PHENOLOGY OF TREES AND OTHER PLANTS IN THE BOREAL ZONE UNDER CLIMATIC WARMING

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Contents

Summary

Various aspects of global change will have several direct and indirect effects on plants in the boreal zone, and some of these effects may be quite dramatic. In this article, the effects of one essential aspect of global change, i.e. climatic warming, on phenology of trees and other plants in the boreal zone are discussed. The scientific information available to date suggests two potential categories of phenomena, with opposite effects on plants: On one hand, climatic warming may cause increased incidence of damage to these plants during overwintering. On the other hand, it may also promote growth and reproduction of plants by improving the growing conditions, especially by prolonging the growing season during spring. Due to the uncertainties involved and lack of information, only uncertain predictions can be presented for any given species. It is, however, probable that there is considerable variation among species in their responses to climatic warming. In this case, climatic warming may cause changes in the species composition of plant communities in the boreal zone, i.e. some of the present species may gain advantage at the disadvantage of others. Furthermore, new species may invade from the south and replace some of the current species. In an extreme case this phenomenon may even change the whole vegetation into a temperate vegetation type, or possibly into a type intermediate to the present boreal and temperate types. However, considering the large within species variation in several plant traits related to climatic adaptation, migration of more southern genotypes of the species presently growing in the boreal zone may partly decrease the establishment of completely new species.

1. Climatic Adaptation of Plants in Boreal Zone

The climate in the boreal zone is characterized by a pronounced seasonality of incoming solar radiation and air temperature. In plant adaptation to these conditions, two parts are distinguished, i.e. survival adaptation and capacity adaptation.

Plants have to overcome the harsh conditions prevailing during winter causing freezing stress and winter desiccation (*survival adaptation*). Frost survival can be based on two strategies, i.e. on avoidance or on tolerance. The strategy of a given terrestrial plant species depends on which parts of the plants over-winter, and the extent to which the over-wintering parts receive shelter from snow and layers of litter and soil (aquatic plants are not considered here).

The various over-wintering strategies are addressed in the classical Raunkiaer's classification of plant life forms. The above-ground meristems (buds and cambium) of trees and shrubs (i.e. *phanerophytes* in Raunkiaer's classification) over-winter above the sheltering snow cover. Thus, with the exception of roots, the frost survival of trees and shrubs has to be based entirely on *frost tolerance*, i.e. on frost hardiness. Actively growing meristems can frost harden only slightly, so a prerequisite for frost hardening is that during late summer and early autumn the trees and shrubs fall into winter dormancy. The dormancy is released during spring, with a simultaneous dehardening of the meristems. In this way, the survival adaptation of the trees and shrubs is realized by their annual cycle of development. In the case of dwarf shrubs like *Vaccinium vitis-idea* (i.e. *chamaephytes*) the above-ground meristems are usually protected by snow cover, but not always. Their frost survival is based both an avoidance (snow cover) and tolerance (annual cycle of hardening and dehardening). With the exception of annuals, most herbs and grasses belong to the group of *hemicryptophytes*, i.e. their shoot senesces and among the above-ground parts, only buds just above the soil surface over-winter.

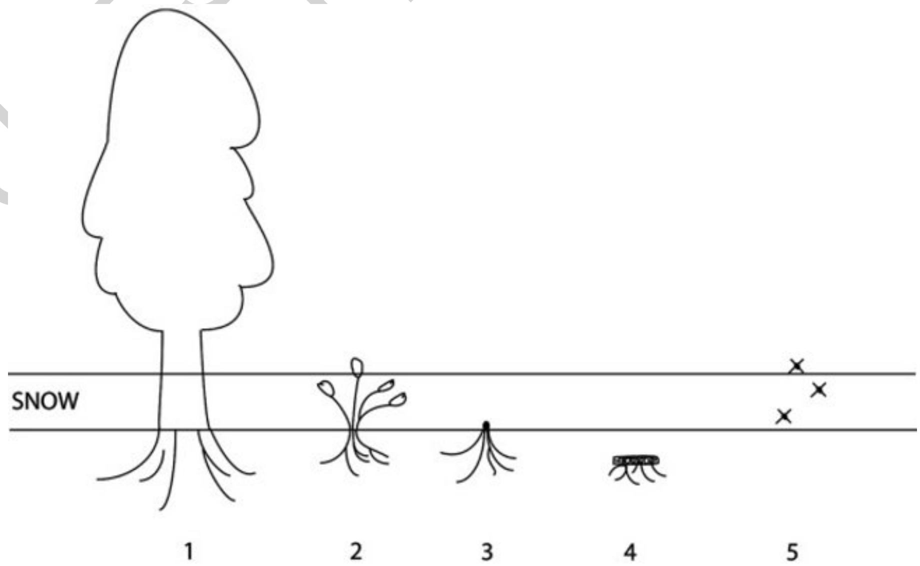

Figure 1. Raunkiaer's classification of plant growth forms. The classification is based on which part of the plant overwinter and how much shelter by snow cover, litter and

soil is provided to the overwintering parts. 1) Phanerophyte, 2) chamaephyte, 3) hemicryptophyte (the black dot denotes the overwintering bud just above the soil surface), 4) cryptophyte, and 5) therophyte (an annual plant, black crosses denote seeds).

In addition to snow cover, they are usually sheltered also by a litter layer. Thus, despite some hardening possibly taking place in the over-wintering above-ground organs, the frost survival of these plants is mainly based on *frost avoidance*. This is even more so among *cryptophytes*, i.e. in species like Lily of the Valley which overwinter in the soil e.g. as rhizomes or bulbs. Annual species form the group of *therophytes*. They over-winter only as seeds, which are generally frost hardy organs (frost tolerance).

Whatever the plant life form and the corresponding strategy of survival adaptation, the plants also have to use the growth resources (light, nutrients, water) as efficiently as possible. This second part of the adaptation of plants is called *capacity adaptation*. Plants with insufficient capacity adaptation are destroyed by inter and/or intra specific competition.

Only species with both a sufficient survival and a sufficient capacity adaptation are able to live in the seasonal climatic conditions of the boreal zone. These two aspects of adaptation are often favoured by contrasting traits, so as a result the plants are subjected to a stabilizing selection. This is especially the case in the phenology of the plants during spring. At this time, the level of ambient solar radiation is high, so plants with an early start to the growing season and a rapid development thereafter gain an advantage over plants with later and slower development. Thus with respect to capacity adaptation, the early starters are selected for and the late starters are selected against. With respect to survival adaptation, however, the situation is reversed. This is because the early starters may be subjected to damage by late frosts. In this way, the optimal phenology is determined as a tradeoff between these two contrasting selective forces.

Air temperature is a major ecological factor affecting the phenology of plants in the boreal zone. For this reason it is evident that the predicted climatic warming will considerably affect the phenology of these plants, especially because the warming is predicted be pronounced at high latitudes. In this article, possible effects of climatic warming on phenology of the trees and other plants in the boreal zone are discussed, with reference both to over-wintering (survival adaptation) and to growth and competition (capacity adaptation).

2. Trees and Shrubs

2.1. Regulation of the Annual Cycle

2.1.1. Phenology of Bud Burst

Classical theory

According to the theory that has prevailed until recently, air temperature has been considered to be the most important environmental factor regulating the bud burst of trees in the boreal (and temperate) zone. After growth cessation during autumn, the buds of trees are in a state of rest, i.e. bud burst and growth are arrested due to physiological conditions inside the bud. This implies that no bud burst takes place even under conditions of high, normally growth-promoting, air temperatures. Prolonged exposure to chilling temperatures (e.g. $0\ ^{o}C < T < 10\ ^{o}C$) causes rest break, i.e. removal of the inherent growth arresting conditions.

The development of the bud during the rest period can be quantified by accumulating various chilling units on the basis of temperature data. The genotype-specific chilling requirement of rest completion varies among species and provenances from a few days to several months. In most cases, rest completion takes place during late autumn. At the time of rest completion the buds attain a state of quiescence, i.e. they remain dormant, but now the dormancy is caused by low ambient temperature, no longer by the physiological condition of the tree. At this state of development exposure to relatively high temperatures (e.g. $T > 0\ ^{o}C$) causes ontogenetic development towards bud burst. Thus, during quiescence the development of the buds can be quantified by accumulating various high temperature units (e.g. day degrees, d.d.). Bud burst takes place, when the genotype-specific high temperature requirement of bud burst is met. This happens usually during late spring.

In conclusion, the classical theory assumes a dual role of air temperature in regulating bud burst: prolonged exposure to comparatively high temperatures causes bud burst, but only after a sufficiently long period of chilling has conditioned the buds to respond to the high temperatures. Large intra- and inter-specific variation exist both in the chilling requirement and in the high temperature requirement.

In evolutionary terms, the chilling requirement has been interpreted as a safety mechanism ensuring that the buds will not burst untimely during warm periods in autumn. Furthermore, according to the prevailing concept, photoperiod plays only a minor role in regulating the rest break and bud burst of trees from the boreal and temperate regions. Beech (*Fagus sylvatica*), however, is an exception to this rule, as in addition to chilling requirement, rest completion in this species requires also attainment of a critical photoperiod.

Recent findings

In the past few decades, the classical theory of regulation of bud burst by accumulation of chilling and by subsequent accumulation of day degrees has been substantiated in hundreds of experimental studies, carried out both with forest and fruit trees. In the last few years, however, the theory has run into difficulties, especially in the case of tests with long-term historic phenological data gathered with mature trees growing in natural conditions. Simple models assuming that rest break takes place each year at a fixed calendar day during spring have provided more accurate predictions of timings of bud burst than more complicated models based on the dual effect of air temperature. These results, however, do not falsify the concept of chilling requirement. Rather, the results suggest, that in the case of adult trees, some additional cues are required, in addition to chilling, for the rest break. Revealing of these additional factors and their effects is crucial for the prediction of the effects of climatic warming (see section 2.2.1.).

2.1.2. Phenology of Growth Cessation

Elongation growth of trees can take place basically in two ways. In *fixed growth* all of the leaf primordia are developed in the bud at the time when the bud is formed during the late phase of the previous growing season. In this case elongation consists merely of the growth of these over-wintered leaf primordia. In the case of *free growth* additional leaf primordia are initiated simultaneously during growth, so the elongation consists of growth of both over-wintered and newly formed primordia. The mode of growth varies among tree species, and in some species even among different individual ages. In this case, the growth is normally free among young individuals and turns more to the fixed mode when the individual gets older. Naturally during the first growing season, the growth belongs always to the category of free growth, since no primordia exist in the seeds.

In the case of fixed growth, growth cessation takes place when all of the primordia have attained their full length. Thus, the timing of growth cessation depends on the growth rate of the individual primordia. The growth rate in turn is determined by ambient temperature, so as with the state of quiescence, the development of the meristem can be quantified during the growth state by accumulating high temperature units (e.g. day degrees), and growth cessation takes place when a genotype-specific high temperature requirement of growth cessation is attained.

Conversely, in the case of free growth, the timing of growth cessation is mainly determined by the cessation of the initiation of new leaf primordia. According to the prevailing theory, this is caused by the attainment of a genotype-specific critical night length. Thus, in evolutionary terms, lengthening of the night during late summer signals to the tree the advent of winter and triggers the cessation of growth and initiation of hardening.

According to the prevailing theory addressing the regulation of cessation of free growth, other environmental factors (air temperature, humidity) may act as additional factors, modifying the major effect caused by night length. However, over the last twenty years increasing support has been presented for a new theory, stating that growth cessation is regulated as a joint effect of night length and air temperature. However, it appears that this new concept has not been generally accepted in the scientific community. This conflict may be to some extent a semantic one, i.e. some scientist consider a given effect as a ‘modifying’ one; whereas others regard it as important as the effect caused by night length, so they prefer to use the concept ‘joint regulation’.

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Biographical Sketch

Heikki Hänninen was born in July 1957. He received his Ph.D. from the University of Joensuu in 1990. He worked as a Research Fellow and Acting Professor in the same University until 1997, when he was nominated as Professor of Terrestrial Plant Ecology at the University of Helsinki. His main research interest is in the climatic adaptation of boreal plants, with a special emphasis on the effects of climatic change. In his studies he applies an approach where whole plant ecophysiological experimental work is combined with simulation modeling. Earlier he worked solely with forest trees but recently he has broadened his scope to cover other boreal plants as well.