

CRC REVIVALS

# Handbook of Flowering

Volume I

*Edited by*  
**Abraham H. Halevy**



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# CRC Handbook of Flowering Volume I

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## 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

## PREFACE

*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<sup>6</sup> and Schwabe's<sup>9</sup> chapters in general encyclopedias of plant physiology, Evan's opening and concluding chapters in his book,<sup>4</sup> the books by Salisbury,<sup>8</sup> Vince-Prue,<sup>11</sup> and Bernier et al.<sup>1</sup> and the several review articles in the *Annual Reviews of Plant Physiology*.<sup>2,3,5,7,10,12</sup> With the exception of Evans,<sup>4</sup> 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;<sup>4</sup> 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.

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He has twice received the Alex Laurie award of the American Society of Horticultural Science, and was recently (1983) nominated as a fellow of the society.

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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<sup>1</sup> 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<sup>2</sup> 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<sup>2</sup> (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<sup>2</sup> 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<sup>3</sup> 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.<sup>4</sup>

Juvenility has been defined as the inability to flower.<sup>5</sup> 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**

Treatment	Species
Gravimorphism	<i>Larix leptolepsis</i> <sup>7</sup>
Girdling	<i>Thuja plicata</i> <sup>8</sup>
	<i>Larix leptolepsis</i> <sup>9</sup>
GA	<i>Pinus elliotii</i>
	<i>Picea abies</i> <sup>10</sup>
	<i>Picea stitchensis</i> <sup>10</sup>
	<i>Chamaecyparis lawsoniana</i> <sup>10</sup>
	<i>Juniperus virginiana</i> <sup>10</sup>
	<i>Libocedrus decurrens</i> <sup>10</sup>
	<i>Thuja plicata</i> <sup>10</sup>
	<i>Cryptomeria japonica</i> <sup>10</sup>
	<i>Metasequoia glyptostroboides</i> <sup>10</sup>
	<i>Sequoia sempervirens</i> <sup>10</sup>
	<i>Taxodium distichum</i> <sup>10</sup>
Mineral salts (fertilizer)	<i>Picea glauca</i> <sup>9</sup>
Temperature	<i>Picea abies</i> <sup>11</sup>
	<i>Picea stitchensis</i> <sup>12</sup>
	<i>Tsuga heterophylla</i> <sup>13</sup>
Drought	<i>Tsuga heterophylla</i> <sup>14</sup>
	<i>Larix leptolepsis</i> <sup>15</sup>
	<i>Larix decidua</i> <sup>15</sup>

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.<sup>2</sup>

This chapter will discuss research concerning “flowering” in the Pinaceae, although as Romberger<sup>6</sup> (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.

Florin<sup>16</sup> 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.<sup>17</sup> 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.<sup>18</sup>

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 axils 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.<sup>18</sup>

“Ripeness to flower” in perennial woody plants has been suggested as a function of either plant size or age.<sup>19</sup> 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.<sup>20</sup> 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<sup>21</sup> 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<sup>22</sup> suggests that the younger trees normally bear fewer than 100 cones (Eis<sup>23</sup> 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.<sup>23,24</sup>

Silen<sup>25</sup> 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'être* 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,<sup>24</sup> Vredenburg and Bastide,<sup>26</sup> and Eis<sup>23</sup> 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<sup>27</sup> notes that reproductive buds can develop on lammas shoots that have had no chilling.

Wommack<sup>28</sup> 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<sup>29</sup> essentially agrees with that assessment, but Lavender and Wareing<sup>30</sup> 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<sup>31</sup> was not able to demonstrate that air temperature in excess of 30°C stimulated 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.<sup>32</sup> 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<sup>33</sup> and Bonnet-Masimbert and Lanares<sup>34</sup> report that drought may stimulate development of reproductive buds. Ebell,<sup>33</sup> 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<sup>34</sup> 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<sup>35</sup> that flower buds may differentiate after the late spring-early summer period suggested by Owens.<sup>36</sup>

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<sup>37</sup> 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<sup>18</sup> 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.<sup>36</sup> Other data also demonstrate that daylength is probably not a factor in differentiation of Douglas-fir flower buds. Silen<sup>35</sup> demonstrated a significant change in bud differentiation in late June, and Bonnet-Masimbert<sup>27</sup> 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<sup>32</sup> observed a change from vegetative shoot to female flower on one plant during budburst in early spring.

Silen<sup>35</sup> 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-inducive 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<sup>38</sup> has reported that neither phosphorus nor potassium stimulated flowering.

Ebell<sup>39,40</sup> 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<sup>35</sup> and Bonnet-Masimbert and Lanares<sup>34</sup> 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<sup>41</sup> 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<sup>41</sup> 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.,<sup>42</sup> 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<sup>23,24,26</sup> 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<sup>43</sup> 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<sup>24</sup> 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<sup>44</sup> 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.<sup>7</sup> 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.<sup>45</sup>

Bonnet-Masimbert et al.<sup>45a</sup> 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<sup>46</sup> and Puritch et al.<sup>47</sup> 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<sup>46</sup> 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<sup>48</sup> 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,<sup>49</sup> 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:<sup>50</sup> 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,<sup>9</sup> 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<sup>51</sup> reports that *P. ponderosa* produced good cone crops 27 months after above-average temperatures in April and May. On the other hand, Daubenmire<sup>52</sup> 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<sup>9</sup> 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<sup>53</sup> 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.<sup>54</sup> Irrigation experiments substantiate these field observations. *P. monticola* and *P. elliotii* produced more pollen strobili when watered during the summer, but the number of female flowers was the same or reduced.<sup>55,56</sup> In another study, irrigation stimulated male cone production in *P. elliotii* 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.<sup>57</sup>

Irrigation of *P. taeda* during April to June, followed by July to September drought, resulted in a larger cone crop the following year.<sup>58</sup> In two other studies of the same species, irrigation substantially increased seed yield in seed orchards.<sup>59</sup> The combination of adequate water supply and appropriately timed drought may prove to be an important technique for inducing flowering in pines. Giertych<sup>60</sup> observed that warmth and drought during the flower induction period favors initiation of both male and female primordia. Greenwood,<sup>61</sup> who subjected potted *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,<sup>62</sup> using a "water balance" method to estimate drought, found that in seed orchards of *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.<sup>32</sup> When root activity was arrested by drought, flooding, or high temperature, more female cones were produced than were produced on control plants.<sup>63</sup> 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 *Pinus* species, but it has yet to be tested.

### Light

The photoperiodic effects on flowering in pines is apparently variable. Mirov<sup>64</sup> 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 *P. attenuata*.<sup>65</sup> But Larson<sup>66</sup> caused a shift from female to male flower production in *P. banksiana* with slightly longer days. More conclusively, Longman<sup>67</sup> found that 10-hr days for 11 weeks induced 6 times as many female flowers in *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, *P. elliotii* was found to produce more female flowers on the side receiving the greatest amount of light.<sup>68</sup> (Thinning to increase light in the crown is now a common method for increasing cone production in seed orchards of southern pines.<sup>59</sup>) A similar effect was reported for *P. silvestris*, and it was noted in addition that male flowers usually formed in shaded areas.<sup>69</sup> Hashizume<sup>70</sup> reports that colored paraffin paper bags covering shoots of *P. densiflora* or *P. thunbergii* caused sex reversal. Giertych<sup>60</sup> observed that high light intensity during the time of cone differentiation for *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.

### Mineral Nutrition

Fertilization is the most commonly utilized technique for increasing pine cone production.

Numerous experiments, however, report varying results with fertilizers,<sup>9,51,71</sup> 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.<sup>9</sup> Chalupka and Fober<sup>72</sup> 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.<sup>59,73</sup> *P. elliotii* and *P. taeda* in southern pine seed orchards generally respond favorably to applications of ammonium nitrate.<sup>57,74</sup>

Irrigation can enhance the fertilizer effect,<sup>59</sup> and a wide variety of pines have shown increased cone yields with fertilizer treatment under certain conditions.<sup>9,71</sup> 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<sup>41</sup> suggest that the amino acid content at the flower induction site leads to periodicity of flower crops, but Lee et al.<sup>75</sup> found low N levels in buds and increased female flower differentiation in *P. elliotii*. Sweet and Hong<sup>76</sup> 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.<sup>59</sup>

### Cultural Treatments

Girdling of pines often induces flowering, but results vary. Hare<sup>74</sup> reports that seed orchards of *P. elliotii* 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.<sup>9</sup> Greenwood<sup>61</sup> 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<sup>77</sup> 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,<sup>8</sup> 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.<sup>9</sup>

Pruning, on the other hand, is less harmful and is effective in some species. It has induced flowering in *P. densiflora* and *P. thunbergii*<sup>70</sup> and increased the number of flowering stems per ramet in a breeding arboretum of *P. radiata*.<sup>78</sup> 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. elliotii*.<sup>79</sup>

### Growth Regulators

Gibberellins (GA) are known to induce flowering in conifers, especially in the Cupressaceae and Taxodiaceae.<sup>80</sup> But their effectiveness in inducing flowering in the pines has been disappointing.<sup>77</sup> Some workers report little or no effect on pine species;<sup>67,70</sup> others report positive effects of GA in *P. contorta*,<sup>81</sup> *P. taeda*,<sup>82</sup> *P. palustris*,<sup>74</sup> *P. silvestris*,<sup>77</sup> and *P. banksiana*.<sup>83</sup> 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 affect on the flower induction process in pines.<sup>66,70,84</sup>

## 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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## ANGIOSPERMOUS FOREST TREES OF TEMPERATE ZONES

Denis P. Lavender

## INTRODUCTION

Temperate-zone forests contain both conifers and a wide range of angiospermous species. Members of four genera, *Betula*, *Fagus*, *Quercus*, and *Salix*, have extensive ranges, especially in the Northern Hemisphere, and comprise many species of important timber trees. But summaries of their flower production must be brief, primarily because little interest has been shown in the physiology of flowering in these genera by botanists or by members of applied disciplines such as forestry.

Early in this century the four genera were placed in the Dicotyledoneae subclass Chlo-ripetalae (Apetalae).<sup>1</sup> Members of this subclass are characterized by flowers which have tepals but no petals and which are borne on structures commonly called aments or catkins. Rickett,<sup>2</sup> reviewing the use (and misuse) of the term "ament", concludes it may best describe a commonly pendant inflorescence that is essentially a slender deciduous spike bearing unisexual, apetalous flowers. But Abbe,<sup>3</sup> in a comprehensive review of the "Amentiferae", concludes that the term is used to indicate a lack of knowledge of the basic morphology of the inflorescence and that the terms "calyx" or "sepal" are not appropriate for the Chlo-ripetalae. He proposes the use of "tepal" (the term used in this chapter), which he defines as "an undifferentiated member of the homochlamydeous floral envelope (collectively, perigon)."

More modern taxonomists consider these anemophilous plants to have lost floral parts through evolutionary reduction, and they classify *Betula*, *Fagus*, and *Quercus* in the subclass Hamamelidae Takhtajan, order Fagales Engler.<sup>4</sup> *Salix*, whose members are considered to bear catkins, not aments,<sup>3</sup> is classified in the subclass Dilleniidae Takhtajan, order Salicales Lindley.

THE GENUS *BETULA*

En. Birch; Fr. Bouleau; Ge. Birke; Sp. Betula

**Flower Initiation and Development**

The genus *Betula* L., belonging to the family Betulaceae, consists of approximately 40 species of shrubs and trees widely distributed in the Northern Hemisphere. Species are found in Eurasia between the Himalaya Mountains and the Arctic Circle and in North America between the arctic regions and the southern U.S.<sup>5</sup> Although members of this genus are never more than medium-sized trees, they form vast forests in northern latitudes, and *B. lutea* Michx. is considered to be an important timber tree.<sup>5</sup>

The flowers are generally vernal (rarely autumnal) and monoecious.<sup>6</sup> Staminate catkins, formed in the fall, may reach a length of 25 mm by winter.<sup>1,6</sup> They remain naked during the winter and elongate to a length of 75 to 100 mm immediately before or during early leaf expansion in spring. Bracts have 3 sessile or nearly sessile florets, each floret composed of a minute 2- to 4-part membraneous perigon (calyx), and 2 to 20 stamens divided at the apex, inserted on a receptacle, and bearing outward-turned anthers and distinct filaments.<sup>1,6</sup> The staminate inflorescences may be either terminal on long shoots of the preceding year or may be on lateral short shoots.<sup>3</sup> The solitary pistillate flowers with thin bracts are borne on short lateral or capitate erect catkins below the staminate flowers on the same twigs.<sup>6,7,8</sup> There may be one (e.g., *B. michauxii* Spach), but more commonly, 3 pistils subtending each conspicuous bract complex.<sup>3</sup> The perigon is either superficially absent or vestigial.<sup>3</sup> The 2-celled ovary, which narrows into a short style divided into 2 elongated branches, has

2 (rarely 4) inverted pendulous ovules. The cone-like pistillate catkins ripen in late summer or early autumn to become pendulous or erect strobili.<sup>9</sup> Each scale of the strobilus may bear a single, small, oval, veined seed that has persistent stigmas. The mature tan to light-brown seed is dispersed primarily by wind, occasionally by water.<sup>9</sup>

The juvenile period of birch in forest stands varies with species. *B. verrucosa* Ehrh. and *B. pubescens* Ehrh. have been reported to bear both staminate and pistillate flowers in their second year.<sup>10</sup> Female flowers borne on second-year seedlings may well be androgynous, with reduced fertility in the pistillate parts, and the flowering seedlings demonstrate a juvenile growth habit.<sup>11</sup> However, Huhtinen<sup>12</sup> argues that the plant response is more mature than juvenile and suggests that techniques for taking tissue culture from the seedlings may cause the material to revert, at least partially, to the juvenile state. Yellow birch (*B. alleghensis* Britton) commonly flowers at 5 to 10 years,<sup>13</sup> paper birch (*B. papyrifera* Marsh) at 15 years,<sup>14</sup> and sweet birch (*B. lenta* L.) at 40 years. Experiments in England designed to determine if the growth habit of *B. verrucosa* seedlings were related to the juvenile state, demonstrated clearly that the initiation of flowering was associated with plant size rather than with plant age or number of artificially induced growth cycles.<sup>15,16</sup>

Birch usually produces a good seed crop at about 2-year intervals. There are few data describing the quantities of seed produced, but it has been estimated to be as high as 1 million seeds per tree under controlled conditions.

## Effect of Environment

### Temperature

Several studies<sup>17-19</sup> have attempted to relate the data of flowering in *Betula* species with air temperature. Both *B. papyrifera* and *B. lutea* Michx. have been shown to initiate flower development in the spring when minimum temperatures were below freezing,<sup>17</sup> but no significant relationship between the onset of anthesis and air temperature has been established. A low threshold temperature range ( $-16$  to  $-19^{\circ}\text{C}$ ) has similarly been estimated for *B. papyrifera*<sup>18</sup> but without close correlation between date of flowering and air temperature. In contrast, a study of *B. verrucosa* in Finland, demonstrated that the initiation and duration of anthesis was closely correlated with a degree-day sum based on a threshold temperature of  $5^{\circ}\text{C}$ .

### Moisture

Rain has been shown to reduce pollen flight,<sup>9</sup> but there are apparently no data relating moisture availability to initiation of flower buds.

### Photoperiod

An investigation of *B. verrucosa* in Great Britain showed that short photoperiods induced flower formation,<sup>20</sup> but it was also demonstrated that continuous growth of birch seedlings, stimulated by long photoperiods, resulted in precocious flower development.<sup>15</sup> Plantlets derived from seedlings with a precocious flowering habit would flower profusely under long photoperiods.<sup>12</sup>

## Cultural Treatments

In common with many perennial plants, *B. verrucosa* responds to girdling by producing reproductive buds.<sup>21</sup> However, because this treatment is effective even with seedlings only 8 months old, it is hypothesized that *Betula* may not have a true juvenile period.<sup>21</sup>

## THE GENUS *FAGUS*

En. Beech; Fr. Hêtre; Ge. Buche; Sp. Faia

### Flower Initiation and Development

The genus *Fagus* L. of the family Fagaceae contains ten species of medium-sized trees, all native to the temperate regions of the Northern Hemisphere. Only one, *Fagus grandifolia* Ehrh. is a native of North America, where it is found on generally moist soils of forests in the eastern U.S. and Canada.<sup>5</sup>

The staminate flowers, which are subject to damage by frost, appear after the leaves unfold in the spring.<sup>5</sup> They are borne in dense, pendulose, globose heads, about 25 mm in diameter, on long bibracteolate stems generally originating from the base of the previous year's shoot.<sup>6</sup> Each flower has 4 to 7 united tepals and 8 to 14 stamens inserted on the base of the perigon. The stamens have slender, free filaments and greenish, oblong, introrse, 2-celled anthers.<sup>3,6</sup>

The genus *Fagus* is monoecious, with flowers in 2 to 4 clusters borne on spikes emerging from the axils of the upper leaves.<sup>5</sup> The pistillate flowers are composed of a 4- to 8-lobed perigon subtended by an involucre of imbricated bracts, and of a 3- to 7-celled ovary, which has an equal number of styles and 1 or 2 pendulous, inverted or semi-inverted ovules in each cell.<sup>3</sup>

The morphology of the staminate flowers of *F. orientalis* Lipsky has been shown to be affected by habitat moisture but not strongly by elevation.<sup>22</sup> In contrast, the numbers of staminate inflorescences, florets, and stamens of *F. sylvatica* L. are reduced with an increase in altitude.<sup>23</sup> The increase in occurrence of hermaphroditic flowers at high elevations in Bulgaria has a decidedly negative effect on the incidence of natural regeneration.<sup>23</sup>

Beech normally has a long juvenile period, the initiation of flowering occurring at about 40 years.<sup>14</sup> The transition from juvenile to mature form may be unstable, as scions taken from the flowering area of mature beech crowns often fail to flower when grafted on vigorous, juvenile rootstock.<sup>24</sup>

Flower-bud production in some *Fagus* species is sensitive to environmental factors, as significant flower crops are generally produced at irregular intervals.

### Effect of Environment

#### Temperature

The incidence of mast years for *F. sylvatica* has been positively correlated with the average temperature and hours of sunshine of the previous July.<sup>25</sup> It is hypothesized that the development of flower buds, which are distinguishable by September, is stimulated by both high temperature and light intensity. Both staminate and pistillate flowers are subject to frost damage in May and June, and temperatures of from  $-1$  to  $-3^{\circ}\text{C}$  are lethal.<sup>25</sup> The degree of metandry is affected by spring temperatures<sup>26</sup> warm, dry springs generally result in a shorter period of metandry than cool, humid spring weather.

#### Moisture

A study with *F. sylvatica* scions in Denmark was designed to evaluate the effect of controlled drought upon the incidence of flowering in the succeeding summer. The results clearly demonstrated that drought from late June to mid-August stimulates formation of both male and female flower buds<sup>27</sup> and that reproductive tissue may be differentiated as late as the end of August.



THE GENUS *QUERCUS*

En. Oak; Fr. Chêne; Ge. Eiche; Sp. Carvalho

**Flower Initiation and Development**

The genus *Quercus* is extremely important economically and botanically. The more than 500 named species (probably about 300 true species, the remainder hybrids or varieties) vary in size from small shrubs to large trees. They are widespread in the northern temperate zone and found at high elevations in the tropics.<sup>5</sup> Worldwide, only the pines are a more important timber source.

Their extreme botanical variability makes members of the genus *Quercus* a complex taxonomic puzzle. They are monoecious, with both staminate and pistillate flowers appearing as the leaves unfold. The staminate flowers are borne on clustered, hairy, slender, pendant spikes that develop from the axils of leaves of the current or previous year or from the axils of scales of the terminal bud.<sup>6</sup> The florets, borne singly in the axils of primary bracts, consist of a perigon with 6 membranous lobes (rarely 4 to 7), 4 to 6 stamens (rarely 2 to 12), and 2-celled, ovate-oblong to subglobose anthers that are usually yellow.<sup>3,6</sup>

The pistillate inflorescences are essentially simple. Each contains a single floret surrounded by an involucre cup in the axis of the primary caducous bract and by 2 bractlets on short or elongated few-flowered spikes that originate from the axils of the top 3 or 4 current-year leaves.<sup>3,6,28</sup> The inferior, tricarpellate, trilocular ovary has 2 anatropous or semianatropous ovules in each cell. The perigon has 4 to 6 or 9 tepals and as many styles as cells of the ovary, each style flat, with the inner face stigmatic. (Flat styles distinguish most species of *Quercus* from other members of Fagaceae.<sup>3,6</sup>)

The staminate flower buds of white oak (*Quercus alba* L.) are initially distinguishable in Virginia in late May.<sup>28</sup> The primordia develop through the summer and into the fall, when most of the components of the florets are visible. Little development occurs during winter, but during bud swell in spring, the anthers complete their growth and achieve their final configuration.<sup>28</sup>

Pistillate buds of white oak are first distinguishable in early August, but may be present earlier.<sup>28</sup> They continue development until mid-October. Growth ceases with the inflorescence only partially formed, then resumes in early spring. In late March and early April, the pistillate bud enlarges rapidly and the spike elongates and forms a series of as many as 5 florets, each with a subtending bract.<sup>28</sup>

Reports from Europe suggest that the initiation and development of staminate buds of *Q. robur* L.<sup>29</sup> and *Q. rubra* L.<sup>30</sup> are similar to that of *Q. alba* L., but that their pistillate buds are initiated and developed in the spring of the flower year. Pistillate flower primordia may be formed during or just before bud flush, and the ovules may be formed so late that they are not fully developed at the time of pollination.<sup>31</sup> But, a review of the reproduction of the British oak (*Q. robur*), states that spring initiation of pistillate inflorescences is not established.<sup>32</sup> Several workers have reported anomalous flowering in oak.

In Europe, late frost injury to *Q. robur* has produced buds with both staminate and pistillate primordia. Many of these buds failed to develop, and those that did produced pistillate inflorescences.<sup>33</sup> In contrast, only the staminate flowers were viable in bisexual inflorescences of *Q. pubescens* Willd.<sup>34</sup>

In North America, two small sclerophyllous oaks, *Q. turbinella* Green subsp. *californica* Tucker and *Q. durata* Jeps. have been reported to bear aberrant inflorescences in late summer.<sup>35</sup> The perfect flower may represent the ancestral condition in the beech family, and anomalous flowering may occur in response to some extreme weather event, such as heavy summer rains.<sup>35</sup> Such events trigger a late season growth flush that bears the anomalous flowers. The multiple flowered inflorescences, which are much longer than the normal single or double flowered inflorescences characteristic of these oaks, may be further evidence of

a reversion to a more primitive form.<sup>35</sup> The incidence of hermaphroditic flowers on Gambel oak (*Q. gambelii*) in Utah confirms observations of *Q. robur* in Europe that the aberrant flowers occurred after frost injury, and observations in California that the flowers were initiated and developed during a single growing season.<sup>36</sup>

Estimates of the minimum age for flowering for the genus *Quercus* vary with species from 5 years for *Q. nuttallii* Palmer and *Q. acutissima* Carruthers to 35 years for bur oak (*Q. macrocarpa* Michx.)<sup>9,14</sup> Perhaps the shortest juvenile period in this genus, however, are those of *Q. robur* and *Q. pedunculiflora* C. Koch., both of which have been reported to flower in Europe during the third or fourth year.<sup>37,38</sup>

A thorough 12-year study in western Pennsylvania of the flowering of white oak (*Q. alba* L.), chestnut oak (*Q. prinus* L.), scrub chestnut oak (*Q. prinoides* Willd.), and bur oak<sup>39</sup> yielded the following observations of the staminate flowers:

1. Staminate buds were the first to flush in spring, the growth proceeding basipetally from the top of the tree.
2. Catkins were borne in groups of 3 to more than 10, the number consistent on all branch tips of any one tree.
3. All species except *Q. alba* flowered at a consistent date from tree to tree and flowered at low elevations first, but each population had early and late flowering trees.
4. Pollen dispersal was hindered by high humidity, which closes the anthers, or by dry weather occurring early in the development of the staminate flowers.
5. Trees produced good to heavy crops of staminate flowers every year of the 12-year study.

A study of the phenology and production of pistillate flowers on the same trees<sup>40</sup> showed that:

1. Pistillate buds opened 5 to 10 days after staminate buds.
2. Pollination occurred within 10 days of the breaking of the pistillate flowers, but fertilization was delayed until late June.
3. Production of acorns was strongly correlated with vigorous growth of the stalk that bears the cupules.
4. Production of pistillate flowers was not consistent from one year to the next.

## Effect of the Environment

### Temperature

No studies relate flower initiation in oak to temperature. A study of forest trees in Minnesota<sup>17</sup> reported no consistent relationship between air temperature and the date of flushing of flower buds of bur oak, but a study of flowering of oaks in Pennsylvania found that the date of staminate bud flush was earlier and the development of catkins more rapid with warm spring temperatures.<sup>39</sup> The development of pistillate flowers, in contrast, was favored by a warm April and cool May, but not by the reverse.<sup>40</sup>

The occurrence of late frosts sufficiently severe to damage staminate or pistillate flowers is rare in western Pennsylvania.<sup>39,40</sup>

### Photoperiod

No evidence has been found that photoperiod affects the initiation or development of flowers in oak.<sup>32</sup>

## Cultural Treatments

There have been few attempts to stimulate flower initiation or shorten the juvenile period

in *Quercus*, but one report describes the successful stimulation of flowers on *Q. suber* L. after girdling, which has successfully stimulated flower initiation on a wide range of perennial plants.<sup>32</sup>

## THE GENUS *SALIX*

En. Willow; Fr. Saule; Ge. Weide; Sp. Salgueiro

### Flower Initiation and Development

The genus *Salix* contains about 300 species largely scattered throughout the cooler areas of the Northern and Southern hemispheres, about 100 of these indigenous to North America.<sup>9,41</sup> A few species are tropical, and a few extend north of the Arctic Circle.<sup>5</sup> In general, all willows require considerable moisture and are found along streams. Many willows are shrubs or small trees; the largest in the U.S., black willow (*Salix nigra* Marsh), has a maximum height of 140 ft and diameter of 4 ft.<sup>14</sup>

Members of *Salix* are dioecious. The staminate catkins, which appear just before the leaves appear, are minute, erect, and covered with a single scale during the winter.<sup>5,7</sup> They may be sessile or stalked, terminal or axillary on leafed branches.<sup>6</sup> There may be 1, 2, or 3 to 12 stamens inserted at the base of a generally hairy, dark scale. The filaments may be free (rarely united) and are usually pale yellow, glabrous, or hairy at the base.<sup>6</sup> The small ovoid or oblong anthers, often rose-colored before anthesis, darken to orange or purple.<sup>6</sup>

The pistillate inflorescence is also a catkin.<sup>7</sup> The flower is in the axil of a bract with 1 or 2 glands on a small, lobed disk at its base.<sup>1</sup> Each floret has a single sessile or stipitate, conic, obtuse to subulate-rostrate ovary and two carpels.<sup>1</sup> The stigmas are characteristically short and are borne on an abbreviated recurved style.<sup>6</sup> 8 to 16 ovules are in each ovary, 4 to 8 on each of 2 placentas.<sup>6</sup>

Little data describe the frequency of flowering or minimum age for flower production, which varies with species from 2 to 10 years.<sup>9</sup> A gradient in flowering potential was found in *Salix tetrasperma* shoots by culturing its buds in vitro at different developmental stages during the active growth and the dormant period and examining the nature of sprouts produced by them.<sup>43</sup> All the buds collected from the first and second nodes of the branches from the top were vegetative. About half of the buds from the third and fourth nodes were reproductive and produced catkins. All the buds obtained from the fifth node and below were reproductive. Reproductive determination of buds during the spring growth flush is not tantamount to flowering, as the catkins produced by them are sterile. The second step of flower development is during the dormant period, in which the determined buds are gradually directed towards flower formation, a process that is completed by December.

### Effect of the Environment

#### Temperature

A report from Norway<sup>42</sup> indicating that temperatures above 15°C depress flower-bud formation on *S. pentandra* L., especially under short photoperiods, is the sole quantitative measurement of effects of temperature upon initiation of reproductive organs on willow.

#### Photoperiod

Short photoperiods (12 hr) have favored flower formation at 15°C temperatures, but long photoperiods (20 to 24 hr) have stimulated initiation of flower buds when plants are grown at 18 to 24°C temperatures.<sup>42</sup>

### Growth Regulators

A study of the relationship of natural or artificial growth regulators upon the incidence

of flowering in willow demonstrated that applications of GA at the rate of 0.1  $\mu\text{g}$  per bud reduced flower bud formation on material taken from mature plants.<sup>42</sup> Cytokinins and auxin, applied at the rate of 1 to 2.5  $\mu\text{g}$  each per plant, or ABA applied at rates of 10 to 25  $\mu\text{g}$  per plant failed to stimulate flower production.<sup>42</sup>

## CONCLUSION

Although this chapter summarizes significant attempts to elucidate the anatomy and morphology of amentiferous species, the physiology of flower initiation and phenology in these species has received little attention. The absence of data precludes conclusions as to the role of endogenous or exogenous factors in the reproductive strategies of species of *Betula*, *Fagus*, or *Salix*.

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## TROPICAL FOREST TREES

K. A. Longman

## INTRODUCTION

Tropical forest trees are the largest and most diverse, but least studied group in this *Handbook*, covering tens of thousands of woody species, belonging to some 85 families.<sup>73</sup> For instance, more species may be present in 25 ha of lowland forest in Malaysia than in the whole flora of the U.S.<sup>119</sup> During the last decade, more information has become available on reproductive phenology and periodicity in both natural forests and plantations, but knowledge of controlling factors is still extremely scanty. Attention will therefore be focused on considering the most fruitful approaches to the difficult problems of studying forest trees, sketching the variety of their reproductive behavior in the tropics, and indicating some of the factors known or likely to affect flowering (including coning of coniferous species).

Because many little-studied and largely unimproved trees are considered here together does not mean that they are unimportant commercially. Export of specialist tropical timbers has yielded many thousands of millions of U.S. dollars in a year, but stocks are now generally declining sharply. Local use of wood is economically even more important: for instance 86% of the wood used in the Third World countries provides essential firewood or charcoal for cooking and/or heating.<sup>91</sup> The inhabitants of tropical forest land also utilize forest produce for many other purposes, ranging from house and boat building to the provision of animal forage and medicinal products.<sup>56</sup> Reproductive parts provide the "crop" in a few instances, where undomesticated fruits like *Dacryodes edulis* (Burseraceae),<sup>97</sup> *Garcinia mangostana* (Guttiferae), and *Solanum quitoense* (Solanaceae)<sup>90</sup>; or oil-seeds (for example, *Caryocar* spp. — Caryocaraceae; and *Shorea* spp. — Dipterocarpaceae) are collected; or where honey or even the sugary flower itself (*Sesbania grandiflora* — Papilionaceae) is eaten. Typically, however, vegetative portions of trees are used, predominantly the main-stem wood, but sometimes bark, branches, or leaves, and occasionally parts of the root system, stem spines, etc.

Tropical forest trees are also being recognized as playing an integral role in the maintenance of soil physical structure and fertility in many agricultural systems,<sup>33,62,109</sup> as well as in the conservation of water, wildlife, and endangered species. Despite these key roles in local and world economies, tropical forests are still typically being exploited with little replacement, rather than being managed as renewable resources.

Increased knowledge of reproductive biology at two levels will help toward changing attitudes. First, how does their diverse and often intermittent flowering behavior maintain and regenerate these complex ecosystems of high net primary production, and how far can they be modified without serious loss? Second, can knowledge of external and internal factors influencing reproductive behavior be used to develop flower induction techniques to help domesticate a wide range of indigenous as well as exotic species for reafforestation and agroforestry?

## APPROACHES TO THE PROBLEM

Reproductive studies with trees are hampered by the long life-cycle, the size and complexity attained, and by considerable variability and spatial dispersion of individuals. Information on floral structure in tropical forest trees is quite extensive, and there have been a number of recent studies on the phenology of flowering (see section "Variation in Phenology"), and some on distribution of inflorescences within trees in relation to vegetative morphology.<sup>30,45,46,118</sup> However, information about the timing of floral initiation and the

identity of the factors controlling it tends to vary from partial to nonexistent, by way of correlations, untested hypotheses, and mere conjecture.

The following suggestions are put forward to encourage physiological research, to provide the knowledge on which to develop reliable techniques for stimulating flowering. Assuming as a starting point that the various visible stages are, where possible, being observed on tagged trees, most attention should be given to identifying the time at which flowers are initiated, and to “miniaturizing” the plants and standardizing the conditions so that experiments can be realistically attempted.

### **Studying Easier Species First**

However strong the commercial pressures, it is not necessarily wise to start with a species where flowering is known to be long-delayed and irregular (see Table 1). *Tabebuia pallida* (Bignoniaceae), for example, will flower readily as a small pot plant, allowing environmental treatments to be applied.<sup>84</sup> Rapid progress with such a convenient species may then be used to tackle a more difficult member of the same genus, while other information may prove to be of family or general significance to floral induction studies. Similarly, *Ateramnus lucidus* (Euphorbiaceae)<sup>118</sup> and members of the Cupressaceae form reproductive parts which can be seen at an early stage without dissection, greatly facilitating research.

### **Propagating Uniform Clones of Trees**

Material of seedling origin is often too variable for experimental purposes (see section “Genetic Control over Flowering”). Vegetative propagation is probably the single most important tool for studying flowering, partly because it allows sources of variation to be distinguished and any interactions clearly seen. Rooting of cuttings is now known to be relatively easy under automatic mist with many tropical tree species<sup>71,80,85,89</sup> and has also been successful with leafy cuttings from young trees in simple polyethylene covers under moderate shade.<sup>54</sup> Material from older trees may not root so easily, but can often be grafted on seedling root-stocks using standard procedures.

### **Selecting Material More Likely to Flower**

It is commonly observed that some individuals come into flowering earlier and produce many more flowers than others. Experience with horticultural crops and temperate forest trees suggests that these tendencies are frequently strongly inherited, and so clones from selected “floriferous” trees can be used to miniaturize and speed up the time-scale,<sup>72</sup> and even allow growth cabinet experiments on reproduction in small potted plants.<sup>81</sup> It is often noted that trees in plantations may commence flowering earlier than in natural forest<sup>2,6</sup> (see Table 1), and this may be an undesirable trait in timber trees.<sup>78</sup> However, strictly for research purposes, it should be relatively simple to propagate floriferous selections, for example with *Tectona grandis* (Verbenaceae) and *Pinus caribaea* var. *hondurensis* (Pinaceae), perhaps by coppicing the vegetative stockplants or pruning them into “bushes” to provide a continuing source of cuttings.

In trees having a long period before flowering, mature material from the crown might be more likely to flower than that originating near the ground. Grafting may be necessary, and would also be useful if clonal rootstocks are developed that promote flowering in the scions.

### **Using the Same Clones Repeatedly**

Once clones useful for flowering studies have been developed, they can be used many times over, providing for forest trees the kind of standardized material long accepted as normal in experiments with other crop and ornamental species. Moreover, they allow direct comparison between work in plantations, trial plots, nurseries, and perhaps controlled environments, and allow flowering studies to be linked to an accumulating general body of information concerning vegetative growth and other characteristics of the clone.

### Harnessing One Flower-Inducing Technique to Test Others

Where a technique is known to stimulate flowering, it can be very usefully employed in screening other possible chemical or environmental treatments. Thus, GA<sub>3</sub> is known to stimulate heavy male and female coning in the Cupressaceae (see section, "Effects of Treatment on Flower Initiation"). A moderate dose of this hormone, injected into small, clonal potted plants, has been used in temperate members of this family to test the effects of other growth substances and of photoperiod and temperature.<sup>78,84</sup> The GA<sub>3</sub> doses were so arranged that coning could be increased or decreased in one or both sexes, and results were obtained on precise interactions between treatments. Complete bark-ringing has also been used in this way in the study of coning in temperate members of the Pinaceae.

## VARIATION IN PHENOLOGY

The timing of key events in the reproductive cycle of tropical forest trees is of central importance in learning how to stimulate or control flowering. Examples illustrating the great range of behavior in various tropical regions are given here together with some indication of possible relationships with vegetative growth and with climatic changes.

### The Onset of the Reproductive Condition

As has been mentioned, many trees go through a substantial period in which flowers or cones are not normally formed, although individuals within a species generally vary considerably in their age at first flowering. Most published information is in the form of observations and experience, rather than of systematically taken records on the same group of trees from the first year. It is difficult in many tropical species to determine age in natural stands, except where clear annual rings are formed, although recent studies hold out some hope in this direction.<sup>13</sup> Nevertheless, it is clear that some species commence reproductive activity after a few years while others remain vegetative for decades (Table 1). The most extreme examples of a long vegetative period are the monocarpic perennials, such as *Tachigalia versicolor* (Caesalpiniaceae),<sup>34</sup> *Strobilanthes* spp. (Acanthaceae),<sup>5</sup> and some bamboos (Gramineae)<sup>59</sup> which flower only once in their life-span, and then die.

From the physiological standpoint, it is probably most satisfactory to regard the onset of reproduction as just one part of the overall ontogenetic change from a "juvenile" to a "mature" tree, and not as the sole criterion for the occurrence of phase-change.<sup>76,112</sup> Vegetative changes with age, such as loss of thorns, alteration in leaf shape and size, and reduction in frequency and length of shoot extension periods<sup>79,82</sup> may perhaps take place sequentially. Semantic difficulties also arise because old trees do not necessarily flower regularly, while very young seedlings occasionally reproduce<sup>47,114,115</sup> (see the chapter "Citrus" by Monseliese in Volume II). Study of vegetatively propagated plants originating from various parts of the same tree, which often retain distinct morphological and physiological differences, would help to clarify these questions.

### Categories of Flowering Behavior

#### *Sex Differentiation*

Quite a high proportion of tropical forest trees produce separate male and female flowers: for example 32% in Central America,<sup>7</sup> 31% in Ghana,<sup>44</sup> and 42% in the mixed tropical/temperate origin trees and shrubs of South Florida.<sup>118</sup> The majority of these tend to be dioecious, with separate male and female trees, in contrast to many temperate forests where the monoecious condition strongly predominates.<sup>7-9,124,125</sup> These distinctions are not always clear-cut, however: for example, there is a strong tendency for one sex to predominate in *Cupania glabra*, and a lesser tendency in *Sapindus saponaria* (both Sapindaceae).<sup>118</sup> Careful study is also needed to distinguish the monoecious status of *Savia bahamensis* (Euphorbi-



**Table 1**  
**ESTIMATED AGE AT FIRST REPRODUCTION**

Family	Species	Reproduction starts (years)	Notes	Ref.
Coniferales				
Araucariaceae	<i>Araucaria cunninghamii</i>	15—25	Plantations in Mauritius and Queensland	96
Pinaceae	<i>Pinus caribaea</i> var. <i>hondurensis</i>	1+	Brazil and E. Kalimantan, Indonesia	36
	<i>P. kesiya</i>	10—18	S.E. Asia	2
	<i>P. merkusii</i>	2—7 10—20	As exotic in Africa Vietnam	22
Dicotyledones				
Combretaceae	<i>Terminalia ivorensis</i>	10	Abundant seed in Sierra Leone	68
Dipterocarpaceae	(several genera)	20—30	Arboretum, Malaysia	92
Meliaceae	<i>Cedrela odorata</i>	10	Plantations	67
Sterculiaceae	<i>Triplochiton scleroxylon</i>	15—30	Rare before this in natural stands in West Africa	72
		8	First record in field-grown cuttings	65
		2—6	Precocious flowering in Scottish glasshouses	72
Verbenaceae	<i>Gmelina arborea</i>	10—15	Natural regeneration prolific around plantations (E. Nigeria and Sierra Leone)	66
		3—4	Can commence in W. African plantations	66
	<i>Tectona grandis</i>	(0.25-) 8—10 (-27 +)	Extremes and normal range for Thailand	47
		4—5	Virtually all individuals in Nigerian plantations	77
		1—2	Precocious individuals in plantations	61

aceae) in which individual branches tend to be all of one sex, and other intermediate types occur in which flowers are apparently perfect but only one sex is functional. In *Colubrina* spp. (Rhamnaceae) the same flowers open first as male and later as female (dianthesis), as in avocado, where the timing is so distinct that two different varieties may have to be interplanted to encourage pollination.<sup>111,118</sup>

Equal proportions of male and female trees do not always occur in dioecious species; thus, of 23 species in Costa Rica, 8 had significantly more male trees and 2 had more female.<sup>99</sup> Moreover, male trees also tended to produce more inflorescences, each containing more flowers than on female trees, and sometimes appeared to commence flowering earlier in life. Change of sexual status of individual trees with time has been found with a “dioecious” temperate zone *Acer* species (Aceraceae),<sup>48</sup> but this has rarely been studied in the tropics. Tropical conifers are predominantly monoecious, although dioecious examples occur, for example, in *Podocarpus* and *Dacrydium* (Podocarpaceae) and *Araucaria* (Araucariaceae).<sup>38</sup> Female cones typically occur in the upper part of the tree and towards the tips of the stronger branches, while male cones generally occupy more proximal sites.

#### *Regularity and Frequency of Production*

Once reproduction has started, flowering in most species of large trees is periodic.<sup>82</sup> Usually less than 2% are “everflowering”; examples are the secondary forest species *Dillenia suffruticosa*, (Dilleniaceae),<sup>23</sup> *Trema orientalis* (Ulmaceae) and *Harungana madagascariensis* (Hypericaceae).<sup>44</sup> Including shrubs as well as trees, 15% of the species in South Florida

flower more or less continuously, including the mangrove *Rhizophora mangle*, (Rhizophoraceae), which however shows a peak in June/July.<sup>118</sup>

When the forest as a whole is considered, three generalizations have frequently been made about the incidence of flowering: (1) some years show higher flowering than others; (2) there is seldom any month when there is no flowering; (3) clear-cut seasonal peaks in flowering are found not only where there is a distinct dry season but also in relatively uniform climates.<sup>1,35,52,57,87,103,107</sup> Regular periodicity of flowering shows up despite the presence of nonseasonal species, great variability between (and even within) individuals, and imperfections in assessments (many studies are based on herbarium collections). It can be expressed as the "Seasonal Flowering Index", the ratio between the number of species flowering in the consecutive 6 months with the most flowering, and that with the least flowering: Values of 1.2 to 4.9 have been found (Figure 1).

A frequent feature of seasonal peaks is that they tend to occur in the dry season, or in the latter part of the drier season and the early part of the wetter season<sup>24,28,35,58,82,108</sup> (Figure 1), although mid-rainy season flowering has been reported in some of the drier forests types in Ethiopia.<sup>16</sup> Seasonality differs in particular classes of tropical trees. Thus, peak flowering is later in dioecious species,<sup>9</sup> and may occur earlier in the dry season in deciduous trees and woody climbers than in evergreen trees or herbaceous forest plants.<sup>24,44,82,118</sup>

At the level of the individual species, there are instances where flowering is so regular that it is used to indicate the planting date for agricultural crops.<sup>82</sup> Besides regular seasonality and the everflowering category, there are also several types of nonseasonal behavior: the proportion of "not clearly seasonal" species appears to be about 33% in Ghana,<sup>44</sup> 14% in South Florida,<sup>118</sup> and 26% from a detailed study including herbaceous species in Barro Colorado Island, Panama.<sup>24</sup>

The frequency of flowering periods can be as short as 3 to 4 months, for example in *Ficus sumatrana* (Moraceae).<sup>87</sup> Fairly regular annual flowering is characteristic of a number of species commonly planted, such as *Cedrela odorata* (Meliaceae),<sup>67</sup> *Gmelina arborea* (Verbenaceae),<sup>66</sup> *Tectona grandis*,<sup>47</sup> *Terminalia ivorensis* (Combretaceae),<sup>68</sup> and *Pinus kesiya*.<sup>2</sup> Biennial flowering has been reported for the majority of the canopy species in Surinam,<sup>113</sup> and non-12-month cycles exist as well as instances in which flowering may not occur on any appreciable scale for 3 to 8 years or even more. The 10 to 15 year interval between flowering of *Homalium grandiflorum* (Flacourtiaceae) in Singapore<sup>52</sup> may be seen as intermediate between most trees and the monocarpic condition.

#### *The Period That Species Remain in Flower*

Some trees have an extremely precise time for flowering, such that the entire crown is in flower for a few days only, as in *Tabebuia serratifolia* in Surinam<sup>113</sup> and *T. ochracea* spp. *neochrysantha* in Central America.<sup>37</sup> If many individuals of a species flower synchronously over a whole district or region, this is termed gregarious flowering, and is characteristic of *Pterocarpus indicus* (Papilionaceae)<sup>52</sup> and many dipterocarps in southeast Asia (see section "Flowering in Dipterocarps: A Special Case").

Related species have been reported to flower at different times, such that a genus may span the whole year (for example, *Arrabidaea*, Bignoniaceae). A contrasting category of trees opens a few flowers each day over 1 to 4 months.<sup>37,49</sup> Individual flowers typically remain open only for a few hours<sup>102</sup> although those of *Bombax buonopozense* (Bombacaceae), for instance, last for several days. Data are available on receptivity and shedding periods<sup>31,69,88,98,100,104,125</sup> and on nectar secretion.<sup>32</sup>

### **Flowering and Vegetative Growth**

#### *Shoot Extension Growth and the Time of Flower Initiation*

There is some circumstantial evidence that flowers may normally be initiated when shoots

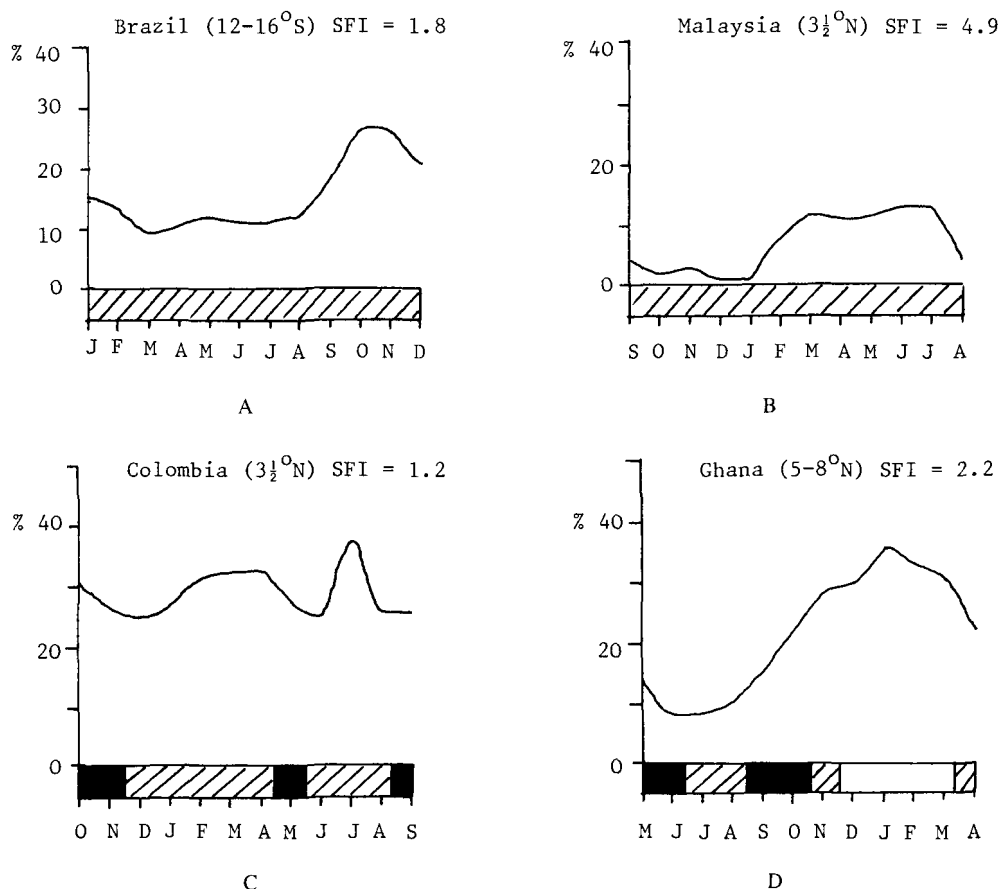


FIGURE 1. Seasonal variation in the percentage of tree species in flower. SFI = Seasonal Flowering Index (ratio of number of species in flower during the consecutive 6-month period with most flowering, to that with the least). Dark zones — wet season; cross-hatched zones — moist; open zones — dry season. Redrawn from authors' data. (A) Alvim and Alvim<sup>1</sup> — Coastal area near Bahia, Brazil. 120 trees of 30 spp for 3 years; (B) Medway<sup>87</sup> — Ulu Gombak Forest Reserve, Selangor, Malaysia. 56 trees of 42 spp. observed from 43-m-high tower for 6 years (Note: many dipterocarps did not flower in 4 of the years); (C) Hilty<sup>49</sup> — Alto Yunda, Valle, Colombia. 621 trees (over 3 m tall) of 164 spp on a 1000 × 6-m-transect for 14 months; (D) Hall and Swaine<sup>44</sup> — Southern Ghana. 169 species from plot records throughout the natural forests of Ghana (excluding "more or less ever-flowering" and "not clearly seasonal" categories); (E) Croat<sup>24</sup> — Barro Colorado Island, Panama Canal Zone. Approximately 270 species of large- and medium-sized trees from herbarium specimens and field observations for 3 years; (F) Tomlinson<sup>118</sup> — S. Florida. 75 species observed over 11 years (excluding "more or less everflowering" and "not clearly seasonal" categories).

of a certain morphological type are at a particular stage of growth, for instance when a new flush has just been completed, and the buds are beginning to form. It has been suggested that young *Pinus taeda* does not reproduce because the intermittent growth habit allows insufficient time for cone initiation,<sup>39</sup> and a disturbance of synchrony is often noted in plantations of *P. caribaea* with cones of both sexes at widely different stages. It has also been observed that trees of *Tabebuia rosea* and *Cordia glabra* (Boraginaceae) which lose their leaves in the dry season in Costa Rica often flower at the same time, whereas those individuals which lose their leaves in the rainy season do not flower. *Erythrina poeppigiana* (Papilionaceae) sheds its leaves twice a year, but only flowers in the dry season.<sup>12</sup> (See chapters on *Tabebuia*, *Cordia*, and *Erythrina* in Volume V.)

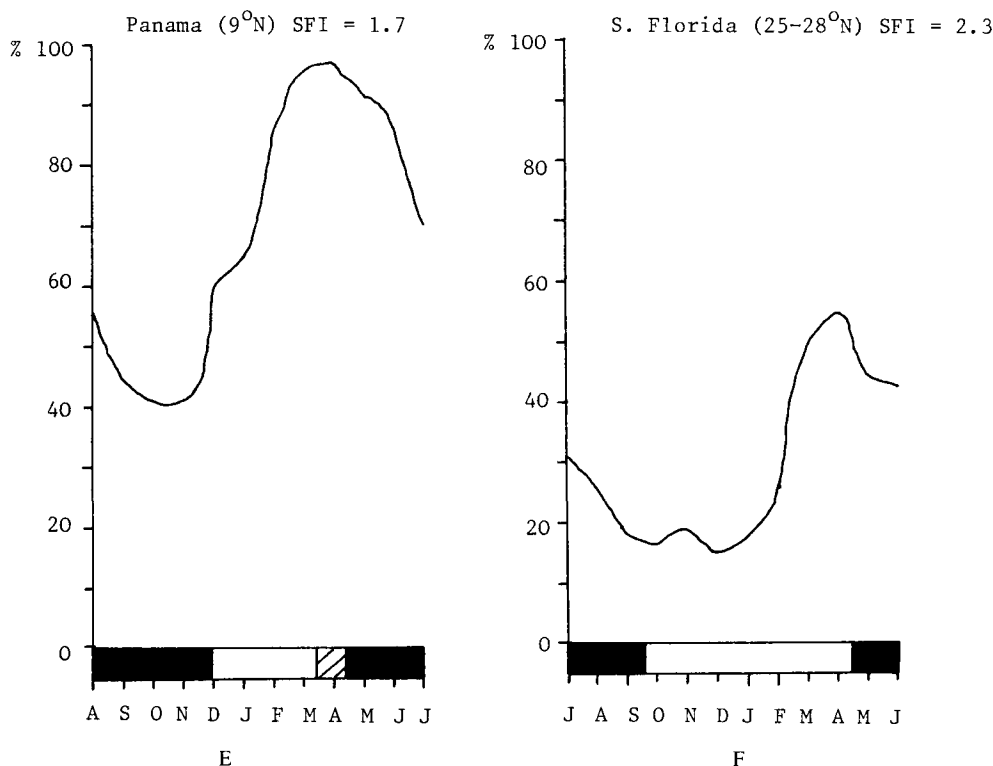


FIGURE 1

### *Vigor of Shoot Growth and Its Correlation with Flowering*

There is a widely held belief that the two processes are somehow in opposition, dating back to early work on the C/N ratio,<sup>64</sup> and drawing credence from observations on trees which have flowered heavily and shown reduced vegetative growth following stress of some kind. Although there may well be some truth in this, it is possible that a reduction in root growth is of greater significance. Moreover, rapid vegetative growth in young seedlings may actually hasten the attainment of a size at which flowering is more likely to occur.<sup>76,121</sup>

### FLOWERING IN DIPTEROCARPS: A SPECIAL CASE

The Dipterocarpaceae, dominant family of many of the tropical forests of southeast Asia, combines in a striking fashion irregularity and precision of reproductive activity. Scarcity of flowers is general, severely restricting reafforestation, improvement and yields in species producing, for example, the *meranti* group of timbers and the oil-rich *illipi* nuts.

By definition, phenological information about irregular events is difficult to obtain and approximate in nature. Thus the onset of first flowering was recorded at 17 to 45 years in the arboretum at Kepong, West Malaysia.<sup>92,93</sup> Estimates for natural forests are longer still (about 60 years<sup>3</sup>), for trees must generally emerge into the middle tree layer or receive extra light from a gap. In more open stands, precocious flowering is sometimes observed, and exceptionally, 20% of some 7-month-old seedlings of *Dipterocarpus oblongifolius* flowered as potted plants in a greenhouse in Serdang, West Malaysia.<sup>115</sup>

Once dipterocarps have started flowering, there are periods of about 1 to 7 years in which there is small-scale and sporadic flowering by individual trees (or branches on a tree). This is followed by a year in which heavy flower production occurs in the family as a whole, often accompanied by marked reproductive activity in other families.<sup>19,87,123</sup> Within a dip-

terocarp species, flowering is typically gregarious, with perhaps well over half the individual trees flowering synchronously across many square kilometers. The period in which flowers were open was found to be 15-25 days in 6 species of *Shorea* in a detailed study in Malaysia by Chan,<sup>18</sup> with peaks of flowering activity lasting 5 to 11 days (Figure 2). Very large numbers of flowers were produced: sample trees of *S. leprosula*, for instance, opened between 63,000 and 4 million flowers each, despite considerable flower bud abortion.

The most striking pattern discovered was that these closely related species were staggered in their flowering periods, so that the peaks did not overlap (Figure 2). This characteristic, which has also been noted in the Bignoniaceae of the New World,<sup>37</sup> is often considered to have evolved through competition for a limited number of pollinators. This group of *Shorea* spp. is strongly self-incompatible, and yet appears to be pollinated predominantly by weakly flying thrips.<sup>19</sup> The flowers, which open between 1700 and 1830 hr apparently reach peak stigma receptivity between 2000 and 2400 hr. Next morning, the corollas with their adnate stamens become detached, and gyrate slowly to the forest floor, bringing many of the thrips with them. Next evening the insects fly up again, assisted perhaps by rising air currents, some presumably reaching and cross-pollinating other trees of the same species.

In attempting to form hypotheses about the physiological signals which evoke such a precisely controlled series of "time-niches" between these closely related but effectively isolated species, the following points emerge:

1. *S. macroptera*, the earliest to flower, took only 18 days from the first signs of flower buds (seen with binoculars) to the start of blooming;<sup>19</sup> the latest to flower, *S. leprosula*, took 46 days (Figure 2). Assuming steady rates of floral development from initiation to anthesis, there is a strong presumption that the timing of floral initiation for all 6 species might well have been during the first 10 days of February, 1976. (A less likely alternative would be release of previously initiated flower buds from dormancy in early February.)
2. The most likely physiological trigger might be a macroclimatic factor, since the responses are so widespread, occurring on many species of trees of different sizes growing on varying soils and sites. A long-term endogenous rhythm seems wholly incapable of explaining the phenomenon.
3. Of the possible environmental factors, daylength is ruled out by the absence or scarcity of flowering in many years. Various authors have suggested correlations with drier spells<sup>17,87,106</sup> or occasional severe drought,<sup>21</sup> but these are also times of greater sunshine<sup>93</sup> and more pronounced diurnal fluctuations in temperature. Greater values of all three of these factors tend to occur in West Malaysia particularly in the period January to March.<sup>25,26,87</sup> Thus an extra 30 to 45 hr of sunshine sometimes occur and diurnal fluctuations in temperature can reach 12°C in February, even as a monthly average. February rainfall only 10% of normal was recorded before a heavy flowering year.<sup>21</sup>
4. On the whole, the most likely hypothesis is that an increased diurnal fluctuation of temperature provides the region-wide signal for flower initiation. This might be associated with clearer skies and less humid air, due perhaps to perturbations in or unusual movement south of the West Pacific Polar Front.<sup>50</sup> It is interesting that further north in Malaya flowering is more frequent,<sup>52</sup> while in Indochina the local dipterocarp species tend to flower annually.<sup>4</sup>

The validity of this hypothesis, and of others, could now perhaps be tested experimentally. As already mentioned, flowering has been recorded in 7-month-old *Dipterocarpus oblongifolius* seedlings from a prolifically flowering forest tree when they still averaged only 37 cm in height.<sup>115</sup> Since several dipterocarps have been rooted as cuttings from young trees, the approaches described in the Section "Approaches to the Problem" now seem possible,

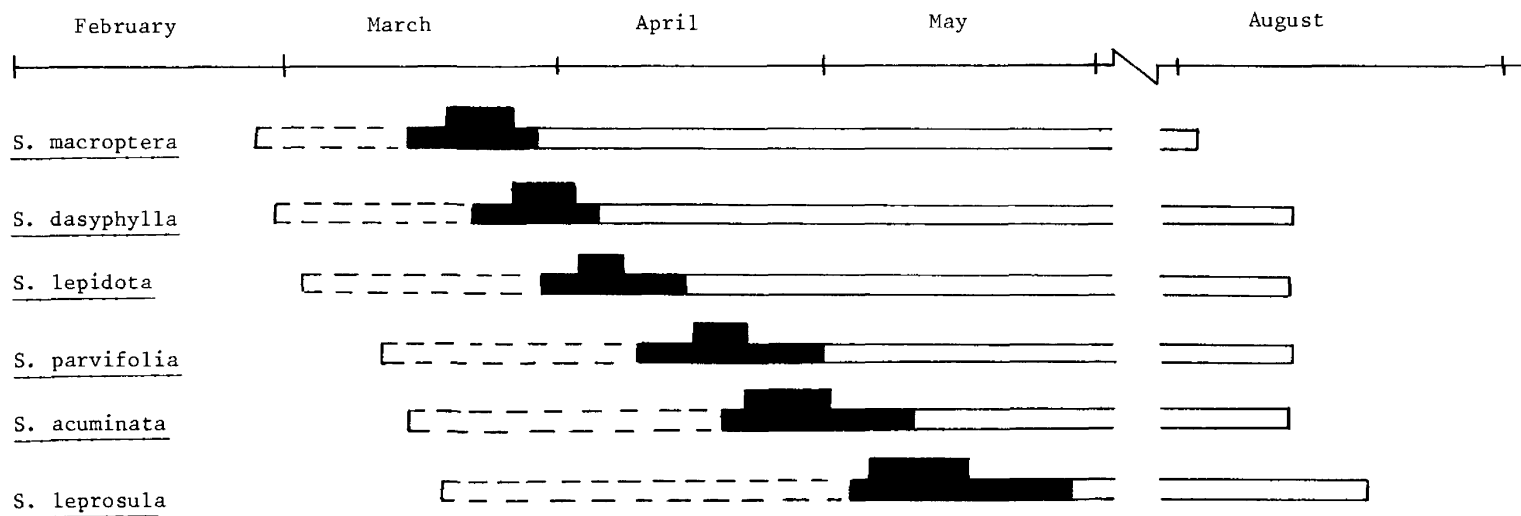


FIGURE 2. Sequential flowering of six related species of *Shorea*, in the gregarious dipterocarp flowering year of 1976 (redrawn from Chan,<sup>18</sup> and Chan and Appanah<sup>19</sup>). Dotted zones – flower buds detectable by binoculars; dark zones – flowers open (plus peak flowering period); open zones – fruit development.

with controlled environment comparisons in precisely known conditions. Once key factors begin to be elucidated, it will become possible to consider practical techniques for flower induction. These might well prove to be applicable not only to dipterocarps in general, but perhaps to other families as well.

## EFFECTS OF TREATMENTS ON FLOWER INITIATION

### Environmental

Because of technical and other problems, the number of experimental studies of flowering in tropical trees has been very limited. Various possible factors, such as light intensity, photoperiod, temperature, and water-stress have been frequently suggested, but seldom tested. Suppression of flowering in branches of *Hildegardia barteri* (Sterculiaceae) close to street-lights has been interpreted as a possible inhibition by continuous illumination of a short-day plant.<sup>43</sup> Certainly a number of tropical forest trees have been shown to be sensitive to daylength in their vegetative growth<sup>74,79,94,116</sup> and a number of economically important shrubs have been reported to be SDP. However, it is probably a mistake to conclude that all will be SDP or day-neutral,<sup>101</sup> for Mathon<sup>86</sup> has shown that a substantial minority of tropical plants are LDP, while the SDP are not necessarily obligate.<sup>42,122</sup>

Precocious flowering has been stimulated in seedlings, and cuttings taken from them, of the timber tree *Triplochiton scleroxylon* (Sterculiaceae) grown under year-round 19½-hr photoperiods in tropicalized glasshouses in Scotland.<sup>72</sup> Fifteen plants representing 9 clones have produced flowers on 24 occasions between February and August. The time from germination to first flowering ranged from 2 to 6 years, the plants being approximately 0.5 to 2.5 m tall. One 0.7-m plant produced 160 flower buds, including an inflorescence terminal on the main stem, so it is clear that the onset of reproduction has occurred sooner than in forest conditions (see Table 1).

As regards the causative factors, it seems probable that *T. scleroxylon* is at least a facultative LDP or day-neutral species. Flowering tended to occur in plants kept in temperatures around 20°C, often in relatively small pots, while other members of the same clones given temperatures of 25 to 30°C, more artificial light supplement, and larger pots, grew vigorously but vegetatively. Preliminary evidence suggests that chilling the soil to about 10°C while keeping the air temperatures higher may possibly be one way to trigger flowering,<sup>70</sup> but the various factors have still to be clearly determined. In this connection, it is interesting that 11 out of 12 container-grown cuttings from a mature clone of *Gmelina arborea* flowered in a nursery in Nigeria, whereas no flowering was observed in those planted out.<sup>53</sup> A promising hypothesis would be that flowering is stimulated by restrictions to root growth, and perhaps also to shoot growth and translocation.

Precocious flowering has also occurred under the Scottish glasshouse conditions in two clones of *Cedrela odorata* and one of *Gmelina arborea*; and twice in a seedling of *Vateria* (*Vateriopsis*) *seychellarum* (Dipterocarpaceae). This is of special interest since this endemic species is on the point of extinction. Precocious flowering in a temperate-zone glasshouse has also been reported for a subtropical eucalypt under 16-hr days, but not in natural daylengths (maximum 15 hr).<sup>11</sup> (See *Eucalyptus*, in Volume II.) Conversely, 1-year-old grafts of *Pinus taeda*, made with scions from nonflowering trees 2 to 6 years old, were stimulated to produce male and female cones by reducing the photoperiod from 20 to about 10 hr, and lowering night temperatures.<sup>39</sup> It was noted that frequent watering and applying fertilizers to mature grafts of the same species tended to stimulate vegetative growth, eliminate female coning, and reduce male coning.

In a study of the effects of herbivores on six species of small trees and shrubs in Costa Rica, complete experimental defoliation once or twice between August and October eliminated reproduction in more than 80% of trees, though not in some instances where the top

was left intact.<sup>110</sup> By contrast, there are reports that severe defoliation using 25% urea sprays stimulated flowering in the tropical fruit tree guava.<sup>20</sup> (See *Psidium*, in Volume V.)

### Hormonal

Spraying 1-year-old *Cupressus lusitanica* seedlings in a nursery in Colombia with 50 to 200 ppm GA<sub>3</sub> induced male coning, with female cones also on two plants receiving 200 ppm.<sup>41</sup> Injection of larger mature grafted trees was not successful, probably because the doses of 250 to 1000 µg per tree were too small. A single injection of 1 to 6 mg GA<sub>3</sub> into smaller shoot systems has stimulated prolific cone formation in four nontropical *Cupressus* species.<sup>83</sup> The subtropical *Callitris glauca* and *C. intratropica* also responded, and since this effect is found in at least 35 species and hybrids of 15 genera, it may well be characteristic of the Cupressaceae.<sup>105</sup> Recommended doses for substantial male and female cone induction are 1 to 5 mg GA<sub>3</sub> per meter of treated shoot for small specimens, and up to 10 times more for trees above about 3 meters in height.<sup>83</sup> A single injection of an alcoholic hormone solution into one or two holes in a branch or main stem is the simplest and probably the most effective method,<sup>27</sup> and the doses and timing can easily be adjusted by trial and error.

These clearcut promotive effects of GA<sub>3</sub> appear not to hold for other conifers (except probably for the Taxodiaceae), while in broad-leaved trees gibberellins are often inhibitory to flower initiation. Some stimulation has been reported for nontropical members of the Pinaceae with mixtures of GA<sub>4</sub> and GA<sub>7</sub>,<sup>105</sup> including the subtropical *Pinus taeda*.<sup>39,40</sup> Slight promotion with GA<sub>4</sub> and pronounced stimulation by a soil drench of 30 ppm of the growth retardant Ancymidol has been reported for the dicotyledenous vine *Clerodendrum thomsoniae* (Verbenaceae).<sup>63</sup> Once suitable plant material becomes available (see Section “Approaches to the Problem”), there is a wide range of growth substances and other chemicals found effective in other woody plants, such as CCC, for example, which can be screened for possible effects in tropical forest trees. Moreover, it is also becoming easier to test for levels of endogenous growth substances in localized parts of plants.

### Bark-Ringing (Girdling)

This centuries-old method of inducing trees to flower is very effective when applied in early spring to various unrelated temperate zone species, sometimes even in young trees.<sup>75,78</sup> Examples include *Betula* (Betulaceae), *Nothofagus* (Fagaceae), *Pyrus* (Rosaceae), *Ulmus* (Ulmaceae); and *Larix* and *Pinus* (Pinaceae), × *Cupressocyparis* and *Thuja* (Cupressaceae), and *Metasequoia* (Taxodiaceae). Success has also been reported for tropical fruit trees, and for *Pinus elliottii* var. *elliottii*,<sup>51</sup> *Faurea speciosa* (Proteaceae),<sup>95</sup> and *Terminalia ivorensis*.<sup>14</sup> The similar technique of strangulation is said to stimulate flowering in *Pinus* spp. and *Tectona grandis*.<sup>117</sup> Removal of a complete “ring” of bark down to the cambium is generally much more effective than partial systems, but the positioning of the ring (immediately above vigorous branches on the mainstem, or at the base of a strong branch or fork) is critical for continuing survival of the treated portion.<sup>75</sup> The width of the ring (generally 5 to 15 mm), timing of the ringing some months before the estimated period for flower initiation, immediate treatment of the ring with a wound paint, and mechanical support for the ringed shoot, are also important. Promotion of reproduction occurs in the first and/or second flowering period after treatment, and may sometimes persist, even after the ring has callused over. At present, a narrow complete ring appears to be the most promising flower induction technique to try out on tropical woody species outside the Cupressaceae.

## EFFECTS OF TREATMENTS ON FLOWER BUD DEVELOPMENT

Considerable confusion is caused because the interval between flower initiation and an-



thesis can differ greatly. A broad distinction can be made between trees comparable with the everflowering group, in which initiation is evidently succeeded by primordium growth and opening of the floral parts without a break; and those similar to most temperate-zone trees with an extended period of flower bud dormancy. Here different external and internal conditions may influence flower bud opening, compared with those prevailing at initiation.

A 7-year study of trees and shrubs by Opler et al.<sup>101</sup> in a tropical forest in Costa Rica with an approximately 5-month dry season has provided valuable information. In *Croton reflexifolius* and *Bernardia nicaraguensis* (Euphorbiaceae), for example, flower buds are already fully formed before the dry season starts. Plants are leafless during the dry season, but were observed to flower gregariously 2 to 5 days after the first rains. The flowering period was as short as 2 days, but occurred in March, April, or May in different years. A number of other woody plants appeared to respond at a slower rate to the same physiological signal of the first rain, and the sequence in which they did so was remarkably similar.

These results were obtained at two different sites, where rainfall occurred first at one site in 1972, and the other in 1973 and 1974. They thus form an unusual controlled "natural experiment", which confirms that the first rains appear to provide a trigger for considerable numbers of individuals and species of trees, which open flowers 2 to 14 days, or even perhaps 6 to 8 weeks later. Investigations in coffee (see Volume II), the orchid *Dendrobium crumenatum* (see Orchidaceae), and in bulbs suggest that the most likely stimuli for forest trees may be the moisture itself and/or the sudden dropping of temperature which accompanies a tropical storm. Detailed experiments are needed to clarify this, and also to show whether dry weather has an effect on flower bud dormancy analogous to that of cold temperatures in breaking the dormancy of buds of temperate-zone trees. Studies of hormonal changes within the shoots may also be helpful, as for coffee flower buds.<sup>15</sup>

Flower bud abortion before opening is quite common in some tropical trees, such as *Shorea* spp. and *Triplochiton scleroxylon*, so that, even without damage or stress, by no means every flower reaches anthesis.<sup>19,55,72</sup> In the glasshouse plants of *T. scleroxylon* described above, 30% of flower buds were abscised before opening. From those that opened and were cross-pollinated, however, over 50 viable seeds and normal seedlings were obtained.

## GENETIC CONTROL OVER FLOWERING

Tropical forest trees can be expected to show high genetic variability, since few of them have been selected, still less bred. Presumably those which are largely or completely self-incompatible, like *Triplochiton scleroxylon*<sup>55,72</sup> and *Shorea leprosula*<sup>60</sup> may be more diverse than self-fertile species, particularly those such as *S. agami* and *S. ovalis* ssp. *sericea* which form seeds with multiple embryos through apomixis.<sup>60</sup>

Where clonal material is available, there is often also strong evidence of genetic variability. For example, mature grafts of *T. scleroxylon* clone no. 4 flowered in Ghana at ages 4, 5, 6, 7, and 8 years from planting; four clones showed slight, occasional flowering; and 44 other clones did not flower at all during the period of observation.<sup>120</sup> In glasshouses in Scotland all 4 plants of mature clone 8057 have flowered, but 5 other mature clones remained entirely vegetative. Meanwhile, after crossing 2 "juvenile" clones, flowering has commenced at 2 years in the next generation, indicating perhaps a response to both genetic and environmental influences.

Instances of very precise synchrony in flowering times have been described above, but in other species individual trees may differ greatly in their behavior.<sup>24,53</sup> Some at least of this variation is genetic, for recognizable selections can be made of wild fruit-bearing forest species, which subsequently flower at different times.<sup>97</sup>

Selection for early, regular, and heavy flowering, although commonly practiced with fruit and ornamental species, may be counter-productive in trees grown for timber. Diversion of

more dry matter resources to reproduction may prove to be negative selection, unless green flowers and fruits contribute substantially to the tree's photosynthesis.<sup>10</sup> Moreover, inflorescences frequently occupy positions which would otherwise be vegetative branches, continuing to contribute to dry weight increment. They may even terminate the main stem so that further height growth is necessarily sympodial. Short or crooked boles may be formed, for instance, in trees showing Leeuwenberg's "architectural model" or branching system.<sup>45,46</sup> Teak (*Tectona grandis*) is a good example: here the widespread early flowering in plantations (see Table 1), particularly of certain provenances,<sup>28</sup> means that the straight main-stem terminates at a height of a few meters, occasionally even at less than 1 meter.<sup>47</sup>

Thus, although these floriferous stands of teak may be less than desirable in terms of economic forestry, they may prove invaluable if in the longer term they enable the keys to floral induction to be identified. Then the more vegetative and most desirable genotypes of tropical forest trees can be stimulated to contribute fully to the gene pools of later generations, forming an increasingly valuable resource.

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## DESERT PLANTS

M. Evenari and Y. Gutterman

## INTRODUCTION

In the last eighty years the physiology, ecology, and ecophysiology of desert plants have been studied intensively and in great detail by many authors. But nearly all of these investigations deal with water balance, photosynthesis, dry matter production, productivity, etc. The process and control of the flowering of desert plants has been largely neglected. One needs only to look through such old reviews of photoperiodism as, e.g., Lang,<sup>38</sup> Lockhart,<sup>41</sup> Naylor,<sup>49</sup> or recent ones like Vince-Prue<sup>63</sup> to see that there is not a single desert plant mentioned in their tables listing the photoperiodic reaction of a great number of plant species.

The only review on the flowering behavior of desert plants in relation to their environment, seed set, dispersal, and germination is a paper by Mott and Chouard<sup>48</sup> in which the authors deal, in a general way, with the question of parameters controlling the flowering of desert plants. (See also Evenari<sup>12</sup>.) We try in this paper to present the data known about the flowering of desert plants.

There is no precise demarcation line between deserts and arid and semi-arid zones. We will therefore deal with plants from all areas with a prolonged dry period without trying to define the terms, "desert," "arid," and "semi-arid."

For the plants of the Middle East we will indicate to which phytogeographic region they belong, i.e., which is their general area of distribution (g.a.d.), using the following abbreviations:<sup>9,10,22,68</sup> SA — Saharo Arabian elements, i.e., plants whose g.a.d. is the large desert belt stretching from the Atlantic coast of North Africa through the Sahara, Sinai, Southern Palestine, and southern Mesopotamia to extratropical Arabia; IT — Irano-Turanian elements whose g.a.d. is the steppical area extending from Mauritania through Palestine, Syria, Iraq, Iran, and eastern and central Turkey to the high plateau of Central Asia. This region is the center of origin for many plant species and genera; M — Mediterranean elements, i.e., plants whose g.a.d. is a narrow belt around the Mediterranean; ES — Euro-Siberian elements, i.e., plants whose g.a.d. is the northern part of Europe, and Asia up to Siberia excluding the Far East; B — Boreal. This is the northern subregion of the ES; TR — Tropical, i.e., elements whose g.a.d. is the tropics of the Old World; S — Sudanian elements, i.e., plants whose g.a.d. is the Sahelo-Sudanian zone including southwestern Arabia and a belt along the gulfs of Suez, Aqaba, the Persian Gulf, and the Gulf of Oman; Pl — Pluriregional elements, i.e., plants whose g.a.d. extends to a number of phytogeographic regions. When an abbreviation is followed by another one in brackets such as SA(IT), it means (e.g.) that the main distribution of the species is Saharo-Arabian but it extends also into the Irano-Turanian region.

## ANNUALS

In tables 1 to 3, the basic photoperiodic dependence of flowering of desert annuals from North America, the Negev desert, and Australia is summarized. Since flowering is not only controlled photoperiodically, and because vernalization, thermoperiod, water stress, and other parameters are also involved in conjunction with the photoperiod, these tables need additional explanations.

All of the winter annuals of the California arid and semi-arid regions (Table 1) are, according to the original paper by Lewis and Went,<sup>40</sup> LDP. But when we pointed out to Went that the Negev desert winter annuals were all FLD plants, he wrote in a personal communication (cited in Evenari and Gutterman<sup>13</sup>): "Quite generally I believe that the



**Table 1**  
**FLOWERING DATES AND THE PHOTOPERIODIC DEPENDENCE OF**  
**FLOWERING OF SOME CALIFORNIA ANNUALS**

Species	Family	Flowering date in nature	Photoperiod dependence of flowering	Ref.
<i>Baeria chrysostoma</i> T. and G.	Compositae	III—IV	FLD	40
<i>Baileya multiradiata</i> Harv. and Gray	Compositae	III—VII	FLD(LD)	40
<i>Coreopsis californica</i> Sharsmith	Compositae	III—V	FLD(LD)	40
<i>Eschscholzia californica</i> Cham.	Papaveraceae	II—IX	FLD(LD)	40
<i>Eschscholzia lobbi</i> Greene	Papaveraceae	III—IV	FLD(LD)	40
<i>Gilia tricolor</i> Benth.	Polemoniaceae	III—V	FLD(LD)	40
<i>Godetia quadrivulnera</i> (Dougl.) Spach.	Onagraceae	IV—VII	FLD(LD)	40
<i>Linanthus montanus</i> Greene	Polemoniaceae	IV—VI	FLD(LD)	40
<i>Madia elegans</i> Don.	Madieae?	VI—IX	Bimodal	40
<i>Mentzelia lindleyi</i> T. and G.	Loasaceae	IV—V	FLD(LD)	40
<i>Monardella lanceolata</i> Gray	Labiatae	VI—VIII	FLD(LD)	40
<i>Phacelia parryi</i> Torr.	Hydrophyllaceae	III—V	FLD(LD)	40
<i>Pectis papposa</i>	Compositae	VI—XI	DN ?	65
<i>Amaranthus fimbriatus</i>	Amaranthaceae	VIII—XI	DN ?	65
<i>Bouteloua barbata</i>	Gramineae	VII—XII	DN ?	65

Note: FLD (LD) means that in the original publication of Lewis and Went<sup>40</sup> the plants were designated as LD whereas we suggest that they are FLD plants.

California desert annuals, at least the winter and spring ones, are LDP. With relatively few exceptions, LDP are facultative and there are relatively few which never will flower in continuous short days.”

The winter annual *Baeria* needs some special attention. Of all the winter annuals, including those of the Negev, it comes closest to that of an ephemeral (very short lived). Already 5 days after germination the seedlings were photoperiodically sensitive, and the first flower primordia appeared 7 days after the beginning of LD treatment. The plant is already sensitive to photoperiods after it has developed cotyledons and one pair of leaves. It needs at least 5 photoperiods for flower initiation. The photoperiods are inductive only at temperatures below 25°C. The minimum light intensity for flower initiation is about 1 klx. Under optimal flowering conditions (17 to 20°C) and continuous light, flower bud opening occurred 19 to 32 days after seeding.<sup>60,65</sup> The age of the *Baeria* seeds has an effect on the time span between germination and flowering. Seedlings derived from fresh seeds flowered under optimal conditions after 19 days, and 3-year-old seeds under identical conditions flowered after 32 days. According to Camus (cited in Went<sup>66</sup>), *Baeria* forms flower primordia after 37 days under SD when amino acids are added to the rooting medium.

It is not clear if the Californian desert annuals need cold vernalization for flowering, but according to Soriano (cited in Went<sup>66</sup>), flowering is delayed by pretreatment of the seeds with rain.

Three Californian summer annuals seem to be DN plants (*Pectis*, *Amaranthus*, *Bouteloua*); one (*Madia*), has two photoperiodic flowering optima, one at 8 hr, the other at 12 to 18 hr of light (bimodal or amphi-photoperiodic reaction).

In contrast to the Californian annuals of which only a few are real desert plants, the annuals growing in the Negev desert<sup>13</sup> (Table 2), are either real desert plants (SA) or steppe-desert plants (IT or M-IT). The plants were grown under the same photoperiods (8 hr and 20 hr) in the greenhouse and outdoors. Since the authors used only one SD and one LD photoperiod, their conclusions concerning the photoperiodic dependence of flowering were not fully conclusive. Gutterman<sup>22b,23a-c</sup> repeated the experiments with *Trigonella stellata*,

*Tr. arabica*, *Polypogon monspeliensis*, *Rumex cyprius* and others using 6, 10.5, 12, 13.5, 15, and 18 hr photoperiods in the greenhouse and outdoors and came to the same conclusions as Evenari and Gutterman.<sup>13</sup> The first 10 species of Table 2 are FLD plants. Table 3 demonstrates this for one representative plant of this group. The second group, i.e., *Carrichtera*, *Gymnarrhena*, and *Reboudia* behaved in the greenhouse as FLDP and outdoors as DNP (see *Gymnarrhena* as representative of this group in Table 2). The six species of the third group (*Malva* in Table 3 as an example) are somewhat intermediate between groups 1 and 2. It is not clear why the plants of groups 2 and 3 behave as FLDP in the greenhouse and as DNP outdoors.

It is most probable that temperature differences are involved since Lona<sup>43</sup> demonstrated for *Carrichtera* and *Ifloga spicata* that both are very sensitive to low temperatures with respect to their photoperiodic reaction. But the possibility that light intensity is one of the parameters controlling flowering of desert plants cannot be excluded.<sup>12</sup> Chouard<sup>5</sup> reported a clear effect of light intensity on the flowering response of *Scrophularia arguta* (see Volume IV).

The amphicarpic *Gymnarrhena* which normally carries underground and above-ground flower heads had a quite interesting photoperiodic reaction. The LD greenhouse plants formed only above-ground capitula. The LD outdoor plants carried only subterranean flower heads, and the SD greenhouse and outdoor plants both types of capitula. One could therefore call *Gymnarrhena*, as far as amphicarpy is concerned, a facultative amphicarpic plant.<sup>11,16,17,34</sup>

The facultative amphicarpic behavior is apparently controlled by photoperiod, temperature, and perhaps, light intensity. We observed in the field that in years with late germination-triggering rainfall, when germination of *Gymnarrhena* took place when daylength was increasing but temperatures were still relatively low, the plants developed only subterranean capitula as under LD and outdoors in the experiment. We never found in the field plants with only above-ground flower heads. Possibly the formation of subterranean capitula is suppressed by a combination of LD, high temperature, and perhaps also low light intensities. Plants in the field are never exposed to such environmental conditions. The amphicarpic reaction to SD is apparently independent of temperature.

A comparison of the photoperiodic dependence of flowering of desert winter annuals with that of winter annuals of the Mediterranean region of Israel shows that there is no difference in this regard between the two groups. The species of the Mediterranean group investigated by Landau<sup>37</sup> were all legumes: *Astragalus hamosus* L. (M-IT), *Lotus peregrinus* L. (M), *Medicago orbicularis* (L) Bart. (M-IT (ES-S), *M. coronata* (L.), Bart. (M(IT), *Melilotus sulcatus* Desf. (M), *Tetragonolobus palestinus* Boiss. (M), *Trifolium lappaceum* L. (M(IT), *Tr. stellatum* L. (M), *Tr. purpureum* Loisel (M(IT-ES), *Tr. palaestinum* Boiss. (M), *Tr. scabrum* L. (M(IT-ES), *Tr. vavilovii* Eig. (M), *Tr. spumosum* L. (M-IT), *Tr. argutum* Banks et Sol. (M) (= *Tr. xerocephalum* Fenzl.), *Trigonella spinosa* L. (M), *Tr. monspeliaca* L. (M-IT), *Trigonella coelesyriaca* Boiss. (M), and *Vicia narbonensis* L. (M(ES-IT). All these winter and spring annuals are FLD plants.

The two arido-active biseasonal *Salsola* species listed in Table 2 are FSDP (Table 3). They cannot be classified as summer annuals because they germinate during the rainy season in winter and spring, are physiologically active during the dry season, and flower late in July/September before the start of the next rainy season. Their flowering clock is apparently set by a combination of shortening days and high temperatures.

The biseasonal behavior of the two *Salsola* species can, under certain artificial conditions which the plants will never undergo in nature, be changed into a quasi seasonal one. When exposed during winter (SD) to high day temperatures (30°C and more), they flowered after 3 months and not after 6 to 8 months as in nature.<sup>24a</sup> They could therefore be called potential facultative biseasonal plants.

*Salsola inermis* and *S. volkensii* are not the only biseasonal species of the chenopods

**Table 2**  
**FLOWERING DATES AND PHOTOPERIODIC DEPENDENCE OF ANNUALS OF THE NEGEV DESERT OF ISRAEL**

Species	Phytogeographical distribution <sup>a</sup>	Family	Flowering date in nature	Photoperiod dependence of flowering	Ref.
<i>Asteriscus pygmaeus</i> (Viv.) O. Ktzel.	SA(IT)*	Compositae	I—IV	FLD	13, 23
<i>Astragalus cruciatus</i> Link.	M—SA(IT)	Papilionaceae	III—V	FLD	13
<i>Ifloga spicata</i> (Forsk.) Sch. Bip.	SA(M)	Compositae	III—V	FLD	13, 40, 41
<i>Lappula spinocarpus</i> (Forsk.) Aschers. ex O. Ktze. (= <i>Sclerocaryopsis spinocarpus</i> (Forsk.) Brand)	SA—IT	Boraginaceae	II—IV	FLD	13
<i>Limonium thouini</i> (Viv.) O. Ktze., (= <i>Statice thouini</i> Viv.)	SA	Plumbaginaceae	III—V	FLD	23b
<i>Plantago coronopus</i> L.	M—IT—SA	Plantaginaceae	I—V	FLD	13
<i>Rumex cyprius</i> Murb. (= <i>R. roseus</i> L.)	SA—IT(M)	Polygonaceae	I—V	FLD	13, 23c
<i>Schismus arabicus</i> Nees.	IT—SA	Gramineae	II—IV	FLD	13
<i>Stipa capensis</i> Thunb. (= <i>St. tortilis</i> Desf.)	IT-SA	Gramineae	III—V	FLD	13
<i>Trigonella stellata</i> Forsk.	SA(IT)	Papilionaceae	II—V	FLD	13, 23c
<i>Trigonella arabica</i> Del.	SA	Papilionaceae	III—IV	FLD	22b
<i>Polypogon monspeliensis</i> (L.) Desf.	M—IT—SA(Tr)	Gramineae	III—VI	FLD	23c
<i>Carrichtera annua</i> (L.) DC.	SA	Cruciferae	II—V	DN/FLD	13, 42, 43
<i>Gymnarrhena micrantha</i> Desf.	SA(IT)	Compositae	III—V	DN/FLD	13
<i>Reboudia pinnata</i> (Viv.) Schulz	SA	Cruciferae	II—IV	DN/FLD	13
<i>Filago pyramidata</i> L. (= <i>F. spathulata</i> Presl.)	M(IT)	Compositae	II—V	Intermediate FLD, DN/FLD	13
<i>Malva aegyptia</i> L.	SA(M)	Malvaceae	III—V	Intermediate FLD, DN/FLD	13
<i>Matthiola livida</i> (Del.) D.C.	SA	Cruciferae	III—V	Intermediate FLD, DN/FLD	13
<i>Medicago laciniata</i> (L.) Mill.	SA	Papilionaceae	III—V	Intermediate FLD, DN(FLD)	13
<i>Ononis sicula</i> Guss.	M—SA—IT	Papilionaceae	III—V	Intermediate FLD, DN/FLD	13, 14, 24
<i>Plantago ovata</i> Forsk.	SA—IT	Plantaginaceae	I—V	Intermediate FLD, DN/FLD	13