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The flowering process: a prolonged incompletion

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Introduction

Flowering, the sexual reproductive development, is a multistep integrated and dynamical networking process, oriented in time (physiological clocks) and space (root, leaves, stem, shoot apex territories), producing as finality a new organ: the flower. Since the cretaceous time ($\sim 1,3 \cdot 10^8$ years), it ensures the reproduction (species survival) and the space expansion of higher plants ($\sim 3,5 \cdot 10^5$ different species). This phase of the plant life cycle is the most important, together with the biomass production by photosynthesis (vegetative growth and development: $2 \cdot 10^{11}$ t dry weight per year).

The dynamic stability of ecosystems and biosphere, as well as environmental adaptation, are widely dependent on the evolution of flowering, in connection with the response capacity to ecospace changes (light, temperature, water, soil, etc.) and to biospace specific structure (mutation, recombination; population genetics; ecological web) [4,14,21,68,140].

The flowering process, putting aside the inconvenience of complexity, is a good model to study and understand the co-action and adaptation between the genetic biospace and the physico-generic activities on one side and the ecospace properties changes on the other side. These properties are, for example, temperature, light and water that are important agents for growth and development, and also signalling by photo-nyctotemperature alternation, photo-nyctoperiodic induction, water stress, etc. [58-60,112].

Despite the numerous publications that have appeared in this field during the last century, the flowering mechanism is still not clearly known. It is only recently, after a long period of morphological and ultrastructural description, followed by a chemical and biochemical analysis and a classical genetic approach, that we are progressively entering into a molecular genetic phase and a biophysical and physiological systemic approach. This new trend, with the help of a lot of new techniques (nucleic acids amplification and analysis, macro-and microarrays, bioinformatics, genomics, proteomics; atomic force microscopy, nuclear magnetic resonance, fluorescence analysis, network and far from equilibrium thermodynamics, metabolic compartmental

analysis, modeling, physiomatics, etc.) will probably allow to solve this always-open question during the new century (the Arabidopsis genome will be totally deciphered in 2001) [35,63,64,90,110,112,133,145,171].

The different components of the flower (sepal, petal, stamen, pistil) are the end-result of floral morphogenesis, determined by the action of some specific genes (floral meristem and organ identity genes) and the consecutive physico-biochemical changes in the apical shoot meristem: a few hundred cells constitute three territories, the initial ring for leaves production (plastochrone), the medullary and the prosporogenic territories for respectively stem and flowers formation. Significant knowledge has been acquired concerning the molecular nature of floral morphogenesis in the apex. Less is known about floral evocation, the phase following the vegetative functioning (leaves production). This period, lying from the onset of induction to the second wave of apical mitosis (onset of the floral pieces construction), is characterized by a dedifferentiation (hydrolytic activities) of the prosporogenic territory and then a stimulation of mitosis to produce, later, the flower. Evocation is coupled to a space-time change in the mitotic distribution and control of the different territories in the shoot apex (change in the phyllotaxis and Fibonacci series) [36]. Good indicators of evocation, as we have proposed, are the localization and amount of glucose-6-phosphate dehydrogenase activity, the mitochondrial and plastid DNA synthesis and the plasma membrane proliferation [5-7,13,39,57,87,151,157,194].

Another important progress has been made by the progressive identification of the genes responsible for the orientation in time (physiological clocks) and those encoding the pigments (phytochrome, cryptochrome, etc.) that enable to cope with environmental parameters triggering floral development (reproduction) or maintaining vegetative mass production [37,41,59,104,108,114,122,150,160].

The environmental conditions may act as optimizing agents which are monitored by the plant to determine the best time for reproduction or for biomass production. Each ecotype has a specific set of different genetic modules interfacing with the environment and allowing various adaptation patterns.

If the shoot apex has all the genetic information to produce flowers, the fitting of the reproductive program within some environmental and obliged internal parameters is an absolute necessity for the survival of the plant species, because they can not escape from the ecospace constraints. Plants are immobile, strictly depending on light and water for their autonomy and, contrarily to animals, have a low degree of global homeostasy against environmental pressure. They are however adapted by other specific ways, such as continuous embryogenesis, cellular totipotency, low degree of tissue and organ differentiation, leaf abscission, cross-resistance and stress resistance patterns, etc., affording a multifactorial solution leading to the same finality (equifinality). That "extraspection" feature offers multiple ways of responding to the fluctuating environment; some aspects of these modular responses are detected by the shoot apex to induce or not flower formation (integration with environmental and internal possibilities) [63,112,133] .

Some signals (floral stimuli or inhibitors) are produced in the plant (leaves, root) by the transduction of eco- and internal sensors information (environment perception; memory, Pavlov-like reactions, learning) and, under the control of biological clocks, are then transferred (communication) to the apex where they trigger or block the

flowering process at the prosporogenic meristem level. The real nature of these stimuli and of the implicated genes (flowering genes) are for the moment not sufficiently known. But when the leaf has been induced to produce the floral stimuli, it is possible by grafting it to a vegetative plant, to induce the flowering of the receptor. This transition of vegetative leaf to floral state, characterized by specific proteins, is irreversible. The graft effect is linked to the plasma membrane symplastic reconnection with the stock. The phloem is an important conduit for the circulation of the floral stimuli. Senescence is accelerated when flowering is launched.

By the dynamic integration of the environmental possibilities it becomes possible to achieve with security (environmental risk) the reproductive development and to guarantee the future of the species. A varied networking of genes under activation or repression control (methylation, etc.) [22,34,38,45,72,146] associated with different functional modules and receptors in space and time (physiological, genetic and thermo-compensated clocks) is in operation (co-action) in the whole plant, integrating the influence of environmental stimuli to decide (at the apex) whether to enter the flowering stage or to remain at the vegetative state, on the wait. This particularity is important for ecological and geographical reasons and for optimization of the biosphere heterogenic and viable structure. Outcomes and applications from a better and perfect understanding of this process are manifold and relate to several fields: industry, agriculture, sylviculture, territory management, etc...[25,51,70, 170,171,175].

Genetics of flowering

During the last decade, molecular genetic studies have increased our understanding of flower development from the vegetative-to-floral transition to the specification of floral organ identity by homeotic genes. The genetic control of flowering time in Arabidopsis has been the subject of intensive research that has been reviewed in details [71,89,101,102,136,144,157] and we will describe here only some aspects and recent findings. The genetics of organ specification in the flower structure will not be considered (for reviews and updating data of the famous ABC model, see [123,129,136,188]). Genetic analysis has also been conducted with other plants such as pea and wheat [159,189] but has not been yet complemented by a molecular approach as in Arabidopsis.

Flowering is under the control of environmental signals such as light and temperature. In many plant species, the initiation of flowering is controlled by daylength, a phenomenon known as photoperiodism. The measurement of daylength by a daily timer, the circadian clock, is now generally accepted [171]. The control of flowering by temperature is operative through vernalization, a response of the plant to low temperature that abolish the repression of developmental processes, such as the initiation of flowering. This phenomenon is most apparent in plants growing at high latitudes, and the repression of flowering occurs even if the plant is grown under favorable photoperiods. The vernalization response can be considered in a way as a biological timer measuring the length of the winter period. Whereas the inductive daylength is perceived in the leaves and generates a signal that travels to the shoot apex, vernalization acts in the mitotically active cells that will form the inflorescence [45,72]. Flowering is also influenced by environmental nutrient deprivation and by endogenous developmental factors associated with the age of the plant.

Arabidopsis is a facultative long-day plant that flowers faster under long days than short days conditions. It will also flower in complete darkness in specific laboratory conditions such as growth on vertical plates which provide sucrose directly to the developing cotyledons [142]. In the mutant *embryonic flower* (*emf*) the vegetative phase will even be skipped and an inflorescence meristem will be produced upon germination [168]. The commonly used laboratories varieties Columbia, Landsberg *erecta* and Wassillewskija are rapid cycling ecotypes in contrast to other ecotypes that show a vernalization response.

Mutagenesis and molecular genetic studies has permitted the identification and cloning of many genes implicated in the control of transition to flowering. There are currently about 80 genes and loci known to affect flowering time in Arabidopsis [101]. In addition to the laboratory-induced mutants, the naturally occurring variation among accessions is becoming an alternative complementary source for mapping of loci and the cloning of large-effect genes (discussed in [2]).

The function of these genes, their distribution in specific genetic pathways, the interplay of these pathways in a complex genetic network has been has reviewed recently [16,89,101,136,157]. Mutants affected in flowering time are either late or early, mostly late. A collection of late-flowering mutations has been identified by the pioneering work of Koornneef and coworkers [88-91]. These late flowering mutants are derived from the early flowering parent Landsberg *erecta* and have been distributed in two groups, according to their response to daylength and vernalization. One group is unaffected by vernalization and short days and is constituted by the mutants *fe, ft, fd, fwa, constans* (*co*) *and gigantea* (*gi*). These mutants define genes required to promote flowering specifically in response to long day and belong therefore to a photoperiod pathway, photoperiod-dependent but temperature-insensitive. The other group is accelerated by vernalization and delayed in short days and is constituted by the mutants *fca, fve, fy, fpa* and luminidependens (*ld*). This group of mutants are recessive and still able to respond to environmental cues, and they are therefore considered to be disrupted in an autonomous promotion pathway, photoperiod-independent but temperature-sensitive. A third pathway consists of a class of mutants reducing the biosynthesis or the response to the growth regulator gibberellin, with most severe effects in short days. A fourth pathway has been defined with mutants that are specifically impaired in their response to a cold treatment and that may be defective either in the perception of cold temperature or in the transduction of the cold signal. No single mutation has been yet described in Arabidopsis that abolish flowering completely, because the promotive pathways are functionally redundant. Due to this redundancy, inactivation of two pathways results however in a more severe phenotype than inactivation of one. The inductive pathways will lead to activation of the meristem identity genes that will change the fate of the meristem from vegetative to floral [135,186,187].

Control by temperature

In Arabidopsis, two major loci act together to delay flowering, *FRIGIDA* (*FRI*) and *FLOWERING LOCUS C* (*FLC*). These loci have been characterized by comparing the naturally occurring varieties having or not a vernalization response. The vernalization-suppressible late-flowering phenotype of winter-annual ecotypes of Arabidopsis

results from the presence of dominant late-flowering alleles at these two loci. Both genes have recently been cloned. The *FLC* gene encodes a putative transcription factor of the MADS–box class acting as a dosage-dependent repressor of the floral transition [111,152]. The *FRI* gene is found as a single copy gene in the Arabidopsi*s* genome and encodes an open reading frame for a protein of 609 amino acids, which shows no significant match to any known protein or domain or protein domain in the available databases [76]. The levels of *FLC* transcripts are regulated positively by *FRI* and negatively by vernalization and genome demethylation. A quantitative relationship has been found between the duration of the cold treatment and the extent of down-regulation of *FLC* transcriptional activity [154]. DNA demethylation is assumed to mediate the vernalization response [34,43,45,153]. It has been shown indeed that a reduction in genome methylation by the demethylating agent 5-azacytidine or by a methyltransferase [MET+] antisense substitutes for a vernalization treatment in promoting flowering [22,42,44]. A correlation was found between *FLC* transcription and decreased genomic methylation in the early-flowering *MET1* antisense plants [152]. A third gene, *VRN2* which has not been cloned yet, acts during vernalization and reduces *FLC* expression. From these observations, *FLC* is now considered to play a pivotal role in controlling the vernalization response. *FLC* is also regulated negatively by genes of the autonomous pathway (*FCA, FVE, FPA, FD, FLD* and *LD*), as indicated by the elevated levels of *FLC* and the vernalization-responsiveness of the late flowering mutants obtained from early ecotypes [111,154]. *LD* and *FCA* have been cloned and encode respectively a putative transcription factor [95] and an RNA binding protein [106], presuming a control of *FLC* at both the transcriptional and posttranscriptional levels. Taken together, *FLC* appears as integrating the vernalization and the autonomous pathways. It has also been proposed that *FLC* may act by antagonizing the promotive effect of gibberellins on flowering, since the *flf-1* mutant, overexpressing the FLC transcripts, requires higher amount of exogenous GA to decrease flowering time [152]. Another MADS-box gene, *SHORT VEGETATIVE PHASE* [*SVP*], has been shown recently to repress flowering and the possibility of forming a FLC/SVP heterodimer has been suggested [69].

It is worth mentioning that contrasting phenotypes have been related to altering methylation, such as the late flowering phenotype of *fwa* mutants, which is caused by gain-of-function epigenetic alleles of a homeodomain gene induced by hypomethylation of two direct repeats in the 5' region of the gene [162]. The function of *FWA* in flowering of wild-type plants is questioned by the authors.

Control by daylength

The molecular relationships between the regulation of flowering time by daylength and the circadian clock has gained evidence from the recent description of mutants in which both circadian rhythms and flowering time are disrupted. The clock is entrained by light input signals that are perceived by the photoreceptors phytochromes (red light) and cryptochromes (blue light), which also regulate flowering [67,103,114,166,171]. The molecular basis of circadian oscillators has been established as oscillating transcription/translation loops of positive and negative elements more or less conserved between Drosophila, Neurospora and mammals [37]. In plants, candidates for a molecular circadian oscillator have been identified recently, but a specific role for

these candidates remains to be asserted. The plant oscillator would apparently be different to the ones established in other organisms, since components are not homologues. One of the best candidate as an oscillator component is *TIMING OF CAB (TOC1)*, which encodes a nuclear protein containing an atypical response regulator receiver domain, and two motifs that suggest a role in transcriptional regulation [165]. The next two candidates are the *CIRCADIAN CLOCK ASSOCIATED 1(CCA1)* and *LATE ELONGATED HYPOCOTYL (LHY)* genes encoding both MYB-related transcription factors [147,185]. Modulation of CCA1 by protein kinase CK2 has been shown and suggested to play a role in vivo [167]. Two other candidates are the *ZEITLUPE (ZTL)* and *FKF*1 genes and its related homologue *LKP1* [85,113,121,161]. These genes encode novel proteins with a PAS domain similar to the flavin-binding domain Arabidopsis blue-light photoreceptor NPH1, an F-box characteristics of proteins that direct ubiquitin-mediated protein degradation, and 6 kelch repeats that could serve as the protein-protein interaction domain recruiting specific protein for degradation. Disruption of any of these putative clock gene results in an altered flowering time. Mutations in *FKF1* is also responsive to vernalization. Its role might therefore be more complex than just acting in the pathway that promotes flowering in response to long days. The well known photoperiod mutant *gi* was characterized recently at the molecular level [46,73,128]. From computer-based prediction, GI was first proposed to be an integral plasmamembrane-localized protein, but recent data have shown that it is a nucloplasmically localized protein [73]. GI was shown to be required for maintaining circadian amplitude and appropriate period length in the expression of its own gene as well as *CCA1* and *LHY,* and also to affect light signalling to the clock, which suggests a role in a feed back, loop in the circadian clock. The photoperiod information is further relayed to *CONSTANS (CO)*, a gene that encodes a zinc finger transcription factor and that activates downstream floral meristem identity genes such as *LEAFY (LFY)*, *TERMINAL FLOWER 1 (TFL1)* and *APETALATA 1 (AP1)* [15,135,138,141,156]. The *FLOWERING LOCUS T (FT)* is also acting downstream of *CO* , but its promotive action is antagonized by the homologous gene *TFL* [79,86]. The *LFY* promoter integrates the floral inductive signals of both the GA and the photoperiod pathways at different cis elements [17] and the protein LFY participate in cell signalling by moving from cell to cell [151].

Using a suppressor mutagenesis approach [127,145], CO has been shown recently to play a pivotal role in promoting flowering by activating at least four early target genes: *SUPPRESSOR OF CONSTANS 1 (SOC1)*, previously known as *AGAMOUS-LIKE 20 [AGL20]*, *FLOWERING TIME [FT]*, *ACS10* and *AtP5C52*, encoding respectively a MADS-box transcription factor a putative phosphatidylethanolamine binding protein, an enzyme involved in ethylene synthesis and an enzyme involved in proline biosynthesis. Floral meristem identity genes within the shoot apex are subsequently activated by *SOC1* and *FT*. A reduction of the expression of *SOC1* and *FT* has been observed in a low *FLC* mRNA background and it has been proposed that levels of *SOC1* and *FT* expression may be determined by a balance of CO and FLC, and represents therefore common components of distinct flowering-time pathways. The role of SOC1/AGL20 as an integrator of the autonomous, vernalization and photoperiod pathways was also shown by another group [94].

Despite all the knowledge acquired from studies on the genetic control of flowering, there is no clear evidence about the identity of genes implicated in the signal generation in the leaves, its transmission and its perception in the shoot apical meristem (discussed in [25,105]). *CO* for example is expressed uniformly in the leaves and in the shoot apical meristem. In maize, *ID1* which encodes a zinc finger protein (like *CO*) acts non-cell-autonomously and has been proposed to regulate the production of a floral stimulus or the repression of a floral inhibitor [25,26], It has been hypothesized [25] that a mechanism for the long distance transmission of the flowering signal could be posttranscriptional gene silencing [40,77,117]. Indeed, the epigenetic state of genes can be transferred form one part of a plant to the other via plasmodesmata and phloem channels and could implicate double-stranded RNA [134,169,178,192]. The epigenetic silencing at the transcriptional level can also be considered as a way of controlling developmental gene expression. It is for example regulated by the polycomb proteins and several of them have been identified in Arabidopsis, namely CURLY LEAF which is required to regulate expression of floral homeotic genes [52,84,126,137]. Chromatin remodelling through methylation-dependent or -independent mechanisms has been observed lately in Arabidopsis and represent a basis for gene activation and repression during development [3,38,74,75,78,163,164,191].

Flowering induction and ecospace

In the case of photoperiodically controlled plants (LDP, SDP, etc...), it is possible to demonstrate that floral induction proceeds in a networking three-step process, as soon as the critical photo- or nyctoperiod is reached (physiological and molecular clocks control). These three steps are the following (Fig. 1):

1) Following a juvenile phase of the leaf (emergence of sensitivity), light on and light off detection of photo-nyctoperiod duration by several specific pigments like phytochromes, cryptochromes and other photoreceptors [41,103,114,166]. Depending on external and internal coincidences of this event with the metabolic effects of clock genes [89,121,128,144] and of biophysical oscillators, photo-nyctoperiodic induction and structuro-functional transduction (flowering genes) of this processing to all the cells of the leaf. Then, production of the floral stimuli of unknown nature and, with some delay, acquisition by the leaves of the floral state, characterized by a few new specific proteins [9,17,96,97,109,141,157]. The induction property is transmissible to vegetative plants by grafting of an induced leaf.

2) Migration-transmission of the floral stimuli through the petiole and stem towards the apical meristems which have become competent. The extraction and characterization of the floral stimuli are the subject of a lot of uncertainty despite the quality of the research [14,24,66,77,105,124,134,184,193].

3) Commitment of the meristem cells and territories to floral evocation, and topological modulation of the mitotic activity; then, after two general waves of mitosis, start of floral morphogenesis as a consequence of the activation of floral meristem and organ identity genes. This last step is well known for the moment [5-7,13,14,156].

Ecospace-Biospace (Higher Plants)

The Flowering Process (Reproduction)
Unsolved problem since > 100 years of studies
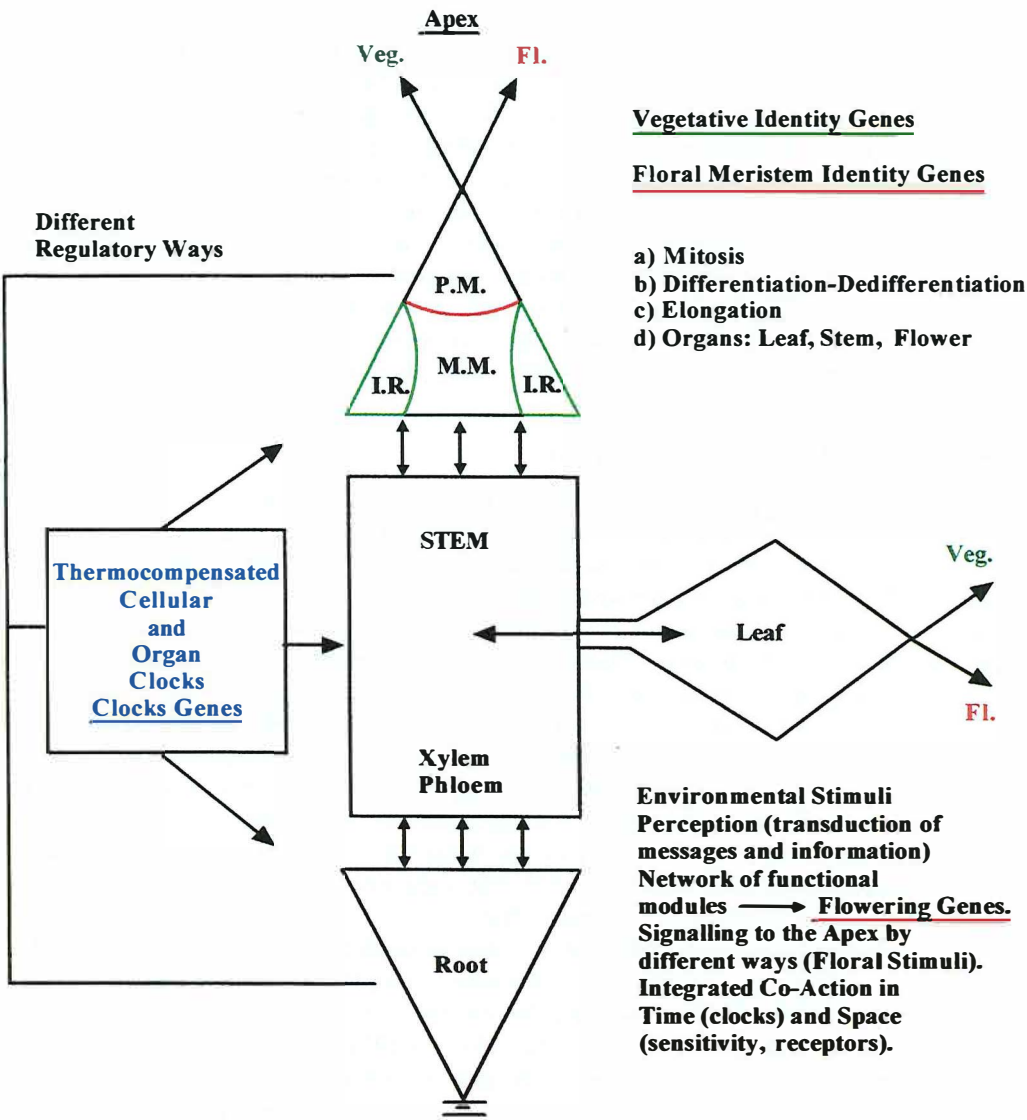**(Autonomous , photoperiodic, vernalization pathways)**

Figure 1. The Plant System and the Flowering Process. P.M.: prosporogenic meristem territory; M.M.: medullary meristem territory; I.R.: initial ring, meristem territory.

Table 1. Some physical, chemical and biochemical parameters correlated with the induction process in leaves of spinach (LDP). Trends to a maximum or minimum value at the onset of induction [10-12,19,20,29,31,32,99,107,133,148,149,176].

Parameter	Critical Photoperiod 11-12 hrs light	Floral induction Effect
1. Energy-signals		
a) Energetic charge	max.	+ 50 %
b)Redox charge	max.	+ 100 %
c) Chloroplastic MDH.NADPH dep.	max.	+ 200 %
d) Cytosolic MDH. NADH dep.	max.	+ 100 %
e) Chloroplastic A.K., C1	min.	- 70 %
f) Cytosolic Adenylate Kinase	max.	+ 50 %
g) New pool of free glucose	→ max.	+ 400 %
2. Proton pumps, AT~P dep.		
a) App. K_m	→ min.	- 68 %
b) Activity	→ max.	
c) I A A desensitization	transition	$10^{-11}M \rightarrow 10^{-6}$ M -30% + 30 %
3. Calcium Pumps. AT~P dep.		
a) App. K_m	→ max	+ 50 %
b) Calcium desensitization		
4. Water organization		
a) $^+$HNMR; T1	min	- 50 %
5. Plasma membrane		
a) Oleic/Linoleic acids in phospholipids ($C_{18:1}$ / $C_{18:2}$)	max.	+ 60 %
b) ^{31}PNMR	Shoulder	Hexagonal II ?
c) Thickness	max.	+ 20 %
d) C_6 ^{19}FNMR (lyophilized); T1	min	- 40 %

Many hypotheses have been put forward during the last 100 years to explain the flowering process and the real nature of the floral stimuli, from J. Sachs to G. Klebs proposals (specific floral substances versus ratio between substances); for example, specific hormones and inhibitors [24,93,195], sink-source chemical interaction [142,143,158], fragments of cell-wall specific oligosaccharides [124], volatile substances [193], plasmamembrane modification [53,56], electrochemical and hydraulic signalling and coded frequency [184], etc...

Different ways and modules of interactions, feed-backs and communications could be activated during the induction of flowering in leaves and roots, implicating immediate and short-term regulation as the slower one. Quantitative increase or decrease and qualitative effects could be observed, depending on the evolution of environmental constraints (light, temperature, water, stress and shock) and on the species and genetic dotation of the strain: different ways could be activated or inhibited to tend, by equifinality, to the same final result, the production of the floral stimuli. We will present here some aspects we have prospected with spinach, a qualitative long-day plant, *Arabidopsis thaliana*, a quantitative long-day plant and *Chenopodium rubrum*, a short-day plant.

Energy-signal and brownian motion

Energy and its control are playing a central and important role during development. Adaptation to new environmental conditions (day, night duration) might be immediately reflected in the alteration of energy transduction. Therefore emphasis should be put on the time-dependent interconversion in adenine and pyridine nucleotide pools. The Energy Status [18-20,65,112,179] has been determined by different approaches and evaluations: chemical analysis of free glucose or saccharose, biochemical analysis of nucleotides and calculation of the energy and redox charges (the energy charge (ATP+½ADP)/(ATP+ADP+AMP); the redox anabolic charge NADPH/(NADP+NADPH); the redox catabolic charge NADH/(NAD+NADH)), spectroscopic analysis, as for example ^{1}H-NMR or C_6^{19}F-NMR (nuclear magnetic resonance), a non-invasive method [54,99]. By this technique, it is possible to get a precise identification of chemicals and to appreciate intramolecular exchange, intermolecular dynamics and statistical entropy variation. The photoperiodic induction time in spinach leaves (Table 1 and Figs 2,3,4) corresponds to the circadian period of the maximum levels in energy and redox charges and of the minimum levels of statistical entropy (frequency of correlation fc). At this time, an important increase of free glucose is observed, which can also be detected when floral induction is provoked by a displaced-short-day treatment. This rise corresponds to a photoperiodic and clock control associated to the processing of floral induction, as it is usual for LDP. The comparison with SDP (Fig. 5) suggests that the photoperiodic free glucose control relates to the cell filling in LDP and the cell emptying in SDP (differential threshold). Another aspect of the sensitivity of this photoperiodic free glucose pool is illustrated by the inhibition of induction by a stress or a pricking (Fig. 6), that can abolish this effect for about 48 hrs [31-33,47,133,158].

The plant cells contain 80 to 90 % of water and a great number of molecules are essentially constituted by hydrogen. Biodynamics attempts to investigate the physical status of living cells by the measurement of random movements, as for example the
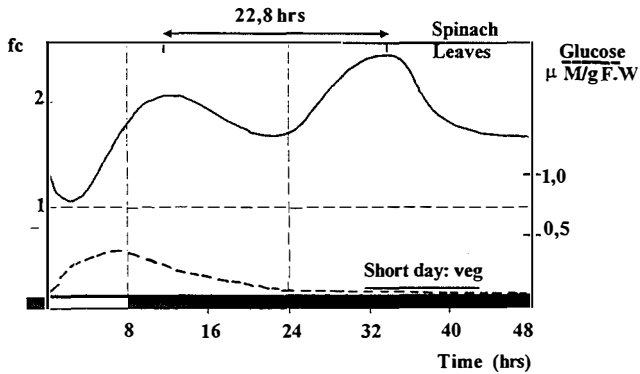
Figure 2. Time-dependent evolution in short days (vegetative state) of the relative correlation frequencies fc (^{1}H-NMR: 90 MHz) and free glucose concentration in spinach leaves (8 hrs light, 16 hrs night, 4 weeks-old); fc rhythm: 22,8 hrs [31,32,99].
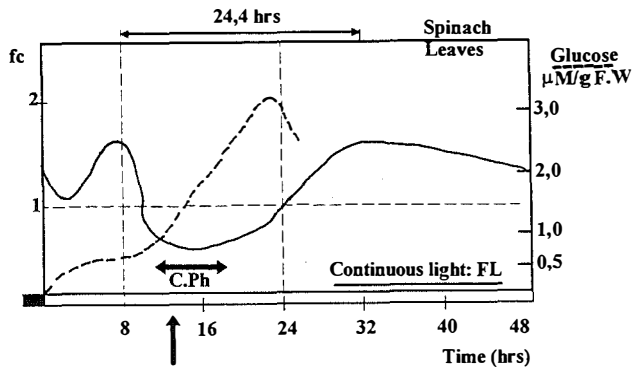

Figure 3. Idem fig. 2, but after an inductive transfer to continuous light (flowering induction). Arrow: onset of the critical photoperiod (C. Ph) for the induction of flowering; fc rhythm: 24,4 hrs
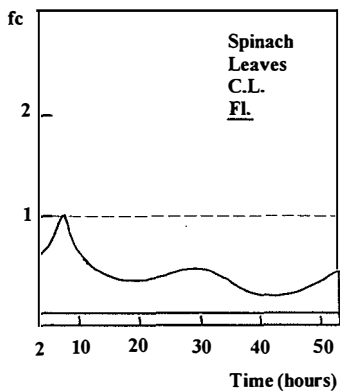

Figure 4. Time-dependent evolution under permanent continuous light (3 weeks) of fc in fully induced plants (floral state).
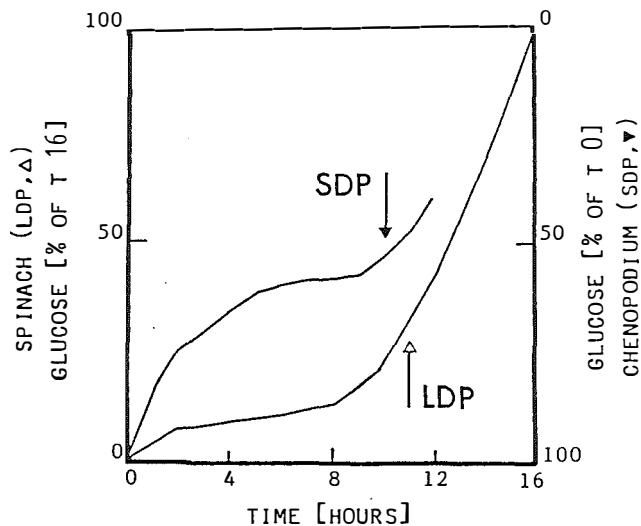
Figure 5. Free glucose content evolution in petioles of spinach leaves (LDP) and *Chenopodium rubrum* (SDP) during flowering induction, respectively by transfer to continuous light or to night. Arrows: critical photo- or nyctoperiod [133].
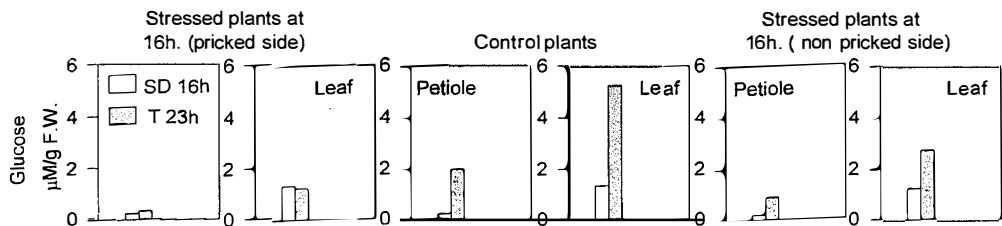

Figure 6. Free glucose content in spinach leaves and petioles at the vegetative state (short days) and after a light inductive transfer (23 hrs). Comparison with pricked plants (stress) [33,133].

brownian motion [63,98]. This particular motion is in relation with the general thermic motion of water (heat reservoir) through the dissipation of energy by the metabolism. NMR spectra and other characteristics such as spin lattice relaxation time (T_1) give us some information about the status of the Brownian system, from random organization to different degree of order and liberty. Macromolecules and membranes are playing an important role in controlling the degree of order of water molecules and the exchange between molecules, at long distance too. Ordered water could in turn organize other molecules and transmit some signals. With a correlation time ranging from 10^{-12} sec to 10^{-6} sec, the motion gives essentially a thermic contribution to internal energy, entropy and pressure ($E = \frac{3}{2} kT$); but from 10^{-5} sec to 10^{-1} sec, it can

provide signals (slow co-operative movement of polymer chains in membranes and chromosomes as momentaneous water molecules alignment).

Brownian dynamics is quantitatively determined by the correlation time τc, the activation energy Ea and the diffusion coefficient D. The dynamic entropy Sd is related with the correlation time and the frequency of correlation: $Sd \cdot \alpha \cdot \dfrac{1}{\tau c} \cdot \alpha \cdot fc$. The correlation time may be determined by NMR spectra (bandwidth Δ) and the measurement of the spin lattice relaxation time T_1: $\Delta \cdot \alpha \cdot \tau c \cdot \alpha \cdot \dfrac{1}{\tau c} \cdot \alpha \cdot \dfrac{1}{fc} \cdot \alpha \cdot \dfrac{1}{Sd}$. The ordered molecular systems are present in membranes with lipid bilayers and in some part of water, in the vicinity of membranes, chromosomes, macromolecules and ions.
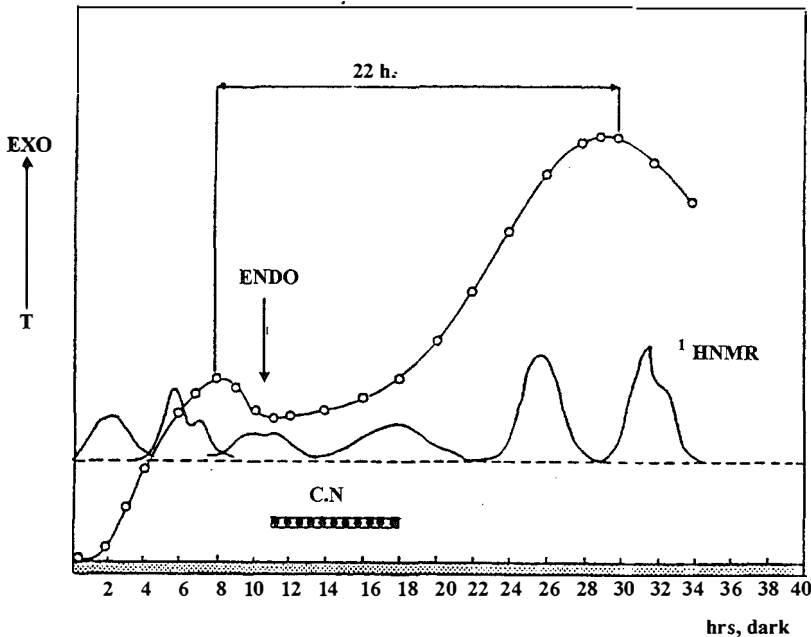

Figure 7. ^{1}H-NMR spectra of *Chenopodium rubrum* plantlets (SDP) in continuous darkness (induction of flowering). C.N.: critical nyctoperiod. Measurement, in a flux calorimeter, of heat exchanges during the same time (continuous curve). Endo-exothermic rhythm of 22 hrs [54].

Proton NMR in spinach leaves and Chenopodium plantlets (Figs 2,3,4,7; Table 2) gives us an information about the biodynamics of water molecules under the control and modulation by macromolecules, membranes and cell energetization. In both cases, it is when the photo- or nyctoperiod are critical that we observe a maximum of restriction of the water motion; it means a change in brownian versus semi-brownian dynamic order. The frequency of correlation fc, and also T_1 and Sd present a minimal value. A maximum is measured for the bandwidth line Δ, and the correlation time τc (free water : τc, 10^{-12} sec; T_1, 2,6 sec; proton exchange time, $2 \cdot 10^{-4}$ sec; the situation in leaves is different because the presence of various populations of water molecules : τc from 10^{-12} sec to 10^{-6} sec, as 10^{-5} sec, 10^{-4} sec, etc.; T_1 from 150 msec to 800 msec).

The dynamically ordered water, because of its specific physical and chemical exchange capacity, could transduce signals reflecting the energetic state in the cell, and through the physico-generic interaction with plasmalemma could operate at distance from leaves to apex (chromosomes could be another target of that water signal). So we hypothesize that the water brownian motion control and modulation could play a role as *primum movens* in the flowering induction process in leaves by its interaction with plasmamembrane (T_1 Fl < T_1 Veg; τc Fl > τc Veg; fc Fl < fc Veg; Δ Fl > Δ Veg; Sd Fl < Sd Veg ratio of negative entropy variation ~ 2)[11,12,19,20,28,29,32,64,99, 107,148,149,167,176].

Table 2. Plasmamembrane thickness evolution in apex or leaves of spinach (LDP) or *Chenopodium rubrum* (SDP) correlated with the induction process. [27,59,107]

Spinach : LDP	Plasma membrane Thickness
Short Days (8h. L, 16h. N): 4 weeks	Leaves: 8,6 ± 0,3 nm
Vegetative plants	Apex: 8,9 ± 0,5 nm
Transfer to continuous light (24hrs)	Leaves: 10,2 ± 0,2 nm
Floral induction	Apex: 10,4 ± 0,4 nm
Short days + GA$_3$ (10^{-5} M, 3 days)	Leaves: 10,2 ± 0,3 nm
Floral induction	Apex: 10,6 ± 0,4 nm
Chenopodium rubrum: SDP	Plasma membrane thickness
Continuous light (3 weeks)	Leaves: 8,2 ± 0,3 nm
Vegetative plants	
Transfer to 12 hrs night	Leaves: 9,6 ± 0,2 nm
Floral induction	
Transfer + red light break of night.	Leaves: 8,3 ± 0,5 nm
Vegetative plants	

Plasmamembrane

During the critical period of leaf induction by light in spinach or Arabidopsis, by night for Chenopodium, some structural, biochemical and physiological modifications are very rapidly occurring in plasmalemma both in leaves and apex. For example, the thickness of the membrane is increasing (~2nm) and the peripheral aspect is more clotted or lumpy after photoperiodic induction (osmic fixation). With NMR spectroscopy, we observe, at this time, a decrease of diffusivity of small molecules such as fluor nuclei (probe) or proton with about the same ratio of bandwidth line or T_1 variation. This restriction of molecular motion corresponds to a higher crosslinking with the macromolecular cellular system after induction, and with a blocking of the molecular dynamics, an increase in structuration and order, a decrease of the entropy of fluctuation. The ^{31}P-NMR suggest the appearance of hexagonal II phase in the plasmalemma (Fig. 8)[8,27-30,48,55,56,99,100,133].
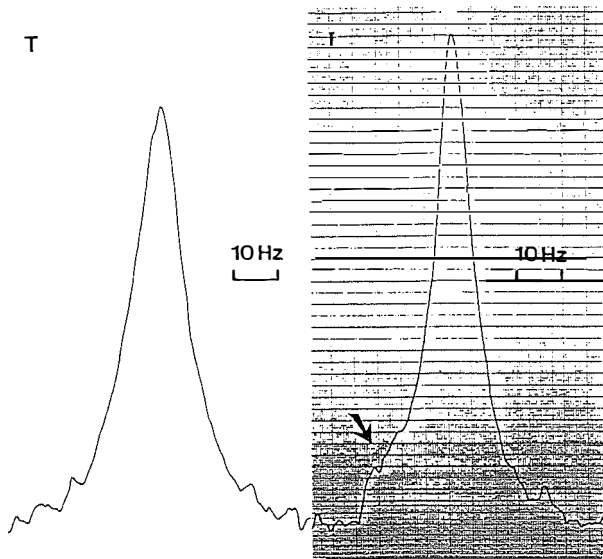
Figure 8. ^{31}P-NMR (200 MHz) of spinach leaves (plasmamembranes) at the vegetative state (T) and after transfer in continuous light (I: induction of flowering. Arrow: shoulder (hexagonal II ?) [28, 133].
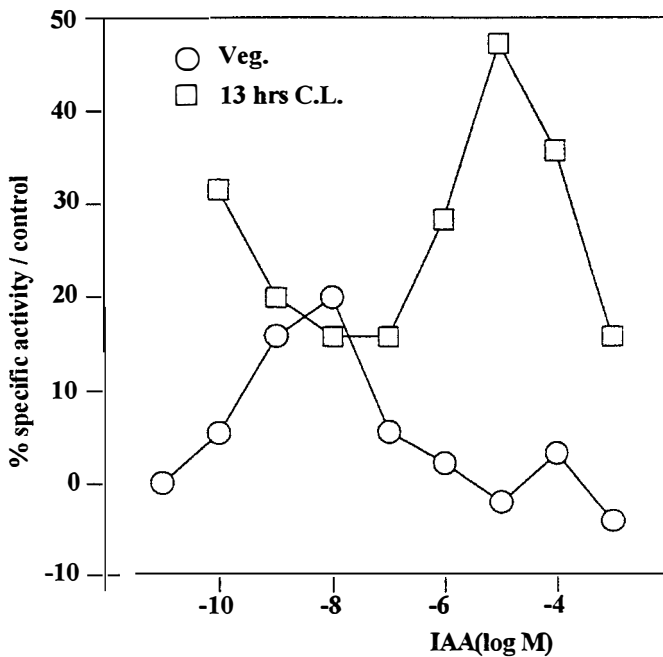

Figure 9. IAA sensitivity evolution of the H$^+$ pumps activity, ATPase dependent, at the vegetative state (spinach plasmamembranes) and during the transition to floral state (transfer from SD to continuous light: CL: 13 hrs, critical photoperiod). Three weeks-old spinach [11,12].

Usually the lamellar alpha phase is typical of membranes of young functioning cells, and the beta phase gel concerns the membranes of senescing cells. Under certain circumstances (temperature transition, increase of intercellular ions, hydratation degree of tissue) a non-bilayer configuration could occur in the membrane mosaïc. Phospholipids molecules could form cylinders with the polar head graps facing a water-filled core. Such inverted micelles could be distributed like hydrophobic buttons strewing the lumpy floral membrane and could serve as endogenous calcium ionophore or Ca channels. A rise of calcium is appearing during the photoperiodic induction and calcium pumps sensitivity is diminishing during this phase. All these modifications could influence the conformation of enzymes and their interactions (calcium and proton pumps, auxin receptors, etc.). The apparent Km of proton pumps ATPase dependent is decreasing and a desensitization to IAA occurs during floral induction (Table 1, Fig. 9). In spinach, the induction is associated with a high level in the endogenous auxin concentration and with a low level of peroxidase activity.
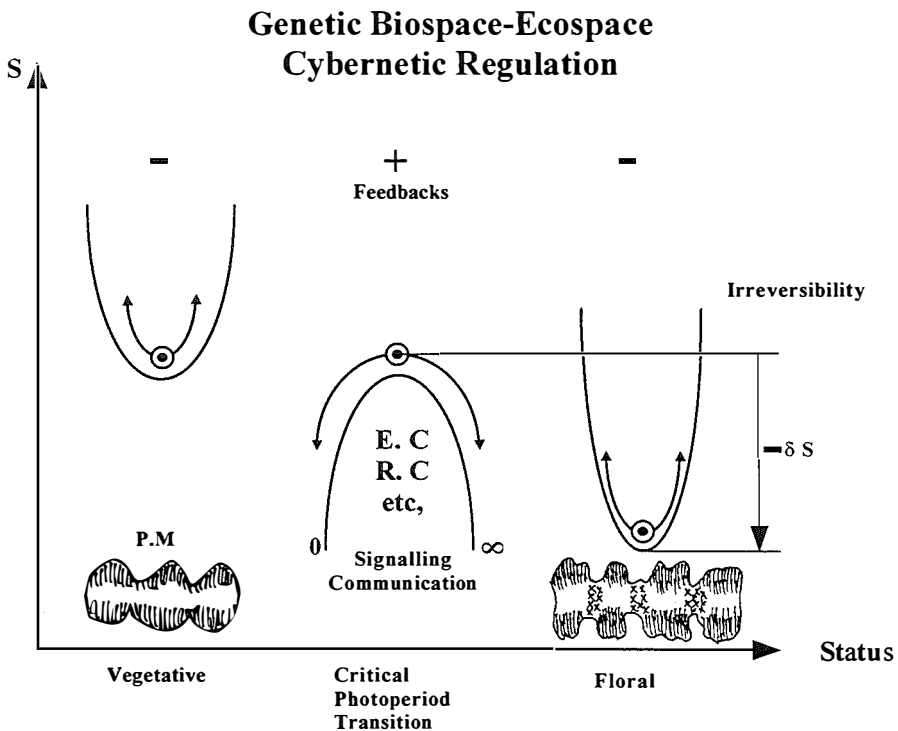

Figure 10. Cybernetical, structural and thermodynamical model. S: statistical entropy. P.M.: plasmamembrane. E.C.: energetic charge. R.C.: redox charge. Vegetative homeostasy and rheostasy (plastochrone): global master negative feedback (specific energetic and structural envelope). Transition: appearance of some positive feedbacks. Floral state: new homeo- and rheostasy in a new envelope, stabilised with new proteins pattern.
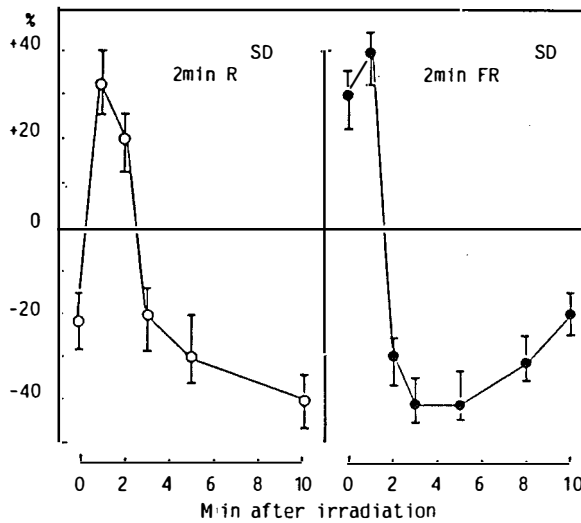
Figure 11. Effect of 2 min R (660 nm; 0,045 W/m²) or 2 min FR (730 nm; 0,015 W/m²) on the activity of free basic peroxidase extracted from leaves of SD-grown spinach (vegetative state). Data are expressed as % variation of the irradiated plants versus non-irradiated ones, extracted at the same time [80-83,131-133].
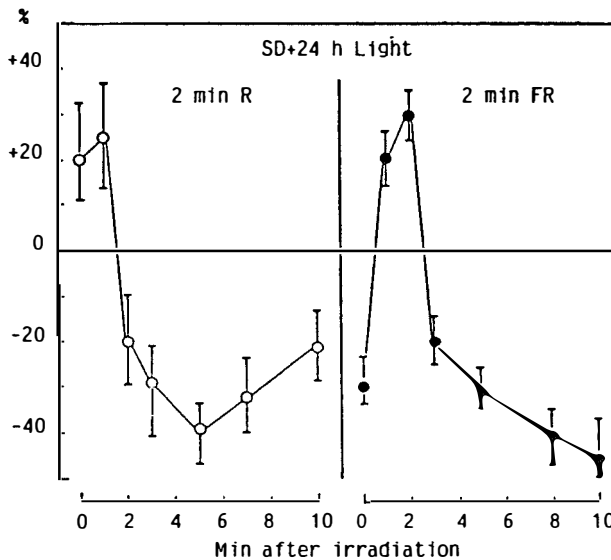

Figure 12. Idem fig. 11, but after induction of flowering with transfer from SD to continuous light (24 hrs). The response is inverted.

During the floral transition the chemical analysis points out a change in plasmamembrane sterols and an increase in the ratio of fatty acids C 18:1 (saturated) to fatty acids C 18:2 (unsaturated). This could influence the structural conformation and the exchange capacity of membranes. For example, the tails of lipids exhibit rotational motion (τc 10^{-9} sec to 10^{-7} sec), translational movement (τc 10^{-7} sec to 10^{-6} sec), exchanges among polar heads (τc 10^{-5} sec), slow flips along whole lipids (τc 10^{-1} sec), with some consequences in the bilayer lipids transmission along the membrane and the interactions with various membrane ligands (receptors, ions, secondary messengers, etc.). This physico-generic aspect and the interaction with the water brownian control and modulation could be the *primum movens* of the induction in leaves that lead to floral information, after the perception of specific light duration and temperature in conjunction with a clock control. Externalities of these primary effects are ionic and electrical messengers and hormonal-receptors modifications in co-action with quantitative gene activation, in a first time, followed by qualitative activation to stabilize the leaf floral state (new specific proteins). The Figure 10 summarizes the regulatory relation between energy, plasmamembrane state and the induction of flowering. We attach importance to a systemic physico-chemical effect during the first step of leaf induction [46,49,58,63,64,101,112,130,155,177,180-183].

Peroxidases and phytochrome

Peroxidases have been implicated with various physiological process and in free radical scavenging and auxin catabolism: control of endogenous free auxin level, cell wall biogenesis, H_2O_2 consumers or producers. The number of genes and isozymes in a plant is very high (60 to 90 genes for *Arabidopsis thaliana*).

Total peroxidase activity in leaves exhibits a clear correlation with the developmental stage of spinach : a minimum value is observed at the time of induction and floral evocation, after this period a progressive increase occurs until the floral morphogenesis and senescence. The balance between anodic and cathodic peroxidases is very rapidly modified during the leaf induction, with a great decrease in the activity of basic peroxidases.

Basic peroxidasic activity is under the control of phytochrome as shown by the 660 versus 730 nm light effect on the activity. The peroxidase activity reacts rapidly to 1 or 2 minutes of *in vivo* irradiation of the leaves (Fig. 11) and this photocontrol is modified at the moment of floral induction in leaves (Fig. 12). The effect of this local photoconversion, was very rapidly propagated to all the parts of the plant (Figs 13,14). This signal transmission was inhibited or delayed by several substances including LiCl, EGTA and the Ca ionophore A23187. Figure 15 gives a temptative model explaining the propagation of the signal and the modification of the kinetics after leaf induction that could be linked to the plasmamembrane modification [23,50,80,81,130-132].

We have demonstrated that it was possible to modulate, both *in vivo* and *in vitro*, a specific binding or release of the basic peroxidases (glycoproteins) on leaf plasmamembrane or tonoplast by far-red and red light (phytochrome), or by Mn^{2+}, Ca^{2+}, and EGTA. This control is modified during the induction process in the LDP spinach as well in the SDP Pharbitis. This association of some peroxidases with membranes is specific to sites in membranes. The plasmamembrane of Pharbitis leaves

present a hemicircadian rhythm of the basic peroxidase association capacity, with a maximum at the moment when the sensitivity to red light in flowering inhibition is at its maximum (Fig. 16). In spinach a similar observation could be associated with red or far-red light effect (Fig. 17). A correlation is observed with the light on, light off control of the plasmamembrane electrical potential [82,83]
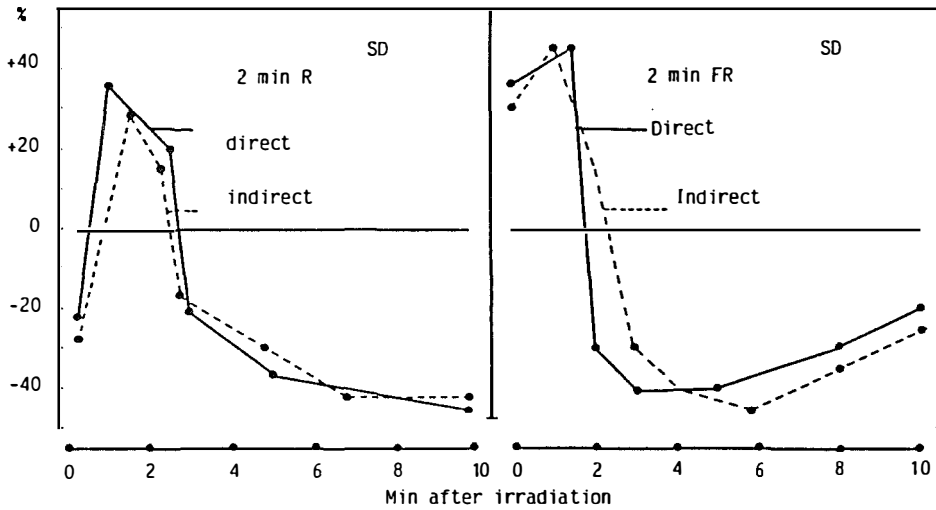

Figure 13. Idem Fig. 11; test with the irradiated leaf (continuous line) as with non-irradiated leaf (broken line) of the same plant (communication at distance). Vegetative state (spinach).
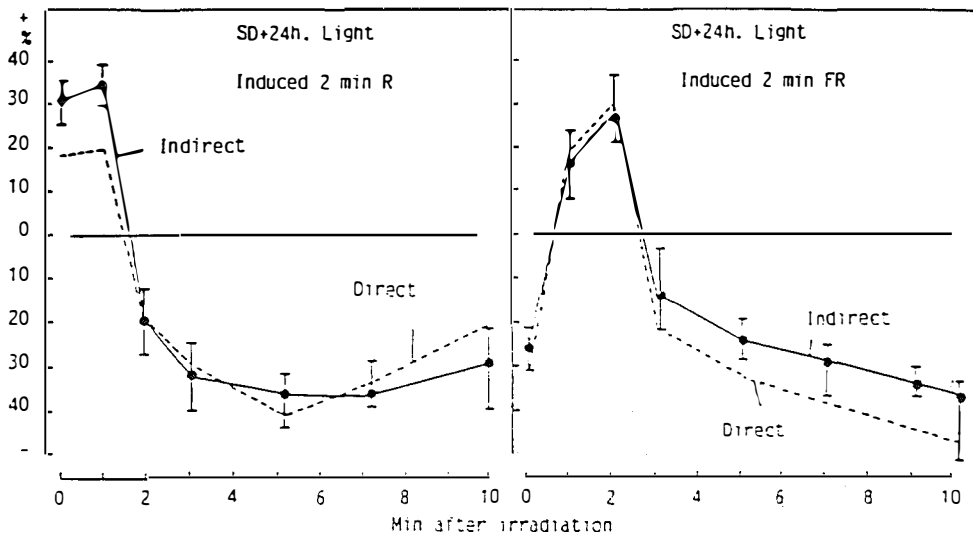

Figure 14. Idem Fig. 12 and same test as Fig. 13, after flowering induction.
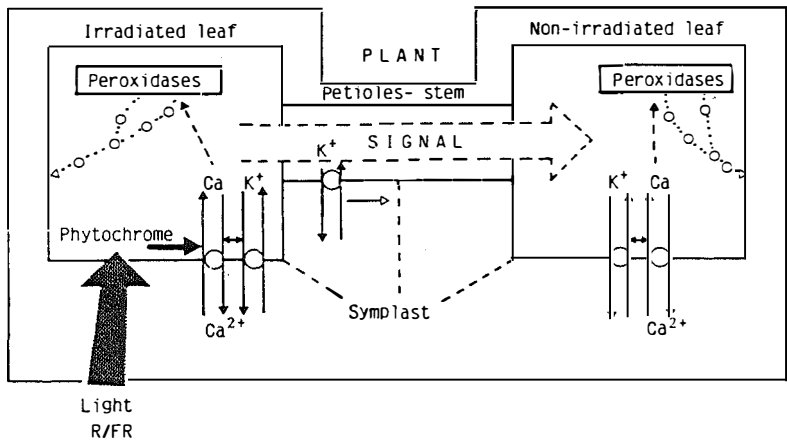
Figure 15. Model of the transmission in the whole plant of the "peroxidase signal": interaction between light, phytochromes and other pigments, ions, plasmamembrane (timing mechanism, receptors, structural organisation, ion pumps, secondary signals, etc.) and peroxidases. The "flowering signals" are transmitted through plasmamembrane and phloem cells (symplast). The transmission of both signals implicates Ca^{++} and could be blocked by LiCl, whereas ouabain blocks only the peroxidase signals.
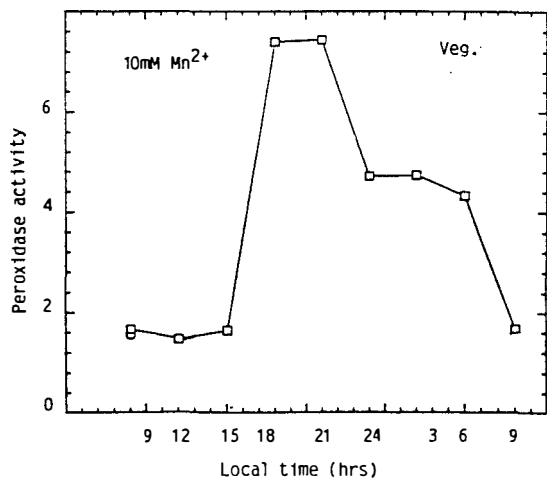

Figure 16. Basic peroxidase binding on purified plasmamembrane (*Pharbitis nil*, SDP) extracted at different times of the day (hemicircadian rhythm). Vegetative state. Red light break (660 nm) during inductive long night has the maximum effect (inhibition of flowering) at 20 hrs. It corresponds to the period when the maximum peroxidase binding could be observed [83,133].
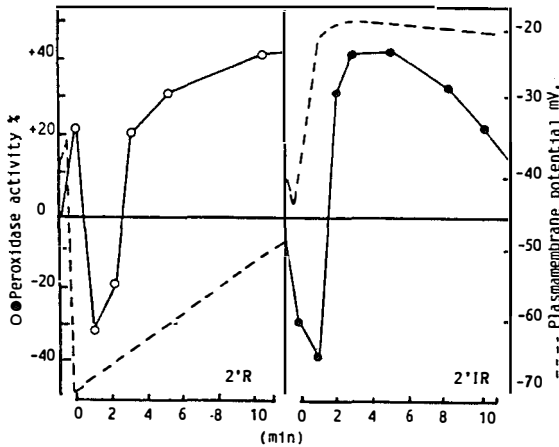
Figure 17. Correlation between the light on effect (Red or Infrared: 660, 730 nm) on the binding or release of basic peroxidases with the membrane, and the light on (left) or light off (right) effect on the bioelectrical potential (micro-electrodes) of leaf plasmamembranes (spinach). Electrochemical and ionic mediation [133].

Bioelectricity

Active cells and organs are surrounded by electrochemical activities essentially stemming from photosynthetic metabolism during daylight and respiratory pathway during the night. About half of the generated energy is spent in electrochemical activities. As a result, because of biological activity far from equilibrium and thermodynamically open....,dynamic electrical potentials (span: ± 150 mV) are generated at different compartmental levels (plasmamembrane, chloroplasts, mitochondria, nucleus, vacuole). The value and evolution of these potentials give us an insight about the intra- and inter- compartmental relation in cells and between the tissues and organs, the interaction with environmental constraints and the stage of growth and development of the plant. The coupling of bioelectrical tests with the use of different LDP or SDP, and mutants or transgenic plants, could be a way of identifying, in different environmental background, what are the primary invariants of leaf induction producing the flowering stimuli. A pattern of gene activity upstream could be determined by microarray.
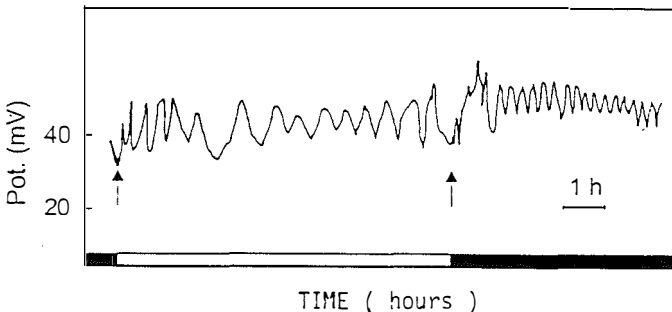

Figure 18. Fluctuation of the bioelectrical potential of plasmamembrane (spinach leaves) during one day, at the vegetative state (4 weeks-old plants. SD: 8 hrs light, 16 hrs night) [125].

In continuous light (floral state) spinach leaves show a rest-potential at the plasmamembrane modulated by a circadian rhythm of 25,2 ± 0,9 hrs, supporting an alternate train of small electrical fluctuations (5 to 10 mV) with a frequency of about $1,4 \cdot 10^{-3}$ Hz, for a first set and $8,9 \cdot 10^{-4}$ Hz for another set (hemicircadian alternation). Under short days (vegetative state), a fluctuation of $8,4 \cdot 10^{-4}$ Hz is observed during the light period and $2,2 \cdot 10^{-3}$ Hz during the night (Fig. 18). If we induce flowering by transfering the plant from short days to 30 hrs continuous light, and then back-transfering the plant in short days, the frequency of electrical oscillation is $2,2 \cdot 10^{-3}$ Hz at the night, as before, and respectively $4,9 \cdot 10^{-4}$ Hz and $6,7 \cdot 10^{-4}$ Hz during the light period of the first and second short-day. This result suggests that flowering induction in leaf has modified the electrical response and regulation in light, which indicated that some irreversible transformation has occurred [125].
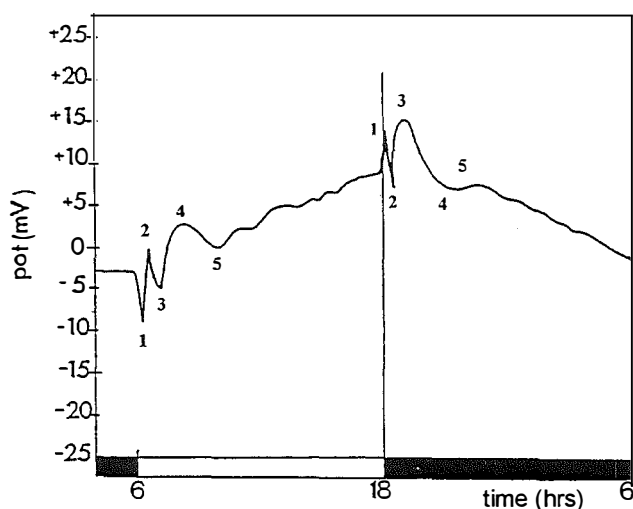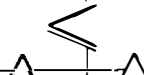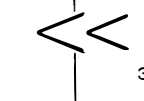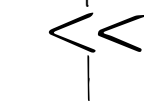

Figure 19. Detail of surface bioelectrical potential (leaf of bean) evolution: light on, light off effect (polarization, depolarization) during ~20 minutes (12 hrs light, 12 hrs night) [62].

In photoperiodic plants the orientation in time is dependent upon the coincidence of light on and light off signals with the internal clock system oscillations. The light-dark breaks produce specific fast variation of the plasmamembrane electrical potential and of the surface potential (Fig. 19). These signals present circadian property in the electrical signature with two series of fluctuations, 0,016 Hz and 0,0041 Hz, which are closely fitted with the photonyctoperiod length (enslaving). Some modifications of the signal structure seem to be correlated with flowering induction (Fig. 20) [66].

These results and the existence of a clock adjustment between the different parts of the plant (multiplicity of rhythmic phenomena) suggest that the periodic organization in electrochemical oscillation could be the basis for communication between leaves and apex via frequency coded signals. Apical cells would be activated to modulate mitosis in the different apical territories, as a consequence of brownian water

modulation, and because of changes in plasmamembrane that provoke coded electrochemical fluctuations and transduction to secondary messengers, hormones and receptors (Figs 21,22) [1,61,62,92,115,116,174,184].

Bioelectrical Potential

Parameter	Amplitude A		Period τ	
Light	Fl.	Veg.	Fl.	Veg.
ON				
OFF		30%		50%

CHENOPODIUM: S.D.P

Figure 20. Light on, light off global analysis at the vegetative state and after flowering induction in *Chenopodium rubrum* leaves (SDP): modification of the amplitude of the signal as the duration of this one [66].

Physiomatics

Macrofunctions, plasmamembranes and clocks are playing an important role in this vision of the primary events of flowering induction in leaves (Figs 21 to 23). Concerning the time measurement, NADH oxidase associated to membranes, could be implicated as an ultradian and thermocompensated rhythm of redox activity [57,58,118-120,139,172,173,177,190].

During these last years, important progress has been made in computering registration and sensors development (macro, micro, nano-sensors), and in mathematical and system analysis. It is possible to fit out a plant with a lot of various probes for continuous measuring and registration of the different physical, chemical and biochemical parameters. Depending on the program, it is possible to stimulate or inhibit the plant with the action of electrodes and other devices. So we can prospect the capacity and pattern of cybernetic accommodation and adaptation of the plant under different and global environmental treatment (light, temperature, chemicals) in relation with genetic properties (mutants, transgenics, ecotypes). The set up of a phytofeedbacks between the measured parameters and the imposed program of stimulation or inhibition, under different global environmental constraints, allows by this self-enslaving the determination of the different self-equilibrium level, by various genes activation or inhibition, and also the nature of the various transition
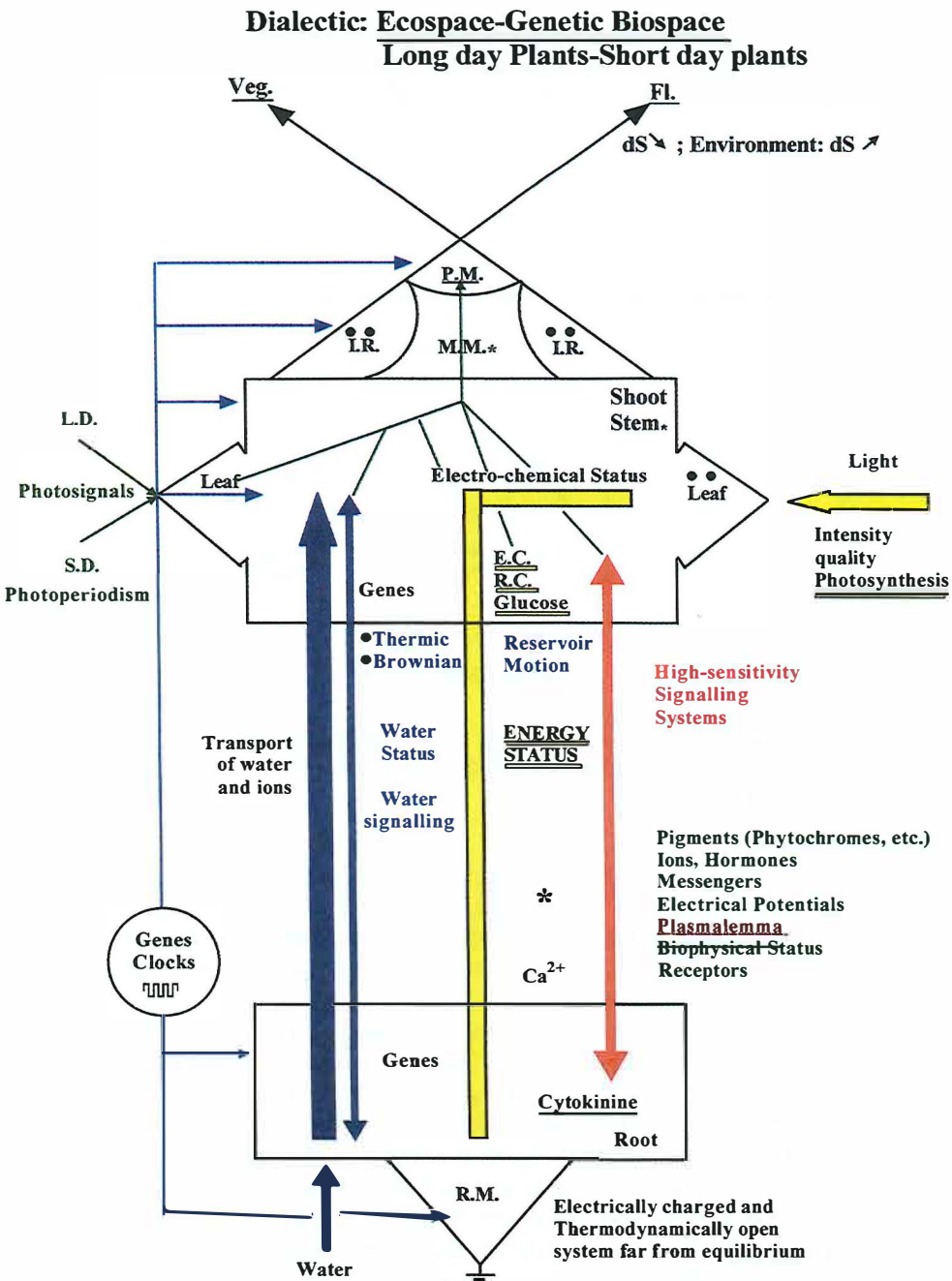
Figure 21. General sketch of the basic events during the flowering induction in leaves. Veg: vegetative; Fl: floral. dS: entropy variation. P.M.: prosporogenic meristem. M.M.: medullary meristem. I.R.: initial ring. E.C.: energetic charge. R.C.: redox charge. R.M.: root meristem. L.D.: long day. S.D.: short day.
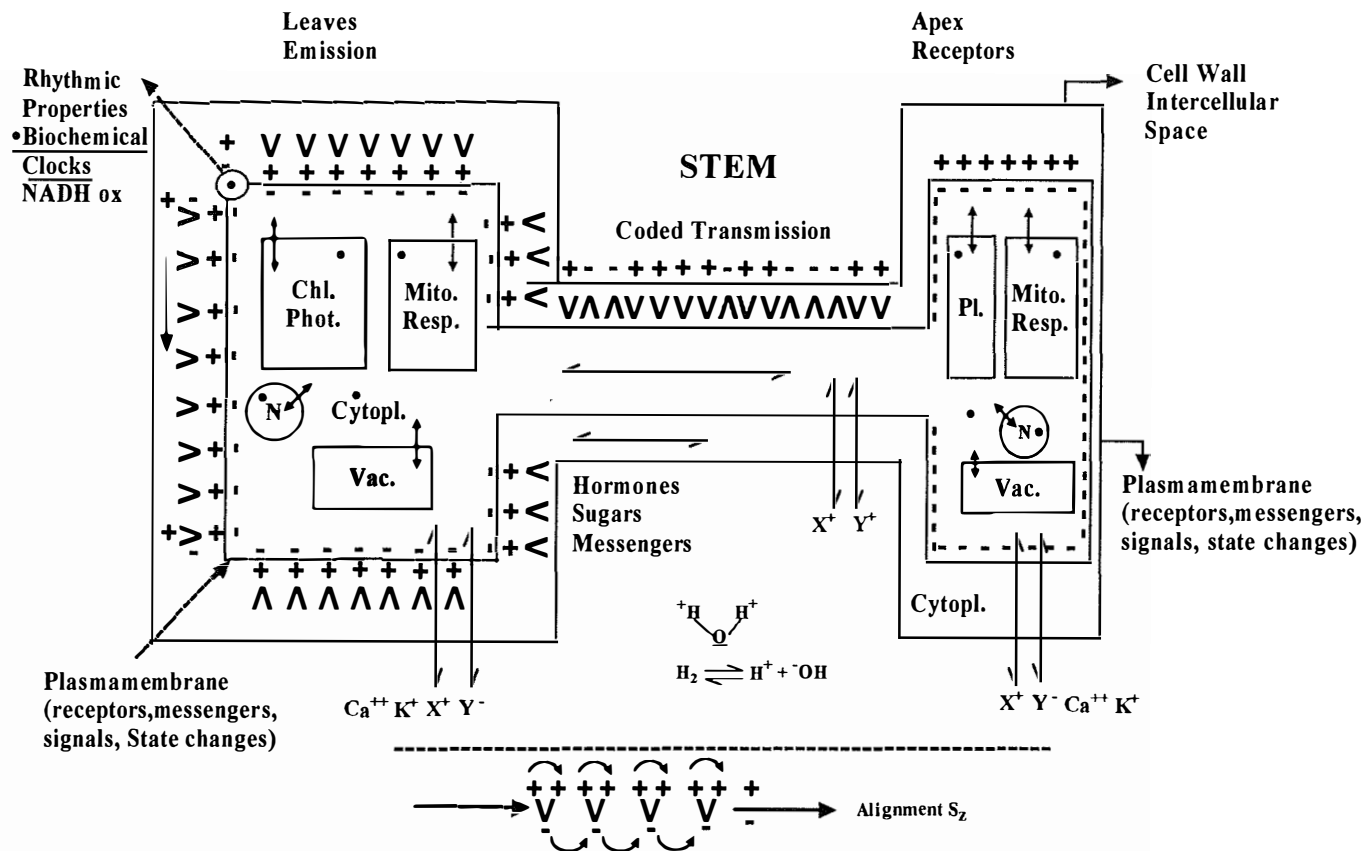
Figure 22. Coded electrochemical model of communication (hypothesis). N: nucleus. Chl.: chloroplast, photosynthesis. Mito: mitochondria, respiration. Vac: vacuole. Cytoplasme [66,183,184].

Organism (Higher-Plant)

Growth-Development   Macro-functions

Cells: 10^{11}- 10^{13}
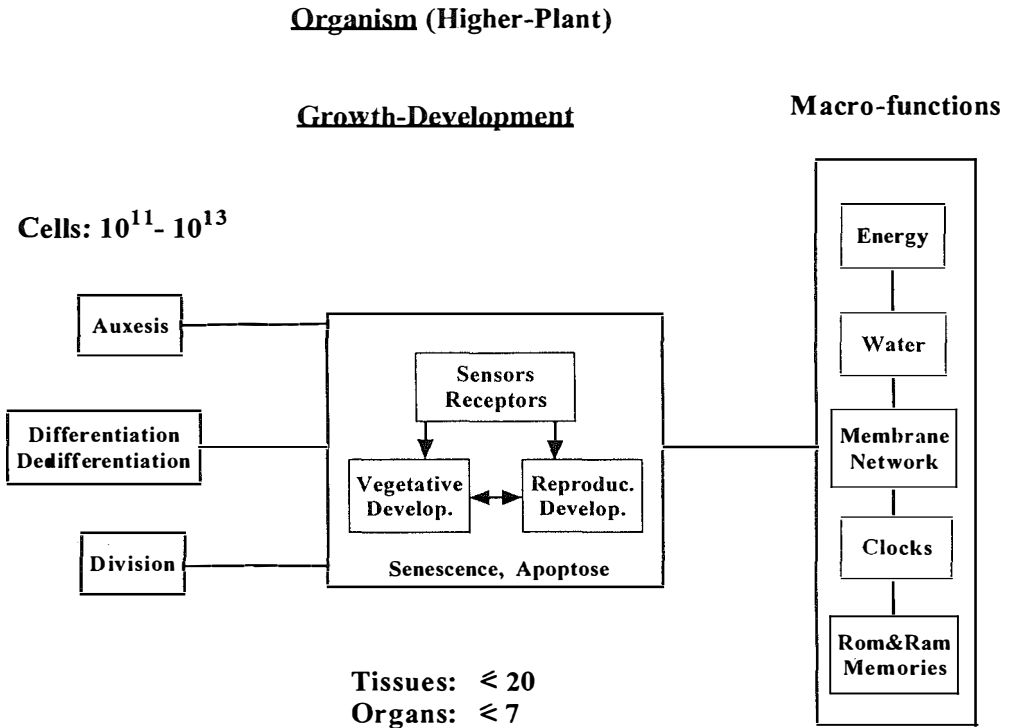
Figure 23. Cellular working programs supervised by a few macrofunctions controlling at distance a few number of tissues and organs [59].

possibilities and the damageable situations. An expected result, in particular when the experimentation is made with the extreme environmental constraints that lead to flowering induction, is the progressive determination of the operators which associate the genetic matrix of information with the dynamical phenotypic expression (non-linear equation) (Fig. 24). It should represent a progress in the discovery of the information grammar of the interacting genes in plant, and also in the dialectic of biospace versus ecospace [51,58, 60,70,134,155,160,170,175,181].

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PHYSIOMATICS
10^{11} - 10^{13} cells

Responses
sensors
1. Growth
2. Leaf Movement
3. Electrical Potential
4. Resistivity
5. Light (λ) Absorption
   Reflection, Fluorescence
6. Sap Movement
7. Water Balance
8. Specific Electrodes
   etc.

Stimuli
A. Light
B. Temperature
C. λ , Short Lighting
D. Electrical Potential
   and Stimulation
E. Mechanical
   Stimulation
F. Chemicals
   etc.

Mutants (Arabidopsis)
Ecotypes (Chenopodium)
Transgenic Plants

Computer
Registration
Analysis
Simulation

Coupling, covariation and guidance system

between stimuli and responses   Feedback

[Genetic Matrix]   Operators   [Phenotypic Expression
                                     non-linear dynamic
                                     equations]

Macrofunctions

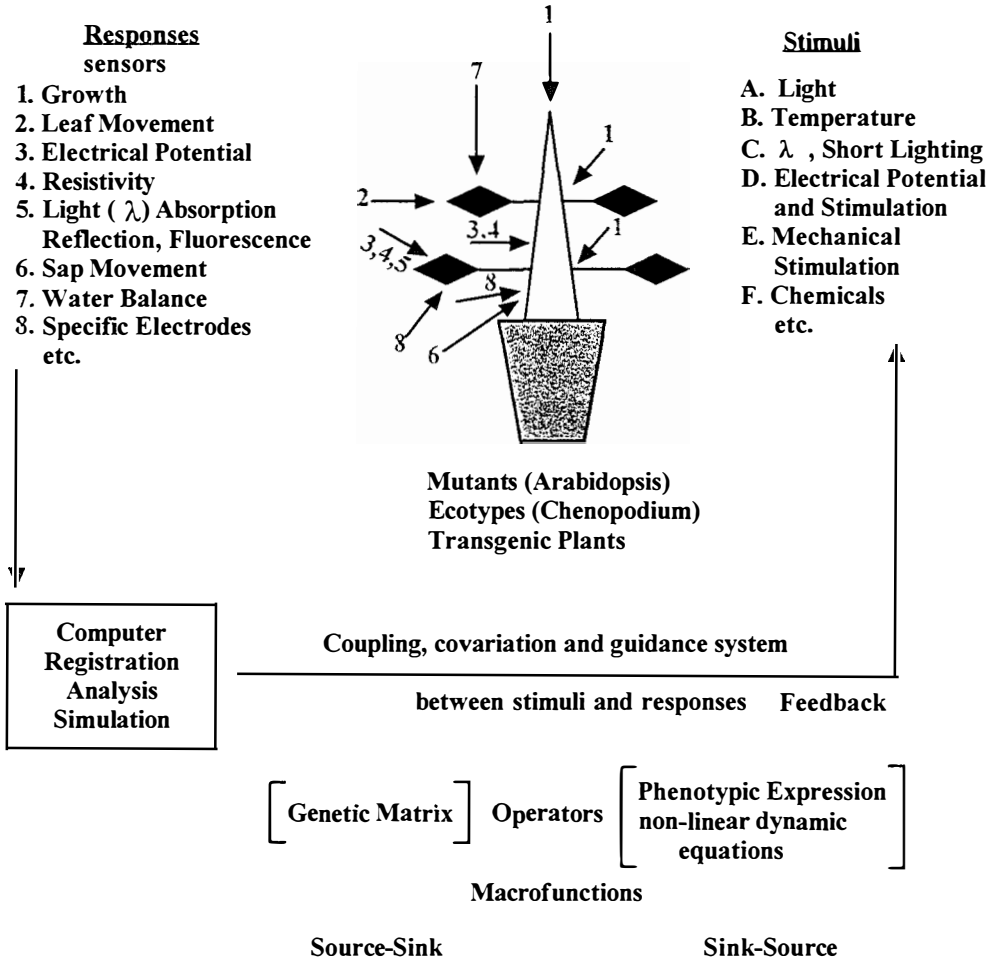Source-Sink   Sink-Source

Figure 24. Physiomatics, a way to prospect the genes networking in relation with global effects on the plant territories [59].

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