A study of different flowering strategies in response to vernalization using mathematical modelling

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This report presents the results from my implementation of a genetic-physiological model of flowering developed by Prof. A. Satake. The outputs generated show 4 different plant life cycles due to the dynamic epigenetic regulation in response to vernalization.

FLOWERING LOCUS C (FLC) is transcription factor that acts as flowering repressor and VERNALIZATION INSENSITIVE 3 (VIN3) is one of the initial repressors of FLC during winters. The repression of FLC activates FLOWERING LOCUS T (FT) and the production of FT protein begins which is then transported from leaves to shoot apical meristem, where it initiates flowering. This model takes into account the simple interactions between VIN3, FLC and FT protein and ignores some components of the actual gene regulatory network such as SUPRESSOR OF OVEREXPRESSION OF CO 1 (SOC1) and photoperiod pathway. The model also assumes that repression signal is digital in nature, i.e. the cells are either repressed or activated.

My implementation of the model and its results have been presented here. The results in this report are similar to that of the original study (see citations).

1 Temperature dataset

Since the original temperature dataset used for the study could not be located, I designed a simple model to generate random temperature dataset array for any number of days. The function is a simple trignometric function, with gaussian noise added to it. It is a sine wave function multiplied by a factor θ_r and added to an average temperature value. The function is written as,

$$\theta_{av} + \theta_r \sin((M + \frac{D}{30})\frac{\pi}{12}) + \mathcal{N}(\mu, \sigma) \tag{1.1}$$

In the equation, θ_{av} stands for the desired average value, $M \in [0, 11]$ denotes the month for which the data is being generated and $D \in [0, 29]$ is the day number for the month. For simplicity, every month is assumed to have 30 days.

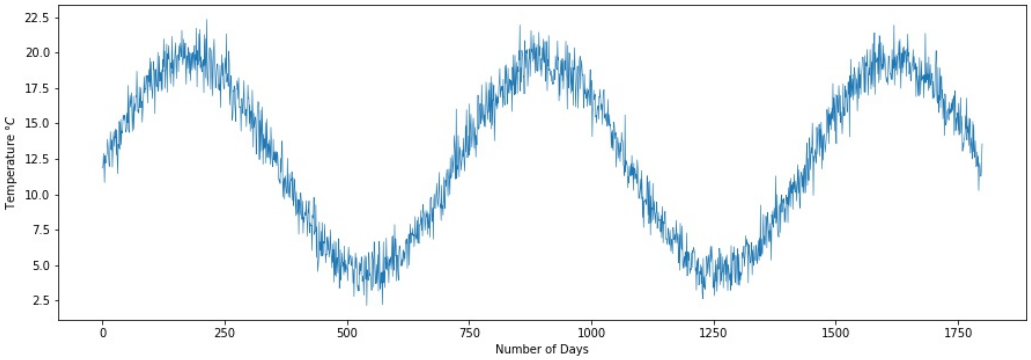


Figure 1: The generated data by implementing the equation 1.1, for $\theta_{av} = 12, \theta_r = 7.5, \mu = 0, \sigma = 2$ for 60 months.

2 Summary of the model

As described by A. Satake, the model focuses on vernalization pathway and showcases the repression of FLC due to prolonged cold temperatures (below the vernalization threshold in the model, K_T) and its subsequent maintenance. VERNALIZATION INSENSITIVE 3 (VIN3) expression induced by cold environment is one of the repressors of the FLC gene. The dynamics of the VIN3 transcript levels vary as,

$$\frac{dVIN3}{dt} = \beta_V \theta(T(t) < K_T) - \alpha_V VIN3 \tag{2.1a}$$

and,

$$\theta(T(t) < K_T) = \begin{cases} 1 & if T(t) \leq K_T \\ 0 & otherwise \end{cases} \tag{2.1b}$$

In equation (2.1a), β_V is the production rate of VIN3 transcript and α_V is the degradation rate of the same. $\theta(T(t) < K_T)$ is a step function as described by equation (2.1b).

VIN3 leads to increased repressive histone modifications at FLC locus and a decrease in modifications associated with active transcription. In the original study the cells were assumed to be either repressed or active i.e. the repression signal is analogus to a digital signal. R_{FLC} are the fraction of cells that are in repressive state, which changes according to,

$$\frac{dR_{FLC}}{dt} = q\theta(VIN3(t) > K_{VIN3})(1 - R_{FLC}) - pR_{FLC} \tag{2.2}$$

The parameters p and q represent the rates at which repressive cells change to active state and the rate at which active cells change to repressed cells respectively. The changing these two rates while keeping all other parameters fixed produces different flowering strategies.

FLC transcript level per unit of leaf biomass is,

$$FLC(t) = r(1 - R_{FLC}(t)) \tag{2.3}$$

r represents maximum transcript level. Based on the transcript levels of FLC, the FT protein concentration per unit leaf biomass changes according to,

$$\frac{dFT}{dt} = \beta_{FT}\theta(FLC(t) < K_{FLC}) - \alpha_{FT} \tag{2.4}$$

where β_{FT} is the production rate and α_{FT} is the degradation rate of FT protein and K_{FLC} is the threshold for FT protein production. According to the model, plants start bolting when,

$$xFT > K_{FT} \tag{2.5}$$

x is the size of total leaf biomass and it changes according to,

$$\frac{dx}{dt} = h[1 - \theta(xFT > K_{FT})]\frac{ax}{1 + bx} - d_x x \tag{2.6}$$

where h represents the fraction of carbon gain used for vegetative growth and $\frac{ax}{1+bx}$ represents carbohydrates gained after subtracting the maintainance costs of plants. d_x is the natural loss of biomass due to natural disturbances. The amount of stored resources (S) changes as,

$$\frac{dS}{dt} = (1 - h[1 - \theta(xFT > K_{FT}])\frac{ax}{1 + bx} - C_f\theta(xFT > K_{FT}) - C_s y - d_s S \tag{2.7}$$

Here C_f indicates the rate of resource investment to produce flowers, C_s is the rate of resource investment to produce fruits and seeds while d_s is the resource investment for respiration. Three of these are subtracted from the main term that represents the resource increment by photosynthesis. Finally, the number of fertilized flowers changes according to

$$\frac{dy}{dt} = \frac{C_f\theta(xFT > K_{FT})}{u_f} - d_y y \tag{2.8}$$

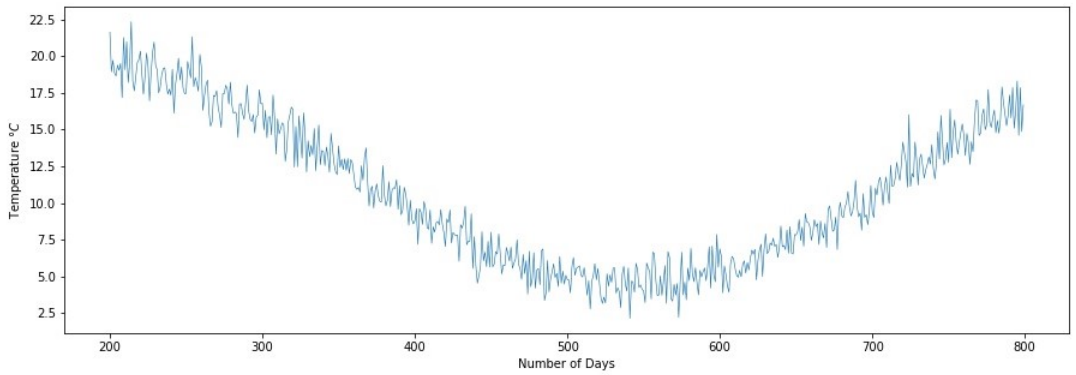
where u_f is the unit cost to produce a single flower. For more details on the model, refer to the original paper cited in the sources. It discusses the model at length. Another book chapter by Dr. A. Satake (in sources) is also an equally good read.

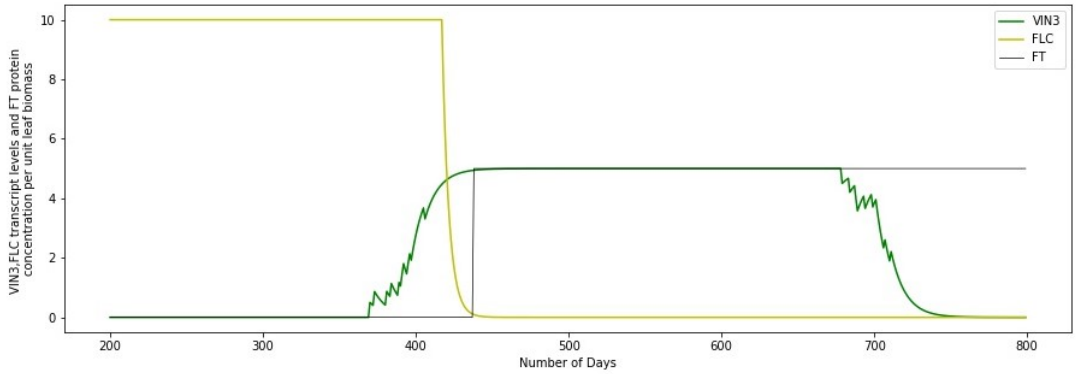
For my implementation, I changed the parameters to reflect the differences in the temperature signal dataset between this study and the original paper. The original parameters are in the cited paper and my parameters can be found in the jupyter notebook, alongside the implementation.

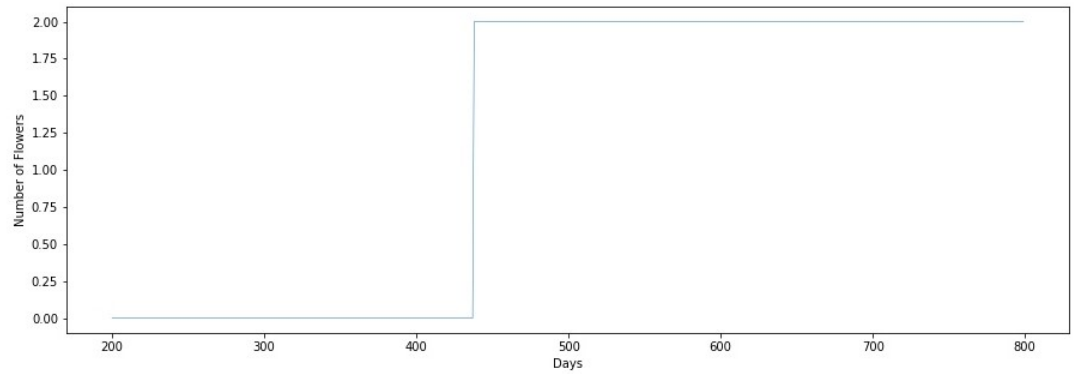
3 Results

My implementation of the model yeilded similar results to that of the original study. Here I present 4 different flowering stratregies produced by changing the values of parameters p (rate at which repressed cells change back to active state) and q (the rate at which active cells are repressed)

For $p = 0.0$ and $q = 0.2$, i.e. when cells once repressed, stay repressed; **Monocarpic** flowering strategy was observed. (For better representation, a subset of the original temperature data was taken, hence days do not start at 0). Here, plants retain the "winter memory", i.e. even after the temperature rises above the vernalization threshold (here, $K_T = 10°C$) and VIN3 transcript level drops to zero, FLC stays repressed.

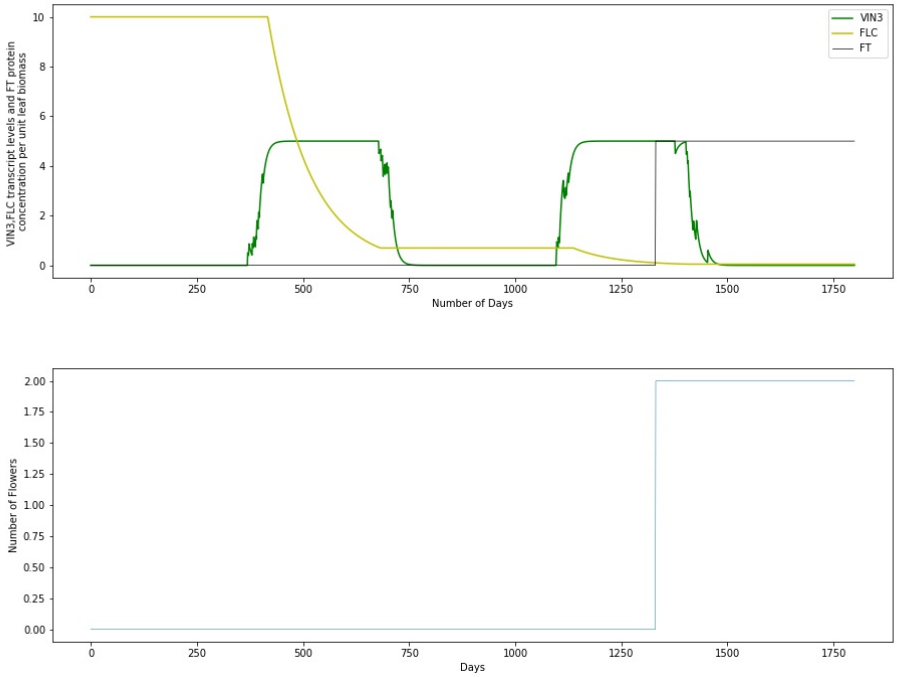




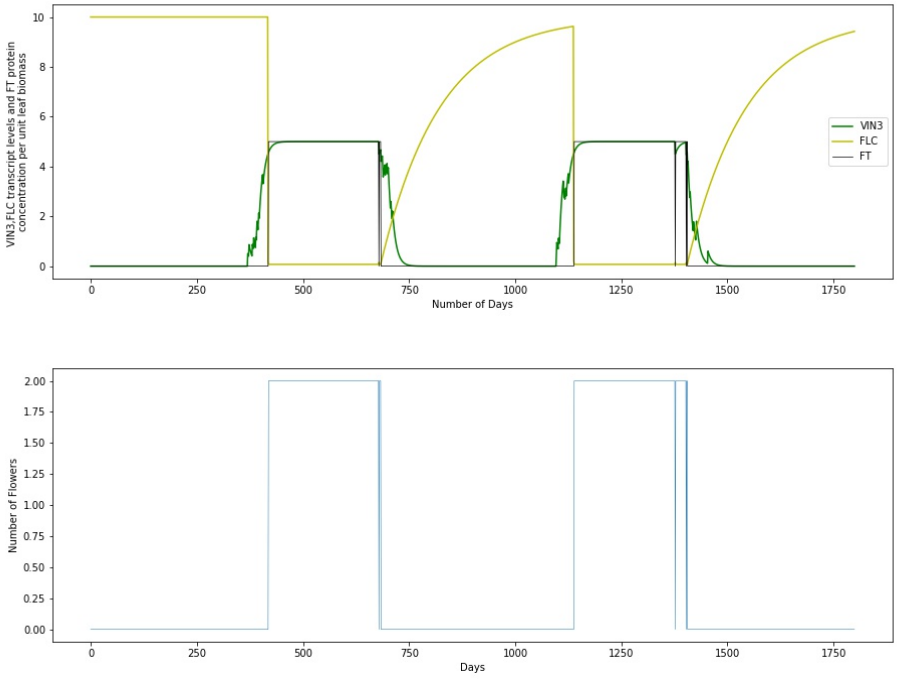


These monocarpic plants require only one winter to flower and thus can be classified as **Monocarpic annuals**, however, here the year in temperature dataset is from a planet where one year spans about 600 days.

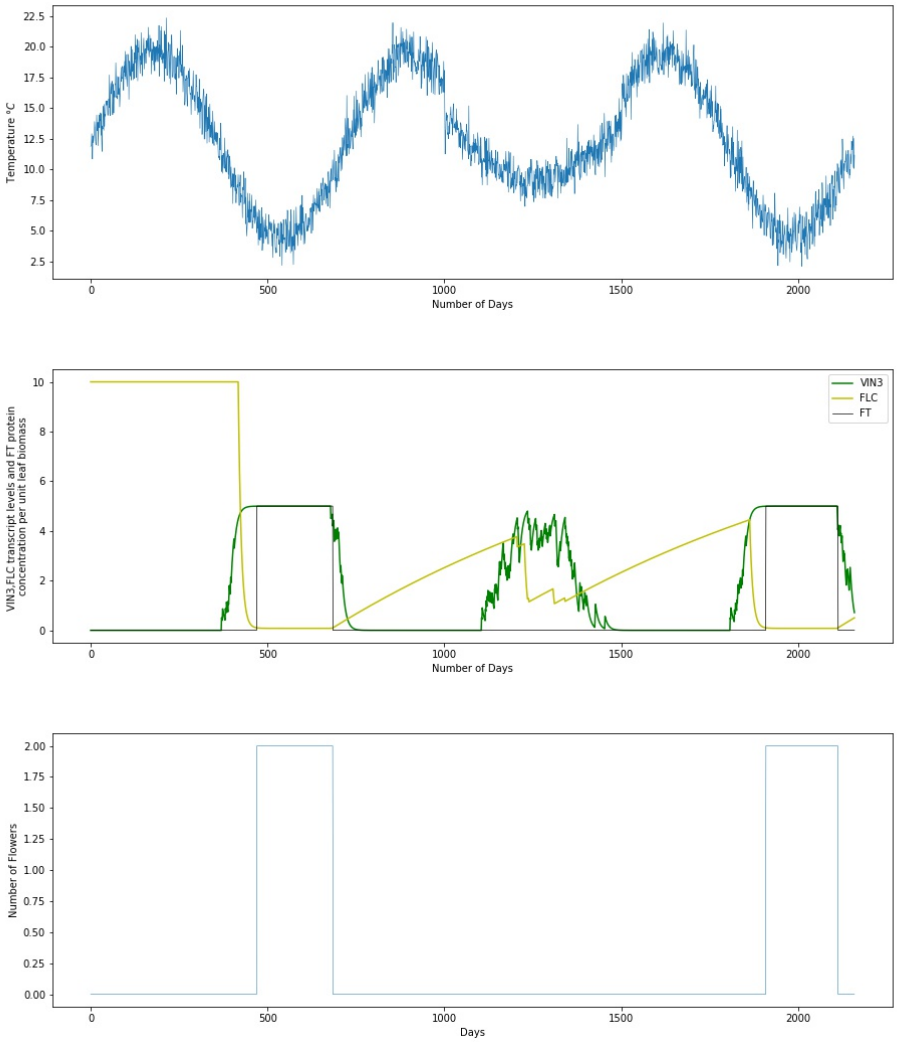
For $p = 0.0$ and $q = 0.01$, that is, when cells once repressed, stay repressed but the rate of repression is low. This results in **Monocarpic perennial** flowering. Here, plants require more than one winter to accumulate the reduction in FLC expression.



For $p = 0.0072$ and $q = 0.98$, that is the cells once repressed for FLC can become active after the winter, thus here the winter memory is not stable. This results in **Polycarpic yearly** flowering. Here, the activation rate of FLC activity is not negligibly small.



Finally, for $p = 0.00089$ and $q = 0.11$, i.e. when rate of repression of FLC activity is not high enough. In such a scenario, whenever a warm winter occurs, as shown in this toy temperature signal, FLC expression is not repressed enough for flowering. This type of flowering behaviour can be classified as **Polycarpic intermittent**.



4 Citations

The model implemented in this project is by Prof. Akiko Satake, 2010.

Satake A., Diversity of plant life cycles is generated by dynamic epigenetic regulation in response to vernalization, Journal of Theoretical Biology, 266 (2010) 595 - 605, https://doi.org/10.1016/j.jtbi.2010.07.019

Satake A. (2018) Flowering Time as a Model Trait to Bridge Proximate and Evolutionary Questions. In: Morris R. (eds) Mathematical Modelling in Plant Biology. Springer, Cham. https://doi.org/10.1007/978-3-319-99070-5_9