Chapter I

General Introduction

Phenology deals with the study of periodicity of different life cycle events of plants throughout the year like seed germination, bud break, leaf expansion, leaf colour changes, and maintenance of biomass, vegetative growth and reproduction, determining the plants adaptation to seasonally changing environments of their habitats. Phenological studies are important to understand plant responses to various biotic and abiotic factors like competition for light or pollinators (Negi and Singh 1992), photoperiod (Write and van Schaic 1994), temperature (Arroyo et al. 1981), and precipitation (Opler et al. 1976, Athokpam and Garkoti 2013). Phenological observations provide background information on functional rhythms of plants and plant communities (Ralhan et al. 1985a, Baruah and Ramakrishnan 1989). Understanding of behaviour of such communities is useful in evolving proper management, and information on phenological pattern is helpful in predicting the interactions of plants and animals to the changing environment. Studies from different parts of the world have shown biotic and abiotic factors to be responsible for vegetative and reproductive phenology (Sundarapandian et al. 2005). Climatic factors such as temperature and precipitation determine seasonality in plant phenology (Marques et al. 2004). Different climatic factors are mainly responsible for vegetative and reproductive phenology at both community and species level (Mishra et al. 2006). The onset and duration of particular phenological events vary from year to year depending on the current weather situation (Larchar 2003). Tropical plants with their high level of species diversity display phenological events such as leaf drop, leaf
flushing, flowering and fruiting, etc in relation to time and space (Justiniano and Fredericksen 2000, Sing and Sing 1992).

Leaf phenology which is described as the biological periodicity of leaf production represents a plant strategy for maximizing net primary production under the temporal variation of limiting environmental factors (Kikuzawa 1995). Leave are central to the adaptation of a plant for growth and competitive success; therefore, it is important to understand the selective pressure that are placed on leaves by different environments (Givnish 1987). In tropical trees leaf phenology is important because it reflects the influence of evolution and environment on plant characteristic and in turn has substantial implications for plant functioning (Reich et al. 2004). In tropical forests deciduousness (leaflessness) is an important strategy of trees to survive in water stress period during summer (Kushwaha et al. 2010, 2011). The life span of leaves is important in that it reflects several ecophysiological attributes. For example, compared to deciduous species evergreen species generally show longer leaf life span, deeper root system, higher stem water potential to rehydrate the stem during the dry season, longer duration of photosynthetic activity at lower rates (Medina 1995, Chapin et al. 1996; Eamus et al. 2001, Borchert et al. 2002, Garkoti et al. 2003, Singh et al. 2006, Athokpam and Garkoti 2013). An increase leaf life span, by increasing the time period for photosynthesis, can compensate for low rates of photosynthesis (Orians and Solbrig 1977, Schulze et al. 1977) or allow plants to initiate photosynthesis early in the spring before conditions are suitable for leaf growth (Chabot and Hick 1982). Thus the phenological terms ‘deciduous’ and ‘evergreen’ have connotations in tree phenology and should be applied to a species with great care.
Plant water stress is caused by seasonal water deficit and it suppresses leaf activity like assimilation and development. The seasonality of tropical tree phenology is mainly determined by the duration and intensity of seasonal drought (Mooney et al. 1995). Deciduousness of plant species is a reflection of interacted effect of seasonal drought, tree characteristics and soil moisture conditions (Kushwaha et al. 2010). Low irradiance is induced more by cloud cover than by day length or incident angle of sunlight (Walsh 1996) and it suppresses photosynthesis and growth of canopy trees (Clark and Clark 1994, Zotz and Winter 1996). Consequently the following assumptions have generally accepted about the tropical leaf phenology. First, in habitat with seasonal water stress, plants concentrate their leaf production in the wet season when water supply for leaf activity is available. Second, in a habitat with a permanent and sufficient water supply, plant concentrate their leaf production in the sunny (dry) season when photosynthetic productivity increases with high irradiance (van Schaik et al. 1993, Wright 1996). Even conspecific trees often experience differing degree of drought stress (Singh and Kushwaha 2005a).

Leaf dry mass is one of the useful and important component of various traits in plant ecology like leaf dry matter content (LDMC), specific leaf area (SLA), specific leaf mass (SLM), relative growth rate (RGR$_L$) and biomass or productivity, which helps in understanding and predicting plant strategies like behaviour of species, communities and finally whole ecosystem in response to climate change and competitors. The global leaf economics spectrum demonstrates correlations and trade-offs between a range of chemical, physical and physiological leaf traits across biomes and functional groups, based on a leaf dry mass economics (Wright et al. 2004). Plants with favourable habitats would be capable of maintaining a high seasonal relative growth (Chapin et al. 1993, Poorter and Garnier 1999, Mediavilla and
Escudero 2003) and associated with a low survivorship of old leaves owing to the strong demands of newly growing organs (Mooney 1983, Chapin et al. 1993). Quantification of the relationship foliar size and the dry mass costs of developing leaf area are important in understanding the relative costs and benefits of larger versus smaller leaves (Pickup et al. 2005).

Leaf may die in many ways, due to external factors like herbivory, temperature or water stress, damage by wind, rain or the thrashing action of neighbouring branches, etc. and leaf death can also occur due to internal cause by plant itself, for example in response to some phenological cue or to shading (whether self-shading or from neighbouring plants). An important difference between the plants having control over the timing of leaf death and having no control is the withdrawal of nutrients contents from leaves before they are shed (Wright and Cannon 2001). The changes in nutrient content of leaves during the growing season are important for studies of nutrient cycling and for studies of adaptation of various species to their environment within the forest community. The pattern of changes varies with the elements. Retranslocation of nutrients from senescing leaves involves most macronutrients (Ostman and Weaver 1982, Ralhan and Singh 1987, Negi and Singh 1992, Nordell and Karlsson 1995, Nelson et al. 1995, Wright et al. 2004). Transfer of nutrients from senescing leaves to woody parts of trees and shrubs reduces the likelihood of nutrients loss in litter dropped on the forest floor (Mitchell et al. 1975, Bormann et al. 1977). Nutrients differ in extents of their retranslocation from senescing leaves (Olsen 1948, Lindgren et al. 1977, Tilton 1977, Ostman and Weaver 1982). A few relevant points often raised are whether or not deciduous species retranslocate more nutrients than the evergreen (Chapin and Kedrowski 1983, Garkoti and Singh 1994). Monk (1966), Haag (1974) and Chapin (1980) have suggested that
species with long lived leaves canopy occupy nutrient poor sites and those with short lived occupy nutrient rich sites. Plants adapted to infertile site show greater proportional loss of nutrients at senescence than those adapted to fertile site (Eickmeier 1979). However, evidence contrary to this process is also available (Chapin and Kedrowski 1983). Further we know little about the interspecific variation within the communities in regard to the extent of nutrient retranslocation. The question that emerges in whether or not various species occupy the same site show broadly similar levels of nutrient retranslocation.

Co-occurring trees in forest typically differ in foliar phenology (Lechowicz 1984, Kikuzawa 1989), but current theory (Harada and Takada 1988, Tateno and Watanabe 1988) offers no explanation for such local phenological variation. The most likely proximate explanation lies in inter-specific differences in vulnerability to xylem dysfunction, a trait that traditionally has been considered to depend primarily on the diameter of the conduction element in the xylem (Zimmermann 1983, Wang et al. 1992) and the species differences in the behaviour of specific conductivity suggest that elasticity of the pit membrane was the main factor causing specific conductivity to be disproportionate to the pressure gradient and to the different pressure regimes (Jean et al. 2007). The changes in the cell type and cell dimensions that accompany formation of tension wood could also have a profound effect on water transport (Barbara et al. 2003).

A considerable amount of information on foliar phenology and other related studies (leaf life span, leaf mass, relative growth rate, xylem conductivity, nutrient content and resorption) is available from different part of the world (Chapin et al. 1980, Chabot and Hicks 1982, Chapin and Kedrowski 1983, Reich and Borchert

The present study was carried out in the tropical forest of this region with following main objectives-
1. To study the seasonal periodicity of leaf and shoot development of selected important plant species of the region.

2. To understand whether or not the seasonal changes in leaf and shoot phenology are related to twig xylem conductivity.

3. To compare the patterns of leaf mass and nutrient dynamics associated with leaf phenology of important trees and shrubs of the region.

4. To test whether evergreen and deciduous species, or canopy, sub-canopy and shrub species differ substantially with respect to commencement and completion of their seasonal growth.

Findings of the present study may help the forest managers and policy makers to understand the leaf and shoot growth phenology, and nutrient dynamics of plant species in the tropical forests and will give them good relevance to know the forest structure and functions and its productivity which ultimately help them in proper management of tropical forests.