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ORIGINAL ARTICLE

Population differentiation and phenotypic plasticity in temperature response of bud burst in *Frangula alnus* provenances of different latitude

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Abstract Flushing in spring marks an important adaptive process in a tree's growth cycle. We studied bud burst in three provenances of a common small tree *Frangula alnus* Mill., originating from Italy, Belgium and Sweden. We observed timing of bud burst and leaf senescence in a common garden, and timing and duration of bud burst in greenhouse conditions (cuttings) with different temperature regimes, all located in Belgium. The early bud burst response of the southern European provenance together with the later leaf senescence compared to the local provenance indicated population differentiation that may, at least partly, be driven by local adaptation to a longer growing season. The duration of the process was longer in the cold greenhouse compared to the local provenance, whereas it responded similar as the local provenance in the warm greenhouse, suggesting adaptation to warmer conditions. Unexpectedly, the northern European provenance expressed a plastic reaction to warmer temperatures in the field trial and in the greenhouse conditions flushing in both cases earlier than the local provenance. The duration of the process in the warm greenhouse compared to the local provenance was shorter, whereas in the cold greenhouse it was similar. This result again suggested that not only the onset, but also the duration of the bud burst process was a plastic reaction to the warmer conditions compared to its site of origin. Together, our results suggest two mechanisms driving bud burst in *F. alnus* provenances, a co-gradient and a counter-gradient variation depending on the latitude of origin.

Keywords Cumulative logistic mixed models · Bud burst · Leaf senescence · Local adaptation · Phenotypic plasticity · Temperature

Introduction

Spring flushing in temperate tree populations is a phenophase marking the onset of the yearly growth cycle. While maximizing the length of the growing season, it minimizes the chance of frost damage in early spring (Bennie et al. 2010). In addition, the onset of bud burst determines to a certain extent the onset of flowering (Vander Mijnsbrugge et al. 2015) and is, therefore, related to fecundity. Bud burst has been intensely studied in recent years as spring phenology of plants advances due to climate warming (Bertin 2008). When evaluated in situ, bud burst and leaf unfolding in temperate tree species occur characteristically earlier in southern latitudes and/or lower elevations compared to more northern sites and/or higher elevations (Vitasse et al. 2009; Alberto et al. 2011; Robson et al. 2011). This is related to the requirement of a given amount of warm temperatures in spring before buds can flush (forcing requirement), usually expressed as a daily or hourly temperature sum above a certain threshold temperature (Murray et al. 1989; Hannerz 1999). Although spring temperatures play a pivotal role in the timing of bud burst in situ, chilling requirement and photoperiod may also be

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involved depending on the species and the provenance within species (Caffarra and Donnelly 2011; Olsson et al. 2013). A negative relation between forcing requirement in situ and latitude was found for several tree species, indicating provenance-specific adaptations (Olsson et al. 2013). It is suggested that southern and central European provenances have higher forcing requirements in situ than northern provenances as they are adapted to slower seasonal transitions and experience higher risks of spring frosts (Hannerz et al. 2003; Olsson et al. 2013).

Phenology is believed to have a polygenic or complex genetic architecture (Neale and Kremer 2011; Olson and Levsen 2012; McKown et al. 2014). Bud burst and leaf unfolding in temperate tree populations originating from different sites but grown in common gardens typically express large intra- and inter-population differentiation and high heritability values (Alberto et al. 2011; McKown et al. 2014). They follow clinal patterns, mainly altitudinal and latitudinal, but also longitudinal (Oleksyn et al. 1998; Robson et al. 2011). The clines are interpreted as being (to a large extent) the result of local adaptation, based on differential and genetically determined responses to environmental factors. It is typical for adaptive traits in trees to exhibit high levels of population differentiation despite extensive gene flow, as a result of strong divergent selection due to biotic and abiotic selection pressures (Savolainen et al. 2007; Kremer et al. 2012). These genetical clines in timing of bud flushing in different provenances of temperate tree species planted in common gardens are described as linear relationships between the bud burst response and geographical variables at the sites of origin of the provenances and mostly show the so-called co-gradient variation, although counter-gradient variation has been described too (Soularue and Kremer 2012). *Quercus petraea* typically expresses co-gradient variation with southern/low altitude provenances flushing earlier both in situ and in common gardens compared to more northern/high elevational provenances (Vitasse et al. 2009; Alberto et al. 2011). Counter-gradient variation has been found for the altitudinal gradient in beech (*Fagus sylvatica*). The higher altitudinal provenances flush earlier compared to lower altitudinal provenances in a common garden because they require less temperature forcing, whereas in situ they flush later because of the colder climate at higher altitude, as a safeguard against frost damage (vonWuehlisch et al. 1995; Vitasse et al. 2009; Robson et al. 2013).

Literature on the duration of the bud burst process is remarkably scarce. Rousi and Pusenius (2005) found large variation both in the timing of bud burst and in the duration of the bud burst process among individual genotypes of birch planted in field trials and interpreted this variation as a defense mechanism against herbivory: insects may encounter difficulties in the unpredictability in timing and duration of bud burst resulting from genetic variation among trees. Duration of bud burst has been negatively correlated with mean caterpillar densities on trees (Hunter 1992). Basler and Körner (2014) studied timing and duration of bud swelling in spring at the species level (*Acer pseudoplatanus*, *Fagus sylvatica*, *Quercus petraea,* and *Picea abies*). The onset and duration of the bud swelling prior to bud burst in trees that had experienced sufficient chilling were driven by concurrent temperature and photoperiod (Basler and Körner 2014). Temperature was also shown to shorten the duration of the bud formation process in autumn in hybrid poplar clones (Rohde et al. 2011).

With the foreseen change in climate, the question can be raised whether to transfer southern provenances to more northern sites as an anticipation to the predicted higher mean temperatures (Williams and Dumroese 2014). On the other hand, it can be suggested that populations may persist in their current growth site and withstand environmental changes if they possess adequate adaptive capacities (Lindner et al. 2010). High genetic diversity among and within populations can improve opportunities of rapid adaptation to new environments, which is typically studied in common garden experiments, whereas phenotypic plasticity allows plants to cope with rapid environmental change (Vitasse et al. 2010). It can be suggested that phenotypic plasticity plays an important role in trees because of their long life span (Vitasse et al. 2010). The degree to which temperature mediates the bud burst response at a given latitude is important to determine the impact of future temperature change on the timing of flushing in woody plants. As clinal responses of different phenophases in common gardens are species dependent and hitherto mainly studied in wind pollinated (and commercially valued) tree species, we questioned which types of phenological responses can be expected in an insect-pollinated small tree species *Frangula alnus* Mill. (glossy buckthorn). More specifically, we questioned whether *F. alnus* expressed population differentiation between three provenances originating from different latitudes in Europe for bud burst and leaf senescence in a common garden, and to what extent the bud burst response reacted plastically to different temperature regimes in a greenhouse experiment. We focused both on the onset and on the duration of the bud burst process.

Materials and methods

Source material

Frangula alnus is a common deciduous small tree species with a high seed dispersal capacity and a wide distribution range, occurring throughout Europe and in northern
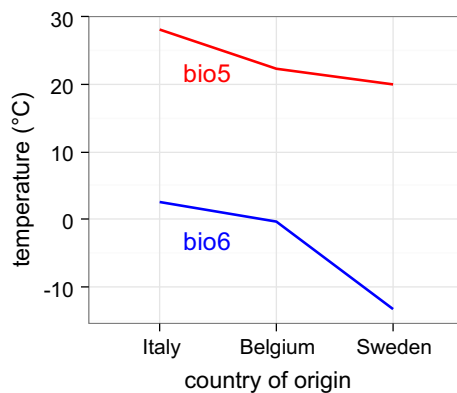
Fig. 1 Climate at the sites of origin of the three different provenances of *Frangula alnus*. Shown are temperature of the warmest (bio5) and coldest month (bio6)

Morocco (Medan 1994). In late summer of 2011, berries were collected from 7, 10 and 10 individual *F. alnus* shrubs in natural populations located in Famelunga, Italy (lat.: 43.12181; lon.: 11.17654), in Heist-op-den-Berg, Belgium (lat.: 51.08424; lon.: 4.793124) and in Ottsjön, Sweden (lat.: 62.44210; lon.:17.23451), respectively, representing populations at the southern edge of its range, at the center, and at the northern edge, respectively. Climate variables related to temperature at the three sites of origin (bio5: maximum temperature of the warmest month, bio6: minimum temperature of the coldest month) were downloaded from WorldClim (Hijmans et al. 2005) with a 2.5 arc-min resolution and are shown in Fig. 1. Seeds were kept separate per mother shrub. They were cleaned after collection, dried, transported to Belgium and stratified upon arrival in late autumn 2011 in trays (one seed per separate tray cell), according to the standard nursery practices at the nursery of the Research Institute for Nature and Forest in Geraardsbergen, Belgium. Trays were kept in an open greenhouse (greenhouse without sides). For the Italian, Belgian and Swedish provenances 8, 17 and 15 seeds germinated, respectively, and were further grown as potted plants in a container field in open air. In July 2013, the 1.5-year-old saplings (with an average height of 80 cm) were pruned at 20 cm above soil level to promote a shrubby habitus. Seedlings were further grown to 2-year-old potted plants (40 pots of 4 L and 21 cm diameter) using standard nursery techniques and standard nursery potting soil. All plants were transplanted to a field trial in January 2014, applying a single tree plot as design (shrubs individually intermingled) with 1.5 × 1.5 m interspace between the plants.

Cutting experiment

Cuttings were taken on the 10th of March 2015 from all shrubs from the Italian (32), Belgian (68) and Swedish

(48) provenances. As the shrubs lacked a clear apical dominance because of the pruning in 2013, each plant had several similar shoots. Per plant two to four comparable shoots were cut at 20 cm from the top and individually labeled. All 148 cuttings were put in glass containers filled with cool tap water. The water was changed weekly during the experiment. Half of the cuttings per plant were kept in eight glass containers in a well-heated greenhouse (minimal temperature of 20 °C), further called the warm greenhouse, whereas the other half were placed in eight containers in a less heated greenhouse (minimal temperature of 10 °C) further called the cold greenhouse. There was no control over the maximum temperature. For each greenhouse, the cuttings of the three provenances were individually mingled and randomly distributed among the eight containers in each greenhouse. Both greenhouses were next to each other with insulation being comparable between the two. On average, the two greenhouses differed 9 °C during the experiment.

Phenological observations in field trial and in greenhouse

Bud burst was observed in the field trial in the spring of 2014 following a scoring protocol of five levels (Table 1). From each shrub, all apical buds of the different shoots at the above half of the plant were observed and an average stage was scored. Observations were performed on 1, 7 and 16 April. Senescence of the leaves was evaluated at a single day in autumn 2014 (30 October) following a scoring protocol of three levels (Table 1). From each shrub, all shoots at the above half of the plant were observed and an average stage was scored. Bud burst was evaluated on the bud of the cuttings in the greenhouses in spring 2015 following the same bud burst protocol (Table 1) on five observation days (16, 20, 25, 30 March and 3 April).

Statistical analysis

Bud burst data from the field trial and from the greenhouse experiment were processed with cumulative logistic mixed models using the ordinal package (Christensen 2013) in R (R Core Team 2013). Ordinal calculates models for ordinal response variables. Bud burst scores were ordered from 5 to 1 so that the probability to have maximally reached a given bud burst score, e.g., score 3, encompassed all plants that reached score 5, 4 and 3. This was equal to all plants that minimally reached score 3.

Bud burst observations in the field trial were modeled as follows:

$$Bbf_{ij} = D + C_i + plantID_{ij}$$

Table 1 Scoring protocols of bud burst and leaf senescence in *Frangula alnus*

Phenophase	Score level	Description
Bud burst	1	Buds at rest
	2	Buds swollen
	3	First leaves visible but not yet protruding
	4	First leaves protruding from the bud, but not yet unfolding
	5	First leaves already unfolding
Leaf senescence	1	Leaves at the top of the shoots still green
	2	Intermediate stage
	3	Leaves at the top of the shoots colored brown and/or fallen

Bbf is the phenological observation in the field trial (bud burst), D is the day of observation counting from day 1 (27th March 2014) and C is the country of origin. D and C are in the fixed part of the model. PlantID is a unique identity code for each shrub in the field trial with plantID nested in C. PlantID remained in the random part of the model (random intercept), taking into account the repeated measurements on the same plants. The probability (p) to have minimally reached a given bud burst score on a given day D was calculated as follows:

$$\text{Log}(p/(1-p)) = \alpha_T - \beta_D \times D - \beta_C \times C$$

β_C and β_D are the estimated parameters in the fitted model for each country (C) and for day (D). α_T is the estimated threshold value to pass over from a given bud burst score to the next in order. To calculate the time lag between two provenances (thus from two countries) in the field trial, the day for each provenance was calculated on which the probability to have minimally reached bud burst score 3 was 50 % ($D_{C-50\,\%}$) and both days were subtracted:

$$D_{C1-50\%} - D_{C2-50\%} = (\beta_{C2} - \beta_{C1})/\beta_D$$

β_C and β_D are the estimated parameters in the fitted model for each country (C) and for day (D).

Bud burst observations on the cuttings were processed for each greenhouse and thus for each temperature treatment separately following the model:

$$Bbg_{ijk} = D \times C_i + \text{plantID}_{ij} + \text{cuttingID}_{ijk}$$

Bbg is the phenological observation in the greenhouse (bud burst), D is the day of observation counting from day 1 when the cuttings were cut and put in water containers and C is the country of origin. D and C are in the fixed part of the model. PlantID and cuttingID are unique identity codes for each shrub in the field trial and for each cutting, respectively, with cuttingID nested in plantID nested in C. PlantID and cuttingID remained in the random part of the model (random intercept), accounting for the repeated measurements on each cutting.

The probability (p) to have minimally reached a given bud burst score on a given day D was calculated as follows:

$$\text{Log}(p/(1-p)) = \alpha_T - \beta_D \times D - \beta_C \times C - \beta_{C \times D} \times C \times D$$

β_C, β_D and $\beta_{C \times D}$ are the estimated parameters in the fitted model for each country (C) and for day (D). α_T is the estimated threshold value to pass over from a given bud burst score to the next in order. To calculate the time lag between two provenances (thus from two countries) in a greenhouse, the day for each provenance was calculated on which the probability to have minimally reached bud burst score 3 was 50 % ($D_{C-50\,\%}$) and both days were subtracted:

$$D_{C-50\%} = (\beta_C - \alpha_{4|3})/(-\beta_D - \beta_{C \times D})$$

β_C, β_D and $\beta_{C \times D}$ are the estimated parameters in the fitted model for each country(C), for day (D) and for the interaction term $C \times D$. $\alpha_{4|3}$ is the estimated threshold value to pass over from bud burst score 4 to score 3 and indicates all plants that minimally reached bud burst score 3 (all plants with score 3, 4 or 5). The time lag between two countries was calculated by subtracting $D_{C-50\,\%}$ from two countries. To calculate the duration of the bud burst process for each provenance in a greenhouse, the days were calculated for which the probability (p) to minimally have reached bud burst score 3 was 5 and 95 %, respectively ($D_{C-5\,\%}$ and $D_{C-95\,\%}$) and by subtracting both days:

$$D_{C-5\%} = (\beta_C - \alpha_{4|3} + \log(p_{5\%}/(1-p_{5\%}))/(-\beta_D - \beta_{C \times D})$$

$$D_{C-95\%} = (\beta_C - \alpha_{4|3} + \log(p_{95\%}/(1-p_{95\%}))/(-\beta_D - \beta_{C \times D})$$

The only senescence observation in the field trial in autumn 2014 was processed with χ^2 statistics in R.

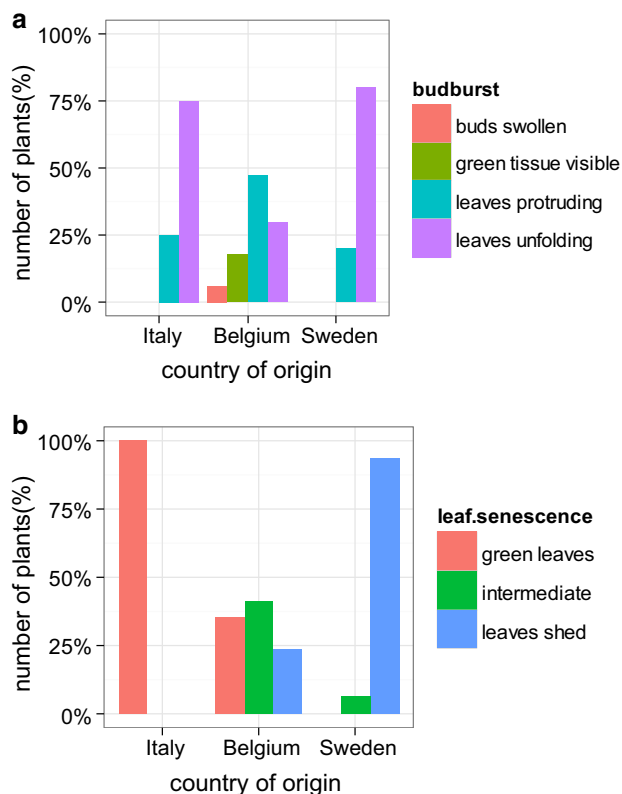## Results

Phenological responses in the field trial

The Italian and the Swedish provenances both flushed earlier than the Flemish provenance (Fig. 2a; Table 2) with a time lag of 4.7 and 4.4 days, respectively, calculated for the days that the probability for a given provenance to

minimally have reached bud burst score 3 was 50 % (which is the probability that half of the plants reached minimally score 3, 4 or 5).

Leaf senescence differed between the three provenances in the field trial on the only observation day in 2014 (30 October, Fig. 2b). A χ^2 test indicated significant differences between the three provenances (Belgium versus Italy: $\chi^2 = 9.24$, $df = 2$, P value $= 0.009$; Belgium versus Sweden: $\chi^2 = 16.00$, $df = 2$, P value < 0.001; Italy versus Sweden: $\chi^2 = 23$, $df = 2$, P value < 0.001). The Italian provenance shed leaves later compared to the Flemish provenance, whereas the Swedish provenance shed leaves earlier.

Phenological responses in the greenhouses

To assess the plasticity of the bud burst response of the different origins of *F. alnus* in different temperature regimes, cuttings from the same shrubs were taken from the field trial and allowed to flush in a warm and a cold greenhouse. The Italian and the Swedish provenances both flushed earlier than the Flemish provenance in both greenhouse conditions (Fig. 3). In the warm greenhouse, the Italian and the Swedish provenances flushed 2.8 and 3.8 days earlier compared to the Flemish provenance, as

Table 2 Model statistics for bud burst of three provenances originating from Italy (It), Belgium and Sweden (Sw) in the field trial (common garden)

Covariate	Estimate	Std. error	z value	P value
D (day)	−0.99	0.23	−4.34	**<0.001***
It	−4.27	1.79	−2.39	**0.017***
Sw	−4.00	1.54	−2.60	**0.009***

Belgium is the standard provenance to which Italy and Sweden are compared to (country is a factor variable)

Significant results are in bold: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

calculated from the days that the probability to minimally have reached but burst score 3 was 50 % (Fig. 3; Table 3). For the cold greenhouse, these time lags were 2.1 and 4 days between the Flemish provenance and the Italian and Swedish provenances, respectively. The differences in slope of the modeled bud burst curves expressed the plasticity of the bud burst response (the interaction terms between day and country of origin in the models, Table 3). In the warm greenhouse, the interaction term between day and country of origin for the Swedish provenance differed significantly from the Flemish provenance, whereas the Italian provenance did not differ significantly from the Flemish provenance, indicating different durations of bud burst in the Swedish provenance compared to the Flemish and Italian provenances. In the warm greenhouse, the time lag between the moments that the probability to minimally have reached bud burst score 3 was 5 and 95 %, was 8 and 7.1 days for the Flemish and Italian provenances, respectively, whereas it was only 5.4 days for the Swedish provenance. In the cold greenhouse, the interaction term between day and country of origin for the Italian provenance differed significantly from the Flemish provenance, whereas the Swedish provenance did not differ significantly from the Flemish provenance, indicating that the duration of bud burst in the Italian provenance differed from the Flemish and Swedish provenances. The time lag between the moments that the probability to minimally have reached bud burst score 3 was 5 and 95 %, was 4.6 days for both the Flemish and Swedish provenances, whereas it counted up to 5.4 days for the Italian provenance.

Discussion

Northern provenance deviates from expected latitudinal cline in bud burst

Linear latitudinal clines are typically observed for bud burst and leaf unfolding in common gardens of temperate tree species (Ducousso et al. 1996; Robson et al. 2011). In

Fig. 2 *Bar charts* indicating the different proportions of *Frangula alnus* plants in the field trial originating from the three countries in the different bud burst (**a**) and leaf senescence score levels (**b**) on the 7th of April and the 30th of October 2014, respectively

Fig. 3 Modeled bud burst of *Frangula alnus* cuttings originating from three different countries, in warm and cold greenhouse conditions (average difference of 9 °C). Day 1 is 10th of March 2015
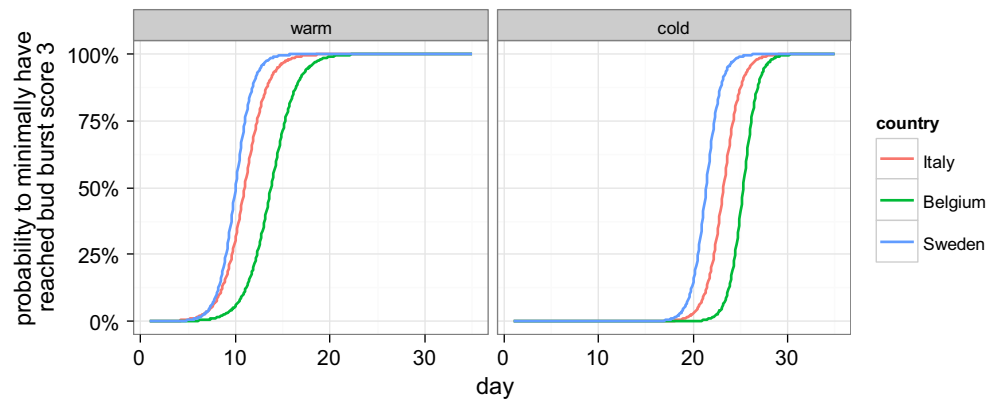
Table 3 Model statistics for bud burst observations on cuttings from three provenances of *Frangula alnus* originating from Italy (It), Belgium and Sweden (Sw)

Covariate	Warm greenhouse				Cold greenhouse			
	Estimate	Std. error	*z* value	*P* value	Estimate	Std. error	*z* value	*P* value
D (day)	−0.74	0.07	−10.76	**<0.001***	−1.28	0.13	−10.02	**<0.001***
It	−1.10	1.17	−0.94	0.347	−7.27	2.13	−3.41	**<0.001***
Sw	0.81	1.14	0.71	0.478	−5.21	1.85	−2.81	**0.005**
D:It	−0.09	0.08	−1.15	0.252	0.20	0.06	3.38	**<0.001***
D:Sw	−0.36	0.09	−3.84	**<0.001***	0.01	0.05	0.16	0.875

Belgium is the standard country to which Italy and Sweden are compared to (country is a factor variable)

Significant results are in bold: *** $P < 0.001$, ** $P < 0.01$

our study, the Italian provenance of *F. alnus* flushes earlier than the local provenance both in the field trial as in greenhouse conditions. At the end of the growing season, this provenance also sheds leaves later in the field trial compared to the local provenance. Timing of both flushing and growth cessation is known to affect growth of the temperate tree species. Early flushing was found to influence significantly forest ecosystem net primary production (Myneni et al. 1997). The length of the growing season was the best predictor of growth in birch clones (Rousi and Pusenius 2005) and timing of growth cessation played an important role in total growth of poplar clones (Ceulemans et al. 1992; DeBell et al. 1997). All indicate population differentiation for the Italian provenance and may point to local adaptation to longer growing seasons in the south and thus co-gradient variation between low and mid-latitudes. Remarkably, the northern provenance from Sweden does not follow the expected latitudinal cline and also flushes earlier than the local Flemish provenance both in the field trial as in greenhouse conditions, indicating again population differentiation and suggesting counter-gradient variation between mid and high latitudes. It can be suggested that this northern provenance expresses a strong plastic response to spring temperature, which supersedes the response expected from local adaptation to a high latitude growth site with a limited growing season length. This can be related to the finding in several tree species that the

requirements for bud break are less stringent in more northern provenances (Olsson et al. 2013). In this way, northern provenances of *F. alnus* may profit from a prolongation of their minimal growing season by earlier flushing in exceptional favorable conditions compared to lower latitude populations. Additionally, the timing of bud burst in northern provenances may be more responsive to photoperiod, experiencing in Belgium a different photoperiod compared to their home site. Bud set in northern provenances of dogwood was shown to be more sensitive to photoperiod than in lower latitude provenances (Tanino et al. 2010).

Duration of the bud burst process

Not only is the onset of the bud burst process earlier in the warm greenhouse condition compared to the cold greenhouse for all studied provenances, but also the duration of the bud burst process is on average shorter. This duration of the bud burst process interestingly differed between the studied provenances. In the warm greenhouse, the duration of bud burst for the Swedish provenance was significantly less long compared to the Flemish provenance, whereas in the cold greenhouse the duration was significantly longer for the Italian provenance compared to the Flemish provenance. For the Swedish provenance, this result seems to underpin the plastic nature of the bud burst response: the

warmer the condition, the shorter is the duration of the flushing process compared to the local Flemish provenance. This result can be related to the observation that northern provenances of *Populus trichocarpa* have greater number of leaves in dormant buds indicating an increase in the spring canopy and/or faster leaf production rates, which is interpreted as a mitigation to the shorter growing seasons in the north (McKown et al. 2014). Although the higher temperatures in the warm greenhouse environment are likely to correspond more to the home-site conditions of the Italian provenance, still the duration of the bud burst process is not shortened compared to the local Flemish provenance. Furthermore, in the cold greenhouse, the Italian provenance takes longer to accomplish the bud burst process compared to the local provenance, suggesting that the warm greenhouse environment is closer to the optimal flushing temperature of the Italian provenance.

Conclusion

Although our dataset consisted of only three genetically differentiated populations, the results may suggest two mechanisms driving bud burst in *F. alnus* provenances, depending on the latitude of the origin. The bud burst response of the southern European provenance in the field trial and in greenhouse conditions (which are at an intermediate latitudinal site in Belgium) may indicate local adaptation to a longer growing season. This result is underpinned by a later leaf senescence compared to the local provenance in the field trial. Unexpectedly, our results indicate that the northern European provenance reacts more plastically to warmer temperatures. Not only is the onset of the process advanced, but also is the duration of the process shorter in warmer environmental conditions. Phenotypic plasticity of quantitative traits has been found in other tree species to vary between different populations within the same species (Matesanz et al. 2010; Matesanz and Valladares 2014).

The transfer of provenances has already been put forward as a climate change adaptation strategy (Seppälä et al. 2009). Southern provenances of *F. alnus* may be adapted to warmer and drier conditions during the growing season, which can be an advantage when transferred more to the north where warmer and drier summers are predicted, as has already been suggested for *Fagus sylvatica* (Robson et al. 2011). However, the predicted higher frequency of extreme climatic conditions, including late spring frosts, can be a disadvantage in early flushing southern provenances when transferred to more northern sites. On the other hand, northern provenances of *F. alnus* transferred to more southern sites may profit from the ability to react plastically to warmer temperatures in spring, although leaf senescence, and thus probably growth arrest, occurs earlier in autumn as well, still limiting the growing seasons length. This putative stronger ability to track climate changes in more northern provenances can be considered advantageous in a rapidly changing environment, but includes the risk of tracking unusually warm springs followed by frost. Additionally, their thermotolerance may be weaker compared to more southern provenances. Despite the controversy whether or not planting stock of local origin is in all cases the best (McKay et al. 2005; Vander Mijnsbrugge et al. 2010), it is likewise clear that large-scale use of non-autochthonous genotypes is not recommendable, especially when reasons to do so are purely economic (Laikre et al. 2010). Taken together, the advantages and disadvantages of transferring provenances as a climate change adaptation strategy and accounting for the inherent ability of local provenances to phenotypically react plastically on a changing environment (Alberto et al. 2013) focusing on local provenances can still be a valuable approach.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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