Inter-individual variability in spring phenology of temperate deciduous trees depends on species, tree size and previous year autumn phenology

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SUMMARY

We explored the inter-individual variability in bud-burst and its potential drivers, in homogeneous mature stands of temperate deciduous trees. Phenological observations of leaves and wood formation were performed weekly from summer 2017 to summer 2018 for pedunculate oak, European beech and silver birch in Belgium. The variability of bud-burst was correlated to previous year autumn phenology (i.e. the onset of leaf senescence and the cessation of wood formation) and tree size but with important differences among species. In fact, variability of bud-burst was primarily related to onset of leaf senescence, cessation of wood formation and tree height for oak, beech and birch, respectively. The inter-individual variability of onset of leaf senescence was not related to the tree characteristics considered and was much larger than the inter-individual variability in bud-burst. Multi-species multivariate models could explain up to 66% of the bud-burst variability. These findings represent an important advance in our fundamental understanding and modelling of phenology and tree functioning of deciduous tree species.

1. Introduction

Phenology is the discipline that studies 'the timing of detectable reciprocal events in the life cycle of plants and animals in connection with the environment, ranging from an individual- to an ecosystem level' (Forrest and Miller-Rushing, 2010). In the deciduous tree species of the temperate zone, primary growth starts with bud-burst, which is therefore an essential determinant of seasonal photosynthetic uptake, energy and water balance but also of tree functional traits (Piao et al., 2019).

Even if trees in forest stands experience gradients of micro-meteorological conditions,the environmental factors affecting tree phenology in spring (e.g.temperature, photoperiod) (Čufar et al., 2008; Prislan et al., 2013; Vitasse and Basler, 2013) do not vary significantly among individuals at the same site, where meteorological conditions are close to identical. Still, there is an inter-individual variability of bud-burst (Fig. 1), which can be up to 20 days (Puchałka et al., 2017). This variability in spring phenology is important for the trees, as it can influence tree performance, resilience and gives competitive advantage during the current and the following year (Barbaroux et al., 2003; Pérez-de-Lis et al., 2016). Moreover, inter-individual variability in spring phenology can crucially affect the function and structure of the forest understory. For instance, variations in the flowering phenology of forest herbs is related to variation in the canopy phenology of primary growth, with fitness advantages (better germination seed rate) for early flowering individuals (Baeten et al., 2015). Finally, inter-individual variability of spring phenology can impact leaf herbivores dynamics and their spatial distribution (Forkner et al., 2008)

Fig. 1. Inter-individual variability of bud-burst at the beech stand of the Park of Brasschaat. 17/04/2018. Photo Lorène J. Marchand.

It is generally thought that inter-individual variability in spring phenology is mainly due to genetic differences among individuals. For instance, the temperature sum requirement for birch bud-burst differs among genotypes (Possen et al., 2014). However, relating variability in spring phenology to genetic variability among individuals is technically very difficult to integrate into the current generation of population-, forest- and terrestrial ecosystem models or meta- and global analyses (Müller et al., 2017). On the other hand, the task of elucidating and modelling inter-individual variability of spring phenology would be greatly facilitated if such variability could be related to differences in tree development and growth among individuals or to variability in tree functional traits that are influenced by genetic variability but are easy to measure and model. For instance, it is known that age and size differences affect inter-individual variability in phenology, as younger and smaller trees need an earlier start of the growing season to compensate for the over-shading from taller and older trees (Augspurger and Bartlett, 2003). Inter-individual variability of phenological events in spring can also be related to inter-individual variability of phenology in autumn. For instance, Delpierre et al. (2017) found evidence that later leaf senescence can also induce later leaf unfolding the following year on mature oak trees. Relationships between inter-individual variability in spring phenology and inter-individual variability in tree growth and developmental characteristics (comprising age, dendrometric data, autumn phenology, annual ring increment and tree competition) might help elucidating the drivers of such variability, its potential modelling and how much of spring phenology variability is dependent from previous' year phenology variability. However, up to date, data on this topic is lacking.

We investigated whether, and to what extent, inter-individual variability of bud-burst is related to inter-individual variability of tree characteristics and autumn phenology of the previous year (onset of leaf senescence and cessation of wood formation). Therefore, we: (i) assessed the timing of bud-burst and of previous' year onset of senescence and their inter-individual variability for three deciduous species (*Quercus robur* L., *Fagus sylvatica* L. and *Betula pendula* Roth.) in two nearby forest areas in Antwerp Province, Belgium; (ii) studied the impact of individual tree (growth) characteristics (age, height, autumn phenology etc.) on the inter-individual variability in spring phenology, and (iii) built statistical models to determine the importance of the explanatory variables on the inter-individual variability of bud-burst. In addition, a comparison between the inter-individual variability of bud-burst and of leaf senescence onset, and their relationships with tree characteristics, was performed. Our approach will help to better

understand fundamental aspects of tree functioning and to model the individual tree phenology.

2. Material and methods

2.1. Study species and study sites

Three of the most common temperate deciduous tree species in Europe were studied in Northern Belgium: Pedunculate oak(*Quercus robur* L.), European beech (*Fagus sylvatica* L.) and silver birch (*Betula pendula* Roth.). Oak and beech are late successional species with a determinate growth (i.e. they produce leaves in 1–2 flushes). Birch is a pioneer species (Dyderski et al., 2018) with an indeterminate growth (i.e. it produces leaves continuously throughout the season). The wood anatomy of these species is also different: oak is a ring-porous species whereas beech and birch are diffuse-porous species. Northern Belgium is characterized by a maritime temperate climate optimal for our studied tree species, with precipitation (778 mm year^{-1}) distributed regularly over the year and average monthly temperatures ranging from +3 °C (January) to +17 °C (July) (Campioli et al., 2012) with an average annual temperature of 10.1 °C. The study comprises two forest areas (51°12′ – 51°21′ N, 4°26′ – 4°37′ E, 18–22 m a.s.l.). The first one is the 'Park of Brasschaat' (PB), the second one is the military domain 'Klein Schietveld' (KS), a Natura2000 reserve. The study areas are at the distance of 9,5 km, in a region with topography flat and without any features possibly causing significant climatological differences (Mariën et al., 2019). Both areas encompass planted (oak and beech) and unplanted stands (birch) on sandy soil, with low management activity. A thick organic layer (60–90 cm) is present at PB, making it more fertile than KS. A total of six stands were investigated, three of which are located in the park: PB-Q (park oak), PB-F (park beech) and PB-B (park birch) and three others in the military reserve: KS-Q (military reserve oak), KS-F (military reserve beech) and KS-B (military reserve birch). In each stand, 8–16 (co)dominant healthy trees without windows in the crown and dead branches, were selected in the summer of 2017. Leaf phenological observations were performed on all trees (56 trees), whereas phenology of wood formation (secondary growth) was only followed on half of the trees due to the labor-intensive nature of these analyses.

2.2. Leaf phenological observations

Phenological observations of bud-burst in 2018 were conducted

weekly for the first half of March and then twice a week from mid-March till the end of May. Binoculars (Tokura explorer bak4, Tokura, Japan) with a magnification of 8–27 × 25 were used to observe five randomly chosen buds in the upper third of the tree crown and five randomly chosen buds in the lower third of the crown (the crown was divided in three equal parts) to account for the possible variability in the timing of bud-burst within the crown due to shadow effects (the top of the crown receives more direct light than the bottom (Davi et al., 2011). Phenology of primary growth (leaves) was monitored according to a 5-stage scale adapted from Vitasse et al. (2009) and Gričar et al. (2017): 0: dormant bud; 1: swelling bud; 2: bud-burst; 3: emerging leaves, and 4: one leaf at least is completely detached from the bud. The date of bud-burst was defined as the date when 50% of the buds in a tree reached stage 2, combining together top and bottom crown buds to have an indication at the tree level (Vitasse et al., 2009). Leaf autumn phenology was monitored by observing the canopy coloration at day t (Xt) (Dox et al., 2020). In late summer and early autumn, canopy coloration was estimated directly, as a percentage. Later in the season, when the process became more intense, Xt was estimated through a combined rating of the percentage of leaves that had changed color (αt) and the percentage of leaves that had fallen (βt), as described in (Vitasse et al., 2011):

$$x_t = \frac{\alpha_t * (100 - \beta_t)}{100} + \beta_t$$

Observations were carried out weekly from late August until Xt was 100% in mid-late November. To determine the onset of leaf senescence a breakpoint analysis, performed with the R package 'segmented' (Muggeo, 2008), was conducted on the seasonal time series of canopy coloration. The onset of leaf senescence was defined as the point in time (breakpoint) when the seasonal canopy coloration sharply increased due to the start of the natural process of leaf senescence (before this point slight coloration already happened due to slow build-up of leaf stress damage). Details about the determination of the leaf senescence onset at the study sites can be found in (Mariën et al., 2019).

2.3. Wood phenological observation and analysis

To assess autumn phenology of wood formation in 2017, stem micro-cores were collected weekly from late August till late November. Sampling took place between a height of 1.3 m and 2 m. Samples were collected using a Trephor (Rossi et al., 2006). An upward spiral sampling was followed over the season to avoid wound reactions. The preparation following Prislan et al. (2014) and the analysis of the micro-cores was done at the Slovenian Forestry Institute (Ljubljana). Samples were observed under a LEICA DM 4000B light microscope (Leica Microsystems, Wetzlar, Germany) using transmission and polarised light. Polarised light induced brightness in the secondary walls (characteristic of mature cells). Histometric analyses were performed with a LEICA DMC 4500 camera and LAS image analysis software (LEICA Application Suite version 4.9.0, copyright 2003–2006) to determine the number of cambial cells in the dormant/active stage. Cessation of wood formation was recognizable by a completely red cell wall of all cells due to a safranin-astra blue staining, whereas cells that were still in the wall-thickening phase had blue colored inner parts of the cell walls. We defined the end of wood formation as the moment in time when latewood differentiation was completed (i.e. the proportion of cells still in the wall-thickening phase was < 0.5%) (Dox et al., 2020).

2.4. Tree competition index

To examine the effect of canopy competition, which is present when the crown of a neighboring tree is in contact with the crown of the study tree, we determined a tree competition index (or tree density index). All trees inside a circular area, with a diameter of 4 m for birch and 8 m for beech and oak respectively, proxy to the projection of the tree crown,

and centered at the study tree, were considered as possible competitors. Small understory trees (trees < 10 cm DBH for birch stands and < 20 cm DBH for beech and oak stands) were excluded. The tree density index was taken as equal to the total basal area of the competitor trees.

2.5. Tree age and tree-ring width

In total 12 beech, 8 oak and 8 birch trees were cored with a Pressler corer, with two increment cores per tree, one in N and one in S direction. The cores were conditioned in a climate chamber at 20 °C and 65% relative humidity for two weeks and then glued on wooden sample holders. The cores were sanded and tree-ring width measurements were performed with a Lintab measuring stage (0.01 mm precision) connected to the TSAP-Win software for data acquisition.

2.6. Data analysis

All analyses were conducted in the open source programming language R, version 3.4.2. A p-value of 0.05 was chosen as the level of significance. Graphs were made with the package *ggplot2* (Wilkinson, 2005). Three different sets of statistical analyses were conducted. (i) The timing of bud-burst and onset of leaf senescence were compared, separately, among stands with a two-way ANOVA followed by a Tukey's HSD (honestly significant difference) test, with species and site as factors. Normality of residuals and homogeneity of variances were verified with Shapiro test (Royston, 1982) and ncvTest (package *car,*(Fox and Weisberg, 2019), respectively. (ii) Univariate linear model between bud-burst (or leaf senescence onset) and the tree characteristics or previous' year phenological events were constructed, normality of residuals and variance homogeneity were done as above. When the conditions of normality were not met, a generalized linear model was performed instead of the linear model. (iii) Multivariate linear models were constructed after checking for collinearity between variables (Table SI in appendix). Normality of residuals and variance homogeneity were performed as above. ANOVA analysis (package *car*) was done on each best model including species as factor to test the model qualitative characteristics as a whole.

3. Results

3.1. Timing of bud-burst

Bud-bursttook place between DOY 96 and 117 across sites and inter-species, with stand average bud-burst dates between DOY 100 and 109 (Table 1). Stand average bud-burst date differed between the two sites ($p = 0.03$) and inter-species ($p < 0.01$; post-hoc test with $p < 0.05$ for all species combinations) (Fig. 2). Inter-individual variability in bud-burst varied among species and, for oak, between sites. Across the six stands, inter- individual bud-burst variability varied from 2 to 13 days (Table 1).

Table 1
Inter-individual variability of bud-burst and of leaf senescence onset for stands of oak (Q), beech (F) and birch (B) at two forest areas ('Park of Brasschaat' (PB) and 'Klein Schietveld' (KS)) close to Antwerp, Belgium, expressed as minimum (min), maximum (max), their difference (range) and mean (± standard error) of bud-burst and leaf senescence onset date for the trees at each stand.

Stand	Bud-burst (DOY)				Onset of senescence (DOY)			
	min	max	mean ± SE	range	min	max	mean ± SE	range
PB-Q	106	113	109 ± 0.77	7	277	318	303 ± 5.38	41
KS-Q	108	110	109 ± 0.31	2	280	317	297 ± 4.92	37
PB-F	104	117	109 ± 1.5	13	266	309	292 ± 5.3	42
KS-F	96	109	105 ± 0.7	13	280	307	293 ± 1.7	27
PB-B	98	102	100 ± 0.5	4	254	305	278 ± 7.9	51
KS-B	99	103	101 ± 0.6	5	260	286	281 ± 3.12	26

SENESCENCE: p<0.01
Species: p<0.01
Sites: p=0.99

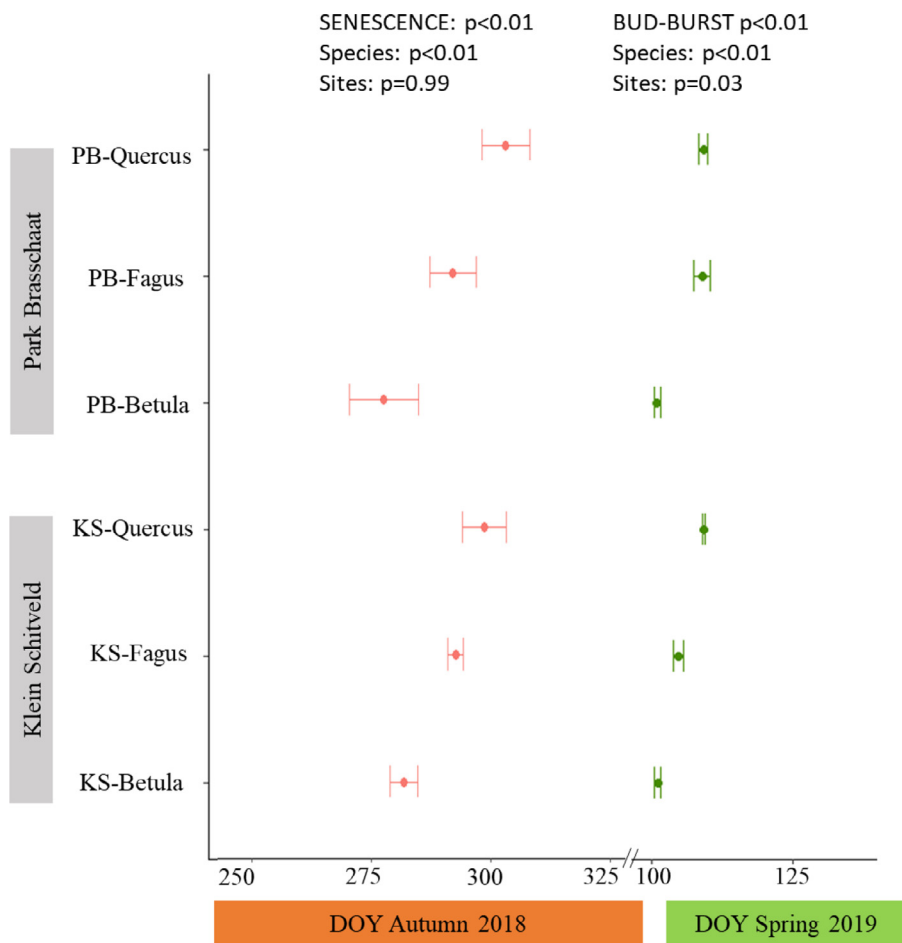BUD-BURST p<0.01
Species: p<0.01
Sites: p=0.03

Fig. 2. Average date (± standard error) of onset of senescence in 2017 (orange) and bud-burst in 2018 (green) for beech, oak and birch at two forest areas (Park of Brasschaat, PB, and military reserve Klein Schietveld, KS) in the vicinity of Antwerp, Belgium. p-values represents the significance level of the factor 'species' and 'site' when a two-way ANOVA was applied to onset of leaf senescence and budburst, separately, at the stand level.

3.2. Univariate models of inter-individual variability of spring phenology

For oak individuals, bud-burst in 2018 was significantly and positively correlated to the onset of leaf senescence in the previous year (Table 2, Fig. 3a). Thus, for this species under these conditions, individuals with a later onset of leaf senescence in the previous year presented bud-burst later in the current year. For beech, bud-burst was positively correlated with the timing of cessation of wood formation in the previous year (Table 2, Fig. 3c). In other words, trees with delayed cessation of wood formationpresented later bud-burst. For beech, weak negative relationships were found between bud-burst and tree height (*p* = 0.065) and tree diameter (*p* = 0.065), with taller and larger trees presenting earlier bud-burst (Table 2). For birch a correlation between bud-burst and tree height was also found, but of opposite sign (thus taller trees presenting later bud-burst) (Table 2, Fig. 3e). When the species were pooled, bud-burst was significantly and positively correlated to the onset of leaf senescence, cessation of wood formationand tree diameter (Table 2, Fig. 3b, d, f). Weaker multi-species relationships were also found between bud-burst and tree height (negative) and age (positive).

3.3. Comparison between bud-burst and onset of leaf senescence

Leaf senescence onset presented a substantially larger inter-individual variability across species and sites (DOY 255–318, 63 days) than bud-burst (21 days) (Table 1). Average onset of leaf senescence varied across species ($p < 0.01$), except for the comparison oak and beech (p = 0.11 with post-hoc test), but it did not vary between sites

Table 2

Characteristics of univariate linear models between bud-burst in 2018 and tree characteristics or autumn phenology in 2017, for oak (*n* = 15), beech (*n* = 23) and birch (*n* = 16), separately and pooled together, from two forest areas close to Antwerp, Belgium. (a) indicates variables with smaller sample size (for oak *n* = 7, for beech *n* = 12 and for birch *n* = 8); the bold font indicates when the p-value is significant (<0.05); the asterisk indicates the use of a generalized linear model quasipoisson instead of a linear model.

| Potential drivers	OAK			BEECH			BIRCH			ALL SPECIES TOGETHER		
	T-value	R^2	P-value	T-value	R^2	P-value	T-value	R^2	P-value	T-value	R^2	P-value
Onset of senescence 2017 (DOY)	2.221	0.2028	**0.0433**	0.563	−0.0321	0.5796	0.366	−0.0659	0.72	3.841	0.2021	**<0.01**
Tree diameter (m)	1.22	0.0315	0.243	−1.939	0.1071	0.0654	0.176	−0.0691	0.863	3.355	0.1647	**0.02**
Tree competition index (m²/ha)	1.355	0.0527	0.197	−1.141	0.0564	0.266	−0.786	−0.0261	0.445	0.303	−0.018	0.763
Tree height (m)	−0.416	−0.0627	0.684	−1.94	0.1073	0.0653	2.164	0.1971	**0.0482**	−1.791	0.0410	0.079
cessation of wood formation 2017 (DOY) (a)	0,197	−0.1592	0.850	2.373	0.2963	**0.039**	−1.866	0.1667	0.111	4.727	0.4508	**<0.01**
Age (year) (a)	0.527	−0.1151	0.617	−0.969	−0.006	0.355	−0.354*	0.0204	0.735	2.028	0.1069	0.0534
10 year average ring width (μm) (a)	−0.021	−0.1666	0.984	0.894	−0.0186	0.392	1.715	0.1329	0.137	−1.038	0.003	0.309
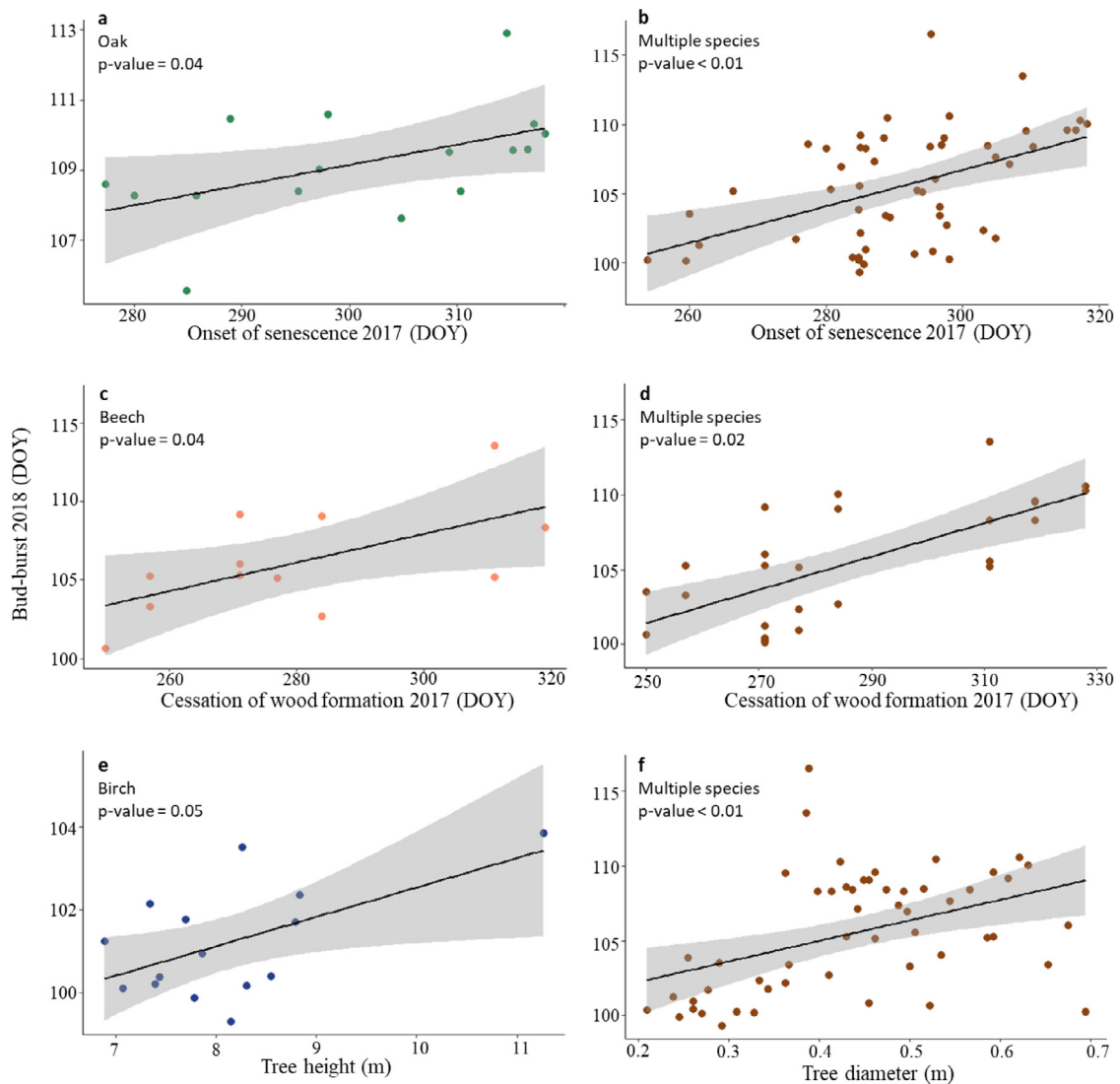
Fig. 3. Significant ($p < 0.05$) relationships between bud-burst and onset of senescence (for oak (a) and all species pooled together (b)), cessation of wood formation (for beech (c) and all species pooled together (d)), tree height (for birch (e)) and tree diameter (for all species pooled together (f)). The black line represent the linear model with its significance value. Thegray bands represent the confidence interval of 95%.

($p = 0.99$). The relationships between onset of leaf senescence and tree diameter, tree height and the tree competition index were not significant when the species were considered separately (Suppl. Table SIII) but a significant ($p < 0.01$) positive relationship between onset of leaf senescence and tree diameter was found when the species were pooled (Suppl. Table SIII).

3.4. Multivariate models of inter-individual variability in bud-burst

When consideringthe independent variables examined, plus the species and site factors, we obtained a model with five significant variables (height, species, site, onset of senescence, cessation of wood formation) but with onset of senescence and species as the most important variables (Table 3). This model could explain 66% of the inter-individual variability. When considering only the independent variables related to the tree size and tree competition, we obtained a simpler model (three variables) but still able to explain 60% of the bud-burst variability. In this case, species and diameter were the key variables. Compared to the previous model, diameter substituted the effect of height (see the correlation between diameter and height; Suppl. Table SI) and of leaf senescence onset (see the correlation between diameter and leaf senescence onset; Suppl. Table SIII). Note that for the onset of

Table 3

Characteristics of multivariate and multi-species linear models of inter-individual variability of bud-burst, for individuals of oak, beech and birch pooled together (Model 1 $n = 53$, Model 2 $n = 27$) from two forest areas close to Antwerp, Belgium. Bold font indicates when the p-value is significant (< 0.05). "NA" indicates no available variables and "ns" indicates no significant variables.

	53 trees		27 trees	
	F-value	P-value	F-value	P-value
Specie	25.15	**<0.01**	10.88	**<0.01**
Site	7.66	**<0.01**	2.286	0.146
Tree height	ns	ns	0.275	0.606
Onset of senescence 2017	nc	nc	29.95	**<0.01**
Cessation of wood formation 2017	NA	NA	2.473	0.131
Age	NA	NA	ns	ns
10 year average ring width	NA	NA	ns	ns
Tree competiton index	ns	ns	ns	ns
Tree diameter	27.07	**<0.01**	ns	ns
R² adjusted	60%		66%	

Table 4

Characteristics of single species multivariate linear models for inter-individual variability of bud-burst considering tree diameter, tree height, tree competition index and with or without leaf senescence onset, for oak ($n = 15$), beech ($n = 23$) and birch ($n = 16$), separately. Bold font indicates when the p-value is significant (< 0.05). "nc" indicates no considered variables on our analyses. "ns" indicetes no significant variables.

	Oak				Beech				Birch			
	With onset of scenescence		Without onset of senescence		With onset of scenescence		Without onset of senescence		With onset of scenescence		Without onset of senescence	
Potential drivers	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value
Site	3.076	0.107	3.284	0.095	6.194	**0.022**	6.382	**0.02**	0.0167	0.900	ns	ns
Diameter	0.015	0.906	0.3485	0.565	3.926	0.062	4.57	**0.04**	1.269	0.289	1.00	0.34
Tree competition index	ns	ns	ns	ns	ns	ns	ns	ns	5.593	**0.042**	2.04	0.18
Height	ns	ns	ns	ns	ns	ns	ns	ns	7.036	**0.026**	10.89	**<0.01**
Onset of senescence 2017	3.831	0.08	ns	ns	0.439	0.516	ns	ns	0.2367	0.638	ns	ns
R² adjusted	22%		20%		26%		29%		40%		44%	

leaf senescence the best model could explain only 24% of the variability (Supp. Table SII).

Single species models could explain much less variability in bud-burst (ca. 20–40%) than multi-species models (Table IV) even if the relevant model variables were the same. As for the multiple-species models, onset of leaf senescence could be substituted without loss of performance also in the single-species models (Table 4).

4. Discussion

The inter-individual variability in bud-burst observed in this study varied among species (in particular, beech seems to have a higher variability than birch). However, it was smaller than the variability reported in other studies (e.g. between 16 and 20 days for beech and up to 10 days for oak (Prislan et al., 2013; Puchałka et al., 2017)). Site differences in inter-individual variability was relevant for oak. Maybe this was partially related to the inter-individual variability of leaf senescence onset, which was strongly linked to bud-burst variability for oak (Table 2).

In fact, for oak individuals, timing of bud-burst was positively related to the timing of onset of leaf senescence in the previous year. Similar results were found for oak in France (Delpierre et al., 2017) and young oak trees in Belgium (Fu et al., 2014). An earlier leaf senescence might induce an earlier endodormancy. Thus the chilling requirement in winter (and heat requirement in spring) could be reached earlier in case of earlier leaf senescence, advancing bud-burst in the following year (Fu et al., 2014). For beech, bud-burst was directly related to the timing of the previous year' cessation of wood formation with an earlier bud-burst related to an earlier cessation of wood formation. To the best of our knowledge, this has never been detected before. As cessation of wood formation occurred earlier than leaf senescence onset (280 ± 7 and 290 ± 3 DOY, respectively) (data not shown), this observation could be explained by a larger reserve storage achieved through the accumulation of photoassimilates produced by the leaves before senescence and not allocated to wood growth (Čufar et al., 2015). In fact, there is evidence that soluble carbohydrate concentration is highly correlated to bud-burst and also than buds richer in non-structural carbohydrates open earlier (Maurel et al., 2004; Pérez-de-Lis et al., 2016). For beech, bud-burst is not correlated with the onset of leaf senescence, in agreement with the study of Delpierre et al. (2017) in France. The different relationship between bud-burst and previous-year onset of leaf senescence for beech (non-significant) and oak (significant) might be due to the higher chilling requirement of beech (Delpierre et al., 2017). In fact, for the latter species, earlier start of endodormancy probably has no positive effect in reaching the chilling requirement earlier and, thus, to trigger earlier bud-burst (Delpierre et al., 2017). Our results differed from the ones obtained from an experiment on young beech trees where bud-burst appeared earlier in case of an earlier leaf senescence in the previous year

(Fu et al., 2014), but age differences might play a confounding role. For birch, inter-individual variability in spring phenology was positive related to height. Taller and more dominant trees have probably less need to start canopy development earlier. However, this relationship seems species-specific, as a negative correlation between bud-burst timing and tree height was found for beech. As suggested above, carbohydrates might play a role in advancing bud-burst for beech and taller, larger beech trees might have more carbohydrates reserve.

To the best of our knowledge, no modelling work has yet been done to capture inter-individual variability in spring phenology, whereas most phenological modelling has focused on determining the environmental cues (e.g. temperature) of spring phenology for a stand or population (Delpierre et al., 2016; Fu et al., 2012; Linkosalo et al., 2008). Our results showed that tree diameter, species and site can explain together the majority of the variability (66%) of bud-burst among trees at the landscape level. An explained variance of 66% is high for an experimental design such as the one used here and for a dynamics (i.e. inter-individual variability of spring phenology) not yet comprehensively explored (see for comparison the forest growth efficiency models in (Campioli et al., 2015). At single species level, our study shows important relationships between inter-individual variability of bud-burst and intra-individual variability of variables related to tree size and autumn phenology of the previous year. However, multivariate models showed that these relationships could explain only a minor portion of the inter-individual variability in bud-burst for each species, separately. It is possible that variables not considered in our study will play a role (e.g. carbon and nutrients reserves, fine root dynamics).

As bud-burst and onset of leaf senescence occurred during a time window, it is possible that trees of the same stand have experienced different meteorological conditions before each phenological event (e.g. trees with later onset of senescence have experienced colder conditions before senescence than trees with earlier onset of senescence). Because of the complex interactions among tree size, annual phenological events and seasonal meteorological conditions, we have not considered the influence of the latter on inter-individual phenology variability. However, the impact of seasonal meteorological conditions on inter-individual phenology variability will be an interesting point for further research, particularly for onset of senescence that showed a large variability. The importance of autumn phenology in affecting bud-burst stresses the relation between the tree life cycle events across the dormant season and the legacy of the previous year's growth conditions on current growth. However, the comparison between bud-burst and onset of leaf senescence showed that the inter-individual variability of the latter is much larger than the former, respectively, and that leaf senescence onset shows less correlation with tree characteristics than bud-burst. This indicates that inter-individual variability of different phenophases has different underlying mechanisms. Onset of leaf senescence might be more variable than bud-burst because of the larger impact on the former of inter-individual variability in nutrient status

and canopy architecture (and thus light environment). Both, nutrient status (Estiarte and Peñuelas, 2015; Weih, 2009) and light environment (Brelsford et al., 2019; Michelson et al., 2018) affect the autumn leaf senescence. In general, onset of leaf senescence is a much more subtle process than bud-burst and we still lack a clear understanding of this process (Gallinat et al., 2015).

5. Conclusion

Our results showed that inter-individual variability of bud-burst significantly related to tree diameter, height and previous' year autumn phenology (onset of leaf senescence and cessation of wood formation) with differences between deciduous species. Based on these variables, multi-species statistical models explained 60–66% of the inter-individual variability of bud-burst. These results extend our understanding of tree phenology, tree functioning and the relation between spring and autumn dynamics. Moreover, these finding could improve simulations of single-tree phenology in landscape or regions with various forest stands, and forest models when inter-individual variability is sought for.

Author contribution

L.J.M., I.D., S.L and M.C., collected data. J.V.D.B. and I.D. processed the tree age data. L.J.M., P.P and J.G. performed secondary growth analyses, while L.J.M. performed all other analyses. L.J. M. and M.C. wrote the text. All authors contributed to discussions and revisions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2020.108031.

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