Modelling of the leaf appearance process or *phyllochron* with interval censored measurements

<u>Sandra Plancade</u>⁽¹⁾, Elodie Marchadier^(2,3), Sylvie Huet⁽¹⁾, Adrienne Ressayre⁽²⁾, Christine Dillmann^(2,3)

(1) Unité MaIAGE, INRA, (2) Génétique Quantitative et Évolution - Le Moulon INRA, Université Paris-Sud,

CNRS, AgroParisTech

5 december 2019

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1 Applied context : leaf appearance process or *phyllochron*

- 2 General modelling of phyllochron
- 3 First parametrisation : gaussian distribution
- 4 Work in progress : Semi-Markov models
- 5 Conclusion

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Applied context : leaf appearance process or *phyllochron* The ITEMAIZE project

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Plant growth and development

• Growth and development : synchronized processes



I. A. Ciampitti *et al*,

Kansas State University (2013)

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Plant growth and development

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- Modelling at various scales
 - Plot/field level
 - Plant level
 - Organ level
 - Cellular level
 - \hookrightarrow Stochastic % f(x) = 0 and deterministic model

Plant growth and development

• Growth and development : synchronized processes



I. A. Ciampitti *et al*,

Kansas State University (2013)

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- Modelling at various scales
 - Plot/field level
 - Plant level
 - Organ level
 - Cellular level
 - \hookrightarrow **Stochastic** and deterministic model
 - $\hookrightarrow \mathsf{Our} \mathsf{ model} : \mathbf{single \ phenotype}$

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Process of leaf appearance or phyllochron

• Phyllochron : times of leaf appearance on the plant/ interval of time between successive leaves



Process of leaf appearance or phyllochron

• Phyllochron : times of leaf appearance on the plant/ interval of time between successive leaves



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Applied context : leaf appearance process or *phyllochron* The ITEMAIZE project

- 2 General modelling of phyllochron
 - Classic approach : thermal time
 - Alternative : stochastic process
- 3 First parametrisation : gaussian distribution
 - Model and estimation
 - Applications
 - Strengths and weaknesses of the model
- 4 Work in progress : Semi-Markov models
 - Semi-Markov model with interval censoring
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• Divergent selection of early/late flowering plants



\Rightarrow hierarchical grouping



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• Idea : main driving factor of phyllochron is temperature

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- Idea : main driving factor of phyllochron is temperature
- TT = accumulation of temperature weighted by temperature efficiency
 - $\hookrightarrow \mathsf{time}\ \mathsf{rescaling}$

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- Idea : main driving factor of phyllochron is temperature
- TT = accumulation of temperature weighted by temperature efficiency
 - $\hookrightarrow \mathsf{time}\ \mathsf{rescaling}$
- Linear phyllochron : Leaf Number_p(t) = $\alpha_p TT_t + \varepsilon_{p,t}$
 - Inference of α_p by linear regression
 - F-test/mixed model on (α_p) to test genotype/environment effect
 - Linear asssumption : questionable

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- Linear asssumption : questionable
- More flexible models : $LN_p(t) = f(TT_t) + \varepsilon_{p,t}$, $\varepsilon_{p,t}$ i.i.d.
 - bi/tri-linear, splines
 - Descriptive analysis
 - Statistical analysis (confidence interval, tests)
 - $\hookrightarrow \mathsf{auto-correlation} \Rightarrow \mathsf{bias}$

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Independent waiting times model

Consider a given genotype and a given year.

LN_p(t)= nb of leaves



 Realistic biological assumption : (Y_{p,f})_{f=1,...,F} independent

 $\left\{ \begin{array}{ll} \{LN_{p}(t)\}_{t>0} & \text{number of leaves} \\ (Z_{p,f})_{f} & \text{Times of leaf appearance} \\ (Y_{p,f})_{f} & \text{Interval between leaves} \end{array} \right.$

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Independent waiting times model

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 ${LN_p(t)}_{t>0}$ number of leaves $(Z_{p,f})_f$ Times of leaf appearance $(Y, c)_f$ Interval but Interval between leaves

• Realistic biological assumption : $(Y_{p,f})_{f=1,\dots,F}$ independent

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$$Y_{p,f} = \mu_f + \varepsilon_{p,f}$$

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Independent waiting times model

Consider a given genotype and a given year.

LN_p(t)= nb of leaves



 $\begin{array}{ll} \{LN_{\rho}(t)\}_{t>0} & \text{number of leaves} \\ (Z_{\rho,f})_{f} & \text{Times of leaf appearance} \\ (Y_{\rho,f})_{f} & \text{Interval between leaves} \end{array}$

- Realistic biological assumption : $(Y_{p,f})_{f=1,...,F}$ independent
- Flexible modelling :

$$Y_{p,f} = \mu_f + \varepsilon_{p,f}$$

• More generally

$$Y_{p,f} \sim \mathcal{D}(heta_f)$$

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		12/39
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• Observations $(LN_{\rho}(t_{\rho,1}), \ldots, LN_{\rho}(t_{\rho,N_{\rho}}))$

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- Observations $(LN_p(t_{p,1}), \ldots, LN_p(t_{p,N_p}))$ $\Leftrightarrow Z_{p,f} \in (\nu_{p,f}, \tau_{p,f}], f = 1, \ldots, F_p$ with
 - ▶ v_{p,f} = last observation time before appearance of leaf f (or 0)
 - *τ_{p,f}* = first observation time after
 appearance of leaf *f* (or +∞)

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 appearance of leaf *f* (or +∞)
- Rk : Observations $\Leftrightarrow Y_{p,f} \in (\nu'_{p,f}, \tau'_{p,f}]$

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Issue : estimation of the model from discrete measurements/ interval censored observations

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Applied context : leaf appearance process or phyllochron

2 General modelling of phyllochron

First parametrisation : gaussian distribution

- Model and estimation
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- Strengths and weaknesses of the model

Work in progress : Semi-Markov models

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The model

Consider a given genotype and a given year, for each plant p

$$\mathbf{Y}_{p} = (Y_{p,f})_{f=1,\dots,F_{p}} \sim \mathcal{N}_{F_{p}}(\mu, D), \quad D = \operatorname{diag}(\sigma^{2})$$



- $Y_{p,f} = \mu_f + \varepsilon_{p,f}, \quad \varepsilon_{p,f} \sim \mathcal{N}(0, \sigma_f^2)$
- Normality assumption for computing reasons

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- $Y_{p,f} = \mu_f + \varepsilon_{p,f}, \quad \varepsilon_{p,f} \sim \mathcal{N}(0, \sigma_f^2)$
- Normality assumption for computing reasons
- $\Rightarrow \mbox{ Leaf appearance times } \textbf{Z}_{p} \sim \mathcal{N}(\overline{\mu}, \Sigma)) \mbox{ with } \Sigma \mbox{ not diagonal }$

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Monte Carlo EM algorithm

- Latent variables : $(\mathbf{Y}_p)_p \Leftrightarrow (\mathbf{Z}_p)_p$
- Observed variables : $((\nu_{p,f}, \tau_{p,f})_f)_p$
- $\Theta = (\mu, \sigma)$



MLE of a univariate gaussian distributions

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MLE of a univariate gaussian distributions

Sample from truncated multivariate distribution P[Z_p|Z_p ∈ [ν_p, τ_p)]
 → Basic rejection methods fail when dimension increases

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Monte Carlo EM algorithm

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- $\Theta = (\mu, \sigma)$



MLE of a univariate gaussian distributions

- Sample from truncated multivariate distribution $\mathbb{P}[Z_p|Z_p \in [\nu_p, \tau_p)]$ \hookrightarrow Basic rejection methods fail when dimension increases
- Various methods for gaussian distribution
 - \hookrightarrow Package truncatedNormal, Botev (2016)

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Applied context : leaf appearance process or *phyllochron* The ITEMAIZE project

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Implementation on ITEMAIZE data



- Test genotypic group effect
- Test assumption of *linear phyllochron* i.e. $\mu_f = constant$
- Imput of climatic variables

Genotypic group effects

Model comparison



- (mod1) $(\mu_f, \sigma_f)_{f=f^{\min},...,f^{\max}}$ depend on genotype
- ► (mod0) (μ_f, σ_f)_{f=f^{min},...,f^{max}} same for all genotypes in the selection group

- Criteria based on likelihood : AIC, χ^2 -likelihood ratio test
 - Almost all tests are significant (some strongly)
 - Permutation test on one comparison
 - \hookrightarrow Results reliable even slightly over-estimated

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Parametric submodels (Linear phyllochron?)

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Parametric submodels (Linear phyllochron?)

- Various parametric models for $f \mapsto \mu_f$:
 - constant
 - linear
 - piecewise constant
 - piecewise linear

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Parametric submodels (Linear phyllochron?)

- Various parametric models for $f \mapsto \mu_f$:
 - constant
 - linear
 - piecewise constant
 - piecewise linear
- Constant model (H0) vs each other model (H1) ($\chi^2\mbox{-likelihood ratio test}$ /AIC)



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Input of climatic variables

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- Regression of 7 climatic variable on μ : for each year and genotype
 - (1) Estimation of μ
 - (2) Regression of climatic variables on μ + variable selection

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 - \hookrightarrow No account for error of the estimate of μ

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 - (1) Estimation of μ
 - (2) Regression of climatic variables on μ + variable selection
 - \hookrightarrow No account for error of the estimate of μ
- Results : in progress

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Strengths of the model

Less biased modelling

Classic approach Leaf number :

$$LN(t) = f(TT_t) + \varepsilon_t$$

with $(\varepsilon_t)_t$ independent

 \hookrightarrow No account for auto-correlation

- More flexible modelling
- Allows to
 - Test conditions/genotypic effects
 - Select parametric models for μ
 - Evaluate climate effect

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Our model

Interval between successive leaves

 $Y_f \sim \mathcal{D}(\theta_f)$

with $(Y_f)_f$ independent. \hookrightarrow Independence : realistic

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- Large number of parameters
 - Price to pay for flexible model
 - Option : equal variance parameters within line

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- Large number of parameters
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- Model comparison via likelihood : less flexible than mixed models

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- Large number of parameters
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- Model comparison via likelihood : less flexible than mixed models
- \bullet Plant level variation : gaussian distribution for a time-to-event $_{\sigma_{f}/\mu_{f}}$



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- Longitudinal covariates
 - Regression on the phyllochron parameters μ
 - \neq include longitudinale covariate in the model

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• Semi Markov property : State and sojourn duration depends only on previous state and sojourn duration

$$\mathbb{P}[S_{[t+1:t+d]} = i | (S_{t'})_{t' \le t}] = \mathbb{P}[S_{[t+1:t+d]} = i | S_{[t-d'+1:t]} = j] := a_{(i,d)(j,d')}$$

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• Unidirectional SMM = transition only from i to i + 1

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 $\bullet\,$ Phyllochron : sojourn time independent of time in previous state :

$$a_{(i,d)(j,d')} = \mathbbm{1}_{i=j+1}f_i(d) \quad ext{with} \quad f_i(d) = \mathbb{P}[Y_i = d].$$

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 \hookrightarrow If f_i geometric : Poisson point process

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Hidden SMM

• $(S_t)_{t=1,...,T_{max}}$ unobserved SMM



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Hidden SMM

• $(S_t)_{t=1,...,T_{max}}$ unobserved SMM • $(O_t)_{t=1,...,T_{max}}$ observed process with

$$\mathbb{P}[O_t = x | (S_{t'})_{t'}, (O_{t'})_{t' \neq t}]$$

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$$\hookrightarrow b_j(\cdot) =$$
emission proba in state j .



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SMM with interval censoring : analogy with $\ensuremath{\mathsf{HSMM}}$

• Interval censoring :

$$\begin{cases} (S_t)_{t=1,dots,T_{\max}} \\ (t_1,\ldots,t_N) \\ (t_i,S_{t_i})_{i=1,\ldots,N} \end{cases}$$

SMM monitoring times Observations



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Interval censoring :

 $\begin{cases} (S_t)_{t=1,dots,T_{\max}} \\ (t_1,\ldots,t_N) \\ (t_i,S_{t_i})_{i=1,\ldots,N} \end{cases}$

- SMM monitoring times Observations
- $(O_t)_t$ observed process (determ. given $(S_t)_t$)

$$O_t = \begin{cases} S_t & \text{if } t \in \{t_1, \dots, t_N\} \\ 0 & \text{otherwise} \end{cases}$$



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Interval censoring :

 $\begin{cases} (S_t)_{t=1,dots,T_{max}} & \text{SMM} \\ (t_1,\ldots,t_N) & \text{monit} \\ (t_i,S_{t_i})_{i=1,\ldots,N} & \text{Observed} \end{cases}$

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• Algorithm forward/backward : very similar to HSMM

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Applied context : leaf appearance process or *phyllochron* The ITEMAIZE project

- 2 General modelling of phyllochron
 - Classic approach : thermal time
 - Alternative : stochastic process
- 3 First parametrisation : gaussian distribution
 - Model and estimation
 - Applications
 - Strengths and weaknesses of the model
- Work in progress : Semi-Markov models
 - Semi-Markov model with interval censoring
 - Application to phyllochron
 - Perspectives

Conclusion

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Application to phyllochron : flexible distribution

- Support $[\![1,D]\!]$
- Beta-binomiale with offset : $\kappa + \mathcal{BB}(\text{size} = n, \text{prob} = \pi, \rho)$, $n + \kappa \leq D$



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Ex : results for group F-late



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Ex : results for group F-late



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Longitudinal covariate in unidir. SMM w. interval censoring

Longitudinal covariate in unidirectional SMM with interval censoring

• **X** = (X_t)_{t=1:T_{max}} longitudinal covariate observed at all times



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Exple. Discrete time Cox model

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Applied context : leaf appearance process or *phyllochron* The ITEMAIZE project

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Work in progress : Semi-Markov models

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Conclusion

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- Improve numerical implementation (general SMM w. interval censoring)
 - $\hookrightarrow \mathsf{Issues \ similar \ to} \ \mathsf{HSMM}$
- Penalized likelihood
 - Flexible distribution (splines, etc)
 - Several longitudinal covariates
- Multi-chain SMM
 - $\hookrightarrow \mathsf{Application}:\mathsf{floral}\;\mathsf{transition}$

Applied context : leaf appearance process or phyllochron

- 2 General modelling of phyllochron
- 3 First parametrisation : gaussian distribution
- 4 Work in progress : Semi-Markov models
- **5** Conclusion

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Phyllochron modelling

- Flexible average phyllochron
 - $\hookrightarrow \mathsf{Enlighten} \ \mathsf{temporal} \ \mathsf{trends}$
- Downstream analysis : less tractable than classic linear phyllochron
- Stochastic process vs regression models
 - Other fields e.g. plant pathogens (Nemis et al 2013)

Semi-Markov model with interval censoring

- More flexible framework for phyllochron
 - Any parametric distribution
 - Longitudinal covariate (unidirectional SMM)
- General interest
 - ► SMM with interval censoring : almost not adressed in literature
 - Application in various fields (disease progression...)
- Algorithm analogous to Hidden SMM
 - Adapt methods for HSMM to interval censored SMM

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