

Michel Thellier

Plant Responses to Environmental Stimuli

The Role of Specific Forms of Plant
Memory

éditions
Quæ

Éditions Cirad, Ifremer, Inra, Irstea
www.quae.com

 Springer

Plant Responses to Environmental Stimuli

Michel Thellier

Plant Responses to Environmental Stimuli

The Role of Specific Forms of Plant Memory

 Springer

éditions
Quæ

Éditions Cirad, Ifremer, Inra, Irstea
www.quae.com

Michel Thellier
Emeritus Professor of the University
of Rouen
Rouen, France

ISBN 978-94-024-1046-4 ISBN 978-94-024-1047-1 (eBook)
DOI 10.1007/978-94-024-1047-1

Library of Congress Control Number: 2017931347

Éditions Quæ, R10, 78026 Versailles cedex, France www.quae.com

© Éditions Quæ, 2017

Jointly published with Éditions Quæ, Versailles, France

This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed. Exempted from this legal reservation are brief excerpts in connection with reviews or scholarly analysis or material supplied specifically for the purpose of being entered and executed on a computer system, for exclusive use by the purchaser of the work. Duplication of this publication or parts thereof is permitted only under the provisions of the Copyright Law of the Publisher's location, in its current version, and permission for use must always be obtained from Springer. Permissions for use may be obtained through RightsLink at the Copyright Clearance Center. Violations are liable to prosecution under the respective Copyright Law.

The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

While the advice and information in this book are believed to be true and accurate at the date of publication, neither the authors nor the editors nor the publisher can accept any legal responsibility for any errors or omissions that may be made. The publisher makes no warranty, express or implied, with respect to the material contained herein.

Printed on acid-free paper

This Springer imprint is published by Springer Nature

The registered company is Springer Science+Business Media B.V.

The registered company address is: Van Godewijkstraat 30, 3311 GX Dordrecht, The Netherlands

Foreword

Yes, plants possess memory ability! In his little book, Michel Thellier has combined recent discoveries with older data dealing with plant memory and its potential role on plant acclimatization to environment stimuli. By placing memory within an evolutionary frame, the author persuades us that a new way of researches has opened in plant physiology.

This programme appears as a new step in an already long (though being badly known) story. The existence of memory implies the ability to perceive signals and therefore some sensitivity. Strangely enough, the scientific reflexion about plant sensitivity has been occulted though a number of philosophers and botanists have taken it into consideration. Strangely also, the simplistic Aristoteles' ideas continue being cited, although they were almost immediately disproven. The first biologists have taken interest in the differences existing between animals and plants. According to Aristoteles (384–322 before Christ), a soul was present in each living being, but with different features in the different beings. The human soul had three functions: vegetative, sensitive and mental. Only the two firsts were present in animals, while plants possessed only a vegetative soul governing generation, feeding and growth; in other terms, plants were devoid of sensitivity, a fortiori of memory. Theophrastus (371–288 before Christ), who was interested by plant phototropism, criticized this oversimple Aristoteles' viewpoint.

Since the very beginning of modern science, the plant mystery has been the object of a lot of discussions, though, obviously, neither the concepts nor the techniques requisite for a rational approach were available at that time. Several key observations occurring during Renaissance are reported; however, in most cases, their interpretation was wrong. Both Giambattista della Porta (1535–1615), who is better renowned for his researches in optics, and William Gilbert (1544–1603), a pioneer about modern electricity, have taken interest in plant polarity; using an audacious comparison with magnet behaviour, they have explored the way towards a mechanistic explanation of plant movements. The Portuguese botanist Cristobal Acosta (1515–1594) was interested in the rapid movements of the leaves of the sensitive plant (*Mimosa pudica*) and in the circadian movements of the leaves of tamarind (*Tamarindus indica*) that coil in the evening and uncoil in the morning.

Francis Bacon (1561–1626) believed that these movements were a mere result from mechanical actions; he proposed the plant vessels and fibres to bear a strong analogy with the nerves and blood vessels of animals. William Harvey (1578–1657), who discovered blood circulation and the mechanical role of the heart, has put forward that the cause of the rapid movements of the leaves of the sensitive plant is similar to that of muscle contraction in animals.

Surprisingly, the question of plant sensitivity did not remain restricted to a few intellectuals: in the middle of the seventeenth century, the general public developed a true infatuation for plant movements. In Great Britain, sensitive plants were extensively grown in greenhouses. Moreover, experimenters like Robert Browne (1605–1682) and Henry Power (1623–1682) began to study phototropism, gravitropism and nutation. King Charles II (1630–1685) even asked the Royal Society to find an explanation to the movements of the leaves of the sensitive plant. The experiments that followed, as reported by Robert Hooke (1635–1703), were devoted to plant sensitivity. All that has supported the idea that, in the great chain of being (the so-called *scala naturae*), the sensitive plant was an intermediate between plant and animal, as this was already the case with the soft-water hydra (*Hydra viridissima*) that was discovered by Abraham Trembley (1710–1784). As a consequence, it was no longer possible to consider sensitivity, or “irritability” according to Charles Bonnet (1720–1793), belonging only to animals. In the eighteenth century, Julien Offray de la Mettrie (1709–1751), the author of the provocative book *L’Homme Machine* [The Machine Man] (1747), also wrote 1 year later *L’Homme Plante* [The Plant Man] in which he compared the irritability of these two organisms with each other.

With the generalization of experimental research, at the onset of the nineteenth century, several naturalists undertook a thorough study of plant sensitivity. As soon as 1806, Thomas Knight (1759–1838) experimented on gravitropism; for that, he invented the so-called Knight’s wheel, demonstrating that the root and the aerial part of a plant orient according to the acceleration to which they are subjected (gravitation only or gravitation combined with a centrifuge force); in 1812, he also showed that the root exhibits a negative phototropism. Henri Dutrochet (1776–1847) suggested an interpretation for plant growth movements via osmotic processes; by longitudinally slicing a young plant in two parts and exposing one part to light and the other to darkness, he discovered that the illuminated part bent, while the other one continued to grow straight on. The German Julius von Sachs (1832–1897) and the Austrian Julius von Wiesner (1838–1916) attempted to determine whether plant movements were active responses to the environment or purely passive consequences of the effects of light and gravity; they examined whether the movement quantity was proportional or not to the intensity of the stimulus; Sachs, pioneering a microscope approach, had a suspicion that the intracellular structure may depend on the environment.

At the same period of time, last but not least, the name of Charles Darwin (1809–1882) came out in the literature. Apart from his famous book *On the Origin of Species by Means of Natural Selection*, Darwin has written a number of publications dealing with botanic and plant physiology, in which the concepts of plant

evolution and adaptation were close to emerging. In the year 1855, he studied the seed longevity in saltwater; clearly, he was wishing to test if plant colonization of the volcanic islands took place via the marine way. In the course of all his life, he was interested in plant reproduction, especially that of orchids and Fabaceae (which were termed Papilionaceae at that time), with particular reference to possible hybridizations and to the essential role of pollinating insects such as Hymenoptera or Lepidoptera. In the years 1860 and following, Darwin conceived a passion for plant movements and sensitivity. Two important books deal with climbing plants (*On the Movements and Habits of Climbing Plants*, 1865) and with insectivorous plants and their capture movements (*Insectivorous Plants*, 1875). He then urged his seventh child, Francis (1848–1925), to carry on broader observations and studies of plant movements; this was the matter of his last book (*The Power of Movements in Plants*, 1880). It is not a surprise to find in the book by Michel Thellier the same dramatic species as studied by Darwin, such as bryony and Venus flytrap.

Darwin has been especially interested in insectivorous plants. He has shown that a drosera (*Drosera rotundifolia*) was able to distinguish between different types of objects and had sensitivity better than that of human skin. The relatively rapid closure of the *Dionaea* traps caused Darwin to speculate on the possible existence of a nervous system in plants. In order to put that idea to the test, he visited the physician John Burdon-Sanderson (1828–1905) at the University of London in 1873. Burdon-Sanderson set electrodes on *Dionaea* leaves, and, each time he touched one of the hairs present in the *Dionaea* traps existing at the extremity of the plant leaves, he registered an electrical wave similar to the action potentials of animal neurons. Darwin related the result of that beautiful experiment on sensitivity, to the plant adaptation to a very peculiar mode of nutrition.

In 1871, St. George Mivart (1827–1900), a professor in London University, raised objections on several points of *On the Origin of Species*. In particular, Mivart stated that natural selection could not explain the way how plant sensitivity appeared, especially in the climbing plants. In his response, Darwin postulated that circumnutation was a universal property of plants and that it is thus an ancestral feature that has subsequently specialized to give the various other types of movements. This is one of the events that have caused Darwin to take gravitropism and phototropism into consideration. A series of experiments allowed him to assume that the root tips was sensitive to gravity, and to other sorts of stimuli such as touching and light, and that a signal was transmitted to the growth area causing the root to bend (the so-called *root cap hypothesis*). After a debate with Sachs, Darwin proposed a *root-brain hypothesis* that is interpreted as follows in the last pages of his book *The Power of Movements in Plants*: “it is hardly an exaggeration to say that the tip of the radicle thus endowed, and having the power of directing the movements of the adjoining parts, acts like the brain of the lower animals”. Darwin did not propose the existence of some sort of memory, but he wasn’t so far from it. Let us finally recall a series of experiments about the coleoptile of Poaceae, as quoted by Michel Thellier. Nowadays, the experiments by Peter Boysen Jensen (1883–1959) and Frits Went (1903–1990) are most often cited, but it shouldn’t be forgotten that Darwin,

with the help of his son, was the first to show that light stimuli were perceived at the level of the root tip and that a corresponding signal migrated towards the neighbouring tissues.

In the English-speaking universities, the plant movements were included up to 1935 in the books dealing with compared psychology. It is only later that the development of plant physiology finally permitted this branch of instruction to become autonomous, with its own biochemistry and hormonology. Though nowadays ranking plant tropisms within psychology would seem absurd, this unitary view of the living world had the advantage not to isolate plants from animals, which isolation risks to astonish the general public when facing the reality of plant sensitivity.

In most cases, plant sensitivity is responsible for non-reversible growth movements such as the circumnutating of voluble plants or the root and stalk tropisms. Darwin was well aware of the adaptive importance of these movements and had set it in an evolution frame. The book by Michel Thellier goes a step further. Plants do have memory; however plant memory is totally different from the animal memory that is familiar to us. If the movements resulting from plant sensitivity have a crucial role in plant life (the root towards ground and the stalk towards light), memory enables plants to produce a more elaborate and more integrated response than would be a straightforward response. No doubt that the book by Michel Thellier will give rise to subsequent works that, from cellular and molecular biology to ecophysiology, will contribute to the understanding of how the 369,000 or so recorded species of angiosperms (according to the recent report of Kew Garden) have settled our planet.

For More Details

Hopper SD, Lambers H (2009) Darwin as a plant scientist: a Southern Hemisphere perspective. *Trends Plant Sci* 14(8):421–435

Kutschera U, Briggs WR (2009) From Charles Darwin's botanical country-house studies to modern plant biology. *Plant Biol* 11:785–795

Kutschera U, Niklas KJ (2009) Evolutionary plant biology: Charles Darwin's forgotten synthesis. *Naturwissenschaften* 96:1339–1354

Whippo CW, Hangarter RP (2009) The “sensational” power of movement in plants: a Darwinian system for studying the evolution of behaviour. *Am J Bot* 96(12):2115–2127

Institut de Biologie Paris-Seine
UMR 7138, “Evolution Paris-Seine”
7 Quai Saint Bernard
F-75252 Paris Cedex 05, France
e-mail: herve.le_guyader@umpc.fr

Hervé Le Guyader

Acknowledgements

In the preparation of this book, I have benefited of the gracious help of colleagues, friends and relatives for the form and the substance. I thank them all heartedly. I am especially indebted to Anne Alexandre, Jean-Louis Bonnemain, Marie-José Costil, Claude Gillet, Michel Gounot, Janine Guespin, Chantal and Yannick Kerdudou, Philippe Lefrançois, Nolwenn Legrand, Hervé Le Guyader, Ulrich Lüttge, Victor Norris, Sandrine Pesnel, Jeanine Rens, Camille Ripoll, Marie-Claire Verdus and Alain Vian.

Contents

1 Me, a Plant	1
1.1 A Little Bit of Plant Morphology	1
1.2 A Little Bit of Plant Physiology	2
1.3 The Plant Cells	3
2 Plant Sensitivity to Stimuli	7
2.1 Animal vs. Plant Sensitivity	7
2.2 The Various Sorts of Stimuli That a Plant Perceives	8
2.2.1 The Relative Length of Night and Day	8
2.2.2 Plant Sensitivity to Gravity	10
2.2.3 Local and Distant Responses to Stimulation	12
2.2.4 Defence Reactions of Plants	13
2.2.5 Plant Movements in Response to Stimuli	15
2.3 How Do Plants Perceive Stimuli?.....	17
2.3.1 Perception of Light Signals.....	17
2.3.2 Perception of Gravitation	18
2.3.3 Perception of Diverse Stimuli	19
2.4 After Stimulus Perception, the Calcium Wave	19
2.5 From the Stimulated to the Reactive Area.....	21
2.6 About a Few Practical Applications	22
3 Discovery of the Existence of Memory in <i>Bidens</i> Seedlings	23
3.1 Correlations Between Organs	23
3.2 Dominant and Dominated Buds	24
3.3 Specification of the Dominance Between Cotyledonary Buds.....	24
3.4 Rate of Information Transfer.....	27
3.5 Storage/Recall of Dominance-Specification Information	27

- 3.6 Properties of the Storage/Recall Form of Memory 30
 - 3.6.1 Properties of the Storage Function..... 30
 - 3.6.2 Properties of the Recall Function..... 32
 - 3.6.3 Interaction of the Storage and Recall Functions 33
- 3.7 Generalizing the Concept of Plant Memory 33
 - 3.7.1 Experimenting with Plants Other than *Bidens* 33
 - 3.7.2 Further Remarks about Plant Memory..... 34
- 4 More About the Storage/Recall Form of Plant Memory 37**
 - 4.1 New Experimental Systems..... 37
 - 4.2 Reduction of Hypocotyl Elongation 38
 - 4.2.1 Evidencing the Existence of Storage and Recall Functions..... 38
 - 4.2.2 Properties of the Memorization of a Reduction of Hypocotyl Elongation..... 40
 - 4.2.3 Extension to Other Plants than *Bidens*..... 41
 - 4.3 Production of Epidermal Meristems..... 41
 - 4.3.1 The Experimental Approach 41
 - 4.3.2 Evidencing the Existence of Storage and Recall Functions..... 42
 - 4.3.3 Properties of the Storage Function..... 45
 - 4.3.4 Properties of the Recall Function..... 46
 - 4.3.5 Memory and Rhythms..... 49
 - 4.3.6 Memory and the Proteome..... 49
- 5 More About the Learning Form of Memory in Plants 51**
 - 5.1 Examples of the Learning Form of Plant Memory..... 51
 - 5.1.1 Memory Effect at the Level of the Calcium Wave 51
 - 5.1.2 Memory Effect at the Level of the Ultimate Response..... 52
 - 5.2 Comparison of the Learning with the Storage/Recall Form of Memory 52
- 6 Plant Memory vs. Animal and Human Memory 55**
 - 6.1 Reminder of some Characteristics of Animal and Human Memory 55
 - 6.2 Plant Memory vs. Animal and Human Memory 56
- 7 What Is the Need for a Plant to Have Memory? 59**
 - 7.1 Straightforward Responses vs. Memorisation..... 59
 - 7.2 Potential of the Learning Form of Plant Memory 60
 - 7.3 Potential of the Storage/Recall Form of Plant Memory 60
 - 7.3.1 Potential of the Storage Function..... 60
 - 7.3.2 Potential of the Recall Function..... 61
 - 7.3.3 Combined Potential of the Storage and Recall Functions..... 62
 - 7.3.4 Effective Biological Role of the Storage/Recall Form of Plant Memory..... 62

8 Attempt at Synthesis 67

 8.1 Conceptual Modelling of Plant Memory 67

 8.1.1 Statement of the Problem 67

 8.1.2 The Model 67

 8.1.3 Adequacy of the Model 70

 8.2 The Present Picture of Plant Memory 72

 8.2.1 The Most Solid Knowledge 72

 8.2.2 A Bit of Speculation 73

 8.2.3 Suggestions for Future Work 75

 Epilogue 76

Appendices 77

 Appendix A1 Ciphers and Secret Messages 77

 A1.1. The 4-Symbol Codes 77

 A1.2. Elaboration and Deciphering of Secret Messages 78

 A1.3. Cryptography 80

 Appendix A2 The Molecular Magic 81

 A2.1. Proteins: What Are They and How Do They Work? 81

 A2.2. What Is a Gene? 82

 A2.3. What Is DNA, and What Is its Structure? 82

 A2.4. How Does DNA Keep Identical to Itself in Cell Division? 84

 A2.5. What Is RNA, and What Is its Structure? 84

 A2.6. How Are Proteins Biosynthesized on the Pattern of DNA? 85

 A2.7. How Does Cell Differentiation Occur? 88

 A2.8. How Can the Evolution of Living Beings Be Explained? 88

 A2.9. Is the Genetic Code Dependent on the Species? 89

 A2.10. What About the Mitochondrial and Chloroplast DNA? 90

 A2.11. What Is a GMO? 90

 Appendix A3 Calcium Condensation/Decondensation 91

 A3.1. Water Condensation 91

 A3.2. Ionic Condensation 91

 A3.3. Biological Implications 93

Glossary 95

References 103