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Changes in autumn senescence in northern hemisphere deciduous trees: a meta-analysis of autumn phenology studies

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● **Background and Aims** Many individual studies have shown that the timing of leaf senescence in boreal and temperate deciduous forests in the northern hemisphere is influenced by rising temperatures, but there is limited consensus on the magnitude, direction and spatial extent of this relationship.

● **Methods** A meta-analysis was conducted of published studies from the peer-reviewed literature that reported autumn senescence dates for deciduous trees in the northern hemisphere, encompassing 64 publications with observations ranging from 1931 to 2010.

● **Key Results** Among the meteorological measurements examined, October temperatures were the strongest predictors of date of senescence, followed by cooling degree-days, latitude, photoperiod and, lastly, total monthly precipitation, although the strength of the relationships differed between high- and low-latitude sites. Autumn leaf senescence has been significantly more delayed at low (25° to 49°N) than high (50° to 70°N) latitudes across the northern hemisphere, with senescence across high-latitude sites more sensitive to the effects of photoperiod and low-latitude sites more sensitive to the effects of temperature. Delays in leaf senescence over time were stronger in North America compared with Europe and Asia.

● **Conclusions** The results indicate that leaf senescence has been delayed over time and in response to temperature, although low-latitude sites show significantly stronger delays in senescence over time than high-latitude sites. While temperature alone may be a reasonable predictor of the date of leaf senescence when examining a broad suite of sites, it is important to consider that temperature-induced changes in senescence at high-latitude sites are likely to be constrained by the influence of photoperiod. Ecosystem-level differences in the mechanisms that control the timing of leaf senescence may affect both plant community interactions and ecosystem carbon storage as global temperatures increase over the next century.

Key words: Autumn phenology, climate change, growing season, leaf senescence, temperature, deciduous tree, woody plants.

INTRODUCTION

Air temperatures around the globe are increasing (Jones *et al.*, 2012), which has measureable effects on a variety of plant processes. Specifically, the effects of climate change on the phenology of vegetation have received increased attention over the past several decades as any factor that alters the timing of early growing season leaf-out and senescence has the potential to affect a variety of ecosystem properties. For example, the timing of leaf-out and senescence of deciduous plants has been shown to affect plant competition (Fridley, 2012), plant growth (Myneni *et al.*, 1997) and ecosystem carbon uptake (Barichivich *et al.*, 2012). Changes in phenology also affect surface albedo through differences in reflectance between closed and bare canopies (Richardson *et al.*, 2013). While leaf-out has been shown to advance over the past century as a result of increasing air temperatures (Linderholm, 2006; Polgar and Primack, 2011), the relationship between temperature and leaf senescence remains less well understood (García-Plazaola *et al.*, 2003; Richardson *et al.*, 2013). Leaf senescence completes the growing season for deciduous trees and therefore factors that delay leaf-off can lengthen the period of plant

photosynthesis and increase rates of gross primary productivity (Richardson *et al.*, 2010). Thus, an extension of the growing season can contribute to reduced atmospheric CO_2 concentrations due to enhanced carbon sequestration in terrestrial plants (Penuelas *et al.*, 2009; Richardson *et al.*, 2013). However, the increase in carbon uptake may be partially offset by increased rates of ecosystem respiration (Piao *et al.*, 2008).

Efforts to examine the effects of increasing air temperatures on leaf senescence have employed a wide array of methodologies and have measured senescence across a range of scales, from ground-based observations of individual trees to regional-scale remote sensing. Ge *et al.* (2014) conducted a meta-analysis of ground-based phenological data sets spanning >20 years throughout China and found that leaf senescence in trees and woody shrubs was delayed by 1·98 d per decade from 1960 to 2011. Menzel *et al.* (2006) used long-term, ground-based observations to determine that autumn senescence in Europe was delayed by 1·3 d per decade and 1·0 d $°C^{-1}$ between 1971 and 2000; however, these trends were not unidirectional as only 15 % of individual sites demonstrated significantly delayed senescence, 12 % showed senescence dates that advanced and

83 % did not change significantly over time. Through the use of 8×8 km^2 grid remote-sensing data, Piao *et al.* (2006) demonstrated that senescence was delayed by 0·37 d year^{-1} over the 27 year period between 1982 and 2009 in deciduous forests in the northern hemisphere. Jeong *et al.* (2011) found evidence of advanced senescence in temperate North America using satellite data from 1982 to 2011. Several additional studies also show weak or insignificant relationships between the timing of autumn senescence and air temperatures (Menzel, 2003; Menzel *et al.*, 2006; Pudas *et al.*, 2008).

The lack of consistent relationships between air temperature and timing of leaf senescence suggests that autumn senescence may be influenced by a variety of factors that obscure its relationship with temperature. The date of first frost in the autumn months in temperate and boreal ecosystems is highly variable and does not always follow a linear cooling trend (Way and Montgomery, 2014). It is therefore likely that the timing of leaf senescence responds to a suite of environmental factors, although the genetic basis of senescence activity and physiology remains unknown (Tuskan *et al.*, 2006; Way and Montgomery, 2014). For example, photoperiod (Hanninen and Tanino 2011; Jeong *et al.*, 2011; Way, 2011) and local meteorological factors such as wind and humidity (Staelens *et al.*, 2003; Travers and Eldridge, 2013) have all been shown to affect dates of senescence. The factors that most strongly influence the onset of senescence may also differ across ecosystems, with high-latitude plants considered to be more responsive to photoperiod and low-latitude plants more responsive to temperature (Stinziano and Way, 2014; Way and Montgomery, 2014). In addition to site-level meteorological factors, recent studies also demonstrate a relationship between the timing of spring leaf-out and the timing of autumn leaf senescence (Fu *et al.*, 2014; Keenan and Richardson, 2015).

Changes in vegetation dynamics have major implications for the global carbon cycle, yet the current generation of terrestrial biosphere models often fail to simulate changes in autumn phenology accurately (Richardson *et al.*, 2012). Many terrestrial biosphere models use temperature as a primary predictor of leaf senescence despite its inconsistency as a strong driver in observational studies (Menzel, 2002; Menzel *et al.*, 2006; Richardson *et al.*, 2013). For example, the Integrated Biosphere Simulator (IBIS) model induces leaf drop when mean daily air temperatures fall below 5 °C (Foley *et al.*, 2010), while other models use combinations of both mean air temperature and threshold temperatures to predict leaf shedding (Estrella and Menzel, 2006). Growing degree-days or cooling degree-days are employed in some models, and provide an integrated measure of temperature history over a growing season (White and Nemani, 2003; Jolly *et al.*, 2005; Richardson *et al.*, 2012). Other models predict leaf drop through an integration of photoperiod and mean air temperature thresholds (BIOME-BGC; White *et al.*, 1997), or photoperiod and cooling degree-day summation (Delpierre *et al.*, 2009). The lack of consensus in phenology modelling schemes reflects the fact that the mechanisms that drive autumn phenology remain poorly understood (Vitasse *et al.*, 2011).

Leaf senescence data are widely collected, although integrating these observations into an interpretable framework poses a challenge due to the variability in measurement methods and criteria used to determine the date of senescence. There is no consistent definition of leaf senescence, nor a standard methodology used for monitoring the process across studies (Gallinat *et al.* 2015). Some data networks standardize methodologies over specific regions or habitat types in an effort to synthesize senescence trends over time and space (e.g. Ibanez *et al.*, 2010; Panchen *et al.*, 2015). Despite these large-scale efforts, there are numerous individual studies that have examined controls on the timing of leaf senescence at local and regional scales that vary in their methodology. In many cases the definition of leaf senescence depends on the plant species examined, as some species' life history traits inherently lend themselves to particular definitions. For instance, the genus *Quercus* typically holds senescing leaves longer than other genera, which may make the date of 50 % leaf colour change the best description of leaf senescence, while members of the genus *Paulownia* drop green leaves, making leaf drop a preferable metric to characterize the end of the growing season. Some studies integrate physiological measurements such as photosynthetic rate and chlorophyll content to delineate the date of senescence (Nagai *et al.*, 2011). While the metrics chosen by individual research groups often optimize senescence estimates for a particular genus or location, the variation in methodology across ecosystems makes large-scale generalization challenging.

Here we synthesize publications from the peer-reviewed literature to evaluate larger scale trends in dates of leaf senescence across leaf senescence studies in the northern hemisphere. We present a meta-analysis to describe patterns of leaf senescence in boreal and temperate deciduous trees and examine relationships between dates of leaf senescence and meteorological measurements to assess physical drivers of leaf senescence. The primary goals of this synthesis were to: (1) characterize the methodologies employed in observations of autumn senescence in boreal and temperate deciduous trees in the northern hemisphere; (2) determine the influence of temperature, precipitation, latitude and photoperiod on the timing of leaf senescence in high- and low-latitude ecosystems; (3) identify how senescence trends differ among taxa and regions; and (4) provide recommendations for future research by identifying biologically relevant methods for monitoring leaf senescence and characterizing key areas of uncertainty in predicting senescence phenology.

MATERIALS AND METHODS

Data collection

We assembled a database of peer-reviewed publications using the Web of Science search engine. We used all combinations of the following search terms as 'topics': 'autumn' or 'fall'; 'phenology' or 'senescence'; 'tree' or 'plant' or 'forest'; and 'leaf'. We limited the search to English-language, peer-reviewed journal articles published before 25 February 2013. The search resulted in 760 publications, but we limited our subsequent analysis to all publications that report either (1) the date of tree leaf senescence in a given year (for one year or a series of years) or (2) a rate of change in tree leaf senescence dates over time or temperature for a reported measurement period. We limited the data set to publications that report estimates of autumn leaf senescence for ecosystems with one annual senescence period. To optimize data resolution, we included only

those publications in which researchers monitored phenology more frequently than 14 day intervals throughout the senescence period. We included measurements from both young and mature trees and, in the cases of experimental studies, used data from reference treatments only. Within publications, we considered unique sites and plant species to represent independent data. We extracted data from tables and text when available and used DataThief (version 1.6; Tummers, 2006) to extract values presented in the figures.

Studies were distributed throughout North and South America, Europe and Asia, with data concentrated in the eastern USA, Europe and Japan (Fig. 1). The distribution of studies was heavily skewed toward the northern hemisphere, with only two studies located in the southern hemisphere. Due to lack of sufficient replication in the southern hemisphere, we focus our analysis on senescence trends in the northern hemisphere alone. We identified 64 publications and 1121 independent measurements that met our criteria.

We compiled data into two categories based on the response type: (1) date of senescence (DOS) and (2) change in senescence. The DOS data set includes 56 publications (Appendix 1), all of which report a date of leaf senescence for a single year or a single mean date of leaf senescence over multiple years. The change in senescence data set includes 21 publications (Appendix 2), all of which report a rate of change in senescence over time or temperature (d year^{-1} or d °C^{-1}, respectively). The change in senescence data set includes five publications that did not self-report a rate of change for which we calculated the change in senescence over time from the dates of senescence for more than five continuous years (Appendix 2). Twelve of the 64 publications reported data that fell into both DOS and change in senescence categories.

Analyses

Date of senescence (DOS). In order to make meaningful comparisons across studies reporting the date of leaf senescence and to assess autumn leaf senescence trends accurately on a large scale, we characterized the metrics used to measure the date of leaf senescence and identified the metrics most widely presented in the literature (Table 1). In some cases, publications reported DOS using multiple metrics (e.g. both 50 and 100 % leaf fall), and we report these to demonstrate the full spectrum of metrics used to estimate date of leaf senescence in the literature (Table 1). For cases in which the authors report a mean date of leaf senescence over a range of years, we used the median year of the measurement period to approximate leaf fall year. We assessed the relationship of colour change-based metrics and abscission-based metrics (leaf fall), the two main classes of senescence measurements, with site latitude.

Meteorological data collection. We examined relationships of air temperature, cooling degree-days (CDDs), precipitation, photoperiod and site latitude to the date of leaf senescence. In particular, we sought to determine the temporal window (e.g. 1 month or 3 months prior to leaf fall) over which meteorological data (i.e. air temperature and precipitation) were averaged that explained the greatest variation in leaf fall dates. Based on the latitude and longitude of the individual sites, we obtained daily meteorological data for each study location from either the National Climate Data Center's (NCDC) Global Summary of the Day (GSOD) database (National Climate Data Center, 2013) or the Global Historical Climatology Network (GHCN) Daily database (Menne *et al.*, 2012). We excluded observations that did not report location co-ordinates or a specific site location, and those which did not have station-based meteorological data reported within 2 ° latitude/longitude for the reported period. For each study site, we used the closest meteorological station (median distance 14 km) reporting daily minimum temperature, maximum temperature and precipitation with >70 % temporal coverage (22 days per month) for the years referenced in the corresponding study. Mean temperature was calculated by taking the mean of the daily minimum and maximum temperatures (World Meteorological Organization, 2011). At each site, we calculated the mean temperature (°C), latitude-based photoperiod (h) and total precipitation (mm) for three periods: 1–31 August, 1–30 September and 1–31 October. CDDs were calculated using mean daily temperature from 1 August to 31

FIG. 1. Distribution of sites used in the meta-analysis. Studies that do not report a specific site location or co-ordinates are not presented on the map.

TABLE 1. *Metrics used to estimate date of senescence across publications reporting the date of fall leaf senescence in the northern hemisphere (DOS studies only,* n = 56 *publications and 861 independent measurements total)*

Leaf senescence metric	No. of publications	Fraction of publications	No. of observations	Fraction of observations
50 % leaf fall	20	0·36	291	0·34
100 % leaf fall	12	0·21	162	0·19
NDVI	6	0·11	83	0·1
80 % leaf fall	4	0·07	62	0·07
50 % green	3	0·05	3	0
50 % colour change	2	0·04	7	0·01
0 % green	2	0·04	2	0
50 % yellow	2	0·04	3	0
PAR transmission plateau	2	0·04	66	0·08
Peak colour change	2	0·04	94	0·11
Start of leaf fall	2	0·04	68	0·08
10 % colour change in 10 % of trees	1	0·02	8	0·01
10 % colour change in 90 % of trees	1	0·02	8	0·01
10 % leaf fall	1	0·02	48	0·06
50 % A_{max}	1	0·02	6	0·01
50 % colour change or leaf fall	1	0·02	103	0·12
75 % leaf fall	1	0·02	9	0·01
90 % leaf fall	1	0·02	9	0·01
Eddy covariance	1	0·02	2	0
Landsat 50 % cover	1	0·02	1	0
More yellow than green leaves	1	0·02	4	0
Photo 'greenness' index	1	0·02	1	0
Photosynthetic rate = 0	1	0·02	16	0·02
Peak red	1	0·02	1	0

The number and total percentage of published studies and independent observations that used each metric are reported.

Note that many studies employed multiple metrics, therefore the number of entries in the table is greater than the total number of publications included in Appendix 1.

See Appendix 1 for list of publications included here.

LAI, leaf area index; PAR, photosnthetically acive radiation; NDVI, normalized difference vegetation index.

October. CDDs represent the thermal sum below a base temperature of 20 °C based on the method of Richardson *et al*. (2006).

We examined the relationships between meteorological variables and date of 50 % leaf fall, the most common metric employed across DOS studies (Table 1). We binned senescence observations by site latitude (low latitude, 25–49°N; high latitude, 50–70°N; roughly corresponding to the distribution of temperate and boreal forests, respectively) and regressed mean DOS at each site against mean August, September and October temperature (°C), cumulative CDDs (°C), photoperiod on the date of leaf senescence (h), site latitude and total monthly precipitation (mm) for August, September and October. In order to assess the relative effect of temperature and photoperiod on the date of senescence across high and low latitude sites, we then used partial correlation analysis to assess the relationship between the DOS and temperature (mean August, September, October and cumulative CDDs) while removing the effect of photoperiod.

Change in senescence. While all studies completed their observation period between 1993 and 2010, the start of senescence observations varied widely across studies from 1931 to 2005 (Appendix 2). In order to evaluate the influence of when observations were initiated and the study duration on study-specific estimates of change in senescence over time or temperature, we binned studies by decades based on the start of the measurement period. We further binned studies by continent (North America, Europe and Asia), major plant order (all orders with more than five independent measurements) and site

latitude (low latitude, 25–49°N; high latitude, 50–70°N) to evaluate the relationships between spatial and taxonomic factors and the date of senescence. We computed the mean change in the date of senescence over time (years) and temperature (°C) across all studies and used one-way analyses of variance (ANOVAs; $P < 0.05$) and Tukey's tests of post-hoc intergroup comparison to assess differences in the change in senescence across continents, plant orders, site latitude range and time periods. All statistical analyses were conducted in R (version 3.1.1; R Development Core Team, 2013).

RESULTS

Date of senescence

Among DOS studies, we identified 24 distinct methods of estimating date of autumn leaf senescence across 56 publications (Table 1; Appendix 1). These publications utilized a variety of metrics, including leaf fall, leaf colour change and annual changes in plant physiology as measures of leaf senescence. Date of senescence was significantly earlier at higher latitudes, regardless of whether colour change or percentage leaf fall was used as a measure of date of senescence ($P < 0.01$ for both; Fig. 2). However, latitude explained more variation in the date of leaf senescence in measurements utilizing colour change ($R^2 = 0.55$; e.g. 50 % colour change, 50 % green, peak colour change, more yellow than green leaves; Fig. 2A) compared to percentage leaf fall ($R^2 = 0.26$; e.g. 10, 50, 80, 90 and 100 % leaf fall; Fig. 2B).
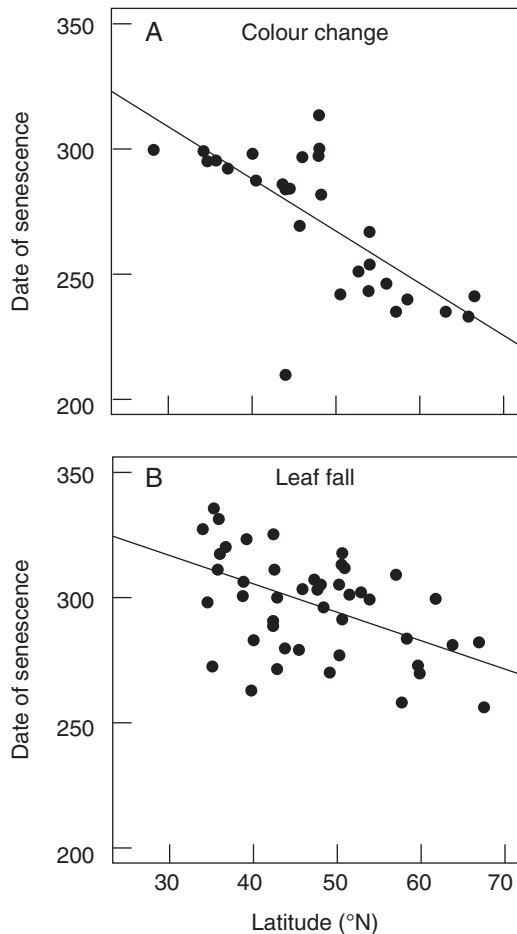
FIG. 2. Relationship between latitude and the date of leaf senescence by studies that estimate date of senescence using (A) leaf colour change and (B) percentage leaf fall. Points represent all studies that estimate the date of leaf senescence using either method. Measurements using leaf colour change explain more variation in the relationship between latitude and the date of leaf senescence than measurements using percentage leaf fall (colour change, $R^2 = 0.55$, $P < 0.001$; leaf fall, $R^2 = 0.26$, $P < 0.001$).

We limited our analysis of the relationship between meteorological variables and the date of leaf senescence to studies reporting the date of 50 % leaf fall in order to compare a common metric of leaf senescence among published studies (20 publications). The date of 50 % leaf fall was the most common metric utilized and accounted for 36 % of publications and 34 % of individual observations of DOS. Thirteen of the other 24 methods used to characterize the date of leaf senescence were unique to a single study; it was therefore not feasible to examine effects of meteorological measurements across these studies together.

Simple linear regression models highlighted relationships between site-level meteorological data and the date of 50 % leaf fall across all sites examined in the northern hemisphere (Fig. 3). Compared with other meteorological variables, mean monthly temperature explained the most variation in the date of 50 % leaf fall, and the relationship strengthened as the temperature window examined shifted later in the year, with a delay of 2.49 ± 0.48 (mean $\pm$ s.e.) d $°C^{-1}$ in mean October temperature

($R^2 = 0.49$, $P < 0.001$; Fig. 3C). Sites with greater CCDs senesced earlier ($R^2 = 0.37$, $P < 0.001$; Fig. 3D). Latitude and photoperiod on the date of 50 % leaf fall explained 25 and 22 % of the variation in the date of 50 % leaf fall, respectively (Fig. 3E, F). Greater precipitation in August through October weakly delayed or did not change leaf fall timing significantly, with precipitation alone explaining $\leq$16 % of the variability in the date of 50 % leaf fall (Fig. 3G–I).

The relationships between date of 50 % leaf fall and all measures of temperature (August, September, October mean temperature and cumulative CDDs) were weaker in high-latitude compared with low-latitude sites (Table 2; Fig. 3A–D). The relationship between date of 50 % leaf fall and each measure of temperature weakened (i.e. P-values increased) once the effect of photoperiod through partial correlation analysis was removed for high-latitude sites (CDD: $R = -0.54$, $P = 0.068$; $R_{partial} = -0.064$, $P = 0.87$; mean October temperature: $R = 0.59$, $P = 0.068$; $R_{partial} = 0.25$, $P = 0.50$; Table 2). In contrast, the relationship between each measure of temperature and date of 50 % leaf fall in low-latitude sites remained statistically significant when the effect of photoperiod was removed (CDD: $R = -0.69$, $P = 0.001$; $R_{partial} = -0.49$, $P = 0.02$; mean October temperature: $R = 0.81$, $P < 0.001$; $R_{partial} = 0.73$, $P < 0.001$; Table 2).

Change in senescence

Six publications reported changes in autumn leaf senescence with temperature (109 independent observations) and 18 publications (291 independent observations) reported changes in autumn leaf senescence with time (Appendix 2). Examining all studies together, we found that leaf senescence was delayed by 0.33 ± 0.03 d year^{-1} and 1.20 ± 0.17 d $°C^{-1}$ (mean $\pm$ 1 s.e.). Date of senescence did not vary over time at high-latitude sites, but was significantly more delayed at low-latitude sites over time ($P = 0.040$; Fig. 4A). The relationship between date of senescence and temperature did not differ significantly between high and low latitudes ($P = 0.96$; Fig 4B). In all sites (low- and high-latitude), date of senescence was delayed with increased temperatures (Fig. 4B). Senescence was delayed with time across all three northern hemisphere continents examined, but the delay was significantly larger with time in North America than in Europe and Asia ($P < 0.001$; Fig. 4C). Both Europe and Asia showed delayed leaf senescence with increased temperatures (Fig. 4D), but there was not a statistically significant difference in response to temperature between continents ($P = 0.095$, Fig. 4B). Both Rosales and Fagales were significantly more delayed per $°C$ than Ginkgoales ($P < 0.0001$; Fig. 4F). The rate of senescence delay (d year^{-1} and d degree^{-1}) was higher in studies initiated in recent decades (1990s–2000s) than those initiated in 1930–1980, although the difference was not statistically significant (Fig. 4G, $P = 0.069$; Fig. 4H, $P = 0.095$, respectively).

DISCUSSION

Drivers of autumn leaf senescence

Among the meteorological measurements examined, October temperatures were the strongest predictors of date of 50 % leaf
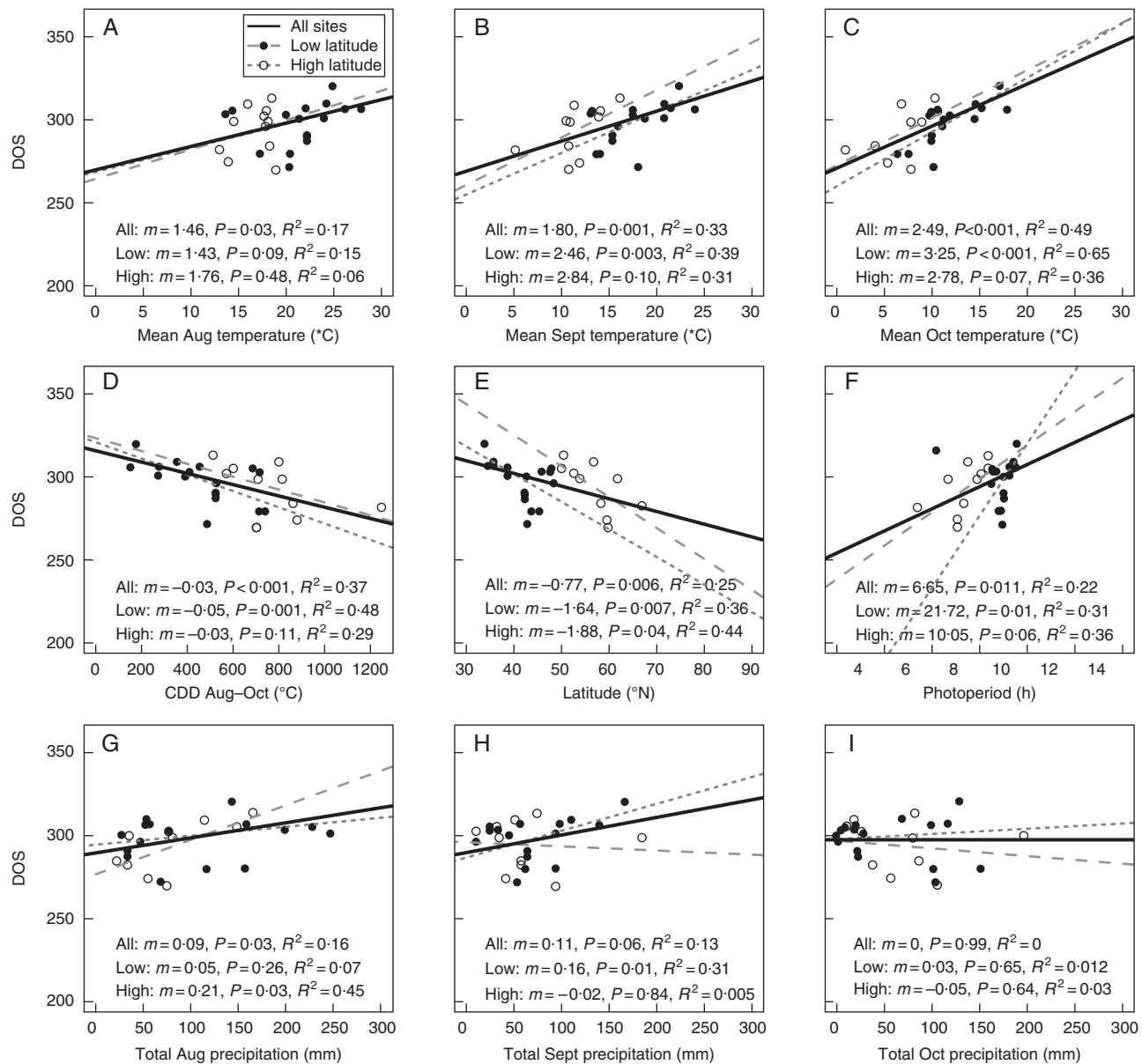
FIG. 3. Relationship between monthly averaged site temperature (°C), cooling degree-days (CDDs, °C), photoperiod (h) on date of senescence (DOS), site latitude, total monthly precipitation (mm) and the date of 50 % leaf fall. Points represent the average date of 50 % leaf fall by site. Low-latitude and high-latitude sites are as indicated in the key in (A).

TABLE 2. *Partial correlation coefficients associated with simple linear regression models*

Parameter	Effect removed	Low latitude		High latitude	
		R	P-value	R	P-value
Cooling degree-days (°C)	None	−0·69	0·001	−0·54	0·068
	Photoperiod	−0·49	0·02	−0·064	0·87
August temperature (°C)	None	0·39	0·098	0·25	0·48
	Photoperiod	−0·31	0·19	−0·072	0·85
September temperature (°C)	None	0·63	0·4	0·55	0·097
	Photoperiod	0·35	0·14	0·012	0·96
October temperature (°C)	None	0·81	<0·001	0·59	0·068
	Photoperiod	0·73	<0·001	0·25	0·5

fall, followed by CDDs, latitude, photoperiod and, lastly, total monthly precipitation, although the strength of the relationships differed between high- and low-latitude sites (Figs 3 and 4; Table 2). Temperature continued to explain significant variation in the date of 50 % leaf fall in low-latitude sites after the effect of photoperiod was removed, but did not explain significant variation in high-latitude leaf fall timing following removal of photoperiod from regression models (Table 2). These results suggest that while temperature alone may be a reasonable predictor of the date of 50 % leaf fall in general (mean October temperature: $R^2 = 0.49$ across all sites), the factors that most strongly control leaf fall may differ by site location. The lack of change in date of 50 % leaf fall over time at high latitudes
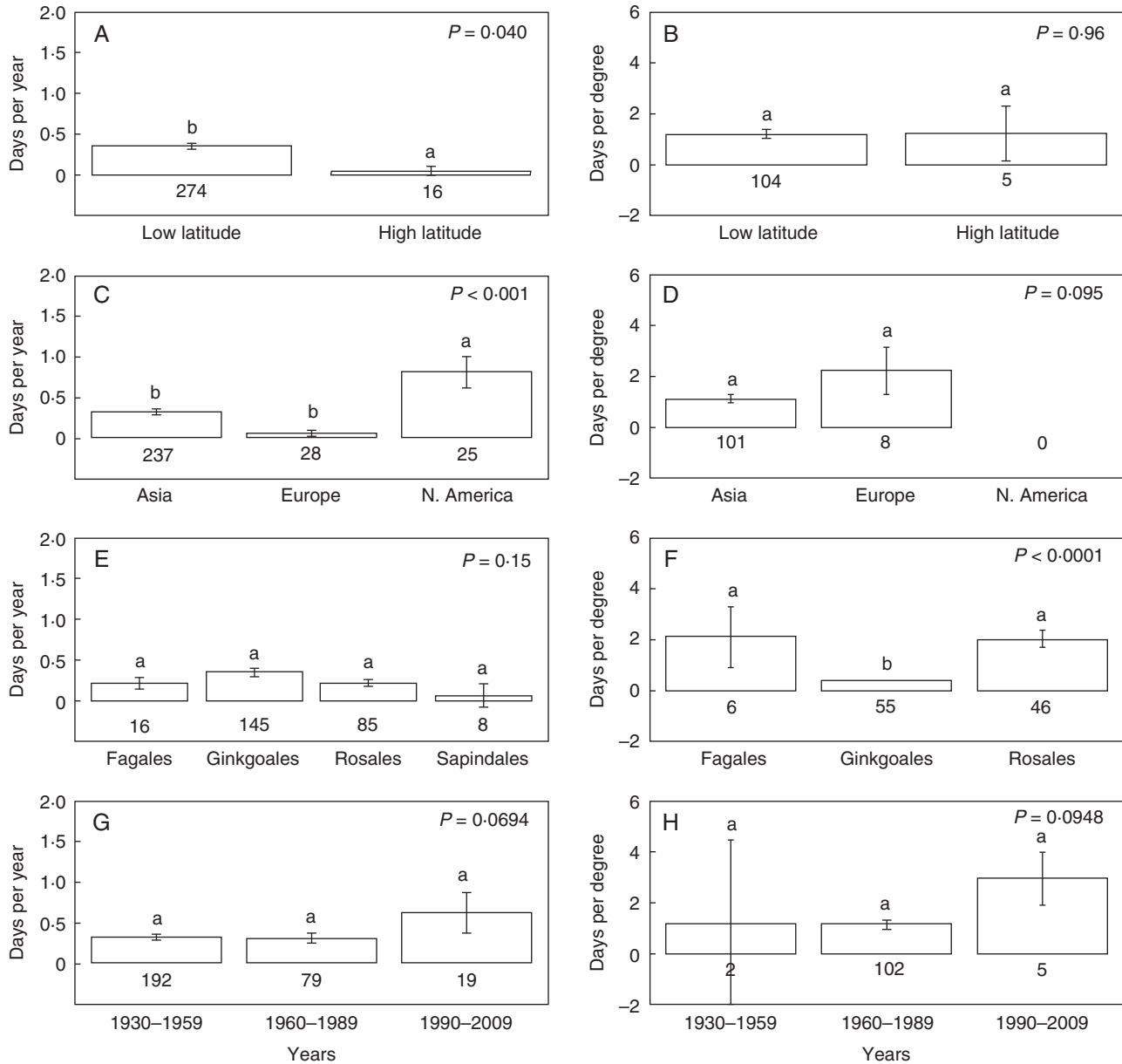
FIG. 4. Change in date of senescence by latitude range, continent, plant order and decade. Shown are orders with more than five independent observations. Time periods in (G) and (H) show the decade in which senescence observations began, with all studies ending between 1993 and 2010. Values are means ± s.e.; different letters indicate statistically significant differences between groups. Values below the bars show the number of independent observations.

despite large changes in temperature (Fig. 4A; Jones *et al.*, 2012) is possibly due to the strong constraint photoperiod imposes on the timing of leaf fall in these latitudes (Stinziano and Way, 2014; Way and Montgomery, 2014). Our results suggest that while temperature and photoperiod are two important variables that could be incorporated in models to predict the date of leaf senescence, it is unlikely that model parameters can be applied uniformly at the global scale. Temperature alone may provide a reasonable predictor for the date of 50 % leaf fall at low latitudes, but the inclusion of the effect of photoperiod in models may be important to assess the timing of leaf-off at high latitudes.

Compared with low-latitude ecosystems, high-latitude ecosystems may continue to experience the largest increases in temperature over the next century (Jones *et al.*, 2012), while photoperiod will remain the same over time. These asynchronous changes in meteorological factors may affect plant communities and their role in carbon sequestration (Stinziano and Way, 2014). For example, as the ranges of more southerly plant species migrate north in response to rising temperatures (Beck *et al.*, 2011), these temperature-responsive species may lengthen their photosynthetic period, while native, photoperiod-dependent northerly species may show less flexibility in the timing of leaf senescence, affecting competitive dynamics

within plant communities (Way and Montgomery, 2014). The strong influence of photoperiod on leaf senescence at high latitudes could also influence ecosystem-scale carbon uptake. Photoperiod-induced leaf senescence will end an individual growing season's period of ecosystem carbon uptake, but carbon losses through soil respiration may remain high with warmer temperatures (Piao *et al.*, 2008). While warming-induced changes in leaf senescence delay the end of the growing season and result in enhanced net carbon uptake in temperate forests (Keenan *et al.*, 2014), these patterns may not hold true in higher latitude boreal forests if trees do not extend their period of photosynthesis at the end of the growing season. In other words, the stronger constraint of photoperiod on date of leaf senescence in high-latitude boreal deciduous forests may limit the response of forest carbon uptake to increases in temperature.

There was a statistically significant delay in leaf senescence with time (days per year) across all three continents in the northern hemisphere, but delays were stronger in North America than in Europe and Asia. This pattern is similar to the results of Piao *et al.* (2007), who used large-scale remote-sensing techniques and quantified senescence delays of 0·28 d year^{-1} in North America but only 0·11 d year^{-1} in Eurasia over the last two decades. Some of the differences observed across continents may be due to differences in tree species composition and the number of species assessed. Differences in geographical distribution of studies within each continent may also explain some of the variation observed. For example, while European studies were distributed throughout the continent, studies tended to be concentrated in coastal regions in Asia and North America (Fig. 1). In addition, our analysis found that high-latitude regions have smaller changes in senescence over time than low-latitude regions (Fig. 4). As the majority of high-latitude studies included in this analysis were conducted in Europe, it is not surprising that we found larger delays in North America and Asia than in Europe. Unlike satellite-derived measurements of senescence that show an intensifying delay in senescence in recent decades (Jeong *et al.*, 2011), we did not find a statistically significant change in the rate of delay over time (Fig. 4G).

Recommendations for future research

Looking forward, as the study of leaf senescence phenology garners additional research interest, one important take-away from this meta-analysis is the need to identify and use common, biologically relevant definitions of the date of leaf senescence. Among the publications we examined in our meta-analysis, date of senescence was estimated by a variety of metrics, including leaf fall, colour change and chlorophyll content, and was measured on a variety of scales, including leaf, branch, individual tree and total canopy. Fifty per cent leaf fall comprised over one-third of senescence measurements, and we show that it is a useful metric to compare date of senescence observations across multiple studies. Leaf fall is easily characterized in the field and contributes to measurements of forest productivity, making it a practical ecological measure. While 50 % leaf fall is the metric most commonly used across studies of fall leaf senescence, our results demonstrate that senescence dates estimated using leaf colour change are more strongly correlated with latitude than percentage leaf fall (Fig. 2). Because the

senescence process is a combination of biodegradation and nutrient resorption, deciduous plants often show a large decline in photosynthetic activity long before they drop their leaves (Wilson *et al.*, 2001). Additionally, species-specific relationships between the end of the photosynthetic period and date of leaf fall may vary, adding bias to patterns not accounted for in this analysis. Therefore, metrics involving leaf colour change may represent more biologically meaningful measures of the end of the growing season for deciduous plants compared with percentage leaf fall. We suggest that researchers consider the biological relevance of senescence metrics when designing future studies to allow for robust cross-study comparisons and enable understanding of large-scale trends.

Deciduous trees in the northern hemisphere are well represented by leaf senescence studies, especially in eastern North America, Europe and parts of Asia (Fig. 1). Additional studies in other regions in North America and the southern hemisphere are needed. This enlarged geographic range of studies would allow researchers to disentangle differences in the response of autumn leaf senescence to changes in temperature at finer resolution across space and deciduous forest biomes (temperate vs. boreal). Due to small sample sizes, we found it was not feasible to estimate senescence trends at the species level. We therefore focused on the level of plant order and found that plants in the order Rosales and Fagales respond to increases in air temperature with later dates of senescence compared with Ginkgoales.

Regional, national and global networks of on-the-ground and remotely sensed data provide important information about changes in autumn phenology, but there is an opportunity to augment these data through smaller scale, independent studies as well. In particular, we recommend that global change experiments that are currently underway to examine the effects of elevated CO_2, warmer temperatures, drought, elevated tropospheric ozone or other global change factors, as well as multifactor investigations, include measurements of leaf senescence. Despite the noted underprediction of changes in spring leaf-out by experimental manipulations compared with observational studies (Wolkovich *et al.*, 2012), ongoing or new experiments could provide additional critical information by disentangling the various environmental and physiological drivers of autumn phenology.

Conclusions

To our knowledge, this is the first study to synthesize existing senescence data derived from individual studies of deciduous trees throughout the northern hemisphere. Our findings demonstrate that across published studies, leaf senescence is delayed over time and in response to temperature, although low-latitude sites show significantly stronger delays in senescence over time than high-latitude sites. We find that while temperature alone may be a reasonable predictor of the date of leaf senescence when examining a broad suite of sites, it is important to consider that temperature-induced changes in senescence at high-latitude sites are likely to be constrained by the influence of photoperiod. Ecosystem-level differences in the mechanisms that control the timing of leaf senescence may affect both plant

community interactions and ecosystem carbon storage as global temperatures increase over the next century.

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APPENDIX 1 PUBLICATIONS INCLUDED IN DATE OF SENESCENCE ANALYSIS

This table includes all publications that met search criteria for date of senescence studies and were included in the senescence metric tabulation in Table 1. Studies highlighted in bold used the most common senescence metric (50 % leaf fall) and were included in the regression and partial correlation analyses. (*) indicates a paper that reported a mean date of leaf senescence over a range of years, and (**) indicates that the range of years varied by site within the study.

No.	Paper	Observations	Continent	Site	Latitude	Longitude	Biome	Order	Year range	Senescence metric
1	Asshoff *et al.* (2006)	9	Europe	Swiss Canopy Crane Reserve	47·46667	7·5	Temperate	Fagales	2002–2004	75 % LF
2	Augspurger *et al.* (2005)	5	North America	Trelease Woods, understorey	40·15	−88·16667	Temperate	Sapindales	1996–1998*	0 % LAI
				Trelease Woods, edge						
				Trelease Woods, canopy				Mixed		
3	Barr *et al.* (2004)	16	North America	Old Aspen Site	53·7	−106·2	Boreal	Fagales	1997–2003	PAR transmission plateau, $P_x = 0$
								Malpighiales	1994, 1996–2003	
4	**Blanke and Kunz (2011)**	**3**	**Europe**	**Klein-Altendorf Research Centre**	**50·62**	**6·988**	**Temperate**	**Mixed**	**1988–2010***	**50 % LF**
									1958–2007*	
									1958–1987*	
5	**Brown *et al.* (1997)**	**4**	**North American**	**Orland E. White Arboretum**	**39·0638**	**−78·0646**	**Temperate**	**Fagales**	**1994**	**50 % LF**
6	Chen *et al.* (2005)	6	Asia	Beijing	40·01667	116·3333	Temperate	Mixed	1982–1993*	NDVI
				Gaixian	40·4333	122·3333			1982–1993*	
				Harbin	45·7	126·6667			1982–1993*	
				Luoyang	34·6667	112·41667			1982–1993*	
				Mudanjiang	44·4333	129·6667			1982–1993*	
				Xi'an	34·21667	108·96667			1982–1993*	
				Xingtai	37·0667	114·5			1982–1993*	
7	**Chmielewski and Rötzer (2001)**	**11**	**Europe**	**Dinaric Mountain Region**	**42·9**	**20·3**	**Temperate**	**Mixed**	**1969–1984***	**50 % LF**
				Great Hungarian Lowlands	**46**	**19·6**				
				North Alpine Foreland	**47·8**	**10·9**				
				Southern Central European Highlands	**48·2**	**8·2**				
				Bohemian Highlands	**48·6**	**15·5**				
				Northern Central European Highlands	**50·4**	**8·7**				
				British Isles	**51·6**	**−3·8**	**Temperate**			
				North Sea/Central European Lowlands	**52·9**	**10·1**	**Temperate**			
				Baltic Sea Region	**57·2**	**15·2**	**Temperate**			
				North Atlantic Mountain Region	**61·9**	**8·1**	**Boreal**			
				North Scandinavia	**67·1**	**26·7**	**Boreal**			

(continued)

Continued

No.	Paper	Observations	Continent	Site	Latitude	Longitude	Biome	Order	Year range	Senescence metric
8	Chmielewski *et al.* (2005)	3	Europe	Saxony	NA	NA	Temperate	Sapindales Fagales	1961–2000* 1961–2000*	50 % CC
9	**Connor *et al.* (1994)**	**6**	**North America**	**Orland E. White Arboretum**	**39·0638**	**−78·0646**	**Temperate**	**Fagales**	**1989–1991**	**50 % LF**
10	Delbart *et al.* (2005)	10	Asia	Turuhansk	65·8	88	Boreal	Fagales	1999	NDVI
				Taseevo	57·18333	94·833333	Boreal			
				Vehme	63·08333	88	Boreal			
				Podtsesovo	58·51666	92·216666	Boreal			
				Aksarka	66·5	67·816666	Boreal			
				Ilir	50·5	100·7	Boreal			
				Kuragino	53·9	92·7	Boreal			
				Krasnoyarsk	56	93	Boreal			
				Tachtip	52·733	90	Boreal			
				Volchno	54	81	Boreal			
11	**Dillen *et al.* (2012)**	**2**	**North America**	**Harvard Forest**	**42·533**	**−72·183**	**Temperate**	**Fagales**	**2010**	**50 % LF**
								Fagales		
12	Doi (2012)	53	Asia	Japan meteorological sites (53 sites)	NA	NA	Temperate	Rosales	1953–2005	80 % LF
13	Doi and Takashi (2008)	2	Asia	Japan meteorological sites	35·4	135·8	Temperate	Ginkgoales Sapindales	1953–2005*	80 % LF
14	Dragoni *et al.* (2011)	10	North America	Morgon Monroe State Forest	39·317	−86·417	Temperate	Mixed	1999–2008	0 % LAI
15	Dragoni and Rahman (2012)	48	North America	28·25°N	28·25	NA	Temperate	Mixed	1989–1999	NDVI
				35·75°N	35·75	NA				
				48·25°N	48·25	NA				
16	Elmore *et al.* (2012)	1	North America	Cheasapeake Bay	39·87	−77·75	Temperate	Mixed	2004–2008*	Landsat 50 % cover
17	**Fridley (2012)**	**6**	**North America**	**Syracuse, NY**	**43·05**	**−76·15**	**Temperate**	**Mixed**	**2008–2010**	**50 % LF, 90 % LF**
18	**Gibson *et al.* (2001)**	**1**	**North America**	**Clemson, SC**	**34·68**	**−82·84**	**Temperate**	**Rosales**	**1998**	**50 % LF**
19	**Gill *et al.* (1998)**	**4**	**North America**	**Hubbard Brook Experimental Forest**	**43·94**	**−71·72**	**Temperate**	**Fagales Lamiales Sapindales**	**1989**	**50 % LF**
20	**Glinwood and Pettersson (2000)**	**1**		**Uppsala**	**59·816667**	**17·633333**	**Temperate**	**Rosales**	**1998**	**50 % LF**
21	Grassi and Magnani (2005)	6	Europe	Nonantola Experimental Site	44·683	11·033	Temperate	Lamiales Fagales	2001–2003	50 % A_{max}
22	**Heide (2003)**	**7**	**Europe**	**Agricultural University of Norway**	**60**	**10·783**	**Boreal**	**Fagales**	**1996–2002***	**50 % LF**
23	Isaacson *et al.* (2012)	8	North America	Flambeau River State Forest	45·733	−90·75	Temperate	Lamiales	2009	NDVI
				Kettle Moraine State Forest	43·598	−88·280		Sapindales		
24	**Juknys *et al.* (2011)**	**92**	**Europe**	**Vytautus Magnus University**	**54·083**	**23·083**	**Temperate**	**Malvales**	**1956–60, 1968–1997, 2000–2010**	**50 % LF, 50 % CC**
25	Kafaki *et al.* (2009)	4	Asia	Guilan Province	NA	NA	Temperate	Fagales	2003–2006	100 % LF
26	Keskitalo (2005)	1	Europe	Umea University	63·820539	20·303591	Boreal	Malpighiales	2003	100 % LF
27	Kodani *et al.* (2002)		Japan	Tohoku Research Center	36·76667	141·13333	Temperate	Fagales	1999	0 % LAI
28	Kozlov and Berlina (2002)	60	Europe	Lapland Biosphere Reserve	67·65	32·61667	Boreal	Mixed	1931–1941, 1946–1952, 1957–1998	Start of LF
29	Kramer (1995)	9	Europe	International Phenological Gardens	NA	NA	Temperate	Malpighiales Malvales Pinales Fagales	1955–1987	50 % LF
30	Laurila *et al.* (2001)	2	Europe	Petsikko	69·47	27·23	Boreal	Fagales	1997–1998	Eddy covariance
31	Lebourgeois *et al.* (2010)	8	Europe	102 sites	NA	NA	Temperate	Pinales	1997–2006	10 % CC in 10 % of trees, 10 % CC in 90 % of trees
32	Lee *et al.* (2003)	88	North America	Harvard Forest	42·53	−72·18	Temperate	Fagales Fagales Cornales Lamiales Fagales Sapindales Rosales	1991–1999	50 % LF
33	Nagai *et al.* (2011)	9	Asia	Takayama	36·1466	137·423	Temperate	Fagales	2005–2007	0 % LAI
								Sapindales		
34	Nakamura *et al.* (2010)	1	Asia	Tomakomai Experimental Forest	42·667	141·6	Temperate	Fagales	2008	80 % LF
35	Nicolai (2010)	8	Europe	Marburg, Hesse	50·816667	8·6	Temperate	Fabales	2002–2009	Start of LF

(continued)

Continued

No.	Paper	Observations	Continent	Site	Latitude	Longitude	Biome	Order	Year range	Senescence metric
36	**Niinemets and Tamm (2005)**	**6**	**Europe**	**Karkna**	**58·46667**	**26·633333**	**Temperate**	**Sapindales** **Fagales Malpighiales**	**1997**	**50 % LF, 80 % LF**
37	**Norby *et al.* (2003)**	**4**	**North America**	**Oak Ridge**	**35·9**	**–84·333333**	**Temperate**	**Sapindales**	**1995–1996**	**50 % LF**
38	**Parker and Tibbs (2004)**	**11**	**North America**	**Anapolis, MD**	**38·883333**	**–76·55**	**Temperate**	**Fagales Cornales Fagales Saxifragales Magnoliales**	**1994**	**50 % LF**
39	**Pataki and Oren (2003)**	**6**	**North America**	**Duke Forest**	**36·017**	**–79·982**	**Temperate**	**Fagales** **Saxifragales Magnoliales**	**1997**	**50 % LF, 100 % LF**
40	Pellis *et al.* (2004)	50	Europe	Antwerp	51·083	4·366	Temperate	Malpighiales	1996–1998, 2001	100 % LF, plateau PAR ratio
41	Richardson *et al.* (2009)	1	North America	Bartlett Experimental Forest	44·064	–71·288	Temperate	Mixed	2007	Photo 'greenness' index, peak red colour
42	Rolshausen and Schaefer (2007)	2	Europe	Freiberg	48	8	Temperate	Rosales	2004	Peak CC
43	Schaberg *et al.* (2003)	1	North America	USDA Forest Service Northern Research Station	44·5	–73·2	Temperate	Sapindales	1999	50 % green, 50 % yellow, 0 % green
44	**Schreiber *et al.* (2013)**	**4**	**North America**	**Alberta-Pacific Forest Industries**	**–**	**–113**	**Temperate**	**Malpighiales**	**2010**	**More yellow than green leaves**
45	Sonnentag *et al.* (2012)	1	North America	Harvard Forest	42·5	–72·2	Temperate	Mixed	2010	100 % LF, 50 % green, 0 % green
46	Soolanayakana-hally *et al.* (2013)	2	North America	Vancouver Indian Head, Saskatchewan	49·26	–123·25	Temperate	Malpighiales	2009	100 % LF, 50 % yellow
47	Soudani *et al.* (2012)	9	Europe	Fontainebleau Hesse Fougeres	48 48 48	2 7 1	Temperate	Fagales	2005–2009**	NDVI
48	Tartachnyk and Blanke (2001)	3	Europe	Bonn	50·733	7·0833	Temperate	Rosales	1997–1999	90 % LF
49	Tateno *et al.* (2005)	48	Asia	Ashui Forest Research Station	35·3	135·72	Temperate	Cornales Ericales Sapindales Aquifoliales Apiales mixed Fagales Rosales Lamiales Magnoliales Laurales	2001	10 % LF
50	Uddling *et al.* (2005)	2	Europe	Ostad Field Station	57·9	12·4	Temperate	Fagales	1997–1998	100 % LF
51	**Vitasse *et al.* (2009)**	**103**	**Europe**	**Pyrenees**	**46**	**6**	**Temperate**	**Fagales Lamiales Sapindales**	**2005–2007**	**50 % CC or LF**
52	**Waddell *et al.* (2001)**	**3**	**North America**	**Sesquicentennial State Park (high elevation) Sesquicentennial State Park (low elevation) Clemson University**	**34·091** **34·091** **34·132**	**–80·907** **–80·907** **–80·869**	**Temperate**	**Fagales**	**1994**	**50 % LF**
53	**Wang *et al.* (1992)**	**23**	**North America**	**Mont St. Hilaire Nursery**	**45·533**	**–73·133**	**Temperate**	**Fagales Lamiales Malvales Rosales Malpighiales Sapindales**	**1988–1989***	**50 % LF**
54	White *et al.* (1997)	2	North America	Hubbard Brook	43·933	–71·67	Temperate	Mixed	1991–1992	NDVI
55	**Zhang *et al.* (2011)**	**4**	**North America**	**Harvard Forest**	**42·533**	**–72·183**	**Temperate**	**Mixed**	**2001–2004**	**50 % LF, 50 % colour change**
56	Zhao *et al.* (2006)	71	Asia	Henan Meteorological Bureau sites	NA	NA	Temperate	Malpighiales Fabales Sapindales	1986–2003	100 % LF

CC, colour change, LAI, leaf area index; LF, leaf fall; PAR, photosynthetically acive radiation; NA, not available; NDVI, normalized difference vegetation index.

APPENDIX 2 PUBLICATIONS INCLUDED IN CHANGE IN SENESCENCE ANALYSIS

(*) indicates that the slope was calculated based on >5 years of DOS data reported in the study, and (**) indicates that the range of years for which data are reported is less than the 5 year threshold period, but the study reported senescence change in d °C^{-1} across an elevation gradient. All studies were included in the analysis regardless of senescence metric.

No.	Paper	Observations	Continent	Biome	Order	Year range	Senescence metric	Regression type
1	Barr *et al.* (2004)*	1	North America	Boreal	Fagales	1994–2003	PAR transmission plateau	Time
2	Chen and Xu (2012)	46	Asia	Temperate	Rosales	1986–2005	"Almost all leaves fallen"	Time and temperature
3	Chen *et al.* (2005)	5	Asia	Temperate	Mixed	1982–1993	NDVI	Time
4	Chmielewski and Rötzer. (2005)	11	Europe	Temperate/boreal	Mixed	1969–1998	50 % LF	Time
5	Chmielewski *et al.* (2005)	3	Europe	Temperate	Sapindales Fagales	1961–2000	50 % CC	Time
6	Dragoni *et al.* (2011)	3	North America	Temperate	Mixed	1998–2008	0 % LAI	Time
7	Dragoni and Rahman (2012)	9	North America	Temperate	Mixed	1989–2008	NDVI	Time
8	Ibanez *et al.* (2010)	183	Asia	Temperate	Ginkgoales Rosales	1953–2005	80 % LF	Time
9	Juknys *et al.* (2012*a*)	3	Europe	Temperate	Sapindales Fagales Malvales	1956–2010	50 % LF	Time
10	Juknys *et al.* (2012*b*)	2	Europe	Temperate	Fagales Malvales	1956–2010	50 % LF	Temperature
11	Kozlov and Berlina (2002)*	1	Europe	Boreal	mixed	1931–1941, 1946–1952, 1957–1998	'Begininning of leaf fall'	Time
12	Kunz and Blanke (2011)	1	Europe	Temperate	Rosales	1958–2008	50 % LF	Time
13	Lee *et al.* (2003)*	11	North America	Temperate	Rosales Sapindales Lamiales Fagales	1991–1998	50 % LF	Time
14	Matsumoto (2010)	55	Asia	Temperate	Ginkgoales	1961–2000	80 % LF	Temperature
15	Menzel *et al.* (2001)	4	Europe	Temperate	Sapindales Fagales	1951–1996	Start of CC	Time
16	Menzel *et al.* (2006)	1	Europe	Temperate	mixed	1971–2000	50 % CC	Time and temperature
17	Nicolai (2010)*	1	Europe	Temperate	Fabales	2002–2009	Start of LF	Time
18	Pudas *et al.* (2008)	3	Europe	Boreal	Fagales	1997–2006	50 % colour change	Time and temperature
19	Richardson *et al.* (2006)	1	North America	Temperate	Sapindales	1957–2004	Photo greenness index	Time
20	Vitasse *et al.* (2009)	2	Europe	Temperate	Fagales	2005–2007**	50 % CC or LF	Temperature
21	Zhao *et al.* (2006)*	4	Europe	Temperate	Sapindales Malpighiales Fabales	1986–2003	100% LF	Time

LAI, leaf area index; LF, leaf fall; PAR, photosnthetically acive radiation; NDVI, normalized difference vegetation index.