Can transition to flowering be modelled dynamically from the gene level?

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Abstract

Quantitative models could predict the functioning of gene networks if those networks were sufficiently understood and appropriately quantified. Such capability would facilitate the application of crop growth simulation models in crop improvement programs, and hence improve the connectivity of research between crop and cell biology. Crop response to photoperiod is a useful physiological case study, as its genetic control is relatively well understood. Based on existing literature, we present here a simplified network for this process in *Arabidopsis thaliana*, a long-day crop. Although the current version of the model is strictly qualitative, it illustrates how a simple gene network can generate critical and ceiling photoperiods as an emergent property of the framework dynamics. We argue that simulating causes of physiological processes, rather than their consequences, will provide simulation models with the functionality required to extend the domain of genotype x environment (GxE) combinations.

Media summary

Crop growth simulation models that dynamically capture phenotypic responses to genetic differences may provide a useful tool to incorporate molecular biology into crop improvement programs.

Key Words

gene network, phenology, simulation model, critical photoperiod, crop improvement

Introduction

Quantitative models could predict the functioning of gene networks if those networks were sufficiently understood and appropriately quantified. Based on this notion, there has been considerable recent speculation about building an entire *in silico* plant starting from the gene level (Minorsky, 2003) as a pathway to plant improvement. Others, including ourselves (Tardieu, 2003; Hammer et al., 2004) have argued that this is not feasible, nor wise, for systems such as entire plants, due to the level of complexity involved in spanning levels of biological organisation. Still, perhaps for components of plant function that are well characterized genetically, dynamic quantitative gene network models are possible and potentially useful. The pathway for the photoperiodic control of the transition to flowering is a prime candidate in this regard. Detailed qualitative models for this pathway have been developed from studies with mutants in the long-day crop *Arabidopsis thaliana* (eg Bl?zquez 2000), and the same pathway is largely conserved in rice (*Oryza sativa* L.), a short-day crop (Cremer and Coupland, 2003).

Most crop growth simulation models simulate phenology empirically as a function of photoperiod and thermal time, with input parameters (base vegetative period, critical photoperiod, photoperiod sensitivity) bearing no direct relationship to known gene action (Major et al., 1990). Although this descriptive photothermal framework provides simulations of anthesis date that are adequate for agronomic purposes, there are several environmental effects on the timing of anthesis that it cannot capture. Examples are the effects of asynchrony between the day/night rhythms of temperature and photoperiod on phenology (Morgan et al., 1987; Ellis et al. 1997), and the delay in development following partial defoliation (Ockerby et al., 2001), which renders such models useless in grazing studies.

A model based on a gene network can potentially predict the effect on phenology of new combination of genes. This was recently illustrated by Welch et al. (2003) and Dong (2003), who developed a genetic neural network model for the control of time to flowering in *Arabidopsis thaliana.* However, that model was quite mathematical in attempting to capture all of the dynamics, including the pathways of RNA synthesis and product transcription. We attempt to construct a model that is similar in the component pathways, but which is less mathematical and does not explicitly incorporate some of the synthesis pathways. It is designed to be incorporated into the APSIM generic crop template (Wang et al., 2002)

A network for genetic control of photoperiodic response in a long-day plant

The gene network was developed from literature data and we present here a preliminary model (Fig. 1) associated with photoperiodic response, while acknowledging that there are other pathways (constitutive or temperature pathway, GA regulated pathway). Numerous papers on the genetic control of the response of *Arabidopsis thaliana* to photoperiod have been published (e.g. Bl?zquez 2000; Hayama and Coupland, 2003) and the current opinion is that the *constans (CO)* gene is essential for the early flowering under long days (Valverde et al., 2004). *CO* is a transcriptional regulator of the expression of the *FT* gene, and its expression is regulated by both the circadian clock and the presence of light (Valverde et al., 2004). There is evidence that the *gigantea (GI)* gene is closely linked to the circadian clock and is located upstream of *CO* (Fowler et al., 1999). Downstream of *CO* is the *FT*-gene, the transcription of which is regulated by *CO* activity (Valverde et al., 2004). High expression levels of *FT* trigger expression of the *LFY*-gene and flower primordia are initiated when *LFY* expression reaches a certain threshold (Bl?zquez et al., 1997).

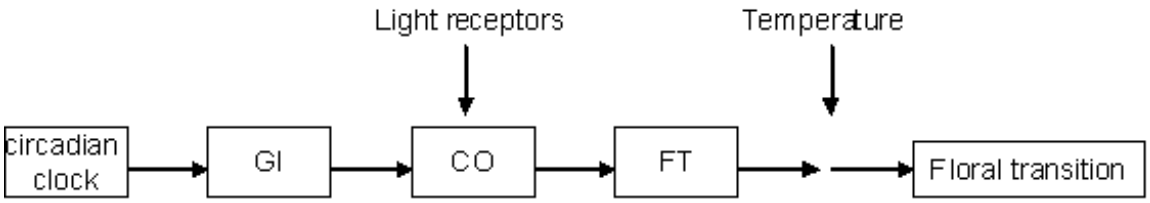

Figure 1. Simplified gene network for the photoperiod pathway in *Arabidopsis thaliana* (long-day plant). Adapted from Cremer and Coupland (2003).

Dynamic simulation of critical photoperiod

Our model estimates the hourly expression of *CO* and calculates the change in expression as the difference between the hourly production and decay rates. From the expression data, a daily average expression of *CO* was calculated, which is inversely related to the time to anthesis (Roe et al., 2003; SM Welch, pers. comm.).

The production of *CO* was determined by (1) the expression of *GI*, (2) a sinusoid function, and (3) a production rate. The expression of *GI* (Fig. 2) was assumed to be under circadian control, increasing from a minimum value at dawn to a maximum at 10h after dawn and then gradually declining until a minimum value was reached at 19 h after dawn (Fowler et al., 1999; Park et al., 1999). Although the timing and height of the peak both depend on photoperiod (Fowler et al., 1999), we kept the expression pattern independent of photoperiod for sake of simplicity. A transfer function (Welch et al., 2003) was used to translate the expression pattern into an input value for *CO*. The sinusoidal function was used to represent the circadian control of CO through light receptors (phytochrome and cryptochrome). It had a phase of 24 h and its angle was set to represent the observation that the expression of *CO* does not start until approximately 8h after dawn (Su?rez L?pez et al., 2001; Yanovsky and Kay, 2002). The production rate of *CO* was selected arbitrarily, with the proviso that rates were high during the day and the night (SM Welch, pers. comm.).

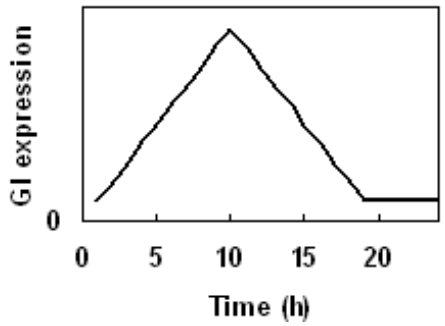

Figure 2. Schematic representation of the circadian rhythm of GI-expression. T=0 represents dawn.

The decay rate of *CO* was calculated as a first-order reaction, and was thus proportional to the amount of *CO* present. Based on data published for both *CO* (Su?rez L?pez et al., 2001; Yanovsky and Kay, 2002) and its homolog in rice, *Hd1,* (Kojima et al., 2002; Hayama et al., 2003) we derived a proportionality constant for this decay which was close to 0.25 (Fig. 3).

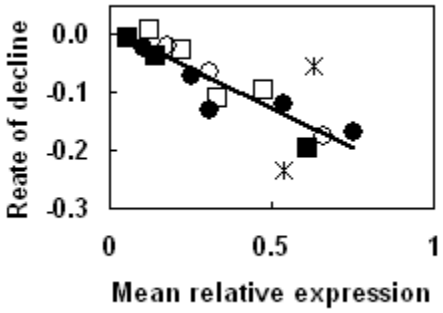

Figure 3. Rate of decline in expression of as a function of the mean relative expression for *CO* (closed symbols) and *Hd1* (open symbols). Data from intervals >6 h after dusk. ■ Su?rez L?pez et al., 2001; ●Yanovsky and Kay, 2002; □ Hayama et al., 2003; ○ Kojima et al., 2002. * = outlier

Regression slope: y = -0.27x + 0.01 R^2=0.87 n=15.

The results of this model showed that the average daily expression of *CO* was relatively constant at photoperiods below 10 h and beyond 18h (Fig. 4). As low levels of *CO* result in low expression of *FT* and hence late flowering, the daily expression of *CO* is inversely related to the timing of flowering. Although Fig. 4 has only qualitative value, it illustrates the possibility to infer the critical and ceiling photoperiods as an emergent property of a simple gene network.

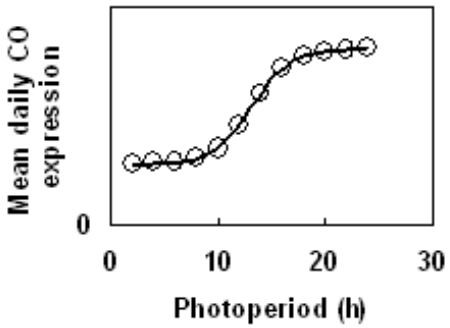

Figure 4. Simulated mean daily CO-expression (unit less) as a function of photoperiod.

Potential for applications of crop growth simulation models

The functionality and dynamics of gene network models potentially allow them to capture the phenotypic consequences of genotypic changes. This is illustrated by a neural network model for phenology in *Arabidopsis*, which captured a cross-over mutant x temperature interaction for phenology (Welch et al., 2003). Such a capability would allow applications of models in breeding programs to explore new GxE interactions and would provide a useful tool in integrating molecular biology research into crop improvement programs. The gene network presented here provides an example of the change in paradigm in model development, from simulation consequences of physiological processes to simulating their causes, that is necessary to obtain the required functionality in crop models.

Conclusion

Our results show that critical and ceiling photoperiods can be generated as an emergent property of the dynamics of a relatively simple gene network model, thus eliminating the necessity of descriptive model input parameters. Our example is only qualitative, and considerable improvements need to be incorporated (eg constitutive temperature response) before the model can be incorporated into a crop growth simulation model. However, it illustrates the potential for the dynamic simulation of phenology through the use of a gene network. A change in paradigm from modelling consequences of physiological process to modelling their causes, as illustrated in this paper, is essential in facilitating the dialectic between crop level and cell level research.

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