDFs will be found on the interfluves while genera more typical of (or shared with) the wet tropical forests will tend to be found along water margins. For Central America, elements of the present TDF appear in the mid to late Eocene. One study used the diversification rate of the genus *Bursera,* which is a common genus in Neotropical dry forests, to argue that the TDF appeared around 25 million years ago in western Mexico, perhaps as a result of aridity associated with the most recent uplift of the Sierra Madre Occidental.

A.1.3. Organization of this review

In this review we will focus almost entirely on trees and lianas, spending little time on herbs, shrubs, and epiphytes. We begin with a discussion of the phenology of leaf emergence and abscission and corresponding changes in the stem and roots. We then examine the life history of trees, starting with flowering and ending with the growth rates of canopy trees. Having discussed "births", we turn to catastrophic deaths; that is, natural and anthropogenic disturbances. We conclude with a discussion of forest structure and diversity, as well as conservation issues.

To a great degree, what we know about TDF is based upon the forests of western Mexico and Costa Rica as this is where the two most fecund research stations—Chamela and Guanacaste—are located. In the last few years one begins to see literature that is modestly more varied in origin; especially work from Thailand and India. Nonetheless, this Neotropical bias is unavoidable in a review at this time.

A point we will repeatedly stress, with some frustration, is how little is understood about this system relative to other vegetation types. Indeed, it is perhaps the least understood terrestrial ecosystem. In contrast, tropical moist and wet forests have been much more thoroughly studied. As an example, only 3% of papers on tropical conservation are concerned with dry forests. The role of advance regeneration versus post-disturbance sexual and asexual regeneration when small gaps occur remains essentially unexamined.

Little is known about seed dispersal by animals. In particular, TDF disturbance regimes (severity, return time, size)—the agents that govern the temporal dynamics of forests elsewhere—have hardly been researched at all.

A.2. Phenology

Phenology is the response of living organisms to an annual cycle of seasonal and climatic change. In plants, this refers to vegetative (leaf, stem, and root growth) and reproductive (**anthesis**, flower development, and fruit maturation) stages that are linked to changing environmental factors. Several phenological patterns within tropical dry forest are highly dependent on the periodicity of annual rainfall, slope position, and a plant's water storage capacity. With a few exceptions, day-length appears to be relatively unimportant. Likewise, pollinator availability may play a role in the phenology of selected species, but generally water-availability is the overriding factor.

A.2.1. Leaves and stems

The dramatic decline in water availability from the wet to the dry season results in a wide variety of leaf structures and schedules ranging from strongly drought deciduous to evergreen. As soil moisture is depleted following the last heavy rains, many trees will undergo a change in water balance and resort to **leaf abscission** to avoid further water loss through transpiration. Trees that abscise their leaves and remain in a leafless state for a period of time are referred to as drought-deciduous. The timing and duration of leaf abscission varies within and between tree species due to several factors. Water availability, stored either within a tree's stem or in the soil, will affect the timing of leaf abscission. Trees with shallow root systems and no stem water storage on sites with little or no soil water available will be the first to abscise their leaves, doing so very early in the dry season. More generally, leaf fall begins at ridge-lines and descends downslope as the drought progresses. Leaf shedding temporarily increases the amount of stem water, and this often leads to an increase in stem and branch diameter. Rehydration due to leaf loss will not be enough to promote flushing in drought-deciduous trees and they will remain in a leafless state until sufficient water becomes available; that is, with the commencement of the rainy season.

Leaf flushing will occur in a synchronous fashion among **conspecific** drought deciduous trees on the same site once old leaves have been abscised and the trees become fully rehydrated with the heavy rains of the wet season. When deciduous trees flush there will be a small and temporary decrease in stem diameter as stem water is used in the production of new leaves. This decrease is generally equivalent to the increase in diameter that accompanied leaf loss. Deciduous trees with no access to soil or stem water storage in the dry season are not in a state of dormancy, but rather in a drought-induced rest period whereby they remain inactive until this period of rehydration. This is supported by research in a Costa Rican dry forest where irrigation of trees during the dry season readily induced flushing. Isolated rain showers falling within the dry season, bringing with them sufficient moisture to hydrate the tree, can also induce flushing.

Stem succulents are a deciduous group of trees within the dry forest ecosystem that, in addition to abscising their leaves, have characteristics to help them deal with the arid conditions of the dry season. The main characteristic of these plants is the high water storage capacity within the low-density wood of the stem. Water storage within the xylem of the stem acts as a buffer against seasonal drought. These species often occur on the driest sites within the forest and, regardless of their water storage abilities, abscise all their leaves early in the dry season and remain leafless for several months. Unlike other deciduous species, stem succulent species have dormant buds that need not rely on hydration to induce flushing; they do not respond to irrigation or rain showers prior to the spring equinox. This indicates that flushing for these species is triggered by the change in daylength after the spring equinox, an event occurring typically well before the first rains of the wet season. Timing the vegetative bud break so that it occurs just before the rainy season ensures a sufficient water supply to support shoot growth. There are many stem succulent species within the families Euphorbiaceae, Bombacaceae and Burserasea.

Some tree species, termed spring flushing species, are not stem succulents but nonetheless they flush their leaves between the spring equinox and the start of the rainy season. In contrast to the stem succulents, the leaf abscission period for this group is not concentrated early in the dry season and spring flushers do not remain leafless for extended periods of time. *Cassia grandis,* a spring flushing hardwood in Costa Rica, was reported to undergo bud break within a 10 day period in consecutive years; this relative constancy is the main reason to assume a daylength cue. In contrast to the majority of Neotropical tree species, most trees in Indian dry tropical forests are spring flushers. This may be due to a higher amount of water storage in the deep soils of the Indian forests which allows leaf flushing prior to the wet season.

Evergreen trees are found in the riparian zones of many TDFs and can access retreating soil water perimeters with an extensive root system. The evergreen habit is more common in Southeast Asian dry forests than in the Neotropics. Evergreen tree leaf loss tends to be concurrently balanced by the deployment of new foliage so that a constant crown mass is maintained. The highest rate of leaf exchange for evergreens occurs during the dry season. Evergreen leaves are often coriaceous (tough and leathery) or sclerophyllous, with a high mass to area ratio. These leaf types help minimize transpiration during the period of low water availability. In contrast, leaves of deciduous trees are generally mesophyllic, that is, thin and possessing a low mass to area ratio.

Some species do not fit neatly into this tripartite scheme of leaf phenological response. An interesting exception includes the species exhibiting a **reverse phenology**. These trees will flush a cohort of new leaves in the dry season and abscise their leaves during the wettest part of the year. *Jacquinia pungens* and *Forchammeria pallida* are Neotropical examples. One of the evolutionary arguments for this unusual schedule is that the behavior reduces leaf loss to herbivores by producing new foliage at a time when herbivore activity is at a minimum

A.2.2. Roots

Fine root growth, like leaf activity, closely follows the seasonal availability of water in tropical dry forest and differs among deciduous and evergreen trees. A fibrous root mass confined to the upper layers of soil is characteristic of many deciduous tree species. Deciduous trees, unlike most evergreens, will produce fine roots throughout the wet season to allow them access to even a very shallow wetting of the soil surface. The production of fine roots on an annual basis can exceed 400 grams per m^2, about double that of wetter tropical forests; indeed, the ratio of root mass to above-ground mass is far higher for TDFs than any other vegetation type. As the dry season commences, however, the upper layer of soil dries out, root growth diminishes, and subsequently there is a high rate of fine root mortality as the seasonal drought intensifies.

Evergreen trees, relying on a deeper and more extensive root system, generally maintain access to water throughout the year. Evergreens, therefore, do not show strong pulses of fine root mortality and regrowth, and are less likely to respond to shallow wetting of the soil by a brief rain.

A.3. Sexual Reproduction

A.3.1. Mating systems

In Neotropical dry forests, about 75% of tree and shrub species are self-incompatible, and thus the heavy investment in flowers and nectar rewards is a necessity. Indeed, the strong reliance on outcrossing is one of the chief causes for concern about the fate of plant populations in small forest remnants well-separated from other potential breeding partners.

An effective method for ensuring outcrossing is dioecy (each individual a single gender). Dioecious species comprise a larger fraction of the flora in TDFs than in mid-latitude forests: about 20% of tree species in the Neotropics. The fraction is far lower, however, in India.

Self-compatibility is far more common among shrubs and herbs than trees.

A.3.2. Flowering and pollination

Flower development from bud formation to anthesis is seldom a continuous process. As in the mid-latitudes, many species are proleptic, i.e. there is a period of inactivity between sexual bud differentiation and subsequent flower development. Phenologically, we can make a few generalizations about flower induction. For species with terminal inflorescences, the flowering process begins in the wet season as vegetative growth on a shoot declines and reproductive growth commences. Carbohydrates are concentrated near the reproductive bud, and hormones induce bud primordia to differentiate into sexual buds. In shoots that are undergoing indeterminate growth, vegetative growth will not be inhibited and sexual bud differentiation (leading eventually to a lateral inflorescence) will occur concurrently with vegetative growth. Terminal inflorescences begin development late in the growing season once vegetative growth has ended. Lateral inflorescences, however, can begin development earlier in the wet season.

Many months after bud differentiation has taken place, development resumes. For most species anthesis occurs with a positive water balance within the stem and this will generally happen in the dry season following leaf abscission. Leaf fall and the consequent hydration of the tree are prerequisites for flowering in many species. In both Neotropical and Paleotropical TDFs, a surprisingly large fraction of tree species flower during the dry season; in some reports (e.g. India and Costa Rica) these species represent a majority. Dry season flowers are usually much larger than rainy season flowers, and they make a fine display on an otherwise arid, leafless hillslope.

Many tree species wait for the rains of the wet season to flower. In a tropical dry forest in Ghana some flowering was reported throughout the year, with a peak occurring in the wet season and little anthesis during very dry periods. Flowers produced in the wet season are comparatively small and fewer in number than those produced in the dry season. Wet season flowering for a population is of a similar duration to that of dry season flowering. It is interesting that the bulk of tree species flowering in the wet season in Costa Rica are considered to be rare whereas those flowering in the dry season include both common and rare species.

The evergreen trees in the riparian zones generally flower in the dry season, but like rainy season flowering species, they tend to have small, inconspicuous flowers. One argument for this pattern is that a crown with full leaf deployment induces a daily water deficit within the tree, and thus these trees will not have excess water to devote to freely-transpiring, larger flowers.

Flowering among conspecifics is generally well-synchronized. The flowering period for any population is typically on the order of six weeks; continuous flowering for a period greater than four months is quite rare. Modestly asynchronous flowering can occur within same tree crown as the lower layer of leaves may experience less evaporative water loss and therefore maintain leaves for a longer period of time; this in turn, leads to later rehydration and flowering for that part of the crown.

Species that share pollinators and/or seed dispersers may stagger their flowering phenologies in time to minimize interspecific competition. Flowering schedules of species in Costa Rica tended to be sequential with relatively little overlap. In a recent study, comparing the phenology of trees from the same family (Bombacaceae) in three different Neotropical forests, differing in dry season length and intensity, it was found that the schedule of any one species changed by site so as to avoid overlap.

There is very little work on the percentage of species that engage in mass flowering episodes or the abiotic cues that might prompt the response. High irradiance clearly promotes flower bud formation (and mass flowering) in teak but few other TDF species have been studied. We know that the inter-annual **coefficient of variation** for fruit and flowers falling into litter baskets is about 4 times greater than for leaves, but careful long-term studies of individual species are almost non-existent.

As in the wet tropics, animal pollination is far more common than wind pollination. Whereas 15-30% of mid-latitude tree species are pollinated by wind, the proportion in tropical forests is as low as 2%. One author has speculated that TDF species possessing inconspicuous flowers with small pollen grains may actually be wind-pollinated, this group comprising as much as 40% of the dioecious species in western Mexico. There is no evidence for this, however, and most ecologists would assume that they are pollinated by small, unspecialized insects.

The large flowers produced in the dry season tend to be visited by long-tongued specialists: bats, hummingbirds, and certain insects. The smaller flowers produced in the wet season and along the riparian zone are more commonly visited by short-tongued insects. Generally, beetles seem to be unimportant pollinators in TDFs.

Microsatellite studies are beginning to show that animals are carrying pollen considerable distances. For example, a surprisingly large proportion of the pollen crop of mahogany (*Swietenia humulis*) in Honduras was carried >1 km. If this is at all typical, it means that fragmentation is perhaps not so detrimental for outcrossing as had been assumed; i.e., pollinators are capable of traveling farther to forage if they must.

A.3.3. Fruits and Seeds

The time of flowering for any given tree species will necessarily affect the timing of the fruiting phase. Generally, the interval between fertilization and the completion of seed maturation is about two months, with larger intervals for larger fruits.

In most TDFs, the peak community-wide fruiting period occurs just before or just after the onset of rains. There are exceptions: e.g. the trees in an Indian monsoon forest had a peak in fruit production in the late wet season. Neotropical shrubs are different from the trees: they are more likely to fruit in the wet season. As with mass flowering, we have little understanding of mass seeding events for TDF species.

Seed and fruit production is, loosely, a function of tree size. Similar to higher latitudes, size (e.g. basal area) is the single best (and certainly most easily measured) correlate of within-population crop size. Nonetheless, the percentage of the variance in seed or fruit production explained by plant size is not high: 20 to 50%.

Unlike the situation with pollination where TDFs are similar to other tropical forests in their tremendous dependence on animal vectors, seed dispersal by wind is much more common among trees in TDFs than in the wetter tropics. Indeed, the percentage of tree species that are wind dispersed approaches the norms of mid-latitude forests. Generalizing broadly, about 45% of TDF tree species have fleshy fruits and are dispersed primarily by birds. Another 40% have clear adaptations (drag-promoting fibers, lift-producing wings) for dispersal by wind. Finally, about 15% are cached by mammals or defecated by large terrestrial mammals. (This latter percentage increases or decreases with the importance of the Leguminosae in the flora). Altogether then, about 60% of the trees are animal-dispersed; in the wet tropics the figure would be closer to 90%.

The percentage of liana species that are wind-dispersed in TDFs is even larger than for trees. Likewise, this percentage is also greater than for the lianas in the wet tropics. As in higher-latitude and wet tropical forests, wind dispersal is extremely rare among shrubs or herbs except in open grass-dominated areas.

For both lianas and trees, the reliance on wind dispersal is especially pronounced for species that flower in the dry season and complete their seed maturation and abscission before the start of the rainy season. It has been argued that the lack of rain and increase in wind speed (due to the absence of leaves) favors wind dispersal of seeds. One notes that it would logically follow that wind pollination would also be favored by these conditions, but, as we saw, very few TDF species use wind to distribute their pollen.

Other modes of dispersal are quite rare in these forests. A few leguminous tree species have explosive **dehiscence**. Dispersal on water or on fur or feathers (via hooks) is almost non-existent except for a few shrubs and herbs.

Fleshy fruit are mainly produced in the wet season. As elsewhere, such fruits tend to have gaudy coloration and odoriferous compounds to signal ripeness. Tree species developing fleshy fruit in the dry season tend to be evergreen and are found along wetter valley bottoms as they require adequate moisture levels for the fruit's growth and development.

There are very few studies of seed dispersal in intact forests in TDFs; more work has been done on recruitment in clearings because of conservation concerns. These studies make it clear that wind dispersal leads to far higher recruit densities in clearings than does animal dispersal—at least up to a few hundred meters from a clearing edge. By offering perching sites, residual trees and shrubs in a clearing increase the fleshy fruited input by birds. In intact forest, we might presume (from studies in the wetter tropics) that animal dispersal is at least as effective as wind dispersal.

Seed size appears to be lower on average in TDFs than in the moist or wet tropics. In particular, there are fewer very large seeds. To some degree this may simply be a consequence of the greater number of species engaging in wind dispersal: necessarily, more massive seeds are more poorly dispersed. Quite small seeds (say, 10 mg or less) are rare in TDFs (as in the wetter tropical forests).

It has been argued that seed predators have a greater impact on TDFs than foliovores or other plant consumers. Certainly, predation is the most common form of mortality for tropical seeds, much more common than damping off (fungal attack). In a very rough way, the predator size correlates with the seed size. Small seeds are taken by insects whose larvae consume the seed from within. Seeds of medium size are consumed by small mammals, while the largest seeds are taken by the largest mammals. There are, of course, exceptions to these generalizations: e.g. the pericarps of coconuts are slowly gnawed through by squirrels. Seed predators, especially the larger mammals, may be of net benefit to a plant when acting as dispersers; that is, if some fraction of seeds fortuitously survive.

The tendency for greater predation of seeds beneath maternal crowns compared to farther away is as pronounced in TDFs as in the wetter tropics. As elsewhere, this **Janzen-Connell effect** has been seen as a selective force for enhanced dispersal capacity as well as a prime arbiter of species diversity.

Seed dispersal permits plant species to search for a suitable germination site in space; seed dormancy permits a search for a better site in time. Storage of viable seeds awaiting favorable conditions for germination can take place in the soil (a soil seedbank) or else the seeds remain on the branches, delaying abscission. This latter strategy, aerial seedbanks, does not occur in the tropics, perhaps because natural fire is too rare a disturbance.

Both wet and dry tropical forests tend to have quite transient soil seedbanks, the seeds seldom maintaining dormancy longer than a few months. Similarly, in wet tropical and mid-latitude forests, very few tree species are capable of seed dormancy extending beyond one year. Dormant seeds are typically found in the first few cm of the soil; given the short dormancy period, there is too little time for burrowing animals to inadvertently take them to greater depths. Likewise, freeze-thaw episodes cannot redistribute dormant seeds through the soil column. The number of dormant seeds per m^2 depends greatly on the time of year the sampling is done (dormant seeds are far more abundant just before the rainy season begins) and on the abundance of herbs, which are far more likely to employ extended dormancy than are trees. Reports of dormant seed abundance are among the lowest values ever recorded for any ecosystem: 50-700 per m^2.

Nonetheless, most tree species in tropical dry forests produce seeds that are capable of at least some type of dormancy that will carry them through an initially unfavorable situation. There are two major types of seed dormancy within tropical dry forests, physiological and physical. Physiological dormancy, the most prevalent type, is caused by some inhibiting mechanism in the embryo that prevents the radical (initial root) from emerging through the seed coat. Seeds of this dormancy type are permeable to water.

Seeds utilizing physical dormancy are especially common among the Leguminosae. The seed coats are initially impermeable to water, usually because of one or more layers of densely-packed palisade cells in their seed coat. There are several mechanisms that will break physical dormancy. A study conducted in an Australian dry forest highlighted the importance of "wet heat" (i.e., conditions of high temperature and humidity, as in the rainy season of tropical dry forests) in breaking seed dormancy. (Dry heat, or even fire, is also known to release seeds from physical dormancy in other vegetation types, especially chaparral, but seems to be unimportant in TDFs.) Finally, scarification of the seed coat by acid or mechanical means is capable of breaking physical dormancy in a variety of TDF tree seeds. This can occur via passage through an animal's intestinal tract as the stomach acid, or the stones in a bird's crop, abrade the seed coat.

With regard to the timing of dormancy breaking, there are essentially four categories of species. One group, maturing its fruits relatively late in the rainy season, disperses the seeds and these remain in a dormant state on the ground until the next rainy season. It would, of course, be lethal to germinate at the start of the dry season. A second group, in many systems the most common, finishes ripening during the dry season and then abscises the seeds. These deposited seeds delay germination via physiological dormancy until the rains begin. The third pattern is for seeds produced early in the rainy season to have no dormancy at all. Radicals appear within a week or two as water is readily imbibed. Species with strong physical dormancy constitute the fourth group. Despite the fact that *Acacia*, to take one example of this group, can remain dormant for several years, they usually germinate much sooner than that, or else they are eaten.

A.4. Subsequent Life History Stages

A.4.1. Germination, Establishment, and Early Herbivory

The dormancy breaking discussed above leads to a sudden pulse of recruits at the onset of the rainy season. The optimal soil temperature for germination is 20-25 C. Subsequently, more germinants are added by species that flower, mature rapidly, and abscise non-dormant seeds in the early part of the rainy season. Toward the end of autumn, germination ceases.

There is very little discussion of germinant size or seedbeds in the literature on regeneration in TDFs but there is much we can intuit. Necessarily, germinant length will be proportional to seed size, and small germinants here, as elsewhere, cannot push though a dense mass of leaves to the light above them. Further, the range of seedbeds available to plants will be quite restricted. For example, decomposition of boles is perhaps slower than in the wetter tropics but is nonetheless sufficiently quick that there is little well-rotted wood on the ground in a TDF. In other vegetation types, elevated (and therefore leaf-shedding) boles are a prime seedbed for small-seeded species in intact forests. It follows, therefore, that except where leaf-cutter ants or termites have greatly reduced its depth, leaf litter should be essentially the only seedbed available. Leaf litter depth slowly increases during the dry season, reaching a maximum at the onset of the rains. The depth of leaf litter is about five times more at the start than at the end of the wet season. This build-up is due to the fact that there is so little decomposition during the dry season. The layer of decomposing leaves is almost completely a product of the leaf abscission from the previous year, as leaf turnover rates are typically less than one year. The accumulation of litter, coupled with the rarity of rotted wood, means that small seeds will seldom germinate successfully on the forest floor of intact stands. Large clearings, especially if recently burnt, would be drier but more hospitable. This seedbed constraint explains why small seeds (seed mass <10 mg and with a subsequent above-ground germinant length <3 cm) are so rare among TDF species.

As elsewhere, within TDFs smaller dicotyledonous seeds tend to have epigeal germination while larger seeds tend to exhibit hypogeal germination. Again, as elsewhere, the ecological significance of this pattern is not understood.

The initial number of germinants at the onset of the rainy season is often quite high. In Ghana, seedling density peaked at this time, with mean woody species seedling density around 15 per m^2. Establishment of a seedling, which we will arbitrarily define as the survival beyond one dry season, is an exceedingly unlikely fate. The first-summer seedling has necessarily a shallow root system and thus faces severe water stress far earlier in the drought period than would a larger plant. That is, mortality rates during the first few months after germination (i.e., during the rainy season) may well be high but they pale next to the losses that will ensue in the first dry season when age-specific mortality typically approaches 100%. This is quite unlike any other vegetation type where mortality rates are expected to decline with plant age.

In other forest types, the limiting factor for young woody plants is normally light availability, with light receipt near the forest floor of intact stands typically <10%. In consequence, gaps in the canopy (i.e. places where one or more contiguous trees have died) are often dense with seedlings because of the enhanced light. Some species in TDFs seem to conform to this convention. A study in Ghana concluded that pioneer species could certainly germinate in intact forest but were generally absent within the forest understory because they were unable to survive in a meager light regime. The situation in many dry topical forests is, however, generally less clear than this example. This is due to the far greater water loss for seedlings in gaps than in the adjacent intact forest. This is exemplified by *Cedrela odorata,* a species found both in the wet and dry tropical forests in Costa Rica. Its survival beyond the seedling stage was limited by low light in the former forest, but was mainly limited by water in the latter forest.

Generalizing broadly across TDFs, the best site for establishment is intact forest because water will not be so limiting. The ideal site for subsequent survival and growth is, however, within a gap where height growth is typically three times greater than under intact canopies. Perhaps, some compromise such as the edge of a gap is the optimum.

Another trait that would determine the relative success rates in gaps vs intact forests would be the timing of leaf flushing for seedlings versus adults. There is, potentially, a window of opportunity in the early rainy season where both light and soil water are ample because, on average, the adults require about two months from initial flushing to full leaf deployment. Any species whose seedlings could deploy their leaves faster than the community-wide adult average would enjoy a tremendous advantage. That is, they could enjoy the high light environment of a gap (at least for a short period) while avoiding the consequent transpiration loss. However, we know of no studies of this.

Some authors in India have noted possible adaptations of seedlings to the conditions of tropical dry forest. With some species, photosynthesis may be restricted to the early morning and late evening hours. Seedling leaves also close their stomata during the day in an attempt to reduce loss of water by transpiration.

Herbivory at the establishment stage in TDFs appears to be relatively unimportant compared to other forest types. As elsewhere, herbivory becomes less of a hazard with plant age. Likewise, fungal attack, especially on germinants, seems to be negligible.

A.4.2. Asexual reproduction

Asexual reproduction by woody plants in TDF is a common way to persist through disturbance. Many species are capable of asexual reproduction in the form of coppicing: the production of shoots from dormant buds along the root collar at the base of the tree or shrub. For a small fraction of species, asexual stems (suckers) may arise from dormant buds along near-surface roots.

Asexual reproduction is more common in TDFs than in wetter forests. Some ecologists have speculated that this higher dependence on coppicing as a means of regeneration in dry rather than wet forests may be due to the higher risk and lower success rate associated with regeneration from seed.

Initially, asexual stems have much higher growth rates and lower mortality rates than sexually-derived stems because (1) they inherit a starch reserve in the roots, and (2) they need not invest in a woody root system. For example, in the first two years following a hurricane, there was 88% survival of sprouts; this is far higher than the expected survivorship of seedlings.

Sprouting capacity increases with crown damage because, presumably, the suppressing effect of auxin is decreased. For example, following a hurricane in Puerto Rico the percentage of individuals sprouting increased with the crown damage class. Harvesting, like dramatic crown damage from wind, leads to prolific sprouting. In Jamaica, 95% of all woody individuals sprouted after a clearcut. Likewise, a low intensity burn will sponsor many sprouts. In Nicaragua, 13 of 15 species examined responded to fire with sprouts and nine of these also had suckers (none had suckers without sprouts.)

While most TDF tree species appear to have the capacity to reliably sprout, there are three cases where a disturbance can reduce the rate of asexual regeneration. First, repeated disturbances (e.g. cutting followed by fire, or quickly cutting the initial sprouts responding to a first harvest) greatly reduces the density of asexual stems. Presumably, this is due to exhaustion of the starch reserve. Second, sprouting declines with fire intensity; one would guess that an intense fire directly kills the dormant buds. Finally, very young sexual stems are not capable of sprouting or suckering.

A.4.3. Subsequent Growth

In other forest types, a crucial distinction for tree species regards their tolerance of shade. Generally, shade intolerant species, relative to tolerant species, grow faster where there is ample light, have lower density wood, reach reproductive status at an earlier age (i.e. achieve some minimum size earlier than do tolerants) and have a shorter time to

senescence. Tolerant species also have slower growth in shade than in light, but, unlike the intolerants, at least some of them survive in shade. Thus, the great advantage of shade tolerance is that when a disturbance kills a canopy tree, there is potentially a bank of suppressed seedlings and taller subcanopy stems, all of them growing poorly, available to seize that vacant crown space.

Does this dichotomous suite of traits apply to TDFs? Generally yes, but there are too few studies to make us confident. A study in Mexico showed that species that are associated with disturbed habitats (treefall gaps) had both growth rates and frequencies that were correlated with light receipt. In Thailand there was a difference in stem diameter between shade intolerant and shade tolerant canopy trees of the same age, and this size difference was attributed in part to a difference in growth rate.

Shoot elongation is confined to the early wet season for many tropical deciduous trees. There is little height or diameter accretion (we ignore rehydration responses) for any deciduous species well into the rainless period. Those species which exhibit annual rings certainly show wider rings in years when the rainy season was more prolonged.

In contrast, trees with extensive root systems and access to deep soil water reserves, usually riparian evergreen trees, will show radial growth throughout much of the year. Indeed, near valley bottoms, evergreens may attain a final height more typical of the wet tropics.

Factors other than precipitation and level of shade tolerance can affect growth rates. In particular, as in other forests, slope position is related to both water availability and cation exchange capacity. Decreasing stature of trees with increasing slope position is such a common feature in TDFs that we can assume this pattern is due to geomorphic control on water and nutrient availability rather than a difference in age or species-specific growth patterns.

Herbivory rates on canopy trees are greater in TDFs than in the wetter tropics, and about double the rate in mid-latitude forests. In TDFs most of the damage to leaves occurs during the long period when they are fully developed, rather than, as in the wetter tropics, when they are first deployed. Possibly, this difference is due to a required time for foliovore populations to increase following the long drought. While drastic loss of leaves to herbivores can deleteriously affect both growth rate and subsequent fruit crop size, nonetheless, such dramatic defoliation is quite rare. Thus, unlike granivores, leaf-eating animals do not appear to play such a crucial role in dynamics.

As mentioned earlier, the mean number of flowers and fruits within a population is loosely correlated with tree size. Presumably here as elsewhere, there is a minimum size and light level required for the onset of reproductive maturity. Given that trees in the wetter tropics grow about two times faster than those in dry tropics, one speculates that the former will reach reproductive maturity about twice as soon as the latter.

A.5. Growth Rings

In the wetter tropical forests there is an on-going debate about whether growth rings, as a reflection of radial tree growth, are produced on an annual basis. Most ecologists have argued that the more constant climate in tropical regions is conducive to year-round plant growth and thus growth rings are unlikely to be annual. In contrast, dry tropical forests have a climate that, like temperate regions, alternates between predictably favorable and unfavorable growing regimes. Drought-deciduous trees show highly seasonal growth, with cambium activity confined to the wet season, and this periodicity in growth should produce annual rings. For example, *Cedrela odorata* and *Swietenia macrophylla*, both obligate deciduous trees in a Venezuelan forest with an annual dry season, show distinct annual growth rings.

Trees on sites with prolonged access to soil water (e.g. along rivers) may continue cambium activity during the dry season; these typically evergreen trees may cease cambial activity for only a short period at the end of the dry season, or not at all. Although still possible, trees exhibiting this type of growth schedule are less likely to produce distinct annual growth rings. *Capparis indica* is an evergreen species in a Costa Rican dry forest that relies on deep soil water reserves for growth and can maintain a positive water balance throughout dry periods. In spite of this access to soil water, this species produces annual growth rings. Likewise, *Pinus caribaea* is an evergreen species growing in a seasonally dry Venezuelan forest that produces distinct annual growth rings.

There are several reliable methods available to quantify the growth of dry tropical trees, including **cambial wounding** and **radiocarbon dating**. Information obtained from the growth rings of trees within tropical dry forest could aid greatly in the interpretation of stand dynamics in tropical dry forests.

A.6. Disturbance and Succession

The original extent of tropical dry forest is unknown but many have argued that much of the land covered by savanna today was dry forest in the past. If so, the extant of TDFs has been dramatically reduced. One argument is that the primary agent for this conversion was anthropogenic fire.

Paradoxically, it is widely accepted at present that natural (lightning-ignited) fire in undisturbed TDFs is quite rare, a conclusion that is rather odd considering the severity and duration of the dry season. Nonetheless, there are almost no reports of natural fires exceeding more than a few ha. As experiments are lacking, we have only speculative arguments for why natural fire is so rare. The first is that perhaps lightning itself is too uncommon; certainly, there is little convective activity during the long dry season. If true, this argument would make the TDF the only ignition-controlled terrestrial biome in the world. Nonetheless, one would expect that convective activity at the onset of the rainy season, while the fuels are still dry, could occasionally lead to a serious fire. This seems to almost never happen.

Another argument, borrowed from the wetter tropics, is that the litter under a closed canopy is too moist, even after a drought of several months. This is incorrect for the TDF; the leafless stands are too open, the relative humidity too low, and the dry season too long. The leaf litter burns readily.

A more likely explanation is that the trunks are still not sufficiently flammable despite the long drought. In particular, the stem-succulent species could release too much water vapor during the passage of the flaming front; the latent heat lost would greatly reduce the intensity of the flaming front. Deliberate burning of pastures (or of garbage at local landfills) is a common activity during the dry season, and yet the fire almost never extends more than a few meters into continuous-canopy forest nearby. This lack of propagation could well be due to stem succulence.

If natural fire is rare, how then did anthropogenic fire convert so much TDF to savanna? The conventional argument is that grazing, repeated fires, and some harvesting of trees could begin to open up the forest. This extra light would, in turn, encourage a ground layer of flammable grasses that would ensure that the next fire burned even more intensely and over a greater area. Eventually, one would be a left with scattered trees representing thick-barked species in a matrix of grass: a savanna.

As mentioned previously, asexual recruitment of trees is inversely correlated with fire intensity, and consecutive disturbances of any kind (grazing, harvesting, etc) within a short interval reduce the asexual response. Meanwhile, pre-existing seedlings are of course killed by fire; they are too young to re-sprout. Finally, grasses are notoriously strong competitors with tree seedlings where moisture is scant.

Thus, at first glance, the argument for savannas as grass-infested relics of TDFs is attractive. But there is one problem: a recent study from Oaxaca in Mexico showed that the woody species of savannas and TDFs were taxonomically quite distinct; i.e. the savanna trees are not merely a thick-barked subset of the TDF species.

Other anthropogenic disturbances include agriculture and logging. A study in Sierra Leone showed that low intensity swidden (i.e. quick abandonment followed by a long fallow interval) led to reliable coppicing and therefore little change in species composition or invasion by grasses. But a reduced fallow interval led to stump death and widespread grass encroachment.

As for logging, given that most TDF tree species can readily recruit asexually after harvesting, it follows that cutting should have a minimal effect. But the situation is complicated by the fact that logging in TDFs has tended to focus on valuable species. For example, populations of teak were greatly reduced in Burma and Thailand in the 19th and early 20th centuries. For any species high-graded in this way, there will be a dramatic reduction in propagule availability for a long time afterward. This is because, even though many harvested individuals might recruit asexually, there still will be some stumps whose sprouts are outcompeted by advance regeneration of other species. That is, for a population to persist, the asexual response needs to be augmented by a compliment of sexual recruits scattered across the local area.

Clearcuts, while more democratic as a mortality agent, can cause different problems. In particular, they act as a sieve, reducing the sexual recruitment of animal-dispersed species and those that are the least tolerant of very dry seedbeds.

Returning to natural causes of canopy tree mortality, one asks: if not fire, then what have been the main agents shaping the community dynamics? The most likely cause of death, more by default perhaps than by any certainty derived from field studies, is wind. (We should pause to explain that by death we refer to the removal of a tree or liana from the canopy. It may well be that the individual is still alive via an asexual response from buds arrayed along the basal collar or roots.) Certainly, most TDF forests are close enough to coasts to be affected by tropical cyclones. Beyond a hundred kilometers from a coast, downbursts ought to be the main way in which wind can kill canopy trees. Unhappily, there are no studies anywhere in the TDF region estimating the point probability of dying due to wind damage of any kind. We have instead regional return times. As an example, we know from diaries that most Caribbean islands have been visited by hurricanes on the order of 50 times during the last 300 years. But this of course does not tell us the average return time for canopy tree death at any one place on any one island.

A few recent hurricanes have been well-studied. Hurricane Georges caused the loss of as much as 22% of the basal area of a TDF in Puerto Rico. As has been found with wind-induced damage in other forests, the amount of crown loss increased with tree size; i.e. with exposure to the higher winds occurring aloft. Mortality was 10 times greater than the background rate. Sprouting increased by 15 times compared to the pre-hurricane rate. Similarly, on the nearby island of Guadeloupe following Hurricane Hugo, regeneration was mainly asexual but was also abetted by a persistent sapling/seedling bank. While falling trunks and branches cause considerable mortality among the latter, this advance regeneration, if tall enough, represents the most likely candidate to ascend into the canopy despite the otherwise great advantages that asexual stems enjoy.

Generalizations from studies of hurricane damage in dry tropical forests lead to three conclusions. First, basal area per area lost is around 15%. Second, bigger trees are damaged more than smaller trees. Finally, advance regeneration, where dense, can be a considerable part of the recruitment, and represent the tallest elements initially. These generalizations should also hold for forests badly damaged by other kinds of wind events; e.g. downbursts. Nonetheless, we have neither permanent plots nor stand reconstructions (using annual rings) to delineate how the next forest is constructed from the recruits we initially see following the event.

Another possible source of canopy tree mortality is catastrophic defoliation by foliovores. As mentioned, however, there is very little evidence for this. Leaf loss in TDFs is usually gradual over the rainy season, and represents only about 15-20% of leaf tissue. Further, tree death due to defoliation normally (at least with studies from higher latitudes) requires consecutive years of catastrophic leaf loss. This seems to almost never occur in the tropics.

Another natural disturbance agent is an extended drought during the rainy season. This season represents, depending on the location, only about 500 to 1500 mm of precipitation, with much of this falling in a few events. In consequence, the coefficient of variation for rainfall during the growing season is about double the value for mid-latitude forests. Speculatively, one might imagine that an extended dry period in the rainy season would lead to much leaf loss, and perhaps death, with some species more affected than others, and seedlings especially impacted. Even if the canopy trees were not killed, the leaf loss could represent a temporary release for any subcanopy trees that were more resistant to the change in water availability.

Volcanic and seismic events (and their indirect effects such as landslides) may be important in certain regions, but undoubtedly are too episodic to be important arbiters of species composition.

The size of a disturbance is of interest because the diameter of a canopy gap affects the light receipt at the forest floor. Unlike the wet tropics, there are no studies of gap size distribution in TDFs. In the only two studies using annual rings (Brazil, Thailand), there was good evidence for an extensive disturbance (cause unknown) leading to a (more or less) single cohort over a wide area.

How important is a catastrophic disturbance relative to the background canopy tree mortality? There are a few studies of background mortality (canopy tree loss over a period of several years due to many unrelated events); we have published estimates of 0.3% for Puerto Rico and 0.4% for Zambia. These are only modestly lower than typical estimates—0.5 to 1.5%—for wetter tropical forests and the deciduous broadleaf forests of higher latitudes.

Following a catastrophic disturbance, how long does it take to reach a level of structural complexity and species composition somewhat similar to the pre-disturbance stands? Clearly, this depends on growth rates and the initial turn-over in species composition. We can obtain a broad hint at the long-term dynamics by using **chronosequences**. A chronosequence in Bolivian TDF, based on time since the last swidden event, showed that basal area per area and mean height reached mature forest values by about 50 years. Species diversity matched the older adjacent forest by about the fifth year with much the same species composition. If the initial regeneration is dominated by asexual regeneration then it would not be surprising that a disturbance quickly replicates the previous composition. This fast recovery is similar to chronosequence studies from Nigeria and Zimbabwe. Likewise, following farm abandonment in a TDF in Columbia, a 56-year chronosequence derived from air photos showed that the woody species composition was beginning to approach the nearby mature forest by about the fifth decade.

Generalizing from these chronosequence studies, species composition is re-attained by about 50 years. Basal area per area and mean canopy height are, likewise, regained by about the fifth decade. If so, recovery times are much more rapid than in other systems. Further, asexual reproduction may be so reliable in this system that natural catastrophes are very unlikely to cause great changes in species composition. Post-disturbance, sexually-derived stems may well be present but they are unlikely to form the canopy; instead they contribute to the advance regeneration available for the next disturbance. Advance regeneration may play an equally large role following certain types of disturbance (e.g. hurricanes). By contrast, dynamics following intense anthropogenic fire lead to a dramatic departure from the previous composition because the clearing will be large and animal-dispersed species may have considerable problems invading the area.

A.7. Forest Structure and Diversity

Tropical dry forest exhibits many structural characteristics and a plant diversity regime that reflect the highly seasonal climate. In general, tropical dry forest is smaller in structure and less complex than wetter forests in the tropics. Primary forest on dry slopes attains a canopy height between 5 and 15 m while riparian stands are much taller. Many of the trees within this ecosystem have multiple stems due to the prevalence of asexual reproduction.

On average, tropical dry forest trees tend to have wood of higher density than trees growing in ever-wet conditions. A high cell wall to cell volume ratio, found in high density wood, is a common indicator of drought stressed plants and may provide a safe method of water conductance in a climate where drastic changes in water availability are common.

Forest strata can be divided into three levels; the continuous canopy, a discontinuous understory of shrubs and suppressed trees, and a discontinuous layer of herbs and young shrubs and trees. Lianas and vines may be found inter-connecting these strata.

Aboveground **biomass**, a reflection of moisture availability, is generally low in dry forests, with basal area per area about half that of wetter forests. Vines and lianas are an important component of this biomass, representing up to 20% of the total vegetation. Epiphytes, somewhat more common in TDFs near coasts, are not as common as climbing plants. Root buttresses are not common on dry forest trees and do not contribute considerably to aboveground biomass.

The species richness of TDFs is considerably less than that of wetter tropical forests, with the former typically containing one third to one half the number of plant species per area found in the latter. The number of tree species present in 1-3 ha of dry forest is between 35 and 90. Generally, species diversity in the tropical dry forest is well correlated with water availability. For example, in a study that examined 20 sites and accounted for over 900 species of trees and lianas within tropical dry forests throughout Mexico, variation in evapotranspiration was a significant predictor of diversity.

Although species diversity is higher in wetter tropical forests, TDFs maintain higher life-form diversity. Life forms that occur within tropical dry forest include plants exhibiting sclerophyllous and coriaceous leaf tissue as well as succulent woody plants. Cacti, a family normally associated with extremely arid climates, contribute arborescent species to Neotropical tropical dry forests.

In addition to great life form diversity, tropical dry forests are home to a high number of **endemic** plant species. This is an extremely important factor in tropical conservation. The number of endemic genera decreases along a precipitation gradient in the New World tropics: in Mexico, endemic genera range from a low of 4% in humid areas to a high of 43 % in arid regions. Chamela (Mexico) is one of the most diverse TDFs in the world due to its high proportion of endemic species.

A.8. Conservation

For the last 10,000 years, dry tropical forests have experienced more alteration by humans than wet tropical areas, especially for food production. Indeed, many of the cultivars presently used globally were first domesticated in tropical dry forests. Aside from agriculture, there are several reasons for the greater alteration of TDFs by humans, including more favorable conditions for clearance (shorter trees are easier to clear), better soils, a more clement climate for livestock, less incidence of malaria and other tropical diseases, and a winter climate that invites tourism from higher latitudes. As a consequence, human population density in TDFs is significantly higher than in the wet tropics.

With deforestation and conversion to agriculture causing serious depletions in tropical dry forest cover, this forest type remains the most threatened within tropical regions. Currently, over 1 million km2 remains of this forest type with less than 300,000 km2 protected globally.

Given the economic importance of these forests, conservation efforts were never a priority for the governments of developing nations; presently, only a small percentage of the remaining TDF is protected from exploitation in any serious way. However, the high number of endemic species within TDFs underscores the need to conserve these remnants.

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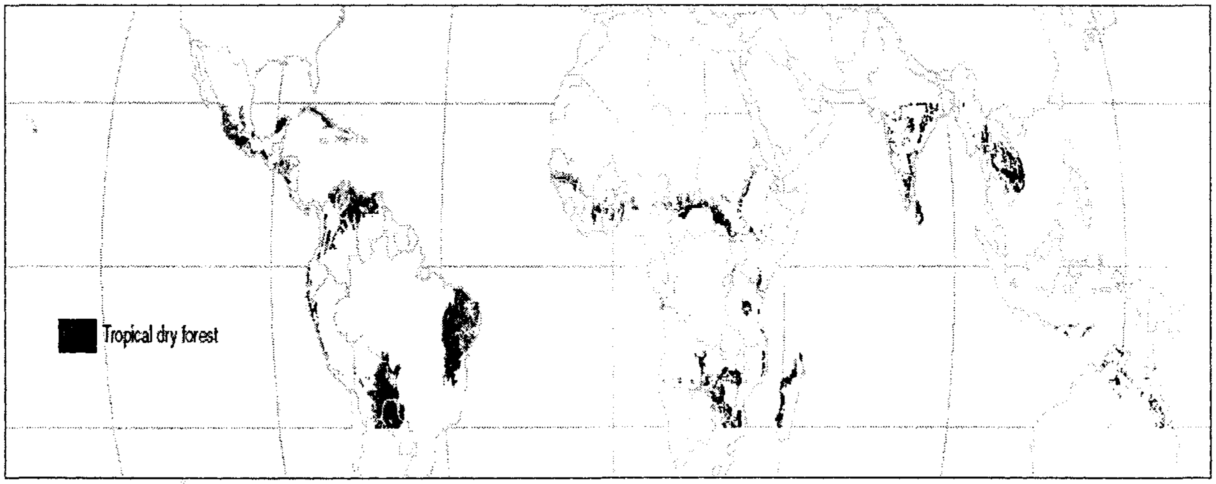
A.10. Glossary

Anthesis: The period during which a flower is open and functional.
Cambial wounding: The method of removing a small amount of bark and underlying cambium used in determining the periodicity of growth rings produced by the tree.
Chronosequence: A set of stands of different ages that are expected to represent the temporal sequence at any one site.
Coefficient of variation: A statistical measurement for comparing the relative amount of variation among two or more groups.
Conspecific: Belonging to the same species.
Dehisence: The opening at maturity of a plant structure (e.g. fruit) to release its contents.
Endemic: Constrained to a relatively small area.
Inter-tropical convergenze zone: The area of low atmospheric pressure located between the Tropics of Cancer and Capricorn, and characterized by the ascent of warm, moist air.
Janzen-Connell effect: A hypothesis that argues that the mortality of seeds and seedlings will be much higher around parents and other conspecifics than farther away. The argument has been used to explain the evolution of dispersal and the maintenance of species diversity.
Leaf abscission: The scheduled removal of leaves after weakening at the point of attachment in the petiole.
Leaf Flush: The rapid emergence of new leaves.
Radiocarbon dating: An absolute dating method based on radioactive decay of the Carbon-14 contained in organic materials.
Senescence: The post-maturity stage for perennial plants characterized by a slow deterioration of tissues and of physiological functions.

Figure 18: The extant of dry tropical forest (taken from Miles et al (2006). The map is based on 10 km cells containing at least 40% forest



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