# A MODEL OF LEAF BUDDING AND DEVELOPMENT FOR A MATURE *QUERCUS* FOREST

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## SUMMARY

(1) Budburst and leaf expansion up to maximal leaf area index were followed from 1976 to 1983 in a 120-year-old *Quercus petraea* stand.

(2) A phenological model was formulated to predict the date of budburst and the increase in leaf area as a function of cumulative temperature and of day-length. Budburst occurs when the temperature sum of the past 10 days exceeds a given threshold, which is a decreasing function of day-length. Leaf area increases with the temperature sum since budburst, and reaches its greatest value when the temperature sum exceeds a given threshold, which is also a function of day-length.

(3) The model was tested during the growing season of 1982 and 1983. Simulated dates of budburst and leaf area index development were in close agreement with the measurements.

## INTRODUCTION

Energy and mass exchanges of a deciduous forest are influenced by the temporal variations in leaf area index (Rauner 1976; Miller & Stoner 1979; Baldocchi *et al.* 1984). The present study is part of an investigation on water balance, carried out in a mature oak (*Quercus petraea* (Matt.) Liebl.) stand in the middle of the Fontainebleau forest (Nizinski & Saugier 1988a,b), 50 km south of Paris, France. This paper deals with prediction of the temporal dynamics of the forest canopy. An empirical model with a 1-day time resolution was developed to predict the dates of budburst, the end of leaf growth and the value of the leaf area index during the shoot elongation period. Mean daily air temperature and day length were used in the model, but environmental variables such as soil-water content and soil temperature were not included as they vary little from year to year. According to Cannell & Smith (1983), the incorporation of soil temperature in budburst predictive models has a negligible effect on their accuracy.

Numerous predictive models exist for the bud elongation process in northern temperate conifers (Owens, Molder & Langer 1977; Thomson & Moncrieff 1982; Cannell & Smith 1983, 1986; Perala 1985), but there are few models for deciduous forests. In the literature on budburst timing in trees, it is implied that a relationship exists between the date of budburst and cumulative mean daily air temperature, measured from the first day of the months of January, March or April up to the date of budburst. According to Castonguay, Boisvert & Dube (1984), these three starting dates yielded the same results; thus, these arbitrary dates are of statistical rather than of biological nature. The short period immediately before budburst was studied. Budburst is the final stage of the tree's physiological 'activation' process, which can be observed by root uptake and transloca-tion of water, nutrients and carbon (Braun 1983, 1984) and change in bud water content and ionic concentration (Essiamah & Eschrich 1986). This period has specific length. It is

included in our empirical model of the bud elongation process based on day-length and cumulative temperatures.

## STUDY SITE

Field work was carried out on plot number 267 ('*Gros Fouteau*'), situated on a rise in the centre of the 22 000 ha Fontainebleau forest near Paris (48°26′N, 2°41′E) at 131 m altitude. The limestone bedrock is covered with quaternary wind-blown silicious sand. The depth of the sandy layer has determined the characteristics of the plot's soils. which are leached or podzolic. The climate of the region is partly maritime, partly subcontinental. The mean annual precipitation (1883–1983) is 720 mm, being fairly evenly distributed throughout the year, with a maximum of 72 mm in January and December and a minimum of 48 mm in March and 46 mm in April. The mean annual temperature is 10 °C (average monthly maximum of 18 °C in July and minimum of 2 °C in January). The overstorey canopy is exclusively 120-year-old oaks (*Quercus petraea*). The mean tree height is 30 m, stand density is 182 trees ha$^{-1}$ and the total basal area is 33·8 m$^2$ ha$^{-1}$. The understorey consists mainly of seedlings and saplings of beech (*Fagus silvatica* L.). According to Lemée (1966), the vegetation of the sample site is characteristic of an oak stand on acid soils (*Querco–Fagetea, Quercion robori-petraeae*).

## METHODS

### Phenological assessments

Bud elongation was assessed using the phenological observation scale of Aussenac (1975):

b0 = bud dormancy phase, the buds keep their winter size;
b1 = bud swelling phase, the scales of buds remain closed;
b2 = first green leaf phase, beginning of bud burst;
b3 = real budburst, young leaves protrude beyond the bud scales;
b4 = young leaves are completely free of bud scales.

The physiological 'activation' period is equivalent to stages b1 and b2. In this study, actual budburst was considered as stage b3. During stage b4, the shoots increase to their final size.

### Sampling techniques

Leafing out was recorded in two ways. Budburst and leaf elongation measurements were made on five mature trees of *Q. petraea*, 240 leaves in 1982 and 150 leaves in 1983. Each sampled tree and shoot was randomly selected and identified by numbering. The date of budburst was defined as the day when 50% of the lateral buds of the trees reached stage b3, and the leaf area index was considered as maximal if the values of the lengths and widths of leaves were stable for 50% of the leaves. Variation in recording of dates was up to 1 day (24 h).

The dates of budburst and of the start of the fully-leafed phase of the period 1976–80 were available (J. Y. Pontailler, unpublished). As these dates were monitored in the same way, although the variation in recording was up to 2 days (48 h), the shoot phenology results could then be extrapolated to the forest-canopy level.
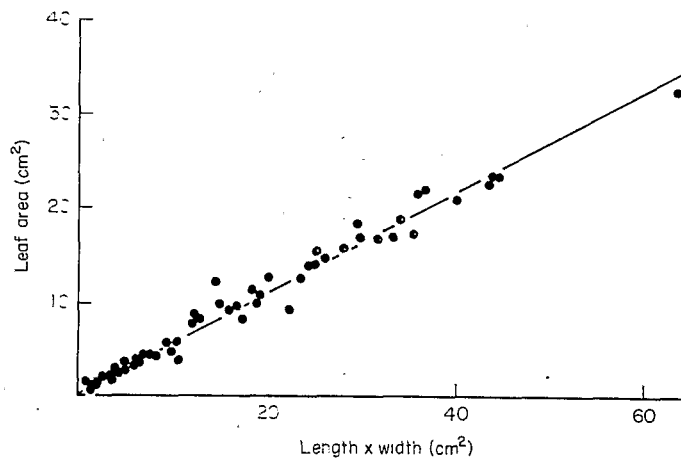
Fig. 1. Relationship between the mature actual leaf area ($LAI_{max}$) of *Quercus petraeae* and the leaf area (*LA*) calculated from the product of leaf length and width (*LW*) ($LA=0.52LW+0.64$, $r=0.990$). The 54 experimental points were recorded in August, 1981 at Fontainebleau forest.

## Leaf area measurements

During the elongation phase, every sampled shoot at the research site was measured with a steel tape (error range ± 1 mm) to determine the length of the main vein without the leafstalk and the width of the widest part of the leaf.

The leaf area (*LA*) was calculated from the product of length and width (*LW*). The relationship between the actual and the calculated leaf area was established using a linear regression for 54 leaves of varying sizes ($LA=0.52LW+0.64$, $r=0.990$). These shoots were harvested in August 1981 during the fully-leafed canopy stage and their actual areas were measured with a leaf-area meter (Delta T Devices; accuracy $0.1$ cm$^2$) (Fig. 1).

## Measurements of maximal leaf area index

Measurement of the maximal leaf area index was based on the assumption that the total leaf number and area measured on the tree would be the same as on the soil surface after autumnal leaf-fall. Two indirect-measurement techniques were used to estimate the maximal leaf area index. First, leaves were collected from fresh litter with a vertically-held needle (the 'needle' technique). The average number of leaves collected with each stab represents the maximal leaf area index. Each measurement was repeated 100 times on 17 January 1983. Second, leaf-fall was monitored at weekly intervals from 1 September to 16 December 1983 using ten baskets with a total collecting area of 25 000 cm$^2$ (the 'basket' technique). The area of the sampled leaves was measured with a leaf-area meter. The leaf area index was thus the total area of harvested leaves per unit ground area. The maximal leaf area index found on a similar plot in 1975 using thirty grids with a total surface of 75 000 cm$^2$ was also used (G. Lemée, unpublished).

## Meteorological data

The mean daily air temperature (($T_{min}+T_{max}$)/2) for the period 1976–83 was calculated from records at the Fontainebleau-Ville meteorological station, 2 km from the study site.

TABLE 1. The eight budburst dates of *Quercus petraea* and its thermal time values
with a starting summation date of 1 March, the base temperature being 0 °C

| Years in order of budburst date | Budburst date | Mean daily air temperature (and number of days) from 1 March to budburst date | Cumulative mean daily air temperature from 1 March to budburst date (°C) |
|---|---|---|---|
| 1981 | 14 April | 10·4 °C (44 days) | 455·5 |
| 1976 | 20 April | 7·4 °C (50 days) | 367·8 |
| 1980 | 20 April | 6·9 °C (50 days) | 345·4 |
| 1977 | 24 April | 8·0 °C (54 days) | 431·7 |
| 1983 | 25 April | 7·6 °C (55 days) | 417·3 |
| 1978 | 27 April | 7·6 °C (57 days) | 432·1 |
| 1982 | 29 April | 7·9 °C (59 days) | 468·8 |
| 1979 | 10 May | 7·4 °C (70 days) | 520·7 |

TABLE 2. The earliest and latest dates of budburst of *Quercus petraea* recorded from
1976 to 1983

| Years | Budburst date | Cumulative mean daily air temperature of the 10 days before budburst date (°C) | Day-length on budburst date (min) |
|---|---|---|---|
| Earliest budburst, 1981 | 14 April | 135 | 815 |
| Latest budburst. 1979 | 10 May | 82 | 899 |

## RESULTS AND DISCUSSION

### *Date of budburst*

Budburst dates were first plotted against temperature sum alone, and then against temperature sum and day-length. The elongation rate of buds was analysed relative to the cumulative mean daily air temperature, using several starting summation dates from 1 November to 15 March and several base temperatures ranging from −5 to +10 °C. Table 1 lists the thermal time values with a starting summation date of 1 March (0 °C base temperature). Regardless of base temperature and the starting summation dates, thermal time varied from one year to the next and the higher the mean daily air temperatures from these starting summation dates, the earlier budburst occurred.

Cannell & Smith (1983) showed for *Picea sitchensis* (Bong.) Carr. that a decreasing exponential relationship existed between the number of day degrees above 5 °C from 1 February to budburst, and the number of cold days with a mean temperature ≤5 °C from 1 November to the time of budburst. If the number of cold days is replaced by day-length (which increases from 21 December), the date of budburst could be explained by the cumulative temperatures and the day-length. We therefore examined relationships between the day length on the day of budburst and (i) the mean daily air temperature summed from a fixed date to budburst and (ii) the mean daily air temperature summed on a given period before budburst. For both relationships, the base temperature varied between −5 and +10 °C. The best prediction was obtained with a period of 10 days before budburst and a base temperature of 0 °C by fitting a regression line using least-squares analysis ($r = 0.99$). The earliest and latest dates of budburst are given in Table 2.

TABLE 3. Budburst date and the first day of fully-leafed phase of *Quercus petraea* with number of days of leaf expansion phase, mean daily air temperature and cumulative mean daily air temperature recorded from 1981 to 1983

| | Year | | |
| --- | --- | --- | --- |
| | 1981 | 1982 | 1983 |
| Budburst date | 14 April | 25 April | 29 April |
| First day of fully-leafed phase | 14 May | 19 May | 18 May |
| Number of days of leaf expansion phase | 31 | 23 | 20 |
| Mean daily air temperature during leaf expansion phase (°C) | 9·7 | 11·4 | 12·0 |
| Cumulative mean daily air temperature during leaf expansion phase with 0 °C base temperature | 289·7 | 262·0 | 240·0 |

Figure 2 shows that the heat sum $S$ (in °C days) required for budburst is a decreasing function of day-length $D$ (in minutes):

$$S = (2·42 \times 10^{-2}D)/[(1·41 \times 10^{-3})D - 1] \qquad (1)$$

The asymptotes of eqn (1) have a specific biological significance. Budburst cannot occur when the denominator of eqn (1) is negative, i.e. for $D \leqslant 711$ minutes (day-length of March 16). When day length tends towards the infinite, $S$ tends towards 17·2 °C days, i.e. budburst cannot occur if the mean daily air temperatures during the previous 10 days were lower than $+1·7$ °C. In this study the maximal day length is 967 minutes (17–23 June). Thus, according to eqn (1), budburst cannot occur if the mean daily air temperatures during the 10 days prior to budburst were below $+6·4$ °C.
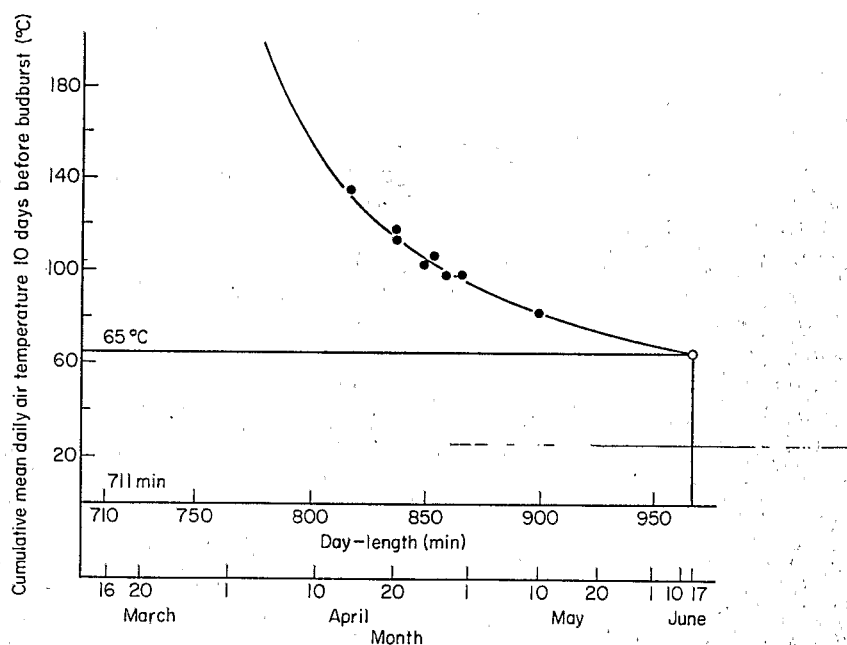


FIG. 2. Relationship between the cumulative mean daily air temperature (during the 10 days before budburst) and the day-length of the budburst date. The eight dates of budburst (●) of *Quercus petraea* were recorded from 1976 to 1983. The fitted line (——) is described by eqn (3) (see text).
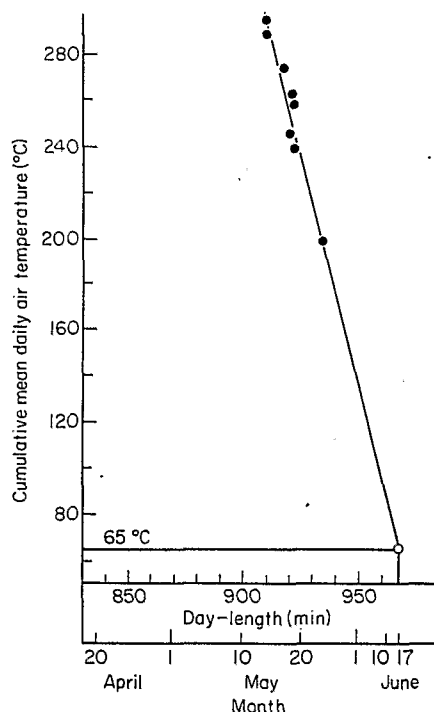
FIG. 3. Relationship between the cumulative mean daily air temperature (from budburst to $LAI = LAI_{max}$) and day-length of the first day with $LAI = LAI_{max}$. The eight dates of the first day with $LAI = LAI_{max}$ (●) of *Quercus petraea* were recorded from 1976 to 1983 at Fontainebleau forest. The fitted line (——) is described by eqn (2) (see text).

## First day of the fully-leafed phase

The leaves were fully elongated 18–31 days after budburst. *Q. petraea* did not produce any more leaves during the year. To estimate the date of the start of the fully-leafed phenophase, a similar analysis to that for the date of budburst was made. The date of the first day of the fully-leafed phase was examined in relation to (i) cumulative mean daily air temperatures for the leaf expansion period and (ii) temperature and day-length during the shoot elongation phase. Thus, for the last 3 years of observations, the higher the mean daily air temperatures, the shorter the shoot expansion phase (Table 3). On the other hand, the cumulative mean daily air temperature for the shoot elongation phase had a fluctuating value. As for budburst, the process was accelerated by an increase of the photoperiod. For the eight recorded dates, a linear relationship ($r = 0.975$) existed between heat sum $S'$ (in °C days) for the leaf expansion period and the day-length $D'$ (minutes) of the first day of the fully-leafed phase (Fig. 3).

$$S' = 4 \cdot 1 \ (983 - D') \tag{2}$$

where $S'$ is the cumulative mean daily air temperature for the leaf expansion period (between the budburst day ($db$) and day $d$), with 0 °C as the base temperature. Thus, in 1981 for example, leaf expansion was reached on 14 May when the day-length was 910 minutes and in 1979 on 24 May when the day-length was 934 minutes. The threshold of 983 minutes in eqn (2) is approximately the maximum day-length for the study site.

*Maximal leaf area index*

The mean maximal leaf area index was slightly above 4. Thus, for 17 January 1983, $LAI_{max} = 4·38 \pm 1·70$, $n = 100$ ('needle' technique) and for 16 December 1983, $LAI_{max} = 4·38 \pm 0·30$, $n = 10$ ('basket' technique). This is close to the maximal leaf area index measured by G. Lemée ($LAI_{max} = 4·26$ in 1975, unpublished). According to Rauner (1976), the maximal leaf area index in 100–200-year-old *Q. robur* forest is between 4 and 4·5.

## Model of the leaf area development

### Description of the model

The model produces a numerical output for the daily leaf area index of the forest. The simulation starts on the first day of the year (day $d = 1$) with the initial condition taken as $LAI_{d=1} = 0$. The model is algebraic, based on the empirical eqn (1) and (2). It requires two parameters, the maximal leaf area index and the longitude and latitude of the study plot. The inputs for the model were mean daily air temperatures and day-length, calculated at the study site using an equation given by Jones (1983).

### Predicting the date of budburst

The date of budburst was determined using the thermal time model given by eqn (1) (Fig. 2). For each day $d$ of day-length $D_d$, thermal time $S_d$ was calculated during 10 days from day $(d-10)$ to day $d$. If $S_d > S$ given by eqn (1) then budburst occurred on day $d$, otherwise the model proceeded to the following day (day $d+1$, day-length $D_{d+1}$) and the computations were repeated until the inequality was satisfied.

### Predicting the canopy leaf area index

The leaf area index for a day $d$ ($LAI_d$) was calculated using eqn (3) which follows from empirical relationship (2):

$$LAI_d = (LAI_{max}\sum_{db}^{d}Ta)/[4·1\ (983 - D_d)] \tag{3}$$

Thus, the calculated leaf area index ($LAI_d$) is the product of the maximal leaf area index ($LAI_{max}$) and of the heat sum between the day of budburst ($db$) and day $d$, divided by the heat sum required on day $d$ to reach the fully-leafed phase. If the value of the simulated leaf area index reached the value of the maximal leaf area index ($LAI_d \geq LAI_{max}$), then the forest leaf area index was considered constant and was taken as the maximal leaf area index for each day of simulation until the beginning of leaf-fall.

## Conclusion from the simulation

The aim of this study was to produce a model with 1-day time resolution for a 120-year-old *Q. petraea* forest which could predict the date of budburst, the date of the first day of the fully developed leaf period and the value of the leaf area index during shoot elongation. The resulting leaf area index was compared with measurements of the leaf area index in the Fontainebleau forest during the springs of 1982 and 1983 (date of budburst and the leaf area index for the leaf expansion phase). The simulated leaf area index was in close agreement with the measurements (Fig. 4). However, the model systematically over-estimated the leaf area index in the beginning of the shoot expansion phase and under-estimated $LAI$ at the end of the same phase. This was caused by the type
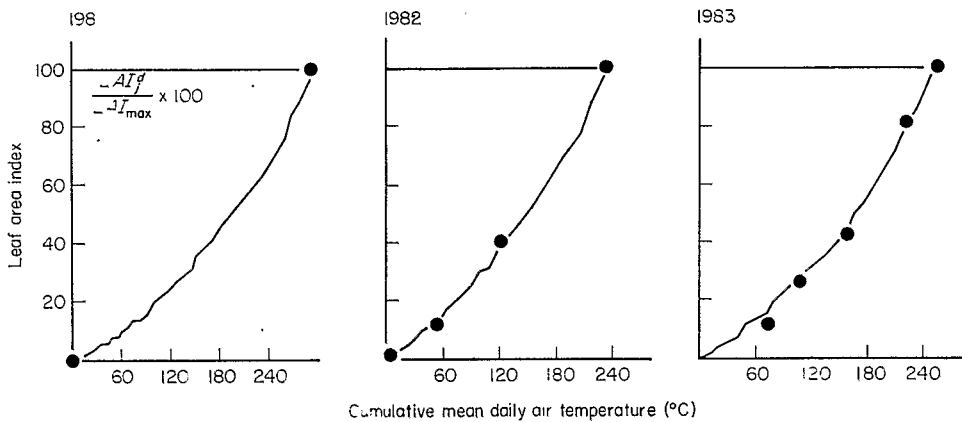
FIG. 4. Simulated (———) and measured (●) leaf area index evolution of *Quercus petraea* at Fontainebleau forest during the springs. (a) 1981: budburst date, April 15; first day of fully-leafed phase $(LAI = LAI_{max})$, May 14. (b) 1982: budburst date, April 30; first day of fully-leafed phase $(LAI = LAI_{max})$, May 19. (c) 1983: budburst date, April 26; first day of fully-leafed phase $(LAI = LAI_{max})$, May 18.

of relation used in the model. Equation (3) assumes a linear relation between shoot elongation rates and the sum of temperatures, whereas the actual relationship is sigmoidal (Durand 1967). The interest of this phenological model rests on its predictive accuracy of the budburst dates (error range ± 2 days, whereas the errors in previous models were up to 3–4 days and on its simplicity (two driving variables: mean daily air temperature, day-length). It is easy to insert into energy and mass exchange models for a deciduous forest. It has already been used by Halldin, Saugier & Pontailler (1984) and Nizinski & Saugier (1988a,b) for *Q. petraea* and Chassagneux & Choisnel (1986) for *F. silvatica*.

Both temperature sum (during 10 days prior to budburst) and day-length were needed to predict budburst date; thus both temperature and day-length have promoted budburst in *Q. petraea*. If the necessary temperature and day-length conditions were not met, is it possible that budburst would not occur? This may theoretically be true, but is highly improbable, since the latest budburst requires + 6·4 °C mean daily air temperature over 10 days only (Fig. 2).

Equation (1) raises two points of discussion; in the literature on budburst timing, authors have freed themselves from restrictions of time by using the cumulative mean daily air temperature measured from a fixed starting date. We again found the budburst process linked to time. This 10-day period could be due to a seasonal internal rhythm which ought to be dependent on genotype as well as on the climatic environment (or environment in general) which selected this genotype. The short period immediately before budburst can be interpreted as the final stage of the tree's physiological 'activation' process (Essiamah & Eschrich 1986); this period has a specific length varying from 6 to 24 days for *Acer pseudoplatanus* L., *Betula pendula* Roth, *Alnus glutinosa* Gaertn., *F. silvatica* and *Fraxinus excelsior* L. It should be added that the mean daily air temperature over 10 days prior to budburst dates was + 10·6 °C (mean value from 1976 to 1983); this may be explained as a seasonal adaptation of *Q. petraea* to the temperatures in the beginning of spring. The coefficients in eqn (1) could express the adaptive characteristics of *Q. petraea* to the average day-length and temperature conditions for growing in Fontainebleau forest. However, it would be interesting to study another

population of *Q. petraea*, as well as another temperate deciduous tree species, to know whether the parameter values in eqn (1) were a specific characteristic of the population, or of temperate tree species in general.

According to eqn (3), temperature in spring regulates leaf growth; the higher the mean daily air temperature, the shorter the shoot expansion phase. In fact, temperature is the essential factor in all biological processes—in this study the shoot elongation rate. On the other hand, increased day-length decreases the sum of the temperatures required to complete the shoot elongation process in a decreasing linear relationship (eqn (2), Fig. 3). Thus, *Q. petraea* behaves as the other temperate tree species for which increasing day-length had a promotive effect on leaf growth.

## ACKNOWLEDGMENTS

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