

Chilling and forcing requirements for foliage bud burst of European beech (*Fagus sylvatica* L.) differ between provenances and are phenotypically plastic

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ABSTRACT

The timing of foliar budburst is an important component of the fitness of trees. Adaptation of budburst to local temperatures and phenotypic plasticity in the date of budburst to changes in temperature can therefore be expected. In this study, we analysed provenance trials of European beech (*Fagus sylvatica* L.) established over a wide geographic and climatic range in Europe. The analysis was based on a phenological model that represents the key processes at budburst phenology of temperate- and boreal zone deciduous trees. We conclude that adaptive differences exist between provenances in the critical chilling- and forcing requirements triggering budburst. Moreover, it is likely that these provenances show a plastic response to local environmental conditions for these two factors. Chilling- and forcing temperature requirements are key traits determining a tree's response of the date of foliar budburst to temperature. We infer from our results that trees would be able to adjust this response when climatic conditions change. Implications for climate change assessment studies and suggestions to incorporate this second order phenotypic plasticity in phenological models are discussed.

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1. Introduction

Budburst of foliage of trees mark the transition from a dormant phase, resistant to adverse environmental conditions such as frost, to an active one which is vulnerable to adverse conditions (Levitt, 1969, 1972; Woolhouse, 1969). Budburst is thereby an important component of plant fitness: too early may lead to frost damage (Parker, 1963; Sakai and Larcher, 1987; Weiser, 1970) too

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late may result in an incomplete utilisation of the growing season and thereby a lower competitive ability relative to species that do take full advantage of the period with favourable conditions for growth (Lechowicz, 1984; Lockhart, 1983). Adaptation of budburst to local environmental conditions can thus be expected (Hänninen et al., 1990; Koski, 1985). A large body of literature indicates that the phenology of trees in the temperate and boreal zone is such that chilling temperatures are required to break rest, a period during which buds remain dormant due to growth-arresting physiological conditions in the bud itself, despite favourable conditions for growth. This rest period is then followed by quiescence, a period during which buds remain dormant due to unfavourable environmental conditions. Photoperiod may interact with the temperature response of budburst, e.g. by compensation for a lack of chilling, though important differences exist between species (Downs and Borthwick, 1956; Hughes et al., 1984; Nitsch, 1957; Salisbury, 1981; Vaartaja, 1959; Wareing, 1956; Yan and Wallace, 1996). See Doorenbos (1953), Perry (1971), Romberger (1963), Samish (1954), Vegis (1964, 1973) and Wareing (1969) for excellent reviews covering decades of research on dormancy of woody plants.

Since the landmark papers by Bradshaw (1965, 1973), phenotypic plasticity of a trait is seen as an adaptive trait in itself that is heritable and has its own specific genetic control (Scheiner, 1993; Schlichting and Pigliucci, 1993). Phenotypic plasticity is expressed as a so-called reaction norm, describing either the differential performance of a genotype in different environments (Sultan, 1992; Via, 1992), or the differential performance of a population (Richards et al., 2006; Valladares et al., 2006), i.e. a provenance in forestry terminology (Wuehlisch et al., 1995). The latter definition is used in this study. The adaptive significance of phenotypic plasticity is generally assumed that it increases mean fitness across heterogeneous environments (Alpert and Simms, 2002; Schlichting, 1986; Via, 1993), though evidently not all plant responses to environmental changes can be considered heritably adaptive (Wright and McConnaughay, 2002). As phenotypic plasticity appears to counteract genetic differentiation, i.e. specialisation, by natural selection, the conditions under which adaptive phenotypic plasticity evolves is much debated (de Jong, 1995, 1999; Lortie and Aarssen, 1996; Pigliucci, 1993; Schlichting, 1986; Via, 1992; Via et al., 1995). In the context of phenology, phenotypic plasticity is often described as the response of the timing of a phenological event to environmental drivers, e.g. leaf unfolding or leaf fall to temperature or photoperiod (Duputie et al., 2015; Kramer, 1995b; Vitasse et al., 2010). As it is increasingly clear that phenology has a strong impact on ecosystem functioning (Kramer et al., 2000; Leinonen and Kramer, 2002; Noormets, 2009; Schwartz, 2013) and that climate change has a strong impact on phenology (Menzel, 2000; Menzel and Fabian, 1999; Schwartz, 1994), models have been developed that describe such phenological responses and applied to assess climate change impacts on the distribution of trees and functioning of forest ecosystems (Chuine et al., 1999; Chuine, 2000; Hänninen, 1990; Kramer, 1994; Murray et al., 1994). See Hänninen and Kramer (2007); Kramer and Hänninen (2009) and Chuine et al. (2013) for reviews on plant development models and their application in climate change studies.

More recently, concerns are expressed that a mismatch in phenology may occur with a future climate and that rates of adaptation are too slow relative to the rate of climate change (Aitken et al., 2008; Kramer et al., 2010; Rice and Emery, 2003) and phenotypic plasticity is insufficient to adjust to climate change (Duputie et al., 2015). To assess the importance of local adaptation and phenotypic plasticity of phenology to a local environment, we analysed a large dataset of provenance trials on European beech (*Fagus sylvatica* L.) (Muhs and von Wuehlisch, 1993). Though provenance trials have been designed to answer practical forestry questions considering the selection of the most suitable provenances for a particular

site, they happen to provide unique insight in the response of genetically different trees to strong changes in their environment, thereby mimicking climate change (Mátyás, 1996; Mátyás, 2010; Savolainen et al., 2007).

In the analyses of this data set we tested two hypotheses. First, that the critical chilling- and forcing requirements for foliar budburst of trees are adapted to local climatic conditions, thereby differing among provenances. Second, that these critical chilling- and forcing requirements themselves are phenotypically plastic, i.e. varying among trial sites for the same provenances. Were these hypotheses not rejected, we could infer that when trees of the same provenance trees were subjected to different local climates, they would be able to attain different values for these critical temperature thresholds. As these parameters determine the phenotypic plastic response of bud burst to temperature, phenotypic plasticity in these parameters indicates plasticity in temperature response of the date of budburst, e.g. due to the changed climatic conditions. The implications are that process-based plant distribution models, which typically assume a single parametrisation to simulate phenology across the entire range of a species, not only need to take local adaptation into account but also phenotypic plasticity in the response of budburst to temperature.

2. Materials and methods

2.1. Phenological data

Since the mid-eighties five series of provenance trials of European beech (*Fagus sylvatica*) were established throughout Europe of which four series could be used for this study (Table 1). The objectives for the establishment of these trial series were to select suitable plant material for tree improvement, to conserve genetic diversity, but not to assess climate change impacts (Wuehlisch et al., 1998). The lay-out of the trials was randomised incomplete (series 1984/'87 and 1985/'88, Table 1), or complete (1993/'95 and 1996/'98, Table 1) block design with three replications. Planting was done in rows with a space of 2 m x 0.5 m (series 1984/'87 and 1985/'88) or 2 m x 1 m (series 1993/'95 and 1996/'98). Each plot was laid out with 100 plants (series 1984/'87 and 1985/'88) or 50 plants (series 1993/'95 and 1996/'98), resulting in a plot size of 10 m x 10 m. The plots are considered large enough to maintain the trials for 60 years. Usually two rows were planted around the trials to avoid edge effects. Some provenances were represented in two or more series for which beech nuts were harvested several times, as beech nuts cannot be stored for several years. Each harvest obtained a so-called 'seed book number'. The observations of different seed-book numbers but for the same provenance were pooled in the analyses. A large number of plant traits were recorded including the budburst score, which is analysed in this study. The phenological data collected was the number of trees per provenance in a particular phenological stage at a date on which the site was visited.

Different scoring scales were used at different locations and periods of time. For the analysis of the data, it was necessary to harmonize the data to obtain a uniform scoring scale and to arrive at a single scoring stage within the selected scale. To obtain a uniform scoring scale, the scores of the 5, 6 and 7-step scales were aggregated towards the 3-step scale (Table 2). Subsequently, all data with score 1 and 3 were converted into score 2 of the 3-step scale to use all the data. This rescaling was done by adding a number of days to stage 1 and subtracting a number of days from stage 3, based on the average difference in these stages (see Appendix A). This modification was not possible for all provenances and sites, so that sites visited only once per year could not be used in the present study (Fig. 1).

Table 1
Overview of all data collected at the provenance trials of European beech. Of the full data set of 1763 observations on 291 provenances at 27 sites, we could use 1402 observations on 240 provenances at 21 sites in our analyses.

Year of seeding/year of planting	Start year of observation	End year of observation	#Observation sites	#Provenances	#Observations
1984/'87	1989	1993	5	51	168
1985/'88	1989	1993	7	79	219
1993/'95	1997	2008	24	161	827
1996/'98	1999	2008	25	84	549

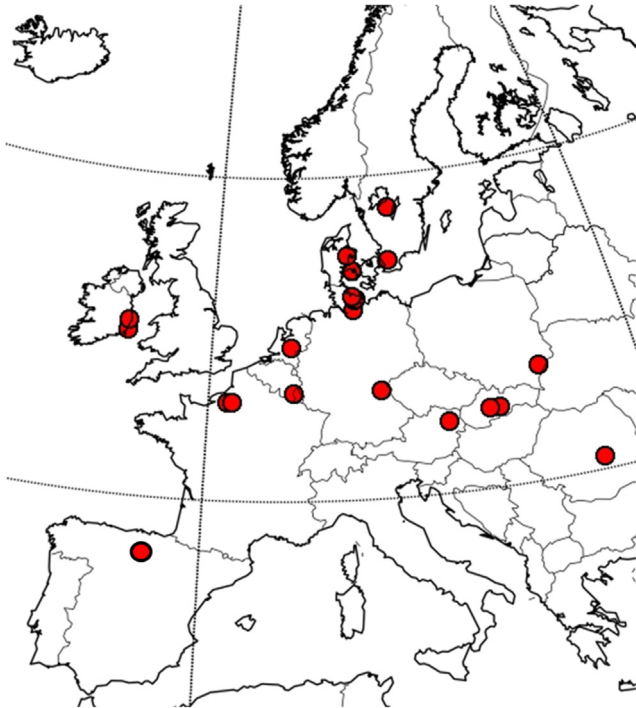


Fig. 1. Location of the European beech (*Fagus sylvatica*) provenance trial sites in Europe that were used in this study. Due to repeated plantings at the same location not all trials are visible.

2.2. Temperature data

The temperature data for the beech provenance trials analysis were collected from the website of the European Climate Assessment & Dataset project (ECA&D) (<http://www.ecad.eu/>). The meteorological stations used for the provenance trials analysis are presented in Table 3 together with the corresponding horizontal and height differences to the provenance trials. See Appendix B for technical information on selecting the meteorological stations and processing the data.

2.3. Model description

In an earlier study, the sequential model was selected as the best model to predict the onset of growth of *Fagus sylvatica* based on a long time series of budburst data in the Netherlands and Germany

(Kramer, 1994). In that study, the sequential model was compared with the alternating, parallel and 4-phase model (Hänninen, 1990; Kramer, 1994). Chuine et al. (1999) and Chuine (2000) later generalised the sequential model in the unified model such that different sub-models emerge as a consequence of a particular choice of parameter values rather than as different equations (Chuine et al., 1999; Chuine, 2000). Here we fitted both the sequential model as developed by Hänninen and Kramer, and the unified model as developed by Chuine.

In the sequential model the duration of dormancy, and thereby the date of budburst marking the end of dormancy, is simulated as a two stage process: a period of rest followed by a period of quiescence. The ontogenetic development during rest is tracked by the state of chilling, S_c , and the quiescence period with the state of forcing, S_f . The rest phase ends if S_c attains a critical value ($t_1: S_c = S_c^*$). Similarly, quiescence ends if S_f attains a critical value ($t_2: S_f = S_f^*$), at which point the budburst is predicted to occur. The onset of accumulating chilling, t_0 , i.e. the end of the growing season, is set at an arbitrary date (November 1st). The equations determining the state of development of S_c and S_f as functions of ambient temperature, T , are:

$$S_c(T) = \sum_{t_0}^{t_1} R_c(T) \quad (1)$$

$$S_f(T) = \sum_{t_1}^{t_2} R_f(T) \quad (2)$$

With the rate of chilling (R_c) and the rate of forcing (R_f) formulated as follows:

$$R_c(T) = \begin{cases} 0, & T < T_{c,min} \\ \frac{T - T_{c,min}}{T_{c,opt} - T_{c,min}}, & T_{c,min} \leq T \leq T_{c,opt} \\ \frac{T - T_{c,max}}{T_{c,opt} - T_{c,max}}, & T_{c,opt} \leq T \leq T_{c,max} \\ 0, & T > T_{c,max} \end{cases} \quad (3)$$

$$R_f(T) = \begin{cases} 0, & T < T_{f,min} \\ \frac{1}{1 + e^{a_f(T+b_f)}}, & T > T_{f,min} \end{cases} \quad (4)$$

Table 2
Phenological stages and how these are aggregated to arrive at a 3-step scoring scale.

3-step	5-step	6-step	7-step
1 = late flushing	1 = dormant winter bud	1 = dormant winter bud	1 = dormant winter bud
	2 = buds expanding	2 = buds swollen	2 = buds swollen
2 = intermediate	3 = bud-burst (first green is visible)	3 = first green is visible	3 = first green is visible
	4 = leaves are flushing	4 = leaves begin to appear, individually visible folded	4 = leaves begin to appear
			5 = individually visible folded
3 = early flushing	5 = leaves are fully expanded	5 = leaves unfolded, fan-shaped	6 = leaves unfolded, fan-shaped
		6 = leaves unfolded, bright	7 = leaves unfolded, bright

Table 3

Meteorological stations providing the daily temperature used for the provenance trial sites, and phenological data used from the trial sites. The temperatures are the long term annual average minimum, average and maximum temperature (°C).

Meteorological station	Country	T _{min}	T _{avg}	T _{max}	Provenance trial site		Horizontal distance (km)	Elevational distance (m)	# Provenances	# Phenological Observations
					site code	site name				
Beauvais-Tille	France	8.8	10.2	11.6	Bu11	Vascoeul/FR	64	86	58	116
Kiel-Holtenau	Germany	−2.3	2.6	7.4	Bu17	Bosau 2/DE	34	−2	68	108
Hamburg Fuhlsbüttel	Germany	6.0	9.5	13	Bu18BSV	Grosshansdorf/DE	18	56	159	224
Kiel-Holtenau	Germany	−2.3	2.6	7.4	Bu1901	Schadtbek/DE	13	13	100	186
Poprad/Tatry	Slovakia	−1.3	0.6	2.4	Bu1905	Vrchdobroc/SK	68	146	97	182
Wien	Austria	9.0	13.5	18	Bu1907	Gablitz/AT	17	151	49	94
Tranebjerg	Denmark	8.6	15.7	22.7	Bu1908	Otterup/DK	39	−6	49	94
Beauvais-Tille	France	8.8	10.2	11.6	Bu1909	F.d.Lyons FR	38	101	100	98
Birr	Ireland	11.3	16.7	22.1	Bu1911	Rathdnum/IE	66	36	46	90
Lviv	Ukraine	−9.0	−3.4	2.2	Bu1915	Oleszyce/PL	84	−123	98	96
Miercurea Ciuc	Romania	0.6	4.7	8.8	Bu1917	Brasov/RO	91	139	44	88
Skovde	Sweden	−1.8	2.3	6.3	Bu1921	Ranna/SE	7	10	36	70
Luxembourg Airport	Luxembourg	2.4	5.4	8.3	Bu1922	Louschelt/LU	42	49	49	94
Kiel-Holtenau	Germany	−2.3	2.6	7.4	Bu2001	Schadtbek/DE	13	13	79	88
Birr	Ireland	11.3	16.7	22.1	Bu2004	Laragh/IE	17	105	34	68
Wageningen- Haarweg	Netherlands	−0.7	3.6	7.9	Bu2008	Oostereng/NL	5	23	58	56
Tranebjerg	Denmark	8.6	15.7	22.7	Bu2009	Lisbjerg/DK	49	69	34	68
Horby A	Sweden	−3.7	0.5	4.6	Bu2010	Ekebo/SE	24	−14	66	66
Oravská Lesná	Slovakia	−4.9	−0.7	3.5	Bu2020	Mlacik/SK	82	70	64	62
Hof	Germany	−1.8	3.7	9.2	Bu2023	Fichtelberg/DE	43	235	44	44
Burgos Villaria	Spain	−3.6	−2.3	−0.9	Bu2024	M.Utilidad/ES	31	460	29	58

In the unified model, the rate of forcing is the same as that of the sequential model (Eq. (4)). However, in the unified model the rate of chilling is described by:

$$R_c(T) = \frac{1}{1 + e^{a_c(T - c_c)^2 + b_c(T - c_c)}} \quad (5)$$

Eq. (5) can take a similar shape as Eq. (3), but is a more flexible function and can also take very different shapes depending on the values of the parameters. The eco-physiological interpretation of the parameters of Eq. (5) is consequently less straightforward than the interpretation of the parameters of Eq. (3) (Hänninen and Kramer, 2007).

The critical state of forcing, S_f^* , is not necessarily independent of chilling as the sequential model suggests. In fact, a decline in the S_f^* with increased chilling is found for several woody species (Campbell and Sugano, 1975; Cannell and Smith, 1983; Harrington, 2015; Landsberg, 1974). Therefore, an exponential decline of S_f^* with the monotonously increasing state of chilling is assumed in the unified model, as originally proposed by Murray et al. (1989):

$$S_f^* = w e^{-k S_c} \quad (6)$$

The dependency of the critical state of forcing on chilling can also be described by a declining function between S_f^* and S_c^* . In this study, a linear function between these model variables was evaluated in combination with the sequential model:

$$S_f^* = a + b S_c^* \quad (7)$$

Neither the sequential nor the unified model include photoperiod as an explanatory factor. Photoperiod may play a role in the timing of budburst of *Fagus sylvatica*, though the empirical evidence is conflicting. Heide (1993) found that both chilling and long days are required for dormancy release on beech buds, whereas Wareing (1953, 1956) concluded based on his experimental studies that long days only are required for dormancy release in beech and the amount of chilling has no appreciable effect on this photoperiodic requirement. Falusi and Calamassi (1990), on the other hand concluded that renewal of bud growth was mainly determined by winter chilling and found only a slight interaction between chilling and photoperiod. In a follow up study on provenances from different latitudes, they concluded that long days are able to substitute

winter chilling, but that once the need for breaking of dormancy has been satisfied, temperature is presumably the principal environmental factor that controls flushing (Falusi and Calamassi, 1996). Based on that finding, photoperiod was included in the sequential model as additive factor to the rate of chilling (Kramer, 1994):

$$R_c(T, P) = R_c(T) + d_c P \quad (8)$$

So that:

$$S_c(T, P) = \sum_{t_0}^{t_1} R_c(T, P) \quad (9)$$

With: $R_c(T)$ as in Eq. (3) and P indicating photoperiod expressed as day length, and S_c is the accumulation of both temperature and photoperiod during the rest period (cf. Eq. (1)).

The value of d_c determines the importance of photoperiod on the accumulation of chilling, relative to the importance of temperature. In case of lack of chilling temperature, S_c is determined by photoperiod, thereby satisfying the experimental results of Heide and Wareing. Whereas if bud dormancy is broken by chilling the value of d_c will be negligible, thereby following the experimental results of Falusi and Calamassi.

See Hänninen and Kramer (2007), Kramer and Hänninen (2009) and Chuine et al. (2013) for reviews on these approaches to model plant development, and Kramer (1994) for considerations how to include photoperiod in phenological models.

2.4. Model evaluation

The two hypotheses presented above were assessed by evaluating the model performance for the following three scenarios: 1) single model evaluation based on all provenances and for all sites; 2) evaluation per provenance across sites; and 3) evaluation per provenance and per site. The first hypothesis of differentiation between provenances, is supported if 2) results in a better model performance than 1). The second hypothesis on phenotypic plasticity, i.e. of differentiation between sites within provenances, of the critical state of either chilling and/or forcing is supported if 3) results in a better model performance than 2).

Table 4

Overview of the parameters for which values were estimated. This scheme was applied to each of the numerical methods tested (downhill simplex; anneal—Chauchy, anneal—Fast, anneal—Boltzmann). The ‘per provenance’ and the ‘per provenance per site’ scenarios were initialised with the parameter values obtained from the ‘all provenances’ scenario for the relevant model using the downhill simplex method only. Black: parameters estimated for: ‘all provenances’, ‘per provenance’ and ‘per provenance per site’ scenarios; grey: parameters estimated for the ‘all provenances’ used in the ‘per provenance’ and ‘per provenance per site’ scenarios. Seq. – sequential model.

	#	1	2	3	4	5	6	7
	Model	Seq.	Seq. + P	Unified	Seq.- fChl	Seq.-fChl + P	Seq.-S* only	Seq.-S*only + P
Parameter	Eqn							
S_c^*	1,2							
S_f^*	1,2							
$T_{c,min}$	3							
$T_{c,opt}$	3							
$T_{c,max}$	3							
a_f	4							
b_f	4							
a_c	5							
b_c	5							
c_c	5							
k	6							
a	7							
b	7							
d_c	8							

The best model for a given scenario was selected based on the root mean square error (RMSE), expressed in day [d]. For the selected models, the improvement of model performance between scenarios was based both on the percentage variance explained, expressed as R^2 , and the systematic and unsystematic mean square errors (Wallach and Goffinet, 1989), expressed relative to the total mean square error.

Both the sequential and the unified models were programmed in Python version 2.7. Parameter values were estimated using both the downhill simplex (Nelder and Mead, 1965) and the simulated annealing methods (Van Laarhoven and Aarts, 1987), as implemented in the scientific Python module SciPy. The downhill simplex method was selected as the best method in Kramer (1994). The simulated annealing method was recommended by Chuine as a suitable method for estimating the parameter values of the unified model (Chuine et al., 1999; Chuine, 2000). SciPy provides three simulating annealing approaches: ‘fast’, ‘cauchy’ and ‘boltzmann’, and all three methods were tested here. For details and references for implementation of these methods, see the *fmin* and *anneal* algorithms of the optimize module in the SciPy documentation (docs.scipy.org/doc/). The model code is available upon request.

Numerical methods to estimate the parameter values of phenological models are sensitive to the initial set of parameter values (Kramer, 1994). Therefore, a single set of parameter values was obtained by considering the observations of all provenances (‘all-provenances’). The set of parameter values obtained from the ‘all-provenances’ run was used to initialize both the runs for each provenance (‘per provenance’) and the runs to determine the parameter values per provenance and per site (‘per provenance per site’). This resulted for each model in 240 sets of parameter values for the ‘per provenance scenario’ and 1095 sets for the ‘per provenance per site scenario’.

The accuracy of the estimate of the parameter values depends on the number of independent observations. Grouping the data first per provenance and then by provenance and site decreases the number of observations available for model fitting. At best 12 observations are available per provenance and per site (i.e. for the

1993/95 series, Table 1). That is insufficient information to estimate eight or more model parameters. Therefore, also the case was tested where only the critical chilling and forcing parameters, S_c^* and S_f^* , were estimated per provenance and site while keeping the other parameters of the same model identical for all provenances. The same test was done at the level of provenance across sites, in addition to the estimation of all parameters per provenance. Table 4 presents an overview of the models evaluated. Table 5 presents a numerical example of the parameter values obtained for the different scenarios.

3. Results

The root mean square errors of the models for the different methods to estimate parameter values and for the different scenarios to assess the hypotheses are presented in Table 6. The high RMSE values for the simulated annealing method are because often no budburst was predicted for a particular year, so that the value 365 was attained. That is also the reason for the high RMSE of the unified model when applying the downhill simplex method to estimate its parameters. Different variants of the unified model, as was done for the sequential model, could therefore not be pursued. Adding photoperiod to the different variant of the sequential model did not improve its performance, irrespective of the scenario used.

The models selected to assess the hypotheses are indicated in bold in Table 6. The following results were obtained for the selected models. When assuming that the observations are a sample from a single, genetically uniform population, we find a large systematic error, MSE_s , of 31% of the total Mean Square Error, MSE_t , between observed and predicted (Fig. 2A, $R^2 = 0.36$, $RMSE = 4d$) dates of budburst. This result indicates that the observations were not obtained from a genetically uniform population. When allowing the model to adjust both the critical chilling and forcing requirements for each provenance separately, across sites, the MSE_s reduced to 15% of MSE_t and the variance explained by the model approximately doubles (Fig. 2B, $R^2 = 0.62$, $RMSE = 3d$). This result indicates that the populations are genetically differentiated with respect to critical

Table 5

Example of parameter values obtained for the Paderborn provenance. Presented are the results for the Seq. – S* model (#6, see Table 4) using the downhill simplex method. The Paderborn provenance was tested at three sites, but with different years of seeding and planting. Consequently, there were three harvests, with seed book numbers 7561, 7582 and 8773. The observations on these seed book numbers were pooled for the analyses of the three scenarios.

	Parameter	$T_{c,min}$	$T_{c,opt}$	$T_{c,max}$	a_f	b_f	S_c^*	S_f^*	n obs.	Year of seeding/year of planting	Year with observation
Scenario	Provenance Site										
all provenances		–19.61	–0.24	77.13	–0.10	–32.58	125.51	3.58	1402		
per provenance	Paderborn	–19.61	–0.24	77.13	–0.10	–32.58	127.08	3.62	8		
per provenance per site	Paderborn Malente (DK)	–19.61	–0.24	77.13	–0.10	–32.58	108.99	5.19	4	1985/'88	1989, 1991
per provenance per site	Paderborn Vascoeuil (FR)	–19.61	–0.24	77.13	–0.10	–32.58	105.87	5.64	3	1985/'88	1991, 1993
per provenance per site	Paderborn Grosshansdorf (DE)	–19.61	–0.24	77.13	–0.10	–32.58	103.67	5.31	1	1993/'95	1995

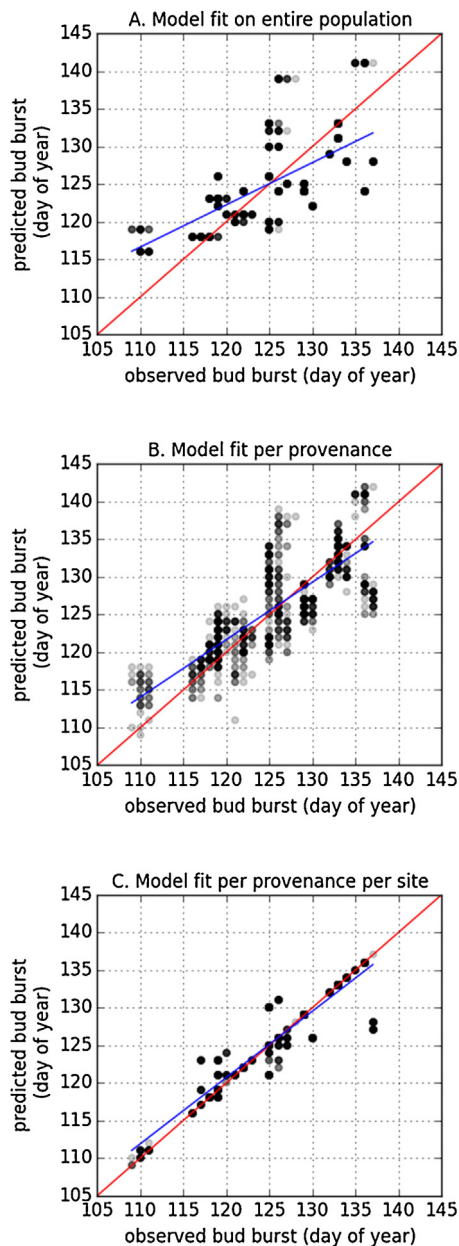


Fig. 2. Fit of the sequential model based on the downhill simplex method for the different scenarios. Each panel presents all 1402 observed and predicted values (see Phenological data). Multiple observations and predictions can fall on the same position. The intensity of the grey scale is proportional to the number of points at the same position to accommodate for that. Blue line: fit through the data points. Red line: observed/predicted 1:1 line. In a perfect model-data fit, the blue and red lines coincide. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 6

Root mean square error (RMSE, [d]) for the different combinations of Model – Method – Scenario evaluated. See Table 4 for the description of the models. In **bold** the models and method selected.

Model	Method	Scenario	RMSE
Seq	downhill simplex	all provenances	4
Seq + P	downhill simplex	all provenances	4
Unified	downhill simplex	all provenances	– ^a
Seq	downhill simplex	per provenance	3
Seq + P	downhill simplex	per provenance	3
Seq – S* only	downhill simplex	per provenance	3
Seq – S* only + P	downhill simplex	per provenance	3
Seq – fChl	downhill simplex	per provenance	–
Seq – fChl + P	downhill simplex	per provenance	–
Seq	anneal–Cauchy	per provenance	224
Seq	anneal–Fast	per provenance	180
Seq	anneal–Boltzmann	per provenance	157
Unified	anneal (3 methods)	per provenance	–
Unified	downhill simplex	per provenance	179
Seq – S* only	downhill simplex	per provenance per site	1
Seq – S* only + P	downhill simplex	per provenance per site	1

^a ‘–’ indicates that in all or the majority of cases the method applied did not converge, i.e. failed to find an optimal set of parameter values. Model performance then mainly depends on that of the initial set of parameter values.

chilling and forcing requirements. Allowing the model to adjust the critical chilling and forcing requirement per provenance per site, further reduces MSE_s to 11% of MSE_t (Fig. 2C, R² = 0.87, RMSE = 1 d). From this last improvement in model fit, we infer that the provenances show phenotypic plasticity of critical chilling and forcing requirements to site conditions of plantation.

The improvement of the model fit is the consequence of the adjustment of both the critical chilling requirement (S_c^*) and critical forcing requirements (S_f^*) in the different scenarios (Fig. 3). Allowing these parameters to vary per site results in a much broader range of values compared to the per provenance scenarios. This strengthens our inference that the provenances show phenotypic plasticity of critical chilling and forcing requirements to local site conditions.

4. Discussion and Conclusions

The timing of phenological events has strong implications on the productivity and survival of agricultural crops, fruit trees and forest trees. Given this importance and the fact that phenological events are easily observable, a large body of phenological literature was developed during the previous century. That historic research provided the basic information to develop phenological models for the assessment of the effects of climate change on plant production systems (see the Introduction for references). More recently, adaptation and phenotypic plasticity of phenology of trees received much attention (Alberto et al., 2011; Alberto et al., 2013; Matesanz et al., 2010; Richards et al., 2006; Savolainen et al., 2007; Valladares et al., 2006; Vitasse et al., 2013). Budburst phenology of trees is

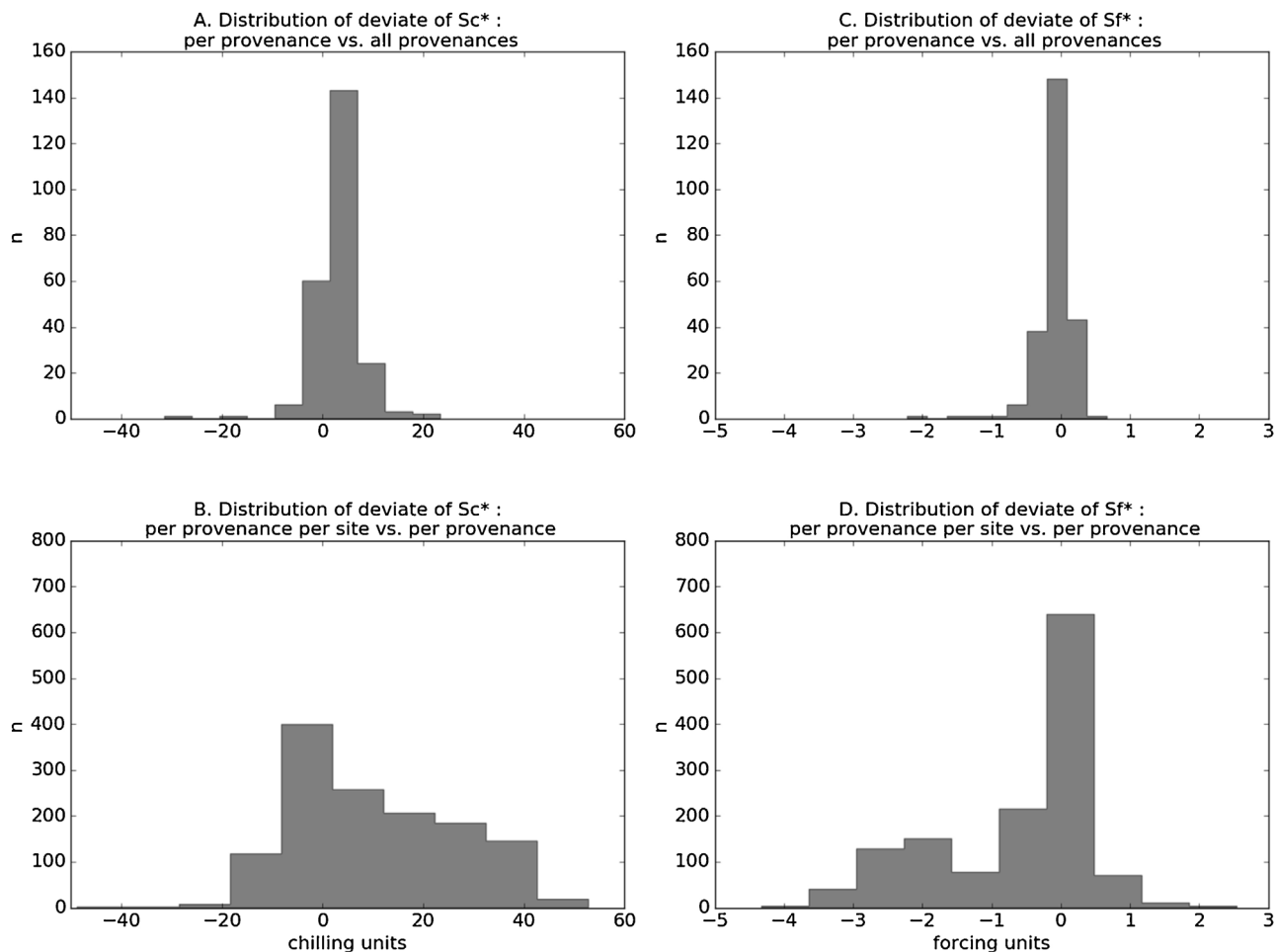


Fig. 3. Distribution of the deviate of both critical state of chilling (S_c^*) and critical state of forcing (S_f^*) between the scenarios. See Table 5 for reference values of these parameters.

found to be phenotypically plastic to temperature, though with strong differences between species (Duputie et al., 2015; Kramer, 1995b; Vitasse et al., 2010). Also modelling studies indicate the importance of adaptation (Kramer et al., 2008; Kramer et al., 2010) and phenotypic plasticity (Duputie et al., 2015) of phenology to evaluate the impact of climate change on forest growth (Kramer, 1995a; Kramer et al., 1996), forest dynamics (Hickler et al., 2004) or species distribution (Chaine and Beaubien, 2001). These phenological models describing the response of budburst to temperature assume fixed temperature thresholds for climate change assessments. However, Schueler and Liesebach (2015) recently found that latitudinal transfer of a beech provenance reduced the temperature sum requirements of that provenance. Thus, phenotypic plasticity occurs with respect to plant traits that determine the response of budburst to temperature. In this study, for the first time, adaptation and phenotypic plasticity of the critical chilling and forcing requirements underlying budburst was analysed on a large spatial scale and with a large number of provenances. Our results suggest that not only adaptive differences exist between provenances of a species for these thresholds, but also that these threshold themselves show phenotypic plasticity to local environmental conditions. This conclusion is likely also valid for other temperate and boreal zone deciduous tree species with the same phenological mechanism to trigger budburst (Kramer, 1995b). Our results thus support the recommendation of Duputie et al. (2015) that species distribution models need to take the response of budburst to temperature into account when forecasting species distribution under

climate change scenarios. Our analyses further support the idea that trees are able to adjust their response to temperature. These findings support the 'lost chilling' mechanism posed by Fu et al. ((2015), their 3rd hypothesis) to explain the decline in the effect of global warming on the phenology of spring leaf unfolding. Including phenotypic plasticity in the plant traits that determine the reaction of phenology is therefore an important mechanism that needs to be included in phenological models.

A possible way to include such second-order phenotypic plasticity in climate change assessment models is by incorporating the genetic architecture in models, as they increasingly become available (Nicotra et al., 2010). Wilczek et al. (2010) proved the feasibility of such a project using the genetic architecture for flowering seasonality disentangled for *Arabidopsis thaliana* to model phenological responses to current and predicted climates at the global scale. Phenotypic plasticity in phenology could thus be modelled based on the limited number of repressors and integrators that determine this process (see Fig. 2. in Wilczek et al. (2010)). Heritable control of phenology may also include an important epigenetic component (Bräutigam et al., 2013). Photoperiod and temperatures during embryogenesis and seed maturation have been shown to affect timing of spring flushing and autumn growth cessation and, consequently, frost damage and hardiness of trees (Johnsen et al., 2005), while germination and juvenile-growth environment exert similar effects on phenology (Gömöry et al., 2015). Although such studies were primarily conducted on conifers, the participation of epigenetic phenomena in the regulation of vegetative phenology

was demonstrated also in the members of the Fagaceae family (Santamaria et al., 2009). Ultimately, insight in the genetics and epigenetics of budburst phenology could circumvent the indirect estimation of plant traits related to dormancy of trees using complex numerical techniques which are applied with variable success (Table 6).

Adaptation as a genetic mechanism can also be incorporated into process-based models, which essentially describe responses of primary plant processes such as photosynthesis, respiration and allocation to environmental drivers. An approach to integrate genetic and physiological processes with an example of adaptation of budburst phenology is presented in (Kramer et al., 2015). It is increasingly becoming clear that micro-evolution is operational at an ecologically relevant time-scale (Carroll et al., 2007), and can in fact be applied for ecosystem restoration in the face of climate change (Rice and Emery, 2003). The understanding of the adaptive mechanism underlying phenotypic plasticity (Nicotra et al., 2010), and the application of this knowledge in models, is thus urgently needed to further develop evolutionary thinking in ecosystem restoration (Wang et al., 2013) and forest management (Chambel et al., 2005) under global environmental change.

Provenance trials provide unique information to assess effects of climate change on the functioning of tree species (Koskela et al., 2014; Mátyás, 1994). Because the trials are established over a large geographic range, provide time series sufficiently long for analyses, and are established under field conditions. However, the main aim to establish the trials was for practical forestry to assess which provenance would grow best under the local environmental conditions (Wuehlisch et al., 1998). Many of the provenance sites are therefore located in remote forested areas, often tens of kilometres away from research stations. That situation makes frequent visiting of the sites and automated logging of sub-daily meteorological data unfeasible, and was considered unnecessary for the original purposes of the trials. The essential reasoning we employ is that differentiation among provenances indicates adaptation, and that differentiation between sites, within provenances, indicates phenotypic plasticity. Improvement of the performance of the selected phenological model led us to conclude that both the hypothesis on adaptation and the one on plasticity are supported by the data. That conclusion may be jeopardized if the meteorological time series used in the model analyses are not representative for the trial sites. However, we analysed the data set over a very large temperature range when considering all of the provenances. For these analyses, the inaccuracy in temperature will be small relative to the full temperature range considered. Inaccuracy in temperature could be an important aspect for the *per provenance per site* analyses. However, that would lead to an increase in systematic and/or unsystematic errors, whilst at this level the lowest deviate between observed and predicted was found. We therefore think that our conclusions are sound. Lack of local meteorological data obtained in forest sites is unfortunately not unique to our study. We support the conclusion by De Frenne and Verheyen (2016) that weather stations urgently need to be installed in forests to promote our understanding of climate change.

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Appendix A. Conversion of the data to score 2 of 3-step scale

As indicated in the section Phenological data, the phenological scores of all data was aggregated toward the 3-step scale (see Table 1). Subsequently, data with score 1 and 3 were converted into score 2 of the 3-step scale. This rescaling was done by adding a number of days to stage 1 and subtracting a number of days from stage 3, based on the average difference in these stages. This difference between stages 1 and 2, and 3 and 2 was not constant (Fig. S1 in Supplementary data). The frequency distribution of each of three phenological stages shows a tri-modal distribution with temperature sum (Fig. S2 in Supplementary data). We defined three clusters based on temperature thresholds of 145 and 260. For clusters 2 and 3 the difference between both scores 1 and 3 with score 2 is reasonably constant (Fig. S3 in Supplementary data). For cluster 1 that is only true above a temperature threshold of about 75 ° days. As the observations below 75° days were all done at one site (Mlacik, SK) and considered less than 2% of the observations, no further breakdown of the data was done. The characteristics of the clusters are presented in Table S2. The difference in temperature sum was used to convert both scores 1 and 3 into score 2 for all provenances and sites falling in a particular cluster.

Appendix B. Processing temperature data

The temperature data for the beech provenance trials analysis were collected from the website of the European Climate Assessment & Dataset project (ECA&D) (<http://www.ecad.eu/>). The data providers are 66 National Meteorological and Hydrological Services, observatories and universities from Europe and the Mediterranean. The website interface for downloading daily series of climate data does not provide the option to find the nearest meteorological stations from a point of interest such as an interactive web-GIS portal, but instead the station can be chosen by picking-up a certain station identified by a toponym related name from a specific country. In this respect, to find the closest meteorological stations from the provenance trials, the coordinates for all the meteorological stations locations were imported into a Geographic Informational System (GIS) software and overlaid with the location of the provenance trials. This allowed to identify the most appropriate station for each provenance trial in terms of horizontal and elevational differences. The climatic data are provided as .txt files and are in two formats: blended and non-blended series. In the blended series the observations from two or more nearby locations can be merged seamlessly for climate change research while the non-blended series consists in separate underlying series. For our study we chose to use the blended series to extract the daily minimum temperature and maximum temperature for the time series used for phenology analysis.

Appendix C. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2016.12.002>.

References

- Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration, or extirpation: climate change outcomes for tree populations. *Evol. Appl.* 1, 95–111.
- Alberto, F., et al., 2011. Adaptive responses for seed and leaf phenology in natural populations of sessile oak along an altitudinal gradient. *J. Evol. Biol.* 24 (7), 1442–1454.
- Alberto, F.J., et al., 2013. Potential for evolutionary responses to climate change – evidence from tree populations. *Glob. Change Biol.* 19 (6), 1645–1661.
- Alpert, P., Simms, E., 2002. The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust? *Evol. Ecol.* 16 (3), 285–297.
- Bradshaw, A.D., 1965. Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.* 13, 115–155.
- Bradshaw, A.D., 1973. Environment and phenotypic plasticity. *Brookhaven Symp. Biol.* 25, 75–94.
- Bräutigam, K., Vining, K.J., Lafon-Placette, C., Fossdal, C.G., Mirouze, M., Gutierrez Marcos, J., Fluch, S., Fernandez Fraga, M., Angeles Guevara, M., Abarca, D., Johnsen, Ø., Maury, S., Strauss, S.H., Campbell, M.M., Rohde, A., Diaz-Sala, C., Cervera, M.T., 2013. Epigenetic regulation of adaptive responses of forest tree species to the environment. *Ecol. Evol.* 3, 399–415.
- Campbell, R.K., Sugano, A.I., 1975. Phenology of bud burst in Douglas-fir related to provenance, photoperiod, chilling, and flushing temperature. *Botanical Gazette* 136 (3), 290–298.
- Cannell, M.G.R., Smith, R.I., 1983. Thermal time, chill days and prediction of budburst in *Picea sitchensis*. *J. Appl. Ecol.* 20, 951–963.
- Carroll, S.P., Hendry, A.P., Reznick, D.N., Fox, C.W., 2007. Evolution on ecological time-scales. *Funct. Ecol.* 21, 387–393.
- Chambel, M.R., Climent, J.M., Alía, R., Valladares, F., 2005. Phenotypic plasticity: a useful framework for understanding adaptation in forest species. *Investigación Agraria. Sistemas y Recursos Forestales* 14 (3), 334–344.
- Chaine, I., Beaubien, E.G., 2001. Phenology is a major determinant of tree species range. *Ecol. Lett.* 4 (5), 500–510.
- Chaine, I., Cour, P., Rousseau, D.D., 1999. Selecting models to predict the timing of flowering of temperate trees: implications for tree phenology modeling. *Plant Cell Environ.* 22, 1–13.
- Chaine, I., Garcia de Cortazar-Atauri, I., Kramer, K., Hänninen, H., 2013. Plant development models. In: Schwartz, M.D. (Ed.), *Phenology: An Integrative Environmental Science*, 2nd ed. Springer Verlag, pp. 275–293.
- Chaine, I., 2000. A unified model for the budburst of trees. *J. Theor. Biol.* 207, 337–347.
- de Jong, G., 1995. Phenotypic plasticity as a product of selection in a variable environment. *Am. Nat.* 145 (4), 493–512.
- de Jong, G., 1999. Unpredictable selection in a structured population leads to local genetic differentiation in evolved reaction norms. *J. Evol. Biol.* 12, 839–851.
- De Frenne, P., Verheyen, K., 2016. Weather stations lack forest data. *Science* 351 (6270).
- Doorenbos, J., 1953. Review of the literature on dormancy in buds of woody plants. *Medelingen van de Landbouwhogeschool te Wageningen Nederland* 53, 1–24.
- Downs, R.J., Borthwick, H.A., 1956. Effects of photoperiod on growth of trees. *Botanical Gazette* 117 (4), 310–326.
- Duputie, A., Rutschmann, A., Ronce, O., Chuine, I., 2015. Phenological plasticity will not help all species adapt to climate change. *Glob. Change Biol.* 21 (8), 3062–3073.
- Falusi, M., Calamassi, R., 1990. Bud dormancy in beech (*Fagus sylvatica* L.). Effect of chilling and photoperiod on dormancy release of beech seedlings. *Tree Physiol.* 6, 429–438.
- Falusi, M., Calamassi, R., 1996. Geographic variation and bud dormancy in beech seedlings (*Fagus sylvatica* L.). *Annales des Sciences Forestières Paris* 53 (5), 967–979.
- Fu, Y.H., et al., 2015. Declining global warming effects on the phenology of spring leaf unfolding. *Nature* 526 (7571), 104–107.
- Gömöry, D., Foffová, E., Longauer, R., Krajmerová, D., 2015. Memory effects associated with the early-growth environment in Norway spruce and European larch. *Eur. J. For. Res.* 134, 89–97.
- Hänninen, H., Häkkinen, R., Hari, P., Koski, V., 1990. Timing of growth in relation to climatic adaptation of northern woody plants. *Tree Physiol.* 6, 29–39.
- Hänninen, H., 1990. Modelling bud dormancy release in trees from cool and temperate regions. *Acta Forestalia Fennica* 213, 1–47.
- Hänninen, H., Kramer, K., 2007. A framework for modelling the annual cycle of trees in boreal and temperate regions. *Silva Fennica* 41 (1), 167.
- Harrington, C.A., 2015. Tradeoffs between chilling and forcing in satisfying dormancy requirements for Pacific Northwest tree species. *Front. Plant Sci.*, 6.
- Heide, O.M., 1993. Dormancy release in beech buds (*Fagus-Sylvatica*) requires both chilling and long days. *Physiol. Plant* 89 (1), 187–191.
- Hickler, T., et al., 2004. Using a generalized vegetation model to simulate vegetation dynamics in northeastern USA. *Ecology* 85 (2), 519–530.
- Hughes, J.E., Morgan, D.C., Lambton, P.A., Black, C.R., Smith, H., 1984. Photoperiodic time signals during twilight. *Plant Cell Environ.* 7 (4), 269–277.
- Johnsen, Ø., Fossdal, C.G., Nagy, N., Molmann, J., Dælen, O.G., Skråp, T., 2005. Climatic adaptation in *Picea abies* progenies is affected by the temperature during zygotic embryogenesis and seed maturation. *Plant Cell Environ.* 28, 1090–1102.
- Koskela, J., et al., 2014. Utilization and transfer of forest genetic resources: a global review. *For. Ecol. Manag.* 333 (0), 22–34.
- Koski, V., 1985. Adaptation of trees to the variation in the length of the growing season. In: Kaurin, A., Junttila, O., Nilsen, J. (Eds.), *Plant Production in the North. Proceedings from 'Plant Adaptation Workshop'*. Norwegian University Press, Tromsø, Norway, 4–9 Sep. 1983. Tromsø Norway, pp. 267–276 (23 ref.).
- Kramer, K., Hänninen, H., 2009. The annual cycle of development of trees and process-based modelling of growth to scale up from the tree to the stand. In: Noormets, A. (Ed.), *Phenology of Ecosystem Processes. Applications in Global Change Research*. Springer Verlag, A. Noormets, pp. 201–228.
- Kramer, K., Friend, A., Leinonen, I., 1996. Modelling comparison to evaluate the importance of phenology and spring frost damage for the effects of climate change on growth of mixed temperate-zone deciduous forests. *Climate Res.* 7 (1), 31–41.
- Kramer, K., Leinonen, I., Loustau, D., 2000. The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview. *Int. J. Biometeorol.* 44 (2), 67–75.
- Kramer, K., et al., 2008. Bridging the gap between ecophysiological and genetic knowledge to assess the adaptive potential of European beech. *Ecol. Model.* 216 (3–4), 333–353.
- Kramer, K., et al., 2010. Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change—range, abundance, genetic diversity and adaptive response. *For. Ecol. Manag.* 259 (11), 2213–2222.
- Kramer, K., van der Werf, B., Schelhaas, M.-J., 2015. Bring in the genes: genetic-ecophysiological modeling of the adaptive response of trees to environmental change With application to the annual cycle. *Front. Plant Sci.*, 5.
- Kramer, K., 1994. Selecting a model to predict the onset of growth of *Fagus sylvatica*. *J. Appl. Ecol.*, 172–181.
- Kramer, K., 1995a. Modelling comparison to evaluate the importance of phenology for the effects of climate change on growth of temperate-zone deciduous trees. *Climate Res.* 5 (2), 119–130.
- Kramer, K., 1995b. Phenotypic plasticity of the phenology of seven European tree species in relation to climatic warming. *Plant Cell Environ.* 18 (2), 93–104.
- Landsberg, J.J., 1974. Apple fruit bud development and growth; analysis and an empirical model. *Ann. Bot.* 38, 1013–1023.
- Lechowicz, M.J., 1984. Why do temperature deciduous trees leaf out at different times? Adaptation and ecology of forest communities. *Am. Nat.* 124 (6), 821–842.
- Leinonen, I., Kramer, K., 2002. Applications of phenological models to predict the future carbon sequestration potential of Boreal forests. *Climatic Change* 55 (1–2), 99–113.
- Levitt, J., 1969. Growth and survival of plants at extremes of temperature – a unified concept. In: Woolhouse, H.W. (Ed.), *Dormancy and Survival*. Nr. XXIII, Symposia of the Society for Experimental Biology. Cambridge University Press, pp. 395–448.
- Levitt, J., 1972. Responses of plants to environmental stresses. In: *Physiological Ecology. A Series of Monographs, Texts and Treatises*. Academic Press, New York (697 pp).
- Lockhart, J.A., 1983. Optimum growth initiation time for shoot buds of deciduous plants in a temperate climate. *Oecologia* 60, 34–37.
- Lortie, C.J., Aarssen, L.W., 1996. The specialization hypothesis for phenotypic plasticity in plants. *Int. J. Plant Sci.* 157 (4), 484–487.
- Mátyás, C., 1994. Modelling climate change effects with provenance test data. *Tree Physiol.* 14, 797–804.
- Mátyás, C., 1996. Climatic adaptation of trees: rediscovering provenance tests. *Euphytica* 92, 45–54.
- Mátyás, C., 2010. Forecasts needed for retreating forests. *Nature* 464 (7293), 1271.
- Matesanz, S., Gianoli, E., Valladares, F., 2010. Global change and the evolution of phenotypic plasticity in plants. *Year Evol. Biol.* 1206, 35–55.
- Menzel, A., Fabian, P., 1999. Growing season extended in Europe. *Nature* 397 (6721), 659–659.
- Menzel, A., 2000. Trends in phenological phases in Europe between 1951 and 1996. *Int. J. Biometeorol.* 44 (2), 76–81.
- Muhs H.-J. and Wuehlisch G.v., 1993. Research on the evaluation of forest genetic resources of beech—a proposal for a long-range experiment. In: H.-J.W. Muhs, G. von (Editor), *The scientific basis for the evaluation of forest genetic resources of beech*. Working document for the EC, DG VI, Brussels Ahrensburg 1993, pp. 257–261.
- Murray, M.B., Cannell, M.G.R., Smith, R.I., 1989. Date of budburst of fifteen tree species in Britain following climatic warming. *J. Appl. Ecol.* 26, 693–700.
- Murray, M.B., et al., 1994. Effects of elevated CO₂ nutrition and climatic warming on bud phenology in Sitka (*Picea sitchensis*) and their impact on the risk of frost damage. *Tree Physiol.* 14, 691–706.
- Nelder, J.A., Mead, R., 1965. A simplex method for function minimization. *Comput. J.* 7, 308–313.
- Nicotra, A.B., et al., 2010. Plant phenotypic plasticity in a changing climate. *Trends Plant Sci.* 15 (12), 684–692.
- Nitsch, J.P., 1957. Photoperiodism in woody plants. *Proc. Am. Soc. Hortic. Sci.* 70, 526–544.
- Noormets, A. (Ed.), 2009. *Phenology of Ecosystem Processes*. Springer Verlag (275 pp).
- Parker, W.H., 1963. Cold resistance in woody plants. *Botanical Rev.* 29, 123–201.
- Perry, T.O., 1971. Dormancy of trees in winter. *Science* 171, 29–36.
- Pigliucci, M., 1993. Plasticity versus genetics. *Trends Ecol. Evol.* 8, 379.
- Rice, K.J., Emery, N.C., 2003. Managing microevolution: restoration in the face of global change. *Front. Ecol. Environ.* 1 (9), 469–478.

- Richards, C.L., Bossdorf, O., Muth, N.Z., Gurevitch, J., Pigliucci, M., 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecol. Lett.* 9 (8), 981–993.
- Romberger, J.A., 1963. Meristems, growth and development in woody plants. USDA Tech. Bull. (Nr, 214).
- Sakai, A., Larcher, W., 1987. Frost survival of plants. Responses and adaptation to freezing stress. *Ecological Studies*, 62. Springer-Verlag, Berlin (321 p).
- Salisbury, F.B., 1981. Responses to photoperiod, *Physiological plant Ecology I. Responses to the physical environment*. In: Lange, P.S., Osmond, C.B., Ziegler, H. (Eds.), *Encyclopedia of Plant Physiology. New Series*, Vol. 12A. Springer Verlag, Berlin, pp. 135–167.
- Samish, R.M., 1954. Dormancy in woody plants. *Annu. Rev. Plant Phys.* 5, 183–204.
- Santamaria, M.E., Hasbun, R., Valera, M.J., Meijon, M., Valledor, L., Rodriguez, J.L., Toorop, P.E., Canal, M.J., Rodriguez, R., 2009. Acetylated H4 histone and genomic DNA methylation patterns during bud set and bud burst in *Castanea sativa*. *J. Plant Physiol.* 166, 1360–1369.
- Savolainen, O., Pyhäjärvi, T., Knürr, T., 2007. Gene flow and local adaptation in trees. *Ann. Rev. Ecol. Evol. Systematics* 38, 595–619.
- Scheiner, S.M., 1993. Genetics and evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.* 24, 35–68.
- Schlichting, C.D., Pigliucci, M., 1993. Control of phenotypic plasticity via regulatory genes. *Am. Nat.* 142 (2), 366–370.
- Schlichting, C.D., 1986. The evolution of phenotypic plasticity in plants. *Annu. Rev. Ecol. Systematics* 17, 667–693.
- Schueler, S., Liesebach, M., 2015. Latitudinal population transfer reduces temperature sum requirements for bud burst of European beech. *Plant Ecol.* 216 (1), 111–122.
- Schwartz, M.D., 1994. Monitoring global change with phenology—the case of the spring green wave. *Int. J. Biometeorol.* 38, 18–22.
- Schwartz, M.E., 2013. *Phenology: An Integrative Environmental Science*, 2nd ed. Springer, Verlag (603 pp).
- Sultan, S.E., 1992. Phenotypic plasticity and the Neo-Darwinian legacy What has survived of Darwin's theory? *Evol. Trend Plant* 6 (2), 61–71.
- Vaartaja, O., 1959. Evidence of photoperiodic ecotypes in trees. *Ecol. Monogr.* 29 (2), 91–111.
- Valladares, F., Sanchez-Gomez, D., Zavala, M.A., 2006. Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. *J. Ecol.* 94 (6), 1103–1116.
- Van Laarhoven, P.J.M., Aarts, E.H.L., 1987. *Simulated Annealing: Theory and Applications*. Kluwer Academic Publishers.
- Vegis, A., 1964. Dormancy in higher plants. *Annu. Rev. Plant Phys.* 15, 185–224.
- Vegis, A., 1973. Effect of temperature on growth and development. In: Precht, H., Christophersen, J., Hensel, H., Larcher, W. (Eds.), *Temperature and Life*. Springer-Verlag, Berlin, pp. 145–170.
- Via, S., et al., 1995. Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol. Evol.* 10 (5), 212–217.
- Via, S., 1992. Models of the evolution of phenotypic plasticity. *Trends Ecol. Evol.* 7 (2), 63.
- Via, S., 1993. Adaptive phenotypic plasticity—target or by-product of selection in a variable environment. *Am. Nat.* 142 (2), 352–365.
- Vitasse, Y., Bresson, C.C., Kremer, A., Michalet, R., Delzon, S., 2010. Quantifying phenological plasticity to temperature in two temperate tree species. *Funct. Ecol.* 24 (6), 1211–1218.
- Vitasse, Y., et al., 2013. Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species. *Oecologia* 171 (3), 663–678.
- Wallach, D., Goffinet, B., 1989. Mean squared error of prediction as a criterion for evaluating and comparing system models. *Ecol. Model.* 44, 299–306.
- Wang, C., He, T., Chen, F., 2013. Evolutionary thinking in restoration under global environmental changes. *J. Plant Ecol.*
- Wareing, P., 1953. Growth studies in woody species V. Photoperiodism in dormant buds of *Fagus sylvatica* L. *Physiol. Plant.* 6, 692–706.
- Wareing, P.F., 1956. Photoperiodism in woody plants. *Annu. Rev. Plant Phys.* 7, 191–214.
- Wareing, P.F., 1969. The control of bud dormancy in seed plants. In: Woolhouse, H.W. (Ed.), *Dormancy and Survival*. Nr. XXIII, *Symposia of the Society for Experimental Biology*. Cambridge University Press, pp. 241–262.
- Weiser, C.J., 1970. Cold resistance and injury in woody plants. Knowledge of hardy plant adaptations to freezing stress may help us to reduce winter damage. *Science* 3952, 1269–1278.
- Wilczek, A.M., et al., 2010. Genetic and physiological bases for phenological responses to current and predicted climates. *Philos. Trans. R. Soc. Lond. Ser. B* 365 (1555), 3129–3147.
- Woolhouse, H.W. (Ed.), 1969. Nr. XXIII, *Symposia of the Society for Experimental Biology*. Nr. 23. Cambridge University Press (598 pp).
- Wright, S.D. and McConnaughay, K.D.M., 2002. Interpreting phenotypic plasticity: the importance of ontogeny.
- Wuehlisch, G., von Krusche, D., Muhs, H.-J., 1995. Variation in temperature sum requirement for flushing of beech provenances. *Silvae Genetica* 44, 343–346.
- Wuehlisch, G., von Liesebach, M., Muhs, H.-J., Stephan, B.R., 1998. A network of international beech provenance trials. In: Turok, J., Kremer, A., de Vries, S. (Eds.), *First EUFORGEN Meeting on Social Broadleaves*, 23.–25. October 1997. IPGRI, France. International Plant Genetic Resources Institute, Rome, Bordeaux, France, pp. 164–172.
- Yan, W., Wallace, D.H., 1996. A model of photoperiod x temperature interaction effects on plant development. *Crit. Rev. Plant Sci.* 15 (1), 63–96.