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The timing of bud burst and its effect on tree growth

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Abstract A phenology model for estimating the timings of bud burst – one of the most influential phenological phases for the simulation of tree growth – is presented in this study. The model calculates the timings of the leafing of beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) and the May shoot of Norway spruce (*Picea abies* L.) and Scots pine (*Pinus sylvestris* L.) on the basis of the daily maximum temperature. The data for parameterisation and validation of the model have been taken from 40 climate and 120 phenological stations in southern Germany with time series for temperature and bud burst of up to 30 years. The validation of the phenology module by means of an independent data set showed correlation coefficients for comparisons between observed and simulated values of 54% (beech), 55% (oak), 59% (spruce) and 56% (pine) with mean absolute errors varying from 4.4 days (spruce) to 5.0 days (pine). These results correspond well with the results of other – often more complex – phenology models. After the phenology module had been implemented in the tree-growth model BALANCE, the growth of a mixed forest stand with the former static and the new dynamic timings for the bud burst was simulated. The results of the two simulation runs showed that phenology has to be taken into account when simulating forest growth, particularly in mixed stands.

Keywords Bud burst · Phenology · Modelling · Tree growth · Leafing

Introduction

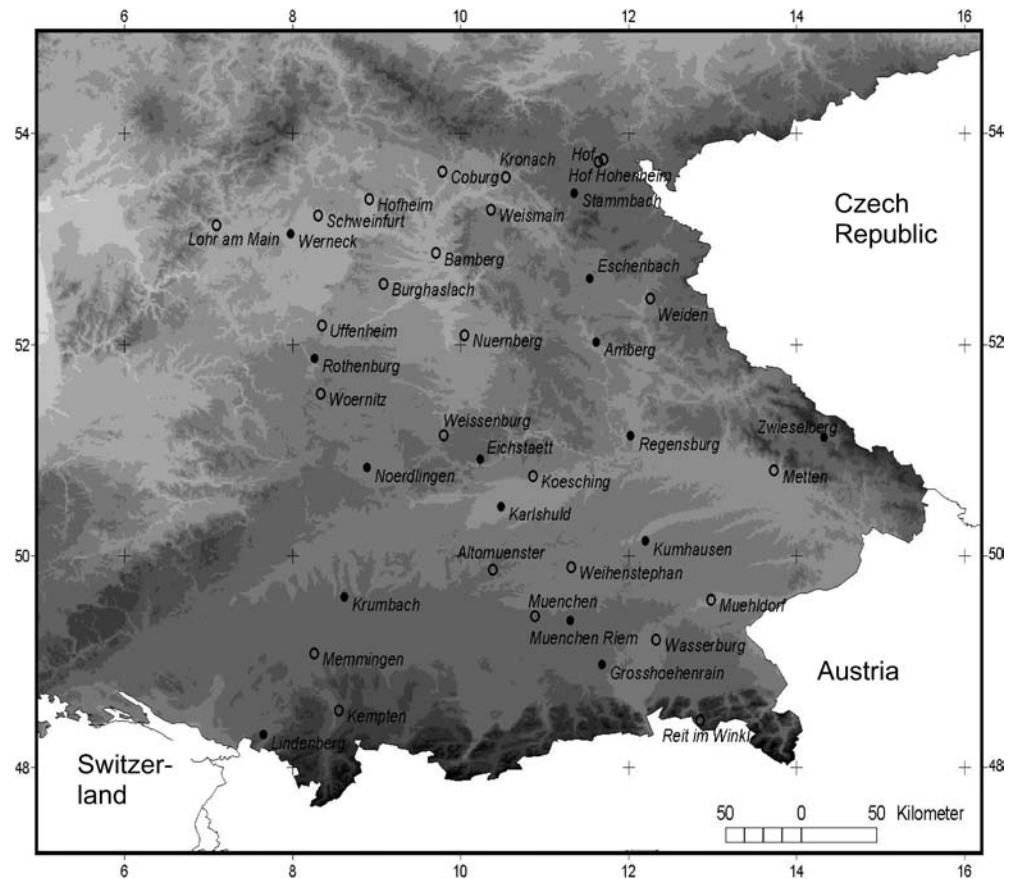
Growth models can be of great importance for ecological monitoring, e.g. the forest intensive monitoring programme (de Vries et al. 2002), to detect the relationships between environmental influences and the fitness of plants and to find causal analytic interpretations and explanations. However, until now statistical approaches have been applied almost exclusively in order to find a correlation between the forest condition and the vitality of trees (Webster et al. 1996; Augustin and Andreae 1998; Mayer 1999; Dammann et al. 2000; Seidling 2000, 2001).

Mechanistic approaches, such as physiological growth models, describe the influences of the site, i.e. climate, soil conditions etc., on plant-specific processes like transpiration, assimilation, respiration, allocation and senescence (e.g. Zhang et al. 1994; Sinoquet and Le Roux 2000; Grote 2003), which in turn are influenced by the developmental stages of the plant. But these phenological phases, for example foliage development, are often inflexibly prescribed in the growth models (e.g. Chen et al. 1994), which leads to a considerable uncertainty in long-term investigations (e.g. Bartelink 2000).

The uncertainties are due to the fact that the beginnings and durations of phenological phases are highly variable in time and space (Schnelle 1955). For Europe, Rötzer and Chmielewski (2001) found regional differences in the average beginning of the growing season (1961–1998) of up to 3 months, and year-to-year differences of 22 days (1990 compared to 1970) for the length of the growing season. Observation data of phenological phases, however, are difficult to obtain for a particular site, such as a forest, so that suitable estimation procedures have to be developed. One of these procedures is to regionalize observation data from (unequally) distributed raster points in space (Rötzer and Würländer 1997), whereas another calculates the phases as a function of available weather data (e.g. Schwartz et al. 1997; Snyder et al. 1999; Chuine et al. 1999; Cenci and Ceschia 2000; Orlandi et al. 2002).

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Fig. 1 Climate stations of southern Germany used for parameterisation (•) and for validation (○)



To account for the importance and variability of bud burst, some tree-growth models calculate the onset of the vegetation period as a function of weather conditions. These are either represented as a defined minimum temperature that is required for physiological activity (Bossel 1994) or by means of the concept of “growing degree days”, which uses the sum of daily average temperatures above a certain temperature limit (Hoffmann 1995; Aber et al. 1996; Friend et al. 1997; Bosc 2000). However, the actual benefit, as far as the bias and accuracy of prognosis of a mechanistic phenological module are concerned, has seldom been investigated (but see Kramer 1995).

We therefore developed a phenological model that simulates the timing of bud burst in order to apply it as a module within the framework of an already published tree-growth model and to test its influence on simulated growth in different years. The preconditions for the module’s construction were that its structure should be simple enough to be applied for the major tree species in Germany over a large range of possible weather conditions. After the validation, by means of an independent data set, it is implemented in the tree-growth model BALANCE (Grote and Pretzsch 2002). The improvements and changes within the model BALANCE will be shown in an example simulating the growth of a mixed forest stand.

Data and methods

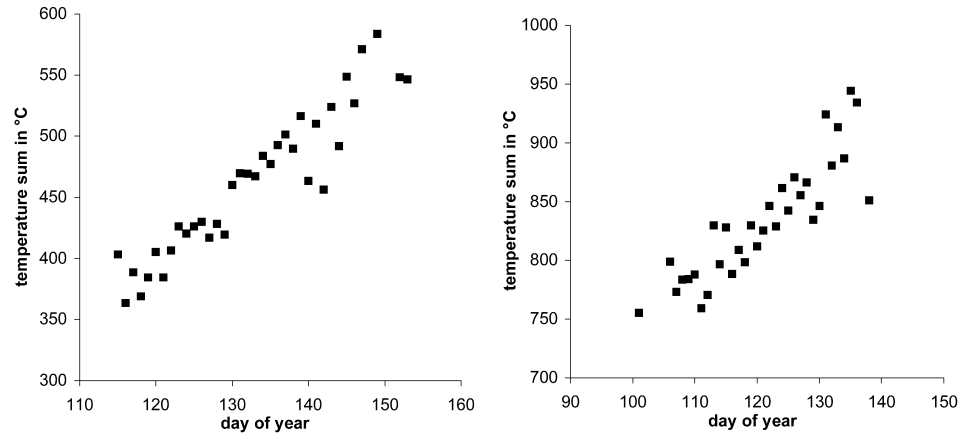
Temperature data (mean, minimum and maximum) from 40 climate stations in southern Germany (Fig. 1), collected by the German Weather Service within the period 1961–1990, are used to develop the phenology model. Thirty-year records of temperature from 25 climate stations were used for model development; data from additional 15 climate stations with time series less than 30 years were used for validation. The altitude of the climate stations used for parameterisation ranged from 161 m to 705 m and that of the climate stations used for validation was 216 m to 760 m.

The climate at the different stations varies considerably. Dry and warm regions, such as the Northwest of Bavaria (altitude: 200 m) with annual mean temperatures between 8 °C and 9 °C and precipitation sums of approximately 600 mm are included, as well as Alpine climate stations (altitude: 700 m) with annual mean temperatures between 6 °C and 7 °C and annual precipitation sums of approximately 1,800 mm (BayFORKLIM 1996).

The phenological information is derived from about 120 phenological stations located in the vicinity of the climate stations. Thus, each climate station could be associated with up to 3 phenological stations. The maximum distance between a phenological station and a climate station is 18.8 km, the maximum difference of altitude is 48 m. On average the distance between a phenological and a climate station is 7.5 km for the modelling stations and 9.4 km for the validation stations, while the mean altitude differences are 16 m and 21 m respectively. Therefore, the error associated with the geography of the phenological and the climate stations in the estimation of the timing of bud burst is smaller than 1 day, according to the results of Rötzer and Chmielewski (2001).

Because of frequently occurring observation errors (Rötzer 1996; Menzel 1997; Rötzer et al. 2000), the mean of at least two values from the phenological stations was used as the annual bud

Fig. 2 Average increase of the threshold temperature sum (maximum for the May shoot of spruce (*Picea abies* L., left) and for the leafing of beech (*Fagus sylvatica* L., right) in the course of the year (basis: 704 resp. 1,415 single observations for spruce and beech)



burst date of a climate station. The difference between the bud burst values for a particular year for any one climate station had to be lower than 20 days, or the value was rejected. This way, plausible annual phenological values were calculated for all climate stations.

The phenophases used for the modelling were the May shoot of Norway spruce (*Picea abies* L.) and Scots pine (*Pinus sylvestris* L.) as well as the beginning of the leafing of beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.). Although there are differences in the annual timings of the phenophases between genotype and/or varieties (Rötzer and Chmielewski 2001), the observations used here can only be distinguished in species according to the phenological observation guidelines (German Weather Service 1991).

The timing of the spring phenophases especially is mainly determined by temperature (e.g. Fitter et al. 1995; Sparks et al. 2000; Chmielewski and Rötzer 2002). For this reason, and because of the precondition that the module structure should be as simple as possible, temperature was applied as the only parameter to model the beginning of bud burst d_{bb} , which can be described as:

$$d_{bb} = d \text{ if } \sum_s^d (T_d - T_b)(d/d_{max})^w > T_{sum,d} \text{ with } T_d > T_b \quad (1)$$

where d is the day of the year, s is the starting date for summing up temperature, d_{max} is the latest observed date of the beginning of a phenological phase, T_d is the daily temperature, T_b is the base temperature above which temperature contributes to bud burst (normally set as 0 °C, 5 °C or 6 °C), w is the weighting factor for the daily temperature with values of 0 (no dependence of d/d_{max}), 1 (linear increase of the dependence of d/d_{max}) or 2 (quadratic increase of the dependence of d/d_{max}), and $T_{sum,d}$ is the threshold temperature sum of the day d .

For the determination of the phenological timings it was assumed that the threshold temperature sum for bud burst rises as the year proceeds. This dependence is demonstrated in Fig. 2 where the average values of the temperature sums for the leafing of beech (1,415 single values) and for the May shoot of spruce (704 single values), that coincide with the respective date, are shown (temperature and phenological data are taken from the climate stations for parameterisation (Fig. 1); Other parameters are $s = 1$ January; $T_b = 0$ °C; $w = 0$).

A distinct increase of the threshold temperature sum can be seen for the leafing of beech as well as for the May shoot of spruce with increasing day of the year. Therefore the threshold temperature sum was calculated according to Eq. 2:

$$T_{sum,d} = ae^{bd} \text{ with } d_{bb,min} < d < d_{bb,max} \quad (2)$$

a and b being parameters specific for every phenological phase and $d_{bb,min}$ and $d_{bb,max}$ are the minimum and maximum dates for the beginning of a phenological phase in which Eq. 2 is valid.

To compute a and b in Eq. 2, mean, maximum and minimum values for T_d are tested as independent variables. Different starting

dates (1 January, 1 February and 1 March), different base temperatures T_b (0 °C and 5 °C) and weighting factors w for the daily temperature (0, 1 or 2) were assumed to optimise the Eqs. 1 and 2. This way the breaking of bud dormancy can be taken into consideration, which requires low temperatures between December and March (Menzel 1997). After summing-up the daily temperatures according to Eq. 1 until the beginning of the phenological observations for all years and stations, a and b in Eq. 2 can be calculated. By means of the coefficient of correlation and the standard error of the regression equations the parameters for Eq. 1 were defined.

Results

Model construction

For the calculation of the timings of the phenological phases, leafing of beech and oak and the May shoot of spruce and pine, by means of the Eqs. 1 and 2 the daily maximum temperature with $T_b = 0$ °C and a quadratic loading, i.e. $w = 2$, turned out to be most suitable for modelling. While the optimal starting date for summing-up the temperature for beech was 1 January, for the three other phenological phases the most favourable starting date was 1 March. Table 1 gives an overview of the parameters and the statistics.

The average of the 491 observations of beech indicates a flushing of the leaf on 3 May, whereas the average of the 440 observations of oak is 10 May. The mean values for the timing of the May shoot are 12 May for spruce (437 observations) and 15 May for pine (370 observations). The standard deviations of the observations range from 7.5 days for the leafing of beech to 8.9 days for the May shoot of pine.

The relationships between the maximum temperature sum and the leafing date of beech and oak can be seen in Fig. 3. The increase of the threshold temperature with increasing day of the year is probably related to the more frequent recurrence of cold periods in the main leafing period from the beginning of April to the end of May (Fig. 4). It can be assumed that these ‘singularities’, which have probabilities of occurrence of up to 84% (Bissoli 1991), cause an increase in the threshold

Table 1 Model parameters and statistics for the fitting of Eqs. 1 and 2 for the calculation of the timings of bud burst of beech, oak, spruce and pine. For all phenological phases the daily maximum temperature is taken as T_d , T_b is set as 0 °C and w is set as 2 (n number of observations; SD standard deviation; s starting day; doy day of the year; obs observations; a , b factors; $d_{bb,min}$, $d_{bb,max}$ minimum and maximum dates for the validity of Eq. 2; SE standard error; r coefficient of correlation; MAE mean absolute error)

Parameter	Leafing of beech	Leafing of oak	May shoot of spruce	May shoot of pine
n	491	440	437	370
Mean (date)	3 May	10 May	12 May	15 May
SD_{obs} (days)	7.5	8.2	7.8	8.9
s (date)	1 January	1 March	1 March	1 March
$d_{bb,min}$ (doy)	115	115	120	125
$d_{bb,max}$ (doy)	135	140	140	145
a	20.8	19.1	19.6	17.3
SD for a	1.64	1.25	1.41	1.46
b	0.0217	0.0228	0.0228	0.0241
SD for b	0.0006	0.0005	0.0005	0.0006
r	0.83	0.91	0.89	0.90
MAE	25.5	23.8	29.0	37.0
SE (°C)	32.1	31.0	36.9	48.0

Fig. 3 Maximum temperature sum and leafing date of beech (*Fagus sylvatica* L., left) respective of oak (*Quercus robur* L., right)

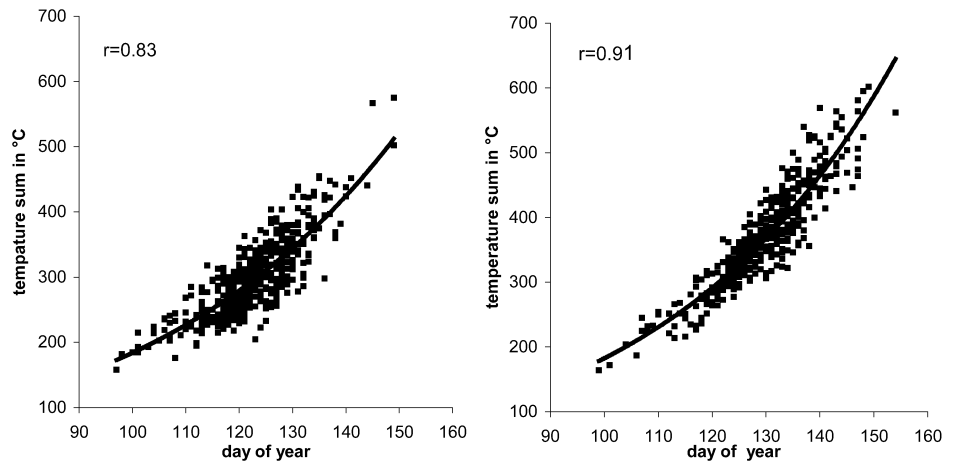
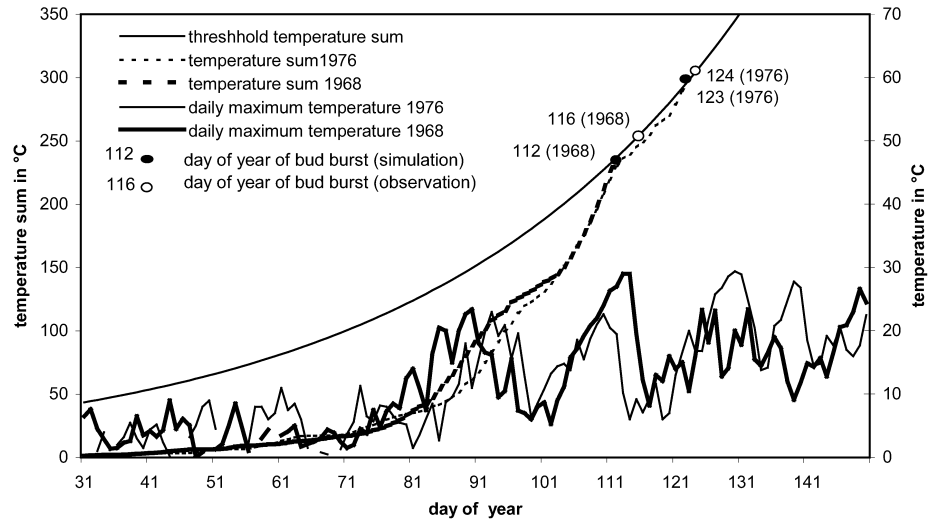


Fig. 4 Daily maximum temperature, temperature sum and threshold temperature sum for the leafing of beech (*Fagus sylvatica* L.) of the years 1968 and 1976 at the Amberg station in southern Germany



temperature sum to overcome the chilling effects of these cold periods.

The regression statistics as well as the factors a and b for the estimation of the threshold temperature sums by Eqs. 1 and 2 are summarised in Table 1. The strong correlations between the temperature sum and the begin-

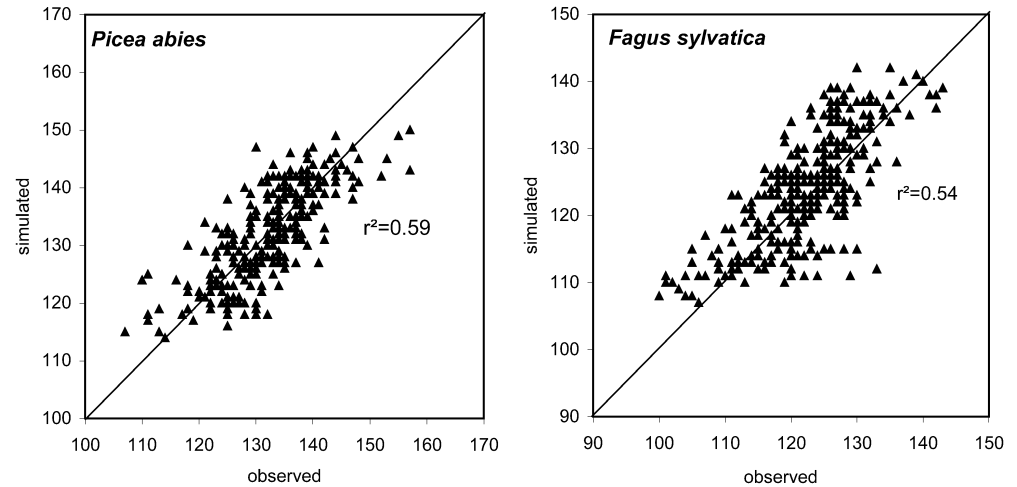
ning of the phenological phases – as can be seen in Fig. 3 and Table 1 – are expressed by the coefficients of correlation with values of 0.83 and 0.91 for the leafing of beech and oak and of 0.89 and 0.90 for the May shoot of spruce and pine. The mean absolute error of the

Table 2 Results of the validation of the regression models for the leafing of beech and oak and for the May shoot of spruce and pine (n number of observations; SD standard deviation; obs observation; sim simulation; r^2 explained variance; MAE mean absolute error)

Parameter	Leafing of beech	Leafing of oak	May shoot of spruce	May shoot of pine
n	340	265	287	226
Mean _{obs} (date)	2 May	8 May	12 May	16 May
SD_{obs} (days)	7.4	7.8	8.2	8.1
Mean _{sim} (date)	4 May	9 May	12 May	16 May
SD_{sim} (days)	8.2	8.3	7.7	8.7
r^2	0.54*	0.55*	0.59*	0.56*
MAE (days)	4.9	4.7	4.4	5.0

* $P < 0.001$

Fig. 5 Simulated and observed values of the May shoot of spruce (*Picea abies* L., left) and the leafing of beech (*Fagus sylvatica* L., right)



regressions ranges from 23.8 °C for the leafing of oak to 37.0 °C for the May shoot of pine.

Validation

A second set of temperature and phenological data was used to validate the regression models (Fig. 1). The mean starting dates for the leafing and the May shoot at all climate stations used for validation as well as the validation statistics are presented in Table 2.

The phenological values observed at the 15 climate stations include 340 leafing dates for beech, 265 leafing dates for oak, 287 May shoot dates for spruce and 226 May shoot dates for pine. The mean values of the observation data are the 2 May for beech, 8 May for oak, 12 May for spruce, and 16 May for pine. The computed starting dates for the May shoot phases have the same average values as the observed values. For the leafing of beech and oak differences between simulated and observed mean starting dates of 2 days and 1 day respectively were calculated. The standard deviations of the observed and simulated mean values are almost the same; the maximum difference is 0.8 day for the leafing of beech. The explained variances of the observed and simulated starting dates vary between 0.54 for the leafing of beech and 0.59 for the May shoot of spruce (Table 2). All correlations are highly significant ($P < 0.001$).

Figure 5 shows the simulated and observed starting dates for the occurrence of foliage of beech and spruce.

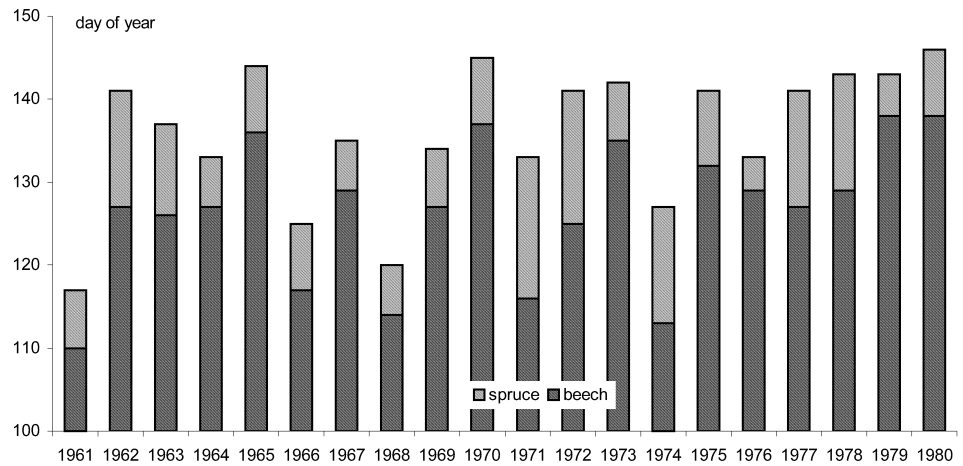
With values from 4.4 days for spruce to 5.0 days for pine, the mean absolute errors between the simulated and the observed starting dates lie within a small range and are distinctly below the standard deviations of the observations (Table 2). Thus, the fitted Eqs. 1 and 2 are able to estimate the leafing dates of beech and oak as well as the May shoot dates of spruce and pine, and can be used as a general module in tree-growth models.

Application

To show the effect of the differences in the timing of bud burst, the phenology model has been implemented in the growth model BALANCE, which simulates growth of individual trees (beech, oak, spruce, pine) under variable environmental conditions (CO_2 , climate, soil, competition), including air pollution and stress. The biomass of all compartments is calculated from measured or estimated dimensional variables (tree position, height, diameter, crown base height, and crown radii). Decisive driving forces are light, temperature and precipitation, optional inputs are relative humidity, wind speed, CO_2 and O_3 concentrations as well as nitrogen deposition.

Relative light availability is calculated separately for several crown sectors as a function of the leaf area and foliage type above the particular sector. This calculation considers the relative position of trees within a stand explicitly. Since light distribution is recalculated as soon as the leaf area changes, the model is particularly suitable

Fig. 6 Calculated beginning of the leafing of beech (*Fagus sylvatica* L.) and of the May shoot of spruce (*Picea abies* L.) in Weihestephan (southern Germany) over the years 1961–1980



for competition effects in mixed stands. While stand conditions are computed daily, physiological processes (assimilation, respiration, senescence, allocation etc.) are calculated for each crown and root system sector in monthly or decadal time steps from the aggregated driving variables. The dimensions of each crown and stem and the mortality of a tree are computed annually on the basis of the individual carbon balance. More information about the model can be found in Grote and Pretzsch (2002).

In contrast to the physiological processes mentioned above, phenology i.e. the beginning of leafing and the May shoot is accounted for the day it is calculated. With the beginning of bud burst foliage biomass and leaf area change as well as the light availability and radiation absorption. Thus, the date of foliage emergence in a tree determines its assimilation and respiration rate but also affects the environmental conditions of the trees in its vicinity.

The following example demonstrates the influence of phenology on the growth of a mixed forest stand, simulated with the model BALANCE. The simulation is initialised with an artificially created, 20-year-old stand with a distance between the trees of 1.4 m, which is composed of 15 spruce and 12 beech trees. The trees are the same size and are planted in rows. Weather data are taken from the Weihestephan climate station (Fig. 1) for the years 1961 to 1980. Tree, stand and soil parameters essential for BALANCE have been taken from the literature or are determined from investigations at the Freising 813 site, a mixed forest of spruce and beech (Pretzsch et al. 1998). Please note that the initialisation and parameterisation are not yet fully evaluated with measured field data. We thus emphasise the relative rather than the absolute growth responses of the species.

Figure 6 shows the beginning of the leafing of beech and of the May shoot of spruce in the period from 1961 to 1980, calculated with the phenology module. Differences between the years of up to 28 days for beech and of up to 29 days for spruce are obtained. The differences between the beginning of leafing and the May shoot of the two species range from 4 days in 1976 to 17 days in 1971.

While the mean leafing date for beech is day 127, the mean date for the beginning of the May shoot of spruce is day 136.

For the simulation of the development of the initialised trees the date of foliage occurrence is taken either as a static value or as a temperature-dependent output of the described phenological module (dynamic value). The observed average values are used for the static-value run. For comparison, the development of average total tree biomass and average diameter at breast height of spruce and beech trees during the simulation period are presented in Figs. 7 and 8.

While in the first decade of the 20-year period the total biomass of spruce (Fig. 7, left) develops almost equally in the two runs, in the second half of the period biomass increases faster in the simulation with the dynamic phenology. At the end of the 20-year period the total biomass dry weight produced with static phenology is only 87% of that produced with the new phenological module (282 kg compared to 324 kg C in average per tree).

In contrast, the biomass development of beech is quite similar in the two runs (Fig. 7, right). The dynamic calculation of phenological dates means that years with more production are counterbalanced by other years, when less biomass is produced. Although, in the end, the dry weight developed with the dynamic phenology model amounts to 370 kg C on average per tree, and is thus approximately 1% higher than that calculated with the static dates (365 kg C on average per tree), a slight tendency for decreasing growth with dynamic phenology calculation is apparent.

When we take a look at the development of diameter at breast height, which is an important parameter used for the estimation of productivity in forests, almost the same development as outlined for total biomass is apparent. Spruce profits by the dynamic phenology calculation – particularly since 1968. For beech, in most cases only small differences occur, indicating a hardly detectable shift in the dynamic phenology calculation from benefit to decrease (Fig. 8).

Fig. 7 Monthly values of total biomass dry weight of spruce (*left*, mean of 15 single trees) and beech (*right*, mean of 12 single trees) over the years 1961–1980 based on calculated dynamic timings and on mean (*static*) starting dates for the leafing and the May shoot

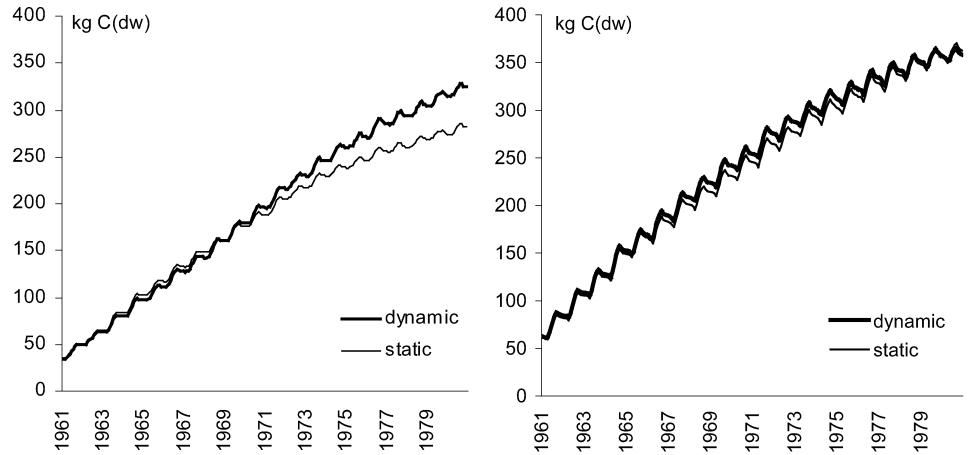
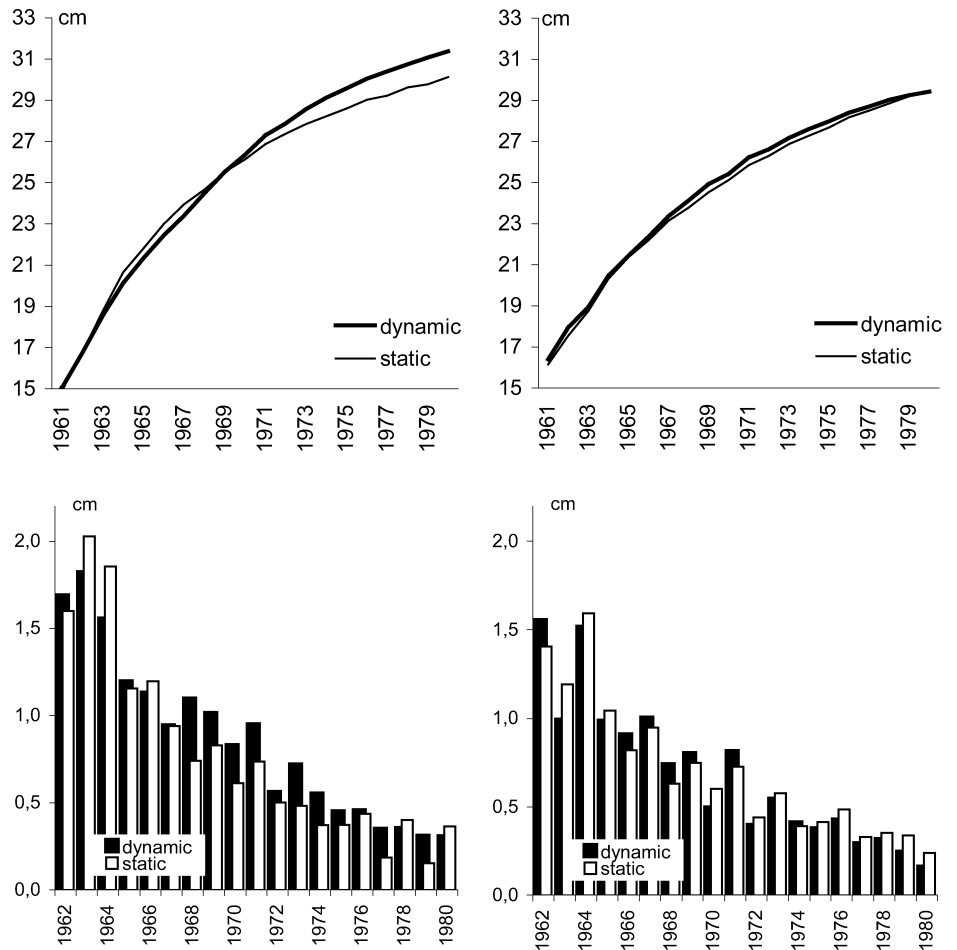


Fig. 8 Increase of the diameter at breast height of spruce (*left*, mean of 15 single trees) and beech (*right*, mean of 12 single trees) over the years 1961–1980 based on the calculated dynamic timings and on the mean (*static*) starting dates for the leafing and the May shoot (*upper figures* sums, *lower figures* annual increments)



Nevertheless, in single years, the differences in the timing of bud burst can lead to considerable deviations between the increments in diameter at breast height of the two simulation runs for both species. The results for the years 1970 and 1971, shown in Table 3, are taken from the model run described above. These years were chosen because the weather conditions of 1970 and 1971 were similar, whereas the leafing and May shoot dates were

different. As can be seen in Table 3 the annual mean temperatures were 7.9 °C in 1970 and 8.1 °C in 1971. Also the temperatures during the summer months – the period in which the main growth occurs – were almost identical in the 2 years. Spring temperatures of the years 1970 and 1971, in contrast, diverge by 2.2 °C, resulting in different starting dates for leafing and the May shoot.

Table 3 Weather conditions, phenology and increase of the diameter at breast height (*dbh*) at the Weihestephan climate station in southern Germany in the years 1970 and 1971 (*doy* day of the year)

Parameter	1970	1971	Difference 1971–1970
Increase in dbh (cm)			
Beech – static	0.60	0.73	0.13
Beech – dynamic	0.50	0.82	0.32
Spruce – static	0.61	0.74	0.13
Spruce – dynamic	0.83	0.95	0.12
Phenology (doy)			
Leafing of beech	137	116	21
May shoot of spruce	145	133	12
Temperature (°C)			
Mean	7.9	8.1	0.2
Spring	5.7	7.9	2.2
Summer	16.3	16.1	–0.2
Precipitation (mm)			
Mean	891	694	–197
Spring	192	191	–1
Summer	342	292	–50

Precipitation sums for the 2 years show differences for the whole year of about 200 mm but only of about 50 mm during the summer month. Furthermore, the huge precipitation sums in spring (almost 200 mm in both years) presumably led to a saturation of the soil with water at the end of spring. Together with the relatively high absolute amounts of precipitation in summer, soil water availability was always high and enabled almost the potential evapotranspiration to be reached. As can be deduced from the works of Rötzer (1996), the maximum potential evapotranspiration in this region is about 120 mm/month in summer for both beech and spruce. Müller-Westermeier et al. (2001) calculated the potential grass reference evapotranspiration sum to be 260–270 mm for the summer months. So neither temperature nor precipitation seems to be the main reason for the differences of the growth development in the years 1970 and 1971.

The simulated increase in diameter at breast height in 1970 was estimated to be 0.61 cm (basis: static phenology) and 0.83 cm (basis: dynamic phenology) for spruce, whereas it was estimated to be 0.60 cm (basis: static phenology) and 0.50 cm (basis: dynamic phenology) for beech. The increase in 1971, on the other hand, was 0.74 cm and 0.95 cm, respectively for spruce and 0.73 cm and 0.82 cm, respectively for beech. This means that while, in most cases, there is a difference between the 1970 and 1971 values of approximately 0.13 cm, in 1971 the difference is almost threefold (0.32 cm) for the dynamic simulation run of beech. This remarkable difference in diameter at breast height for beech in 1971 can be ascribed to the obviously earlier leafing. In 1971 the leafing of beech was 21 days earlier than in 1970. The May shoot of spruce, however, was only 12 days earlier. Hence, in 1970 beech trees had a developmental advantage of only 8 days compared to spruce, whereas in 1971 the advantage was 17 days (see Fig. 6), which certainly

influenced the strong increase of the diameter at breast height of beech in 1971.

Discussion

Phenology model

The regression models for the calculation of the timings of bud burst of beech, oak, spruce and pine, which are described in this paper, are intended to provide a simple but useful improvement to growth models. The equations described are particularly suitable because of their generality and low input requirements. This is a major advantage over “phenology models” that have a complex structure and/or need several input variables and/or hourly information (e.g. Kaduk and Heimann 1996; Menzel 1997; Snyder et al. 1999; Chuine et al. 1999; Orlandi et al. 2002). Furthermore, the calculation of the timings is not very time-consuming and can easily be implemented in tree-growth models.

On the other hand, the validation of the regression models showed results similar to those obtained with more sophisticated phenological models. For example the root-mean-square error that Snyder et al. (1999) obtained for estimated phenological periods of cherry and kiwi was between 2.8 days and 8.8 days, and the mean absolute errors of the “full-bloom models” for peach cultivars (Schwartz et al. 1997) were between 3.5 days and 3.9 days with an explained variance between 43% and 51%. The calculated mean absolute error values of the regression models of 4.4–5.0 days, as well as the values of the explained variance: 54%–59% (Table 2), are close to the mean absolute errors of 4.8–7.5 days and the explained variances of 36%–82% for the bud burst models for beech, spruce, oak and pine presented by Cannell and Smith (1983, cited in Menzel 1997), Kramer (cited in Menzel 1997) and Menzel (1997). The expected variance that Chuine et al. (1999) presented for the flowering of 12 tree species by using different models was 58% on average over all species and models and ranged from 0% to 93%.

Reasons for deviations of simulated values from observations are manifold. The climatic conditions of the phenological site and the climate station, for example the exposure and inclination (Schnelle 1955; Chen 1994), the underlying surface (Snyder et al. 2001) or the surroundings (Rötzer 1996), can differ so that the temperature data do not exactly describe the phenological site. Furthermore, the age and height of a tree influence its leaf phenology (Seiwa 1999), and the genotype of the plant species can also affect the timing of phenological phases. For example, Rötzer and Chmielewski (2001) found mean differences of 6 days in the beginning of leaf unfolding of two varieties of *Fagus sylvatica* as well as in the May shoot of two varieties of *Picea abies*. Other climatic parameters, like air humidity, precipitation (Wielgolaski 2001), radiation (Cenci and Ceschia 2000) or even depth of snow pack (Inouye et al. 2002), can have

an influence on a phenological phase, and non-climatic parameters such as soil moisture and nutrient level (Wielgolaski 2001) or CO₂ (Jach and Ceulemans 1999; Sigurdsson 2001) can also change the timings of phenological phases.

The contribution of all the influences mentioned above can not easily be determined and is not likely to be constant across the region and plant species. Thus, a significant impact of these factors can not easily be demonstrated within a larger region and we do not expect that they will soon be included in regression models such as those presented here. At least for mid-Europe, temperature seems to be the major driving force for the onset of spring phenophases (Chmielewski and Rötzer 2001, 2002) and further climatic parameters do not lead to significant improvements (Menzel 1997). So, considering the high year-to-year variability of the timings of phenological phases, the regression models presented provide satisfactory estimations of the beginning of leafing and the May shoot for the use in growth models.

Application

For the modelling of growth within the year the timing of the phenological phases (emergence, leafing, tillering, flowering, leaf fall etc.) plays an important role (see e.g. Kuchar 1989 and Maier 1997 for crops or Kramer et al. 1996 and Grote 2003 for forest stands). Particularly in mixed forests the competition between the species is likely to change in different years or under climatic change if their phenological behaviour is differently sensitive to these environmental conditions. This is of particular importance in medium-term simulations over several years, when year-to-year variations can be neither neglected nor empirically initialised. It should be considered that an earlier beginning of bud burst cannot only be profitable to the tree because of the longer period of assimilation but also because the surrounding trees are receiving less light and thus are likely to be less effective in their struggle for available resources. These mechanisms mean that a responsive species in a mixed forest should be able to gain a valuable advantage over species with a less adaptive behaviour.

As shown in Fig. 7 and Fig. 8 the consideration of a dynamic phenological behaviour can be an important improvement for estimating growth in forests. The simulations also showed, however, that this is not inevitable but depends on the sensitivity of the tree species and the variability of the climate. Furthermore, it should be remembered that the sensitivity of growth indicators like biomass or diameter at breast height depends on the relative growth that is obtained at a particular site. This means that tree growth under site conditions close to the optimum may be less affected by phenology than growth under low-resource conditions. Thus, averaged over the years the dynamic calculation of bud burst is not profitable in the case of beech, although in some years (1971) the growth obtained with this

method was considerably higher than when a static (mean) value was used for bud burst.

In our calculations, spruce lent itself much more to the dynamic determination of its phenology than beech. This indicates that the implementation of a mechanistic phenological behaviour is of particular importance if the development of mixed forests is being analysed. In contrast to growth in a pure stand, the impact of weather conditions on growth and phenology in mixed stands changes the competition between species in the same direction and thus provides a positive feedback loop. In our example, this led to spruce having an increasing advantage over beech. The increased growth of spruce counterbalanced any advantage that beech would have had from dynamic phenology in a pure beech stand. At the end of the simulation the increased competitiveness of spruce even led to a tendency of beech growth to decrease.

White et al. (1999) found that an increase in the length of the growing season increased net ecosystem production and gross primary production of deciduous forest stands in the eastern USA. But whether spruce or beech, i.e. coniferous or deciduous trees, or light- or shade-tolerant tree species in a mixed stand profit from an earlier beginning of bud burst, is – as shown in the example – probably closely connected to the stand structure, i.e. the spacing, the height of trees, the number of trees in the understorey or predominant trees, etc. To analyse these multiple influences and their interrelations on phenology and tree growth, further investigations have to be carried out. In this article we only intended to demonstrate that the calculation of the timings of bud burst has to be taken into account when the development of forest stands, in particular mixed forest stands, is modelled.

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