CRC REVIVALS

The Physiology of Flowering

Volume I: The Initiation of Flowers

Georges Bernier, Jean-Marie Kinet,
Roy M. Sachs

CRC Press
Taylor & Francis Group

The Physiology of Flowering

Volume I
The Initiation of Flowers

Authors

Georges Bernier, Ph.D.
Professor of Plant Physiology
Director, Centre de Physiologie Végétale Appliquée (I.R.S.I.A.)
University of Liège
Liège, Belgium

Jean-Marie Kinet, Ph.D.
Assistant
Centre de Physiologie Végétale Appliquée (I.R.S.I.A.)
University of Liège
Liège, Belgium

Roy M. Sachs, Ph.D.
Professor and Plant Physiologist
Department of Environmental Horticulture
University of California
Davis, California

CRC Press
Taylor & Francis Group
Boca Raton London New York

CRC Press is an imprint of the
Taylor & Francis Group, an **informa** business

First published 1981 by CRC Press
Taylor & Francis Group
6000 Broken Sound Parkway NW, Suite 300
Boca Raton, FL 33487-2742

Reissued 2018 by CRC Press

Library of Congress Cataloging in Publication Data

Bernier, Georges, 1934-
The initiation of flowers.

(The Physiology of flowering; v. 1—2)
Bibliography: p.
Includes index.
1. Plants, Flowering of. I. Kinet, Jean-Marie, joint author. II. Sachs, Roy M., joint author.
III. Title. IV. Series: Physiology of flowering; v. 1—2.
QK830.B47 582.13'04166 80-24351
ISBN 0-8493-5709-8 (v. 1)
ISBN 0-8493-5710-3 (v. 2)

A Library of Congress record exists under LC control number: 82159289

Publisher's Note
The publisher has gone to great lengths to ensure the quality of this reprint but points out that some imperfections in the original copies may be apparent.

Disclaimer
The publisher has made every effort to trace copyright holders and welcomes correspondence from those they have been unable to contact.

ISBN 13: 978-1-315-89657-1 (hbk)
ISBN 13: 978-1-351-07567-1 (ebk)

Visit the Taylor & Francis Web site at http://www.taylorandfrancis.com and the
CRC Press Web site at http://www.crcpress.com

OBJECTIVES AND ORGANIZATION OF THE WORK

Scientific advances often come from uncovering a hitherto unseen aspect of things as a result, not so much of using some new instrument, but rather of looking at objects from a different angle.

F. Jacob*

From the point of view of basic biology, plant scientists have given much attention to flowering because this is the first step towards sexual reproduction in plants. Also, since the onset of flowering is under absolute environmental control in many species, some biologists with a deep interest in morphogenesis chose the flowering process as their field of research. Interest in this developmental step has a strong economical basis, too, since many aspects of agronomic and horticultural crop production are intimately associated with flowering. Fundamental investigations provide a conceptual framework for the development of practical applications, particularly following the discoveries of photoperiodism and vernalization early in this century. From this period to the present, research has expanded rapidly. Just before World War II, the concept of the floral hormone or florigen was defined; this idea has received experimental support and is apparently the most widely accepted theory for the control of floral initiation. Despite numerous attempts to isolate and identify the hypothetical hormone, we still have no idea of its chemical nature.

With the introduction of more refined investigation techniques in the field, it is apparent that the flowering process is extraordinarily complex. It includes several interrelated steps, each of which is influenced by several factors of both internal and external origin. The simple florigen concept seems no longer commensurate with the complexity of the phenomenon it was supposed to explain. Possibly because of its simplicity it has remained the favorite theory. The physiology of flowering is thus in the uncomfortable situation, perhaps unique in biology, that it is still dominated by a concept proposed more than 40 years ago. It is recognized more and more that this concept puts severe constraints on further developments in both fundamental and applied research programs in which the onset of flowering is the key process.

In all experimental sciences, the appearance of new evidence that is irreconcilable with a theory, no matter how well established the theory may be, requires consideration of alternate hypotheses. Following this rule we suggest that a reconsideration of accepted notions of the physiology of flowering is absolutely and urgently required.

The present work is organized such that the whole phenomenon of flowering is divided into two major steps: (1) the initiation of flower primordia and (2) the development of these primordia into mature flowers until anthesis. Despite the fact that a separation of these two stages does not appear possible on theoretical or evolutionary grounds, the absence of clear distinction between the various stages of the flowering process in several investigations makes interpretation difficult or impossible, and therefore, the results are of little value. These stages are not all alike and do not always react similarly to external and internal variables. They should thus be considered independently to avoid confusion.

The first two volumes are devoted to "flower initiation" which includes not only the production by meristems of clearly recognizable flower primordia, but also all preceding reactions that are required if flowers are to be initiated. This has been by

* From Jacob, F., *Science*, 196, 1161—1166, 10 June 1977. Copyright 1977 by the American Association for the Advancement of Science.

far the most studied stage because many physiologists view it as the critical turning-point from vegetative to reproductive growth.

Volume I is concerned essentially with a review and critical analysis of the classical data and concepts. The aim here is to pinpoint the firmly established facts and controversial issues as well as to stress the shortcomings of classical work and interpretations. Research has indeed focused very heavily throughout the past 60 years on the effects of physical and chemical factors of the environment, while unfortunately little attention has been paid until quite recently towards gaining an understanding of the basic internal mechanisms that underlie the floral transition.

The first section of Volume II deals with these more intimate aspects of the onset of reproductive growth. The basic role of correlative influences in flower initiation, even in the simplest experimental systems, is demonstrated. Then, we proceed by a description of the floral transformation of shoot apices at levels ranging from the macromorphological to the molecular. The idea is that a rather complete description is central to an understanding of the process of flower initiation and that it may further give some insights into the controlling agents of this process.

The second section of Volume II begins with a search for exogenous chemicals that control in part, or totally, the events of the floral transition. This is followed by a review of the work on endogenous substances that are considered as possible promoters or inhibitors of flower initiation. An attempt is made to see how far we have come in the understanding of the ultimate processes whereby a meristem begins to initiate flowers instead of leaves. The not surprising conclusion is that we are still a long way from the goal, but despite the fragmentary nature of the available evidence, the analysis developed in Volume II may provide a useful conceptual framework for future investigations in this important area of plant science. Also, it is anticipated that this new approach will result in development of more rational and efficient controls of flowering for agricultural and horticultural purposes. These applied aspects will be discussed in the third volume of this series.

The treatment of the different chapters is neither simplistic nor exhaustive. Our general philosophy has been to avoid extreme positions, either abusive generalizations that mask the real complexity of the problem and the diversity of plant behaviors or complete descriptions of all possible types of plant responses that create confusion and discourage the readers. Evidently, when one attempts to cover such an extensive subject in a limited number of pages there is inevitably a problem of topic selection. While our aim was to provide a balanced account of the most important and recent contributions in all aspects of the subject, some topics have wittingly received special treatment. Their selection reflects essentially our personal interest; other writers would have certainly made other choices and presented a differently balanced book. We like to think, however, that it will be recognized as timely and essential for the field to be reexamined from widely divergent points of view.

It is important to underline that constant reference to source material and use of a rich illustration should assist the unspecialized reader to obtain a full understanding of the discussed topics. Concluding sections are also inserted in many places and hopefully will be considered as resting spots. The busy reader may begin with these sections and the short Chapter 9, Volume II, and return to the main text for examination of important details. A glossary is also included for the reader who is unfamiliar with the scientific jargon of the field. In a work like this, there is some unavoidable repetition of material, but this has been reduced by frequent use of cross references. The species most commonly used in flowering studies will be usually referred to by their generic names alone.

The third volume will be concerned with the stages of flowering that follow initiation, essentially flower organization and maturation until anthesis. While the necessity of considering separately these successive stages was stressed above, it is also obvious that flowering is a unitary phenomenon and that its component steps are necessarily related to one another. After all flowering is about sexual reproduction in plants and we must expect that in evolution the entire physiological process is designed to expedite recombination of genetic characters and reproduction of the organism.

In this work we deal mainly with angiosperms, although gymnosperms are occasionally considered.

We hope that these three volumes will convey some of the excitement that we have felt during their preparation as well as during our investigations on flowering.

THE AUTHORS

Georges Bernier, Ph.D., is Professor of Plant Physiology, University of Liège, and Director of the Centre de Physiologie Végétale Appliquée (I.R.S.I.A.), Liège, Belgium.

Dr. Bernier graduated in 1956 from the University of Liège, with a "license" degree in botany and obtained his doctoral degree in 1963 from the same university. He performed an in-depth investigation on the uses of plants in nutrition, medicine, and other aspects of life in semiprimitive human societies in Zaire (1957 to 1958). He worked in the laboratories of Professors Buvat and Nougarede, Ecole Normale Superieure, Paris, France (1960 to 1961), and of Professor Jensen, University of California, Berkeley (1964 to 1965).

Dr. Bernier is a member of the American Society of Plant Physiologists, French Society of Plant Physiology, Society for Experimental Biology (U.K.), Federation of European Societies of Plant Physiology, Belgian Society of Biochemistry, and the Belgian Society of Cell Biology.

Dr. Bernier has presented many invited lectures at International Meetings, Universities, or Institutes. He has published more than 70 research papers and book chapters, and a book on *Cellular and Molecular Aspects of Floral Induction* (Longman, London, 1970) including the proceedings of a symposium that he organized at the University of Liège. His current major research interests include the molecular and cellular changes occurring in meristems at floral evocation and subsequent flower initiation, and the nature of the factors that control these developmental steps.

Jean-Marie Kinet, Ph.D., is a member of the Centre de Physiologie Végétale Appliquée (I.R.S.I.A.), Liège, Belgium.

He graduated in 1964 from the University of Liège, with a "license" degree in botany and obtained his doctoral degree in 1972 from the same university. He worked in the laboratory of Professor Wareing, University College of Wales, Aberystwyth, U.K. (1975).

Dr. Kinet is a member of the American Society for Horticultural Science, Belgian Society of Cell Biology, Federation of European Societies of Plant Physiology, and the International Society for Horticultural Science.

He has published more than 30 research papers. His current major research interests include the physiological and cellular aspects of flower initiation, inflorescence and flower development, and the inference that fundamental studies have on research concerning species with an economical interest.

Roy M. Sachs, Ph.D., is Professor and Plant Physiologist, Department of Environmental Horticulture, University of California, Davis.

Dr. Sachs graduated in 1951 from the Massachusetts Institute of Technology, Cambridge, with a B.Sc. in Biology; obtained the Ph.D. degree in Plant Physiology in 1955 from the California Institute of Technology, Pasadena, under the guidance of Dr. Went. In 1958 he began his academic career with the University of California, Los Angeles (1958 to 1961) and was with the Department of Floriculture and Ornamental Horticulture, and moved to Davis to join the Department of Landscape Horticulture (later renamed Environmental Horticulture). He was a Fulbright Fellow at the Università di Parma, Instituto di Botanica, Italy in 1955 and 1956 working with Dr. Lona. From 1956 to 1958 he was a Research Botanist at the University of California, Los Angeles with Dr. Lang. In 1969 to 1970 he was a visiting research scientist at the Vegetation Control Laboratories, U.S. Department of Agriculture (USDA), Fort Detrick, Frederick, Md., in 1975 a North Atlantic Treaty Organization (NATO) visiting

Professor at the Facoltà di Agraria, Universita di Padova, Italy, and in 1979 a visiting Research Scientist at the Département de Botanique, University of Liège, Belgium.

Dr. Sachs is a member of the American Society of Plant Physiologists Association and editor of *Scientia Horticulturae.* He has been the recipient of numerous grants for research on control of vegetative and reproductive development in higher plants. He has presented over 20 invited lectures on the control of vegetative and reproductive development.

Dr. Sachs is the author of more than 100 publications in scientific and technical journals, including review articles on reproductive development in higher plants. His current major research interests are in the areas of reproductive development, biomass production, and fuel conversion systems.

ACKNOWLEDGMENTS*

In preparing this work we acknowledge the support of our colleagues, first in our own departments (M. Bodson, W. P. Hackett, A. Havelange, and A. Jacqmard), and secondly those who have contributed so much to the original data based on flowering. But in a particular way we have appreciated the efforts of H. A. Borthwick, M. Kh. Chailakhyan, P. Chouard, L. T. Evans, K. C. Hamner, W. S. Hillman, A. Lang, A. Nougarède, F. B. Salisbury, D. Vince-Prue, S. J. Wellensiek, and J. A. D. Zeevaart, who have "paid their dues" in writing provocative and sometimes encyclopedic reviews of the subject.

We are greatly indebted to A. Bouniols, A. Nougarède, and M. Tran Thanh Van for supplying unpublished materials, and to these and many copyright owners for permission to reproduce illustrations and data from their publications. These sources are fully acknowledged in the captions of the figures and tables. One of us (Georges Bernier) would especially like to express appreciation to the University of Liège for providing facilities during the preparation of this manuscript. The assistance of Michelyne Dejace and Maggy Grossard in typing the manuscript and preparing the graphs is also gratefully acknowledged.

* Quotation on divider page, Section I from Went, F. W., *Union Int. Sci. Biol. Ser. B,* 34, 169, 1957. With permission. Quotation on divider page, Section II from Wardlaw, C. W., *J. Linn. Soc. London Bot.,* 56, 154, 1959. With permission. Quotations on divider page, Section III from Lang, A., *Communication in Development,* Lang, A., Ed., Academic Press, New York, 1969, 244. With permission. From Letham, D. S., Higgins, T. J. V., Goodwin, P. B., and Jacobsen, J. V., *Phytohormones and Related Compounds: A Comprehensive Treatise,* Vol. 1, Letham, D. S., Goodwin, P. B., and Higgins, T. J. V., Eds., Elsevier/North-Holland Biomedical Press, Amsterdam, 1978, 1. With permission.

TABLE OF CONTENTS

Volume I

SECTION I — CLASSICAL EXPERIMENTAL SYSTEMS AND DATA; ANALYSIS OF COMMON CONCEPTS

TABLE OF CONTENTS

Volume II

SECTION I
Classical Experimental Systems and Data; Analysis of Common Concepts

It is obvious that the problem of flowering [. . .] is a very complicated phenomenon, and [. . .] I do not believe that anything is gained by considering it simple.

F. W. Went

Chapter 1

EXPERIMENTAL SYSTEMS

TABLE OF CONTENTS

I. PLANT MATERIALS

Flower initiation is best investigated in the minority of species or varieties in which this process is under relatively strict control of the environment, as in absolute photoperiodic and cold-requiring plants. Many investigations require that plants start to flower at the same time and are at the same stage of development. In these species during a period of growth in noninductive conditions, an apparent uniformity in response to inductive conditions is achieved giving the required synchrony.

In the majority of higher plants, photoperiod and temperature affect the rate of the transition to flowering, but do not control it in an absolute sense. In such species, the lack of strict developmental control usually hinders the design of critical experiments because there is no precise zero time and insufficient synchronization of plants that must be analyzed as a group. Facultative photoperiodic or cold-requiring plants, while more common, do not represent anything basically different from the absolute ones since many species may have absolute daylength or temperature requirements in one set of environmental conditions and exhibit facultative behavior when some of the parameters are changed.

Early work is mostly with photoperiodic plants requiring several inductive cycles, but recent investigators favor species requiring exposure to only a single photoinductive cycle, because they are presumably the species with the greatest achievable uniformity and ease of timing of postinductive events.

An often-raised question concerns the real significance of the observed structural and chemical changes in relation to the transition to flower formation: are these changes an integral part of the developmental switch or simply accompanying unrelated changes? An unambiguous answer usually requires considerable experimental work and even then is quite difficult to reach. Very often the way to simplify this problem is to examine comparatively developmental transition in a variety of physical or chemical environments and see whether the changes in question are always present. Fortunately in many species, including most of the "single-cycle" ones, flowers initiate in response to more than one experimental treatment (Table 1), and this property makes these systems more exploitable.

Depending on the kind of experiments to be performed, plants may have to meet other prerequisites besides responsiveness to "one-shot" photoinduction. Speaking generally, small size at the responsive stage is essential in experiments that involve many treatments and in studies using a spectrograph or any similar equipment where the area irradiated with any wavelength of light is very limited. Consequently, the SDP *Pharbitis nil*,[1] *Chenopodium rubrum*,[2] and the LDP *Brassica campestris*,[3] which can be induced to flower by a single appropriate photocycle only a few days after sowing are particularly well-suited for such experiments.

Small fast-growing duckweeds, such as the LDP *Lemna gibba*, strain G3, first used by Kandeler,[4] or the SDP, *Lemna paucicostata*, strain 6746 (formerly designated as *L. perpusilla* 6746)[5] offer quite the same advantages as these seedlings. For the busy physiologist, duckweeds have the additional and inestimable advantage that if the flowering index of the cultures cannot be evaluated immediately at the end of an experiment, they may be stored until examination in a refrigerator for periods up to 2 weeks without any change of this index.[5] In addition, duckweeds floating aseptically in test tubes on defined nutrient media present themselves as ideal material for determining the effects of nutrition, and more generally of the chemical environment, on the flowering process.

When translocation of promoters or inhibitors of flower initiation is to be followed, seedlings or duckweeds are, however, frequently not suitable because they lack a transporting system of sizable length. The SDP *Xanthium strumarium*,[6] LDP *Lolium te-*

Table 1
ALTERNATE PATHWAYS TO FLOWER INITIATION IN SOME SINGLE-CYCLE SPECIES

Response Type	Species	Pathway	Discussed in chapter
SDP	*Pharbitis nil*	Continuous light and poor nutrition	2
		Continuous light at low temperature	3
		Continuous light at low light flux	3
		Continuous light at high light flux	3
		Continuous darkness	3
	Lemna paucicostata 6746	LD + copper	2
		LD at low light flux	3
		Skeleton photoperiods	4
		LD + salicylic acid	13[a]
LDP	*Lolium temulentum*	SD and anaerobiosis during one night	3
		SD + GA_3	13[a]
	Sinapis alba	SD at high photon flux	3
		Continuous darkness	3
		SD at low temperature	3
		Displaced SD	4

[a] Volume II, Chapter 6.

mulentum,[7] and *Sinapis alba,*[8] which respond to a single inductive cycle are more appropriate for such studies. These plants are also suitable for investigating changes associated with increased sensitivity to induction with age.

An important advantage, alluded to earlier, in using plants grown in strictly noninductive regimes is that such plants may be in a *more or less steady state of growth* during the experimental period. They usually produce leaves of the same size and shape and at a constant rate, their stem elongates at near constant rate, and their meristem may be at a steady state with respect to size and growth rate, as in *Perilla,*[9] *Chenopodium amaranticolor,*[10] *Xanthium,*[11] *Silene coeli-rosa,*[12] and *Sinapis.*[13] On the other hand, seedlings during germination, do not lend themselves to certain kinds of postinductive analyses precisely because these growing characteristics are changing quite rapidly in both the induced and noninduced plants.

Studies on floral evocation and morphogenesis are more significant with species producing a terminal flower or inflorescence since the complete transformation can be traced in these plants in one and the same meristem. Plants having a decussate or distichous arrangement of leaves at the vegetative stage are especially appropriate for microscopic work that requires an accurate orientation of the meristem for sectioning.

Species requiring a single photoinductive cycle, interesting as they are, may not be the best material for gaining insight into some particular problems. For instance, the processes of fractional induction and partial evocation are easiest to attack in species requiring several inductive cycles or having a dual photoperiodic requirement as LSDP and SLDP.

Certain studies are possible only when the plant material possesses still additional attributes, for example, ease of grafting to a partner. Unfortunately, this attribute is not common in "single-cycle" plants, with the exception of *Xanthium.*

Quite often unsatisfactory results are obtained because of genetic heterogeneity of the plant material, the seed having been commercially purchased or collected from wild plants. In these cases a genetically uniform material must be produced by clonal propagation or inbreeding before the work itself can start. Interest in using plants in which the genetics of flowering are well-known is self-evident, but unfortunately there