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Review

Deciduousness in tropical trees and its potential as indicator of climate change: A review

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ABSTRACT

In tropical forests, deciduousness is an outcome of integrated effect of drought, tree characteristics and soil moisture conditions and thus it is a reliable indicator of seasonal drought experienced by different tree species. Variations in the deciduousness are associated with several ecophysiological characteristics, such as varying allocation pattern of metabolic products, resource capture and conservation, water relations and stem water storages, annual carbon sequestration, timing of reproductive event initiation, extent of separation of vegetative and reproductive events and leaf strategies, and it helps in maintenance of water balance and protection of tree organs during the seasonal drought. Tropical forests support mosaics of tree functional types showing marked differences in the duration of deciduousness (from leaf exchanging to >8 months deciduous), as a result of varying degree of water stress experienced by physiognomy, distribution and wood anatomy of tropical trees. Wide variations in deciduousness in the same species growing at different sites suggest the high sensitivity of tropical trees to small changes in growing habitat. In the present review we have explored the ecological significance of deciduousness in tropical trees with emphasis on: (a) inter- and intraspecies plasticity in deciduousness, (b) various capacity adaptations related with the duration of deciduousness, (c) relationship between tree stem water status and deciduousness, and (d) probable effect of impending climate change on tropical trees. An attempt has also been made to establish deciduousness as climate change indicator in the dry tropics. There is need to develop capabilities to detect and predict the impact of climate change on deciduousness through long-term phenological network in tropics. Remote sensing techniques can generate valuable ecological information such as leaf level drought response and phenological patterns. Deciduousness has the potential to emerge as an important focus for ecological research to address critical questions in global modeling, monitoring, and climate change.

Contents

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1. Introduction

Deciduous tree species growing in temperate and tropical forests exhibit seasonal complete loss of foliage and ensuing brief to prolonged leafless state. Leaf shedding (reflecting growth cessation at the end of growing season) and the subsequent leaf flushing (indicating growth resumption) are separated by a discrete but variable duration of leaflessness or deciduousness (suggesting rest period). Strongly growth limiting conditions (low temperature or severe drought) prevail during the rest period. The time lag between the completion of leaf fall and the initiation of leaf flushing (i.e. the duration of deciduousness) is an important attribute of deciduous tree species, bearing on the adaptations related to the cold or dry seasons. Water stress is most recurrently cited as a principal factor driving the sequence of phenological events in tropical dry forests (Murphy and Lugo, 1986). Deciduousness is an important adaptation to survive severe drought because it helps in avoidance of desiccation (Lohbeck et al., 2015). Tropical deciduous forests are composed of mosaics of tree functional types which differ considerably with respect to the duration of deciduousness and time of bud break of vegetative bud (Borchert et al., 2002; Singh and Kushwaha, 2005a). In seasonally dry tropics tree species survive through growth suppressive drought prone dry season alternating with growth favouring, plentiful water supply wet season (Kushwaha and Singh, 2005). Because water stress induces the fall of old leaves and restricts the extension of new shoots and expansion of leaves, the leafless period in tropical trees usually occurs during the dry season. The degree of water stress experienced by tropical forest trees differs widely due to their varying adaptations, resulting in marked differences in the duration of deciduousness (upto >8 months deciduous).

Majority studies related to tropical forests have focused on the analysis of a variety of functional aspects during the foliated active growth period; but deciduousness, indicated by visual signals, remains least studied (Gallinat et al., 2015). The need for more research at the end of growing season (i.e. pre-deciduousness period) in tropical and semi-arid systems has been stressed to understand the way woody species phenology is controlled (Pau et al., 2011; Seghieri et al., 2012). In regions showing seasonality, the termination of deciduousness (the transition from rest to active growth) is well marked and determines the length of vegetative growth period (Barba et al., 2015). The impending impact of global climate change (e.g. changes in temperature and precipitation) on the extent of deciduousness and vegetative growth period ranks high amongst critical questions in the ecology of dry tropics (Do et al., 2005) because phenological patterns of deciduous plants remain weakly understood in stress or drought (Guan et al., 2014). As frequency and intensity of climatic stress factors may enhance (Garcia et al., 2014), there is a need to develop more predictive, mechanistic models of phenology (Xie et al., 2015).

Here we review the ecological significance of deciduousness in tropical trees with emphasis on inter- and intra-species variability in phenological responses and various adaptations, including stem water status, related with duration of deciduousness. We also discuss the suitability of tree deciduousness as climate change indicator in dry tropical region.

2. Deciduousness in tropical and temperate regions

Since deciduousness of trees in temperate and tropical forests is imposed by seasonal severe cold and drought, respectively, these forests should be viewed from contrasting phenological perspective. In temperate regions almost all trees begin leaf flushing (with the onset of spring) and leaf fall (onset of winter season) around the same time through the annual cycle; possibly they are exposed to similar temporal patterns of cold stress, resulting in closely comparable growing and deciduousness periods in a region. In temperate regions length of growth season has been increasing mainly due to the earlier onset of spring as a result of rising temperature (Penuelas et al., 2004; Menzel, 2003). The beginning of growing season for the whole of Europe is expected to advance by seven days with an increase of 1 °C in spring temperature (Menzel, 2003).

Compared to the seasonal temperate climates, the association between temperature and seasonal availability of soil water is almost reversed in dry tropical forests. The degree of drought to which trees are exposed varies widely, depending on temperature and availability of soil, water, and also tree characteristics (van Schaik et al., 1993), showing many adaptations (e.g. access to subsoil water, water storage in trunk). In the Indian Vindhyan deciduous forests, for instance, amongst different tree species considerable variations occur in the time of bud break of vegetative bud and the deciduousness duration varies from <1 month to >7 months (Kushwaha and Singh, 2005), implying significant differences in the growing period of constituent tree species. Unlike strong synchronization of vegetative growth due to winter cold in cold-temperate forests, severe summer drought fails to synchronize the vegetative growth in tropical deciduous forests.

3. Deciduousness based classification

Although the phenological responses are highly diversified in tropical trees the environmental cues related to phenology are considerably few (temperature, precipitation and photoperiod) and different tree species occupy locations on a gradient of deciduousness duration. The wide variety of phenology of tropical trees can be assigned to combinations of few deciduousness duration based phenological tree functional types and triggering factors for the bud break of vegetative buds. Structural–functional approach may be convenient for the classification of tree functional types, since it permits the use of visible structural attributes as surrogate for functional patterns (Box, 1996). The lack of precise documentation of deciduousness in tropical trees has resulted in self-contradictory reports on leaf phenological nature of widely distributed dominant species (Singh and Kushwaha, 2005b). Categorization of Indian tropical forests as moist evergreen, semi-evergreen, moist deciduous, dry deciduous and thorn forests based on annual canopy fullness and deciduousness (Champion and Seth, 1968) can be regarded as marker of the amount and distribution of annual rainfall and seasonal variation in soil moisture availability. Proportion of deciduous species and the extent of deciduousness – both increasing with greater severity of annual drought – significantly affect structure and functioning in these forests (Singh and Singh, 1988).

Even a small variation in deciduousness amongst species may result in significant physiological and ecological variations. Bud break of vegetative bud may be triggered by different control mechanisms (e.g. by leaf fall, by first significant rainfall, or by changes in photoperiod, Rivera et al., 2002). The triggering factor can be identified by careful observation of the timing, synchrony and inter-annual variation of bud break in conspecific individuals (Borchert et al., 2004). Due to patchiness and inter-annual variation of rainfall at the landscape level, tree species showing vegetative or flower bud break due to rain onset or leaf fall are expected to exhibit high conspecific asynchrony. On the other hand, trees showing photoperiod induced bud break are likely to be least asynchronous, as reported in equatorial forests (Borchert et al., 2005). Tropical forest tree species can be classified on the basis of deciduousness duration, triggering factors for the bud break of vegetative and flowering buds, and flowering types. Such a classification will also give an insight about the prevailing climatic conditions of that system.