

Variation in bud burst and flower opening responses of local versus non-local provenances of hawthorn (*Crataegus monogyna* Jacq.) in Belgium

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Abstract To study the impact of provenance selection of planting stock in (re)forestation and landscape plantings, the variation in bud and flower phenology, height increment and shrub morphology was examined within and between the local and non-local provenances of *Crataegus monogyna* in a provenance trial. Seven Belgian provenances were included, five in Flanders and two in Walloon, completed with three commercial provenances originating from Italy, Hungary and the United Kingdom. A completely randomized design (single tree plots) was adopted. Data were processed using mixed modelling techniques. South European provenances flushed up to 7 days earlier than the Flemish provenances, whereas the Walloon provenances flushed 4 days later. Compared to the Flemish provenances, Southern provenances and Walloon provenances flowered 4 days earlier and 2 days later respectively. Height increment and shrub morphology did not vary significantly between the Belgian and commercial provenances. Bud burst varied less than flowering among the Flemish and the Walloon provenances. This possibly indicates a higher selection pressure on bud burst than on flowering. The higher time lag between the different provenances for bud burst in comparison to flowering indicates a stronger plastic response for the latter. The results point out the importance of bud burst as an indicator of local adaptation to geo-climatologic components.

Finally, it appeared that old hedges are likely to be good sources of locally adapted seed.

Keywords *Crataegus monogyna* · Bud burst · Flowering · Phenology · Local seed source · Local adaptation

Introduction

After many years of neglect, the use of native species in afforestation and landscape programmes is gaining importance throughout, based on the underlying ecological principle that native species and genotypes are adapted to local growing conditions and have co-evolved with other components of the local ecosystems. This has led to large-scaled plantations of indigenous tree and shrub species in Western Europe, not only for forestry purposes but also for native woodland restoration and other landscape plantings, such as thickets, wooded banks and hedgerows. A major problem is that, especially for shrub species, non-indigenous foreign reproductive material is used mainly because of the low seed prices. The Council Directive 1999/105/EC (Council of the European Union 2000) regulates the marketing and transport of forest reproductive material through an obligatory certification of reproductive material for a number of species ensuring the origin of the material. However, this certification is not mandatory for shrub species. In North-West European countries shrub seed is commonly imported from Eastern and Southern Europe where it is cheaper. Nursery managers often do not know or are not interested in the exact origin of the seed they purchase.

Autochthonous populations of trees or shrubs have regenerated naturally since their establishment after the

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last glaciation or have been artificially regenerated using strictly local material only. For long-lived species such as trees, autochthony assumes a continuous presence at a given site since post-glacial immigration (Kleinschmit et al. 2004). This implies a continuous local genetic diversity after thousands of years of natural selection. Introduction of non-local material can have numerous negative consequences. Non-autochthonous planting stock may be poorly adapted to local growing conditions, leading to negative consequences such as decreased fitness (e.g. McKay et al. 2005; Krauss and He 2006; Edmands 2007; Laikre et al. 2010; Vander Mijnsbrugge et al. 2010). Problems may only become evident many years after apparently successful establishment. However, intra-specific hybridization of local and introduced genotypes may result in outbreeding depression, i.e. a reduced fitness in subsequent generations and loss of genetic diversity and adaptation and introgression of less adapted characteristics into the autochthonous populations. The introduction of non-local material may also have negative effects on associated plant and animal species. Hawthorn imported in the U.K. appeared to flower several weeks earlier than native provenances (Jones et al. 2001), potentially threatening insects and birds whose reproductive cycles are synchronized with this event (Hubert and Cottrell 2007). To assess putative negative consequences of using non-local planting stock, the variation of traits within and among autochthonous and non-autochthonous populations has to be evaluated. Provenance trials well-serve this purpose. Traditionally these trials merely aimed at comparing the economic value of different provenances in terms of wood production. However, at the same time, they serve research on adaptive variation of populations.

Phenology is a major determinant for the distribution area of tree species (Chuine and Beaubien 2001). Date of bud burst affects the length of the growing season, the flowering time and the reproductive success. Large clinal variation for this trait is observed in provenance tests of many tree species with moderate to high heritability values (Ducouso et al. 1996; Alberto et al. 2011; Savolainen et al. 2007; Robson et al. 2011; McKown et al. 2014). For softwood species provenances from the South-East of Europe in Mediterranean and warm-continental regions flush early compared to late-flushing provenances from the North and West of Europe where oceanic influences on the climate are strong. In *Fagus sylvatica* multi-site provenance tests, the ranking of provenances within one site is maintained, indicating a genetic control which supersedes the effect of local climate and soil conditions (Robson et al. 2011). Bud burst in *Populus trichocarpa* is triggered by both temperature and photoperiod (McKown et al. 2014). Photoperiod, however, overrides temperature

for the time of bud burst, so that trees moved towards latitudes different from their site of origin experience a mismatch (McKown et al. 2014). The predicted global warming may prolong the growing season of temperate woody species (Chuine and Cour 1999) and thus increase vulnerability to late spring frosts, early autumn frosts or to certain phytopathogens, but frequency and duration of climatic extremes may also augment while photoperiod will remain the same at given latitude. The last decades, many plantations of shrub species in several western European countries, including Flanders, are established with stock from more southern origins than the plantation site. It can be assumed that large-scale plantations of these provenances exhibit early bud burst, increasing their vulnerability to late spring frosts as opposed to their advantage of being adapted to higher average temperatures.

Despite the controversy whether or not planting stock of local origin is in all cases the best, it is likewise clear that large-scale use of non-autochthonous genotypes is not recommendable, especially when reasons to do so are purely economical (Laikre et al. 2010). This study attempts to help clarifying this issue based on the results from a provenance trial using both autochthonous and commercially non-autochthonous provenances of *Crataegus monogyna* Jacq., a traditionally commonly planted shrub species in hedges. As with many common woody species, hawthorn has been somewhat discarded in terms of conservation of patterns of regional forms and ecotypes because conservation efforts tend to focus primarily on rare species. Nonetheless, hawthorn is planted in huge quantities in hedge rows, wooded banks and in the edges and understory of forest stands in Flanders, to improve species diversity, to restore historical landscapes and to preserve wildlife habitat. Commercially available provenances are often non-autochthonous, originating from Southern and South-Eastern European countries where cheap seed is available. The variability among autochthonous and non-autochthonous provenances is assessed in a provenance trial for a biomass trait (height growth rate), two adaptive traits (bud burst and flowering) and a morphological trait (shrub habitus).

Materials and methods

Selection of source populations

Five populations of *C. monogyna* were selected in Flanders based on the inventory of autochthonous trees and shrubs (Vander Mijnsbrugge et al. 2005). Hawthorn plants in old farm hedges were considered to be autochthonous as they were created in former times with planting stock of local

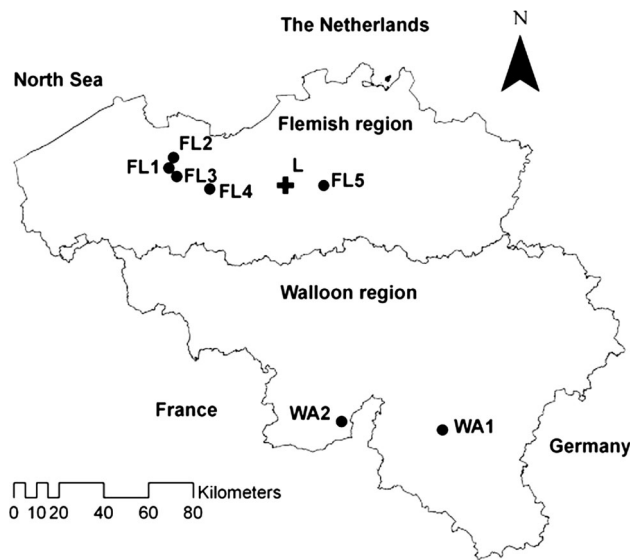


Fig. 1 Map of Belgium indicating the location of the sampled populations of *C. monogyna* (filled circled) and of the provenance trial (filled plus) (L: Londerzeel). Abbreviations of sampled locations are in Table 1

origin. Nowadays, old farm hedges have become rare and endangered in Flanders. Often owned privately and, thus, with little to no protection, they disappear quickly from the landscape. In Flanders, ancient forests with autochthonous gene resources of woody plants are scarce. Therefore, old farm hedges were selected for seed collection provided they were not pruned rigorously. In Wallonia, two additional old farm hedges were chosen for seed collection (Fig. 1 and Table 1). Finally, three commercial provenances originating from Italy, Hungary and the United Kingdom were included in the experiment. The exact location of these commercial seed sources is unknown as a certificate of provenance is not compulsory for *C. monogyna* according to the Council Directive 1999/105/EC (Council of the European Union 2000).

Establishment of the provenance trial

Seeds were collected on the seven Belgian hedges in autumn 2004 and sown in spring 2005. Plants from Southern Europe and the U.K. were obtained from a Flemish commercial nursery. In spring 2008, the provenance trial was established in Londerzeel, using three-year-old, bare-rooted plants of each of the 10 provenances (Fig. 1). A completely randomized design (single tree plots) was adopted with a spacing of 1.5×1.5 m. Low mortality was observed (Table 1). On the other hand, for some plants which were damaged during mowing of the plantation site, a minimum or even negative height increment was recorded after two growing seasons. Because of the single tree plot design, these incidents were considered to have occurred at random among the provenances and so these plants were not excluded from the dataset.

Measurements and scoring

Total tree height was measured in spring 2008 (right after plantation), 2010 and 2012. Bud burst and flower opening were observed on individual plants on 16 and 23 March 2012 and on 4, 12 and 19 May 2012 respectively, using a five class scoring system for both traits (Table 2). As not all plants were already flowering in 2012, the flower opening data set is smaller than the bud burst data set (Table 1). Shrub morphology was evaluated in winter 2010 applying a three-class scoring scheme (Table 2). Data of different provenances within one phytogeographical region were pooled and called provenance regions.

Data analysis

All statistical analyses were performed using the open-source software R 3.0.2 (R Core Team 2013). Phenological data consist of ordered classes that can be modelled with cumulative logistic regression. To partition the variance in

Table 1 Descriptive data of the sampled provenances of *C. monogyna* in the provenance trial

Village	Provenance abb.	Region	Region abb.	Altitude (m)	<i>n</i> Planted	<i>n</i> Dieback ^a	<i>n</i> Flowering ^a
Hansbeke	FL1	Flanders	FL	10	34	1	17
Zomergem	FL2	Flanders	FL	7.5	52	4	35
Landegem	FL3	Flanders	FL	10	55	1	39
Melle	FL4	Flanders	FL	10	55	1	32
Muizen	FL5	Flanders	FL	12.5	54	0	30
Smuid	WA1	Wallonia	WA	370	54	0	19
Viroin	WA2	Wallonia	WA	305	51	2	6
–	HU	Hungary	HU	–	53	7	6
–	IT	Italy	IT	–	54	2	39
–	UK	United Kingdom	UK	–	53	6	2

For the commercial provenances no precise data on seedstock populations is available

– no data available

^a in 2012

Table 2 Scoring scale for bud burst, flower opening and habitus evaluation of the shrubs

Trait	Score	Description of stage
Bud burst	1	Majority of buds in winter rest
	2	Majority of buds swollen
	3	Majority of buds open with leaves visible but not yet protruding
	4	Majority of leaves protruding from buds, but not yet unfolding
	5	Majority of leaves unfolding
Flower opening	1	Majority of flowers closed and coloured greenish-white
	2	Majority of flowers closed but already coloured white
	3	Less than half of the flower heads with flowers that are already opening
	4	More than half of the flower heads with flowers that are opening
	5	All flowers open thus fully blooming
Shrub shape	1	Shrub showing an apical dominance and relatively little branching
	2	Intermediate stage
	3	Very branching habitus with no clear apical dominance

its different components and to estimate the time lag in bud burst and flower opening between the provenance regions, phenological scores were modelled using a cumulative logistic mixed model in the ordinal package in R (Christensen 2013). The phenological observations were modelled as ordered data ranging from level 5 to 1 so that fitted phenological values for a defined provenance region at a defined day indicated the chance that a shrub from that provenance region minimally reached a particular score level.

$$PH_{ijk} = D + PR_i + P_{ij} + ID_{ijk}$$

PH is the phenological observation (bud burst and flower opening), D is the day of observation counting from day 1 at the first observation, PR_i is the provenance region, P_{ij} is the provenance nested in PR_i , ID_{ijk} is the individual shrub number, nested in P_{ij} . D and PR_i are in the fixed part of the model, whereas P_{ij} and ID_{ijk} are in the random part (random intercept).

The time lag in phenological response between the different provenance regions was defined as the difference in days in which half of the plants has reached the same score level, and was calculated as follows:

$$D_{pr1} - D_{pr2} = (\beta_{pr2} - \beta_{pr1}) / \beta_D$$

D is the day counting from day 1 at the first phenological observation, pr is provenance region, β_{pr} is the estimated coefficient of the fitted model for the provenance

region and β_D is the estimated coefficient for D. Confidence intervals were calculated for the time lag in phenological response between the different provenance regions using parametric bootstrapping based on the fitted phenological models. When zero days of time lag between two provenance regions was present within the confidence intervals, the time lag was considered not significant.

To test a putative differentiation in growth rate between the different provenance regions, height data were modelled using linear regression in the nlme package (Pinheiro et al. 2013) in R.

$$H_{ijk} = Y + PR_i + P_{ij} + ID_{ijk}$$

H_{ijk} is height of the individual plant, Y is year of measurement and PR_i is provenance region. Provenance (P_{ij}), nested in PR_i , and number of individual plant (ID_{ijk}), nested in P_{ij} , are in the random part of the model (random intercept).

Shrub morphology was evaluated once and data were processed by χ^2 statistics

Results

Time of bud burst and flowering

At the level of provenance regions clear differences were observed for bud burst and flower opening between the Flemish, the Walloon and the Southern European origins (Fig. 2a, b). The U.K. provenance behaved very similar to the Flemish provenances. Similarly, comparable were the Italian and Hungarian provenances. Bud burst and flower opening were modelled using a cumulative logistic regression. All provenance except U.K. differed significantly from the Flemish provenances for both phenological traits (Table 3). From the estimated parameters of the fixed effects in the model, the time lag between Flanders, Wallonia, United Kingdom and the Southern European provenances was calculated. In comparison to the Flemish provenances, the Walloon provenances flushed 6.5 days later, whereas the Italian and Hungarian provenances flushed 8.7 and 7.0 days earlier, respectively. The U.K. provenance behaved similar to the Flemish ones (0.1 day later). Flowers from the Flemish provenances open 2.1 and 2.4 days later than the Hungarian and Italian ones respectively, whereas they open 2.7 days earlier than the Walloon provenances. Again, the U.K. provenance is similar to the Flemish ones (0.3 day later). The modelled bud burst and flower opening are shown in Fig. 3. Confidence intervals were calculated for time lag between two provenance regions for both bud burst and flower opening, and were considered significant when the confidence interval of the time lag excluded zero days (Fig. 4). Remarkably,

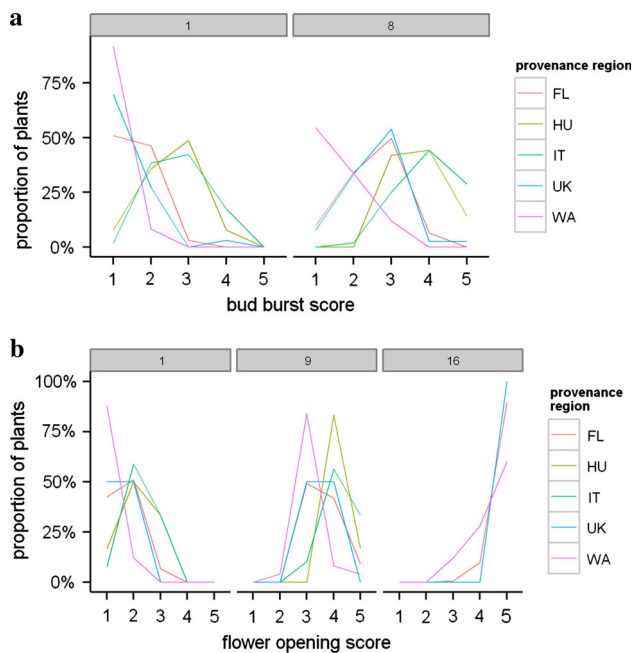


Fig. 2 Proportion of plants in the different score levels of bud burst (a) and flower opening (b) on the two and three scoring days respectively (first observation on day 1). Provenance region abbreviations are in Table 1

variation of bud burst among provenances within the same region (five Flemish provenances and two Walloon provenances) was negligible whereas flower opening varied comparatively more (Fig. 5a, b respectively, for the Flemish provenances). This is expressed in the lower estimated variance component for provenance (P) in the random part of the fitted phenological model for bud burst in comparison to flower opening (Table 4).

Height growth

A box plot of the measured height increment of the different provenance regions in 4 years after plantation is shown in Fig. 6. First, a height growth model was fitted

with and without a weight factor for heterogeneity in the variance of height growth in the provenance regions, using restricted maximum likelihood (REML). Both models were compared using a likelihood ratio test (LRT) which gave a likelihood ratio (LR) of 11.6 with a *p* value of 0.02 [degrees of freedom (df) of 22 and 18 for the models with and without weight factor, respectively]. This indicates no substantial differentiation in variation of height growth among the provenance regions. The weight factor was not retained in further analysis.

Second, the model was fit with and without interaction between the fixed covariates *Y* and *PR_i*. These models were run with maximum likelihood (ML) for correct comparison. The LRT yielded a RT of 32.0 with a *p* value of 0.0001 (df of 18 and 10 for the models with and without an interaction between *Y* and *PR* respectively). This significant difference implies a differentiation in height growth rate between the provenance regions. The model with interaction term was fit with REML to look for significant interaction term parameters. In comparison to the Flemish provenances, displaying a modelled height increment in 4 years after plantation of 66 cm, only the U.K. provenance grew slightly slower (modelled height increment of 46 cm, *p* value of 0.005). The other provenances did not differ significantly (modelled height increment in four years of Italian, Hungarian and Walloon provenances of 51, 82 and 74 with *p* values 0.015, 0.014 and 0.088, respectively).

Shrub habitus

As the shrub habitus was evaluated only once (2 years after plantation), data were processed with χ^2 statistics. The Flemish provenances differed significantly from the Walloon region and Hungary. A slightly higher apical dominance was observed for the Flemish provenances whereas the Walloon and Hungarian provenances are somewhat more bushy and branchy (Fig. 7 and Table 5).

Table 3 Estimated beta coefficients for the fixed part of the phenological models

Covariable	Bud burst				Flower opening			
	Estimated parameter	Std. error	<i>z</i> value	<i>p</i> value	Estimated parameter	Std. error	<i>z</i> value	<i>p</i> value
D (day)	0.97601	0.09504	10.269	0***	−1.4910	0.1385	−10.765	0***
PR_HU	6.87383	0.97271	7.067	0***	−3.1422	−2.036	1.5430	0.04
PR_IT	8.44905	1.04346	8.097	0***	−3.6194	0.9063	−3.994	0***
PR_UK	−0.12744	0.78850	−0.162	0.87	0.4124	2.4967	0.165	0.87
PR_WA	−6.38736	0.88726	−7.199	0***	3.9472	0.9502	4.154	0***

The provenance region (PR) of Flanders is standard (estimated parameter PR_FL = 0), to which the other regions are compared. Abbreviations of provenance regions are in Table 1

Significance codes: *** $p \leq 0.0001$, ** $0.0001 < p \leq 0.001$, * $0.001 < p \leq 0.01$

Fig. 3 Modelled bud burst and flower opening, indicating for every score level the proportion of plants of a provenance region that reached the given score level (first observation on day 1). Provenance region abbreviations are in Table 1

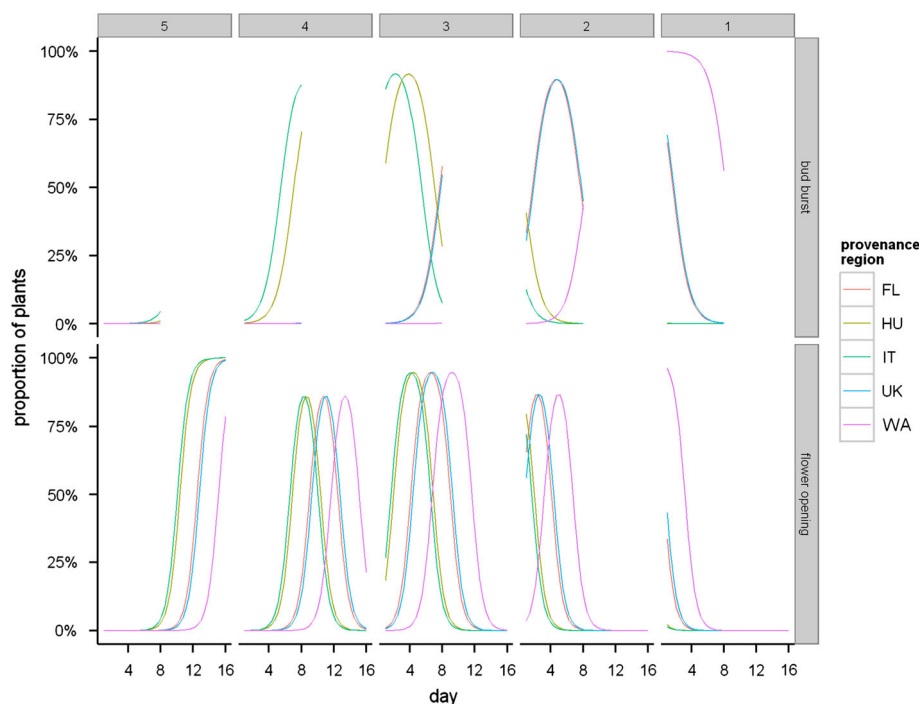
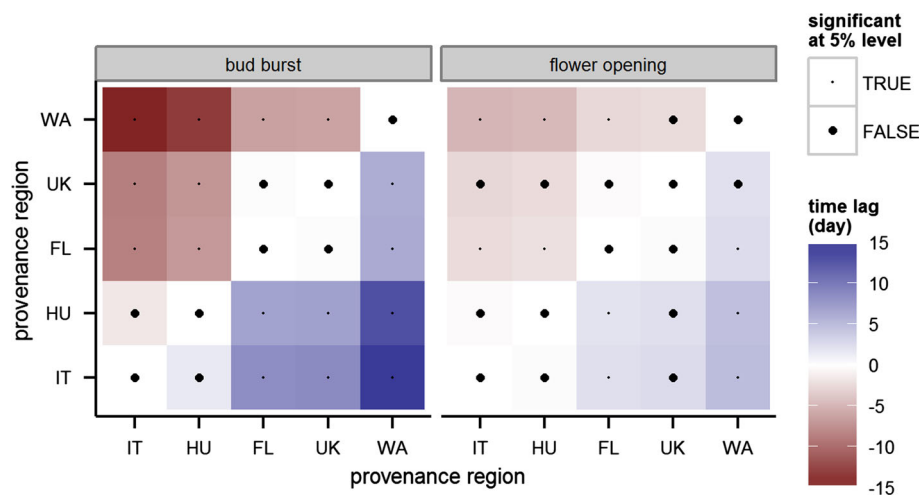


Fig. 4 Diagram showing time lag in bud burst and flower opening between provenance regions. When confidence intervals exclude zero days, the time lag is significant



Discussion

Flanders is characterised by a high anthropogenic impact on the landscape. This not only evolves from deforestation and forest fragmentation, but also from large-scale exploitation of natural resources as a consequence of extensive mechanisation in agriculture during the last century. In this process, many old hawthorn hedges disappeared from the countryside. This was enhanced specifically in the sixties and seventies of the previous century as a precaution and phytoremediation for fire blight infections. All this resulted in huge losses of wooded banks and old hedges, a process which still continues to date.

Only the last decades local programs are initiated to reconstruct the once typical bocage landscape consisting in Flanders largely of *C. monogyna* hedges. These restoration efforts evolve from cultural historical reflections and from the awareness of the present losses of biodiversity in agricultural landscapes. Unfortunately, the origin of the commercial planting stock used for hawthorn hedge restoration is not being taken into account, resulting in the introduction of foreign ecotypes. Consequences in the long run may include both maladaptation and eventually inbreeding depression (Vander Mijnsbrugge et al. 2010). During the last decade, several Western European countries have been pursuing programs on the collection and

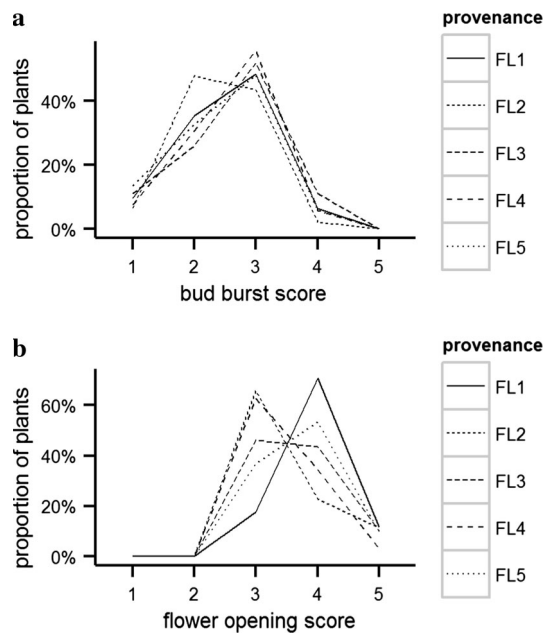
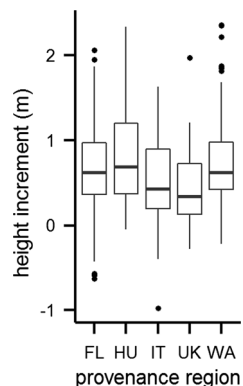


Fig. 5 Proportion of plants in the different score levels of bud burst (a) and flower opening (b) on the second scoring day. Provenance abbreviations are in Table 1

Table 4 Estimated variance components for the random part of the phenological models

Phenophase	No. of provenances (P)	σ_P^2	No of individual shrubs (ID)	σ_{ID}^2
Bud burst	10	0	472	16.3
Flower opening	10	0.3	225	8.8

Fig. 6 Box plot showing height increment of the provenance regions in 4 years after plantation. Provenance region abbreviations are in Table 1



marketing of local seed for the production of forest reproductive material. Much debate has arisen on whether local planting stock is really better in terms of adaptation to the local growth conditions. This study focuses on growth and phenological characteristics of autochthonous and commercially available non-local provenances in a provenance trial.

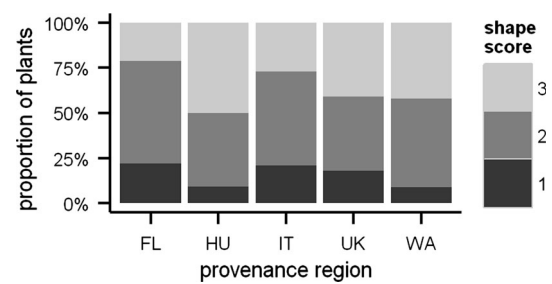


Fig. 7 Bar plot showing shape score classes of the provenance regions. Provenance region abbreviations are in Table 1

Table 5 χ^2 statistics for shrub shape 2 years after plantation

p value	χ^2 statistic	FL	HU	IT	UK	WA
FL			16.87	0.81	7.25	19.31
HU	0***			6.22	1.59	0.86
IT	0.67	0.04			2.02	6.25
UK	0.03	0.45	0.36			2.46
WA	0***	0.65	0.04	0.29		

Provenance region abbreviations are in Table 1

Significance codes: *** $p \leq 0.0001$, ** $0.0001 < p \leq 0.001$, * $0.001 < p \leq 0.01$

Clines in bud burst

Clear adaptational clines in phenological traits of *C. monogyna* are demonstrated, while, neither height growth nor shrub habitus vary significantly or meaningfully among the provenance regions. The observed phenological clines are similar to the ones examined in many provenance trials of economic tree species. Part of the observed phenotypic variation for the studied phenological traits reflects selective processes. Both a latitudinal (Flemish versus South and South-Eastern European provenances) and an altitudinal (Flemish versus Walloon provenances) influence are evident. It can be assumed that the Flemish provenances exhibit a home-site advantage for this trait. The later bud burst in comparison to the Italian and Hungarian provenances is likely to be associated with a higher cold tolerance in spring, whereas the earlier bud burst in comparison to the higher altitude provenances of the Walloon region prolongs the growing season without major risks of frost damage in spring. These results are in accordance with Jones et al. (2001) who demonstrated the superiority of the local provenance of *C. monogyna* in comparison to eight non-local and commercially available provenances in a provenance test in the U.K. Surprisingly, Jones et al. (2001) observe up to 5 weeks of difference in bud burst date between the local high altitude provenance and some Southern European provenances, whereas bud burst data

recorded in this study show a time lag of merely 1 week between the Flemish and the South and South-Eastern European provenances or one and a half week between the higher altitude Walloon provenances and the Southern provenances (approximately 300 m altitude difference). Apart from the fact that provenances in this study are not the same as in the trial of Jones et al. (2001), local climate and soil conditions in both provenance trials may strongly influence bud burst date, implying that a combination of genetic and plastic responses may lead to variation in time lag between bud burst dates of provenances of different latitudinal or altitudinal origin in provenance trials established on different locations. This can possibly be related to the observed shifts in phenology in *Populus balsamifera* depending on the location of the planting site, resulting in varying dates for phenology from genetically identical trees (Olson et al. 2012; Soolanayakanahally et al. 2013). This can be attributed to a larger number of genes and/or varying contributions of gene action being at the base of the phenological responses to local environmental heterogeneity (McKown et al. 2014).

Phenological response and selection pressure

Two results indicate a less stringent selection pressure on flower opening than on bud burst. First, the time lag between the different provenances region studied was clearly higher for bud burst than for flower opening. It can be assumed that the two main and antagonistic drivers of flushing are the minimising of frost damage by late flushing, and the maximising of the growth season by early flushing. The balancing of these two driving forces results in the latitudinal and altitudinal clines when provenances originating from different geographical regions are compared in the same site. The lower differentiation between the provenance regions for flower opening might indicate a stronger impact of a plastic response. Once the growing season has started and shrubs have flushed, favourable temperatures may lead to a stronger plastic response inducing flower opening more synchronised in comparison to bud burst, although the effect of provenance origin is still significantly present. Second, the variation among the five Flemish and the two Walloon provenances is slightly higher for flower opening than for bud burst. Here we look at different provenances originating from similar latitudes and altitudes. Bud burst has been fine tuned to a greater synchronised response in comparison to flower opening, suggesting that selection pressure on bud burst is higher than on flower opening. Not only does flowering occur later in spring compared to flushing, when the risk of frost damage is lower, shrubs also start flowering several years after establishment, implying that frost damage may not be as detrimental as

in younger seedling and sapling stages. As the pollination period is restricted in time, a stronger plastic response may enhance the possibilities to profit from favourable climatic conditions and thus may augment the chances of successful fertilisation.

Old hedges as a source of autochthonous seed

Flanders is a relatively small geographical region marked by an uniform topography. Consequently, all Flemish provenances show a similar bud burst pattern, and height increment during the first 4 years after plantation does not vary considerably among them. This suggests that the sampled old hedges were not planted with foreign stock displaying deviating phenological responses and confirms the assumption that in former times farmers used locally sourced planting stock for their farmland hedges. Our results confirm the autochthonous nature of remaining old hedges. If they are not regularly pruned, they can serve as sources of local seed for the production of planting stock. Fortunately, the regional legislation in Flanders on the marketing of forest reproductive material (Anonymous 2003) implementing the European Council (Council of the European Union 2000), allows a non-obligatory certification of shrub species under the category 'source identified'. This permits private nurseries to collect seeds on officially approved seed sources, such as old hedges, and sell their stock with a guarantee of local origin.

Conclusion

In view of the predicted climate change and accounting for the phenological responses of provenances that express adaptation to latitude and altitude at the site of origin, two concerns can be raised. First, local autochthonous populations may experience two drawbacks in a climate change scenario. Warmer mean spring temperatures may make them flush and flower earlier, putatively rendering them more susceptible to late spring frosts. And, more severe summer droughts may diminish the length of the growing period more in the local late flushing provenances. Second, transferring Southern provenances to Northern sites may create a trade-off between at the one hand a better thermotolerance towards drought periods and a longer growing period and at the other hand a higher vulnerability towards late spring frosts. Precaution should prevail in the transfer of Southern provenances to plantation sites in the North-West of Europe where they may be susceptible to frosts. Clearly, awareness among forest nurseries and other stakeholders involved in plantations of woody vegetations on these aspects is still in its infancy.

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References

- Alberto F, Bouffier L, Louvet JM, Lamy Delzon S, Kremer A (2011) Adaptive responses for seed and leaf phenology in natural populations of sessile oak along an altitudinal gradient. *J Evol Biol* 24:1442–1454
- Anonymous (2003) Besluit van de Vlaamse regering betreffende de procedure tot erkenning van bosbouwkundig uitgangsmateriaal en het in de handel brengen van bosbouwkundig teeltmateriaal. *Belgian Law Gazette* 11:54793–54824
- Christensen RHB (2013) ordinal: Regression models for ordinal data. In: R package version 2013. pp 10–31. <http://www.cran.r-project.org/package=ordinal/>
- Chaine I, Beaubien E (2001) Phenology is a major determinant of tree species range. *Ecol Lett* 4:500–510
- Chaine I, Cour P (1999) Climatic determinants of budburst seasonality of temperate-zone trees. *New Phytol* 143:339–349
- Council of the European Union (2000) Council Directive 1999/105/EC of 22 December 1999 on the marketing of forest reproductive material. *Off J Eur Comm* L11:17–40
- Ducousso A, Guyon JP, Kremer A (1996) Latitudinal and altitudinal variation of bud burst in western populations of sessile oak (*Quercus petraea* (Matt.) Liebl.). *Ann Forest Sci* 53:775–782
- Edmands S (2007) Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. *Molec Ecol* 16:463–475
- Hubert J, Cottrell J (2007) The role of forest genetic resources in helping British forests respond to climate change. Forestry Commission Scotland, Edinburgh
- Jones AT, Hayes MJ, Sackville Hamilton N (2001) The effect of provenance on the performance of *Crataegus monogyna* in hedges. *J Appl Ecol* 38:952–962
- Kleinschmit JRG, Kownatzki D, Gegerius HR (2004) Adaptational characteristics of autochthonous populations – consequences for provenance delineation. *Forest Ecol Manag* 197:213–224
- Krauss LS, He TH (2006) Rapid genetic identification of local provenance seed collection zones for ecological restoration and biodiversity conservation. *J Nature Conserv* 14:190–199
- Laikre L, Schwartz MK, Waples RS, Ryman N (2010) Compromising genetic diversity in the wild: unmonitored large-scale release of plants and animals. *Trends Ecol Evol* 25:520–529
- McKay JK, Christian CE, Harrison S, Rice KJ (2005) “How local is local?”—a review of practical and conceptual issues in the genetics of restoration. *Restor Ecol* 13:432–440
- McKown AD, Guy RD, Klapste J, Geraldine A, Friedmann M, Cronk QCB, El-Kassaby YA, Mansfield SH, Douglas CJ (2014) Geographical and environmental gradients shape phenotypic trait variation and genetic structure in *Populus trichocarpa*. *New Phytol* 201:1263–1276
- Olson MS, Levens N, Soolanayakanahally RY, Guy RD, Schroeder WR, Keller SR, Tiffin P (2012) The adaptive potential of *Populus balsamifera* L. to phenology requirements in a warmer global climate. *Molec Ecol* 22:1214–1230
- Pinheiro J, Bates D, DebRoy S, Sarkar D, the R Development Core Team (2013) nlme: Linear and Nonlinear Mixed Effects Models. In: R Core Team, R package version 3.1-113. R Foundation for Statistical Computing, Vienna
- Robson TM, Alia R, Bozic G, Clark J, Forsteuter M, Gomory D, Liesebach M, Mertens P, Rasztovits E, Zitova M, von Wuhlisch G (2011) The timing of leaf flush in European beech (*Fagus sylvatica* L.) saplings. In: Genetic Resources of European Beech (*Fagus sylvatica* L.) for Sustainable Forestry, Proceedings of the COST E52 Final Meeting, Serie Forestal 22:61–80
- Savolainen O, Pyhäjärvi T, Knürr T (2007) Gene flow and local adaptation in trees. *Annu Rev Ecol Syst* 38:595–619
- Soolanayakanahally RY, Guy RD, Silim SN, Song M (2013) Timing of photoperiodic competency causes phenological mismatch in balsam poplar (*Populus balsamifera* L.). *Pl Cell Environ* 36:116–127
- R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/>
- Vander Mijnsbrugge K, Cox K, Van Slycken J (2005) Conservation approaches for autochthonous woody plants in Flanders. *Silvae Genet* 54:197–205
- Vander Mijnsbrugge K, Bischoff A, Smith B (2010) A question of origin: where and how to collect seed for ecological restoration. *Basic Appl Ecol* 11:300–311

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