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Edited by Stephen H. Bullock, Harold A. Mooney and Ernesto Medina

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## 1

## Introduction

HAROLD A. MOONEY, STEPHEN H. BULLOCK  
& ERNESTO MEDINA

Most ecosystems of the tropical and subtropical latitudes are seasonally stressed by drought (Schimper, 1898; Köppen, 1931; Murphy & Lugo, 1986). Research on population and ecosystems dynamics, and conservation efforts, however, rarely address these ecosystems, but rather concentrate on what is usually understood as tropical wet forest or rain forest. There has been enormous scientific and public attention directed toward documenting the effects of destruction of wet forests on soil fertility, biotic diversity, and global biogeochemistry. These concerns are certainly justified as the rates of forest and species loss accelerate. In contrast, relatively little attention has been given to forests subject to prolonged dry seasons (Ridpath & Corbett, 1985), and to their changing status. Degradation and conversion of 'dry forest' is far more advanced than that of wet forest: only a small fraction remains intact (Murphy & Lugo, Chapter 2; Sampaio, Chapter 3; Menaut, Lepage & Abbadie, Chapter 4; Rundel & Boonpragob, Chapter 5; Gentry, Chapter 7), and the area explicitly conserved is hardly perceptible. This is unfortunate because the forests with prolonged annual drought occupy more area than wet forests, have been of greater use to humans, and are still poorly known over most of their distribution.

The extent of forest in the drier tropics, and even its character, are difficult subjects for debate and research. Particularly in Africa, India and Asia, the relations between savannas, woodlands and dry forests (of various leaf habits) are notoriously complex (Furley, Proctor & Ratter, 1992). Savannas and their degradation are certainly priority subjects of tropical and global ecology, but as with wet forests, they are well studied compared with dry forests. The present volume reviews the available information on tropical forests under climates with highly seasonal rainfall, often making contrasts with wet and moist forests, as a stimulus

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to furthering our understanding and hence management of these systems. Several regional overviews are provided. Largely in accord with the available literature, the coverage by discipline and by site is uneven; thus any synthesis is preliminary. The principal regional bias is to the neotropics, or portions thereof, except for systems ecology.

What are tropical dry forests? In the simplest terms they are forests occurring in the tropical regions where there are several months of severe, even absolute, drought. Drought stress has been indexed mostly by precipitation and temperature (representing evaporation), for the purposes of correlating physiological and phenological patterns with climate and of mapping the distribution of dry forests. The fundamental variable of soil moisture has been sparsely documented, and this substantially hinders intersite comparisons, because soil physical characteristics as well as topography take on great importance in drier forests as determinants of spatial heterogeneity in water availability. Drought normals also are affected by other factors, such as rainfall intensity, cloudiness, continentality, latitude and elevation. The response in terms of leaf habit is predominantly drought-deciduousness, but there are extensive dry evergreen forests, and a noticeable increase of evergreen and succulent plants in very dry deciduous forests.

Reviews of the distribution and structure of dry forests in northern Latin America, Africa and Thailand make clear that the only unifying characteristic of the dry forest climate is the strong seasonality of the rainfall distribution (Murphy & Lugo, Chapter 2; Sampaio, Chapter 3; Menaut *et al.*, Chapter 4; Rundel & Boonpragob, Chapter 5). Differences in rainfall amount, and the average duration of the rainy season, may account for the large differences in canopy height, total biomass, and productivity found among forests.

Seasonally dry forests and savannas occur under the same climatic conditions. While the former are essentially tree-dominated systems, the savannas never have a continuous tree canopy and are characterized by the presence of a xeromorphic, fire-tolerant grass layer. Separation of seasonal forests and savannas under little-disturbed environmental conditions is possible on the basis of the fertility status of the soil. Deciduous dry forests are found on soils of significantly higher fertility than savannas (Ratter *et al.*, 1973; Furley, Ratter & Gifford, 1988). Sarmiento (1992) developed a simple model based on the number of months with water deficit and soil fertility which allows the separation of evergreen forests, deciduous forests, and seasonal savanna systems in South America. However, in most places the balance between forest and

savanna is regulated by human intervention and the fire regime (Menaut *et al.*, Chapter 4; Rundel & Boonpragob, Chapter 5). Agriculture and grazing have greatly decreased the extent of neotropical deciduous forests, converting them to exotic grasslands of one or a few exotic species. Deforestation and frequent burning lead to nutrient impoverishment and soil loss, among other biological, physical and geochemical changes (Maass, Chapter 17).

Neotropical dry forests are generally less species-rich than moister forests in terms of plants and vertebrates (Gentry, Chapter 7; Ceballos, Chapter 8), but the most diverse dry forests are not the wettest ones. Centers of diversity and endemism are strikingly not equatorial but nearer to the tropics, in western México and southeast Bolivia. The geography of species diversity in arthropod taxa remains poorly known. Diversity of plant life-forms appears to be greater in dry than in wet forests (Medina, Chapter 9). Diversity of life forms is both structural (wood specific gravity, plant habit) and physiological (photosynthetic types, water relations, growth seasonality). Adaptations for reproduction are not peculiar in terms of sexuality or compatibility (Bullock, Chapter 11), but the spectrum of mechanisms of gene and seed dispersal is distinct: conspicuous flowers and wind-dispersed seeds are relatively more frequent in trees of drier forests. Among animals, physiological adaptations have not been widely studied, but evidence from mammals suggests no distinctive features of dry forest species.

Dry forest elements have been recorded for the Mid to Late Eocene in Panamá, probably growing in edaphically controlled habitats within an otherwise mesic environment (Graham & Dilcher, Chapter 6). These elements appear to have increased in diversity throughout the Tertiary. In the southern United States tropical dry forest developed in the Mid Eocene but disappeared later in response to increasingly cooler climates and other factors. Unfortunately, the critical expanse of México lacks study.

Leaf water relations and gas exchange characteristics do not seem to differ markedly from those of plants of wetter regions (Holbrook, Whitbeck & Mooney, Chapter 10). Interactions between water availability and structural and physiological characteristics such as rooting depth, stem water storage, hydraulic architecture, and sensitivity to water stress lead to a wide variety of phenological behaviors. The relationship of reproductive to vegetative phenology and to water availability depends on life form, with trees and other high water-storage plants showing the most diversity (Bullock, Chapter 11). However, as the

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duration of soil water deficit increases flowering periods are shorter and more synchronous within and among species. Leaf damage by insects is higher in deciduous than in evergreen species (Dirzo & Domínguez, Chapter 12), but folivory is intense only at the beginning of the rainy season. Levels of folivory can be severe in some cases, and can strongly affect reproduction, but the majority of trees lose less than 20% of leaf area.

The responses of the forest as a system to seasonal droughts are analysed in this volume in relation to biomass distribution, nutrient cycling, dynamics of belowground processes (both fine root and microbiological dynamics) and the emission of nitrogen-containing gases (Martínez-Yrizar, Chapter 13; Jaramillo & Sanford, Chapter 14; Cuevas, Chapter 15; Matson & Vitousek, Chapter 16). Dry forests have consistently lower biomass than wetter forests, because their production of organic matter is limited by the length of the growing season and their stature is smaller. These forests in general allocate larger fractions of photosynthates to development of underground biomass than wetter forests. On the basis of nutrient use-efficiency estimates these forests appear not to be especially nutrient limited, and as in wetter forests, phosphorus use-efficiency is the highest among the nutrients studied. All biological activity in the underground system is strongly limited by water availability and interactions with carbon and nutrient availability. Synchronization between activity of decomposers and fine root production, at the beginning of the rainy season, seems essential for an efficient balance between nutrient uptake by the plants and nutrient immobilization in microbial biomass. Nitrification and  $N_2O$  fluxes are related to soil moisture, but are high only at the beginning of the wet season. Conversion of forest to maize or pasture apparently does not affect gas fluxes much, except where accompanied by fertilization.

The array of oscillating phenomena is not only impressive but complex. Activation of the soil microbiota leads to rapid cascades of decomposition of above- and belowground litter produced during the previous growing season, and consequently, fluxes of gases derived from soil respiration. There is some evidence that decomposition rates are grossly unequal between species (Singh, 1969; Malaisse *et al.*, 1975; Martínez-Yrizar, 1982), so that system behavior may depend on species composition. A simplistic view of water supply driving plant development must be adapted to the notoriously diverse patterns of plant development present in dry forests, particularly if we expect to understand or predict the effects of minor and major climatic variations.

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## INTRODUCTION

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Progress has been made towards general models (Holbrook *et al.*, Chapter 10), but wide testing is needed. Drivers of some important developmental events, such as secondary growth, internal nutrient and energy fluxes, and meristem differentiation are not well known. The phenology of other organisms not subject to rapid dehydration is poorly known. Activity of insects generally is greater in the rainy season, but some groups are less seasonal than others, e.g. bark, seed and pollen feeders vs folivores.

Dry forest is also characterized by the occurrence of phenomena determined by sudden increases and by slow reductions in resource availability. These are driven by pulses in water availability, determined by the principal seasons, as well as by anomalous rains in the dry seasons and frequent drought spells in the rainy season. Some phenomena might be entrained by photoperiod (Peacock & McMillan, 1965; Stubblebine, Langenheim & Lincoln, 1978), but cues of moisture and temperature may be most common.

Relative to wet forests, efforts at modeling ecosystem interactions of dry forests are scarce (Bandhu *et al.*, 1973), because many important processes and their geographic variations are not well understood. For example, there is no general consensus on the importance of different nutrient cycling mechanisms, or even basic information on aboveground respiration. Also, crucial animal groups have not been studied in all major regions. Moreover, despite much work on the dynamic relationship between herbaceous and woody vegetation, there is no scheme for the internal dynamics of dry forest comparable to 'gap' theories in wetter forests.

The possibility of modeling water-limited tropical deciduous forest by analogy with temperature-limited northern deciduous forests has not received much attention. In fact, inherent flaws in the analogy are not difficult to find. In the tropics, water stress varies at very local and regional scales; among other consequences, there are typically several tree life-forms at any site, and the frequency of different leaf habits varies greatly among sites. Growing periods in the tropics may vary greatly between years due to flushing in response to anomalous rain in the dry season, or variations in the rate of drying out. This also applies to decomposers in the soil. Shade is less important with lower precipitation because forest stature is reduced. Fully hydrated long-lived organisms probably experience large losses in carbohydrate and fat reserves during prolonged dry periods, due to high temperatures. Also, the activity of many animal species – phytophagous, pollinating, and predacious – is not

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in phase with precipitation. These and other problems are recognizable, although poorly studied; but to direct new research efforts discussions of modeling will be useful. A general need is for more attention to inter-annual variations, rather than 'typical' yearly cycles, because they probably dominate population and system properties.

Tropical dry forests have been exploited in several ways. One is the extraction of a variety of plant and animal products, for local use or international commerce (Saravia-Toledo, 1985; Sampaio, Chapter 3; Bye, Chapter 18), sometimes transforming the structure of the forest or leading to local extinction of useful species. Local inhabitants use a variety of forest species for purposes of consumption, medicine or fuel, and some make a living commercializing such resources. Medicinal products are important where traditional knowledge of the flora is profound (Arenas, 1987; Schmeda-Hirschmann, 1993; Bye, Chapter 18). Control of land use by external economies, e.g. export markets for meat, timber or charcoal, has rapidly transformed large regions (Schofield & Bucher, 1986). The effective agents of such change are not only technologies of steel: patterns of herbivory and seed dispersal may also be crucial (Saravia-Toledo & Del Castillo, 1988). These forests also have been annihilated to be replaced by herbaceous, succulent or tree crops, or pastures (Sprague, Hanna & Chappell, 1978; Maass, Chapter 17). The progress of integrated plans for a rational and sustainable use of dry forest (e.g. Eiten & Goodland, 1979; Bucher & Schofield, 1981; Hardesty, 1988) awaits review.

We may conclude that within the tropics there are resource gradients affecting, among other things, moisture availability. Temporal limitations on development by moisture availability are widespread, and the resulting dry forest ecosystems are intrinsically complex and varied. These ecosystems are not so outstanding for their species diversity as for their organization, and response to stress and disturbance. Alas, this evolutionary milieu is fast disappearing from the Earth. If we are interested in preserving the world's biodiversity, for direct exploitation or insurance against the unknowns of global change, this exceptionally endangered portion of the tropics deserves its own research priority, more conservative management, and adequate preservation.

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## 2

## Dry forests of Central America and the Caribbean

PETER G. MURPHY &amp; ARIEL E. LUGO

## Introduction

Holdridge (1947, 1967) developed a bioclimatic classification system by which the world's terrestrial biota may be categorized into approximately 120 life zones, each distinguished by climatic parameters that coincide with particular vegetational characteristics. Approximately 68 life zones are in the tropics and subtropics, of which 30 are dominated by forest of various types. Lugo, Schmidt & Brown (1981) estimated that 28 tropical and subtropical forested life zones are represented in Central America and the Caribbean, and 13 are found on the islands of the Caribbean. Despite this diversity, approximately half of the vegetation of Central America and the Caribbean is within the dry forest life zone (*sensu* Holdridge, 1967).

Dry forests are not infrequently referred to as deciduous forests, but the degree of deciduousness varies greatly (see below). Not all dry forests are conspicuously deciduous, and not all deciduous forests are dry forest. By Holdridge's criteria, tropical and subtropical dry forests are found in frost-free areas where mean annual biotemperature (a special calculation that reduces the effects of extreme temperatures) is above 17 °C, annual rainfall ranges from 250 to 2000 mm, and the ratio of potential evapotranspiration to precipitation is greater than one, to a maximum value of two. By these criteria, 49% ( $8.2 \times 10^5$  km<sup>2</sup>) of the vegetation of Central America and the Caribbean is considered dry forest (Brown & Lugo, 1980). Africa has the most dry forest ( $16.5 \times 10^6$  km<sup>2</sup>; 73% of the continent's vegetation); worldwide, about 42% of all intratropical vegetation is dry forest. Global patterns in dry forest distribution and overall ecological characteristics relative to wetter tropical and subtropical forest ecosystems were reviewed by Murphy & Lugo (1986a).

In the general literature, many different names have been applied to

Holdridge's dry forest and adjoining life zones. The names tend to emphasize different features: overall water limitation (e.g. dry or sub-humid forest); seasonality (e.g. seasonal wet or seasonal drought forest); foliage longevity (e.g. evergreen, semievergreen, semideciduous or deciduous forest); vegetation structure (e.g. forest, woodland or thicket); substrate (e.g. limestone or alluvial forest); or some combination of these (e.g. dry limestone forest). Some of the equivalencies in nomenclature among forest classification systems have been reviewed previously (Rzedowski, 1978; Hartshorn, 1988). Hartshorn (1988) grouped related life zones into major vegetation types. For example, the designation lowland subhumid forest encompasses tropical dry forest, subtropical dry forest, and subtropical thorn forest life zones. Included in the 'low mountains' subhumid forest category are subtropical thorn woodland, subtropical dry forest, and subtropical lower montane dry forest.

Beard (1955) classified tropical American vegetation types based on their structural characteristics and primary environmental determinants. His system includes associations (floristic groupings), formations (physiognomic groupings, e.g. 'deciduous seasonal forest'), and formation series (habitat groupings, e.g. 'montane formations'). Of particular relevance to this review are his seasonal formation series and his dry evergreen formation series. The former consists of five formations, ranging from evergreen seasonal forest on the moister sites to cactus scrub on the driest; the intermediate formations constitute semi-evergreen seasonal forest, deciduous seasonal forest, and thorn woodland. Among the formations of this series, the number of tree stories, the horizontal continuity of each story, and other aspects of forest structure are presumed to decrease in a regular fashion as annual moisture supply decreases and seasonality of rainfall increases. The five formations of Beard's dry evergreen formation series include, from most to least developed, dry rain forest, dry evergreen forest, dry evergreen woodland, dry evergreen thicket, and evergreen bushland. In this formation series, edaphic factors (e.g. porous white sands), as well as annual rainfall, are responsible for the differences in forest structure among formations.

Beard's approach, particularly as reflected in his diagrammatic profiles of formation series, brings emphasis to the fact that all of these vegetation units occur as segments of continua along various environmental gradients, rather than as distinct, easily defined entities. This becomes apparent in attempting to condense the literature on the broad array of tropical and subtropical dry forest ecosystems (see Rundel & Boonpragob, Chapter 5). For these reasons, we use the term dry forest in