A model framework for tree leaf colouring in Europe

Cecilia Olsson*, Anna Maria Jönsson

Department of Physical Geography and Ecosystem Science, Lund University, SE-223 62 Lund

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ABSTRACT

Ecosystem productivity is influenced by the start and end of the growing season, and ecosystem models that simulate productivity need reliable representations of the phenology. For the seasonal development, autumn events are less understood than spring events, with comparatively fewer modelling attempts have been made for leaf senescence than for budburst. The few existing models for autumn phenology represent the influence of temperature and photoperiod. In this study, the aim was to evaluate which type of temperature response, photoperiod requirement and interaction between temperature and photoperiod captured the variation in leaf colouring more accurately. We tested existing models on a large dataset and developed new models by combining seven model components: linear or sigmoid temperature response above or below a base temperature, with or without modification by photoperiod, and photoperiod requirements (starting day of temperature response). Potential photoperiod requirement for leaf senescence induction was assessed by using a calibrated starting day or day of budburst that instead of a requirement represent the start of the ageing processes. Day of leaf colouring was simulated using 37 models for birch, beech and oak in Austria, Germany and the United Kingdom, in total 111 model runs that was compared to average day of leaf colouring. In 109 out of 111 simulations, average day of leaf colouring provided a better estimate. Some of the better performing models resembled average day of leaf colouring by counting number of days. Overall, the results indicate that the models estimated response to temperature and photoperiod do not support the use of a fixed degree-day requirement, especially across large regions. No photoperiod requirement could be inferred, and photoperiod in combination with temperature response provided little or no improvement on model performance.

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1. Introduction

Warmer temperatures extend the growing season of many plants (Chmielewski and Rötzer, 2001; Menzel et al., 2008). The timing of growth cessation and leaf senescence express a trade-off between early senescence that allow full remobilisation of nutrients that are stored and used for growth the following spring, and the seasonal carbon gain that is likely reduced with a shorter photosynthetic active period (Larcher, 2003). The response to environmental cues in trees are however not fully understood, less so for the induction and development of autumn events than for spring events (Delpierre et al., 2009; Estrella and Menzel, 2006; Smart, 1994). The response differ among and within provenances and vary with tree age, time of the year and the stage of leaf senescence considered (Archetti et al., 2013; Estrella and Menzel, 2006). Epistemic uncertainty that arise from our incomplete understanding of the processes influence the simulation accuracy. For instance, the

uncertainty in simulated daily and annual net ecosystem exchange related to temperature sum requirements, was about five times higher for leaf fall than for budburst in a beech forest in eastern France (Dufrêne et al., 2005). This exemplifies a need for more reliable phenology representations in ecosystem models that simulate productivity and plant-atmosphere interactions (Aber et al., 1995; Jeong et al., 2012; Migliavacca et al., 2012; Richardson et al., 2012; White et al., 1999).

Leaf senescence is considered to be primarily induced by low temperatures and short days (e.g. Fracheboud et al., 2009; Körner and Basler, 2010), but can also be induced by stress factors since many of the hormones involved in leaf senescence are also activated by stressors such as drought, early autumn frost or herbivory (Lim et al., 2007). The interaction between temperature and photoperiod varies, and potentially, trees may only respond to photoperiod within a certain temperature range, and low temperatures may promote leaf senescence irrespective of photoperiod (Heide and Prestrud, 2005; Vegis, 1964; White et al., 1999). In general, later leaf colouring is associated with warmer autumn months (Archetti et al., 2013; Cufar et al., 2012; Estrella and Menzel, 2006; Menzel, 2003; Menzel et al., 2008), but the association to warmer spring and

Table 1

Summary of the phenological data used in this study for all (All) and each country separately (Austria, Germany and the United Kingdom), with total number of sites (S, count), observations for each phenological phase (O, count) and mean values (and standard deviations) across sites for: observations per site (O/S, count), day of budburst (DBB, doy), day of 50% leaf colouring (DLC, doy), mean temperature July to September (MT, °C), mean days per year with temperature below 0 °C between budburst and leaf colouring (≤ 0 °C, count), mean first frost day of year after summer solstice ($\leq$ -2 °C, doy). Negative trends (Trend, days year^{-1}) in timing of phenological events indicate that they on average occurred earlier.

Species	Country	S	O	S/O	DBB	Trend DBB		DLC	Trend DLC		MT	≤ 0 °C	$\leq$ -2 °C
Birch	All	2055	66455	32 ± 16	110 ± 7	−0.21	***	281 ± 10	0.07	***			
	Austria	142	1333	9 ± 5	109 ± 10	−0.06	ns	274 ± 12	0.01	ns	16.64 ± 1.84	0.01 ± 0.19	326 ± 19
	Germany	1594	63972	40 ± 8	111 ± 6	−0.21	***	279 ± 7	0.06	**	16.03 ± 1.35	0.01 ± 0.23	335 ± 15
	United Kingdom	319	1150	4 ± 1	103 ± 8	−1.14	***	294 ± 11	0.68	*	15.93 ± 1.10	0.01 ± 0.13	350 ± 13
Beech	All	1886	54464	29 ± 17	118 ± 7	−0.14	**	284 ± 10	0.08	***			
	Austria	369	4809	13 ± 10	117 ± 9	0.01	ns	278 ± 10	−0.06	***	16.34 ± 1.61	0.02 ± 0.26	329 ± 17
	Germany	1217	48566	40 ± 8	119 ± 5	−0.17	***	282 ± 7	0.05	***	15.98 ± 1.36	0.02 ± 0.25	335 ± 15
	United Kingdom	300	1089	4 ± 1	114 ± 8	−0.61	***	298 ± 10	0.22	ns	15.83 ± 1.14	0.01 ± 0.12	350 ± 13
Oak	All	1603	51841	32 ± 16	124 ± 8	−0.23	***	291 ± 10	0.11	***			
	Austria	112	1001	9 ± 5	121 ± 10	−0.17	**	285 ± 11	0.03	ns	16.85 ± 1.76	0.12 ± 0.74	328 ± 18
	Germany	1251	49978	40 ± 8	125 ± 7	−0.22	***	288 ± 7	0.09	***	16.08 ± 1.32	0.05 ± 0.40	336 ± 15
	United Kingdom	240	862	4 ± 1	115 ± 9	−0.73	***	308 ± 10	1.28	***	16.13 ± 0.98	0.03 ± 0.21	350 ± 13

Significance; ns (p > 0.05), * (p $\leq$ 0.05), ** (p $\leq$ 0.01), *** (p $\leq$ 0.001)

early summer months vary among species and locations (Archetti et al., 2013; Estrella and Menzel, 2006). Simulations of leaf colouring based on statistical correlations with e.g. temperature are not reliable for spatial and temporal extrapolation and more mechanistic models are needed to capture the variation in phenology. However, as the statistical association can be strong and the mechanistic understanding incomplete, simple models may, despite lacking the appropriate causal effects, capture the phenology better than more complex models that are considered more biological realistic (Hunter and Lechowicz, 1992), especially for spatial simulations when provenance-specific requirements are not known. To date, only a handful of mechanistic models have been developed for autumn phenology. Most of them include the effect of temperature sums and photoperiod of the preceding months, with the estimated daily temperature response assumed linear and increasing with temperatures lower than a base temperature (cold degree-days, CDD) (Dufrêne et al., 2005; Jeong and Medvigy, 2014; Richardson et al., 2006), and enhanced by photoperiod (Delpierre et al., 2009). Sometimes, the opposite temperature response is used, thus, a stronger temperature response with higher temperatures (growing degree-days, GDD), as in the ecosystem model ForSAFE (Aber et al., 1995; Wallman et al., 2005). CDD and GDD assume that colder and warmer days, respectively, advance leaf senescence, which emphasise the uncertainty in the underlying processes of leaf senescence.

The main objective of the present study was to evaluate and discuss different model components for simulating timing when 50% of the leaves of a tree have shifted to autumn colours, for birch, beech and oak in Austria, Germany and the United Kingdom. Simulations by existing models (e.g. DM by Delpierre et al., 2009 and GSI by Jolly et al., 2005), and newly developed models were compared in an attempt to identify model concepts that capture spatial and temporal variation in leaf colouring across the study region. Specifically, we evaluated the effect of using different temperature response (linear or sigmoid), for temperatures above or below a temperature threshold (GDD or CDD), photoperiod requirement (starting day of temperature response) and interaction between temperature and photoperiod. Potential requirements in photoperiod were evaluated both by defining the starting day of degree-day accumulation at each site, and by start of the growing season (approximated by day of budburst). Model simulations were discussed in relation to the underlying theory and biological relevance. To our knowledge, this is the first study where autumn phenology models have been extensively tested using data from more than 1500 sites and with time-series up to 60 years.

2. Material and methods

2.1. Phenology and climate data

The phenological data comprised of observations of budburst and leaf colouring, defined as leaf unfolding on the first visible leaf stalk (BBCH 11) and the day of year (doy) when 50% of the leaves have shifted to autumn colours (BBCH 94), respectively (PEP725 Pan European Phenology Data, data set accessed 2013-06-13 at http://www.zamg.ac.at/pep725/). We included observations of birch (*Betula pendula*), beech (*Fagus sylvatica*) and oak (*Quercus robur*) between 1950 and 2012 in Germany, Austria and the United Kingdom to capture gradients in latitude, altitude and continentality. Records were excluded if budburst or leaf colouring were not observed the same year, and if considered too early or too late (indicating error in data input): budburst <60 or >180 doy and leaf colouring <180 doy. The German dataset is very extensive and to make simulations computationally feasible, only sites with more than 30 years of observations were selected from Germany, while all sites with more than three years of observations were selected from Austria and the United Kingdom (Table 1). The data sets of budburst and leaf colouring followed a Gaussian distribution, with a combined 0.02%, 0.05% and 0.01% of the years classified as outliers (Grubbs' test with α=0.05, Grubbs, 1969) for birch, beech and oak, respectively. These outliers were not specific for a country, site or year, and no site-year had both observations of budburst and leaf colouring classified as outliers. No observation exceeded the 30-day rule from the site-average, which would have indicated a likely protocol error (Schaber and Badeck, 2002). PEP725 data are volunteer based and does not include information of local conditions, provenance and tree age. Since it is difficult to determine the cause of deviation without knowledge of site-specific micro climate and the original observation reports, we considered these observations to be accurate.

Model calculations were based on gridded observed daily mean and minimum air temperature (E-OBS, Version 10.0), with a spatial resolution of 0.22° (Haylock et al., 2008). Trees respond to local temperature while the E-OBS grid-cells represent a spatial average of about 25 × 25 km of temperature and elevation. To better capture site-specific temperature conditions, the gridded temperature were adjusted based on the elevation difference between the site and the grid-cell using a temperature lapse rate of 6.4 °C/km. The adjustment could not be carried out for sites in the United Kingdom due to missing information about the sites elevation, but this did not affect the model comparison. Photoperiod was calculated as a function of latitude of the sites and day of the year using