

Modelling as a tool for predicting and understanding phenology: A review

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Modeller's triangle



Levins (1966)

(1) Predicting: statistical approach

- Observational long-term phenological and climatic records
- Correlations between phenological timing and climatic indices
- Climatic indices for various preseason periods
 - T_{min}, T_{max}
 - Temperature sums (day degrees)
 - Precipitation
 - Sunshine hours
- No a priori theory of underlying causal mechanisms
 - Theories may be developed on the basis of the results
- Statistical approach
 - A multitude of statistical technigues (e.g. ridge regressions, machine learning)
 - Statistical skills needed

(2) Predicting and understanding: Process-based tree spring phenology modelling

Physiological processes addressed by explicit variables

Dynamic models with two categories of variables

- Rate of development, R(t)
- State of development, S(t)
- Classical example: temperature sum (thermal time)
 - Predicting spring phenology with the accumulation of day degrees

Phenological event predicted: Bud burst



Photos by Eeva Pudas

 $S_{DD}(t) = H_{crit}$ \rightarrow Predicted bud burst

Process simulated: Ontogenetic development ('bud growth')



Photos by Sirkka Sutinen

Ecophysiological explication of the day degree - model



$$R_o(T(t)) = 100 \frac{R_{dd}(T(t))}{H_{crit}}$$

Hänninen (2016)

Ecophysiological explication of the day degree - model



Explicit quantification of the predicted ontogenetic development until predicted bud burst

Bi-phase models of spring phenology: Two processes addressed

Ontogenetic development ('bud growth')

- Accumulation of forcing (e.g. day degrees)
- High temperature requirement
- Rest break = endodormancy release
 - Removal of growth-arresting physiological conditions in the bud
 - Accumulation of chilling
 - Chilling requirement
- (Effects of photoperiod: not in this presentation)

Chilling-forcing models: Two crucial research questions

I Model formulation: three phenomena

- Chilling (rest break)
- Forcing (ontogenetic development)
- Relationship between these two
- How are these three phenomena modelled?

II What kind of data is used for the modelling?

- Observational
- Experimental

Chilling-forcing models I: Model formulation

Formulation of the alternating model: *Picea sitchensis* in Britain



Cannell and Smith (1983)

Realism of the alternating model?



Cannell and Smith (1983)

Alternating model: Good accuracy - insufficient realism

OK tool for predictions (always?)

- There is no explicit variable for quantifying the ontogenetic development towards bud burst
- Timing of chilling vs. timing of forcing neglected

Nature does not work like this





An ecophysiologically explicit approach: The HK-framework

- Hänninen-Kramer framework
- Hänninen (1990, 1995, 2016)
- Kramer (1994a,b)
- Hänninen & Kramer (2007)
- Modular framework, three sub-models

The HK-framework

 $R_o(t) = C_o(t) \times R_{o,pot}(t)$



The two classic bi-phasic models in the HK-framework



A continuum of intermediate models in the HK-framework

Close to the sequential end

Close to the parallel end

Hänninen (1990, 2016)

Ongoing study with four subtropical tree species

Experimental determination of the three sub-models

- Zhang et al. (2022)

- Zhang et al. (in preparation)
- Leaf-out in seedlings
- Flowering of adult trees for one species
- Applying the models for scenario simulations
 - Zhang et al. (in preparation)
 - Hangzhou, south-eastern subtropical China
 - 2020 2100
 - RCP4.5, RCP8.5

Projected timing of spring phenology in four subtropical tree species in 2020 - 2100 in Hangzhou

Experimentally determined sub-models for subtropical tree species Sub-model I ('chilling')

Experimentally determined sub-models for subtropical tree species Sub-model II: 'forcing'

Vegetative buds of seedlings

- Castanopsis sclerophylla
- Phoebe chekiangensis
- Pseudolarix amabilis
- Torreya grandis

Flower buds of trees

···· Torreya grandis

Experimentally determined sub-models for subtropical tree species Sub-model III: ontogenetic competence

Understanding

Imply - explain

Confirmation: sensitivity analysis

'Usual suspect' of limited acceleration: High chilling requirement Not in this study

The HK-framework vs. the Unified Model (Chuine 2000)

Overall philosophy the same Chilling effects Forcing effects Relationship between these two

Details left to be determined by data 'Model', or 'Framework' ?

Unified Model mathematically more sophisticated One set of equations All differences covered by values of parameters Facilitates fitting the overall model to data

In the HK-framework each sub-model can be addressed separately

Facilitates experimental work and sensitivity analyses

Time

Chilling-forcing models II: Use of data

Developing process-based tree phenology models: (i) Observational approach

Inverse modelling

- Fitting the models into long-term observational phenological and air temperature records
- Big data readily available
- Efficient and 'economic' approach
- Main line approach currently

Pittfals revealed already in 1992

- Often unrecognized, or neglected

Journal of
Applied Ecology
1992, 29,
597-604Predicting the timing of budburst in temperate treesALISON F. HUNTER and MARTIN J. LECHOWICZ
Department of Biology, McGill University, 1205 Avenue Dr. Penfield, Montréal, Québec, Canada H3A 1B1

3. Analysis of artificial datasets, in which budburst dates were generated according to the biological assumptions of each conceptual model, reveals little connection between the ability to predict budburst with accuracy and the underlying biological response to temperature. This should be a general caveat to modellers; even biologically incorrect models can give reasonably good predictions of budburst phenology.

Trends in Plant Science (2019)

Opinion

Experiments Are Necessary in Process-Based Tree Phenology Modelling

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An additional example: A critique of Chen et al. (2017)

Agricultural and Forest Meteorology 234: 222 - 235.

Leaf unfolding and flowering of Melia azedarach in subtropical China

Observational data for 1981 - 2005 from 42 phenological stations

Fitting the Unified Model (Chuine 2000) Tabulated values of parameters reported No figures of the responses reported Some figures available in Supplementary material of Zhang et al. (2022). (Agricultural and Forest Meteorology 314: 108802)

Temperature (°C)

Chen et al. (2017) Zhang et al. (2022)

Critique of Chen et al. (2017)

Good accuracy in model fitting with observational big data

 Inconsistent and biologically unrealistic temperature responses

 Reliability of the projections obtained for climatic warming with the models?

Purpose of the critique of Chen et al. (2017)
To demonstrate the pitfalls of inverse modelling

Most studies applying inverse modelling

The response curves are not published

- Main interest in predicting, not in understanding
- For ecophysiology the curves are the most interesting results
- An exception
 - Luedeling et al. (2021) Agricultural and Forest Meteorology (2021): 108491
 - 30 °C a chilling temperature in an apple cultivar?
 - Probably not, explanation given by the authors:
 - 'In this location, winter temperatures are usually fairly low, rarely exceeding 10 °C'
 - This is the very reason why experimental studies are needed
 - Other reason: correlation of chilling accumulation and photoperiod in natural conditions

Developing process-based tree phenology models: (ii) Experimental approach

Several constant temperatures in growth chambers

Measuring the time required for

- Rest completion (Sub-model I)
- Bud burst of fully chilled seedlings (Sub-model II)

Rate of development = 100 / time required

- Unit: % day⁻¹, % hour⁻¹

Experimentally-determined sub-models for Torreya flower buds

Problems in the experimental approach

◆ Time-consuming and labour-intensive approach
◆ Unnatural conditions → reliability of the results?
- How about plant physiology?
◆ Tudependent tests in petural conditions needed

Independent tests in natural conditions needed

Early work of Sarvas (1972)

Temperature

Concluding remarks: Future of phenological modelling

Diversity of research needed in the future: (i) Inverse modelling with observational data

Quality control of the responses obtained
Zhang et al. (2022), Nature Climate Change 12: 193-199

Request: please report the response curves

- Transparency of the reporting

Uncertainty caused by the limitations of the approach

SEPPO RUOTSALAINEN & JUHANI HÄGGMAN (TOIM.)

hole-tree

Diversity of phenological modelling needed in the future

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