Vegetative bud-burst variability of European elms

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Abstract

The bud-burst dates of clones of *Ulmus minor*, *Ulmus glabra*, and *Ulmus laevis* were recorded in the field during the spring of 2000, 2001 and 2002 at six locations in five European countries. Meteorological data were obtained from stations close to the plots. Thermal time to bud-burst (T) and chilling (C) were calculated. A relationship on the form $T = a + b\, e^{rC}$ was fitted for each species. In the three species, winter rest release seems to be controlled by two opposite quantitative effects of the temperature, which interrelate according to an inverse exponential relation. Besides, the bud-burst date was found to be stable between years characterised by different winter thermal trends. These three Elm species have small chilling requirements. *U. minor* has chilling requirements lower than those of the other two species, in agreement with the more southern distribution.

Key words: *Ulmus minor, Ulmus glabra, Ulmus laevis,* thermal time, chilling.

Resumen

Variabilidad en la brotación de las yemas vegetativas de los olmos europeos

Durante las primaveras de los años 2000, 2001 y 2002 se registró en campo, en seis localidades de cinco países europeos, la fecha de apertura de yemas en un número de clones pertenecientes a *Ulmus minor*, *Ulmus glabra* y *Ulmus laevis*. Simultáneamente se obtuvieron datos meteorológicos en estaciones próximas a las parcelas. Se calculó los grados día (T) y el requerimiento de frío (C). Para cada especie se estableció una relación de la forma $T = a + b\, e^{rC}$. En las tres especies, la interrupción de la quiescencia parece estar controlada por dos efectos termales cuantitativos opuestos, relacionados por una exponencial inversa. Se ha encontrados que la fecha de apertura de yemas ha sido estable incluso en años con características térmicas invernales considerablemente diferentes. Los requerimientos de frío son pequeños en las tres especies de olmo. *U. minor* requiere fríos menores que las otras dos especies, lo que es consistente con su distribución más meridional.

Palabras clave: *Ulmus minor, Ulmus glabra, Ulmus laevis,* grados día, requerimiento de frío.

Introduction

In temperate and boreal climates, woody plants are dormant during late autumn and winter. In this physiological condition, the opening of buds is prevented even if favourable temperatures occur (Wareing, 1956; Nitsch, 1957; Vegis, 1964). Some experiments have demonstrated that the deficiency of winter cold produces considerable anomalies in bud-burst, shoot growth, and in the entire development of the tree in many arboreal species (Falusi and Calamassi, 1990; Champagnat, 1993). Generally, temperatures between 0°C and 10°C are considered efficacious for releasing dormancy, with an optimum at about 5°C (Perry 1970). Once dormancy is released, buds resume growth at a

rate that may be positively correlated to temperature in a linear manner (Cannell and Smith, 1983). It is assumed that bud-burst occurs after accumulation of a certain thermal sum above a threshold temperature. High correlations between the bud-burst period and the thermal time to bud-burst have been previously demonstrated. Furthermore, in many woody species from temperate regions, the effect of cold and heat on the growth of buds are not independent, and the amount of heat necessary for bud-burst decreases —within certain limits— with the increase in chilling received during the dormancy period (Cannell and Smith, 1983; Murray *et al.*, 1989; Hunter and Lechowitz, 1992; Heide, 1993a, 1993b).

Phenology of trees has gained interest during the past years within the context of «global climatic change». Many models that simulate phenological events have been developed in order to evaluate the responses of the vegetation to climatic changes and to the relative changes in the energy balance-sheet. Models that provide bud-burst dates of the trees (Murray *et al.*, 1989; Hänninen, 1990; Hunter and Lechowicz, 1992; Kramer, 1994a; Chuine *et al.*, 1999) identify temperature as the principal environmental factor regulating the timing of bud-burst. Several models consider only the action of the active temperatures on the springtime growth of buds (Cannell and Smith, 1983; Hunter and Lechowicz, 1992), while others also consider the action of the chilling temperature (Landsberg, 1974; Sarvas, 1974; Cannell and Smith, 1983; Murray *et al.*, 1989; Kramer, 1994a, 1994b). The classic bud-burst models have shown a certain degree of accuracy in predicting the bud-burst dates of different species on a local scale, but have been less reliable in making predictions on a global scale.

Within the framework of the RES GEN project, financed by the European Union and devoted to the «Coordination for conservation, characterisation, collection and utilisation of genetic resources of European elms», the plant material conserved in different national collections of clones has been evaluated for the purpose of identifying desirable characteristics of the clones in the perspective of their reintroduction into the environment.

Particular attention has been given to the timing of vegetative bud-burst, because this is considered to be of primary concern in evaluating the risk probability of damage from late frost, and also considering that some sort of relation may exist between the time of bud-burst and the susceptibility to Dutch elm disease.

In this study, the variation in timing of vegetative bud-burst has been analysed for the three European species of elm —*Ulmus minor, Ulmus glabra* and *Ulmus laevis*— within six locations in five European countries. The relation between the bud-burst date and the trend of chilling and thermal time was studied.

Materials and Methods

Clones and experimental facilities

During the spring of 2000, 2001 and 2002, bud-burst phenology of 875 clones (including 315 clones represented in two or more collections) belonging to *Ulmus minor* Mill. *sensu latissimo* (386 clones), *Ulmus glabra* Huds. (386 clones) and *Ulmus laevis* Pall. (103 clones) was observed in the field, at six locations. Due to the large variability and controversial taxonomy of the field elms (Armstrong and Sell, 1996), the binomial *Ulmus minor* Mill. *sensu latissimo* recommended by Richens (1980) was used for all the field elm clones included in the collections.

The clones of putative natural hybrids between *U. minor and U. glabra* were not analysed in the present study.

Trees were planted in Geraardsbergen (Belgium; 50° 46' N, 3° 55' E, 30 m), Guémené-Penfao and Nogent sur Vernisson (France; 47° 38' N, 1° 50' W, 15 m and 47° 51' N, 2° 45' E, 130 m, respectively), Hann Münden (Germany; 51° 26' N, 9° 38' E, 132 m), Antella (Italy; 43° 43' N, 11° 22' E, 170 m), and Puerta de Hierro (Spain; 40° 28' N, 3° 45' W, 600 m).

Plots contained varying numbers of 3- and 4-year-old clones, selected throughout the natural area of the species within each country and from bordering countries as Portuguese clones in the Spanish collection, Swedish in the German, and some English in the French. For each species a different number of clones was common to more than one plot (210 *U. minor*, 70 *U. laevis*, and 35 *U. glabra*). A variable number of ramets (from 2 to 8) of each clone in each plot was considered.

Phenological notations

Phenological notations were taken for each tree according to a common protocol: at least once a week until complete emergence of the leaves, following a fi-

ve-step scale (1 = dormant buds; 2 = buds swollen, but scales closed; 3 = bud scales open and extremities of the first leaf visible at the apex of the buds; 4 = extremities of all leaves visible; 5 = two or more leaves completely spread out).

Calculation of bud-burst dates, chilling and thermal-time

For each tree, the bud-burst date was defined as the day, counted since January 1 (Julian day), when half of the lateral buds had reached stage 3.

The mean bud-burst date of each clone and the mean and mode of the bud-burst date of all clones of each species were calculated at each location for each year. For each species the bud-burst date at each location in each year was defined as the Julian day corresponding to the mode of the distribution.

Chilling (C) and thermal time (T) to bud-burst were calculated utilising two different methods.

1. As chill days and day degrees respectively, both based on the arithmetic mean of daily maximum and minimum temperatures. Chill days were counted as the number of days from November 1 to bud-burst, when the mean daily temperature was equal to or below 2°C, 5°C and 7°C. Day degrees were calculated as the sum of the differences between the mean daily temperature and 2°C, 5°C and 7°C for each day with a mean daily temperature above the threshold temperature from February 1 to bud-burst.

2. As chill hours and hour degrees respectively, using a sine-logarithmic approximation of the daily heating wave between night minimum and day maximum temperatures, based on maximum and minimum temperatures and daylength (Linvill, 1990). Chill hours were counted as the total number of hours when the mean daily temperature was equal to or below 5°C from November 1 to bud-burst. Hour degrees were calculated as the sum of the differences between the hour temperatures above 5°C and 5°C from February 1 to bud-burst.

November 1 was chosen as the starting date for chilling accumulation (Murray *et al.*, 1989), because few chill days occur before this date in central and southern Europe, and also because during October buds can be «non-dormant», especially in the case of elm trees, which can protract growth up into late autumn. February 1 was chosen as an arbitrary date for the thermal time accumulation, because it has been already used in the literature (Cannell and Smith, 1983). Several authors concur that arbitrary starting dates for heat sum accumulation are of a statistical rather than of a biological nature. Choosing other dates from January to March do not yield significant differences in the assessment of the relationship between the bud-burst date and heat sum to bud-burst (Castonguay *et al.*, 1984; Nizinski and Saugier, 1988).

Maximum and minimum daily temperatures were recorded in meteorological stations located in the study areas or in their immediate vicinity.

Data analysis

The relation between the bud-burst date and the thermal time to bud-burst in all stations and during the different years was examined graphically for each species, assessing the thermal time by each of the methods described above. In order to verify the possible effect of winter chilling, the relationship between the thermal time to bud-burst and the chilling received up to bud-burst was considered for each species, applying each of the described method for calculating chilling and thermal time. The different methods were compared by means of the accuracy, expressed as coefficient R^2, with which the relative exponential functions adjusted to data explained the variance of the bud-burst date.

For each species, utilising non linear estimation procedure-least squares estimation in Statistics 6.0, a non linear regression was fitted, on the form:

$$T = a + b \, e^{rC} \qquad (1)$$

T being day degrees > 5°C since February 1, C chilling days ≤ 5°C from November 1 to the bud-burst date, and *a*, *b*, *r* constants.

Results

Variation in the bud-burst dates

At each location and in each year a wide variation was registered between the clones from the first to the last bud-burst date (i.e. 23-39 days for *U. glabra*; 10-32 for *U. laevis*; 15-52 for *U. minor*). The lowest ranges were associated with collections of clones from uniform geographical origin, and the highest ranges with collections in which clones from many different regions were represented.

Table 1. Bud-burst dates of the elm clonal collections planted at Guémené-Penfao, Nogent-sur-Vernisson and Antella, during springs 2000 and 2001

Site	Year	Chill days ≤5°C	Date of bud-burst		
			Ulmus glabra	*Ulmus laevis*	*Ulmus minor*
Guémené Penfao	2000	33	April 2	April 4	April 11
(France)	2001	28	April 1	April 4	April 5
Antella (Italy)	2000	48	April 3	April 10	March 30
	2001	15	March 31	April 4	March 26
Nogent-sur-Vernisson	2000	62	April 3	April 7	April 6
(France)	2001	41	March 25	April 4	March 29

At Antella, Guémené Penfao and Nogent-sur-Vernisson phenological observations were repeated in 2000 and 2001. At these locations the bud-burst date resulted stable between years for the three species, although a marked variation in the winter thermal conditions was observed (Table 1). The 1999-2000 winter was colder than the 2000-2001 winter in these three stations, and specially in Antella. Nevertheless in the spring 2001, bud-burst occurred only slightly in advance for the clones of each species (Table 1).

Relations between thermal time and bud-burst date

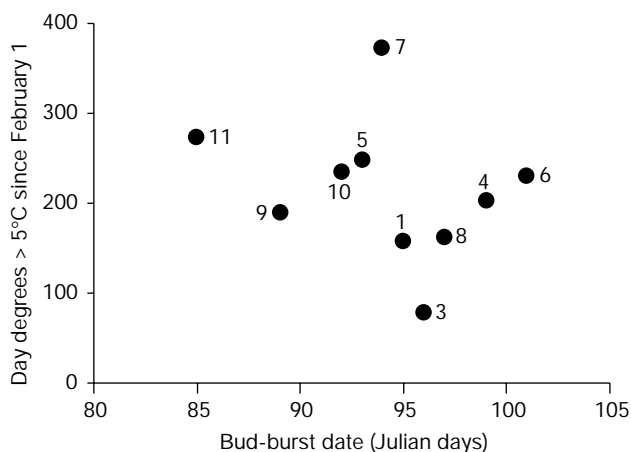For all the species it was not possible to interpret the observed variation in the bud-burst date among stations and years simply by the differences in thermal time from February 1st to budburst, whichever method was utilised for calculating it and whichever the threshold temperature was. As an example, for *U. laevis* no correlation was observed between the bud-burst dates and the thermal time to bud-burst, when it was calculated as day degrees > 5°C (Fig. 1). For the other species and methods the results were analogous.

Relations between thermal time and chilling to bud-burst

Whichever was the method for calculating chilling and thermal time, for each species the thermal time

Figure 1. Lack of relationship between simple thermal time values and bud-burst dates for *Ulmus laevis* clones. Each point represents a year at a location: 1 Geraardsbergen 2000; 3 Hann Muenden 2001; 4-5 Guémené 2000-2001; 6-7 Antella 2000-2001; 8-9-10 Nogent 2000-2001-2002; 11 Puerta de Hierro 2001.

$$y = 409.2e^{-0.0152x}$$
$$R^2 = 0.69$$
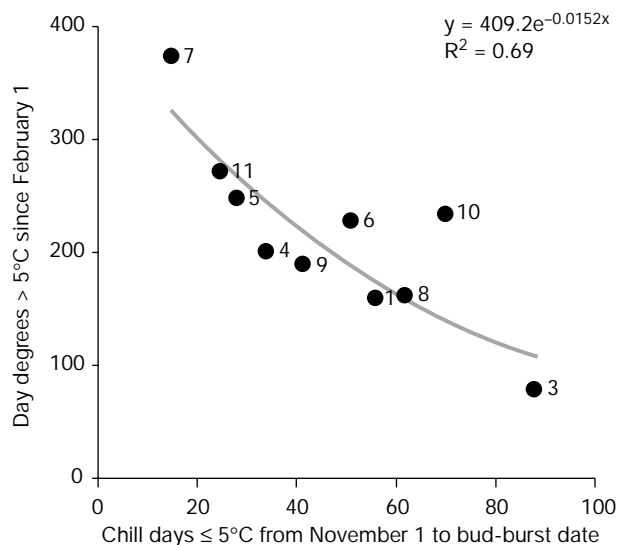
Figure 2. Exponential inverse relationship between thermal time and chilling for *Ulmus laevis* clones. Each point represents a year at a location: 1 Geraardsbergen 2000; 3 Hann Muenden 2001; 4-5 Guémené 2000-2001; 6-7 Antella 2000-2001; 8-9-10 Nogent 2000-2001-2002; 11 Puerta de Hierro 2001.
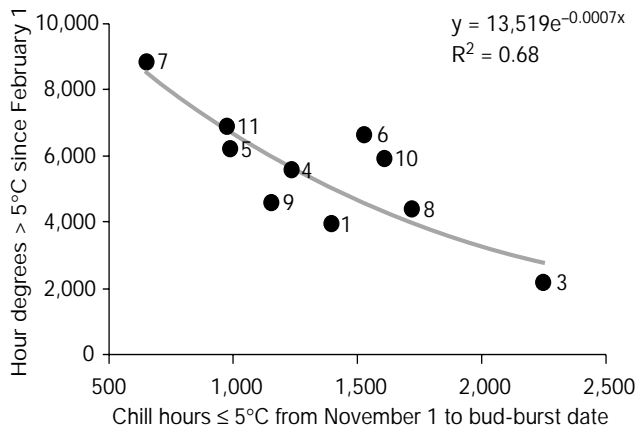
Figure 3. Exponential inverse relationship between thermal time and chilling for *Ulmus laevis* clones. Each point represents a year at a location: 1-2 Geraardsbergen 2000-2001; 3 Hann Muenden 2001; 4-5 Guémené 2000-2001; 6-7 Antella 2000-2001; 8-9-10 Nogent 2000-2001-2002; 11 Puerta de Hierro 2001.

Table 2. Explained variance (R^2) of the exponential relationships between thermal time and chilling, depending on the method used to calculate chilling and thermal time

Species	Method	Base temperature		
		2 °C	5 °C	7 °C
Ulmus glabra	1	0.87	0.76	0.80
	2	—	0.70	—
Ulmus laevis	1	0.73	0.69	0.83
	2	—	0.68	—
Ulmus minor	1	0.60	0.63	0.74
	2	—	0.48	—

to bud-burst decreased exponentially with increasing values of chilling. Two examples for *U. laevis* are provided (Figs. 2 and 3). The R^2 values of the adjusted exponential curves between thermal time and chilling, for each species and method are reported in Table 2.

Figure 4. Relationship between thermal time (T) and chilling (C) to bud-burst for *Ulmus glabra, U. laevis* and *U. minor* clones. ○ Dotted line *U. glabra.* □ continuous line *U. laevis.* ◇ broken line *U. minor.*

Estimates of thermal time-chilling regressions

Equation (1) provided a good explanation for the expected decrease in day degrees to bud-burst with the increase in number of chill days (Fig. 4). For *U. glabra* and *U. laevis*, the obtained function justified 83.17% and 89.01% of the observed variance, respectively (Table 3), whereas for *U. minor* it justified only 62.90% of the variance, similar to a linear regression. Although the curves explained a high percentage of variance, the values of parameters *a* and *r* were not significant (Table 3).

Discussion

Ranges observed yearly at each location between the extreme bud-burst dates of the clones of each elm

Table 3. Percentages of variance explained (e.v. %) by the fitted functions on the form $T = a + be^{rC}$ and parameter estimates ± Standard Error for *Ulmus glabra, U. laevis* and *U. minor*

Species	Parameter values ± SE			
	a	b	r	e.v. %
U. glabra	66.93 ± 155.39 ns	439.28 ± 163.12*	−0.033 ± 0.048 ns	83.17
U. laevis	74.02 ± 85.33 ns	434 ± 76.72**	−0.030 ± 0.021 ns	89.01
U. minor	74.55 ± 240.17 ns	299.86 ± 77.24**	−0.025 ± 0.059 ns	62.90

Significance level of parameter estimates: * Significant for $p < 0.05$. ** Significant for $p < 0.01$. ns: not significant.
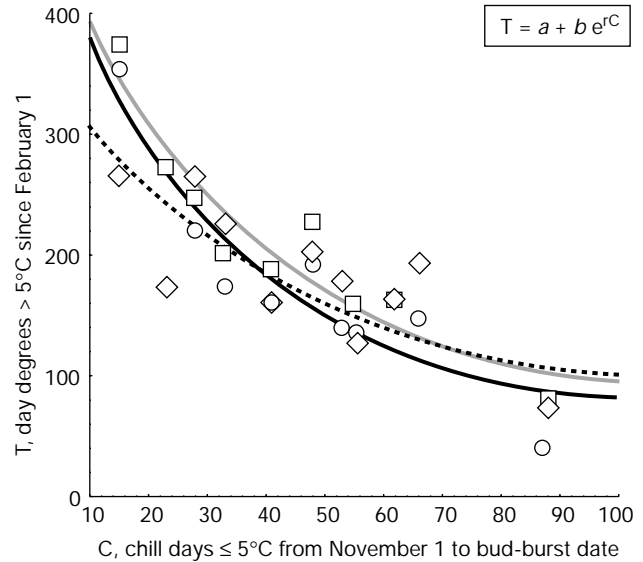
species are comparable to values obtained for other species, e.g. for *Fagus sylvatica* (Von Wühlisch *et al.*, 1995).

For the three elm species the bud-burst dates in the same location appeared to be stable between years characterised by different duration of winter chilling (Table 1), in comparison with other tree species from temperate and northern regions, for which dormancy release is mainly controlled by chilling (Heide, 1993a). Vice versa, bud opening occurred noticeably earlier in those species after warmer winters. For *Prunus padus*, *Betula pubescens* and *B. pendula* growing in field at Ás (Norway, 59° 30' N), Heide (1993b) reported differences from the first to the last bud-burst date equal to 33, 18 and 18 days, respectively. The differences observed for the three European elm species are more comparable to those for *Alnus glutinosa* and *A. incana* (10 days), if not for *Fagus sylvatica* (3 days). In the latter, the bud-burst date is particularly stable thanks to a dual control of dormancy release, in which chilling and photoperiod are involved (Heide, 1993b). For some tree species the promotional effect of chilling in dormancy release may be partially replaced by long photoperiods (Downs and Borthwick, 1956; Garber, 1983; Falusi and Calamassi, 1997). Nevertheless, it seems improbable that such a control system applies to European elms, either on the basis of the limited information known for *U. americana* (Roberts and Main, 1965), or on the basis of the preliminary results of research in progress (Ghelardini *et al.*, unpublished data).

Results did not permit to interpret the variation observed in the bud-burst dates among locations and years by attributing the control of bud-burst exclusively to the requirement of a specific thermal time (Fig. 1). Conversely, Chuine *et al.* (1999) found that the most efficient phenological models for explaining the variability observed in the flowering dates for *U. minor* and *U. glabra,* were those based only on the effect of the springtime rise in temperature. In comparison, the models based on a chilling effect on dormancy release complemented with an inverse chilling/thermal time relation, demonstrated a lesser validity or were found to be not significant. (Chuine *et al.*, 1999). Notwithstanding, even Chuine *et al.* (1999) emphasise the fact that phenological data they referred to came from a single zone, the region of Montpellier for *U. minor* and the region of Lyon for *U. glabra*, in which the duration of winter chilling probably differs little from year to year. Presumably, this was the main reason for which the models not taking into account the chilling action

were found to be more efficient. Our results confirmed that the «thermal time» models applied by Chuine *et al.* (1999), although reliable when winter climate conditions are uniform, do not furnish a valid general indication relative to bud-burst control in *U. minor* and *U. glabra*. Our results showed that an inverse relation exists between chilling and thermal time, and that this relation is clearly demonstrated under natural conditions, exclusively if the data are obtained from a wide variety of environments, equivalent to well-distributed and differentiated values of chilling.

Comparisons among R^2 values of the exponential functions thermal time/chilling showed that resorting to methods for estimating chilling and thermal time based on hourly temperatures, which are more accurate and more capable of discriminating between the real thermal trends in different locations, rather than on the simple daily mean temperatures, did not enable us to obtain more efficient regressions. Analogous comparisons between different methods for estimating thermal time and chilling units previously demonstrated that models estimating the effect of the temperature as chill days and day degrees were superior (Cannell and Smith, 1983). This result might be due to the fact that the more accurate quantification of the effects of both high and low temperature is, the more manifest is the inadequacy of a merely quantitative evaluation of the action of temperature in the processes that lead to dormancy release and bud-burst.

Our results indicated that using different threshold temperatures than 5°C could improve the accuracy of the chill days/day degrees regressions (Table 2). The threshold temperature leading to the most accurate regression was 2°C in *U. glabra* and 7°C in *U. laevis* and *U. minor*. Nevertheless, choosing 2°C and 7°C as threshold temperatures, rather than 5°C, did not allow obtaining regressions whose efficiency improved within a specific direction, a result interpretable in the sense of a progressive approach to the real value of the most efficient temperature. Moreover, an opposite result is reported by Cannell and Smith (1983) for *Picea sitchensis*, where the most accurate models were based on a threshold temperature equal to 5°C. Results prompted us to use, in the following analyses, the simplest method for calculating the amount of chilling and thermal time, i.e. chill days and day degrees, which was always the most accurate. However, the uncertain and conflictive results obtained regarding the choice of threshold temperatures led us to adopt for the successive analyses a base temperature equal to 5°C, the

value more often used. This choice permitted comparing our results with analogous ones reported in the literature.

Considering Fig. 4, *U. minor* clones at low levels of chilling require lower values of thermal time than *U. glabra* and *U. laevis* clones. This result is congruent with the different geographical distributions of the three species. Furthermore, the thermal time for *U. minor* decreases with the increase in chilling at a lower rate with respect to the one observed for *U. glabra* and *U. laevis*. Lastly, at high chilling levels, *U. glabra* requires lower thermal time to bud-burst compared to *U. minor* and *U. laevis*.

The functions presented in this paper are considered to be only approximate, because of the narrowness of the chilling range considered. However, over this range, the functions can be compared between the three species, for which to our knowledge no indication is available in the literature about the relationship that links chilling and thermal time to bud-burst.

The chilling/thermal time regressions of elm species can also be compared to those presented for *Picea sitchensis* (Cannell and Smith, 1983) and for 15 species of trees and shrubs (Murray *et al.,*1989). In both works, the threshold temperature utilised for the final regressions was 5°C. Using this model, the authors explained a very high percentage of the variance observed in the bud-burst date, from 83% to 98% depending on the species. The relative lack of accuracy of the regressions presented in this paper, specially noticeable for *U. minor*, can be explained as follows. Firstly, the defects in the regression curve might partly ascribed to the heterogeneous provenance of the material. In fact, in many species the timing of bud-burst may vary according to the origin of samples from different altitude or latitude (Campbell and Sugano, 1979; Myking and Heide, 1995; Von Wühlisch *et al.,* 1995; Falusi and Calamassi, 1996; Myking, 1997), and in the species with wide distribution areas, distinct climatic ecotypes may develop (Vaartaja, 1954, 1959; Downs and Borthwick, 1956; Heide, 1974; Myking and Heide, 1995). Moreover, in the case of field elm, whose complex taxonomy is still under discussion, this heterogeneity could be due, in the observed sample, to the presence of different varieties within the species, considered in its largest acception. Differences in timing of bud- burst are reported for the different field elm varieties (Richens, 1983). Therefore, the variability observed in the bud-burst dates between stations and years could be partially attributed to clone parti-

cularities linked to their geographic origin, amplified in the case of *U. minor* by the greater size and diversity of the collections. Considering that the chilling requirements of clones cultivated in the same environmental conditions could be different depending on the geographic origin, the variability observed in the bud-burst dates in heterogeneous clonal collections could be partly attributable to differences in ecotypes, and consequently it is logical that a single function was relatively inefficient in explaining it. For *U. minor*, this hypothesis seems to be confirmed by additional investigations in progress (Santini *et al.* unpublished data). Thus, improvement in the parameter significance and accounting for variance can probably be obtained by reducing the variability in origin of plant material. Furthermore in this study, differences between locations are more marked than differences in previous research (Cannell and Smith, 1983). In the study reported by Murray *et al.* (1989), such variability was not present, because before being transferred to the greenhouse, plants received various chilling duration under external conditions, always in the same locality.

Lastly, in order to obtain a curve that correctly describes the chilling/thermal time relation, it is necessary to experiment with a wide range of chilling levels. The principal limitation of our phenological data was that they were recorded in localities covering a narrow chilling range. Furthermore, the sites involved in the trial provided many points corresponding to medium or low chilling values, and only a few points corresponding to high chilling values. Consequently, the curves obtained stand aloft from the point corresponding to the greater chilling duration, ensuing in reducing the percentage of explained variance and overestimating the value of the asymptote *a*. The narrowness of the chilling range and the unbalanced distribution of chilling points within the range are probably the main reasons, causing a disappointing estimate of parameters *a* and *r* for all the species. Consistently, the estimate of parameter *b*, which represents the maximum theoretic requirement of thermal time to bud-burst in the absence of chilling, is significant for all the species.

Attempting to classify the three European elm species among the most numerous species for which Murray *et al.* (1989) obtained analogous regressions, the species-specific curves were found to be comparable with those of their group 3 or 4. A general comparison is possible, although within a limited chilling range, since in Murray *et al.* the lowest chilling duration ex-

perimented exceeded 50 chill days. The species included in groups 3 and 4 have a relatively low dormancy level. Their thermal time requirements stabilise when chilling exceeds 100 chill days. Over the chilling range considered here, the regression curves for *U. minor, U. laevis* and *U. glabra* seem to be like the curves obtained for those species.

By recurring to the criteria adopted by Murray *et al.* (1989) to predict the effect of site and of an hypothetical climate warming on the bud-burst date of groups 3 and 4, the indications obtained for *U. minor* are consistent with those of the authors cited (Tab. 1). In the colder year 2000, the closest to average in the last century, bud-burst was more precocious by 7-12 days in the most southern and warm Italian site with respect to the two French stations. In the warmer year 2001, the advance of bud-burst in comparison with the preceding year was less at Antella (4 days) than at the two French stations (6-8 days). The modest extent of the variations between the colder and the warmer year depended on differences related to methodology between the two trials. Murray *et al.* (1989) simulated an identical warming in the two stations. Instead, we reported real thermal variations which were considerably different in the three stations: a true collapse in chilling at Antella (from 48 to 15 chill days), a consistent reduction (from 62 to 41 chill days) at Nogent, a limited variation (from 33 to 28 chill days) at Guémené.

In this paper a model simple and purely quantitative showed that in elm trees a relationship exists between the effect of high and low temperatures in releasing winter dormancy and promoting bud-burst. Notwithstanding this result, such a model is but a rough approximation, considering that the threshold temperatures and the starting dates for evaluating chilling and thermal time accumulation were arbitrary. The results obtained, for other tree species, in experimental testing under controlled conditions, showed that all temperatures ranging from –3°C to 15°C may be effective as chilling. Furthermore, the effectiveness of the chill temperatures can vary during the winter, so that the same amount of chilling may have a different effect, depending on the period in which it occurs. Some experimental tests indicated also that dormancy release is a partly reversible process, a feature that is not assumed by a quantitative model. The exposure to a mild period in midwinter may negate the effect of previous chilling (Erez *et al.*, 1979a, 1979b; Young, 1992; Couvillon, 1995; Tamura *et al.*, 1995). Similarly, the estimate of the springtime warming effect as a simple heat sum above a daily mean temperature overlooks the influence of the daily temperature ranges, which on the contrary appears important under controlled conditions (Champagnat, 1993). Furthermore, the temperature sum, above a done threshold, required to budburst largely decreases from January to March, and the range of the temperatures compatible with growth is believed to extend progressively, upward and downward, as springtime gets nearer (Champagnat, 1993). These brief mentions of the results obtained under controlled conditions show that the effect of temperature on the release of bud winter rest is not exclusively quantitative, and explain why the bud-burst dates observed under external conditions may present such a wide variation that a simple quantitative model of the temperature effect can only partially account for.

Acknowledgements

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