Chapter 9
Tropical Dry Climates

Arturo Sanchez-Azofeifa, Margaret E. Kalacska, Mauricio Quesada, Kathryn E. Stoner, Jorge A. Lobo, and Pablo Arroyo-Mora

Abstract Tropical dry climates are home to unique forest ecosystems, many of which are affected by strong phenological patterns. In the Americas, tropical dry forest ecosystems account for 40 % of their original extension, and are highly affected by deforestation patterns given the fact that they are located on high fertile forests. Moreover, forest presented in these ecosystems can be considered natural barometers to understand the impact of climate change. In this chapter we first presented an overview of the ecological characteristics of forests present in tropical dry climates. We explore also linkages between environmental change, conservation biology and land-use/cover change (including the role of remote sensing) in tropical dry environments. We conclude this chapter with an overview of future research avenues to improve our knowledge of the ecological mechanisms associated to forests in tropical dry climates.

9.1 Introduction

Based on the Holdridge life zone system (Holdridge 1967) approximately 111,599,269 km^2 around the world have a climate favorable for dry forest (Leemans 1992, Fig. 9.1). Of that area, 94 % is located in the tropics. Tropical

---

A. Sanchez-Azofeifa (✉) • M.E. Kalacska
Earth and Atmospheric Sciences Department, University of Alberta, Edmonton, AB, Canada
e-mail: arturo.sanchez@ualberta.ca

M. Quesada • K.E. Stoner
Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Morelia, Mexico

J.A. Lobo
Biology Department, Universidad de Costa Rica, San Jose, Costa Rica

P. Arroyo-Mora
Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269, USA

M.D. Schwartz (ed.), *Phenology: An Integrative Environmental Science*,
DOI 10.1007/978-94-007-6925-0_9,

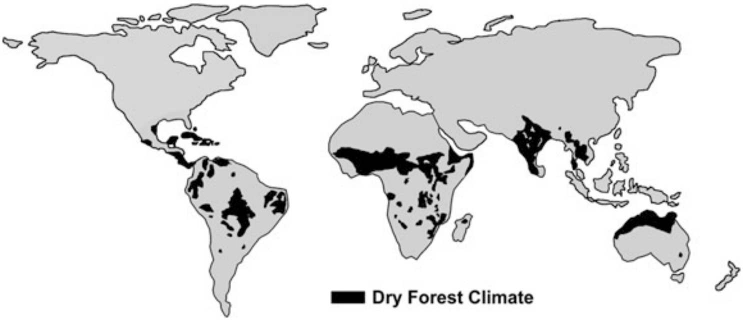

Fig. 9.1 Areas around the world with a climate favorable for supporting a dry forest ecosystem. Spatial resolution: 0.5° latitude by 0.5° longitude (Modified after Leemans 1992)

dry forests are found between the two parallels of latitude, the Tropics of Cancer and Capricorn (23°27′ N and S) where there are several months of little or no precipitation (Holdridge 1967). In general, tropical dry forests present two well-defined seasons: dry and wet season. During the dry season, usually with duration between 3 and 7 months, these forests drop between 85 and 100 % of their leaves. The dominant factor controlling leaf onset and fall is soil moisture (Janzen 1983). The degree of deciduousness is in general controlled by ecosystem composition, topography and forest age (Janzen 1983; Murphy and Lugo 1986; Lüttge 1997; Piperno and Pearsall 1998).

In general, Neotropical dry forests are less species rich than moist or wet forests. For example, 430 species of woody plants have been recorded in the wet forest of La Selva Biological Station, Costa Rica (Hartshorn and Hammel 1994), while in the dry forest of the Santa Rosa National Park, Costa Rica, 160 species (51 families) have been inventoried (Kalácska and Sánchez-Azofeifa, unpublished data). In addition, Gentry (1995) reports a range of 21–121 species (9 and 41 families) from various 0.1 ha plots around the Neotropics. However, there is more structural (e.g., wood specific gravity) and physiological (e.g., growth seasonality) diversity in the plant life forms of dry forests than in wet forests (Medina 1995).

Tropical forests that once formed a continuous habitat across Mesoamerica and some regions of the Pacific and Atlantic regions of South-America, are now found in fragmented patches (Whitmore and Sayer 1992; Heywood et al. 1994; Trejo and Dirzo 2000). Tropical deforestation is likely to affect both biotic and abiotic factors that control the phenological expression of plant communities with severe consequences to plant populations and the communities that interact or depend on them (Cascante et al. 2002; Fuchs et al. 2003). However, fortunately in certain regions of the Neotropics such as in Costa Rica, the secondary forests are in a state of regeneration through which the dry forests are also starting to recuperate (Arroyo-Mora 2002).

Both savannahs and dry forests (T-df) can co-occur in areas with the same climate, but the dry deciduous forests have a tendency to be found in areas with greater soil fertility (Ratter et al. 1973; Mooney et al. 1995). In many areas however, the occurrence of either savannah or dry forest is principally controlled by human disturbance (Maass 1995; Menaut et al. 1995).

The tropical dry forest ecosystem is one of the most fragile and least protected ecosystems in the world. Due to the favorable climatic conditions in which they are found, tropical dry forests have been heavily exploited for agriculture (Ewel 1999). Piperno and Pearsall (1998) argue that historically, tropical wet and dry forests had completely different associations with human activities. They state that the deciduous and semi-evergreen forests (especially the T-df) were the locations of the majority of the early human settlements in addition to being the home of the wild ancestors of many crop plants as well as the origin of animal husbandry. Even today, in most tropical countries, the majority of the agriculture and pasturelands are located in areas that used to be dry and moist forest. This pattern of both higher population density as well as higher intensity food production in the T-df as compared to wetter life zones may be a reflection of the historical tendency for humans to settle these areas (Piperno and Pearsall 1998). It appears that the tuberous plants that are rich in starch for human consumption seem to be more common in the seasonal forests, since the tuber is developed in part for energy storage during the dry season. The long dry season aided in burning of the vegetative cover in order to prepare the fields for agriculture (Piperno and Pearsall 1998). In addition, weeds and pests are less aggressive in the drier environments (Murphy and Lugo 1986).

Tropical dry forest phenology is an area that is still in its early stages of academic discovery, since historically more emphasis has been placed on tropical evergreen forests, especially the Amazon Basin (Lüttge 1997). Therefore, there is a need for efforts to understand tropical dry forest's phenological patterns and integrate its mechanisms at two levels: (1) In the context of conservation biology and (2) the context of land use and land cover change that are taking place on this rich agricultural frontier. In this chapter we document different aspects related to leaf phenology in the tropical dry forest ecosystem and its implications for satellite remote sensing. Emphasis is placed on presenting a description of the causes of leaf phenological change in this threatened ecosystem, and how these can be linked with conservation biology and land use/land cover change at the regional level.

9.2 Causes of Phenological Change

Several studies have indicated that the phenological expression of leaves, flowers and fruits are affected by biotic and abiotic factors. Abiotic factors such as changes in water level stored by plants (Reich and Borchert 1984; Borchert 1994, but also see Wright and Cornejo 1990; Wright 1991), seasonal variations in rainfall (Opler et al. 1976), changes in temperature (Ashton et al. 1988; Williams-Linera 1997), photoperiod (Leopold 1951; Tallak et al. 1981; van Schaik 1986), irradiance (Wright and Vanschaik 1994) or sporadic climatic events (Sakai et al. 1999), have been proposed as the main causes of leaf production or leaf abscission in tropical dry forest plants. In contrast, biotic factors, such as competition for pollinators or pollinator attraction (Robertson 1895; Janzen 1967; Gentry 1974; Stiles 1975; Appanah 1985; Murray et al. 1987; Sakai et al. 1999; Lobo et al. 2003), competition for seed dispersers, and avoidance of herbivory (Marquis 1988; Aide 1993; van Schaik et al. 1993) have been considered as the factors regulating the intensity and duration of leaf and flower production. The abiotic and biotic factors are not mutually exclusive, and it is likely that several are interacting to regulate the expression of each phenological phase.

In tropical dry forests, apart from foliage seasonality, relationships between water availability and structural and physiological characteristics such as hydraulic architecture or sensitivity to water stress produce a variety of phenological behaviors (Murphy and Lugo 1986; Bullock 1995; Holbrook et al. 1995; Lüttge 1997, among others). One of the major causes of the leaf phenological patterns (as mentioned above) in all tropical dry forest is the length of the dry season. This difference may be partly responsible for the differences in physical characteristics such as canopy height or biomass. Apart from leaf phenology, the length of the dry season and the seasonality of precipitation are also important for evolutionary adaptations of gene and seed dispersal, which are distinct in dry forests from the wet forests. In general, in dry forests most trees have conspicuous flowers and wind-dispersed seeds. Dry forests also have a lower biomass and a smaller stature than wet forests (Gentry 1995). Two other main factors that influence leaf phenological patterns are edaphic associations and topography since they determine the spatial heterogeneity of the available water (Murphy and Lugo 1995).

Water stress can vary at both regional and local scales. This variability induces a multitude of tree life forms with different leaf phenological patterns (Mooney et al. 1995). At the regional scale, the structure of the forest is greatly affected. It has been shown that as water availability decreases, so does the number of canopy stories as well as the horizontal continuity of the canopy (Murphy and Lugo 1995). Figure 9.2 compares the climate diagrams (Walter 1971) for fourteen sites from different life zones, ranging from wet to dry forests in Costa Rica as well as the dry forest in Chamela, Mexico. The mean monthly temperature (°C) and the monthly precipitation (mm) are scaled to represent the potential evapotranspiration. Dry months are represented by dotted areas, humid months by the vertical lines, and months with rain in excess of 100 mm are in solid black. Differences in the severity of the dry season as well as the pattern of the rainfall can cause the different leaf phenological patterns observed at various sites. For example, in Guanacaste, Costa Rica, Gentry (1995) estimates that 40–60 % of the tree species are deciduous whereas over 70 % are deciduous in Chamela, Mexico, where the severity of the dry season is more pronounced (Fig. 9.2).

The general response of tropical dry forest trees to the dry season is drought deciduousness where the woody plants lose between 85 and 100 % of their leaves. Some exceptions (wet season deciduous defined as inverse phenology, Fanjul and Barradas 1987) are present on dry evergreen forests and evergreen succulent plants in dry forests (Gentry 1995; Holbrook et al. 1995). Occasional anomalous rains in

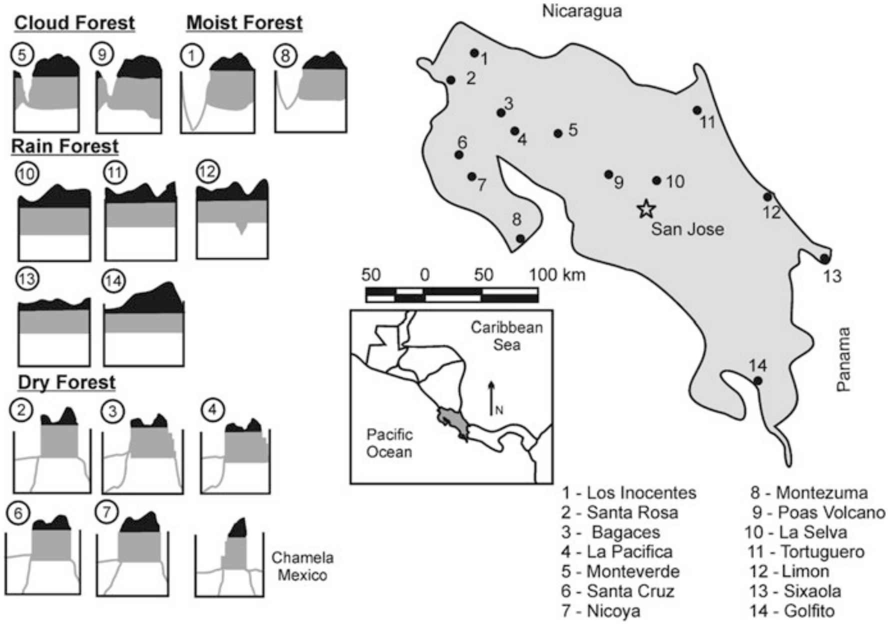

Fig. 9.2 Climate diagrams for 14 representative sites in Costa Rica and Chamela, Mexico

the dry season and drought spells in the wet season complicate this variation in resource availability. Growing periods are thus affected by the variability in flushing as it occurs in response to anomalous rains in the dry season or variation in the drying out process (Murphy and Lugo 1995). In a comparison between wet (La Selva) and dry (Comelco) sites in Costa Rica, Frankie et al. (1974) found that the forest at La Selva maintained its evergreen appearance throughout the year. However, even this wet forest experienced increased leaf flushing with the onset of the wet season. In Comelco they found that while leaf fall began as early as October, the majority of the trees lost their leaves in the dry season, with the peak in leaf fall occurring in March. Of the 113 species they inventoried at Comelco, 83 partially or completely lost their leaves and 19 were evergreen (ex. *Clusia rosea*, *Styrax argenteus*). The trees in the Riparian zones lost their leaves, but were simultaneously replaced. One species, *Lysiloma seemannii* had an unusual leaf-flushing pattern in that after it lost its leaves in the dry season, the new leaves did not appear until 1 month after the rainy season began. Certain species also brought new leaves in January and March but most of these species (for example, *Anacardium excelsum, Coccoloba padiformis*) were from the Riparian zones. In total, Frankie et al. (1974) found that 75 % of the species are affected by the seasonality of the precipitation in the dry forest, compared to 17 % in the wet forest. The timing of leaf flushing was also found to be very different: in the wet forest, most of the leaves were produced in the dry season, whereas in the dry forest the leaves were produced at the beginning of the wet season.

9.3 Phenology and Conservation Biology

In this section, we review the literature and present some of the main consequences that change or disruption of plant phenology may have on the viability of plant populations and animal communities that interact with them.

Biotic factors, such as competition for pollinators or pollinator attraction have been interpreted as important adaptive forces responsible for phenological patterns in tropical plants (Robertson 1895; Janzen 1967; Gentry 1974; Stiles 1975; Appanah 1985; Murray et al. 1987; Zimmerman et al. 1989; Sakai et al. 1999; Lobo et al. 2003). A disruption of the flowering phenological patterns (delayed or early flowering) caused by disturbance or fragmentation is likely to affect the behavior and visitation rate of pollinators. Fragmented landscapes reduce the amount of resources available, as well as appropriate areas for roosting and perching for nectarivorous bats and birds that serve as important pollinators for many tropical plant species (Feinsinger et al. 1982; Andren and Angelstam 1988; Bierregaard and Lovejoy 1989; Rolstad 1991; Saunders et al. 1991; Helversen 1993; Quesada et al. 2003). If the flowering pattern of plants that share pollinators of the same guild is displaced over time (Frankie et al. 1974; Stiles 1975; Fleming 1988), competition for the same pollinators will occur, resulting in negative consequences for the reproductive success of the plants and the ability of the pollinators to obtain resources over time. For example, in the tropical dry forest of the Chamela-Cuixmala Biosphere Reserve, Mexico, trees of the family Bombacaceae provided the main resource to the nectarivorous bats *Leptonycteris curasoae* during 8 months and *Glossophaga soricina* during 6 months. Both bat species concentrated on one bombacaceous species each month (Stoner et al. 2003). The sequential use of bombacaceuos species by these bats coincided with the flowering phenology of the tree species. These data suggest that changes in the flower phenology (e.g. reduction on the overall flower production) caused by habitat disruption may result in competition between these bat species and ultimately may result in local extinction, especially of endemic species that are common in this dry forest. A rare endemic nectarivorous bat that is only found in 4 states in Mexico, *Musonycteris harrisoni*, foraged on the bombacaceous tree *Ceiba grandiflora* during 3 months of the year (Stoner et al. 2002). Since this species has such a restricted distribution and is a specialist nectarivore, changes in flower phenology could be catastrophic for populations of this bat.

Timing of leaf flushing directly affects insect herbivores that depend upon flushing species to complete part of their life cycle (Janzen 1970, 1983; Dirzo and Dominguez 1995). Phenological changes caused by habitat loss will also disrupt the pollination patterns of many long-distance pollinators and trap-liners such as some large bees, hawkmoths, nectarivorous bats, and hummingbirds that have been shown to follow the flowering phenology of plants (Stiles 1977; Haber and Frankie 1989; Fleming et al. 1993; Frankie et al. 1997; Haber and Stevenson 2003). For example, in Costa Rica, hawkmoths regularly move from the lowland tropical dry forest to surrounding areas at higher elevations, following patterns of flowering resources (Haber and Stevenson 2003). Similarly, in México and the southwestern U.S. some nectarivorous bats have been shown to migrate following the availability of flower resources, mainly from the family Cactaceae and Agavaceae (Fleming et al. 1993).

Intra-specific variation in the frequency, duration, amplitude and synchrony of flowering by individuals also has been proposed as an important factor that affects the reproduction and the genetic structure of tropical plant populations in disturbed habitats (Murawski et al. 1990; Murawski and Hamrick 1992; Newstrom et al. 1994; Doligez and Joly 1997; Nason and Hamrick 1997). Flowering phenology directly determines the effective number of pollen donors and the density of flowering individuals, both of which affect the patterns of pollen flow between trees (Stephenson 1982; Murawski and Hamrick 1992). Plants with asynchronous flowering may experience a decrease in reproductive output, the amount of pollen, the number of pollen donors and the levels of outcrossing compared to individuals blooming during the same period. Fuchs et al. (2003) suggested that pollinator behavior is likely to change the mating patterns of *P. quinata*. This study showed that in disturbed fragmented habitats or in trees with early or late peak flowering, bat pollinators are more likely to promote selfing within trees (i.e., geitonogamy) and they have a tendency to produce singly sired fruits, whereas in undisturbed natural forests outcrossing is higher and multiple paternity is more common. The long-tongued bat (*Glossophaga soricina)*, one of the main pollinators of *P. quinata*, has been shown to adopt a territorial behavior within a single plant in disturbed isolated environments with limited resources (Lemke 1984, 1985).

The timing of fruiting during the year (e.g. early or delayed fruiting), which may be altered as a result of environmental changes (e.g. edge effects on micro-meteorological variables such as air temperature and relative humidity, soil temperature, and solar radiation) associated with habitat disturbance, may affect potential vertebrate seed dispersers that, in turn, may affect the reproductive success of the plants they disperse (Fleming and Sosa 1994). Frugivorous Old World and New World bats are known to migrate or change habitats depending on the availability of fruit resources (Eby 1991; Stoner 2001). Similarly, the abundance of temperate and altitudinal migrant birds in tropical forests is closely associated with fruit abundance (Levey et al. 1994). Furthermore, displacement of fruiting phenology of tree species that are keystone resources because they provide fruits when resources are relatively scarce, could have negative consequences on populations of birds and mammals that disperse their seeds and ultimately negative effects on recruitment of the species they disperse (Howe 1984). Seed dispersal by animals is negatively affected by deforestation and results in lower recruitment in forest fragments.

Another factor affected by forest fragmentation is seed predation. In a tropical dry forest seed predation by bruchid beetles on the tree *Samanea saman* was higher in populations of trees found in continuous forest and found to be much less in isolated trees (Janzen 1978). The bruchid beetles, *Merobruchus columbinus* and *Stator limbatus* (Bruchidae) are specific seed predators of *S. saman*. It is likely that the populations of these bruchid species are affected by density dependent factors related to the availability and fluctuation of food resources within fragments, including seeds and flowers. Another explanation is that adult bruchids have to fly greater distances to find isolated trees than trees in continuous populations. This pattern of higher seed predation in populations from continuous forest also has been observed in the dry forest tree, *Bahuinia pauletia*.

Finally, the ultimate consequences of habitat reduction and phenological disruption is a decrease in reproductive plants, increasing the negative effects of endogamy, reducing the quantity and quality of pollen, and lowering the genetic variability of the progeny (Cascante et al. 2002). This likely will affect the viability and establishment of plant populations over time.

9.4 Phenology and Land Use/Cover Change

Remote sensing data provides the possibility for an instantaneous look at a large area with the opportunity of acquiring frequent repeat imagery for the same area. This is important for phenological studies because the temporal variability of the ecosystem can be captured at large scales. In particular, it is essential to consider leaf phenology in order to correctly characterize areas of deciduous forest. Since they measure surface reflectance, optical sensors have been widely used for land cover classification and characterization. However, it must be taken into consideration that one of the greatest limitations to optical sensors is cloud cover. And in the tropics, cloud cover is especially prevalent in the wet season where leaves are on making it difficult to obtained appropriate images for remote sensing applications. In contrast, cloud free imagery is more easily acquired during the dry season, with the drawback that the majority of the trees are leafless (Arroyo-Mora 2002). In addition, vegetation studies using reflectance data have generally focused on green leaves, with both dry vegetation and non-green components being neglected in comparison (van der Meer 1999). However, in areas of deciduous forest green leaves will not always dominate the spectral signature of the forest. In the dry season, only a small fraction of the spectra will be representative of green foliage. The majority of the pixels will be representing leaf litter, bark, branches and soil in various combinations. Therefore, this temporal variability of the spectral signatures that can be extracted from imagery must be taken into consideration in such environments.

As an example, two false color composite images of the same area of dry forest surrounding the Chamela Biological Station, Mexico, were acquired during the dry (March) and wet (August) seasons from the Landsat 7 ETM + sensor (not shown). While the two images visually look completely different, more importantly, the spectral signature of the forest also changes with the seasons. This is key because many algorithms rely on spectral signatures to classify areas. If the same unsupervised classification algorithm (Isodata) is run on the two images, 180 km^2 of forest cover is extracted from the wet season image, while only 26 km^2 of land cover

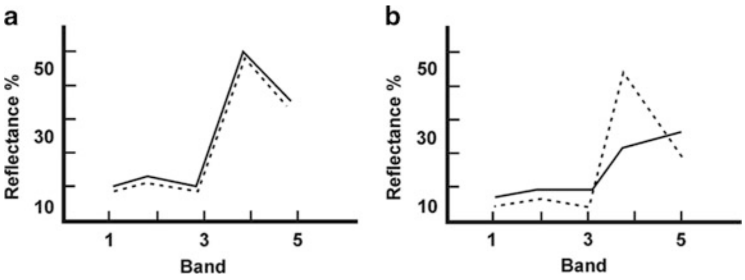

Fig. 9.3 Spectral signatures of the dry forest at the Santa Rosa National Park from 5 TM images. (**a**) Wet season (October) and (**b**) dry season (April). *Solid line* deciduous forest, *dashed line* evergreen forest

exhibits the spectral signature of forest in the dry season (Kalacska et al. 2001). In the dry season image, only the Riparian areas appear to have forest cover.

In a similar case study from the Santa Rosa National Park, Costa Rica, two images (dry season – April and wet season – October) of Landsat 5 TM were classified using an unsupervised classification into forest and non-forest classes. From the wet season image, 61 km^2 of forest were extracted, whereas from the dry season image only 18 km^2 were classified as forest (Kalacska et al. 2001). The discrepancy in the amount of forest extracted from the images in the two seasons is because dry deciduous forests (where trees lose their leaves), may seem to have the spectral signature of pasturelands or agricultural fields in the dry season (Fig. 9.3).

In the wet season, (Fig. 9.3a) the spectra for both the evergreen and deciduous components of the forest are similar. However, in the dry season (Fig. 9.3b), the spectral signature of the deciduous forest no longer resembles that of the evergreen forest. In fact, there is more than a 20 % difference in the near infrared band (band 4) between the two forest classes in the dry season. While these results are important at a local scale, their implications become more profound if regional or global scales are considered. For example, Sader and Joyce (1988) reported the total forest cover for Costa Rica as 17 %. If their map of forest distribution is examined, it can be seen that the province of Guanacaste and the Nicoya Peninsula, both with large extents of deciduous forest, are shown as almost completely non-forest. In a more recent classification of Guanacaste and the Nicoya Peninsula, using Landsat 7 ETM + imagery, Arroyo-Mora (2002) shows that the forest cover is actually 45 %. At the national scale, in the most recent remotely sensed forest cover inventory to date of the entire country of Costa Rica, Sanchez-Azofeifa and Calvo (2002) report a total forest extent 58 % greater than the other previous studies (Castro-Salazar and Arias-Murillo 1998). Seasonal changes in leaf phenology in the deciduous forest are part of the reason for those differences. Even at the spatial resolution of most global monitoring systems (1 km) significant areas of forest can be missed if only dry season images are used or if the phenological changes in leaf cover are not taken into consideration. This forest, which has been ignored by previous remote sensing analysis, is not uniform and includes different stages of succession with different levels of deciduousness

(Arroyo-Mora 2002). For example, in the recent global land cover classification from the MODIS Land Cover Classification Program, neither the area encompassing the Chamela Biological Station, Mexico nor the Santa Rosa National Park, Costa Rica is classified as forest. These complications are important not only for classification purposes, but also in many cases outputs from such data sets are used in global models like CENTURY. The calculations from such models are then further used to calculate baselines and benefits of a given policy for carbon sequestration, for example.

9.5 Final Remarks

Since so many organisms depend upon phenological patterns in tropical forests, it is crucial to document how these phenological patterns may be changed by deforestation and the resulting habitat fragmentation. In addition, studies aimed to understand shifts on phenological patterns (e.g. long terms of duration of growing season, length of dry season, and overall ecosystems productivity) are necessary to quantify the level of stress that tropical dry forests are under both climate and land-use/cover change. Because of their strong phenological patterns, these forests should be considered the number one barometer in tropical environments to quantify many important ecosystems responses to environmental change.

Future studies on phenological patterns of tropical plants should attempt to document intra-specific variation within distinct habitat types and under different levels of disturbance, in order to provide a clear understanding of ecosystem phenological response to different levels and types of disturbance. This information will be important in quantifying the effects of forest fragmentation on phenological patterns and ultimately on tropical ecosystems.

A wealth of information is available on studies conducted with remotely sensed data in both the temperate and tropical regions. And while the image processing techniques may be similar, the ground validation techniques are very different in certain aspects. The complexity (structural and temporal) of the tropical deciduous forests also requires special consideration when field data are being collected. In certain cases, for example when collecting Leaf Area Index (LAI), new sampling techniques need to be developed to account for the spatial and temporal heterogeneity of the forest. This is also the case if there are certain specific phenological patterns of interest. Both the scale of the sampling, as well as the technique should be determined by the required data. For example, biophysical parameters of the canopy such as LAI, vegetation fraction (VF) and the fraction of photosynthetically active radiation (f_{PAR}) have been successfully linked to remotely sensed data in many studies in conifer stands, temperate broad leaf forests and agricultural fields (Chen and Black 1991; Price and Bausch 1995; Chen and Cihlar 1996; Chen et al. 1997). However, similar techniques have not been as thoroughly explored in tropical dry forest environments, nor is there a clear understanding of the impact of phenology in these important biophysical variables. In addition, with the exception of a few studies such as Arroyo-Mora (2002) or Clark (2002) optical remote sensing studies in tropical environments have been predominantly conducted with either the Landsat (TM and ETM+) or AVHRR sensors. However, high spatial resolution multispectral sensors such as IKONOS (4 and 1 m spatial resolution and 4 spectral bands) and Quickbird (2 m and 60 cm spatial resolution, 4 spectral bands) have begun acquiring substantial worldwide archives and can play a key role in monitoring phenological processes in tropical dry forest environments. Also, with the introduction of ASTER (15 m spatial resolution, 14 spectral bands) data can be obtained quite economically. All three of these sensors may be used to capture detailed temporal changes in the dry deciduous forest. In addition, ALI (Advanced Land Imager) a new sensor from the EO-1 platform provides a more cost effective alternative for acquiring Landsat-type data.

Increased spectral resolution may also be an option to characterize deciduous forests from a remote sensing point of view. Hyperspectral sensors such as Hyperion (30 m spatial resolution and 220 spectral bands) or the air-borne sensor HYDICE (1 m spatial resolution and 220 bands) offer new possibilities for describing the phenological changes in the deciduous forest, but their application will be limited to the short life span of this sensor type. More small changes at the canopy level can be observed with these sensors than can be captured by multispectral sensors. These changes can be correlated to ground measurements such as chlorophyll concentrations as a function of age and complexity in order to begin modeling the seasonal changes in the ecosystem in greater detail. Hyperspectral data sets will provide a greater range of possibilities for deriving indices that may be more sensitive to the vegetation characteristics, as well as to phenological changes in dynamic environments.

References

Aide TM (1993) Patterns of leaf development and herbivory in a tropical understory community. Ecology 74:455–466

Andren H, Angelstam P (1988) Elevated predation rates as an edge effect in habitat islands – experimental-evidence. Ecology 69:544–547

Appanah S (1985) General flowering in the climax rain forests of Southeast Asia. J Trop Ecol 1:225–240

Arroyo-Mora P (2002) Forest cover assessment, Chorotega region, Costa Rica. Master's thesis, University of Alberta, Edmonton

Ashton PS, Givnish TJ, Appanah S (1988) Staggered flowering in the dipterocarpaceae – new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. Am Nat 132:44–66

Bierregaard ROJ, Lovejoy TE (1989) Effects of forest fragmentation on Amazonian understory bird communities. Acta Amaz 19:215–242

Borchert R (1994) Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology 75:1437–1449

Bullock SH (1995) Plant reproduction in neotropical dry forests. In: Mooney HA, Bullock SH, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge

Cascante A, Quesada M, Lobo JJ, Fuchs EA (2002) Effects of dry tropical forest fragmentation on the reproductive success and genetic structure of the tree *Samanea saman*. Conserv Biol 16:137–147

Castro-Salazar R, Arias-Murillo G (1998) Costa Rica: toward the sustainability of its forest resources. FONAFIFO, San Jose

Chen JM, Black TA (1991) Measuring leaf-area index of plant canopies with branch architecture. Agric For Meteorol 57:1–12

Chen JM, Cihlar J (1996) Retrieving leaf area index of boreal conifer forests using Landsat TM images. Remote Sens Environ 55:153–162

Chen JM, Rich PM, Gower ST, Norman JM, Plummer S (1997) Leaf area index of boreal forests: theory, techniques, and measurements. J Geophys Res-Atmos 102:29429–29443

Clark D (2002) Applications of 1m and 4m resolution satellite imagery to studies of tropical forest ecology, management and secondary forest detection. In: Tropical forests: past, present, future. The Association of Tropical Biology Annual Meeting, Smithsonian Tropical Research Institute

Dirzo R, Dominguez CA (1995) Plant-herbivore interactions in Mesoamerican tropical dry forests. In: Bullock SH, Mooney HA, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, New York

Doligez A, Joly HI (1997) Genetic diversity and spatial structure within a natural stand of a tropical forest tree species, Carapa procera (Meliaceae), in French Guiana. Heredity 79:72–82

Eby P (1991) Seasonal movements of gray-headed flying-foxes, *Pteropus poliocephalus* (chiroptera, pteropodidae), from 2 maternity camps in northern New South Wales. Wildl Res 18:547–559

Ewel JJ (1999) Natural systems as models for the design of sustainable systems of land use. Agrofor Syst 45:1–21

Fanjul L, Barradas VL (1987) Diurnal and seasonal-variation in the water relations of some deciduous and evergreen trees of a deciduous dry forest of the western coast of Mexico. J Appl Ecol 24:289–303

Feinsinger P, Wolfe JA, Swarm LA (1982) Island ecology – reduced hummingbird diversity and the pollination biology of plants, Trinidad and Tobago, West-Indies. Ecology 63:494–506

Fleming TH (1988) The short-tailed fruit bat: a study in plant-animal interactions. University of Chicago Press, Chicago

Fleming TH, Sosa VJ (1994) Effects of nectarivorous and frugivorous mammals on reproductive success of plants. J Mammal 75:845–851

Fleming TH, Nunez RA, Sternberg LS (1993) Seasonal changes in the diets of migrant and non-migrant nectarivorous bats as revealed by carbon stable isotope analysis. Oecologia 94:72–75

Frankie GW, Baker HG, Opler PA (1974) Comparative phenological studies of trees in tropical wet and dry forests in lowlands of Costa Rica. J Ecol 62:881–919

Frankie GW, Vinson SB, Rizzardi MA, Griswold TL, O'Keefe S, Snelling RR (1997) Diversity and abundance of bees visiting a mass flowering tree species in disturbed seasonal dry forest, Costa Rica. J Kans Entomol Soc 70:281–296

Fuchs EJ, Lobo JA, Quesada M (2003) Effects of forest fragmentation and flowering phenology on the reproductive success and mating patterns of the tropical dry forest tree *Pachira quinata*. Conserv Biol 17:149–157

Gentry AH (1974) Flowering phenology and diversity in tropical Bignoniaceae. Biotropica 6:5

Gentry AH (1995) Diversity and floristic composition of neotropical dry forests. In: Bullock SH, Mooney HA, Medina F (eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge

Haber WA, Frankie GW (1989) A tropical hawkmoth community: Costa Rican dry forest Sphingidae. Biotropica 21:17

Haber WA, Stevenson R (2003) Diversity, migration, and conservation of butterflies in northern Costa Rica. University of California Press, Berkeley

Hartshorn GS, Hammel BE (1994) Vegetation types and floristic patterns. In: McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS (eds) La Selva: ecology and natural history of a neotropical rain forest. The University of Chicago Press, Chicago

Helversen OV (1993) Adaptations of flowers to the pollination by glossophaginae bats. In: Barthlott W (ed) Animal-plant interactions in tropical environments. Alexander Koenig Museum, Bonn

Heywood VH, Mace GM, May RM, Stuart SN (1994) Uncertainties in extinction rates. Nature 368:105–105

Holbrook NM, Witbeck JL, Mooney HA (1995) Drought responses of neotropical dry forest trees. In: Mooney HA, Bullock SH, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge

Holdridge L (1967) Life zone ecology. Tropical Science Centre, San Jose

Howe HF (1984) Implications of seed dispersal by animals for tropical reserve management. Biol Conserv 30:261–281

Janzen DH (1967) Synchronization of sexual reproduction of trees within dry season in Central America. Evolution 21:620–637

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. Am Nat 104:501–528

Janzen DH (1978) Reduction of seed predation on *Bauhinia pauletia* (Leguminosae) through habitat destruction in a Costa Rican deciduous forest. Brenesia 14–15:325–335

Janzen DH (1983) Costa Rica natural history. University of Chicago Press, Chicago

Kalacska M, SánchezAzofeifa GA, Rivard B, Arroyo-Mora P, Hall R, Zhang J, Dutchak K (2001) Implications of phenological changes in the extraction of Mesoamerican Tropical Dry Forests through remote sensing: a case study from Costa Rica and Mexico. Proceedings of the international conference, Wageningin University, Wageningin

Leemans R (1992) Global Holdridge life zone classifications. Digital Raster Data on a 0.5 degree Cartesian orthonormal geodetic (lat/long) 360x720 grid. In Global ecosystems database version 2.0, NOAA National Geophysical Data Center, Boulder

Lemke TO (1984) Foraging ecology of the long-nosed bat, *Glossophaga soricina*, with respect to resource availability. Ecology 65:538–548

Lemke TO (1985) Pollen carrying by the nectar-feeding bat Glossophaga Soricina in a suburban environment. Biotropica 17:107–111

Leopold AC (1951) Photoperiodism in plants. Q Rev Biol 26:247–263

Levey DJ, Moermond TC, Denslow JS (1994) Frugivory: an overview. In: McDade L, Bawa KS, Hespenheide HA, Hartshorn G (eds) La Selva: ecology and natural history of a neotropical rain forest. University of Chicago Press, Chicago

Lobo JA, Quesada M, Stoner KE, Fuchs EJ, Herrerias-Diego Y, Rojas J, Saborio G (2003) Factors affecting phenological patterns of bombacaceous trees in seasonal forests in Costa Rica and Mexico. Am J Bot 90:1054–1063

Lüttge U (1997) Physiological ecology of tropical plants. Springer, Heidelberg

Maass JM (1995) Conversion of tropical dry forest to pasture and agriculture. In: Mooney HA, Bullock SH, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge

Marquis RJ (1988) Phenological variation in the neotropical understory shrub *Piper arieianum* – causes and consequences. Ecology 69:1552–1565

Medina E (1995) Diversity of life forms of higher plants in neotropical dry forests. In: Mooney HA, Bullock SH, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge

Menaut J, Lepage M, Abbadie L (1995) Savannas, woodlands and dry forests in Africa. In: Mooney HA, Bullock SH, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge

Mooney HA, Bullock SH, Medina E (1995) Introduction. In: Bullock SH, Mooney HA, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, New York, pp 1–8

Murawski DA, Hamrick JL (1992) Mating system and phenology of *Ceiba pentandra* (Bombacaceae) in central Panama. J Hered 83:401–404

Murawski DA, Hamrick JL, Hubbell SP, Foster RB (1990) Mating systems of 2 Bombacaceous trees of a neotropical moist forest. Oecologia 82:501–506

Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. Annu Rev Ecol Syst 17:67–88

Murphy PG, Lugo AE (1995) Dry forests of Central America and the Caribbean. In: Mooney HA, Bullock SH, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge

Murray KG, Feinsinger P, Busby WH, Linhart YB, Beach JH, Kinsman S (1987) Evaluation of character displacement among plants in 2 tropical pollination guilds. Ecology 68:1283–1293

Nason JD, Hamrick JL (1997) Reproductive and genetic consequences of forest fragmentation: two case studies of neotropical canopy trees. J Hered 88:264–276

Newstrom LE, Frankie GW, Baker HG, Colwell RK (1994) Diversity of long-term flowering patterns. In: McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS (eds) La Selva: ecology and natural history of a neotropical rain forest. The University of Chicago Press, Chicago

Opler PA, Frankie GW, Baker HG (1976) Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. J Biogeogr 3:231–236

Piperno DR, Pearsall DM (1998) Origins of agriculture in the lowland neotropics. Academic, New York

Price JC, Bausch WC (1995) Leaf-area index estimation from visible and near-infrared reflectance data. Remote Sens Environ 52:55–65

Quesada M, Stoner KE, Rosas-Guerrero V, Palacios-Guevara C, Lobo JA (2003) Effects of habitat disruption on the activity of nectarivorous bats (Chiroptera: Phyllostomidae) in a dry tropical forest: implications for the reproductive success of the neotropical tree *Ceiba grandiflora*. Oecologia 135:400–406

Ratter JA, Richards PW, Argent G, Gifford DR (1973) Observations on vegetation of northeastern Mato Grosso. Woody vegetation types of Xavantina Cachimbo expedition area. Philos Trans R Soc B 266:449–492

Reich PB, Borchert R (1984) Water-stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. J Ecol 72:61–74

Robertson C (1895) The philosophy of flower seasons and the phaenological relations of the entomophilous flora and the anthophilous insect fauna. Am Nat 29:97–117

Rolstad J (1991) Consequences of forest fragmentation for the dynamics of bird populations – conceptual issues and the evidence. Biol J Linn Soc 42:149–163

Sader SA, Joyce AT (1988) Deforestation rates and trends in Costa Rica, 1940 to 1983. Biotropica 20:11–19

Sakai S, Momose K, Yumoto T, Nagamitsu T, Nagamasu H, Hamid AA, Nakashizuka T (1999) Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. Am J Bot 86:1414–1436

Sanchez-Azofeifa GA, Calvo J (2002) Final report on the extent to Costa Rica forest cover: year 2002:20

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation – a review. Conserv Biol 5:18–32

Stephenson AG (1982) The role of the extrafloral nectaries of *Catalpa speciosa* in limiting herbivory and increasing fruit production. Ecology 63:663–669

Stiles FG (1975) Ecology, flowering phenology, and hummingbird pollination of some Costa Rican Heliconia species. Ecology 56:285–301

Stiles FG (1977) Coadapted competitors – flowering seasons of hummingbird-pollinated plants in a tropical forest. Science 198:1177–1178

Stoner KE (2001) Differential habitat use and reproductive patterns of frugivorous bats in tropical dry forest of northwestern Costa Rica. Can J Zool 79:1626–1633

Stoner KE, Quesada M, Rosas-Guerrero V, Lobo JA (2002) Effects of forest fragmentation on the Colima long-nosed bat (*Musonycteris harrisoni*) foraging in tropical dry forest of Jalisco, Mexico. Biotropica 34:462–467

Stoner KE, Salazar KAO, Fernandez RCR, Quesada M (2003) Population dynamics, reproduction, and diet of the lesser long-nosed bat (*Leptonycteris curasoae*) in Jalisco, Mexico: implications for conservation. Biodivers Conserv 12:357–373

Trejo I, Dirzo R (2000) Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico. Biol Conserv 94:133–142

Tallak NE, Muller WH (1981) Phenology of the drought deciduous shrub Lotus scoparius: climatic controls and adaptive significance. Ecol Monogr 51:323–341

van der Meer F (1999) Physical principals of optical remote sensing. In: Stein A, van der Meer F, Gorte B (eds) Spatial statistics for remote sensing – Remote sensing and digital image processing, vol 1. Kluwer Academic Publishers, New York

van Schaik CP (1986) Phenological changes in a Sumatran rain forest Indonesia. J Trop Ecol 2:327–348

van Schaik CP, Terborgh JW, Wright SJ (1993) The phenology of tropical forests – adaptive significance and consequences for primary consumers. Annu Rev Ecol Syst 24:353–377

Walter H (1971) Ecology of tropical and subtropical vegetation. Oliver and Boyd, Edinburgh

Whitmore TC, Sayer JA (1992) Deforestation and species extinction in tropical moist forests. In: Whitmore TC, Sayer JA (eds) Tropical deforestation and species extinction. Chapman & Hall, London

Williams-Linera G (1997) Phenology of deciduous and broadleaved-evergreen tree species in a Mexican tropical lower montane forest. Glob Ecol Biogeogr Lett 6:115–127

Wright SJ (1991) Seasonal drought and the phenology of understory shrubs in a tropical moist forest. Ecology 72:1643–1657

Wright SJ, Cornejo FH (1990) Seasonal drought and leaf fall in a tropical forest. Ecology 71:1165–1175

Wright SJ, Vanschaik CP (1994) Light and the phenology of tropical trees. Am Nat 143:192–199

Zimmerman JK, Roubik DW, Ackerman JD (1989) Asynchronous phenologies of a neotropical orchid and its euglossine bee pollinator. Ecology 70:1192–1195