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Phenology in Plants: Concepts and Uses

[a]Igboabuchi, N.A., [b]Echereme, C.B.*, Ekwealor, K.U.

[a]Department of Biology, Nwafor Orizu College of Education, Nsugbe, Anambra State, Nigeria

[b]Department of Botany, Nnamdi Azikiwe University, P.M.B. 5025, Awka, Anambra State, Nigeria.

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ABSTRACT

Phenology refers to the periodic appearance of life-cycle events. Phenology as a discipline observes these events and relates their annual variation to variation in climate, and the influence of temperature and moisture has been studied by many authors. Phenology currently receives abundant attention as the effects of global and regional climate changes on vegetation are so apparent. Besides being influenced by climatic factors, phenology can be influenced by geographical factors, and the influence of elevation, latitude, and longitude on vegetation phenology has been studied by several authors. Periodicity and seasonality of phenology are mainly determined by the pattern of rainfall in the tropics. Temperate phenologies, unlike in the tropics, are mainly determined by temperature and photo period. Clear yearly cycles in plant phenology predominate in temperate and boreal zones. Complex interactions between organ functions and environmental factors are mainly responsible for a variety of species-specific phenological patterns in tropical trees. Placing plants into phenological functional types, based on leaf habit, has been suggested by authors as an invaluable tool in the comparison of phenologies within and among forests, and this may help our understanding of phenological diversity and relevant changes in global patterns and processes. In view of the varying methodologies in the phenological study in the tropics, phenological observation at functional types will be helpful to develop a common language to communicate concepts and make interpretation of data more compatible among researchers in the region. Apart from the usefulness of phenology in climate change studies, the timing of life-cycle events plays an important role in many environmental, scientific and socioeconomic disciplines.

INTRODUCTION

Plants show a rhythmic appearance of their vegetative and reproductive cycles over time. This phenomenon is termed phenology. Phenology is the study of the relationship between climatic factors and periodic phenomena in organisms. Interest in phenological patterns and the processes controlling them has increased dramatically in recent years, in part due to growing interest in how changing climate affects the timing of life cycles on plants (Corlette and Lanfrankie, 1998; Price and Waser, 1998; Gordo and Sanz, 2005) and animals (Cotton, 2003; MacMynowski and Root, 2007). Leaf development, the flowering of plants, fruit ripening, color changes, and leaf fall, as well as appearance and departure of migratory birds and the timing of animal breeding are all examples of phenological events (Menzel and Dose, 2005). The task of plant phenology is to observe and record the periodically recurring growth stages and study the regularities and dependency of the annual cycles of development on environmental conditions.

The study of plant phenology provides knowledge about the patterns of plant growth and development as well as the effects of environment and selective pressure on flowering and fruiting behavior (Zhang *et al*., 2006). The initiation of growth in plants and changes in phenology are governed by various environmental factors, and the influence of temperature and moisture has been studied by several workers (Dewald and Steiner, 1986). Studies show that geographical factors like altitude, latitude, and longitude can influence phenology at various scales. Recent phenological studies have primarily focused on temperate communities, in which phenologies are constrained by seasonality of temperature and moisture regimes (Ting *et al*., 2008). In contrast, conditions remain favorable for growth and reproduction over the entire year in the tropics. Also, tropical phenology is influenced by a broader set of selective pressures than those of temperate-dwelling organisms. For these reasons, tropical plants constitute a mosaic composed of several phenological functional types adapted to seasonal drought in different ways (Borchert *et al*., 2002).

The importance of phenology lays its effectiveness as a tool to monitor the impacts of climate change on plants and animals (Menzel, 2003). Phenological events, when accurately timed, can be of importance for issues in tourism and recreation, giving information on events that potentially can interest people; biodiversity and ecology, assessing the impacts of mismatch of timing of phenological events on species interactions and community patterns; and education, involving students and public in scientific research by a cost-effective and easy-to-observe method. The information on characteristics of the current year (especially early or late year), may increase people's awareness and may act as a motivation for people to actively observe natural processes (Vliet *et al*., 2003).

PHENOLOGICAL METHODOLOGIES AND COVERAGE

Two different approaches are used to estimating vegetation phenological parameters: small on-the-ground or in-situ field studies (Chmielewski and Rotzer, 2001) and large-scale remote sensing (Dash *et al*., 2010; Brown *et al*., 2012). On-the-ground measurements are made by visual observation and recording of the different stages of the plant's life cycle (Chmielewski *et al*., 2004). Remote-sensing-based phenology, on the other hand, is based primarily on deriving vegetation indices (VIs) and other vegetation parameters like the leaf area index (LAI) or the fraction of absorbed photosynthetically active radiation (FAPAR) from satellite-based sensors (Huete *et al*., 2011). The principal approach for documented phenological changes in plants is direct observation of particular taxa over periods of decades to centuries. A minimum observation period of two decades is recommended by Sparks and Menzel (2002), and most time series used to examine the issue of temporal change have been, at least, this long. Some observations were recorded by single or multiple observers at single locations and others as part of phenological observations of the same species from different locations (see Figs. 1and 2).

Figure 1. A Single observer on a ground-based phenological study of forest trees

Figure 2. Multiple observers on a ground-based phenological study

However, all methods of measuring phenology are subject to various sources of error (reviewed by Dose and Menzel, 2004) and the extent of these potential errors is not precisely known. Interpretations of results are affected by some issues. Different studies have different starting dates, ending dates, durations, and frequencies of observation and temperature change have not been constant over the past few centuries. If the threshold level to recognize activities is different between observers, the length of the event recorded by the two may be different. The number of the events, however, is one for both observers (see Fig. 2), unless the event is strongly bimodal. Calculated rates of change vary depending on what time period is included in the particular set of records (Menzel, 2000; Roetzer *et al.*, 2000; Sparks and Menzel, 2002; Badeck *et al.*, 2004). Menzel *et al*. (2006) eliminated this problem in their comprehensive analysis of European phenological records by standardizing the time period over all sites.

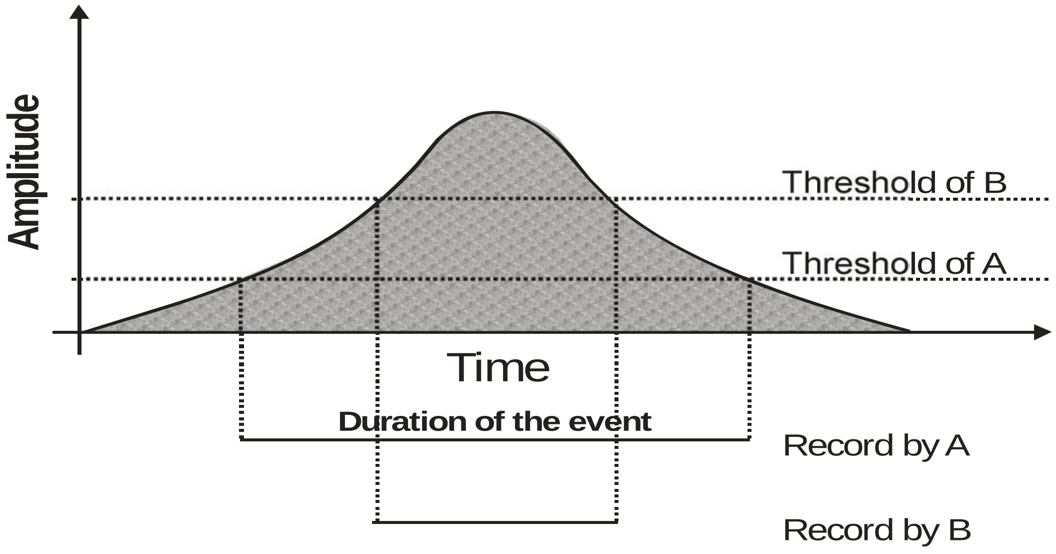

Figure 3. Diagram showing the temporal change in a multitude of phenological events and duration of the event recorded by observers with different methods. The threshold of *observer B* is higher than that of *observer A*; thus, duration of the event recorded by *B* is shorter than *A*. The number of the event, however, is one for both observers, unless the event is strongly bimodal. Source: Sakai (2001).

Seasonality and phenology in the temperate climates

In temperate regions, clear annual cycles in plant phenology predominate. Presumably, regular rhythms in temperature and day length and existence of winter, which limits all biological activities, impose such patterns. Trees in temperate and boreal climates undergo a period of dormancy and enhanced freezing resistance to withstand the harsh climate conditions during winter. The phenological events that coincide with induction and release of dormancy (bud set and bud burst) are finely tuned to the seasonality of the tree's environment, minimizing the risk of potentially fatal freezing damage in autumn and spring, while maximizing the length of the growing season (Basler and Koner, 2014).

In humid extra-tropical climates, the induction and release of seasonal dormancy are triggered by environmental signals, mainly temperature and photo period. In most temperate and boreal trees, dormancy is induced by the decreasing length of the photo period in autumn and cool temperatures, resulting in cessation of growth and the formation of winter buds (Wareing, 1956; Vaartaja, 1959; Thomas and Vince-Pruce, 1997).

Seasonality and phenology in the tropical climates

Periodic shoot growth arrest, as well as a resumption in tropical trees, is mainly caused by endogenous inherent developmental constraints which are the consequence of size- and time-dependent changes in the functional interactions among tree organs, often referred to as correlation control (Borchert, 2000). The largest fraction of tree water is stored in the wood, especially in the sapwood, and changes in stem water status (SWS) plays a central role in the correlative control of tropical trees during the dry season, when water is the principal factors limiting tree growth. The seasonal variation in SWS of trees forms a causal link between seasonality and phenology. SWS depends on the balance between water absorption by roots and transpiration water loss from leaves, depending on tree characteristics and environmental factors (Singh and Kushwaha, 2005b).

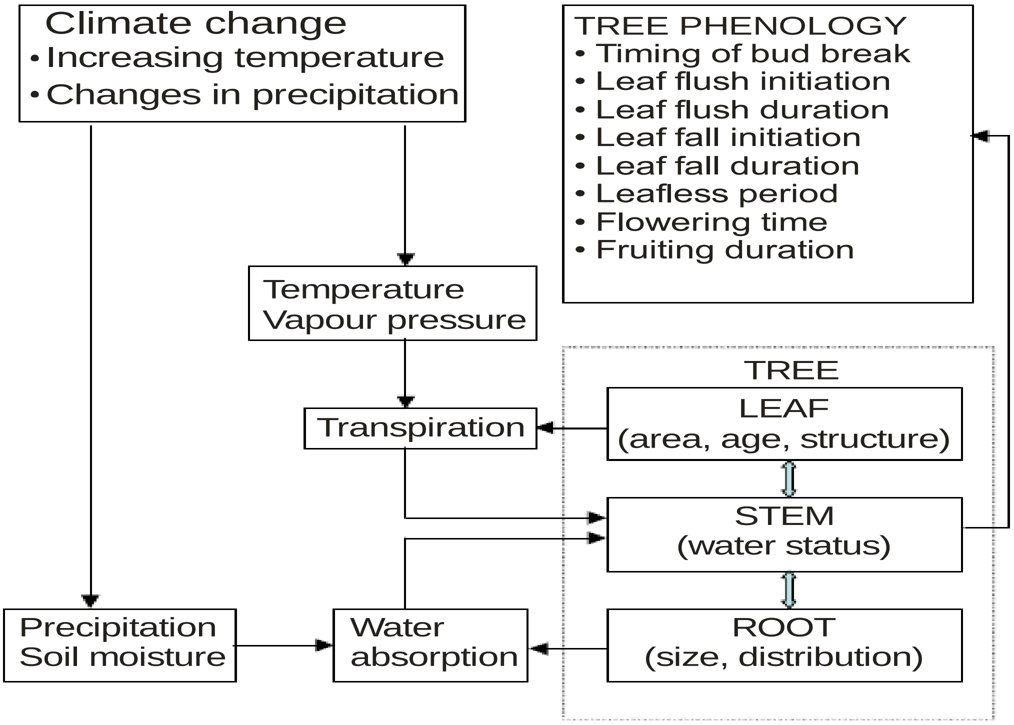

Figure 4. Climate change in relation to interactions amongst environmental inputs, stem water status of trees and its determinants, and phenological characteristics in the tropics. Figure credit: Singh and Kushwaha (2005) (adapted from Borchert, 1999). The direction of the arrow is from the affecting to the affected factor.

Complex interactions between organ functions (e.g., transpiration, water, absorption, SWS) and environmental factors (e.g., seasonal variations in rainfall, day length, and temperature and soil water storage) are mainly responsible for a variety of species-specific phenological patterns in tropical trees (Singh and kushwala, 2005) (see Fig. 4). An opportunistic response to water availability is the simplest explanation for most observed patterns where water is seasonally limiting, while the great diversity of phenological patterns in a seasonal tropics suggests an equal diversity of control.

The influence of temperature and day length on tropical tree phenology

In the tropics, instead of temperature, the light condition is usually more important (Nemani *et al*., 2003; Wright and Van Schaik, 1994; Zimmerman *et al*., 2007). Some authors have addressed the importance of day length variation in manipulating bud-break or flowering in tropical trees (Bollen and Donati, 2005; Rivera and Borchert, 2001; Rivera *et al*., 2002). In regions near the equator where day length variation is small across the year, Borchert *et al*. (2005) proposed an assumption based on times of sunrise or sunset to explain synchronous flowering. Recent studies in tropical America suggested that daily isolation, which is a function of day length, to be the main factor controlling bud-break and flowering of many perennials in the tropics instead of day length only (Calle *et al*., 2009, 2010). In the tropics, seasonal fluctuation in mean temperature is often less than the fluctuations within a single day, and changes in photo period are very small. In contrast to temperate forests, periodic change in rainfall caused by movements of the Inter-Tropical Convergence Zone (ITCZ) often plays an important role as proximate and ultimate factors for tropical plant phenology (Van Schaik *et al*., 1993). In their study on phenology and ecophysiology of *Tabebuia chrysantha* (Bignoniaceae), Reich and Borchert (1982) found no evidence for control of seasonal development by environmental factors such as variation in temperature and photoperiod. The decline in soil moisture and increasing water stress was strongly related to leaf fall phenology in *Tabebuia chrysantha* (Reich and Borchert, 1982).

The relationship between phenology and geographical factors

Studies show that geographical factors like altitude, latitude, and longitude can influence phenology at various scales. Latitudinal changes in plant distribution have been demonstrated in only a few instances and it has been suggested that precipitation changes may have limited range shifts in response to warming in some areas (Bertin, 2008). Effect of elevation along with latitude and longitude on the phenology of plants and animals is described by Hopkins (Hopkins, 1920). He formulated the relationship of elevation, latitude, and longitude to seasonal events such as the arrival of springtime. The relationship was coined the "Law of Bioclimatics", which states that spring advances or phenological events vary at the rate of four days for each degree of geographical latitude westward and 400 feet (121.92 m) higher in elevation. This law is extremely generalized, has geographical limitations and is difficult to apply to individual plant species, but still, it could be useful to predict the tentative date of flower onset for trees that during spring.

The responses of species to existing climate gradients along altitudinal and latitudinal gradients can be used to predict the likely effects of future climate change. A number of studies have previously investigated the responses of insect life cycles to climate changes with altitude (Parkinson and Whittaker, 1975; Hill and Hodkinson, 1995) and latitude (Hodkinson, 1997). There are some influences of geographical factors like elevation and latitude on the phenology of tree, which could alter the date of flower onset and help in range shift of species (Ranjitkar, 2013). In high mountains, flowering phenology changes along elevation gradients, with plants at lower elevations typically flowering earlier than plants of the same species that grow at higher elevations (Ziello *et al*., 2009). Temperature has been documented as the most critical factor during the early stage of the growing season (Miller-Rushing and Primack, 2008). In the mountains, it is elevation gradients that govern the change in temperature (Miller-Rushing and Primack, 2008). Generally, the air temperature in mountain regions decreases with increasing elevation at a lapse rate of about 0.6ºC every 100 m (Du *et al*., 2007), which makes lower elevation areas colder than high elevation areas. As a consequence of the decline in temperature with altitude, species occurring over a 500 m altitude range will experience mean temperature differences of 3ºC, which is comparable with the temperature increases predicted to occur as a result of global warming.

Phenological functional types

Plant functional types are defined as species groups with similar traits and functions to multiple environmental factors (Skarpe, 1996), and functional diversity refers to the number of different plant functional types present in a community (Lavorel *et al*., 1997). It is a system used by climatologists to classify plants according to their physical, phylogenetic and phenological characteristics as part of an overall effort to develop a vegetation model for use in land-use studies and climate models. Identification of plant functional types and estimation of their abundance are useful in the evaluation of ecosystem functions (Gitay and Noble, 1997). The need for data sets of plant functional types has been emphasized by the

International Geosphere-Biosphere Programmer, to evaluate and predict the nature of vegetation responses to future global change (Box, 1996; Woodward and Cramer, 1996).

Leaf phenological variation has been considered as an important variable in distinguishing plant functional types (Condit *et al*., 1996; Chapin *et al*., 1996). The grouping of species according to functional groups contains a fair amount of subjectivity, and ideally, it would be preferable to consider species individually. However, in systems with high species diversity, analyses at the species level would mean a low number of species, thus no possibility of generalization (Gourlet-Fleury *et al*., 2005). The allocation of several species to a small number of groups increases the size of the sample used to exhibit patterns. Using functional groups instead of species also allows comparisons with other similar forests and the formulation of general hypotheses based on the results. Four major leaf phenological functional types, characterized by specific combinations of phenological features, seasonal variation in stem water status (SWS), and structural properties affecting tree water relations have been recognized in dry tropical forests (Borchert, 2000; Borchert *et al*., 2002; Rivera *et al*., 2002) (see Fig. 5). Couralet *et al*. (2013) considered the maximum potential size of trees, which was an indication of the forest layer (understorey or canopy) a species was mostly found at maturity, and this approach resulted in three major functional types among the studied species: (1) group CAN: long-lived shade-tolerant species that dominated the forest canopy at maturity, (2): group HEL: long-lived heliophilous or semi-heliophilous species mostly found in the canopy at maturity and (3) group UND: long-lived, shade-tolerant and generally small-statured species that occupied the understorey at maturity.

Currently, the terminology used to describe phenological functional types lacks uniformity. In the most phenological study, terminology varies with the investigator and the climatic conditions of the habitat studied. For instance, the use of deciduousness to classify functional types has become increasingly unsatisfactory, because every author uses deciduousness as it fits his particular forest. There is a need to standardize the terminology and incorporate, as far as possible, a quantitative perspective. A new way of expressing deciduousness, which has the advantage of being quantitative and applicable to all tropical deciduous forests can be involved using ‘deciduous' in combination with the ‘duration of leaflessness’ in months (Singh and Kushwaha, 2005) (see Fig. 5).

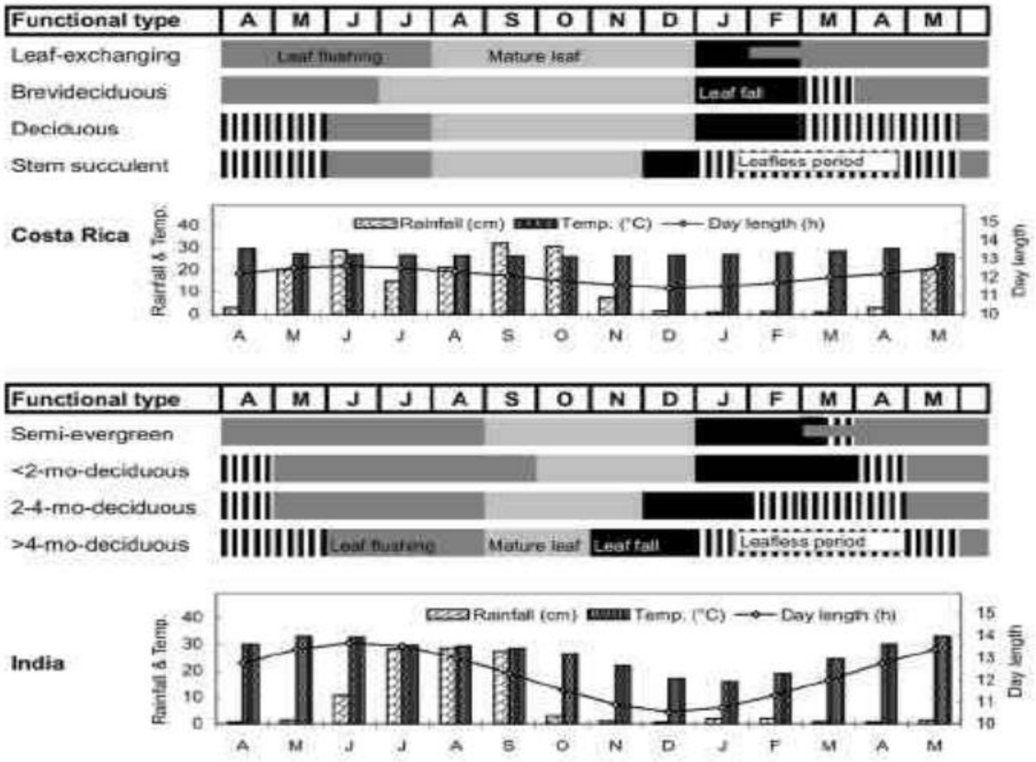

Figure 5. Leaf phenological events and duration of deciduousness in four major phenological functional types recognized in tropical dry forests of Costa Rica and India. Figure credit: Singh and Kushwaha (2005). Data source: Costa Rica, Rivera *et al.* (2002); Climate, Enquist, and Leffler (2001); India, Kushwaha, and Singh (2005).

Climate change influencing phenology: consequences for species interactions and community patterns

Changes in plant phenology will be one of the earliest responses to rapid global climate change and could possibly have huge consequences both for organisms that depend on periodically available plant resources. Because different species respond to climate change at different rates and to different degrees, the makeup of communities and the nature of species interaction must inevitably change (Root *et al*., 2003; Parmesan, 2007; Fitter and Fitter, 2002). Relationships with pollinators, herbivores, and pathogens may shift because some of these animals are likely to respond to different phenological cues than their associated plants. Such a mismatch could work to a plant's benefit or detriment depending on the nature of the relationship.

Rising winter temperature may in some cases delay the leafing-out of plants that have chilling requirements, though they could advance egg-hatching and development of associated insects if these variables are more closely tied to heat sums (Harrington *et al*., 1999). Wall *et al*. (2003) showed that primary pollinators of *Clematis social* change according to the timing of flowering, which in turn reflects late winter temperature. Kudo *et al*. (2004) showed that seed-set in two bee-pollinated spring ephemerals declined in a warm year. They suggested that *Bumblebee* emergence was tied to daily temperature maxima in the hibernating areas, producing a different phenology than in plants responding to heat sums and loss of snow cover. Several dominant New Zealand kinds of grass exhibit mass flowering or mass seeding after hot summers, a phenomenon associated with decreased herbivory (Mckones *et al*., 1998).

Recent increases in spring temperatures in the Netherlands are associated with poor synchronization between egg-hatching of winter moths *Operophtera brumata* and budburst of the Oaks *Quercus spp*. on which they feed (Visser and Holleman, 2001). Honeybee emergence advanced more than flowering seasons of spring-blooming plants in Spain (Gordo and Sanz, 2005). In her meta-analysis, Parmesan (2007) found that phenophases of herbaceous plants did not advance as much as those of butterflies and birds. She and Peñuelas and Filella (2001) suggested that the prediction of the effects of global warming on community patterns will be difficult given the different responses of different taxa to climate change.

Applications of vegetative phenology

Apart from the usefulness of phenology in climate change studies, phenology can contribute to many scientific disciplines from biodiversity, agriculture, and forestry to human health (Rumi and Vulić, 2005). It can also contribute to many environmental and socioeconomic disciplines.

The use of phenology in understanding ecosystem structures and functions

Phenology of individuals plays a key role in determining how ecosystems are structured and how they function (Cleland *et al*., 2007). Phenology can impact species abundance and distribution significantly. For example, phenology is a factor in the fitness and reproductive success of both plants and animals, and in competitive interactions within and among species and across trophic levels, thereby driving species distribution (Chuine, 2010) and community assemblages (Gill *et al*., 1998; Auspurger *et al*., 2005). Phenology is a major driver in determining population dynamics, species interactions, animal movement and the evolution of life histories (Schwartz, 2003; MØller *et al*., 2008). Population-limiting factors are closely linked to seasonal or interannual phenological events, and shifts in phenology can affect ecosystems through changes in ecological interactions such as predator-prey and plant-pollinator dynamics (Cushing, 1990; Edward and Richardson, 2004; Memmott *et al*., 2007; Encinas-Viso *et al*., 2012) and the epidemiology of infectious diseases (Harvell *et al*., 2002; de La Rocque *et al*., 2008). Changing phenologies will contribute to shifts in species distributions, population viability and reproductive successes (Schaper *et al*., 2012; Mair *et al*., 2012), and, in turn, will affect climate via biogeochemical processes and the physical properties of the biosphere (Peñuelas *et al*., 2009). As such, phenological changes will have profound consequences for human societies and economies, including agricultural production (Stokes and Howden, 2010), fisheries production (MacNeil *et al*., 2010) and human health (Ziello *et al*., 2012).

The use of phenology in agriculture and forestry

Agriculture and forestry sciences have applied phenological data for the timing of agricultural work, the selection of suitable crops and cultivars, and in conservation and management programmes. It has been seen that knowledge of plant reproductive phenology is the key to achieving their conservation. Knowledge of reproduction is crucial to our understanding of the causes of rarity and for the conservation of rare plant taxa (e.g. Drury, 1974; Kruckeberg and Rabinowitz, 1985). Knowledge of phenology and floral morphology are essential for conducting studies on breeding systems, particularly on pollination study. Such studies would prove to be successful in planning various programmes specific to different habitats. Studies in reproductive biology will also help in developing strategies to preserve the genetic potential of rare species and are crucial for restoration and reintroduction. Therefore, reproductive phenological studies help in developing strategies to preserve the genetic potential of rare species which are crucial for restoration programmes.

The use of phenology in increasing environmental interest

Phenology is a good instrument to communicate climate characteristics in general, and especially the impacts of climate change on vegetation to the broad public (Vliet *et al*., 2003). There is substantial public interest in phenological bulletins in some countries, indicating the actual state of vegetation development during the growing season. The information on the characteristic of the current year (especially early or late year), may increase the public awareness of nature and its seasonal chronology and may act as a motivation for people to actively observe natural processes. Furthermore, phenology already is (and might become) an even more important topic to enhance the public activities of the meteorological services. Several newspaper articles throughout the year indicate the relevance of this topic for the media.

The use of phenology in tourism and recreation

Tourism is increasingly seen as a tool for development and poverty alleviation. Tourists are often interested in what are essentially phenology-driven events, such as Birdwatching, spring wildflower displays, or autumn tree color. Being able to predict the timing of such events is thus important to tourism visitors. Many plants have high ornamental value during specific phenophases, such as first leaf, flowering, and leaf coloring. Thus, plant phenology correlates highly with seasonal aspects of the landscape (Zexing *et al*., 2015).

The beauty of blooming flowers causes spring to be one of the most picturesque and pleasant seasons in which to travel (Huanjiong, 2016). Therefore, recent climate change may shift flowering time and, as a result, may affect the timing of spring tourism for tourists. The best date of spring flower tourism was significantly correlated with spring temperature ($R = -0.66$, $P < 0.01$) with an increase in spring temperature of 1^0C causing the best date earlier by 4.0 days (Huanjiong, 2016). Thus in the context of future global warming, it is crucial to enhance the ability to predict the flowering time, so as to provide a reference to tourism administrators and the tourists to make better tourism arrangement.

The use of phenology in medicine and health

Pollen forecasting is an example of the application of phenology in the medical sector. The observed earlier onset of spring in the moderate temperate climate zones have prolonged the pollen season, bringing with it the negative effects on well-being and health of allergic people, and causing additional costs in health care (Beggs, 2004). Pollen forecasts can be used by, for example, physicians (allergists), health professionals, allergic people, pharmaceutical industry, scientists and authorities (health, environment) and for a wide variety of purposes for example, prevention, preventive medication, management of therapy (e.g., pre-seasonal hyposensitisation), planning of holidays or travels, planning of medicine production and distribution and start of short-term forecast models (WHO, 2003).

CONCLUSIONS

In this paper, we have outlined the approaches utilized in estimating vegetation phenological parameters and pointed out that interpretations of results usually vary among observers as a result of different threshold levels for recognizing activity.

Changes in plant phenology are generally governed by various environmental factors and the influence of temperature and moisture on phenological patterns has been profound. Temperature and photoperiod are the major environmental factors that drive plant phenological patterns in the temperate and boreal climates. In the tropics, the seasonal variations in stem water status of trees form a causal link between seasonality and phenology.

Phenological functional types based on leaf habit can be an important tool in distinguishing plant functional types in the tropics. Observing plants at their functional types can serve as a standardized methodology in communicating ideas and make interpretation of data more compatible and generalizable in the tropics.

The phenological responses of different plant species to climate changes at different rates and to different degrees ultimately result in a mismatch in food chains, with serious ecological consequences for population dynamics, ecosystem functions, and biodiversity.

Apart from the usefulness of phenology in climate change studies, the timing of life-cycle events plays an important role in many scientific, environmental and socioeconomic disciplines.

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