Functional traits influence patterns in vegetative and reproductive plant phenology – a multi-botanical garden study

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Summary

- Phenology has emerged as key indicator of the biological impacts of climate change, yet the role of functional traits constraining variation in herbaceous species' phenology has received little attention. Botanical gardens are ideal places in which to investigate large numbers of species growing under common climate conditions. We ask whether interspecific variation in plant phenology is influenced by differences in functional traits.
- We recorded onset, end, duration and intensity of initial growth, leafing out, leaf senescence, flowering and fruiting for 212 species across five botanical gardens in Germany. We measured functional traits, including plant height, absolute and specific leaf area, leaf dry matter content, leaf carbon and nitrogen content and seed mass and accounted for species' relatedness.
- Closely related species showed greater similarities in timing of phenological events than expected by chance, but species' traits had a high degree of explanatory power, pointing to paramount importance of species' life-history strategies. Taller plants showed later timing of initial growth, and flowered, fruited and underwent leaf senescence later. Large-leaved species had shorter flowering and fruiting durations.
- Taller, large-leaved species differ in their phenology and are more competitive than smaller, small-leaved species. We assume climate warming will change plant communities' competitive hierarchies with consequences for biodiversity.

Introduction

The timing of phenological events (such as leaf emergence, flowering, fruiting and leaf senescence) is crucial for species resource acquisition and reproductive success (e.g. plant–pollinator interaction, Nord & Lynch, 2009; Liu *et al.*, 2021). Phenology also has important implications for biotic interactions (e.g. herbivory) as well as for competitive hierarchies and ecosystem processes (Heberling *et al.*, 2019; Kudo & Cooper, 2019). Many studies

have demonstrated that plants are now leafing out earlier and flowering earlier in response to a warming climate (Blinova *et al.*, 2003; Root *et al.*, 2003; Wolkovich *et al.*, 2012; Bucher *et al.*, 2018; Menzel *et al.*, 2020; Rosbakh *et al.*, 2021). Plant functional traits (i.e. the morphological and physiological properties of plant species), affect species growth, reproduction and survival (Violle *et al.*, 2007). There is some evidence that differences in functional traits among species may also be associated with interspecific variation in plant phenology (Sun & Frelich, 2011;

Craine *et al.*, 2012; Wolkovich & Cleland, 2014; Bucher *et al.*, 2018; König *et al.*, 2018; Bucher & Römermann, 2020; Segrestin *et al.*, 2020; Liu *et al.*, 2021).

Although > 85% of the species found in temperate ecosystems are herbaceous (Ellenberg & Leuschner, 2010), phenological research has disproportionately focused on trees and shrubs (Estrella *et al.*, 2007; Vitasse *et al.*, 2011; Panchen *et al.*, 2014). While flowering times of herbaceous species, especially the onset of flowering or fruiting, are well studied (Fitter & Fitter, 2002; Craine *et al.*, 2012; Segrestin *et al.*, 2020; Renner *et al.*, 2021), there is relatively little data available on leaf out times and later stages of phenology, such as leaf senescence and fruit maturation (Gallinat *et al.*, 2015; Bucher & Römermann, 2021). Previous studies have found evidence which indicates that phenology is phylogenetically conserved, such that more closely related species tend to flower or leaf out at similar times (Bolmgren & Cowan, 2008; Davies *et al.*, 2013). Therefore, species cannot be regarded as statistically independent, and one has to account for phylogenetic relationships when investigating predictors of phenological timing (Davis *et al.*, 2010, 2013).

To expand our knowledge of herbaceous plant phenology, studies are needed in environments which are easily accessible, which can be replicated, and in which plants are easily identifiable and can be monitored throughout a growing season. Botanical gardens fulfil all of these requirements: they contain taxonomically and ecologically diverse collections of species, and plants are often maintained in specific locations, making them easier to find in a relatively small area throughout the year (Primack & Miller-Rushing, 2009; Huang *et al.*, 2018; Primack *et al.*, 2021).

The PhenObs initiative (www.idiv.de/en/phenobs.html) is an open network of botanical gardens across the Northern Hemisphere, where researchers and citizen scientists monitor the phenology of a large set of herbaceous species following standardized protocols (Nordt *et al.*, 2021). With this approach, the PhenObs network broadens the geographic and climatic scope of phenological research on herbaceous species that previously often focused on local observations or small sets of species. As part of this network, plant phenology is also being linked to the study of plant functional traits to understand observed interspecific variations. Functional traits have been used to assign species to ecological groups and as proxies for more complex species characteristics such as species environmental tolerances, competitive ability and dispersal ability (Table 1). Key functional traits that are widely used include plant height, leaf area, specific leaf area (SLA; i.e. the ratio between leaf dry weight and leaf area), leaf nitrogen (N) content (Gaudet & Keddy, 1988; Bolmgren & Cowan, 2008; Moles *et al.*, 2009; Sun & Frelich, 2011; Bucher *et al.*, 2018; König *et al.*, 2018; Liu *et al.*, 2021), leaf dry matter content (LDMC, i.e. the ratio between leaf dry and leaf fresh weight), leaf carbon I content (Pérez-Harguindeguy *et al.*, 2013) and seed mass (Primack, 1987; Moles & Westoby, 2003; Bolmgren & Cowan, 2008).

Previous studies have focused mainly on just one stage, or a few stages, of plant phenology and functional traits. As a result, it is unclear to what extent plant functional traits are associated with successive stages in plant phenology and which plant functional traits are the most important when aiming to predict plant phenology from traits. Studies on successive phenological stages are crucial in advancing the field of plant phenology as they allow researchers to focus on key functional traits associated with plant phenology. Further, such studies will clarify the mediating role of plant functional traits for responses in plant phenology to changes in climate. We therefore carried out a large-scale study of herbaceous plant phenology and functional traits at multiple

Table 1 Traits used in this study, their function in the plant community, and their reported link to phenology.

Trait	Function, ecological meaning	Reported link to phenology
Plant height	Competitive ability, productivity (Gaudet & Keddy, 1988; Moles *et al.*, 2009)	Smaller plants are associated with earlier flowering (Bolmgren & Cowan, 2008; Sun & Frelich, 2011; Segrestin *et al.*, 2020; Liu *et al.*, 2021) and earlier fruiting (Vile *et al.*, 2006; Liu *et al.*, 2021)
Leaf area	Competitive ability Díaz *et al.* (2004), productivity, light interception, leaf energy and water balance (Díaz *et al.*, 2016)	Large-leafed species are associated with later leaf out (Sun *et al.*, 2006; ZhiGuo *et al.*, 2011)
Specific leaf area (SLA; ratio between leaf dry weight and leaf area)	Productivity, competitive ability, growth performance (Wright *et al.*, 2004; Pérez-Harguindeguy *et al.*, 2013)	Species with higher SLA are associated with later flowering (Sun & Frelich, 2011; König *et al.*, 2018) and earlier leaf senescence (Bucher & Römermann, 2021)
Leaf dry matter content (LDMC; ratio between leaf dry and leaf fresh weight)	Competitive ability, resistance to physical hazards, productivity (Pérez-Harguindeguy *et al.*, 2013)	Species with higher LDMC are associated with later leaf senescence (Bucher & Römermann, 2021)
Mass-based leaf carbon content	Structural compounds, performance (Larcher, 1994)	Species with higher leaf carbon content are associated with earlier flowering (Bucher *et al.*, 2018) and later leaf senescence (Bucher & Römermann, 2021)
Mass-based leaf nitrogen content	Productivity, photosynthetic capacity (Wright *et al.*, 2004; Bucher *et al.*, 2018)	Species with higher leaf nitrogen content are associated with earlier flowering (Craine *et al.*, 2012; Bucher *et al.*, 2018) and earlier leaf senescence (Bucher & Römermann, 2021)
Seed mass	Regeneration (Leishman & Murray, 2001)	Species with heavier seeds are associated with earlier flowering (Primack, 1987; Vile *et al.*, 2006; Bolmgren & Cowan, 2008)

botanical gardens using the standard protocols of the PhenObs initiative (Nordt *et al.*, 2021). Here, we focus on seven functional traits that capture the essence of plant form and function, and that were identified in previous studies as relating to phenology (Table 1). For example, we expect plant height, a trait related to plant biomass production and competitive ability, to be positively associated with the onset of flowering, a relationship that has been found in several studies (see Table 1). More specifically, we investigate whether these functional traits are associated with various vegetative and reproductive stages in phenology and whether they might be used in the future as a substitute for time-intensive phenological monitoring.

We monitored the phenology of 212 perennial herbaceous plant species throughout the whole growing season across five botanical gardens in Germany, capturing the onset, end, and duration of vegetative (i.e. initial growth, leafing out and senescence) and reproductive (i.e. flowering and fruiting) phenological events. We combined information on species phenology with functional trait measurements for the same populations.

We addressed three key questions:
• Can functional traits predict vegetative and reproductive phenology of herbaceous species through the entire growing season? Phenology is assumed to be phylogenetically conserved; therefore, we expect that closely related species show greater similarities in the timing of phenological events than expected by chance. Further, we ask: are specific traits more important than the underlying phylogeny in predicting phenology?
• Which functional traits are most important at predicting herbaceous species phenology at each stage of the growing season?
• Are associations between phenology and functional traits consistent across the growing conditions of the different botanical gardens?

Materials and Methods

Phenological data

We investigated the phenology of 212 perennial plant species from 57 families in five botanical gardens in Germany (Berlin, Frankfurt (Main), Halle (Saale), Jena, Leipzig) in 2020, following the PhenObs protocol described in Nordt *et al.* (2021) (see Supporting Information Fig. S1 for the geographic location of the gardens, and Table S1 for the species included in this study). To cover a larger variability of growth forms occurring in the herbaceous layer, our set of study species also included seven dwarf-shrub and 20 subshrub species (e.g. *Lavandula angustifolia* Mill., *Solanum dulcamara* L., and *Vaccinium oxycoccos* L.). The studied species are widely available in the five gardens. A total of 110 (51%) species were shared among at least three gardens, 69 (33%) species were found in four gardens and 22 (10%) species were found in all five gardens. Phylogenetic information for all species was received from the mega-tree provided in the package V.PHYLOMAKER (Jin & Qian, 2019; see Fig. S2 for a phylogenetic tree of the study species and the number of gardens in which a species was monitored in 2020). We matched synonymous species names according to The Leipzig Catalogue of Vascular Plants (LCVP) taxonomic reference list (Freiberg *et al.*, 2020; available via doi: 10.25829/idiv.1806-40-3009). In the study year 2020, the five locations differed primarily in terms of their annual precipitation and their monthly precipitation in May to September, whereas annual and monthly minimum and mean temperature levels were similar among all gardens. Halle (Saale) was the driest location in 2020, with 401 mm precipitation, while Jena was the wettest of the five gardens, with 597 mm. Especially from June to July 2020, Halle (Saale) received little precipitation (51 mm), while 134 mm precipitation was measured at Jena (see Table S2 for temperature and precipitation data in 2020; data from DWD Climate Data Center; DWD, 2021). Also, long-term observations (1979–2013) showed that climate conditions across the locations mainly differed in terms of their mean annual precipitation, ranging from 532 mm in Halle (Saale) to 607 mm in Leipzig; see Table S3 for long-term bioclimatic data received from the Climatologies at high resolution for the Earth's land surface (CHELSA) database (Karger *et al.*, 2017; Karger *et al.*, 2018). Since there is no strong latitudinal gradient, the photoperiod between the locations did not differ much.

We monitored phenology weekly on a population level (i.e. *c.* 1 m^2 plot per species) following the PhenObs protocol (Nordt *et al.*, 2021). For vegetative phenology, we observed the onset of the stages 'initial growth', 'leaf unfolding' and 'senescence'. According to the PhenObs protocol, initial growth was defined as the first appearance of a new shoot aboveground. Leaf unfolding was recorded when the first leaf of a species was fully visible in its typical form, and senescence was documented when species' leaves were changing colour, drying out or falling off. For reproductive phenology, we observed the onset and end of flowering and fruiting. The monitoring of flowering started when the first flower was fully open and ended with the last open flower of a population. Fruiting was monitored over the whole period when ripe fruits were observed. We calculated the length of the species' flowering and fruiting duration from the number of days between the onset and the end of the respective stage. We also recorded the intensity (i.e. the percentage) of open flowers and leaf senescence. From this intensity we calculated the peak of flowering (i.e. the stage at which 50% of all flowers in a population were open), the onset of leaf senescence and the peak of leaf senescence (i.e. 5% or 50% of the leaves were fallen off, dried or coloured). Additionally, we captured the length of the species' growing season, calculated as the number of days between the onset of leaf unfolding and the date on which 5% leaf senescence was reached. For an overview of all phenological stages included in this study, see Tables 2 and S4. See Fig. S3 for histograms showing the variation in the number of species and gardens for each phenological stage.

Functional trait measurements

For each species and in each garden, plant functional traits were measured from the populations which were monitored for phenology. As explained above, we were interested in traits that were proposed to have a relationship with phenology (Table 1)

Table 2 Phenological stages included in this study.

Phenological stage	Abbrev.[a]	Unit[b]	Min.	Median	Mean	Max.	N_spec[c]
Initial growth	InitGr	doy	2	52	52	162	196
Onset of leaf unfolding	LeafUnf	doy	2	78	74	197	197
Onset of flowering	FlOn	doy	2	135	134	280	196
End of flowering	FlEnd	doy	15	176	184	364	198
Flowering duration	FlDur	days	7	42	55	252	193
Peak of flowering	FlPeak	doy	35	155	151	288	200
Onset of fruiting	FrOn	doy	97	196	199	351	179
End of fruiting	FrEnd	doy	106	281	264	365	173
Fruiting duration	FrDur	days	7	49	60	245	186
Onset of senescence	SenOn	doy	43	197	200	358	205
Peak of senescence	SenPeak	doy	64	247	245	358	197
Growing season length	GSL	days	1	119	126	323	190

[a]Abbreviations of phenological stages names.
[b]Units of measurement of observed stages: day, number of days; doy, day of year.
[c]Number of species out of the 212 study species.

Table 3 Plant functional traits used in this study.

Trait	Abbrev.[a]	Unit	Min.	Median	Mean	Max.	N_spec[b]	N_rep[c]
Plant height	PlantHeight	cm	3.25	45.80	57.43	256.00	197	5
Leaf area	LeafArea	mm^2	5.30	2452.20	11137.90	1345966.00	196	5
Specific leaf area	SLA	$cm^2\,g^{-1}$	4.08	18.43	19.39	73.12	199	5
Leaf dry matter content	LDMC	$mg\,g^{-1}$	56.71	215.32	220.97	514.08	198	5
Mass-based leaf carbon content	C_{mass}	%	33.76	42.54	42.66	52.56	179	1
Mass-based leaf nitrogen content	N_{mass}	%	0.34	2.39	2.46	5.96	179	1
Seed mass	SeedMass	mg	0.01	1.22	10.30	326.47	101	1

[a]Abbreviations of trait names.
[b]Number of species out of the 212 study species.
[c]Number of replicates per species.

and are relatively easy to measure. All measurements were conducted on five randomly selected shoots per species, from which a mean value was calculated (see Table 3). For the leaf trait measurements, two sun leaves per shoot were collected in a random manner. Leaf area (mm^2) was determined on scans of fresh leaves at 300 dpi using the R package LEAFTRAITS (M. Bernhardt-Römermann, unpublished). Using leaf area as well as fresh and dry leaf mass, SLA and LDMC were calculated. For the mass-based leaf carbon concentration (C_{mass}) and mass-based leaf nitrogen concentration (N_{mass}), all leaves from the five individuals per species that were harvested for the previous analyses were pooled, and milled dry leaf tissue was analysed with a vario EL cube (Elementar, Hanau, Germany). Reproductive height (i.e. the distance between the upper boundary of the inflorescence of a plant and the ground level) and vegetative height (i.e. the distance between the upper boundary of the main photosynthetic tissues of a plant and the ground level) was measured at the peak of a population's flowering. As reproductive and vegetative height were highly correlated ($r = 0.89$, $P < 0.001$), we chose the larger of the two values per species as the maximum plant height (cm). Individual dry seed mass (mg) was calculated from 20 to 50 ripe seeds from the measured individuals. For details on trait measurements per species and for

each botanical garden, see Table S4. Histograms illustrating the variation in the number of species and gardens for each functional trait are shown in Fig. S4.

Data analysis

For a general overview of the data, we used Pearson correlations to test whether and to what degree (1) the phenological stages and (2) the functional traits were related to each other. As the Shapiro–Wilk normality test revealed a right-skewed, nonnormal distribution in trait values, all trait variables were ln-transformed before analysis. Two correlation matrices which displayed the degree and direction of the correlations were calculated with the function 'rcorr' from package HMISC v.4.5–0 (Harrell, 2021). Two separate principal component analyses (PCAs) of (1) the 12 phenological stages and (2) the seven functional traits were performed using the package FACTOEXTRA v.1.0.7 (Kassambara & Mundt, 2020), allowing the visualization of their contributions (loadings) to the first and second principal components.

We tested for phylogenetic signal in the phenological stages and the functional traits. We used the function 'phylo.maker' from the package V. PHYLOMAKER (Jin & Qian, 2019) to create a phylogenetic tree of the studied species and linked the trait data

to the species' phylogeny. We used the function 'phylosig' from the package PHYTOOLS v.0.7–80 to calculate Pagel's Lambda statistic (Pagel, 1999), which revealed a phylogenetic signal in the majority of traits and phenological stages (see Table S5).

We used boosted regression trees (BRTs; Elith *et al.*, 2008) to assess whether and to what extent plant functional traits were associated with phenological stages. Boosted regression trees are advantageous for analysing datasets with numerous predictors as they can model linear relationships between numeric and categorical predictors and are relatively insensitive to collinearity. Furthermore, BRTs automatically handle missing values in the dataset (Elith *et al.*, 2008; Bianchini & Morrissey, 2020). The respective phenological stage was the dependent variable, and the garden-specific mean trait values per species were the explanatory variables. To investigate whether the associations between phenology and functional traits are consistent across the gardens, we also included 'garden' as another explanatory variable in the models. We did not include climatic factors in our analysis since our study sites had quite similar temperature conditions based on monthly mean, annual mean and available long-term temperature observations (see Table S2). Since plant species in these five botanical gardens are maintained by gardeners, including irrigation, spacing and weeding, differences in management regimes are probably more important in affecting plant phenology than differences in climate among the gardens.

The phylogenetic analysis of functional traits and phenological stages revealed a phylogenetic nonindependence that must be controlled for in the analyses. However, there is currently no option for directly including phylogeny into BRTs. We therefore followed a procedure applied by Pistón *et al.* (2019) and Bianchini & Morrissey (2020) to account for phylogeny that is based on the phylogenetic eigenvector regression by Diniz-Filho *et al.* (1998): We computed a pairwise distance matrix from our phylogenetic tree and extracted eigenvectors from this distance matrix (see Table S6) with a principal coordinates analysis (PCoA) using the function 'pcoa' from the APE package v.5.6–1 (Paradis & Schliep, 2019). Phylogenetic eigenvectors represent the phylogenetic relationships among species and control for phylogenetic autocorrelation when a sufficiently high number of eigenvectors is included in the analysis (Diniz-Filho *et al.*, 1998; Bianchini & Morrissey, 2020). We therefore included the first 44 of a total of 211 eigenvectors, which explained 90% of the phylogenetic structure in the distance matrix, as covariates in our BRT models (see Tables S7, S8).

BRT models were fitted using the package GBM v.2.1.8 (Greenwell *et al.*, 2020), with a Gaussian error distribution and a fraction of training data (bag fraction) of 0.5, a tree complexity of 1, a learning rate of 0.01, and a tolerance of 0.01. We used cross-validation (cv) as a predictor of model performance. For each model, we present partial dependency plots which display the response between each predictor variable and the respective response variable, independent of the other predictors. To assess which functional traits are most important for predicting species phenology, the relative importance (%) is given for all explanatory variables included in the model (see Figs S5–S16). All statistical analyses were conducted in R 4.1.0 (R Core Team, 2021).

Results

Relationships among phenological stages and among functional traits

Pearson correlation revealed significant positive relationships between pairs of most phenological stages, while there were also some significant negative and nonsignificant relationships (see Table 4 for correlation coefficients). The early stages of initial growth and leaf unfolding were not clearly related to later stages of flowering, fruiting and senescence. Species that started initial growth earlier also leafed out earlier ($r = 0.72$, $P < 0.001$). Species that started flowering earlier reached the peak of flowering earlier ($r = 0.92$, $P < 0.001$). Species that started fruiting earlier ended fruiting earlier ($r = 0.64$, $P < 0.001$). Species that flowered longer also fruited longer ($r = 0.61$, $P < 0.001$). The onset of flowering and fruiting were not clearly related to the flowering and fruiting duration ($r = -0.02$, $P = 0.58$; $r = -0.01$, $P = 0.44$). Species that started and ended flowering and fruiting earlier also underwent onset of senescence earlier. Principal component analyses results for phenology variables showed that the first and second principal components accounted for 66.8% of the total variation in phenology. The first component corresponded mainly with onset, end and peak of flowering, fruiting and senescence and accounted for 48.6% of the total variation. The second component corresponded mainly with leaf unfolding, initial growth and growing season length, and accounted for 18.2% of the total variation (Fig. S17a; see Table S9 for the contributions (loadings) to all 12 PCs).

Pearson correlation revealed significantly positive and negative but also nonsignificant relationships between the functional traits (see Table 5 for correlation coefficients). Specific leaf area was negatively correlated with LDMC ($r = -0.45$, $P < 0.001$) and leaf area ($r = -0.34$, $P < 0.001$). Species with higher LDMC had higher leaf carbon content ($r = 0.34$, $P < 0.001$) and lower leaf nitrogen content ($r = -0.15$, $P < 0.001$). Species with higher SLA had lower leaf carbon content ($r = -0.11$, $P < 0.05$) and higher leaf nitrogen content ($r = 0.28$, $P < 0.001$). Taller species had larger leaves ($r = 0.55$, $P < 0.001$), higher leaf nitrogen content ($r = 0.20$, $P < 0.01$), lower leaf carbon content ($r = -0.04$, $P < 0.01$) and lower LDMC ($r = -0.09$, $P < 0.01$). Plant height was not clearly related to SLA but was related to seed mass ($r = 0.41$, $P < 0.01$). Species with heavier seeds had larger leaves ($r = 0.42$, $P < 0.001$) and a higher leaf nitrogen content ($r = 0.41$, $P < 0.001$), but there was no significant relationship between seed mass and any of the other traits. The PCA of functional trait variables showed that the first and second principal components accounted for 51.5% of the total variation in trait values. The first component corresponded to leaf area, seed mass and plant height and accounted for 29.2% of the total variation in trait values. The second component, corresponding to SLA and LDMC, accounted for 22.3% of the total variation in trait values (Fig. S17b; see Table S10 for the trait contributions (loadings) to all seven PCs).

Table 4 Correlation matrix, based on Pearson correlations, including the correlation coefficients (*r*) of all pairwise combinations of phenological stages.

	LeafUnf	FlOn	FlEnd	FlDur	FlPeak	FrOn	FrEnd	FrDur	SenOn	SenPeak	GSL
InitGr	0.644 ***	0.248 ***	0.124 *	−0.048 (0.150)	0.249 ***	0.240 ***	0.181 **	0.023 (0.800)	0.258 ***	0.139 ***	−0.239 ***
LeafUnf		0.178 ***	−0.012 (0.054)	−0.178 *	0.167 ***	0.178 **	0.018 (0.546)	−0.159 *	0.180 ***	0.103 **	−0.556 ***
FlOn			0.717 ***	−0.018 (0.519)	0.923 ***	0.748 ***	0.595 ***	0.110 **	0.381 ***	0.350 ***	0.196 **
FlEnd				0.578 ***	0.752 ***	0.534 ***	0.624 ***	0.480 ***	0.306 ***	0.319 ***	0.267 ***
FlDur					0.136 **	0.008 (0.443)	0.290 ***	0.608 ***	0.056 **	0.070 ***	0.173 **
FlPeak						0.737 ***	0.634 ***	0.228 ***	0.379 ***	0.362 ***	0.202 ***
FrOn							0.635 ***	0.134 *	0.419 ***	0.340 ***	0.228 ***
FrEnd								0.596 ***	0.405 ***	0.413 ***	0.330 ***
FrDur									0.204 ***	0.222 ***	0.285 ***
SenOn										0.667 ***	0.717 ***
SenPeak											0.491 ***

Significant correlations are indicated by bold text (*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001), negative correlations are highlighted in red, and positive correlations are highlighted in blue; the colour gradient indicates the strength of the correlation.
FlDur, flowering duration; FlEnd, end of flowering; FlOn, onset of flowering; FlPeak, peak of flowering; FrDur, fruiting duration; FrEnd, end of fruiting; FrOn, onset of fruiting; GSL, growing season length; InitGr, initial growth; LeafUnf, onset of leaf unfolding; SenOn, onset of senescence; SenPeak, peak of senescence.

Table 5 Correlation matrix, based on Pearson correlations, including the correlation coefficients (*r*) of all pairwise combinations of functional traits.

	SLA	LDMC	LeafC	LeafN	PlantHeight	SeedMass
LeafArea	0.065 (0.147)	−0.341 ***	−0.199 ***	0.244 ***	0.545 ***	0.421 ***
SLA		−0.447 ***	−0.114 *	0.279 ***	0.117 (0.866)	−0.063 (0.161)
LDMC			0.343 ***	−0.145 ***	−0.085 **	−0.251 (0.294)
LeafC				−0.017 (0.761)	−0.039 **	−0.060 (0.962)
LeafN					0.196 **	0.406 ***
PlantHeight						0.413 **

All trait variables were ln-transformed before analysis. Significant correlations are indicated by bold text (*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001), negative correlations are highlighted in red, and positive correlations are highlighted in blue; the colour gradient indicates the strength of the correlation.
LDMC, leaf dry matter content; LeafArea, leaf area; LeafC, mass-based leaf carbon content; LeafN, mass-based leaf nitrogen content; PlantHeight, plant height; SLA, specific leaf area.

Relationships between phenological stages and functional traits, and the influence of phylogenetic relatedness

The most parsimonious BRT models of the effects of functional traits on vegetative and reproductive stages revealed moderate to good cross-validation (cv = 0.30–0.71; Figs S6–S18). The BRT models showed that the functional traits plant height and leaf area were strongly associated with most of the vegetative and reproductive stages, while leaf carbon and nitrogen content were

less important (Fig. 1). The different growing conditions, as represented by the five gardens, were among the most important factors in explaining the onset and duration of vegetative and reproductive stages. Initial growth and leaf unfolding started earlier in species in Frankfurt (Main) and Halle (Saale), and started later in Jena, Berlin and Leipzig (relative importance 24.9% and 37.4%, respectively; see Figs 1, S6–S17 for partial dependency plots). Leaf senescence started earlier in species in the drier gardens, Berlin and Halle, than in other gardens (11.9%). Species in

the wetter gardens, Jena and Frankfurt, held their leaves longer (i.e. longer growing season length), compared to the species in Berlin (35.4%).

Taller species leafed out later (relative importance 8.9%), as did large-leafed species (6.1%, Fig. 1a). Leaf unfolding also started later in taller (7.8%), and large-leafed species (5.3%, Fig. 1b). Shorter species (13.3%), such as *Primula vulgaris* or *Tussilago farfara* (Fig. S19), and species with lower LDMC (5.3%) started flowering earlier (Fig. 1c). Species with smaller leaves (13.7%), such as *Hypericum perforatum* and *Helianthemum nummularium* (Fig. S5b), species with lighter seeds (7.4%) and taller species (7.3%) showed longer durations of flowering (Fig. 1d). Shorter species started fruiting earlier (12.8%), as did species with higher LDMC (6.1%), and large-leafed species (5.1%, Fig. 2e). Species with lighter seeds (9.6%), small-leafed species (8.1%), species with lower SLA (7.4%), and taller species (5.8%, Fig. 1f) showed longer durations of fruiting. Taller species (8.9%, Fig. 1g) underwent senescence later. Species with smaller leaves (6.3%) and taller stature (6.2%, Fig. 1h) held their leaves longer (i.e. longer growing season length). Our results reveal that the timing of phenological events was strongly influenced by phylogenetic relatedness. The pie charts in Fig. 1 represent the overall contributions of the variables grouped by 'functional traits', 'garden' and 'phylogeny' deduced from the BRT models. 'Phylogeny', that is, the sum of explained variation by the included 44 eigenvectors (each explaining between 0.3% and 15% of the variation in the phylogenetic data, see Table S8), explained between 45.5% (for 'growing season length') to 71.7% (for 'peak of senescence') of the overall variation in the respective BRT models. Still, when considering each of the predictors from the three different groups (traits, garden, phylogenetic eigenvalues) separately, traits, especially plant height and leaf area, were more important than phylogenetic information in the BRT models. We refrained from presenting all phylogenetic eigenvectors in Fig. 1, but details regarding the explained variation of the single eigenvectors can be obtained from Figs S6–S17 for each phenological stage.

Discussion

Our results confirm a close association between species' trait composition and phenology in herbaceous, dwarf–shrub and subshrub species occurring in the herbaceous layer. Overall, we found that those traits which are related to biomass production and competitive ability, such as plant height and leaf area, had substantial explanatory power for phenological stages in the models: they were closely associated with the onset, end, duration and intensity (e.g. peak of flowering) of phenological stages. In particular, we identified plant height as being among the most important traits for both vegetative and reproductive phenology. Shorter species started all phenological stages earlier and had a shorter duration of fruiting and flowering than taller species. Our results confirm the findings of previous studies which found that plant height, as a measure of species productivity and competitiveness, was positively related to the onset of flowering (Bolmgren & Cowan, 2008; Sun & Frelich, 2011; Segrestin

et al., 2020). Further, we found that different environmental conditions were important factors in explaining the timing of phenological stages.

In general, shorter species are more likely to leaf out earlier than taller species, and, particularly in herbaceous species, shorter species need less time to reach flowering height than taller species (Sun & Frelich, 2011). Huang *et al.* (2018) even proposed that studies on phenological stages should be based primarily on plant size, as this trait seems to be the most important factor influencing species interactions, survival, and reproduction. Our findings agree with this notion. However, a closer look at the manifold trait data in our study highlights that this conclusion needs to be carefully modified. For example, leaf area, a proxy for species' competitive ability for light and biomass production (Díaz *et al.*, 2016), was among the set of traits with a high degree of explanatory power for species' onset of senescence and growing season length, as well as flowering and fruiting duration. Similar to Sun *et al.* (2006) and ZhiGuo *et al.* (2011) we found that large-leafed species were associated with later leaf out, while senescence occurred earlier in species with larger leaves than in species with smaller leaves. Leaf senescence can be induced by drought in summer or decreasing temperature in autumn, which might leave species with larger and often thinner leaves more vulnerable to drought or changes in temperature than species with smaller and thicker leaves that are more resistant to drought stress (Grime, 1974) and less sensitive to temperature decreases (Wright *et al.*, 2017). In our study, we also included SLA, with low SLA species having typically smaller and denser leaves in comparison to high SLA species. In our dataset, SLA was not significantly related to leaf area and was of minor importance in all models. The negative relationship between leaf area and flowering duration as well as fruiting duration may mirror a trade-off between growth and reproduction (Aragón *et al.*, 2009), that is, a species invests in either vegetative (leaves) or reproductive (flowers, seeds) compounds. We found seed mass to be an important trait for the prediction of species flowering and fruiting duration: species with heavier seeds flowered for a shorter period of time, which can be explained by the longer development time required for heavier seeds (Elzinga *et al.*, 2007; Bolmgren & Cowan, 2008).

Our results support previous findings from Bolmgren & Cowan (2008) and Davies *et al.* (2013) that the timing of onset of leaf unfolding and flowering is phylogenetically conserved. This finding is extended here as the results suggest that flowering and fruiting duration, the timing of leaf senescence and the length of the growing season are phylogenetically conserved. The importance of species phylogeny was shown in all models. However, plant height in particular, a trait showing no phylogenetic signal in our analysis, was more important than species phylogenetic relatedness in explaining species' onset of flowering and fruiting, and flowering duration. Hence, our study offers new insights into the relative importance of species relatedness and life-history strategies for determining phenology, and points to the paramount importance of functional characteristics in explaining phenology.

We found a strong positive relationship between the early stages of initial growth and leaf unfolding and the later stages of onset and peak of leaf senescence, a finding that is in line with
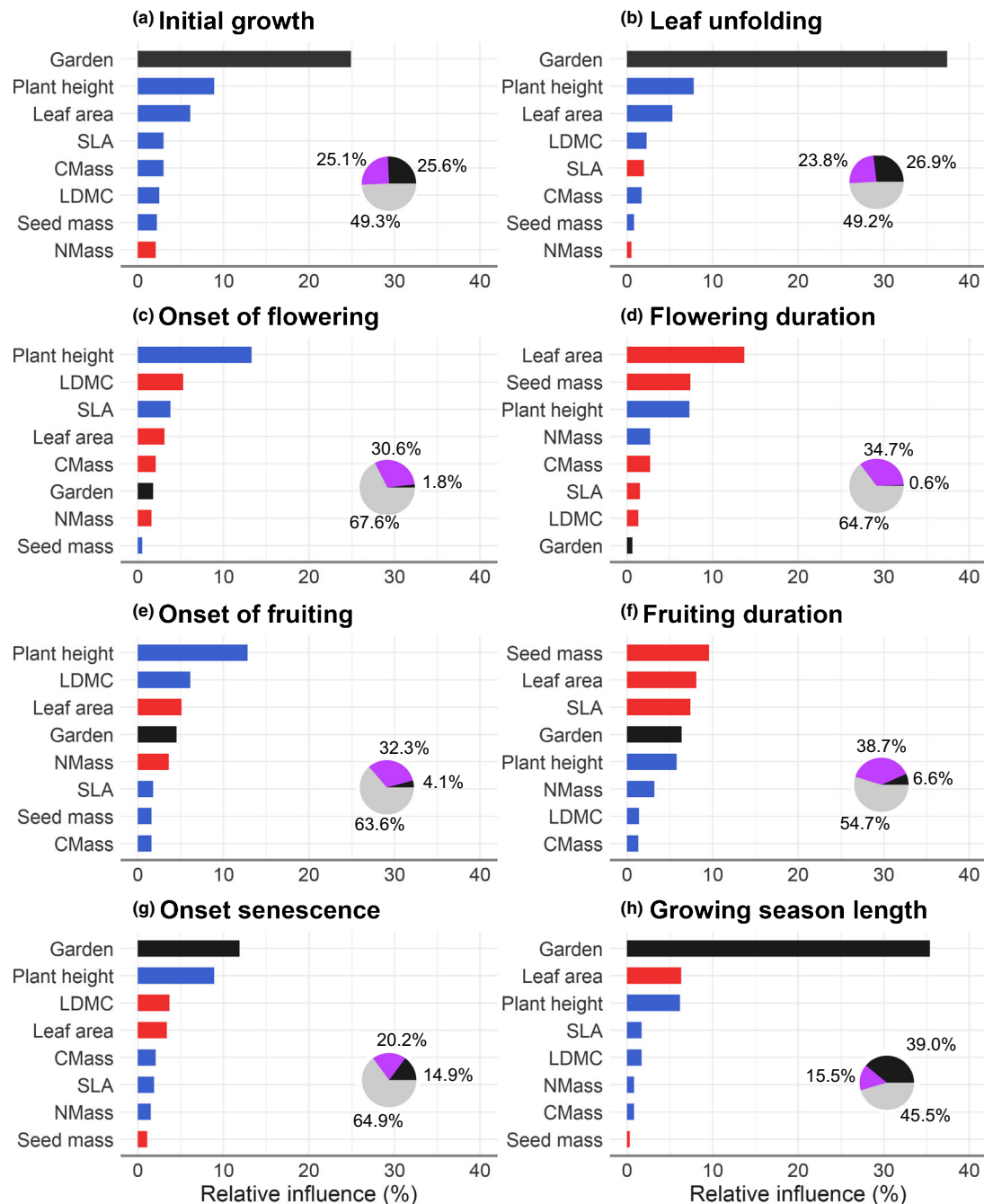
Fig. 1 Relative importance (%) of plant functional traits and the factor 'garden' on the onset or duration of phenological stages, deduced from boosted regression trees (BRTs), in which 44 phylogenetic eigenvectors were also included. Pie charts represent the overall contributions of the variables grouped by 'functional traits' (purple), 'garden' (black) and 'phylogeny' (grey) deduced from the BRT models. Supporting information Figs S5–S16 give an overview of the relevance of the phylogenetic eigenvectors compared to functional traits and the factor 'garden'. Boosted regression tree models were fitted for (a) onset of initial growth ($n = 439$, cross-validation correlation (cv) $= 0.30$), (b) onset of leaf unfolding ($n = 463$, cv $= 0.54$), (c) onset of flowering (day of year; $n = 474$, cv $= 0.69$), (d) flowering duration (days; $n = 466$, cv $= 0.49$), (e) onset of fruiting (day of year; $n = 421$, cv $= 0.64$) and (f) fruiting duration (days; $n = 396$, cv $= 0.39$), (g) onset of senescence (day of year; $n = 538$, cv $= 0.50$), and (h) the duration (days) of growing season length ($n = 426$, cv $= 0.46$). Blue colouring represents a positive influence of the predictor variable, red represents a negative influence of the predictor variable, and black represents the categorical variable 'garden'. CMass, mass-based leaf carbon content (%); LDMC, leaf dry matter content (mg g^{-1}); NMass, mass-based leaf nitrogen content (%); SLA, specific leaf area (cm^2 g^{-1}).

studies by Primack (1987) and Ettinger *et al.* (2018), in which strong linkages among successive stages of tree species were reported. However, the early stages were not related to, or were only weakly related to, later stages of flowering, fruiting or onset of senescence. Therefore, instead of focusing on single stages alone, monitoring species' phenology throughout the whole growing season is crucial to allow profound predictions and general conclusions on species growing season length or flowering

duration from functional traits. As we found several phenological stages to be strongly positively correlated for a large number of herbaceous species (i.e. onset of flowering and fruiting, duration of flowering and fruiting), we recommend monitoring the onsets of leaf unfolding, flowering, fruiting and leaf senescence, as well as the duration of flowering, to capture species' whole growing season phenology. Since intraspecific variation in phenological responses occurs among years (Cleland *et al.*, 2012; Liu *et al.*, 2016; Bucher *et al.*, 2018), we also emphasize the importance of long-term phenological monitoring to evaluate whether phenological patterns are consistent among years that may vary in climate (Ettinger *et al.*, 2018). For this purpose, botanical gardens are well placed to offer the possibility of performing phenological research and measurements of traits on a large number of species and for long time periods. The further international expansion of the PhenObs network will allow these investigations over a wider range of environmental conditions, including those aspects of climate that are modulated by climate change.

The different environmental conditions as represented by the five botanical gardens were important factors in explaining the onset and duration of vegetative stages, in particular, and reproductive stages to a certain degree. Drier conditions can lead to earlier autumn leaf senescence, and this may decrease the growing season length (Estiarte & Peñuelas, 2015; Liu *et al.*, 2016). The differences in precipitation may explain our findings that senescence was observed earlier in species in the drier gardens Halle (Saale) and Berlin, whereas the growing season was longer in species in the wetter Jena garden. Nevertheless, plant species in botanical gardens are maintained by gardeners, who perform tasks including irrigation; thus, differences in natural precipitation should not play out as prominently as in natural settings. Therefore, we see microclimatic and soil conditions as well as garden-specific maintenance as potential causes of the strong effect of the gardens on phenology. Hence, future studies should include information on species' specific environmental conditions (e.g. light availability, fertilization and irrigation treatments, and soil conditions such as texture) in addition to information on temperature and precipitation.

Our study demonstrates that for herbaceous plants and dwarf–shrub and subshrub species occurring in the herbaceous layer, certain functional traits have a high degree of explanatory power for predicting phenological events. Our results demonstrate that plant phenology studies can focus on a few key phenology stages, as many of the phenological stages are highly correlated. In addition, the easily measured characteristics of plant height and leaf area were more important in predicting plant phenology than other functional traits that require laboratory measurements. Further, we highlight the importance of species' shared evolutionary history and recommend that phylogenetic relatedness is accounted for when searching for drivers of phenology.

Our findings have important implications for plant communities as competitive hierarchies are likely to be destroyed with changes in climate: with ongoing global warming, plant species advance their phenology towards earlier days in the year. Given that species respond in species-specific ways to variations in climate (Root *et al.*, 2003; König *et al.*, 2018) and that taller and larger-leaved species are more effective in changing their phenology towards earlier days in the year (König *et al.*, 2018), we can expect that these will outcompete the early flowering small growing species in the future. The effects of climate change acting on these functional characteristics will change the competitive hierarchies with consequences for global biodiversity. The one caveat is that we also found that variation in growing conditions among gardens played a large role in phenological variation. The most likely explanation is different watering, shading, and fertilization regimes. Including microsite conditions is a topic that researchers should consider in subsequent studies.

Author contributions

C Römermann, MS, DJ, IH and SFB developed the research idea for this paper. Data collection and laboratory work was supervised in the respective botanical gardens by BN (Berlin), AK and KH (Frankfurt am Main), CP and MS (Halle (Saale)), DJ (Jena), and MF (Leipzig). MS, DJ and CP harmonized the data. MS cleaned the data. MS carried out statistical analyses with support by C Römermann and SFB. MS produced the graphs and led the paper writing. AB, SFB, MF, IH, BN, RBP, C Römermann, A-DS and CW (in alphabetical order) conceived the ideas for the PhenObs project. MS, DJ, SFB, IH, MF, KH, AK, BN, CP, IB, AB, BK, TK, AL, TM, RBP, C Rosche, MAS, A-DS, KT, ST, CW and C Römermann critically discussed the research and contributed critically to the drafts.

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Data availability

The data that support the findings of this study are available in the Supporting Information that accompanies this article and via the iDiv data repository (doi: 10.25829/idiv.3509-e2owu1).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Geographical location of the five botanical gardens in Germany.

Fig. S2 Phylogenetic tree of the 212 study species.

Fig. S3 Variation in the number of species and gardens for each phenological stage.

Fig. S4 Variation in the number of species and gardens for each functional trait.

Fig. S5 Partial dependency plots of boosted regression trees for the relationship between 'initial growth' and traits and phylogeny.

Fig. S6 Partial dependency plots of boosted regression trees for the relationship between 'leaf unfolding' and traits and phylogeny.

Fig. S7 Partial dependency plots of boosted regression trees for the relationship between 'onset of flowering' and traits and phylogeny.

Fig. S8 Partial dependency plots of boosted regression trees for the relationship between 'peak of flowering' and traits and phylogeny.

Fig. S9 Partial dependency plots of boosted regression trees for the relationship between 'end of flowering' and traits and phylogeny.

Fig. S10 Partial dependency plots of boosted regression trees for the relationship between 'flowering duration' and traits and phylogeny.

Fig. S11 Partial dependency plots of boosted regression trees for the relationship between 'onset of fruiting' and traits and phylogeny.

Fig. S12 Partial dependency plots of boosted regression trees for the relationship between 'end of fruiting' and traits and phylogeny.

Fig. S13 Partial dependency plots of boosted regression trees for the relationship between 'fruiting duration' and traits and phylogeny.

Fig. S14 Partial dependency plots of boosted regression trees for the relationship between 'onset of senescence' and traits and phylogeny.

Fig. S15 Partial dependency plots of boosted regression trees for the relationship between 'peak of senescence' and traits and phylogeny.

Fig. S16 Partial dependency plots of boosted regression trees for the relationship between 'growing season length' and traits and phylogeny.

Fig. S17 Principal component analysis of the phenological stages and functional traits, respectively.

Fig. S18 Relative importance of functional traits, phylogenetic relatedness and factor 'garden' on the timing of phenological stages, deduced from boosted regression trees.

Fig. S19 Scatterplot showing relationship between (a) plant height and first flowering day and (b) leaf area and flowering duration.

Table S1 Overview of the species monitored in each botanical garden.

Table S2 Temperature and precipitation conditions for 2020 in the five botanical gardens.

Table S3 Information on bioclimatic variables from long-term observations for the cities where the botanical gardens are located.

Table S4 Results of phenological monitoring and trait measurements for the investigated species.

Table S5 Phylogenetic relatedness of the phenological stages and functional traits.

Table S6 Phylogenetic distance matrix of the 212 study species.

Table S7 Eigenvalues along each phylogenetic eigenvector.

Table S8 Total and cumulative proportion of the variance in the phylogenetic distance matrix.

Table S9 Contributions of phenological stages to the first to twelfth principal component analyses axes.

Table S10 Trait contributions to the first to twelfth principal component analyses axes.

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