RESPONSES OF TROPICAL TREES TO RAINFALL SEASONALITY AND ITS LONG-TERM CHANGES

ROLF BORCHERT

Department of Biochemistry, Cell and Molecular Biology, University of Kansas, Lawrence, KS 66045-2106, U.S.A.

Abstract. Seasonality and physiognomy of tropical forests are mainly determined by the amount of annual rainfall and its seasonal distribution. Climatic change scenarios predict that global warming will result in reduced annual rainfall and longer dry seasons for some, but not all, tropical rainforests. Tropical trees can reduce the impact of seasonal drought by adaptive mechanisms such as leaf shedding or stem succulence and by utilization of soil water reserves, which enable the maintenance of an evergreen canopy during periods of low rainfall. Correlations between climate and responses of tropical trees are therefore poor and the responses of tropical rainforests to climatic changes are hard to predict. Predicted climate change is unlikely to affect the physiognomy of rainforests with high annual rainfall and low seasonality. Seasonal evergreen forests which depend on the use of soil water reserves will be replaced by more drought-tolerant semideciduous forests, once rainfall becomes insufficient to replenish soil water reserves regularly. As the limits of drought tolerance of tropical rainforests are not known, rate and extent of future changes cannot be predicted.

1. Climate and Tropical Rainforests

Periods of low rainfall, during which evapotranspiration exceeds precipitation and soil water available to plants declines, constitute the principal climatic constraint in tropical lowland forests with minimal variation in temperature. Minima of annual rainfall affect the degree of deciduousness and hence the physiognomy of tropical forests. Seasonal variation in rainfall controls the annual cycle of development (phenology) comprising shoot growth (flushing), flowering and leaf fall in individual trees (Borchert, 1994a,b) and synchronizes tree phenology within forests to some degree (Figure 1). Annual development of individual trees is quite asynchronous in aseasonal rainforests, where temperature and rainfall only rarely decline to suboptimal levels. Although year-to-year variation in the growth rates of many trees (Clark and Clark, 1994) and irregular, supraannual peaks in flowering or fruit set (Hartshorn, 1992; Corlett and LaFrankie, 1998) indicate the effect of interannual climatic variation in these forests, the specific climatic causes of such events have been rarely identified and their irregularity makes them unpredictable. Climate change scenarios predict that global warming is unlikely to alter the climate of aseasonal tropical rainforests significantly, but will result in declining annual rainfall and prolonged seasonal drought in parts of the equatorial tropics covered by seasonal rainforests, especially in Amazonia (Hulme and Viner, 1998). The following assessment of the potential effects of climate changes on phenology and physiognomy, geographic distribution and species composition will be therefore
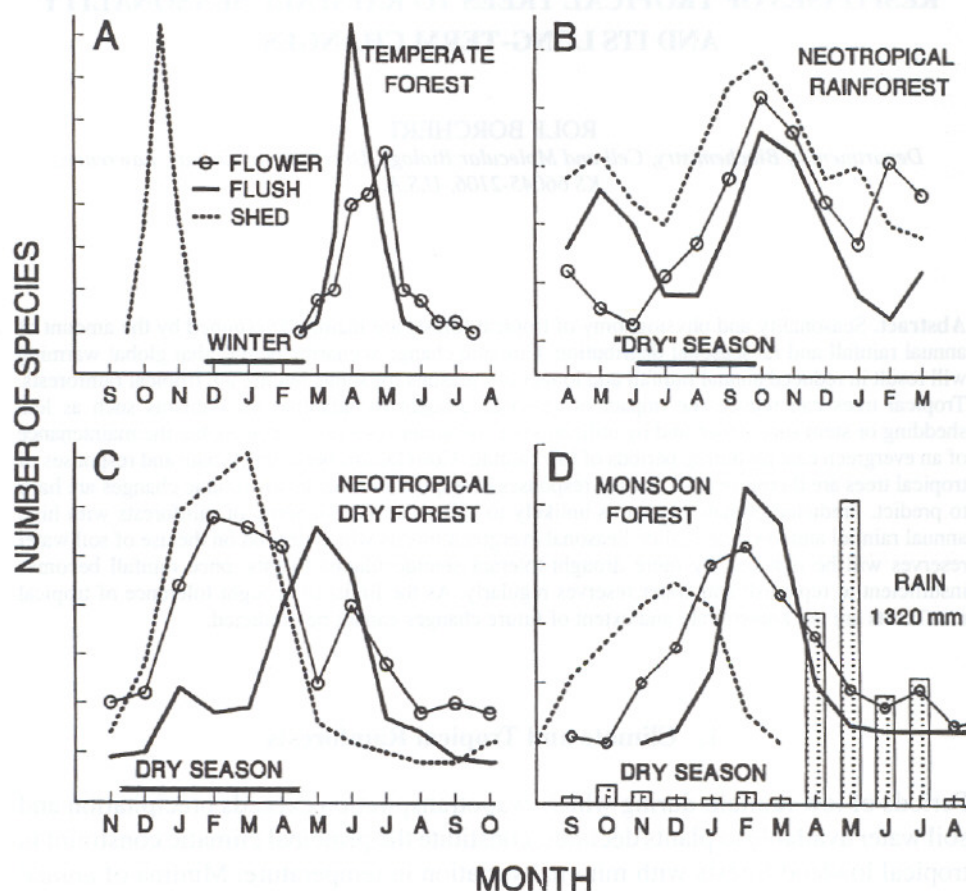
Figure 1. Seasonal development of broadleafed trees in a cold-temperate forest (A), a neotropical rain forest in French Guiana with a short, moderate dry season (B), and in dry forests with a long and severe dry season in Costa Rica (C) and India (D). The sequence of months on the x-axis was chosen such that periods of seasonal climatic stress (horizontal bars) coincide in all graphs. Data from Mori et al. (1982) (B), Frankie et al. (1974) (C) and Troup (1921) (D).

restricted to seasonal rainforests. As long as the ecophysiological mechanisms linking climatic inputs and tree responses are not well understood, predictions must be based on observed correlations between climatic variation and plant responses (Woodward, 1987). For example, the well established, strong correlations between temporal and spatial variation in temperature and the responses of cold-temperate trees constitute the basis for inferring paleoclimatic change from changes in distribution and species composition of fossil plant communities and for predicting the effects of global warming on temperate forests (Woodward, 1987, 1992; Webb, 1992).

Recent studies have shown that responses of tropical trees to seasonal drought are more complex than tree responses to low temperature, because the impact of

drought is generally mitigated by soil water reserves and a variety of drought-avoidance mechanisms in trees (Borchert, 1994a; Nepstad et al., 1994). Many tree responses are therefore not well correlated with climate and the effects of climatic change are hard to predict (Corlett and LaFrankie, 1998). In the following analysis, variation in phenology and distribution of tropical trees observed along small- and large-scale gradients in annual rainfall and the severity of seasonal drought will be used to illustrate the complex effects of rainfall on tropical forests.

2. Tropical Climate and Tree Phenology

Tropical rain forests are evergreen, i.e., canopy density remains high throughout the year, even though most individual trees exchange leaves annually and many canopy trees are deciduous for brief periods (Nepstad et al., 1994, 1995). With increasing length and intensity of the dry season the degree of deciduousness increases. Tropical trees generally exchange leaves during the dry season, and many trees flower and flush during 5–7 months of severe seasonal drought, which therefore does not arrest tree development as completely as seasonal cold does in cold-temperate forests (Figure 1B–D). Peaks of phenological events are usually broad (Figure 1B–D), because in marked contrast to cold-temperate forests (Figure 1A) the phenology of individual species within tropical forests is not well synchronized by climatic seasonality.

Within-species variability of phenology as a function of gradual increases in seasonal drought is illustrated by *Erythrina poeppigiana* and *Tabebuia rosea* growing along an altitudinal gradient at the Pacific slope of Costa Rica (Figure 2; Borchert, 1980, 1991). Both species display the same developmental sequence, leaf shedding > flowering > flushing, but in *Erythrina* the short-lived, mesic leaves are exchanged twice a year, whereas the scleromorphic leaves of *Tabebuia* are replaced annually. The timing of consecutive developmental stages varies strongly with altitudinal variation in climate. At higher elevations, where seasonal drought is moderate, leaf exchange, accompanied by flowering, is rapid (Figure 2A, B, E) and the phenology corresponds to that observed in rain forests (Figure 1B). Increasing seasonal water stress at lower elevations accelerates leaf shedding and delays flushing (Figure 2A–D, E–H), i.e., trees remain leafless for progressively longer periods, as commonly observed in dry forests (Figure 1C, D). Similar variation in seasonal development is observed among conspecific trees growing at wet and dry microsites at the same elevation, i.e., under the same set of climatic conditions (Figure 2B, C). Like many other tropical trees, these species thus tolerate a wide range of seasonal drought and their phenology, specifically the degree of deciduousness, varies widely with microsite and the severity of seasonal drought. The phenology of individual trees and of tree communities is thus not well correlated with climatic seasonality (Figures 1, 2).
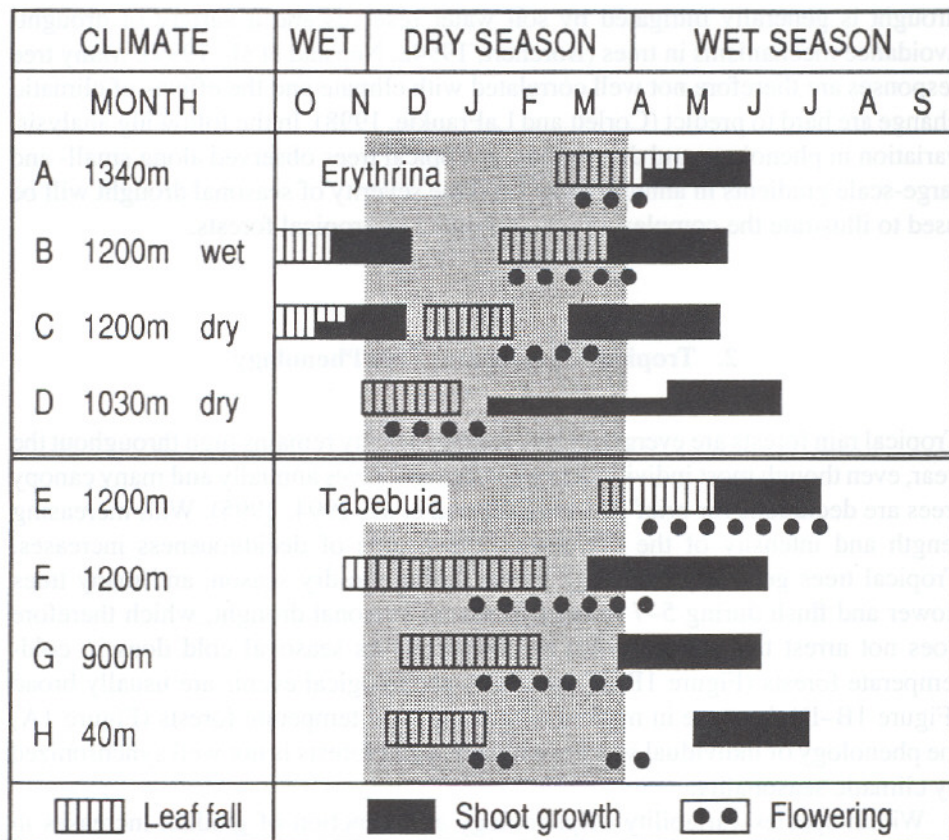
Figure 2. Variation in phenology among trees of *Erythrina poeppigiana* and *Tabebuia rosea* growing along an altitudinal gradient of increasing seasonal drought along the Pacific slope of Costa Rica. Both species are evergreen (A) or leaf exchanging (E) at higher elevations, where seasonal drought is moderate, but deciduous at lower elevations with marked seasonal drought (D, H). After flushing, trees were in full leaf until leaf fall (redrawn from Borchert, 1991).

Seasonal variation in tree water status should constitute the causal link between climatic seasonality and phenology. The temporal relations between rainfall, tree water status and tree development were therefore analyzed in a tropical semideciduous forest in Costa Rica, where mean annual rainfall has been near 1300 mm during the last decade and less than 10% of annual precipitation falls during the 6-months-long dry season (Figure 4A; compare Figure 1D; Borchert, 1994a). Observed phenological patterns range from drought-deciduous to brevideciduous or evergreen trees which exchange leaves and flower during the dry season (Figure 1C). Within four weeks after the last major rainfall, the upper soil layers dry out and tree water balance becomes negative in all trees, as indicated by declining stem water potential (Ψ_{stem}; Figure 3A, E). In many trees, elimination of water loss by leaf shedding in combination with absorption of water from the subsoil enables
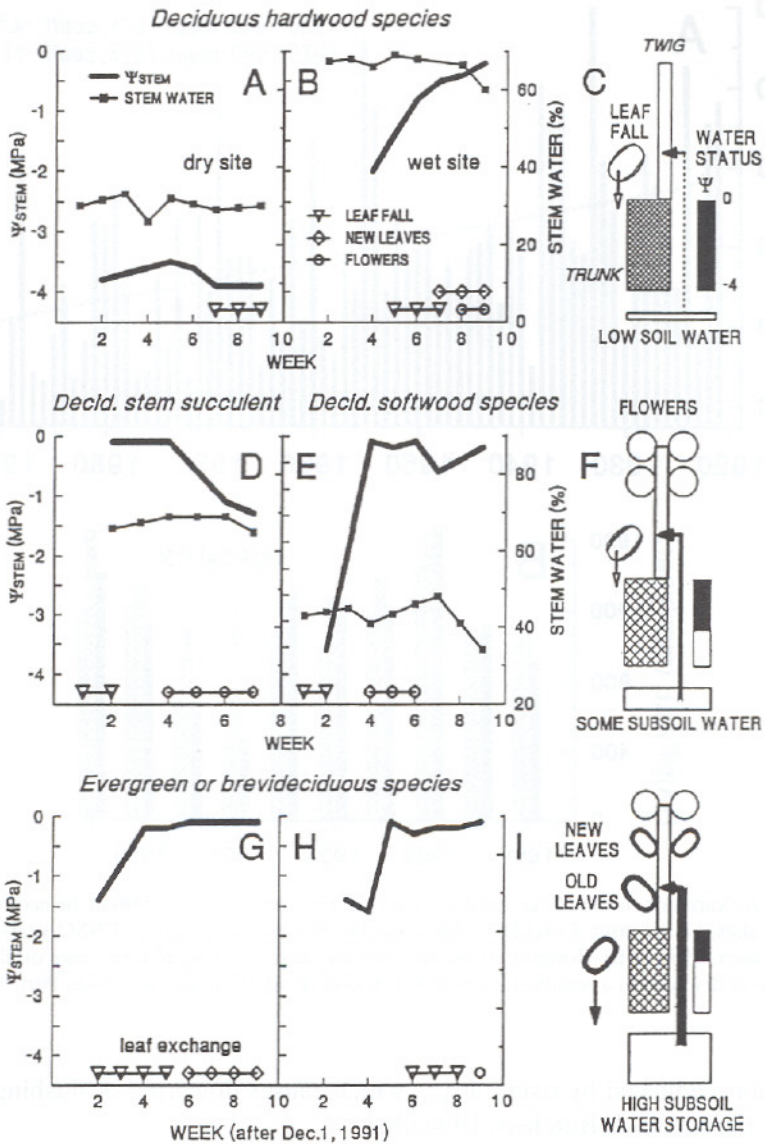
Figure 3. Effect of soil water availability on the temporal correlations between water status and phenology in dry forest trees of different functional types during the early dry season in Guanacaste, Costa Rica. Tree water status is indicated by water potential (thick curves in graphs, gauges in diagrams) and stem water. Phenological events (leaf shedding, flowering, flushing) are described above the x-axis of graphs and on 'twigs' in diagrams. Diagrams illustrate the effect of increasing soil water availability (C to I) on the trees' ability to rehydrate during the dry season (thickness of arrows) and to flower or flush during the dry season. A–C – Deciduous hardwood species (*Apeiba tibourbou*) growing at a dry (A, C) and a moist site (B). D – Deciduous stem-succulent lightwood species (*Bombacopsis quinatum*) at a dry site. E, F – Deciduous softwood species (*Myrospermum frutescens*) at a dry savanna site. G–I – Leaf-exchanging, brevideciduous softwood species at moist sites (*Thouinidium decandrum, Cassia grandis*). Redrawn from Borchert (1994a).
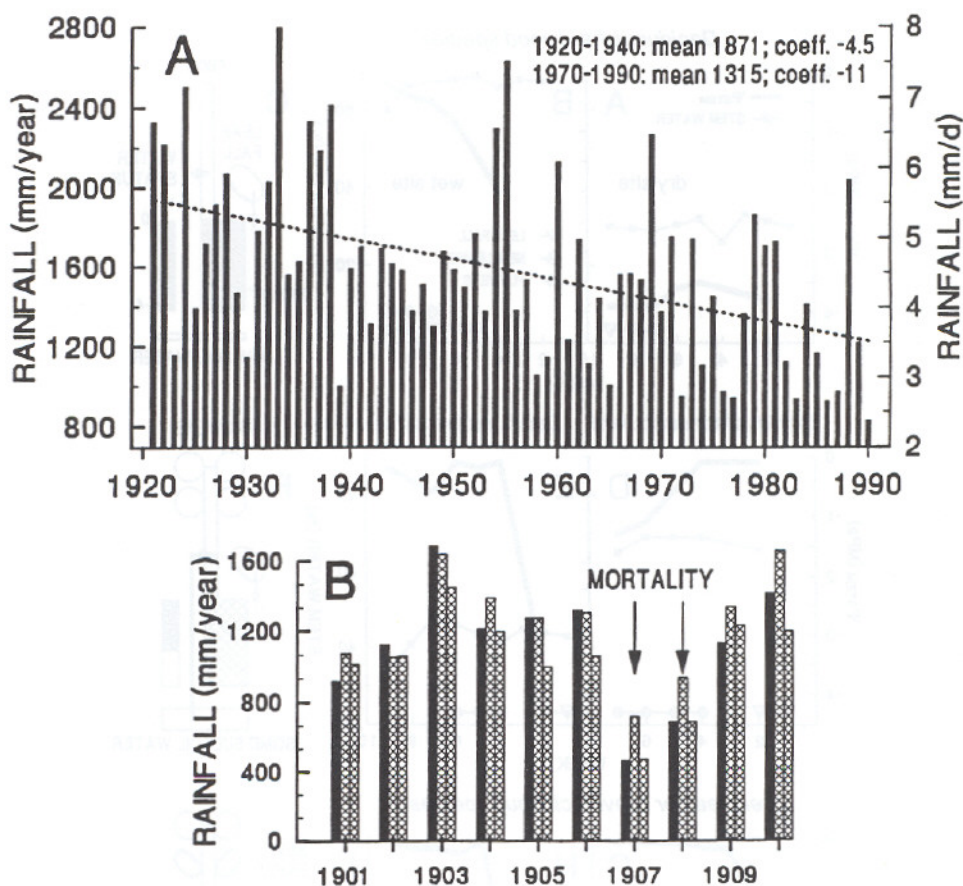
Figure 4. (A) Variation in annual rainfall and its decline between 1920 and 1990 in the neotropical dry forest of Cañas, Guanacaste, Costa Rica. Most rainfall minima occur during ENSO years (redrawn from Hagnauer, 1993). (B) Mortality of *Shorea robusta* caused by consecutive years of abnormally low rainfall at dry sites in a semideciduous forest in Uttar Pradesh, India (data from Puri, 1969).

rehydration, indicated by rising Ψ_{stem}, which causes flowering or flushing during drought (Figure 3E–I; Borchert, 1994a,b).

Within the dry forest biome, the degree of desiccation and subsequent changes in tree water status and tree development during the dry season vary widely with site water availability and functional tree type. Tree species cluster into a number of functional types, characterized by specific combinations of phenology, seasonal changes in water status, and structural features affecting tree water relations. Trees of different functional types are found mainly or exclusively at certain microsites, and the diversity of phenological patterns thus appears to be strongly correlated with species distribution (Borchert, 1994a). In dry upland forest with low soil water reserves, deciduous hardwood species desiccate strongly (low values of Ψ_{stem} and stem water content (SW)) and shed their leaves during early drought

(Figure 3A, C). They remain inactive for the remainder of the dry season until they rehydrate, flush and flower after the first heavy rains (Borchert, 1994c). At moist sites, such trees may become functionally evergreen, i.e., they rehydrate during leaf shedding (high Ψ_{stem}, SW) and flush and flower during the dry season (Figure 3B). At dry upland sites shallow-rooted, deciduous, stem-succulent lightwood species with high trunk water storage (>120% dry weight) maintain a high Ψ_{stem} and SW while shedding their mesic leaves and flowering during early drought (Figure 3D). Widely spaced, deep-rooted deciduous softwood species in dry upland savannas desiccate moderately and use residual subsoil moisture to rehydrate and flower after shedding their leaves (Figure 3E, F). Evergreen or brevideciduous species are confined to moist lowland sites where roots have access to the water table. Trees dehydrate only moderately during early drought, rehydrate before leaf shedding and then flower and exchange their coriaceous, drought-resistant leaves at various times during the dry season (Figure 3G–I). Similarly, in a semideciduous forest in Panama, shallow-rooted species are deciduous, whereas deep-rooted species with access to subsoil water reserves remain well hydrated and retain leaves throughout the dry season (Jackson et al., 1995).

Use of subsoil water reserves to avoid severe drought stress constitutes the ecophysiological basis for maintaining the evergreen habit in seasonally dry tropical forests (Figures 1B; 3I). Within semi-deciduous forests subject to the same rainfall regime, phenology thus varies widely with local variation in subsoil water reserves and with interspecific variation in drought avoidance or resistance. Climatic seasonality and tree phenology are not well correlated, because water storage in the subsoil or in tree trunks buffers trees against the impact of seasonal drought (Figures 1–3).

3. Climate and Distribution of Tropical Forest Types and Tree Species

Evapotranspiration in tropical lowland rainforests averages 3.5–4 mm/d or 1300–1500 mm/year (Shuttleworth, 1988) and most tropical rainforests occur where average annual rainfall is well above 1500 mm (Hulme and Viner, 1998). The deciduousness of tropical forests generally increases with declining annual rainfall and increasing duration of the dry season, but most information on the relations between climate and the distribution of physiognomic forest types, such as Walter's correlations between rainfall, length of the dry season and forest types in India (Houston, 1994, Figure 14.8) or the Holdridge classification of world life zones (Hartshorn, 1992), is anecdotal. There are many different, yet to be classified forest communities within tropical rainforests (Hartshorn, 1992), and forest physiognomy cannot be predicted reliably from the amount and seasonal distribution of rainfall. For example, it is not well understood why reduction in average rainfall by only 180 mm, from 1830 to 1650 mm, causes the transition from tall, evergreen rain forest in SE Amazonia to the physiognomically and floristically different, low, ever-

green Cerrado to its South (Rawitscher, 1948; Nepstad et al., 1994). Whereas most forests with annual precipitation of 1200–1500 mm and a prolonged dry season are likely to contain mainly deciduous species, some are dominated by evergreen species such as *Shorea robusta* (sal; Figure 1D, 4B), which, like brevideciduous species in the semideciduous forest of Costa Rica (Figure 3G–I), depend on the use of subsoil water reserves during the long dry season (Troup, 1921; Seth et al., 1960). In a pioneering study, Nepstad et al. (1994) demonstrated that maintenance of an evergreen canopy in the seasonally dry rain forests of eastern Amazonia depends on the extensive utilization of subsoil water reserves. During a severe, 5-months-long dry season tree roots extending to a depth of >8 m were found to extract >500 mm water from a potential reservoir of >800 mm of plant available water. Like riparian trees in semideciduous forests (Figure 3G–I), such evergreen forests are thus well buffered against seasonal drought.

A comparison between the distribution of species within two families of evergreen canopy trees (Chrysobalanaceae, Lecythidaceae) and dry-season rainfall in Amazonia shows that several wide-ranging species are restricted to the wet parts of Amazonia, and species number declines dramatically from the wet northwestern Amazonia (dry-season rainfall >1.5 mm/d) to the drier southeastern Amazonia (0.5–1.5 mm rain/d) and approaches zero in the savannas (Cerrado) bordering Amazonia (Prance, 1990, Nepstad et al., 1994). Similarly, species composition, the incidence of deciduousness and the seasonality of girth growth change along a gradient in annual rainfall across Panama (Devall et al., 1995; Condit, 1998). Correlations between latitudinal variation in the timing of seasonal drought and the phenology of several wide-ranging species were revealed by the analysis of herbarium collections (Borchert, 1996), but the extent to which herbaria might be used to establish correlations between tropical climates and species distribution remains to be explored. Species distribution within tropical forests also varies locally with topography and site water availability. For example, on Barro Colorado Island in Panama some species are found mainly on moist slopes or in swamps (Condit et al., 1996), and in French Guiana several species of Lecythidaceae grow mainly along ridge tops, whereas others occur exclusively at lowland sites (Mori, 1986). However, for lack of information on the ecological roles and sensitivities of different taxa such observations cannot be related to climate and microsite variability as yet (Nepstad et al., 1995).

4. Interannual Variability of Rainfall and Catastrophic Drought

Interannual variability of rainfall is generally large in the tropics, particularly in regions affected by the El Niño Southern Oscillation (ENSO; Figure 4A; Windsor, 1990; Hagnauer, 1993). For example, 13 of 16 rainfall minima recorded in a tropical semideciduous forest in Costa Rica coincide with ENSO events (Figure 4A; Diaz and Markgraf, 1992). Tree species adapted to such rainfall regimes should cope

well with the exceptionally long dry seasons and depletion of soil water reservoirs occurring during severe drought, as indeed observed during recent ENSO events. During the 1992 record drought in eastern Amazonia annual rainfall was 1100 mm, well below the long-term average of 1700 mm, soil water reserves declined strongly (see above) and many trees remained leafless longer than normal, but there was no exceptional tree mortality. Restoration of soil water reserves to pre-drought levels required two years of normal rainfall (Nepstad et al., 1994). In the semideciduous forest of Barro Colorado Island, Panama, the 1982–1983 ENSO event caused the most severe dry season on record. Although higher than normal (3 vs. 2% per year), forest-wide tree mortality was far from catastrophic, animal populations were scarcely affected, and the forest showed little lasting damage (Leigh et al., 1990; Condit et al., 1997). In contrast, the same ENSO event caused large-scale tree mortality and extensive forest fires in the rainforests of eastern Borneo, which are not regularly exposed to and hence not preadapted to long and severe dry seasons and had been rendered susceptable to fire by wide-spread logging (Leighton and Wirawan, 1986). Large-scale tree mortality has been repeatedly observed in monsoon forests during consecutive years of exceptionally low rainfall, when soil water reserves were depleted to levels far below normal (Figure 4B; Seth et al., 1960; Puri, 1969; Tang and Chong, 1979; Leighton and Wirawan, 1986). As expected, mortality is usually greatest at microsites with relatively low soil water storage capacity, such as upland or sandy lowland sites.

In parallel with large-scale deforestation, annual rainfall in many tropical forests has declined significantly during the last decades, often at rates that exceed those predicted to result from global warming (Figure 4A; Windsor, 1990; Hagnauer, 1993). With the increased frequency of ENSO events, progressively lower rainfall minima have become more frequent (Figure 4A, 1960–1990). However, because of forest destruction and lack of baseline data, the effects of reduced rainfall on forests are hard to evaluate. In the only study relating rainfall decline to species composition at an undisturbed forest site, just one subset of moisture-loving species was found to suffer exceptional losses during the past eight years (Condit et al., 1997). Although fossil records from several tropical lowland sites indicate repeated alternation between tropical rainforests and savannas, and hence between moister and drier climate, during the last 5000 years, the extent of paleoclimatic changes causing these vegetation changes are not known (van der Hammen, 1991; Bush et al., 1992; Flenley, 1998).

5. Predicted Effects of Global Warming on Tropical Rain Forests

In much of Amazonia and equatorial Asia, but not in equatorial Africa, current annual rainfall is well above the theoretical minimum of 1500 mm needed to maintain evergreen rain forests. Climate change scenarios predict that global warming will affect rainfall in equatorial Africa and Asia only little, but will cause a

significant reduction in rainfall and increase in seasonality in eastern Amazonia (Hulme and Viner, 1998). This will enhance the existing rainfall gradient from NW to SE Amazonia (Nepstad et al., 1994) and predictions of the possible consequences of future climate changes can be therefore based on the observations discussed above. In the wet Amazonian rain forests, reduction of annual rainfall from >2500 mm to about 1800 mm should not affect forest physiognomy, but may result in increased synchronization of leaf exchange during the dry season (Figure 1B) and a long-term shift in species composition towards more drought-resistant evergreen species (Prance, 1990; Condit, 1996). The seasonally dry, tall, evergreen forests of eastern Amazonia, which strongly depend on the availability of subsoil water during the dry season, appear to be threatened most by climatic change. In combination with increasing evapotranspiration resulting from predicted increases in temperature, even a moderate decline in annual rainfall, from 1600–1800 to values below 1400 mm, may result in the gradual depletion of subsoil water reservoirs, which would start a dangerous positive feedback mechanism (Nepstad et al., 1995; Bonell, 1998). Vegetation responses currently observed only during extreme drought years will occur more frequently, especially if the frequency of ENSO events should continue to increase. Brevideciduous canopy trees will remain leafless for longer periods and evergreen subcanopy trees might suffer excessive water stress and increased mortality. Reduction in canopy density during the dry season will enhance the desiccation of the accumulated leaf litter and thus increase forest flammability and, especially in heavily logged forests, the likelihood of forest fires causing catastrophic, large-scale tree mortality (Leighton et al., 1986). Where late-successional, evergreen species disappear, they will be replaced by early successional species, which tend to be more deciduous and hence less dependent on the extensive use of soil water reserves (Nepstad et al., 1995). Canopy reduction during the dry season will diminish the quantity of water returned to the atmosphere by evapotranspiration and thus may exacerbate rainfall reduction. Eventually, deciduous colonizers are likely to be replaced by late successional, drought-resistent, facultatively deciduous species of the drier forests bordering Amazonia. Because of the wide range in annual precipitation tolerated by such species, the resulting semideciduous forest should be quite tolerant of future reduction in rainfall (Williams et al., 1995). The range of rainforests will thus shrink and semideciduous forests will expand.

Although the above sequence of changes in phenology and forest physiognomy can be inferred with some confidence from recent observations, rate and extent of the changes caused by global warming are hard to predict for several reasons. First, compared to the available information on low temperature tolerance of cold-temperate trees, we know next to nothing about the threshold of drought-tolerance of evergreen tropical trees and about the complex interactions between depletion of soil water reservoirs, tree water stress and drought-avoidance by leaf shedding (Figure 3), which eventually result in drought-induced mortality of trees and displacement of species. The critical combination of minimum annu-

al rainfall, length of the dry season and soil water storage capacity that permits maintenance of evergreen rainforests is not known. Without such information the potential impact of climatic change on rainforest ecosystems cannot be modelled sucessfully (Markham et al., 1994, Ch. 1). Second, the quality of predictions of climate change in the tropics is generally low. Whereas global warming can be predicted with a high level of confidence, all predicted scenarios of changes in seasonal and interannual variability of rainfall and soil moisture status have very low confidence levels. Changes in the frequency or intensity of ENSO events, a major cause of catastrophic drought, cannot be predicted at all (Hulme and Viner, 1998). Finally, it appears near impossible to separate the effects of present and future man-made forest destruction from those of future climate change. The observed tolerance of extreme drought years by undisturbed forests as compared to the increased drought-induced fire-susceptibility of heavily logged forests suggest that the immediate threat to rainforests by extensive logging may by far exceed the future threat by global warming.

Note added in proof

The effects of the 1997 ENSO event confirm several of the ideas discussed above. In Malaysia and Indonesia, because of the ENSO-induced severe drought thousands of fires set to clear rainforest escaped control and blanketed much of equatorial Asia with thick smoke for several months (see press reports). In Guanacaste, Costa Rica, the rainy season beginning in June (Figure 1C) ended after only two weeks of rain, which were followed by three months of severe, ENSO-induced drought, during which newly emerged leaves of many dry forest trees remained wilted. In contrast to the normal phenological pattern (Figure 1C), most trees exchanged all or part of their foliage during the wet months of September/October, but suffered no apparent damage even though 1997 rainfall will be the lowest on record.

References

Bonell, M.: 1998, 'Possible Impacts of Climate Variability and Change on Tropical Forest Hydrology', *Clim. Change*, this volume.

Borchert, R.: 1980, 'Phenology and Ecophysiology of Tropical Trees: *Erythrina poeppigiana*', *Ecology* **61**, 1065–1074.

Borchert, R.: 1991, 'Growth Periodicity and Dormancy', in Raghvendra, A. S. (ed.), *Physiology of Trees*, John Wiley, New York, pp. 221–245.

Borchert, R.: 1994a, 'Water Storage in Soil or Tree Stems Determines Phenology and Distribution of Tropical Dry Forest Trees', *Ecology* **75**, 1437–1449.

Borchert, R.: 1994b, 'Water Status and Development of Tropical Trees during Seasonal Drought', *Trees* **8**, 115–125.

Borchert, R.: 1994c, 'Induction of Rehydration and Bud Break by Irrigation or Rain in Deciduous Trees of a Tropical Dry Forest in Costa Rica', *Trees* **8**, 198–204.

Borchert, R.: 1996, 'Phenology and Flowering in Neotropical Dry Forest Species: Evidence from Herbarium Collections', *J. Tropic Ecol.* **12**, 65–80.

Puri, G. S.: 1969, *Indian Forest Ecology*, Oxford Book and Stationary Co., New Delhi.

Rawitscher, F.: 1948, 'The Water Economy of the Vegetation of the Campos Cerrados in Southern Brazil', *J. Ecol.* **36**, 237–268.

Sabatier, D. and Puig, H.: 1986, 'Phénologie et Saisonnalité de la Floraison et de la Fructification en Forêt Dense Guyanaise', *Mem. Mus. Hist. Nat. Ser. A* **132**, 173–184.

Seth, S. K., Khan, M. A. W., and Yadav, J. S. P.: 1960, 'Sal Mortality in Bihar', *Indian Forester* **86**, 645–679.

Shuttleworth, W. J.: 1988, 'Evaporation from Amazonian Rain Forest', *Proc. Roy. Soc. Lond. B* **233**, 321–346.

Tang, H. T. and Chong, P. F.: 1979, 'Sudden Mortality in a Regenerated Stand of *Shorea curtisii* in Senaling Inas Forest Reserve, Negeri Sembilan', *Malaysian Forester* **42**, 240–248.

Troup, R. S.: 1921, *The Silviculture of Indian Trees*, Clarendon Press, Oxford.

Van der Hammen, T.: 1991, 'Paleoecological Background: Neotropics', *Clim. Change* **19**, 37–47.

Webb III, T.: 1992, 'Past Changes in Vegetation and Climate: Lessons for the Future', in Peters, R. L. and Lovejoy, T. E. (eds.), *Global Warming and Biological Diversity*, Yale University Press, New Haven, pp. 59–75.

Williams, R. J., Cook, G. D., Braithwaite, R. W., Andersen, A. N., and Corbett, L. K.: 1995, 'Australia's Wet-Dry Tropics: Identifying the Sensitive Zones', in Pernetta, J., Leemans, R., Elder, D., and Humphrey, S. (eds.), *The Impact of Climate Change on Ecosystems and Species: Terrestrial Ecosystems*, IUCN, Gland, Switzerland, pp. 39–65.

Windsor, D. M.: 1990, 'Climate and Moisture Availability in a Tropical Forest: Long-Term Records from Barro Colorado Island, Panama', *Smithsonian Contrib. Earth Sci* **29**, 1–83.

Woodward, F. I.: 1987, *Climate and Plant Distribution*, Cambridge University Press, Cambridge.

Woodward, F. I.: 1992, 'A Review of the Effects of Climate on Vegetation: Ranges, Competition and Composition', in Peters, R. L. and Lovejoy, T. E. (eds.), *Global Warming and Biological Diversity*, Yale University Press, New Haven, pp. 105–123.