

## 21 Control of Plant Development by Hydro-Electrochemical Signal Transduction: a Means for Understanding Photoperiodic Flower Induction

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### 21.1 Introduction: photoperiodic flower induction

The hypothesis that flowering involves a specific stimulus is based upon the demonstration that (a) in photoperiodism the flowering response depends upon the day length conditions given to the leaves, whereas the response occurs in the apices, and that (b) a floral stimulus can be transmitted via a graft union from an induced partner (donor) to a non-induced one (receptor). Transmission of the floral stimulus by grafting has been demonstrated within various photoperiodic response types, as well as between different photoperiodic response types in interspecific and intergeneric grafts. The physiological evidence for a floral stimulus is clear-cut, but up to now the nature of the stimulus has remained obscure (Bernier 1988).

The specific kind of photoperiodic behavior depends very much on the exact environmental conditions, as was shown for four different North American ecotypes of *Chenopodium rubrum* (Tsuschiya and Ishiguri 1981). The southern ecotypes display an obligate short-day behavior under white (W), red (R) and blue (B) light. The most northern ecotype is day neutral in B and W and has an amphiphotoperiodic response in R light. Another northern ecotype has an amphiphotoperiodic response in B and a short-day response in W and R light. The amphiphotoperiodic response in B is modified to day neutral by changing the temperature from 20 to 12 °C. These data clearly indicate that photoperiodic behavior is extremely flexible in adapting to specific environmental conditions.

Irrespective of the flexibility of plants in modifying their photoperiodic behavior in adapting to specific environmental conditions as just mentioned, the following essentials of the photoperiodic reaction have to be kept in mind as a basis for further considerations:

- (a) Short-day (SDP) and long-day plants (LDP) show opposite reactions to a given photoperiod.
- (b) Reactions result from coincidence or non-coincidence of light and dark phases of the photoperiod with corresponding phases of an endogenous circadian rhythm and the main photoreceptors are the plant sensory

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pigment systems phytochrome and cryptochrome. Circadian rhythm and photoreceptors have the same properties in SDP and LDP.

- (c) Critical photoperiodic induction produces irreversible changes in the leaves of SDP and LDP leading to a common state both in SDP and LDP, as proven by grafting experiments. There is no difference between SDP and LDP in their response towards a common inductor from a grafted leaf from an induced short- or long-day plant.

Analyzing the kinetics of change at the shoot apical meristem (SAM) during flower initiation can give hints on the mechanism(s) of signal transduction from leaves to SAM during photoperiodic flower induction.

## 21.2 Model system *Chenopodium*: induction of flowering from physiology to molecular biology

The model system *Chenopodium spec.* had been established to study photoperiodic control of flowering on the physiological, the biochemical and molecular level.

First *Chenopodium* was developed as a “Petri-dish plant” by Cumming (1959) for large scale screening of photoperiodic flower induction with several latitudinal ecotypes showing short-day, long-day and day-neutral responses (Cumming 1967; Tsuschiya and Ishiguri 1981).

Subsequent studies demonstrated that phytochrome photoreversibility could not act as an hour glass timer in photoperiodism, but was gated in its light sensitivity by an endogenous (circadian) rhythm presenting photophile and skotophile phases in daily 24-h light:dark cycles (Cumming et al. 1965). Following Bünning’s (1942) and Hendricks’ (1963) early concepts on metabolic control of timing in photoperiodism, *C. rubrum* has been used to establish an analysis of energy metabolism demonstrating a circadian rhythm in redox state and energy charge as macroparameters timing photoperiodic behavior (Wagner et al. 1975). Recently, *C. rubrum* was also used in molecular studies on signal transduction in photoperiodic flower induction. An ortholog of *LEAFY*, a transcription factor involved in a signaling cascade leading to flowering in *Arabidopsis* (Nilsson et al. 1998), was identified in *C. rubrum*. Expression kinetics of *LEAFY* ortholog *CrFL* at SAM is related to photoperiod (Veit et al. 2004). Transgenic plants were produced using RNA interference in order to analyse function of *CrFL* in signal transduction in *C. rubrum*.

With studies on the hydro-electrochemical integration of communication in *Chenopodium* plants, we could demonstrate that action potentials precede turgor mediated leaf movements and changes in stem extension rate (Wagner et al., 2005) (Fig. 21.1). Molecular and physiological studies at SAM of *C. rubrum* in transition to flowering presented evidence of changes in turgor and in aquaporin expression (Albrechtová and Wagner 2004;