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THE EFFECT OF PHOTOPERIOD ON VEGETATIVE GROWTH AND GENERATIVE DEVELOPMENT IN CONIFEROUS TREE SPECIES

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ABSTRACT

In assessing the effect of photoperiod on the vegetative growth and generative cycle of coniferous trees a distinction is made between dormancy release and flushing, and between cessation of shoot elongation and true winter dormancy. It is suggested that under natural conditions temperature is the most important environmental factor influencing dormancy release and flushing and that cessation of shoot elongation with the formation of a terminal bud, which is closely linked to the onset of the generative cycle, is under the control of photoperiod. The view, therefore, that all theories and concepts of flowering are theories and concepts of photoperiodism could equally apply to coniferous tree species. Both dormancy, and dormancy release are discussed in relation to the microevolution of the species. It is suggested that because cessation of shoot elongation is closely linked with the onset of the generative cycle, and because of the temperature conditions prevailing in the fall, the photoperiodic control of growth cessation confers a survival advantage on the species. A similar survival advantage is not conferred on the species by the photoperiodic control of dormancy release and flushing. The period during which there is gradual cessation of shoot elongation with the formation of a terminal bud is synchronized with the period during which primordia are most plastic in regard to their future development. There is marked meristematic activity during the period prior to true winter dormancy, and it is suggested that at this time substances are synthesized which mediate the onset of the generative cycle. It is during this period, therefore, that treatment could have maximum effect on the development of reproductive buds. In any study designed to influence the periodicity of cone crops it is necessary to distinguish between initiation of reproductive buds and their development and maturation. Factors which may influence initiation may have no effect on development and maturation and *vice versa*. It is possible that for many coniferous species cone crop periodicity is more closely related to development and maturation rather than to initiation of reproductive buds.

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All present theories and concepts of flowering are theories and concepts of photoperiodism since flowering or its absence are criteria of photoperiodism. Chailakyan (1968).

INTRODUCTION

In numerous countries attempts have been made to stimulate early and abundant flowering in seed orchards of coniferous species, and to increase cone production in seed production areas. The methods applied vary from those which often inhibit vegetative growth, e.g. girdling, to those that stimulate it, e.g. the application of fertilizers. In general, it can be said that these methods are frequently applied without reference to the environmental and endogenous factors which are known to influence growth and development in woody plants. Hence, perhaps, the lack of consistant success of these methods in the control of the flowering process in coniferous species.

There seems little doubt, however, that progress in the artificial control of flowering in coniferous species will continue to be very slow until the natural factors influencing both the vegetative growth rhythm and generative development in coniferous trees are more clearly understood.

Photoperiod, dormancy release and flushing.

It is necessary to distinguish between dormancy release and flushing (Smith and Kefford 1964). Dormancy release occurs many weeks prior to flushing and appears to result from the build up of endogenous gibberellins in response to rising temperatures and following winter chilling (Eagles and Wareing 1963). The transitional phase between dormancy release and flushing is, therefore, a non-dormant state. Certain environmental factors which can influence flushing have little or no effect on dormancy release. There is also evidence that environmental conditions, including photoperiod, during bud maturation have an effect both on the time of flushing as well as the amount of growth during the flush (Dormling *et al* 1968).

Despite, however, the reported positive and direct effect of artificially long photoperiods on time of flushing for a small number of tree species, particularly *Fagus sylvatica* (Wareing 1953), and the effect of photoperiod during growth cessation on flushing in the subsequent growth cycle (Dormling *et al* 1968), the bulk of the evidence indicates that the photoperiod prevailing at the time of dormancy release in natural populations of coniferous species has little effect on this phenomenon. Rather it is temperature, (Sarvas 1969, Nienstaedt and King 1969) which is the overwhelmingly important environmental factor (Roche 1969).

Photoperiod, growth cessation and dormancy.

There is a transitional phase, termed summer dormancy, between cessation of shoot growth with the formation of a terminal bud and true winter dormancy. There is marked meristematic activity during this phase (Wareing 1956) and seedlings in a state of summer dormancy can be induced to flush by environmental factors which have little or no effect on seedlings in a state of true winter dormancy.

In one of the most detailed studies of the climatic factors influencing the growth rhythm of a coniferous species under controlled conditions Dormling *et al* (1968) showed that induction of terminal bud set in Norway spruce (*Picea abies* (L) Karst) is a short day response. This result was clear cut and confirmed the tentative conclusions of many other workers that photoperiod is a major environmental factor influencing the onset of dormancy in coniferous species in middle and northern latitudes.

The question arises, therefore, as to why photoperiod is a major component of the environment in regard to growth cessation and dormancy, and temperature the effective instrument in dormancy release and flushing in coniferous species.

The probability of the occurrence of damaging or lethal temperature increases with the passing of time in the fall, and it is clear that in respect to dormancy a perennial plant adapted to photoperiod has a greater survival advantage than one adapted to temperature alone. In the spring, the probability of the occurrence of freezing temperatures decreases with the passing of time, and dormancy release and flushing are the result of the cumulative effect of temperature. Therefore, no overwhelming survival advantage is conferred on the plant by the photoperiodic control of flushing.

Chailakhyan (1968) has stated that all present theories and concepts of flowering are theories and concepts of photoperiodism since flowering or its absence are criteria of photoperiodism. It has been shown that cessation of terminal shoot elongation with the formation of a terminal bud is photoperiodically controlled. In the following section it will be shown that this physiological event is closely synchronized with the generative cycle in coniferous trees. It is not too fanciful to speculate, therefore, that the generative cycle in coniferous trees is to some extent under the influence of photoperiod, and that this is another reason why photoperiod is so closely linked to growth cessation and dormancy, and has little influence on dormancy release and flushing. Chailakhyan's dictum, therefore, could also apply to coniferous tree species as it does to so many other plant species.

Hendricks and Borthwick (1963) have shown that a bright-blue protein termed phytochrome regulates many aspects of plant growth and development, including dormancy. Phytochrome has two forms, P660 and P730, interconvertable under the action of photoperiod, or more correctly nyctoperiod.

It appears likely that the metabolic processes leading to increased levels of inhibitors and eventual dormancy in coniferous species are mediated by a phytochrome-like substance following reception of the stimulus of decreasing day length. For example Tobin and Briggs (1969) have recently demonstrated the occurrence of phytochrome in the embryos of long leaf pine (*Pinus palustris* Mill.) and elucidated its effect on seed dormancy and germination in that species.

It is possible that the photoperiodic reaction is determined, not only by the dark conversion of P730 to P660, but is the result of an interaction between an endogenous circadian rhythm and phytochrome (Bunning 1961, Hamner 1963). For example, there is some indication that populations of coniferous trees from northern latitudes and high elevations are more closely adapted to photoperiod than provenances from areas of long growing season, i.e. populations from low latitudes and low elevations. In the latter instance other factors may be of greater importance than photoperiod, though it must be pointed out that the theories of Bunning in regard to circadian rhythms and photoperiod have not been universally accepted (Romberger 1963).

Photoperiod and generative development

Many of the pine species of the world are represented at the Institute of Forest Genetics at Placerville, California, latitude 38°44'. In this locality, the longest day in summer is approximately 15 hours. Mirov (1956) has shown that flowering in these species is not inhibited at Placerville. For example, *Pinus silvestris* var. *Lapponica*, which has a northern distribution between latitudes 60°00' and 70°00', produced abundant male and female flowers at 29 years of age, despite the fact that the longest day in summer at latitudes spanning its range is approximately 19 hours. Mirov (1956) concluded that the pines at Placerville behaved not as long-day or short-day plants, but as neutral plants whose flowering is not affected by the length of day.

Mirov's conclusion was given as tentative, and it is possible to interpret somewhat differently the data presented. For example, almost the only species which did not flower well at the Institute were the four native pine species which occur naturally at the same latitude as the Institute, e.g. Pinus albicaulis, P. lambertiana, P. monophylla and P. edulis. Furthermore, there is some evidence that flowering was stimulated in species of extreme northern origin by the conditions at Placerville, for they flowered better than the four native pines mentioned. This, in the absence of a photoperiodic effect as a result of a transfer south, is difficult to explain.

It has already been observed that photoperiodic control of dormancy is strongest in species of northern and middle latitudes and less strong in species from southern latitudes. Furthermore, if dormancy is considered not merely in the negative sense of growth cessation, but as a developmental phase closely related to physiological aging, and generative development in coniferous species, the data presented by Mirov may be reinterpreted as follows. Flowering in northern pines is enhanced by a displacement south whereas a displacement to the north of southern pines has no effect on flowering until temperature becomes a limiting factor. Mirov's data, therefore, is not, as commonly thought, incompatible with the view that photoperiod has an effect on flowering in coniferous trees, for it is not unlikely that the disruptive effect of the photoperiodic regime at Placerville on the natural vegetative cycle of northern pines, e.g. Pinus silvestris var. Lapponica, has affected the generative cycle, and stimulated precocious and abundant flowering in these species.

Langlet (1944) has pointed out that when northern populations of Scots pine are grown in southern latitudes female strobili are initiated at an age earlier than normal for the species.

Pharis and Morf (1967) who investigated methods of inducing flowering in a number of coniferous species, concluded that induction and development of strobili in western red cedar (Thuja plicata Donn) is under photoperiodic as well as hormonal control. Full development of strobili occurred only when seedlings were subjected to a photoperiod sequence of long-day - short-day - long-day.

Giertych (1967) has suggested that flowering in pine is photoperiodically controlled, and that the initiation of male strobili is a short-day response, and the initiation of female strobili a long-day response. Owens (1969), however, has demonstrated that in Douglas fir (Pseudotsuga menziesii (Mirb) Franco), the exact time of initiation of male and female strobili as determined by histochemical tests does not vary from the proximal to the distal end of the shoot axis.

Owens (1969) has clarified the annual growth cycle in a coastal provenance of Douglas fir. Lateral bud initiation and the onset of vegetative bud activity occur simultaneously at the end of March. Seven weeks later flushing occurs, and ten weeks later lateral buds are cytochemically distinct, that is, by the end of May. Whether buds become vegetative or reproductive appears to be determined sometime during the eleven weeks after lateral bud initiation, that is, between the beginning of April and the end of June when vegetative shoots are fully elongated. Owens goes on to point out "that this is the period during which lateral primordia are most plastic with regard to their future development and when environmental and internal nutritional and hormonal changes could determine the particular pathway along which a primordium will develop".

Since gradual cessation of shoots elongation, and the formation of a terminal bud begins sometime in mid-June, there seems little doubt that this event is related physiologically to subsequent differentiation and development of reproductive buds. For example, Wareing (1950) has suggested that the effects of short days on dormancy and flowering may be mediated by a common regulator.

If such a constant environmental factor as photoperiod has an effect on the generative cycle of coniferous trees the question arises as to why cone crops are so erratic. Owens (1965) has shown that a period of seventeen months elapses between the initiation of reproductive buds and the development of mature seed cones in Douglas fir. It is clear that fluctuating environmental factors during this long period have a very large effect on the final cone crop. Therefore, in considering the possible effect of photoperiod on the generative cycle of coniferous trees it is necessary to clearly distinguish between the initiation of reproductive buds, and their subsequent development. In Douglas fir at least cone crop periodicity is a function of development rather than initiation (Silen 1967, Owens 1969).

CONCLUSIONS

1. Dates of flushing, and cessation of shoot elongation are population characteristics exhibiting a normal distribution within each population the mean of which varies parallel with the varying environments occupied by the species. The dates of flushing and cessation of shoot elongation characteristic of any one population must, therefore, be based on a relatively large number of individuals within the population.

2. In populations of coniferous trees of northern and middle latitudes temperature is the principal environmental factor influencing dormancy release and flushing.

3. Dormancy release is probably the result of a build up of gibberallins in response to rising temperatures and following winter chilling.

4. It is necessary to distinguish between dormancy release and flushing. Environmental factors which can have an effect on flushing may have little effect on dormancy release.

5. In populations of coniferous trees of northern and middle latitudes photoperiod exercises a major effect on cessation of terminal shoot elongation, and dormancy.

6. In regard to the microevolution of coniferous species there is no overwhelming survival advantage conferred by the photoperiodic control of flushing. On the other hand the photoperiodic control of growth cessation and dormancy, which is closely linked to the onset of the regenerative cycle, confers a survival advantage on the species.

7. The view, therefore, that all theories and concepts of flowering are theories and concepts of photoperiodism, since flowering or its absence are criteria of photoperiodism, could equally apply to coniferous tree species.

8. The transitional phase between cessation of terminal shoot elongation with the formation of a terminal bud is not true winter dormancy. This phase, therefore, can be influenced by environmental factors which have little effect during dormancy.

9. There is marked meristematic activity during the transitional phase prior to true winter dormancy, and it is possible that during this phase substances are synthesized which mediate the onset of the generative cycle.

10. The period during which there is gradual cessation of terminal shoot elongation with the formation of a terminal bud is synchronized with the period during which primordia are most plastic in regard to their future development. It is during this period that treatment could have maximum effect on the development of reproductive buds.

11. In any study designed to influence the periodicity of cone crops, it is necessary to distinguish between initiation of reproductive buds and their development and maturation. Factors which may influence initiation may have no effect on development or maturation and *vice versa*.

12. It is possible that for many coniferous species cone crop periodicity is more closely related to development and maturation rather than to initiation of reproductive buds.

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