FOREWORD

Life would be awfully dull without flowers. The love of flowers is common to all people all over the world, no matter how different their cultural patterns may be. *Artistically*, flowers play an important role in poetry and in decorative arts for their attractive structure, color and odor in endless variation: for their eternal beauty.

*Agriculturally*, and perhaps still more so *horticulturally*, flowers play an essential part in the production of all crops. This is, of course, most evident in floriculture, where the flower is the final product. In all fruit crops, whether deciduous or evergreen, and in crops like grains and the fruit-vegetables, the fruit is the final product, but flowers are the indispensable introductory step to fruit formation. For the many crops which are grown for their seeds, including all breeding projects, flowers and fruits cannot be missed for seed formation.

On the other hand, there are crops where flowers and fruits are undesirable — for instance, those which are grown for their roots, stems, or leaves. However, in seed growing and breeding of these crops, flowers again are indispensable.

The above implies that *control of flowering*, whether positively promoting or negatively preventing flowering, is a cultural measure which has to be applied in the growing of most, if not all, crops. No wonder that in several cases more or less sophisticated methods for controlling flowering are rather well known. Quite generally, such empirically developed methods are genetical and ecological, but an endless variation occurs in the requirements for flowering among different species and even among the cultivars of one species.

The human mind is not satisfied by answering the question as to which factors influence flowering — as approached empirically — it also wants to know the *physiological background* of the actions of these factors. This is a much more difficult problem, and disciplines like biophysics, biochemistry, and molecular biology enter the picture. It is self-evident that this approach has made much less progress than the empirical one. However, it has become clear that also in this respect an endless variation occurs among different species and that a general mechanism of action — if it exists — has not been found yet. Be that as it may, the study of flowering, whether empirical or — on a higher level — physiological, contributes to the development of the human mind by the attempt to understand some of the mysteries of Life.

In the foregoing I used “endless variation” no less than three times, and students of flowering, who concentrate on their own plant(s), run the risk of becoming one-sided. It is, therefore, highly important to provide them with a catalogue of the flowering behavior of as many other plants as possible. The present *Handbook* fills the existing gap by bringing together our knowledge of the individual cases. The “Table of Contents” illustrates that it was no simple effort to compose this edition. A. H. Halevy, “Abe” to his friends, has had the courage and the energy to undertake this task. All those who are interested in flowering in some or other way owe him their gratitude.

S. J. Wellensiek
Rise up, my love, my fair one, and come away.
For, lo, the winter is past,
The rain is over and gone;
The flowers appear on the earth;
The time of singing is come,
And the voice of the turtledove is heard in our land;
The fig tree puts forth her green figs,
And the vines in blossom give forth their fragrance.

(Song of Songs 2:10—13)

From antiquity, poets have expressed humanity’s association of flowering with spring, renewal, singing, beauty, fragrance, and love. This book deals with the more prosaic aspects of flowering: flower formation and development and the environmental and physiological factors which regulate them.

Several excellent reviews and books on flowering have been published in the last 25 years. These include Lang’s and Schwabe’s chapters in general encyclopedias of plant physiology, Evan’s opening and concluding chapters in his book, the books by Salisbury, Vince-Prue, and Bernier et al. and the several review articles in the Annual Reviews of Plant Physiology. With the exception of Evans, these authors have presented a general review of the flowering process and attempted to integrate the data into a unifying theory. Such unifying theories have generally suffered from the disadvantages noted by Evans in the preface to his book; they deal primarily with the earliest events of the flowering process, and they are based on data obtained from a small number of “model” plants. Evan’s book, which contains flowering “case histories” of the majority of these species, includes chapters on only 20 plants, of which only one is a woody plant, two are monocotyledons, and none is a gymnosperm. A great wealth of data on the regulation of flower formation and development can be found in the practical literature of agriculture, horticulture, and forestry. Much of this has been often ignored by flowering physiologists. The flowering process is indeed much more diverse than that revealed in the 20 “model” plants presented in Evan’s book. It was my aim in planning this book to make a more comprehensive view of the flowering process possible by presenting relevant data from as many plants as possible. This includes the majority of the cultivated plants on which such information is available: field crops, fruits, vegetables, ornamentals, industrial plants, and forest trees, not only of the temperate regions, but also of subtropical and tropical climates. To accomplish this goal I have invited scientists from all over the world to contribute chapters on specific plants or groups of plants. Many of the authors have not only reviewed the available literature, but have also included previously unpublished data. Many of the chapters present the first general review of the flowering process in their specific subject area.

The book deals with all aspects of flowering, including juvenility and maturation, flower morphology, flower induction, and morphogenesis to anthesis. Flower morphogenesis has been taken to include also development of individual flower parts, sex expression, and flower malformations. When possible the authors have attempted to present information on all stages of the flowering process. In many cases, however, this has not been feasible, since little or nothing is known about some of the stages. In most cases the “flowering story” is terminated at anthesis. In some plants, however, flower structure and anthesis are directly related to pollination, and in these cases pollination is also included. In some commercial
food crops the description is also extended somewhat beyond anthesis to include important factors in crop production. In many cultivated plants, mostly ornamentals, practical methods for manipulation of flowering are included.

The length of the individual chapters and the emphasis on specific aspects depends in most cases on the availability of experimental information and not on the importance of the plant as a crop or the significance of the physiological stage described. Some important economic plants are absent from this book since little or no information is available on their flowering. In some cases most of the chapter is devoted to a single aspect of flowering, such as juvenility, flower induction, flower development, sex expression, cleistogamy, development of certain flower parts, or flower opening. Some chapters concentrate on physiological aspects, others on ecological, morphological or genetic ones. Other aspects are covered only briefly or even absent, not because they are not important but because they have not been studied in detail.

I am well aware that this book is far from being a comprehensive encyclopedia of flowering. I would greatly appreciate comments from readers on errors found in articles, missing information, and plants not included in the book, whose flowering process have been documented.

The handbook consists of five volumes:

- **Volume I** — contains general chapters on groups of plants, and individual chapters on plants beginning with the letter A
- **Volume II** — contains plants of letters B to E
- **Volume III** — contains plants of letters F to O
- **Volume IV** — contains plants of letters P to Z
- **Volume V** — will be a supplementary volume and will include chapters on plants not included in Volumes I to IV, listed in alphabetical order, and will appear after the first 4 volumes

The merit of the book rests upon the work of the individual authors. I am grateful to them for their efforts, cooperation, and forbearance. I would like to thank my colleagues in the Editorial Board who helped me to select the authors and to review the chapters, and the many other colleagues who helped in reviewing (and sometimes rewriting) specific chapters.

I hope that this Handbook will serve as a reference and source book for scientists interested in the flowering process of particular plants, and will draw their attention to the lack of information on important aspects of the flowering process in many important plant species. I also hope that the wealth of information accumulated here will be useful in future attempts to synthesize general theories of the physiology of flowering.

**REFERENCES**


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Editor's note — The following genera beginning with letter “A” will appear in Volume V: Actinidia, Anacardium, Anona, Aquilegia, Asclepias, Aster novi-belgii, and Aurina.
TEMPERATE CONIFER FOREST TREES*

Denis P. Lavender and Joe B. Zaerr

INTRODUCTION

In a 1971 review, Evans\textsuperscript{1} noted that more than 1200 papers pertaining to flowering in higher plants appeared in a 6-year period in the late 1960s. The majority of the papers were devoted to angiosperms, but conifers were not neglected. Recent reports have related production of strobili in conifers to shade, root pruning, girdling, nutrition, drought, climate, root environments, and growth regulators. Virtually all trials have dealt with single factors at a discrete point in the ontogeny of the experimental material. Romberger and Gregory\textsuperscript{2} suggest three reasons that such an approach may be inappropriate for elucidating mechanisms of flowering in perennial plants.

First, woody perennials could not survive if flowering were controlled solely by a single factor such as photoperiod (which has been shown to be the prime environmental stimulus for flowering of many annuals). Reproductive development must not include all vegetative apices; many or most must remain vegetative if a plant is to make reasonable growth and to avert senescence and death. Therefore, it is probable that numerous biochemical or physiological systems control flowering in every bud on the tree.

Second, trees sufficiently mature to flower carry a "burden of history" (perhaps a correlation of meteorological events 2 years before production of reproductive structures with abundance and frequency of flowers in a forest stand). Romberger and Gregory\textsuperscript{2} (pp. 134—135) state, "Tissues that were differentiated or modified in response to last month's or last year's conditions (drought, heat, cold, photoperiod, etc.) are still present and are a part of the microenvironment of the meristematic tissues today. Metabolites and growth regulators synthesized in response to yesterday's conditions may still be present today and may influence responses to today's environment. Because of the much longer integration time of environmental influences upon tree development as compared to herb development, it is not likely that flowering in trees can be understood by studying environmental influences over a short time period.

Third, Romberger and Gregory\textsuperscript{2} point out that much published data on the formation of reproductive structures on trees concerns developmental stages in flower buds which occur substantially later than floral initiation. Owens\textsuperscript{3} notes, for instance, that sporangia appeared first about mid-March of the year of flowering in the latitude of Victoria, B.C., whereas flower initiation started nearly a year earlier.

The problem of elucidating the mechanism of flowering in forest trees is complicated still further by imprecise definitions of "maturity" and "aging". The burden of evidence suggests that transition from the juvenile to the mature phase is permanent, whereas material from an "aged" plant, i.e., one which has lost vigor during the course of development, may be rejuvenated if it is grafted on juvenile rootstock.\textsuperscript{4}

Juvenility has been defined as the inability to flower.\textsuperscript{5} This definition can lead to confusion when treatments are described as stimulating flower production during the juvenile phase of a plant; it is especially confusing with reference to conifers, which manifest no clear distinction between juvenile and mature material other than, perhaps, the ability of cuttings to root.

Researchers have obviated the problem of the distinction between juvenile and mature phases by working with mature trees. But this presents other problems because of the size

\* A supplementary chapter by R. P. Pharis on some aspects of this subject will be included in Volume V of this Handbook.
Table 1
TREATMENTS THAT HAVE STIMULATED FLOWERING OF SPECIES IN GENERA OF THE PINACEAE AND IN OTHER FAMILIES OF THE CONIFERALES

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gravimorphism</td>
<td>Larix leptolepis⁷</td>
</tr>
<tr>
<td>Girdling</td>
<td>Thuja plicata⁸</td>
</tr>
<tr>
<td>GA</td>
<td>Larix leptolepis⁹</td>
</tr>
<tr>
<td></td>
<td>Pinus elliottii</td>
</tr>
<tr>
<td></td>
<td>Picea abies¹⁰</td>
</tr>
<tr>
<td></td>
<td>Picea stichensis¹⁰</td>
</tr>
<tr>
<td></td>
<td>Chamaecyparis lawsoniana¹⁰</td>
</tr>
<tr>
<td></td>
<td>Juniperus virginiana¹⁰</td>
</tr>
<tr>
<td></td>
<td>Libocedrus decurrens¹⁰</td>
</tr>
<tr>
<td></td>
<td>Thuja plicata¹⁰</td>
</tr>
<tr>
<td></td>
<td>Cryptomeria japonica¹⁰</td>
</tr>
<tr>
<td></td>
<td>Metasequoia glyptostroboideis¹⁰</td>
</tr>
<tr>
<td></td>
<td>Sequoia sempervirens¹⁰</td>
</tr>
<tr>
<td></td>
<td>Taxodium distichum¹⁰</td>
</tr>
<tr>
<td>Mineral salts (fertilizer)</td>
<td>Picea glauca⁸</td>
</tr>
<tr>
<td>Temperature</td>
<td>Picea abies¹¹</td>
</tr>
<tr>
<td></td>
<td>Picea stichensis¹²</td>
</tr>
<tr>
<td></td>
<td>Tsuga heterophylla¹³</td>
</tr>
<tr>
<td></td>
<td>Tsuga heterophylla¹⁴</td>
</tr>
<tr>
<td></td>
<td>Larix leptolepis¹⁵</td>
</tr>
<tr>
<td></td>
<td>Larix decidua¹⁵</td>
</tr>
</tbody>
</table>

of the experimental material, unless grafting is used. Probably all of a score or more of endogenous factors must be permissive if flowering is to occur. Current data do not define such factors with precision, so it is not surprising that empirical trials frequently yield conflicting results.²

This chapter will discuss research concerning “flowering” in the Pinaceae, although as Romberger⁶ (p. 7) notes, “In its strictest traditional morphological sense, a ‘flower’ is a determinate and sporogenous modified shoot which bears carpels. If this definition were accepted, sporogenous strobili of gymnosperms would not be flowers, because they have no true carpels. Likewise the pollen-producing catkins of many hardwood trees would be excluded, because they lack even rudimentary carpels.” The meristems that produce reproductive structures in this group are borne laterally on developing current-year shoots. Development differs with species but has in common that meristems giving rise to male strobili are entirely expended in the process, whereas those producing female strobili are not. In fact, vegetative shoots are occasionally found on the distal ends of ovulate strobili.

Table 1 summarizes various treatments that have stimulated the formation of male or female flowers on species in several genera of the Pinaceae and in other families of the Coniferales.

THE GENUS PSEUDOTSUGA (Douglas-fir)

Flower Initiation and Development

The genus Pseudotsuga Carrière (1867) belongs to the subfamily Abietidae of the family Pinaceae. The species menziesii is native over a wide range extending from central British Columbia to northern Mexico and from the Pacific Ocean to the eastern Rocky Mountains.

Florin¹⁶ reviewed the extensive literature covering the morphology of the female cone in
conifers. He concludes (p. 382) that "living conifers are characterized by having more or less distinctly cone-shaped compound strobili and megasporangia borne terminally on extremely reduced fertile appendages (megasporophylls), themselves lateral organs on the rudimentary axis of the axillary simple strobilus."

Lateral bud initiation for the following year is first evident in vegetative Douglas-fir buds in early spring, about 1 month before they break or about when current-year female cone buds break. Cataphylls are initiated and develop until early July, when leaf, bract, or male bud initiation begins. Development of the male and female cone buds continues at a declining rate from August until early November.

The male cone buds are commonly clustered on the sides of the proximal portion of a lateral shoot and consist of bud scales that enclose a simple strobilus which has a single axis bearing a spiral series of microsporophylls.

Female cone buds are also borne on the sides of the shoot, generally singly or in twos and threes near the proximal end. The bud scales enclose a compound strobilus, which consists of a spiral series of bracts initiated and developed between July and late September, and ovuliferous scales borne in the axil of the bracts. The seed scales, each of which bears two ovules, are initiated in early October and develop until mid-November. Further development occurs in early spring before bud break.

"Ripeness to flower" in perennial woody plants has been suggested as a function of either plant size or age. The aging of Douglas-fir seedlings has been accelerated by cycling them through more than one annual cycle per year in greenhouses and growth chambers at Oregon State University. It was possible to achieve two growth periods annually in a study that was conducted for 8 years (the plants completed 16 annual cycles), but no flower buds appeared on the treated plants after outplanting.

Isaac notes that open-grown Douglas-fir saplings may begin flower production when they are 10 to 15 years old. We have observed that young Douglas-fir, growing from seed in association with grasses, may produce flowers as early as the fifth growing season. Such precocious production is not common, but flower production in 6- to 8-year-old plants in Christmas tree plantations is not rare.

Flower production on Douglas-fir is commonly greatest on open-grown trees, but, regardless of competition, trees 250 to 400 years old commonly bear many more flowers than do trees about 40 years old. Garman suggests that the younger trees normally bear fewer than 100 cones (Eis suggests as many as 2000 cones may be borne during a "good" cone year, while older trees may produce between 10,000 and 15,000 cones.) However, Douglas-fir, perhaps the most erratic flower producer of all Pacific Northwest conifers, produces a good cone crop, on average, only once every 7 years.

Silen notes that the difference between years of abundant and few female and male flowers arises not from the number of flower buds initiated but from the number aborted. Most flower buds initiated during the growing season before a good flower-crop year develop during the summer and mature in the fall, but flower buds initiated during the year before a poor flower crop cease development in July, and the buds then abort.

**Effect of Environment**

**Temperature**

No data have led researchers to infer that Douglas-fir flower buds have a cold requirement. Nor do they suggest that the chilling requirements for initiation of potential flower-bud primordia in the quiescent vegetative bud in early spring, or for their subsequent differentiation during extension of the vegetative shoot in late spring and early summer, differ from that of a vegetative bud containing only vegetative primordia. One can infer, however, that the raison d'etre for the cold requirement of vegetative Douglas-fir buds, i.e., protection against activity during an unseasonable midwinter warm spell, obtains equally well for
reproductive buds. Studies by Lowry, Vredenburgh and Bastide, and Eis suggest that the meteorological sequence 2 years before cone maturity influences the size of cone crops, but the sequence does not constitute a chilling requirement for reproductive buds. Further, such meteorological data do not necessarily reflect conditions required for flower bud initiation or differentiation, since abortion of buds or flowers could result in a poor cone crop. Bonnet-Masimbert notes that reproductive buds can develop on lammas shoots that have had no chilling.

Wommack demonstrated that although speed of bud burst did differ with provenance, seedling Douglas-fir generally required 12 weeks of chilling to satisfy the cold requirements of vegetative buds. Van den Driessche essentially agrees with that assessment, but Lavender and Wareing note that the chilling requirement of Douglas-fir buds is strongly affected by the environment during quiescence and early rest. Reproductive buds resume activity in late winter, earlier than vegetative buds, either because of a differing chilling requirement or differing thermal requirement for bud activity.

Webber and Bonnet-Masimbert and Lanares report that drought may stimulate development of reproductive buds on Douglas-fir; no data demonstrate the promotive value of a given thermoperiod (air temperature). But maintenance of soil temperature at about 3°C for potted seedlings during the period March to October will stimulate production of both male and female buds. The flowers develop not on seedling tissue, but on scion material cut from mature trees and grafted onto the seedlings. Such response is not associated with either significant moisture or mineral stress and is evidence for movement of a promotive substance from the roots to the scion (or for lack of an inhibitor) and for a “ripeness to flower state” of shoot tissues before promotive substances can trigger flower production.

Moisture

Ebell and Bonnet-Masimbert and Lanares report that drought may stimulate development of reproductive buds. Ebell, working with potted grafts, subjected populations to drought between April 28 and June 28. In the following spring, 40% of the drought-stressed plants had male or female flowers, while no control plants flowered.

Bonnet-Masimbert and Lanares report that flower buds appeared on the lammas shoots of Douglas-fir saplings after a midsummer drought in southwestern France. They speculate that the intermittent rainfall and warm summer climate of this region stimulates reproductive development. Their observations confirm those of Silen that flower buds may differentiate after the late spring-early summer period suggested by Owens.

The apparent correlation between summer drought and flowering of Douglas-fir has prompted location of seed orchards on the northeastern coast of the Olympic peninsula and on southeastern Vancouver Island, both of which lie in the rain shadow of the Olympic Mountains.

Light

Jackson and Sweet note that photoperiod does not appear to affect flowering in many forest trees, and certainly there is no clear evidence that it does so in Douglas-fir. Allen and Owens state that both potential reproductive and vegetative bud primordia first appear in a vegetative bud in spring at about the time of the breaking of flower buds. Axillary bud primordia develop simultaneously along the length of the extending shoot during a period characterized by neutral, albeit rapidly lengthening, days. Differentiation of the primordia does not occur until late June and may be associated with cessation of shoot elongation. Other data also demonstrate that daylength is probably not a factor in differentiation of Douglas-fir flower buds. Silen demonstrated a significant change in bud differentiation in late June, and Bonnet-Masimbert observed that flower buds were initiated on lammas shoots under 16-hr photoperiods and on shoots of the initial growth flush under an 11-hr day. Lavender and Ching observed a change from vegetative shoot to female flower on one plant during budburst in early spring.
Silen reports that shading a Douglas-fir branch under a double-layered white muslin bag for 1 month between March and September resulted in fewer female flowers both in the year of treatment and in the following year. He states (p. 533) that "events associated with floral development are more pertinent in Douglas-fir cone crop enhancement than specific floral-inductive or bud-initiative events."

**Mineral Nutrition**

Investigations of the effect of mineral nutrition on flowering in Douglas-fir have been concerned primarily with nitrogen, although Ebell has reported that neither phosphorus nor potassium stimulated flowering.

Ebell notes that application of nitrate nitrogen (but not ammoniacal nitrogen) at bud break greatly increased production of flowers the following year on 20-year old Douglas-fir trees. Though the treatment did not stimulate bud initiation, it apparently permitted more buds to develop to maturity. The dependence upon treatment during the period of vegetative bud break in mid-May for positive results is in sharp contrast to the treatment results of Silen and Bonnet-Masimbert and Lanares discussed earlier. Ebell speculates that coning may result from a sharp change in levels of nitrogenous compounds rather than from increased vigor after nitrogen uptake, but he does not present data to substantiate his hypothesis. However, an earlier report shows that levels of the amino acids arginine, lysine, and ornithine and of soluble nitrogenous compounds, especially other guanidino substances, were higher in trees treated with nitrate nitrogen than in those treated with ammoniacal nitrogen. In contrast, the saplings treated with ammoniacal nitrogen incorporated a higher percentage of absorbed nitrogen in protein than did the nitrate-treated plants. Ebell and McMullan suggest that specific amino acids participate in development rather than initiation of flower buds. However, their hypothesis that arginine levels may regulate flowering in Douglas-fir is not upheld, at least for seedling plants, by the data of Ching et al., which show that fertilization increased free amino acid levels 10-fold and arginine levels 40-fold. In later observations, however, no flowers were noted on either treated or control populations. Further studies are needed to clarify the role of mineral nutrients.

**Weather**

Several workers have found that cone crops correlate with weather sequences occurring as long as 27 months before cone maturity, but none elucidate possible causative effects of weather on flower production.

Lavender and Ching used both ordinary seedlings and seedlings with scion material from mature trees grafted into their crowns to test the 2-year weather sequence that Lowry suggests stimulates flower production. Four seedling populations were subjected to the prescribed sequence of weather modifications, one population initiating the sequence in each of 4 successive years. Flowers appeared only occasionally and were not related to the treatments.

**Cultural Treatments**

Numerous reports substantiate the hypothesis that perennial woody plants may be induced to flower by girdling individual branches or the main stem. Presumably, this treatment checks the basipetal movement of substrate, making more carbohydrate available to support development of reproductive buds. The low soil temperature that stimulates flowers on Douglas-fir may in fact be a girdling mechanism that reduces transport of carbohydrate in the roots, leaving more carbohydrate available to support reproductive development. However, girdles, whether applied directly or indirectly, as in the instance of graft incompatibility, may kill the affected part. Flowers produced immediately before death are often seen as "distress crops," and they may not be a result of normal stimulation and development.
Ebell\textsuperscript{44} girdled one member of each of several pairs of 20-year-old Douglas-fir trees. The trees generally produced more flowers in the 4 years after girdling, though treated and control trees initiated the same number of buds. Timing was important, the largest number of flowers being stimulated by girdling about 1 month before expansion of vegetative buds. Girdling later than 1 week after bud break depressed the numbers of flowers the following year. Girdling treatment and carbohydrates in treated and control trees were apparently not correlated.

Longman et al.\textsuperscript{7} reported that tying the branches of Japanese larch (Larix leptolepis [Sieb. & Succ.] Gordon) horizontally or downward stimulated production of flower buds, but similar treatments of 10- to 20-year-old Douglas-fir did not.\textsuperscript{45}

Bonnet-Masimbert et al.\textsuperscript{55a} demonstrated that a lack of active root growth during the treatment period was necessary for a positive flowering response to applications of gibberellin to Douglas-Fir and, further, that treatments which prevented root growth could, by themselves, stimulate production of flowers.

**Growth Regulators**

McMullan\textsuperscript{46} and Puritch et al.\textsuperscript{47} review a large body of literature describing effects of plant growth regulators on the initiation of Douglas-fir flower buds. The consensus of the papers is that gibberellins, primarily the less polar molecules such as GA 4, 7, or 9, may be associated with the development of reproductive structures on Douglas-fir. However, topical applications of these compounds to Douglas-fir produce erratic, unpredictable results. McMullan\textsuperscript{46} demonstrated significant enhancement of both male and female flower production after treatment with a GA 4/7 mixture, but as concentrations of these materials in the treated buds were 5000 times the endogenous level, the flowering response may have been a "distress crop" (several twigs were killed by the treatment) rather than a true response to a hormone. Analyses of sap from a tree that consistently bore good flower crops and from a nonflowering tree did not show differing gibberellin levels. However, gibberellin analyses are based upon bioassays whose accuracy and specificity at the nanogram level are questionable; therefore the results may be an artifact of the analysis system.

Unpublished research at Oregon State University\textsuperscript{48} has shown that Douglas-fir male, female, and vegetative buds differ in levels and complements of both auxins and cytokinins, but it has not shown that such differences are responsible for bud differentiation.

Unpublished observations also indicate that precocious flowering of Douglas-fir seedlings is most likely to occur in association with grass species (as on golf courses or Christmas-tree farms). At Oregon State University,\textsuperscript{49} spring bud break of potted seedlings grown with rye grass or irrigated with water leached through a grass sod was retarded, and shoot extension was reduced, responses typical of an allelopathic relationship. However, neither these treatments nor plantation culture of Douglas-fir seedlings with grass competition resulted in enhanced or early flower production.

**Conclusions**

The available information on flower production in Douglas-fir agrees in these respects:

1. Shoot tissues must have achieved a state of "ripeness to flower", and they must have produced bud primordia that may differentiate into reproductive structures. Generally, reproductive structures, especially male flowers, are associated, both spatially within the crown and, temporally, with reduced vigor of shoot growth.

2. Differentiation and development of reproductive buds is dependent upon materials, produced elsewhere in the plant, which are often associated with reduced root activity.

3. Early development of reproductive structures is dependent upon specific timing of promotive events. The course of later development depends upon a generally promotive environment rather than a specifically timed event, and it is labile, i.e., vegetative buds may become reproductive and vice versa.
THE GENUS *PINUS*

En. pine, Fr. pin, Ge. Föhre, Sp. piño

**Flower Initiation and Development**

Species of *Pinus* are divided into two groups according to the date of their seed cone differentiation: the hard pines, represented by *Pinus contorta*, and the soft pines, represented by *P. monticola*. Pollen cones of hard pines differentiate in late summer and seed cones in the fall, just before dormancy. Pollen cones of soft pines are also initiated in late summer, but seed cones do not differentiate until the following spring, just before pollination.

Of course, the exact timing of the morphological development of trees, including flower formation, is modified by environmental and other factors, but clearly, the approximate time of differentiation must be known before attempts to modify the process are likely to succeed. The times of seed cone differentiation for *P. contorta* and *P. monticola* stated here are therefore only guidelines, and treatments on other species need to include a study of timing of initiation.

The juvenile period for *Pinus* species commonly persists for 4 to 20 years, after which the plant has the potential, depending upon its environment, to differentiate reproductive structures.

Cone crops are usually periodic rather than evenly distributed from year to year, and heavy cone crops are often followed by crop failure or very light production. The reasons for this periodicity are many: insects, squirrel damage, climatic conditions, and inherent characteristics of the species.

**Effect of Environment**

*Temperature*

Temperature may be one important factor controlling flower induction. Maguire reports that *P. ponderosa* produced good cone crops 27 months after above-average temperatures in April and May. On the other hand, Daubenmire found that April-May temperatures had no effect, but that higher than average temperature from June to September closely correlated with good cone crops 2 years later. Puritch suggests that the opposing requirements of cool summers for bud initiation and warm summers for flower differentiation and development are the major causes for periodicity. Although studies appear to relate high temperature with good flower production, the correlations are based only on field observation and are not demonstrations of cause and effect. It is possible that internal moisture relations, which are strongly affected by temperature, are more important in flower initiation than temperature as such (see following section).

More recently, Longman showed that *P. contorta* cuttings produced more male flowers when given cool treatment (15°C day/8°C night) than when given warm treatment (22°C day/15°C night) during the time of flower initiation, but apparently female flower initiation was not affected. Thus, though it seems to be related in some way to cone differentiation, little information is yet available on how to induce flowering by controlling temperature.

*Moisture*

Water supply also appears to correlate with flower production, but the evidence is not clear. High rainfall from May through July correlated with high flower production in *P. palustris* the following year, but high rainfall in April and May, followed by low rainfall in June and July, correlated with low flower production. Irrigation experiments substantiate these field observations. *P. monticola* and *P. elliottii* produced more pollen strobili when watered during the summer, but the number of female flowers was the same or reduced. In another study, irrigation stimulated male cone production in *P. elliottii* and produced more seeds per cone, but the seed was slightly lighter. Plants should not be irrigated in the
summer during flower initiation, but adequate water should be available when ovule fertilization occurs in the spring.\textsuperscript{57}

Irrigation of \textit{P. taeda} during April to June, followed by July to September drought, resulted in a larger cone crop the following year.\textsuperscript{58} In two other studies of the same species, irrigation substantially increased seed yield in seed orchards.\textsuperscript{59} The combination of adequate water supply and appropriately timed drought may prove to be an important technique for inducing flowering in pines. Giertych\textsuperscript{60} observed that warmth and drought during the flower induction period favors initiation of both male and female primordia. Greenwood,\textsuperscript{61} who subjected potted \textit{P. taeda} grafts to different levels of moisture stress during the induction period (mid-July through August), reported that plant moisture-stress levels of $-10$ bar (as opposed to $-3$ to $-5$ bar for the control) promoted the induction of female flowers. In combination with other treatments, such as girdling and treatment with gibberellins, the effect of high plant moisture stress was even greater. Callegos,\textsuperscript{62} using a “water balance” method to estimate drought, found that in seed orchards of \textit{P. taeda}, drought during the flower differentiation period, combined with irrigation during cone maturation, resulted in increased differentiation and development of ovulate cones.

These experiments indicate that pines apparently need drought stress for favorable flower differentiation. But drought may not, in fact, be the primary physiological factor in flower induction. In Douglas-fir, reduced root temperature increased production of male cones.\textsuperscript{32} When root activity was arrested by drought, flooding, or high temperature, more female cones were produced than were produced on control plants.\textsuperscript{63} The same physiological mechanism could be operating in pines. If so, any treatment that reduces root activity during the period of cone initiation should increase flowering. This hypothesis may account for many observations on flowering in \textit{Pinus} species, but it has yet to be tested.

\textbf{Light}

The photoperiodic effects on flowering in pines is apparently variable. Mirov\textsuperscript{64} grew 58 pine species and reported that pines are day neutral, their ability to flower being unaffected by photoperiod. In a more detailed study, no photoperiodic effect was found in \textit{P. attenuata}.\textsuperscript{65} But Larson\textsuperscript{66} caused a shift from female to male flower production in \textit{P. banksiana} with slightly longer days. More conclusively, Longman\textsuperscript{67} found that 10-hr days for 11 weeks induced 6 times as many female flowers in \textit{P. contorta} as long days (19.5-hr photoperiod). It appears that under certain conditions photoperiod may modify the induction of flowering structures for at least a few pine species, but the extent to which it can be used to manipulate flowering in other species of pine is not clear. Oddly, though much has been learned about the effects of photoperiod in woody plants during the last 50 years, little is known about its relation to flower initiation in pines.

Light intensity may have minor effects on cone differentiation and development. In one study, \textit{P. elliottii} was found to produce more female flowers on the side receiving the greatest amount of light.\textsuperscript{68} (Thinning to increase light in the crown is now a common method for increasing cone production in seed orchards of southern pines.\textsuperscript{59}) A similar effect was reported for \textit{P. silvestris}, and it was noted in addition that male flowers usually formed in shaded areas.\textsuperscript{69} Hashizume\textsuperscript{70} reports that colored paraffin paper bags covering shoots of \textit{P. densiflora} or \textit{P. thunbergii} caused sex reversal. Giertych\textsuperscript{60} observed that high light intensity during the time of cone differentiation for \textit{P. silvestris} had promoted only female flowers. He suggests that the stimulus was perhaps increased temperature associated with high light intensities rather than the light itself. Because heat and light were not separated in any of these experiments, a conclusion with respect to the effect of light intensity on flower initiation in pines is not yet possible.

\textbf{Mineral Nutrition}

Fertilization is the most commonly utilized technique for increasing pine cone production.
Numerous experiments, however, report varying results with fertilizers, probably due to differences in the natural fertility of the soil, different seasons of application, different forms of fertilizer (such as ammonium instead of nitrate nitrogen), or differing environmental conditions. Chalupka and Fober report that potassium slightly increased flowering on *P. silvestris* but conclude that fertilization was not necessary for flowering on their relatively fertile site. Despite the often uncertain effects on cone production, fertilizer is widely used because it is easy to apply and because it usually produces other beneficial effects, such as increased growth and tree vigor. *P. elliottii* and *P. taeda* in southern pine seed orchards generally respond favorably to applications of ammonium nitrate.

Irrigation can enhance the fertilizer effect, and a wide variety of pines have shown increased cone yields with fertilizer treatment under certain conditions. It appears, therefore, that careful fertilizer application can be expected to improve cone yield when soil fertility is the limiting factor in tree growth and vigor, which is true for most forest sites.

Although addition of fertilizers in seed orchards is common practice, the mechanism of its action is not understood. Ebell and McMullan suggest that the amino acid content at the flower induction site leads to periodicity of flower crops, but Lee et al. found low N levels in buds and increased female flower differentiation in *P. elliottii*. Sweet and Hong fertilized *P. radiata* grafts and cuttings and showed that the concentration of free arginine increased considerably in buds with potential for flower production but that the increase was not associated with more cone production. They suggest that nitrogen may increase crown size and the number of sites in the crown where flowers may be initiated rather than influence flower initiation directly. This may explain the generally stimulating effect of fertilization on clones already producing cones and the failure of fertilization to induce differentiation in clones not already producing flowers.

**Cultural Treatments**

Girdling of pines often induces flowering, but results vary. Hare reports that seed orchards of *P. elliottii* and *P. taeda* increased male flowering tenfold or more after combined branch girdling and chemical treatments or fertilization. He concluded, however, that girdling was too often lethal and too time consuming for use in seed orchards.

Girdling must be timely, usually just before flower differentiation. Greenwood girdled the main stem as well as branches of *P. taeda* at the beginning of summer (just before flower differentiation) and the number of female cones per branch increased. Chalupka induced both male and female flowers with branch girdling of *P. silvestris*. The girdle is usually two slightly overlapping grooves around the stem through the phloem; Longman, however, completely ringed the bark in the spring to increase male and female cones in *P. silvestris*.

Strangulation, restriction of the translocation pathway of a tree, has been tested on pines, but results are varied and generally ineffective. Moreover, strangulation may cause irreparable and fatal damage to the tree.

Pruning, on the other hand, is less harmful and is effective in some species. It has induced flowering in *P. densiflora* and *P. thunbergii* and increased the number of flowering stems per ramet in a breeding arboretum of *P. radiata*. The obvious problem with pruning is that it may remove potential sites for flower initiation, thus reducing the total production of cones per tree, which was the case in a seed orchard of *P. elliottii*.

**Growth Regulators**

Gibberellins (GA) are known to induce flowering in conifers, especially in the Cupressaceae and Taxodiaceae. But their effectiveness in inducing flowering in the pines has been disappointing. Some workers report little or no effect on pine species; others report positive effects of GA in *P. contorta*, *P. taeda*, *P. palustris*, *P. silvestris*, and *P. banksiana*. Where GA are effective, their use is usually enhanced by simultaneous
treatments such as drought stress or girdling. It is likely that other pines may respond to GA application, but because their sensitivity is low, this kind of chemical stimulus is not likely to be important for flower induction programs in seed orchards unless improved techniques are developed or more effective hormones are discovered. Other chemicals such as auxins and cytokinins may be important flower inducers in years to come, but information currently available indicates that growth hormones other than GA have only a minor effect on the flower induction process in pines.66,70,84

Conclusions
At present, the most effective agents of increasing pine flower production are fertilizer, drought during the time of flower differentiation, irrigation during dry seasons, and pruning or girdling of branches. Short photoperiods and use of GA may be helpful in certain species and may be more important in the future.

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