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Genetic Resources of European Beech (*Fagus sylvatica* L.) for Sustainable Forestry

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ABSTRACT

Beech is a dominant forest tree species of high economic as well as ecological importance with a wide distribution range linking Scandinavia and the Mediterranean. Due to its functional flexibility and large genetic plasticity, beech can be utilized to study wide reaching influences affecting ecosystems, *e.g.* climate factors in different parts of Europe. The COST Action E52 «Evaluation of Beech Genetic Resources for Sustainable Forestry» commenced March 2006. During the final meeting of this COST action (Burgos, Spain, 4th to 6th of May, 2010) results of numerous research areas were presented, of which a special selection is published here. Among them, the evaluation of data from provenance trials located in most of the regions of beech occurrence show how well populations have adapted to certain site-inherent environmental features, *e.g.* limited water availability, late frost occurrence, acidic or calcareous soil, as well as how non-adapted populations react to such situations, and how successfully they might cope with them. This is of great significance for assessing the value of both, a given beech population and its ecosystem with respect to the conservation of beech ecosystems in a broad sense and particularly the genetic resources of beech.

The timing of leaf flush in European beech (*Fagus sylvatica* L.) saplings

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Ervin Raszovits[9], Martina Zitová[10] and Georg von Wühlisch[7]

ABSTRACT

Spring phenology is considered one of the most important determinants of growth and survival in young stands. It is relatively easy to monitor and is expected to respond to climate changes that will affect the favourable period for growth in temperate regions. The response of trees to the environmental cues that govern spring phenology is largely under genetic control and inter-populational differences exist within species. This suggests that the trait undergoes site-specific selection. Data obtained through monitoring of bud burst at multiple beech provenance-trials were compared with specific site and weather data to reveal geographical clines in beech phenology. We fitted the Weibull function to harmonise phenology data collected using various flushing scales and at different intensities of monitoring. By comparing data from 20 annual census of phenology performed across 13 sites throughout Europe, we showed that accumulated temperature sum > 5°C modelled the timing and duration of flushing more consistently than other temperature sum models > 0°C or > 8°C, or simply Julian Day. Inconsistency in the number of degree hours required for flushing among sites, reinforced the need for testing of more complex mechanistic models that include photoperiod, chilling period, and summer drought in addition to temperature sum. South-North, East-West, and low-high elevational clines were confirmed from the analysis. These findings; reinforce the need for caution in planting provenances from the south-east of Europe, suited to warmer-drier summers, in more north-westerly sites; and highlight the location of some potentially valuable late-flushing populations that also tolerate warm dry temperatures.

Key words: spring phenology, bud-burst, range shift, provenance trials, temperature sum model, clines, glacial refugia.

INTRODUCTION

The European beech (*Fagus sylvatica* L.) provenance trials, established under the EU Concerted Action AIR-CT94-2091, offer an exciting opportunity to compare the performance of a cohort of trees

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growing in common gardens together under a wide span of environmental conditions covering the species range across Europe. Monitoring the phenology of leaf development and senescence among this group of trials is a straight forward and insightful way to compare differences in beech populations due both to provenance and growing location. Leaf phenology is largely genetically determined and is thought to be under selection pressure (Doi *et al.,* 2010). In beech, as in other European temperate tree species, variation in the trait produces differences among populations and strong trends over both large and small geographical scales have been identified (Kramer, 1995).

Spring phenology has been considered one of the most important traits to influence growth and survival in young stands. Extension of the growing season in the spring can potentially add as much as $5\ \mathrm{g\ C\ m^{-2}\ day^{-1}}$ to the net ecosystem production (NEP) of a beech forest (Badeck *et al.,* 2004; Barr, *et al.,* 2009), as greater C assimilation is translated to extra biomass accumulation. However, premature flushing in habitats prone to late frosts can kill young trees or damage their shoot tips giving them a distorted form (Hänninen 1991). Furthermore, a trees' phenological strategy interacts with its competitiveness for water, soil nutrients, and light as well as coordination with the phenology of herbivores (White and Nemani 2003).

This paper (1) combines multiple site data to achieve a picture of the timing of beech flushing across Europe, and reveals how beech flushing is affected by the transfer of provenance populations to new habitats that are geographically and edapho-climatically different from their origin. (2) We explore the methods needed to harmonise data from different years and sites, and the standardisation of techniques required for cross-site comparisons of flushing on a large scale. (3) This allows us to suggest standard protocols for the collection and analyses of spring phenology data for beech that allows maximum information to be obtained in the most time-efficient manner. (4) We apply some of the currently-available models of the controls on flushing, to help understand those environmental factors influencing phenology, and highlight the strongest correlations with climatic variables across sites in a Europe-wide comparison. (5) Using case studies where multi-year census have been performed at a single site, and where the same provenances have been compared in multiple locations, we identify those factors which seem to act as determinants of flushing for particular provenances.

Collating data on bud-burst across Europe

Data were collected on beech spring phenology, prior to and during the EU COST Action E52 (2006-2010), using an ordinal scale to rank the stage of bud development (Teissier du Cros et al. 1988). As each individual research group refined their own protocol, the sophistication of the scale of bud development differed and the number of censuses made per year varied (Table 1). Attempting to compare the timing of phenology across sites and years directly from data based on different scales and collected on different days of the year would be complicated, so to enable multi-site comparisons these data were transformed to give the date of bud-burst (stage 2.5 on all the scales) for each tree at each site. This transformation was achieved by fitting the time-series of ordinal bud-burst data to Julian Dates using an S-shaped curve. The function used to model bud development was the Weibull function ($y = a - b\mathrm{e}^{-(cx^{\wedge}d)}$), although other functions of similar shape can also be used to serve this purpose (as explained in greater depth later). The Weibull Function is asymptotic in the upper and lower limits and the fit was estimated using the open-source software R version 2.8.1. (The R foundation for statistical computing, Vienna, Austria), non-linear fitting self-starting function SSweibull with estimates for the four constants: [a] the horizontal asymptote (Asym) for large values of x; [b] the difference from Asym to the y intercept x = 0 (Drop); [c] the natural logarithm of the rate constant (Lrc); [d] the power (pwr)

TABLE 1

Multi-census and multi-site data on spring phenology. In the first column, the location/name of the trial site is given followed by its nationality, and the trial site code. Sites in the BU19 series were planted out in 1995 and the BU20 series in 1998. The following columns give the year when monitoring was performed (Year) and the number of censuses in that year (Census), the flushing scale used by each national group (Scale), the number of days between flushing censuses (Spacing), and the number of trees where phenological development was successfully modelled using the Weibull function (Fits). The final column gives, the number of provenances (Provs) monitored at each site in every year

Site (country) trial code	Year	Census	Scale	Spacing	Fits	Provs
Schädtbek (DE) BU2001	1999 2008	4 3	1-7 1-5	3-4 days 7-10 days	1,967 1,407	45 45
Little Wittenham (UK)	2004 2006 2008	4 3 6	1-7 0-5 1-7	7 days 7 days 7 days	544 184 1,064	28 6 28
Lisbjerg (DK) BU2009	2002	2	1-5	7 days	2,671	28
Straza (SI) BU2012	2005 2007	7 7	1-7 1-7	4-10 days 6-10 days	405 3,040	10 38
Poiana (RO) BU2018	2007	3	1-5	6 days	3,541	28
Jiloviste (CZ) BU2019	2008	6	1-5	10-15 days	1,444	31
Mlacik (SK) BU2020	2007 2008	13 8	1-6 1-6	3 days 6 days	3,113 3,087	32 32
Hahnengruen (DE) BU2023	2007 2008	2 3	1-6 1-6	25 days 9 days	2,531 3,488	30 30
Pazuengos (ES) BU2024	2008	3	1-7	6 days	3,683	32 (7*)
Schädtbek (DE) BU1901	2005 2006	2 5	1-6 1-7	9 days 4-7 days	605 598	6 6
Vrchdobroc (SK) BU1905	2008	2	1-7	15 days	418	98
Oleszyce (PL) BU1915	1997	2	1-5	3 days	4,145	44
Louschelt (LU) BU1922	1997	2	1-7	10 days	1,858	28

* At Pazuengos multiple census data were only collected for seven provenances.

to which x is raised (Crawley, 2007). This transformation has the disadvantage of requiring more than one census of bud development to provide a fit. Consequently, those sites and years where just one census was taken were excluded from the multi-site comparison. It also requires that single tree data are collected and fitted to obtain a reliable estimate of mean burst date for a population and the range of variability within that population. Nevertheless, some information can still be usefully gleaned from site-average provenance-level data by fitting a single mean curve for the provenance (although this generalisation should be avoided whenever possible as information on population-level variability in flushing duration is lost). Multi-census data should provide a good estimate of the mean timing and duration of flushing for a provenance at a specific site (or ideally at several sites) assuming a good fit to the function. If the provenance-specific estimates turn out to be fairly well-conserved through time and location for each provenance, the bud-burst date could be back-calculated for provenances at those sites where only one census was performed (as long as hourly/daily temperature during bud development at each site is known – see model description later).

Although the age and size of a tree can influence the timing of its spring phenology (Augspurger 2008), these factors were not considered in this analysis since all of the trees were between two and 12 years-old when censured; still small enough to be thought of as juvenile.

Data were harmonised from 13 different trial-sites where multi-census data had been collected, and in six of these sites data were available from multiple years (Table 1). The timing of the phenology census as well as the number of assessments made determine the accuracy of modelling bud-burst date and flushing duration. Even if only two censuses were made (between one and two weeks apart) during the period of bud-burst, it was possible to model bud burst using the Weibull function if an end point on a date when all leaves are known to have fuller developed and a start point know to be prior to bud swelling are used in order to establish the upper and lower limits to the curve. Nevertheless, to predict flushing duration with high confidence ($R^2 > 0.9$), three well-spaced (7-10 days) assessments of phenology during the period of bud development were required. However, making more than three census of phenology only marginally improved the fit to bud development, except in situations when cold weather meant that flushing had proceeded particularly slowly.

The Weibull function has certain benefits over other S-shaped functions to fit bud development. It is asymptotic in the upper and lower limits, and requires initial estimates of the parameters to iteratively fit the data. Where few data, badly-timed or poorly-spaced data were collected, the initial parameter estimates required to commence fitting of the function had to be adjusted manually to ensure the correct fit to the data. In practice, each function was plotted after fitting and was visually inspected to ensure that data did not misfit.

Other S-shaped functions can be used to obtain a model of flushing duration with a similar outcome (see Supplemental Material T1). Plotting the results of the Weibull model (stage 2.5) against a sigmoid spline curve, as used by Gömöry (unpublished data) to model spring phenology with data from the Slovakian beech trial (BU2020), reveals that the results of the two models are very similar (Supplemental Material F1). If two well-timed censuses are performed during the period of bud development, it has been suggested that a linear model is sufficient to provide an estimate of bud-burst date; however this should be avoided, since the variability in flushing duration among provenances can be 10-15 days and while the middle stages of development usually do proceed evenly, there is an initial lag stage prior to and during bud-burst which is not captured by a linear model. Even in this situation where data are limited to just two censuses, the fixed S-shape of the Weibull function is superior to a linear model in capturing the pattern of development among trees.

RESULTS AND DISCUSSION

How does bud burst vary across Europe?

The flushing date of beeches in trials planted in 1998, where 84 widespread provenances from across Europe were monitored (Fig. 1a), and in 1995, with a greater number of provenances from central Europe and 117 in total were monitored (Fig. 1b), exhibited clinal variation along geographical gradients. The estimates given on these maps were produced by normalising the flushing date of each provenance relative to the local provenance for each trial site and standardising against the mean trial-site flushing date (Table 1). In this way information from all of the trial sites monitored could be synthesized in an unbiased manner and a comparison made of as many equivalent provenances as possible (Figs. 1 and 2). In the relatively-warm south and south-east of Europe, suitable habitat for beech tends to occur at high altitude, whereas in the north and north-west of Europe beech tends to occur at low altitude (Lat:Alt, $r = -0.81$). Consequently, large geographical clines in the data set are often further differentiated because they are complemented by concurrent trends due to changes in altitude. Nevertheless, irrespective of altitude, there is a general trend for provenances from the south-east of

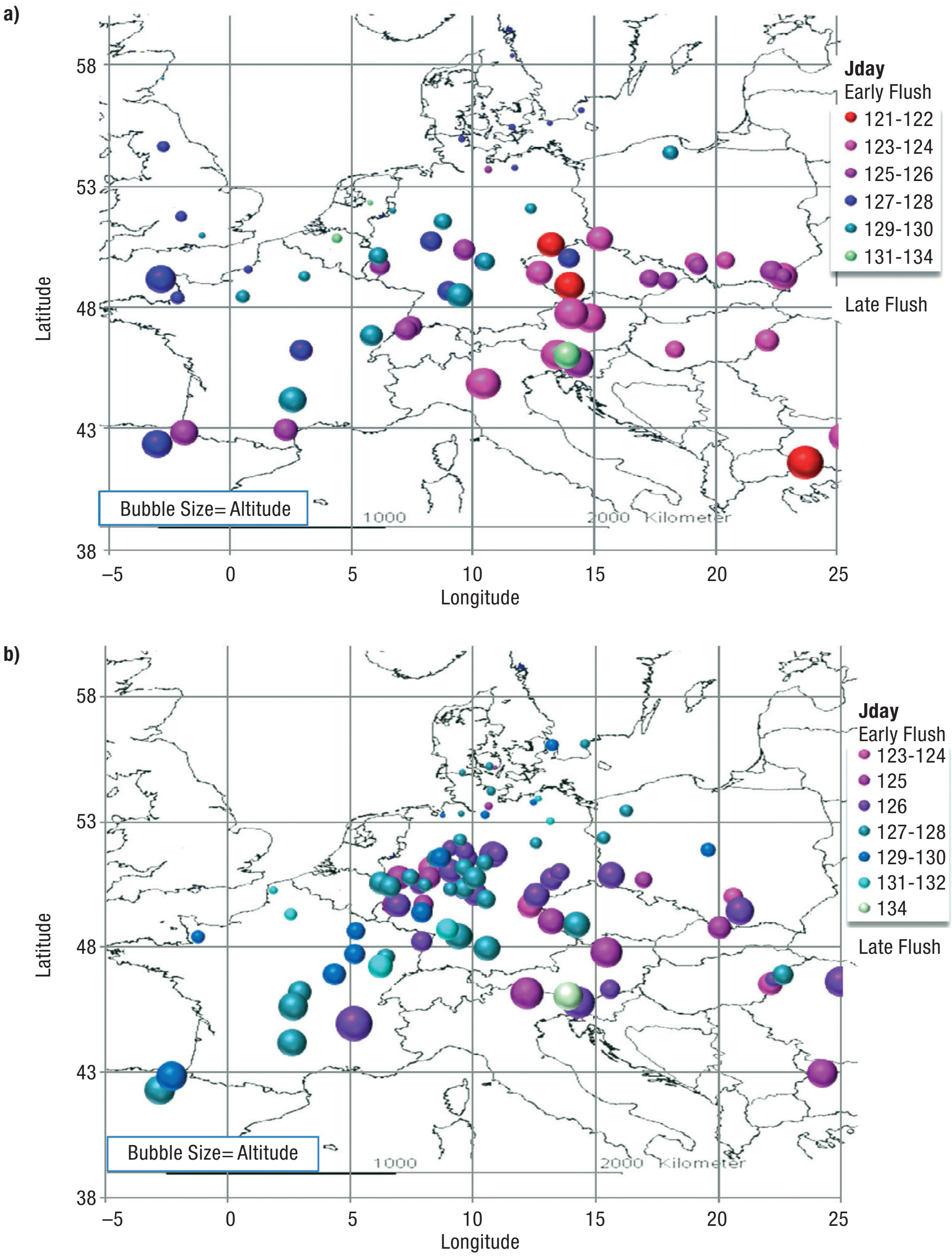

Figure 1. Map showing (a) the provenance origin of 84 populations planted in the 1998 series of COST Action E52 beech common-garden trials, and (b) 117 provenances planted in the 1995 series of trials. The average bud-burst date across sites for each provenance was calculated from the Weibull function fitted to multiple census data and normalised against the local provenance at each site (see text for details). Bud-burst data is represented along a spectral gradient from red (early) through blue to green (late) with circle size representing the elevation of the site of provenance origin.

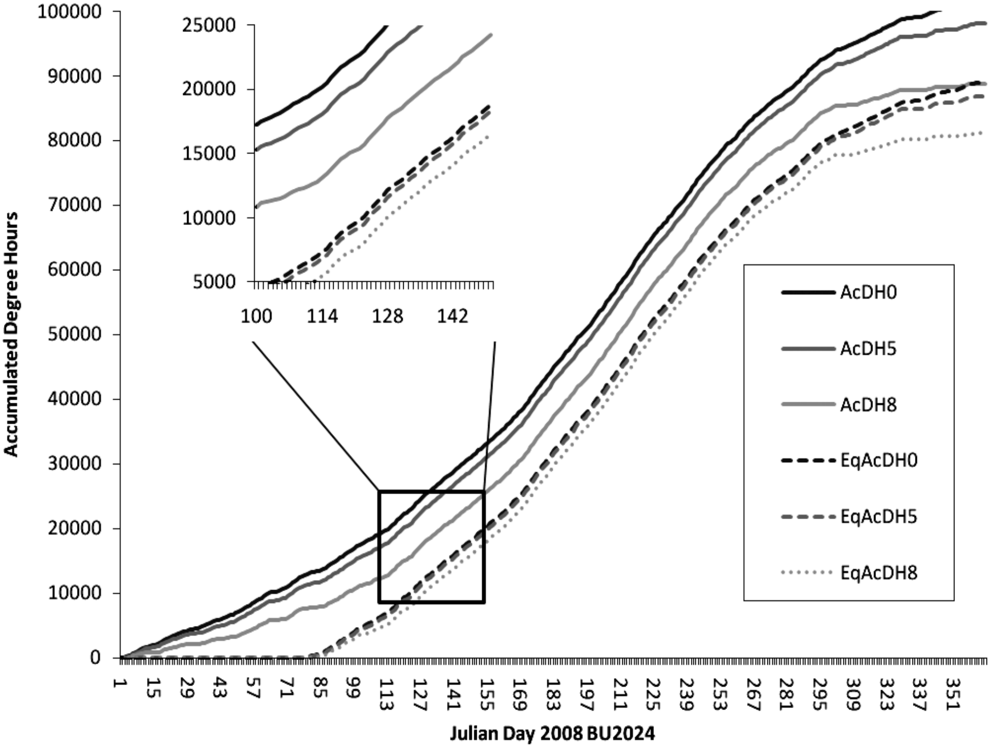

Figure 2. An example of the accumulated temperature sum from the site BU2024 at Pazuegos, Spain, showing the accumulation of degree hours starting from January 1st above 0°C, 5°C and 8°C (AcDH0, AcDH5, AcDH8) and from the vernal equinox (March 21st) above the same temperature thresholds (EqAcDH0, EqAcDH5, EqAcDH8). Inset, details the differences in temperature sum during the main period of bud burst.

Europe in Mediterranean and warm-continental regions to flush early compared with late-flushing provenances from the north and west of Europe where Oceanic influences on the climate are strong (Figs. 2 and 3: Jday:Long $R^2 = 0.164$, Jday:Long × Lat , $R^2 = 0.279$, Jday:Alt $R^2 = 0.149$). At the heart of beeches' range, close to the Alps, in southern Germany, Austria and the Czech Republic, the explanation for regional-scale variability is more complex and local climate has an important role influencing flushing date. Apart from the unusual provenance Idrija-II/2, Oceanic north-western Europe provided all of the late flushing provenances planted at multiple sites (Tables 2 and 3), although provenances from around the Baltic sea and from Spain were similarly late flushing but only monitored in single trials.

The reasons why the provenance Idrija-II/2, from Slovenia, flushes unusually late compared with nearby provenances have been the focus of several studies (Sittler 1981; Brus 2010). The most-likely explanation is that Idrija-II/2 represents a relict population that persisted in a sheltered *micro-refugium* where it was able to survive the last glaciation (Middle Würm period) (Magri, 2008; Brus, 2010). Idrija-II/2 originates from close to the Paleolitic site, *Divje babe I*, where the presence of permanent forest cover since as early as the Middle Würm (*ca.* 80 to 40 ka BP) has been confirmed by paleobotanical analysis (Culiberg, 2007), and from where beech charcoal (> 38 ka ^{14}C BP) has been excavated (Šercelj and Culiberg, 1991). Today the site, a mountain pass (saddle) at 940 m asl, receives high precipitation

TABLE 2
The bud-burst date of the local provenance (Local burst date – Julian Day) at each trial site, and how that compares with the earliest provenance's bud-burst date for that provenance trial (Relative to first Prov - Days). The best temperature sum model from January 1st (AcDH5) and March 21st (EqAcDH5) for bud burst of the local provenance

Site (country) trial code	Year	Local burst date	Days after 1st prov.	Flushing duration	AcDH5 bud burst	EqAcDH5 bud burst
Schädtbek (DE) BU2001	1999	120.7 ± 0.4	5.8	10.6 ± 0.6	10,295	7,060
	2008	117.2 ± 0.3	5.8	15.1 ± 0.6	10,484	4,165
Little Wittenham (UK) BU2005	2004	121.4 ± 1.0	6.2	11.1 ± 0.6	17,586	9,176
	2006	133.2 ± 0.7	5.1	3.4 ± 0.3	16,112	11,559
	2008	119.1 ± 0.7	7.4	9.9 ± 0.6	17,012	6,667
Lisbjerg (DK) BU2009	2002	122.6 ± 0.3	4.4	16.1 ± 0.8	10,306	5,573
Straza (SI) BU2012	2005	113.7 ± 0.5	1.6	12.9 ± 0.7	20,213	7,286
	2007	107.7 ± 0.4	3.8	13.2 ± 0.4	11,407	8,229
Poiana (RO) BU2018	2007	114.3 ± 0.3	4.3	5.9 ± 0.3	14,228	7,348
Jiloviste (CZ) BU2019	2008	110.2 ± 0.6	0.7	19.3 ± 1.1	8,428	3,766
Mlacik (SK) BU2020	2007	113.1 ± 0.6	4.2	10.1 ± 0.2	9,400	5,088
	2008	122.6 ± 0.4	1.2	10.0 ± 0.3	9,999	6,545
Hahnengruen (DE) BU2023	2007	111.7 ± 0.5	4.9	9.1 ± 0.3	10,232	5,570
	2008	121.7 ± 0.3	3.9	10.7 ± 0.3	8,393	4,926
Pazuengos (ES) BU2024	2008	121.7 ± 0.4	7.3	12.6 ± 0.4	20,233	8,962
Schädtbek (DE) BU1901	2005	120.6 ± 0.2	1.4	12.2 ± 0.4	9,106	6,425
	2006	123.7 ± 0.3	1.3	11.4 ± 0.3	6,253	6,145
Vrchdobroc (SK) BU1905	2008	121.6 ± 0.6	1.8	12.3 ± 0.8	7,453	5,201
Oleszyce (PL) BU1915	1997	135.4 ± 0.3	0.9	4.3 ± 0.4	10,980	8,504
Louschelt (LU) BU1922	1997	129.9 ± 0.6	4.1	9.2 ± 0.9	13,588	7,774

year round, much of which falls as snow and sleet. Late flushing may have developed in this population as an adaptation to survive long cold winters during the last glaciation. The possibility that Idrija-II/2 harbours other valuable traits (e.g. cold tolerance: Brus, 2010), whether as adaptations to current high precipitation at Idrija or past climate, merits further investigation.

Modelling the environmental controls on bud burst

From an ecological viewpoint, comparisons of the date (Julian Day) of bud burst can be interesting since they allow differences in growth strategy and potential productivity at locations differing in growing season length to be identified, and tell us something about the broad influence of climate on development. However, they are not particularly informative for understanding the mechanisms controlling bud development from year to year and across-site variability in the timing of flushing. To overcome this problem several modelling approaches have been adopted that identify different potential controls on development (Kramer, 1995; Chuine, 2000; Hänninen and Kramer, 2007). The most universal control is temperature which is usually incorporated as a daily or hourly temperature sum above a certain threshold temperature. To obtain the best model of spring phenology using temperature sum, the starting date from which warm temperatures are expected to help break dormancy must be

TABLE 3

Bud burst date of those selected provenances from the trial planted in 1998 that were censured in six or more trial sites. Dates are expressed as days after the date of bud-burst of the earliest flushing provenance in each trial. This allows the relative performance of these provenances, in terms of its tendency to flush early or late, to be easily compared and synthesized across sites. The provenance names and nationalities are given in the left hand columns followed by their unique code-number

Provenance	Trial site			N Germany	UK	Denmark	Slovenia	Poland	Romania	Czech	Slovakia	S Germany	Spain	X days after 1st Mean ± SE
	Prov	Code	N	BU2001 1999	BU2005 2004	BU 2009 2002	BU 2012 2007	BU 2014 2007	BU 2018 2007	BU 2019 2008	BU2020 2007	BU2023 2007	BU2024 2008	
Domazlice-Vyhledy	CZ	46	7	0.0 ± 0.5		1.4 ± 0.6	0.0 ± 0.3	0.6 ± 0.4		2.1 ± 0.2		1.2 ± 0.3	1.2 ± 0.4	**0.9** ± 0.3
Horni Plana-Cevny	CZ	51	9	1.0 ± 0.3	0.6 ± 0.7	1.1 ± 0.4	2.0 ± 0.3	0.4 ± 0.1	3.5 ± 0.5	0.0 ± 0.5	0.7 ± 0.6	1.2 ± 0.3		**1.2** ± 0.3
Eisenerz	AT	36	9	1.2 ± 0.4		2.3 ± 0.4	0.2 ± 0.3	0.2 ± 0.1	4.7 ± 0.4	1.7 ± 0.3	1.5 ± 0.4	3.7 ± 0.3	2.2 ± 0.4	**1.9** ± 0.5
Jablonec N.N.	CZ	48	8	0.9 ± 0.5	0.5 ± 0.9	2.7 ± 0.4	0.3 ± 0.3	3.6 ± 0.4	5.0 ± 0.3	1.2 ± 0.7	4.2 ± 0.6			**2.3** ± 0.6
Jawornik, 92b	PL	43	6				0.1 ± 0.4	1.3 ± 0.0	4.9 ± 0.3	1.8 ± 0.3	3.5 ± 0.4		3.6 ± 0.4	**2.5** ± 0.7
Jaworze/Bielsko2	PL	39	8	1.5 ± 0.3		2.5 ± 0.4	2.4 ± 0.4	0.9 ± 0.2	4.9 ± 0.3	2.0 ± 0.0	3.3 ± 0.5		3.7 ± 0.4	**2.6** ± 0.4
Oberwil, Arberg3	CH	34	7	2.3 ± 0.3		3.8 ± 0.3	1.5 ± 0.3	0.1 ± 0.1	5.8 ± 0.3	1.7 ± 0.1			4.3 ± 0.4	**2.8** ± 0.7
Buchlovice	CZ	70	6	2.6 ± 0.5				0.2 ± 0.1		0.7 ± 0.6	5.5 ± 0.5	5.0 ± 0.4	2.6 ± 0.4	**2.8** ± 0.9
Hinterstoder	AT	35	9	3.4 ± 0.4	0.0 ± 1.2	3.8 ± 0.3	1.3 ± 0.4	1.3 ± 0.4	6.5 ± 0.3	1.7 ± 0.1	7.4 ± 0.7	5.7 ± 0.4		**3.5** ± 0.9
Brumov-Sidonie	CZ	49	7	2.6 ± 0.3		3.6 ± 0.3	3.8 ± 0.5	1.2 ± 0.5	7.7 ± 0.3	1.8 ± 0.2			5.0 ± 0.3	**3.7** ± 0.8
Postoj Masun.	SI	53	7	3.0 ± 0.3		3.9 ± 0.3	3.8 ± 0.4	0.0 ± 0.1	7.1 ± 0.4		5.0 ± 0.8	4.3 ± 0.6		**3.9** ± 0.8
Pyrénéss-Or. Corbie	FR	8	6	4.9 ± 0.4	3.1 ± 0.8	4.7 ± 0.2	3.9 ± 0.4	0.7 ± 0.2					6.0 ± 0.4	**3.9** ± 0.8
Tarwa Lesko	PL	40	7	2.4 ± 0.8		4.4 ± 0.5	0.7 ± 0.4	0.1 ± 0.1	7.0 ± 0.6		4.3 ± 0.6	8.2 ± 0.6		**3.9** ± 1.1
Farchau (SH)	DE	26	6	5.8 ± 0.4	2.3 ± 1.3	4.6 ± 0.2				3.5 ± 0.5	7.9 ± 0.5		5.2 ± 0.3	**4.9** ± 0.8
Gråsten, F 413	DK	21	8	3.7 ± 0.4	6.0 ± 1.8	4.2 ± 0.3	6.3 ± 0.7	0.7 ± 0.4	9.2 ± 0.4	2.8 ± 0.8	8.6 ± 0.7			**5.2** ± 1.0
Nižbor	CZ	64	8		2.8 ± 0.8	4.5 ± 0.3	4.0 ± 0.4	0.4 ± 0.1	8.4 ± 0.4	3.1 ± 0.7	12.3 ± 0.7	7.5 ± 0.5		**5.4** ± 1.3
Torup	SE	23	10	5.1 ± 0.3	6.5 ± 1.0	5.4 ± 0.4	5.8 ± 0.4	0.6 ± 0.2	9.2 ± 0.3	2.6 ± 0.4	14.5 ± 0.8	10.8 ± 0.6	5.2 ± 0.4	**6.6** ± 1.3
Bordure Man	FR	2	9	3.4 ± 0.4	7.6 ± 1.2	5.7 ± 0.5	8.1 ± 0.7	2.1 ± 0.4	9.4 ± 0.4	2.8 ± 0.7	12.9 ± 0.7		8.1 ± 0.4	**6.7** ± 1.2
Bathurst E95	UK	18	6	6.7 ± 0.4	6.2 ± 1.2	6.7 ± 0.6				4.2 ± 1.0	9.8 ± 0.4		7.4 ± 0.4	**6.8** ± 0.7
Plateaux du Jura	FR	6	9	4.2 ± 0.5	6.9 ± 0.9	5.5 ± 0.6	8.4 ± 0.8	0.3 ± 0.2	10.9 ± 0.4	3.9 ± 1.0	15.8 ± 0.6	10.6 ± 0.7		**7.4** ± 1.5
Perce Belleme	FR	1	7	7.1 ± 0.4	7.0 ± 0.9	6.7 ± 0.6	8.4 ± 0.6	2.5 ± 0.2	10.8 ± 0.3			11.9 ± 0.6		**7.8** ± 1.2
Westfield	UK	17	9	5.8 ± 0.3	7.2 ± 1.1	6.0 ± 0.5	10.1 ± 0.5	1.3 ± 0.3	10.5 ± 0.4	3.1 ± 0.7	11.8 ± 0.6	14.5 ± 0.7		**7.8** ± 1.4
Bilowo/Kartuzy	PL	67	8	4.3 ± 0.6		5.9 ± 0.5	7.5 ± 0.8	1.0 ± 0.4	12.4 ± 0.5	5.0 ± 0.9	14.3 ± 0.6	13.3 ± 0.7		**8.0** ± 1.7
Heinerscheid	LU	11	6	6.6 ± 0.4	9.6 ± 0.9	5.5 ± 0.5	9.8 ± 0.7		11.4 ± 0.4				7.3 ± 0.4	**8.4** ± 0.9
Urach (BW)	DE	31	10	8.2 ± 0.4	8.3 ± 0.8	8.2 ± 0.7	10.5 ± 0.7	0.7 ± 0.2	10.2 ± 0.3	6.9 ± 0.8	10.5 ± 0.6	13.3 ± 0.8	7.3 ± 0.4	**8.4** ± 1.1
Aarnink	NL	14	10	6.5 ± 0.4	9.5 ± 0.4	6.5 ± 0.5	7.9 ± 0.5	0.4 ± 0.2	11.8 ± 0.6	6.7 ± 0.7	13.8 ± 0.7	14.7 ± 0.6	9.2 ± 0.4	**8.7** ± 1.3
Sud Massif Central	FR	4	6	5.7 ± 0.8	8.1 ± 1.1				11.7 ± 0.3	6.0 ± 2.4	14.4 ± 0.7		7.4 ± 0.4	**8.9** ± 1.4
Soignes	BE	13	10	7.9 ± 0.5	11.8 ± 1.5	7.6 ± 0.8	14.7 ± 0.4	1.3 ± 0.3	13.6 ± 0.4	10.5 ± 0.9	18.2 ± 0.6	16.6 ± 0.8	10.1 ± 0.4	**11.2** ± 1.6
Idrija-II/2	SI	54	7				15.1 ± 0.6	1.7 ± 0.2	15.8 ± 0.4	10.4 ± 1.5		18.8 ± 0.8	10.3 ± 0.4	**12.0** ± 2.3
Local after 1st				**5.8 ± 0.4**	**6.2 ± 1.0**	**4.4 ± 0.3**	**3.8 ± 0.2**	**0.3 ± 0.2**	**4.3 ± 0.3**	**0.7 ± 0.6**	**4.2 ± 0.6**	**4.9 ± 0.5**	**7.3 ± 0.4**	
Local Jday				**120.7 ± 0.4**	**121.4 ± 1.0**	**122.6 ± 0.3**	**107.7 ± 0.2**	**130.2 ± 0.2**	**114.3 ± 0.3**	**110.2 ± 0.6**	**113.1 ± 0.6**	**111.7 ± 0.5**	**121.7 ± 0.4**	
Earliest Jday				**114.9**	**115.2**	**118.2**	**103.9**	**129.9**	**110**	**109.5**	**108.9**	**106.8**	**114.4**	**113.2**
Mean				**4.1 ± 0.4**	**5.8 ± 1.0**	**4.7 ± 0.4**	**5.5 ± 0.5**	**0.9 ± 0.2**	**8.9 ± 0.4**	**3.6 ± 0.7**	**9.1 ± 0.6**	**9.5 ± 0.6**	**5.9 ± 0.4**	**5.78**

N: number of sites where each provenance was monitored. The mean and standard error are given for each provenance at each site, ranked from earliest to latest overall bud-burst date. There are four summary rows at the foot of the table. Earliest Jday: the mean Julian Day (Jday) of the earliest flushing provenance at each site. Local Jday is the mean Julian Day of the flushing of the local provenance at each site. Local diff: [Local Jday] minus [Earliest Jday]. Mean: mean of the number of days after the earliest provenance at which the suite of provenances at each site flush (last column) or each provenance in all applicable sites flush (last row): this gives an idea of variability in bud-burst at each site or for each provenance.

TABLE 4

The duration of flushing in those selected provenances from the trial planted in 1998 that were censured in multiple trial sites. Flushing duration is defined as the period between bud-burst and leaf unfolding. Comparisons are made relative to the shortest flushing period of a provenance in each trial, allowing the relative rate of bud opening for each provenance to be compared across provenances and sites. The provenance names and nationalities are given in the left hand columns followed by their unique code-number

Provenance	Trial site			N Germany	UK	Denmark	Slovenia	Poland	Romania	Czech Rep.	Slovakia	Bavaria	S Germany	Min + X days
	Prov	Code	N	BU2001 1999	BU2005 2004	BU 2009 2002	BU 2012 2007	BU 2014 2007	BU 2018 2007	BU 2019 2008	BU2020 2007	BU2023 2007	BU2024 2008	Mean ±SE
Domažlice-Vyhl.	CZ	46	6	1.4 ± 0.9		7.4 ± 0.8	0.2 ± 0.2	0.1 ± 0.3		0.4 ± 0.4		0.3 ± 0.3		**1.6 ± 0.5**
Horni Plana-Cevny	CZ	51	9	0.5 ± 0.4	2.6 ± 1.0	6.2 ± 0.7	1.1 ± 0.2	2.9 ± 0.4	1.1 ± 0.4	2.7 ± 0.6	3.0 ± 0.3	0.0 ± 0.2		**2.2 ± 0.5**
Eisenerz	AT	36	8	1.6 ± 0.7		8.1 ± 0.7	0.1 ± 0.2	1.8 ± 0.3	0.7 ± 0.5	1.5 ± 0.5	3.0 ± 0.2	0.8 ± 0.1		**2.2 ± 0.4**
Jablonec N.N.	CZ	48	8	2.0 ± 1.1	0.0 ± 0.7	7.0 ± 0.8	0.7 ± 0.4	5.1 ± 0.2	1.6 ± 0.5	2.5 ± 0.7	3.2 ± 0.2			**2.7 ± 0.6**
Jawornik, 92b	PL	43	5				0.8 ± 0.5	2.5 ± 0.3	1.1 ± 0.4	1.0 ± 0.5	2.8 ± 0.2			**1.7 ± 0.4**
Jaworze/Bielsko2	PL	39	8	0.8 ± 0.5		8.7 ± 0.6	1.3 ± 0.4	2.9 ± 0.2	0.2 ± 0.3	0.0 ± 0.1	2.7 ± 0.3		0.0 ± 0.4	**2.1 ± 0.3**
Oberwil, Arberg3	CH	34	6	0.6 ± 0.2		7.3 ± 0.8	1.0 ± 0.2	1.4 ± 0.3	0.4 ± 0.4	2.3 ± 0.9				**2.2 ± 0.5**
Buchlovice	CZ	70	5	1.1 ± 0.5				2.0 ± 0.3		3.6 ± 1.1	2.5 ± 0.3	1.9 ± 0.3		**2.2 ± 0.5**
Hinterstoder	AT	35	9	1.0 ± 0.5	1.0 ± 0.8	9.2 ± 0.6	0.7 ± 0.3	3.5 ± 0.5	2.0 ± 0.5	1.4 ± 0.5	2.8 ± 0.4	2.2 ± 0.4		**2.7 ± 0.5**
Brumov-Sidonie	CZ	49	7	0.8 ± 0.4		5.7 ± 0.8	2.0 ± 0.4	2.2 ± 0.7	2.0 ± 0.5	2.3 ± 0.8			0.2 ± 0.4	**2.2 ± 0.6**
Postoj Masun	SI	53	7	0.0 ± 0.3		8.1 ± 0.7	1.6 ± 0.4	0.8 ± 0.3	1.6 ± 0.4		3.4 ± 0.4	1.0 ± 0.4		**2.4 ± 0.4**
Pyrénéss-Or. Corbie	FR	8	6	1.7 ± 0.3	3.4 ± 0.4	6.0 ± 0.9	1.4 ± 0.3	1.7 ± 0.3					1.7 ± 0.4	**2.6 ± 0.4**
Tarwa Lesko	PL	40	7	1.6 ± 0.8		8.5 ± 0.8	0.6 ± 0.3	1.6 ± 0.4	1.3 ± 0.4		3.1 ± 0.3	2.7 ± 0.4		**2.8 ± 0.5**
Farchau (SH)	DE	26	6	3.4 ± 0.6	4.0 ± 0.8	4.8 ± 0.9				5.0 ± 0.8	2.6 ± 0.2		0.9 ± 0.4	**3.5 ± 0.6**
Gråsten, F 413	DK	21	8	0.4 ± 0.3	3.2 ± 0.7	5.8 ± 1.1	4.7 ± 0.7	0.9 ± 0.4	2.9 ± 0.6	2.2 ± 0.9	3.0 ± 0.3			**2.9 ± 0.6**
Nižbor	CZ	64	8		2.2 ± 0.6	5.8 ± 0.9	2.4 ± 0.5	2.7 ± 0.3	1.7 ± 0.6	1.0 ± 0.6	2.0 ± 0.3	2.1 ± 0.3		**2.5 ± 0.5**
Torup	SE	23	9	1.7 ± 0.4	2.7 ± 0.8	2.8 ± 1.0	2.6 ± 0.3	0.0 ± 0.2	0.8 ± 0.4	3.1 ± 0.7	2.0 ± 0.5	3.7 ± 0.4		**2.2 ± 0.5**
Bordure Man	FR	2	8	1.5 ± 0.5	2.5 ± 0.7	6.8 ± 1.1	0.0 ± 0.4	3.4 ± 0.6	0.1 ± 0.4	4.1 ± 1.2	1.2 ± 0.3			**2.5 ± 0.6**
Bathurst E95	UK	18	5	2.4 ± 0.5	2.2 ± 0.8	2.3 ± 0.8				3.8 ± 1.0	2.8 ± 0.3			**2.7 ± 0.7**
Plateaux du Jura	FR	6	9	2.0 ± 0.5	3.3 ± 0.7	4.4 ± 1.3	2.8 ± 0.6	2.0 ± 0.6	1.8 ± 0.5	1.1 ± 0.6	1.1 ± 0.4	2.9 ± 0.5		**2.4 ± 0.6**
Perce Belleme	FR	1	7	2.8 ± 0.6	3.2 ± 0.7	1.0 ± 0.9	3.5 ± 0.5	5.1 ± 0.3	2.7 ± 0.5			5.1 ± 0.6		**3.3 ± 0.6**
Westfield	UK	17	9	3.1 ± 0.6	2.4 ± 1.0	5.6 ± 1.5	1.9 ± 0.3	3.0 ± 0.5	3.1 ± 0.6	2.7 ± 0.9	3.0 ± 0.4	3.0 ± 0.4		**3.1 ± 0.7**
Bilowo/Kartuzy	PL	67	8	0.0 ± 0.4		5.0 ± 1.0	3.0 ± 0.6	1.7 ± 0.5	2.8 ± 0.7	1.8 ± 0.9	1.6 ± 0.3	6.5 ± 0.6		**2.8 ± 0.6**
Heinerscheid	LU	11	5	2.5 ± 0.5	2.8 ± 0.5	1.0 ± 1.3	1.8 ± 0.6		0.0 ± 0.4					**1.6 ± 0.6**
Urach (BW)	DE	31	9	2.5 ± 0.6	3.4 ± 0.5	0.0 ± 0.7	3.0 ± 0.5	1.2 ± 0.2	2.7 ± 0.5	3.0 ± 0.8	3.0 ± 0.3	5.4 ± 0.6		**2.7 ± 0.5**
Aarnink	NL	14	9	1.6 ± 0.6	2.7 ± 0.5	2.1 ± 0.8	4.1 ± 0.5	0.7 ± 0.2	2.0 ± 0.9	4.5 ± 0.8	1.9 ± 0.4	3.2 ± 0.4		**2.5 ± 0.6**
Sud Massif Central	FR	4	5	1.3 ± 0.4	3.1 ± 0.7				1.6 ± 0.4	3.5 ± 2.3	1.7 ± 0.4			**2.2 ± 0.9**
Soignes	BE	13	9	3.5 ± 0.8	2.1 ± 0.6	2.8 ± 1.1	3.3 ± 0.4	2.3 ± 0.3	2.9 ± 0.7	1.9 ± 1.1	0.0 ± 0.3	5.1 ± 0.6		**2.7 ± 0.7**
Idrija-II/2	SI	54	5				3.9 ± 0.5	2.8 ± 0.3	2.1 ± 0.5	2.4 ± 1.5		8.5 ± 0.7		**3.9 ± 0.7**
LOCAL				3.4 ± 0.6	3.7 ± 0.6	8.1 ± 0.8	1.6 ± 0.4	1.0 ± 0.5	0.2 ± 0.3	3.6 ± 1.1	3.2 ± 0.2	4.7 ± 0.4	1.2 ± 0.4	
Longest				**10.7 ± 0.5**	**11.4 ± 0.7**	**17.2 ± 0.9**	**16.3 ± 0.4**	**8.9 ± 0.4**	**8.8 ± 0.5**	**20.7 ± 0.9**	**10.3 ± 0.3**	**16.0 ± 0.4**	**13.1 ± 0.4**	
Shortest				**7.2 ± 0.3**	**7.4 ± 0.7**	**8.0 ± 0.7**	**11.6 ± 0.4**	**3.8 ± 0.2**	**5.7 ± 0.4**	**15.7 ± 0.1**	**6.9 ± 0.3**	**7.5 ± 0.2**	**11.4 ± 0.4**	
Range				**3.5 ± 0.5**	**4.0 ± 0.7**	**9.2 ± 0.9**	**4.7 ± 0.4**	**5.1 ± 0.4**	**3.1 ± 0.5**	**5.0 ± 0.8**	**3.4 ± 0.3**	**8.5 ± 0.4**	**1.7 ± 0.4**	

N: number of sites where each provenance was monitored (note that fewer provenances in the Spanish site were monitored than for bud burst). The mean and standard error of days longer than the duration than the slowest provenance are given for each provenance at every site, ranked from shortest to longest overall flushing duration. There are four summary rows at the foot of the table. Shortest: shortest duration of flushing of a provenance at each site. Local: the number of days more than the fastest flushing provenance required for the local provenance to flush. Longest: the flushing duration of the slowest provenance to flush at each site. Range: the difference in duration between the fastest and slowest flushing provenance at each site (to give an idea of variability in flushing duration at each site).

selected and the minimum temperature above which increased warming will accelerate development chosen. In both cases a variety of values have been used with various justifications across the published literature (von Wühlisch *et al.,* 1995; Falusi and Calamassi, 1996; Liesebach *et al.,* 1999; Schieber, 2006). These range from 0-10°C threshold temperature, and 1st January to 1st April for the inception of temperature summation. In reality, all provide rather crude approximations compared with the plants' own sensory mechanisms, since only once a period of rest is complete (chilling - provided by cold late-autumn and winter temperatures), can physiological priming (warming) commence, and this rest period will also differ among provenances (Hänninen and Kramer, 2007). These two phases may overlap with each other and furthermore interact with photoperiod (which depends on latitude) and various other abiotic stresses which influence the formation of buds in autumn. All these factors will combine to alter the timing of spring phenology. The complexity of controls involved in bud development make realistic physiology modelling difficult, so to allow a large volume of data to be processed and compared, here we restrict ourselves to simple models. Despite their lack of refinement, simple models can still prove useful for the comparison of phenology among populations (Hänninen and Kramer, 2007), so we tested models of bud-development based on accumulated degree hours above 0°C (AcDH0), 5°C (AcDH5) and 8°C (AcDH8) from, 1st January and 21st March (EqAcDH0, EqAcDH5, EqAcDH8: Fig. 2). The model from 1st January should capture all occasions during the winter and spring-time when the threshold temperature is surpassed, under the assumption that chilling and temperature accumulation run concomitantly; whereas only summing temperatures after the vernal equinox assumes that photoperiodic- and chilling controls prior to that date interfere with temperature accumulation.

Of the three temperature sum models tested, degree hours above 5°C consistently performed better than the two others for fitting the duration of flushing, while both the AcDH5 and AcDH0 performed well in fitting bud-burst date (data not shown). These criteria differ, since the duration of flushing at a site is likely to be directly related to temperature during flushing, whereas other environmental factors outside the model are likely to affect the timing of bud burst. To allow for direct comparison on a common scale the degree hour model parameters were back-transformed to their Julian Day equivalents after fitting. From a subset of data from the Pazuengos trial (BU2024 Spain), the standard deviations (SD) in bud-burst date calculated for each provenance were reduced from 0.46 days (SD for Jday) to 0.25 days (SD for AcDH5), and variability in the duration of flushing was reduced both within and among provenances from 0.16 days (SD for Jday) to 0.07 (SD for AcDH5) (data not shown). At some sites temperature sum from 1st January gave more consistent AcDH5 required for bud burst between years (Table 2: e.g BU2001, BU2005) whereas at others the results of the later starting model were more consistent (Table 2: e.g. BU2012, BU1905); although even a direct comparison of back-transformed data is not definitive since the models operate on different scales.

Site-specific trends in the timing and duration of bud burst

Variability among sites in the date of flushing of each local provenance and in the temperature sum they required was quite high (Table 2: Local Provenance). Differential accumulation of chilling units among sites through the winter is a likely contributory factor to this. The average number of frosts (supplemental material F2) at each trial site between December and March is indicative of this difference and also helps to delimit continental sites (cold winters) from oceanic sites (mild winters), a possible explanation for some of the clinal variation in phenology. The relationship between frosts and flushing time does not always hold true so other factors must also be having an influence. For instance, despite their high elevation there are relatively few frosts at the Mediterranean sites but this belays the relatively late flushing of Spanish and Pyrenean provenances (Figs. 1 and 2).

Several sites where monitoring was performed over multiple years provide the opportunity to assess consistency in the order and timing of flushing among provenances from year to year (Tables 1 and 2). In the cool Oceanic trial site at Little Wittenham (BU2005) in Oxfordshire, UK (month temp range 3.9-16.6°C, precip. 642 mm year^{-1}: supplemental material F3), bud-burst data were collected from all 28 provenances in two years (and from six provenances in an additional year). This site was consistently one of the later flushing trials both in terms of Julian day and temperature sum required for flushing (Tables 3 and 5). On average, flushing at the site was just two days later in 2008 than 2004 and the difference between the two years in temperature sum from January (AcDH5) required for bud break was just 12.3 DH5 per day (9%), whereas the EqAcDH5 difference was greater at 31.0 DH5 per day (37%) (Table 2). This suggests that temperature sum accumulation during the winter was also important for bud-burst at this site. Notably, the order of bud-burst date among provenances at the site remained largely the same between the two censuses, as did their degree of separation over time (Supplemental Material F3). Similarly, at the climatically distinct continental site in Mláãik, Slovakia (BU2020), bud burst was very consistent between years both in terms of early Julian Date and low temperature sum requirement (Tables 2, 3 and 6; Supplemental Material F4). Two of the northern European trials, in Schädtbek (north Germany) and Lisbjerg (Denmark), flush quite late (Table 2), but both required a rather low temperature sum for flushing (Table 5). Of those sites monitored over two years, only the Slovenian trial (BU2012) differed in both Julian Date and temperature sum requirement for bud burst between the years, and in 2005 only seven common provenances were considered from this site, too few for broad generalisation (Tables 2 and 5). Unsurprisingly, at most of the trials censured in multiple years the order of bud-burst among provenances within a site was quite conserved, irrespective of location across Europe (Supplemental material F3, F4, F5). This suggested that although in theory the combination of environmental cues triggering development would be expected to differ from site to site and between years and provenances, in practice these differences appear not to have significant differential effects on the relative development of provenances.

Provenance variation in the timing and duration of bud burst

The comparison of individual provenance variability in flushing is based on the assumption that provenances were planted across a variety of trial-site types (rather than late flushing provenances only in late flushing sites, for example). The differences in phenology evident in provenances grown at several locations were as expected, given the behaviour of local provenances at their point of origin and information taken from the published literature (e.g. von Wühlisch et al. 1995). The latest flushing provenances, from Idrija in Slovenia and Soignes in Belgium, flushed on average 11-12 days later than the first provenances wherever they were growing (Table 3). Likewise, the earliest flushing provenances were always among the first to flush irrespective of site location (Table 3). When the temperature sum required for flushing is compared over multiple sites, there are some minor changes in ranking of the provenances (notably Hinterstoder from Austria was generally early flushing, and Heinerscheid from Luxemburg late flushing), but a largely similar pattern was conserved (Table 5). There is scope in the future for much deeper site-specific analysis of provenance behaviour coupled with weather data, to determine how movement between climatic zones affects the phenology of particular provenances from this data set, and to identify the time of year when differences in temperature and precipitation among sites have the greatest influence on phenology.

TABLE 5

Accumulated Degree Hours above 5°C from January 1st (AcDH5) until bud burst for those selected provenances from the trial planted in 1998 that were censured in six or more trial sites. The provenance names and nationalities are given in the left hand columns followed by their unique code-number

Provenance	Trial site			N Germany		UK		Denmark	Slovenia		Poland	Rumania	Czech	Slovakia		S. Germany		Spain	Mean	SE	CV	Rank
	Prov	Code	N	BU2001		BU2005		BU2009	BU2012		BU2014	BU2018	BU2019	BU2020		BU2023		BU2024				
				2008	1999	2004	2008	2002	2005	2007	2007	2007	2008	2007	2008	2007	2008	2008				
Domažlice-Vyhledy	CZ	46	7	9,263	8,903			9,610		18,705	16,565		8,712			9,635	7,432	18,296	**12,232**	1,719	**0.38**	5
Horni Plana-Cevny	CZ	51	9	9,308	9,131	15,696	14,384	9,547		19,542	16,502	14,066	8,322	8,874	10,099	9,649	7,625		**11,953**	1,266	**0.32**	2
Eisenerz	AT	36	9	9,797	9,160			9,797		18,747	16,434	14,425	8,617	8,971	9,984	10,009	8,103	18,617	**12,079**	1,334	**0.34**	3
Jablonec N.N.	CZ	48	8	9,522	9,105	15,626	14,373	9,888		18,801	17,628	14,489	8,549	9,400	9,999				**12,786**	1,332	**0.30**	9
Jawornik, 92b	PL	43	6							18,737	16,769	14,474	8,642	9,280	10,314			19,173	**13,913**	1,838	**0.32**	19
Jaworze/Bielsko2	PL	39	8	9,770	9,235			9,852		19,658	16,670	14,464	8,712	9,261	10,217			19,191	**13,029**	1,546	**0.34**	11
Oberwil, Arberg3	CH	34	7	10,243	9,442			10,165		19,308	16,419	14,777	8,617					19,465	**14,028**	1,699	**0.33**	20
Buchlovice	CZ	70	6		9,512						16,443		8,428	9,759	10,633	10,246	8,541	18,770	**11,542**	1,579	**0.34**	1
Hinterstoder	AT	35	9	9,917	9,710	15,434	14,437	10,173		19,215	16,786	14,979	8,625	10,339	10,633	10,362	8,368		**12,422**	1,161	**0.28**	8
Brumov-Sidonie	CZ	49	7	10,323	9,526			10,126		20,213	16,754	15,444	8,642					19,669	**14,339**	1,793	**0.34**	23
Postoj Masun	SI	53	7	9,559	9,632			10,192	11,407	20,213	16,394	15,180		9,640	10,882	10,110	7,733		**12,138**	1,417	**0.31**	4
Pyrénéss-Or. Corbie	FR	8	6	10,130	10,118	16,478	14,438	10,365	11,727	20,243	16,583							19,936	**14,986**	1,670	**0.28**	26
Tarwa Lesko	PL	40	7		9,452			10,294		18,989	16,426	15,174		9,406	10,356	11,118	8,936		**12,239**	1,382	**0.30**	6
Farchau (SH)	DE	26	6	10,484	10,295	16,201	16,106	10,365					9,065	10,549	10,671			19,755	**12,876**	1,525	**0.30**	10
Gråsten, F 413	DK	21	8	10,010	9,838	17,147	15,688	10,257		21,028	16,600	15,965	8,846	10,748	11,345				**13,746**	1,416	**0.30**	16
Nižbor	CZ	64	8	10,395		16,388	15,991	10,328	11,106	20,278	16,476	15,664	8,981	11,796	11,678	10,882	8,980		**13,212**	1,250	**0.27**	14
Torup	SE	23	10	10,285	9,896	17,268	16,160	10,562	11,877	20,898	16,531	15,938	8,804	12,058	11,736	12,069	9,030	19,755	**13,756**	1,237	**0.29**	17
Bordure Man	FR	2	9	11,610	9,733	17,524	16,304	10,638		21,676	17,143	16,029	8,871	11,897	11,862			20,404	**14,735**	1,419	**0.29**	24
Bathurst E95	UK	18	6	10,686	10,462	17,192	16,809	10,874					9,245	11,221	11,187			20,281	**13,409**	1,593	**0.30**	15
Plateaux du Jura	FR	6	9	10,570	9,935	17,349	16,224	10,574		21,783	16,443	16,524	9,155	12,428	12,183	11,979	9,161		**13,645**	1,296	**0.29**	7
Perce Belleme	FR	1	7	10,709	10,533	17,367	16,915	10,857		21,783	17,241	16,504				12,496	9,496		**14,799**	1,548	**0.28**	25
Westfield	UK	17	9	10,586	10,295	17,430	16,946	10,686		22,418	16,786	16,422	8,981	11,759	11,381	13,155	9,502		**13,813**	1,350	**0.30**	18
Bilowo/Kartuzy	PL	67	8	10,693	9,948			10,669		21,462	16,701	16,782	9,430	12,010	12,047	12,917	9,502		**13,147**	1,353	**0.30**	12
Heinerscheid	LU	11	6	10,660	10,427	18,093	16,721	10,586		22,332		16,609						20,255	**16,432**	1,900	**0.30**	30
Urach (BW)	DE	31	10	12,221	10,709	17,708	16,784	11,238	12,360	22,565	16,583	16,291	9,862	11,448	11,442	12,917	9,700	20,244	**14,275**	1,253	**0.28**	21
Aarnink	NL	14	10	10,541	10,406	18,059	16,619	10,828	11,997	21,612	16,488	16,734	9,817	11,993	12,096	13,226	9,670	20,724	**14,305**	1,264	**0.28**	22
Sud Massif Central	FR	4	6		17,648	17,648	16,685					16,697	9,671	12,046	12,134			20,281	**15,351**	1,480	**0.24**	28
Soignes	BE	13	10	12,259	10,692	18,541	17,661	11,095		24,215	16,769	17,017	10,862	13,043	12,673	13,606	9,749	21,020	**15,149**	1,373	**0.29**	27
Idrija-II/2	SI	54	7						15,499	24,373	16,957	17,725	10,854			14,288	9,913	21,140	**16,344**	1,842	**0.30**	29
LOCAL DH > 5		NA	11	10,484	10,295	17,996	17,012	10,562	11,407	20,213	16,464	14,228	8,428	9,400	9,999	10,233	8,393	20,233	**13,205**	1,281	**0**	13
Range				**2,996**	**8,745**	**3,107**	**3,288**	**1,691**	**4,393**	**5,668**	**1,234**	**3,659**	**2,540**	**4,169**	**2,689**	**4,653**	**2,481**	**2,844**				
MEAN				**10,398**	**10,144**	**17,064**	**16,069**	**10,383**	**12,282**	**20,752**	**16,684**	**15,766**	**9,096**	**10,815**	**11,161**	**11,686**	**8,908**	**19,832**	**13,663**			
SE				159	317	212	239	88	558	330	59	204	139	278	175	371	195	190				
CV				**0.07**	**0.16**	**0.05**	**0.06**	**0.04**	**0.12**	**0.08**	**0.02**	**0.06**	**0.08**	**0.12**	**0.07**	**0.13**	**0.09**	**0.04**				
Rank				4	5	13	11	3	9	15	12	10	2	6	7	8	1	14				

N: number of sites where each provenance was monitored. The range, mean, standard error, and coefficient of variation across all sites where present are given for each provenance at every site, and ranked from least to most AcDH5. At the foot of the table, the mean, standard error, and coefficient of variation across all these provenances are given for each site, and site ranking from least to most AcDH5.

Comparison of the duration of flushing and the timing of bud burst revealed that for most provenances where bud burst was late, the duration of flushing was also relatively long (Table 4), and the contrary was true, that early-flushing provenances developed quickly from bud burst to leaf unfolding (Table 4). Hence, rather than compensating for late initiation of flushing by rapid leaf unfolding, the rate of development post-bud burst appeared to further differentiate the separation in bud-burst date among provenances. One adaptive explanation for this may be that leaves are more vulnerable to frost damage once buds have burst open than prior to leaf unfolding, so early flushing provenances need to pass through this stage quickly. Alternatively, this result may just suggest that similar temperature controls are acting on bud development and leaf unfolding. This explanation is potentially interesting from an ecophysiological perspective because it suggests that not only do winter chilling and photoperiod segregate provenances but that temperature sum later in the spring also has a provenance-specific influence.

CONCLUSIONS RECOMMENDATIONS AND FUTURE DIRECTION

The evidence from these extensive observations of beech phenology confirms the strong geographical trends in beech flushing previously reported, and demonstrates that these differences are maintained when beech provenances are transferred to other sites around Europe. Since the high variability in this trait expresses an adaptation to the climate of provenance origin, two concerns can legitimately be raised about the future performance of beech. (1) Will climate change reduce the fitness of local populations because of (a) summer drought restricting the growing period for late-flushing populations, and/or (b) warmer spring temperatures allowing beech buds to reach the threshold temperature accumulation required to flush sooner, thus making them more susceptible to spring frosts? (2) If foresters attempt to transfer selected seedlings from beech provenances growing in relatively warm sites with dry summers to cool moister sites, will the anticipated fitness advantage gained from improved traits for drought and thermo- tolerance and increased production due to a longer growing period be compounded by frost damage or mortality due to their earlier flushing? Utilising the analyses from these trials we can demonstrate that certain populations, *e.g.* from the south west of Europe, are adapted to Mediterranean environments and yet flush relatively late. Thus, they may be candidates to withstand climate change without being susceptible to late frost. However, these provenances are typically not among the most productive and so have tended to be overlooked in the past.

While the relationships between differential flushing of provenances and survival, growth, and form, require further investigation, our results reinforce the need for caution in planting provenances from the south-east of Europe, expected to be suited to warmer continental conditions, in more north-westerly sites where they might be frosted. Finally, we note that the extensive database now available on the phenology of common-provenances at multiple sites, when coupled with daily weather data for each site, is ripe for exploration to further our understanding of the environmental controls on the physiological mechanisms controlling dormancy and bud-burst in beech.

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REFERENCES

AUGSPURGER C.K., 2008. Early spring leaf out enhances growth and survival of saplings in a temperate deciduous forest. Oecologia, 156, 281-286.

BADECK F.-W., BONDEAU A., BÖTTCHER K., DOKTOR D., LUCHT W., SCHABER J., SITCH S., 2004. Responses of spring phenology to climate change. New Phytologist 162, 295-309.

BARR A., BLACK T.A., MCCAUGHEY H., 2009. Climatic and phenological controls of the carbon and energy balances of three contrasting boreal forest ecosystems in western Canada. In: Phenology of ecosystem processes (Noormets A.,ed). Springer, Berlin.

BRUS R., 2010. Growing evidence for the existence of glacial refugia of European beech (*Fagus sylvatica* L.) in the south-eastern Alps and north-western Dinaric Alps. Periodicum Biologorum 112(3), 239-246.

CHUINE I., 2000. A unified model for budburst of trees. Journal of Theoretical Biology 207, 337-347.

CRAWLEY M.J., 2007. The R book. Chapter 20: Non-linear Regression. Jon Wiley and Son Inc, Chichester, UK. pp. 661-684.

CULIBERG M., 2007. Paleobotaniãne raziskave v Divjih babah I In: Divje babe I: paleolitsko najdišče mlajšega pleistocena v Sloveniji: Opera Instituti archaeologici Sloveniae, 13: Part 1: Geologija in paleontologija, Ljubljana. I. TURK, (ed.) Inšitut za arheologijo ZRC SAZU. pp. 167-184.

DOI H., TAKAHASHI M., KATANO I., 2010. Genetic diversity increases regional variation in phenological dates in response to climate change. Global Change Biology 16, 373-379.

FALUSI M., CALAMASSI R., 1996. Geographic variation and bud dormancy in beech seedlings (*Fagus sylvatica* L.). Annals of Forest Science 53, 967-979.

HÄNNINEN H., 1991. Does climatic warming increase the risk of frost damage in northern trees? Plant Cell and Environment 14, 449-545.

HÄNNINEN H., KRAMER K., 2007. A framework for modelling the annual cycle of trees in boreal and temperate regions. Silva Fennica 41, 167-205.

KRAMER K., 1995. Phenotypic plasticity of the phenology of seven European tree species in relation to climatic warming. Plant Cell and Environment 18, 93-104.

LIESEBACH M., DEGEN B., SCHOLZ F., 1999. Zur genetischen Anpassungsfähigkeit der Rotbuche (*Fagus sylvatica* L.) [On the Adaptability in Flushing of Beech (*Fagus sylvatica* L.)]. Berichte über Landwitschaft 75, 128-133.

MAGRI D., 2008. Patterns of post-glacial spread and the extent of glacial refugia of European beech (*Fagus sylvatica*). Journal of Biogeography 35, 450-463.

SCHIEBER B., 2006. Spring phenology of European beech (*Fagus sylvatica* L.) in a submountain beech stand with different stocking in 1995-2004. Journal of Forest Science 52, 208-216.

ŠERCELJ A., CULIBERG M., 1991. Palinološke in antrakotomske raziskave sedimentov iz paleolitske postaje Razprave - Slovenska akademija znanosti in umetnosti, Razred naravoslovnih ved, 32, 129-152.

SITTLER B., 1981. Experimentell ökologische Untersuchungen an 15 slowenischen Buchenprovenienzen zur Beurteilung ihrer Anbaufähigkeit in der Bundesrepublik Deutschland (Experimental ecological studies on the origin of 15 Slovenian beech provenances to assess their growth in the Federal Republic of Germany). PhD Dissertation. Albert-Ludwig University of Freiburg. 205 pp.

TEISSIER DU CROS E., THIEBAUT B., DUVAL H., 1988. Variability in beech: budding, height growth and tree form. Annals of Forest Science 45, 383-398.

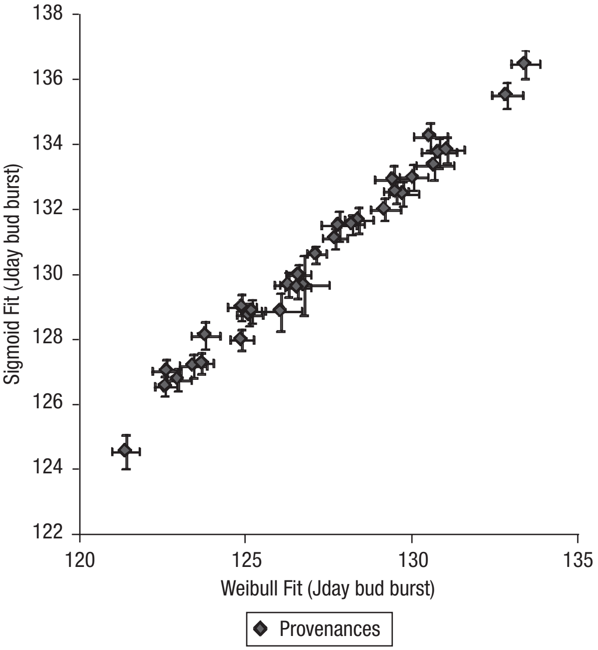
VON WÜHLISCH G., KRUSCHE D., MUHS H-J., 1995. Variation in temperature sum requirement for flushing of beech provenances. Silvae Genetica 44, 343-347.

WHITE M.A., NEMANI R.R., 2003. Canopy duration has little influence on annual carbon storage in the deciduous broad leaf forest. Global Change Biology 9, 967–972.

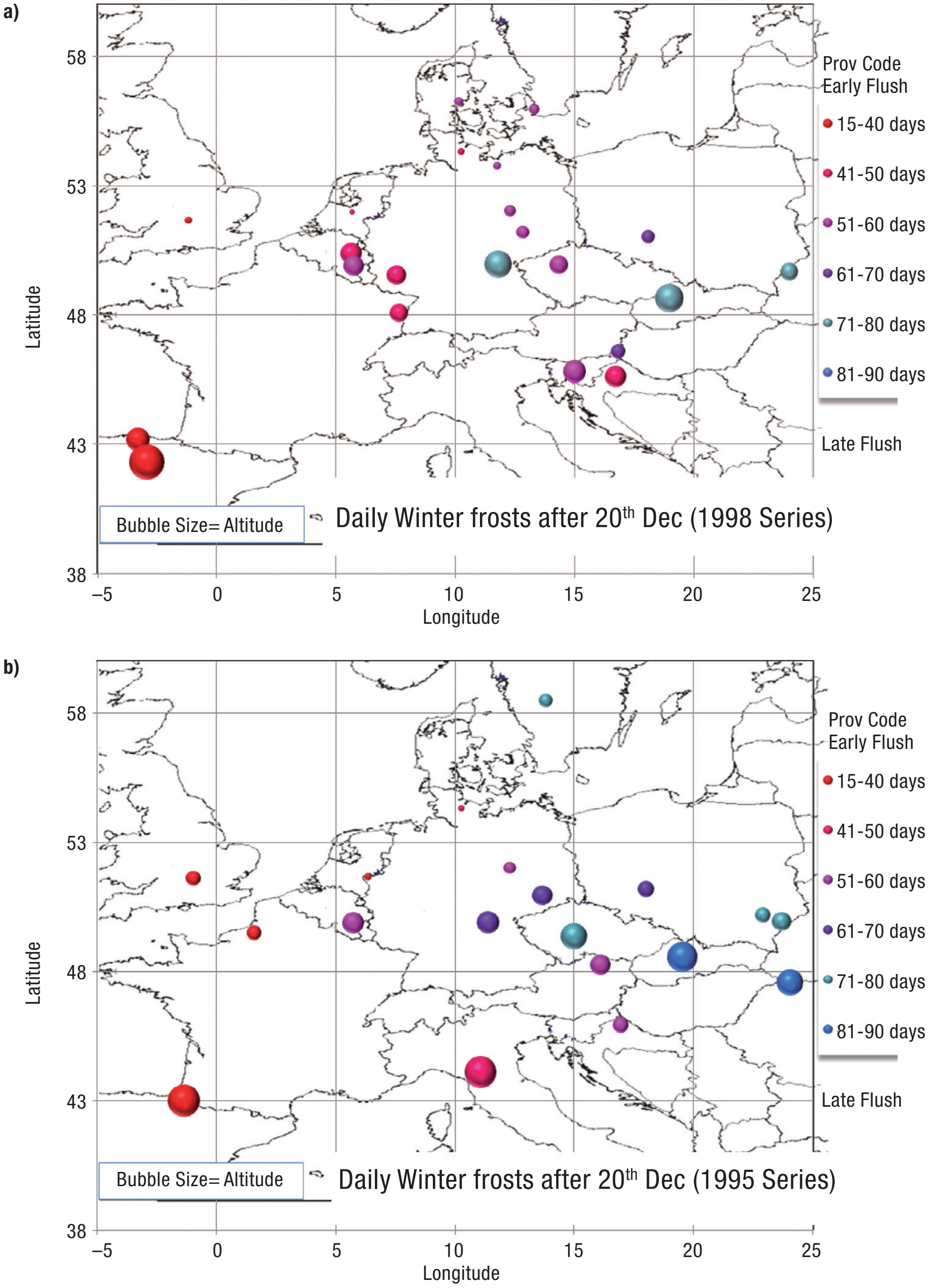
PROCEEDINGS PAPER: SUPPLEMENTAL MATERIAL

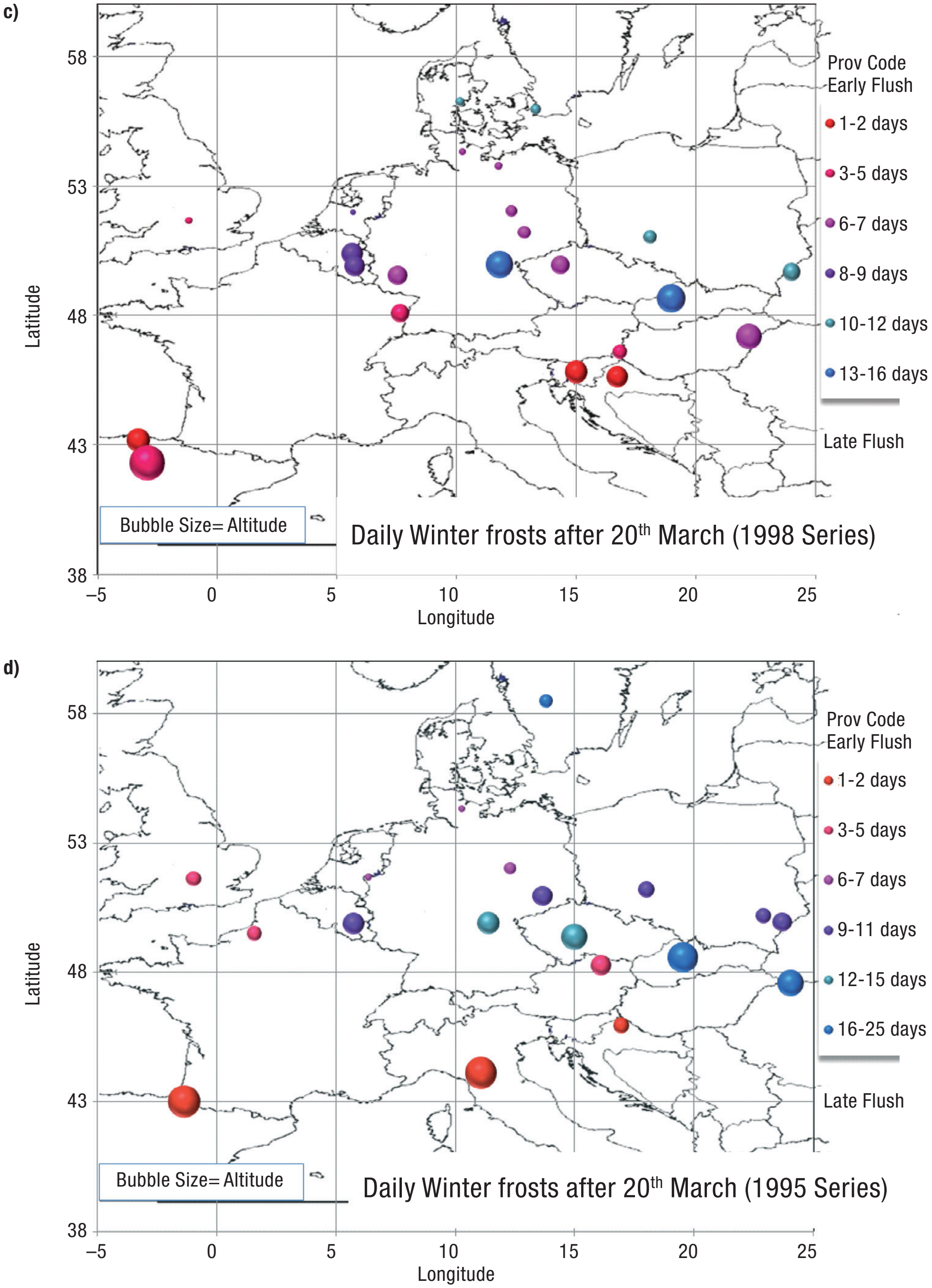
T1
Published results from beech provenance trials using various models

Authors	Location	Model type	Temp-Start date	Temp limit	Burst date
Von Wuehlisch *et al.,* 1995	Grosshansdorf, DE	Degree hours	1st Jan (JD 1)	AcDH5 compared with others	30/04-09/05 7600-146000 DH
Ĉufar *et al.,* 2008	Ljubljana, SI 1960-2006				20/04 JD111 ± 5
Schieber, 2006	Kremnickévrchy Mts., SK 1995-2004	Degree days	1st Feb (JD 32)	AcDD8 compared with others	77-150 DD cv 13%
Falusi and Calamassi, 1996	Florence, IT	Chilling + Julian Day	1st Feb (JD 32)	AcDD5	05/04-21/04 292-296 DD
Liesebach *et al.,* 1999	Grosshansdorf, DE	Degree hours	Controlled	AcDH5 AcDH10	Controlled AcDH5: 350-800 DH

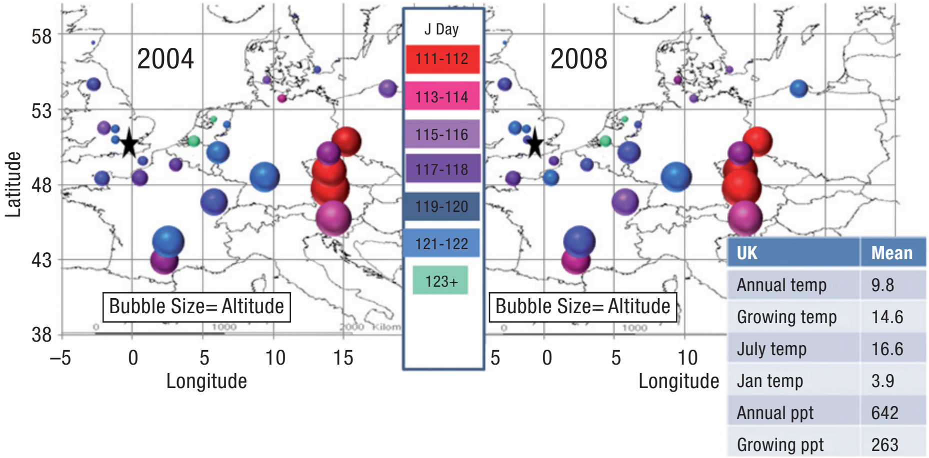


F1. Comparison of bud-burst date modelled by fitting individual tree data from entire trial BU2020 (Slovakia) using Weibull Function and using a Sigmoid Function (Gömöry - unpublished data).


a)
Latitude
58
53
48
43
38
–5
0
5
10
15
20
25
Longitude
Prov Code
Early Flush
15-40 days
41-50 days
51-60 days
61-70 days
71-80 days
81-90 days
Late Flush
Bubble Size= Altitude
Daily Winter frosts after 20th Dec (1998 Series)
b)
Latitude
58
53
48
43
38
–5
0
5
10
15
20
25
Longitude
Prov Code
Early Flush
15-40 days
41-50 days
51-60 days
61-70 days
71-80 days
81-90 days
Late Flush
Bubble Size= Altitude
Daily Winter frosts after 20th Dec (1995 Series)

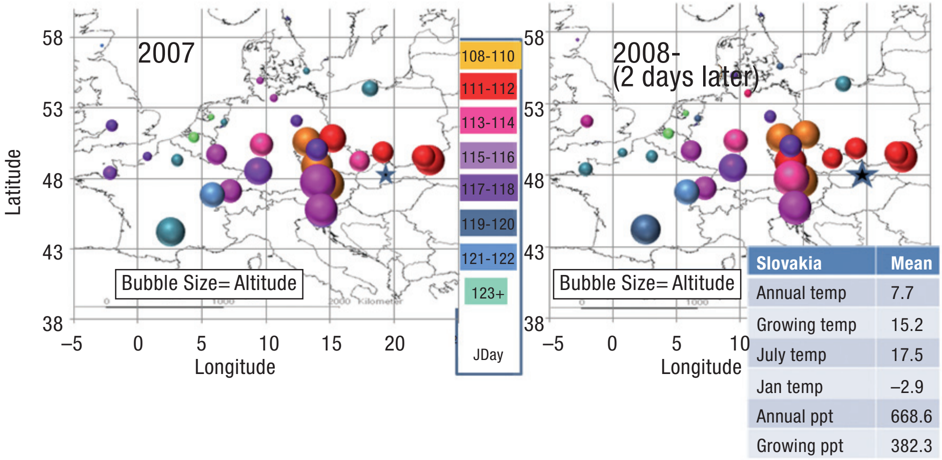


F2. Maps showing number of frosts 50 year average daily weather data at each trial site. Winter frosts (December 21st to March 21st), a) 1998-Series, b) 1995-Series. Spring frost (after March 21st), c) 1998-Series, d) 1995-Series.



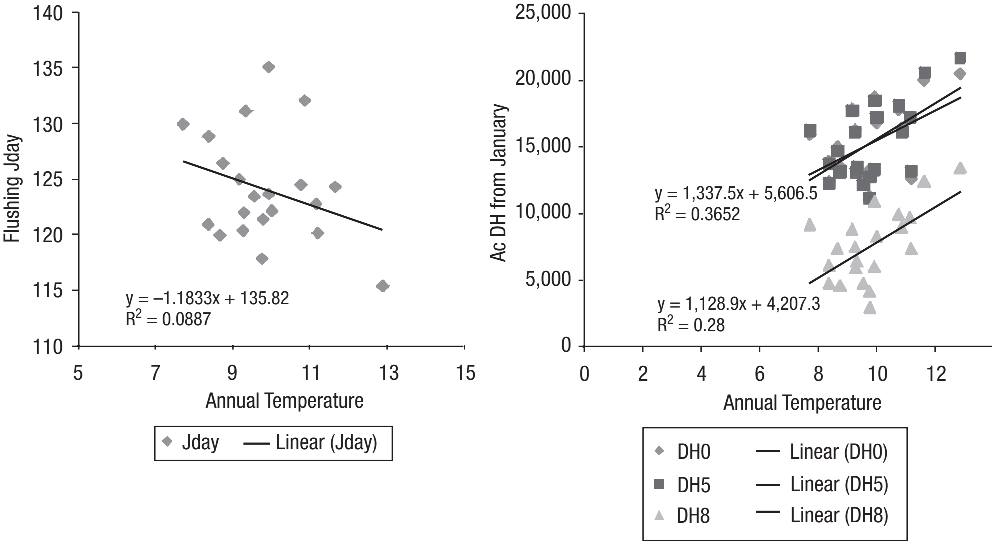
UK	Mean
Annual temp	9.8
Growing temp	14.6
July temp	16.6
Jan temp	3.9
Annual ppt	642
Growing ppt	263

F3. Comparison of the full suite of provenances growing at trial site BU2005 Little Wittenham, Oxfordshire, UK. 2004 v 2008. The star shows the location of the trial site.



Slovakia	Mean
Annual temp	7.7
Growing temp	15.2
July temp	17.5
Jan temp	–2.9
Annual ppt	668.6
Growing ppt	382.3

F4. Comparison of the full suite of provenances growing at trial site BU2020 Mlacik, Slovakia. 2007 v 2008. The star shows the location of the trial site. Colours on the right-hand map (2008) represented bud-burst dates 2-days later than in the key for the left hand map.



F5. The relationship between mean flushing date at 19 trial sites and the mean average temperature at each site (calculated from 50-year mean climatic data). The left panel shows the very weak negative correlation (NS) with Julian Date, while the right panel shows a positive relationship between AcDH requirement and temperature, suggesting that warmer sites require a greater temperature sum for bud burst.