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Extended leaf phenology has limited benefits for invasive species growing at northern latitudes

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Abstract Many understory woody invasive plants in North America leaf out earlier or retain leaves later than their native associates. This extended leaf phenology is thought to grant invasive species an advantage over native species because spring and fall are crucial times for light access and carbon acquisition in understory habitats. However, it is unclear whether this advantage persists at northern latitudes where freezing temperatures constrain growing season length and low light levels reduce carbon gain. To investigate the costs and benefits of extended leaf phenology at northern latitudes, we observed leaf phenology, estimated total carbon gain, measured growth, and tested susceptibility to freezing temperatures for four native and four invasive woody shrubs in a disturbed forest in northern Minnesota, USA. We found that the invaders leafed out simultaneously with the natives in the spring but retained their leaves later in the autumn than native species. This extended fall phenology did not enable greater total carbon gain for the invaders because they assimilated less carbon earlier in the year than the natives. There was also no significant difference between native and invasive species in their susceptibility to freezing temperatures. Instead freezing tolerance related more to native range then leaf phenology. Our results suggest that freezing temperatures do not limit invasive species' northern expansion and instead indicate that at the northern edge of their ranges, these species may lose any competitive advantage granted by extended leaf phenology over their native associates. This study demonstrates the importance of considering latitude and forest structure when investigating phenology and growth.

Keywords Carbon assimilation · Photosynthesis · Distribution · Leaf out · Senescence

Introduction

Many understory woody invasive plants in North America, such as *Rhamnus cathartica, Lonicera x bella,* and *Berberis thunbergii,* leaf out before and/or retain functional leaves after their native associates (Harrington et al. 1989; Xu et al. 2007; Fridley 2012) because they evolved in Europe and Asia, where growing seasons are longer than in North America (Zohner and Renner 2017). This extended leaf phenology may increase these species' competitive advantage over natives in North America by granting

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greater access to understory light and lengthening their growing season (Wolkovich and Cleland 2011; Smith 2013). There is also evidence that invasive species respond more strongly to warming temperatures, enabling them to be more successful than natives under future climatic conditions (Cleland et al. 2012) and thus continue expanding north in the future (Merow et al. 2017). However, little is known about how invasive plants near the northern edge of their distributions respond to cold temperatures and low light levels because there is sparse data on their physiology in the northern parts of their ranges. To examine whether extended leaf phenology could help facilitate invasive species' continued northern expansion, we need to better understand the costs and benefits of this growth pattern at northern latitudes, where irradiance levels are lower, cold temperatures limit growing season length, and seasons transition rapidly.

Light availability, which changes with latitude and fluctuates throughout the growing season (Fig. 1), heavily influences carbon gain in the understory (Miyashita et al. 2012). Many early-leafing understory plants access as much as 80% of their yearly light (Augspurger et al. 2005; Lopez et al. 2008; Kwit et al. 2010) and assimilate 27–100% of their yearly carbon (Harrington et al. 1989; Heberling et al. 2018) before the forest canopy closes in the spring. Similarly in the fall, plants can acquire up to 21% of their total carbon after the overstory canopy reopens (Fridley 2012). However, freezing temperatures occur later in the spring and earlier in the fall at northern latitudes and shorten the period of unshaded understory growth during both seasons (Kwit et al. 2010). In general, light in the fall is less crucial to carbon gain than in the spring because photosynthetic rates decline in older leaves (Wilson et al. 2001), daylength shortens, and light transmission decreases (Baldocchi et al. 1984; Lopez et al. 2008), especially at northern latitudes (Lappi and Stenberg 1998). All of these factors could impact the success of invasive species at northern latitudes.

Many woody invasive plants exhibit high plasticity in response to seasonal changes in light (Martinez and Fridley 2018) and can survive under a range of light conditions, including low light at northern latitudes (i.e., lower solar elevation angle and shorter spring and fall day length). However, these species often display greater growth under high light (*Berberis thunbergii*: Silander and Klepeis 1999; *Frangula alnus*: Cunard and Lee 2009; *Lonicera maackii*: Luken et al. 1995; Lieurance and Landsbergen 2016; *Rhamnus cathartica*: Kurylo et al. 2007; Pretorius 2015). Decreased light availability may even dampen invasion success in mature forests (Meiners et al. 2002; Cunard and Lee 2009). As a result of these limitations, invasive species often grow where light transmittance is high, such as in gaps (Sanford et al. 2003), disturbed habitats (With 2002; Fan et al. 2013), and early successional forests (Meiners et al. 2002). It is unclear how invasive species' sensitivity to light impacts their productivity in lower light conditions of northern latitudes.

The timing and severity of freezing temperatures can also play a critical role in determining whether a species can expand into northern latitudes (Fig. 1). Species that leaf out early should have freezing tolerant leaves or an ability to reflush leaves after freezing damage (McEwan et al. 2009; Vitasse et al. 2014a). These species also often have smaller diameter vessel elements which reduce the risk of embolism during freezing events (Davis et al. 1999; Panchen et al. 2014; Yin et al. 2016). Freezing tolerance is an expensive investment that often correlates with slower growth rates in many species (Koehler et al. 2012; Savage and Cavender-Bares 2013; Reich 2014). Although invasive species are known to display high growth rates (Grotkopp et al. 2002; Dawson et al. 2011) and have small diameter vessels (Smith et al. 2013; Yin et al. 2016), few studies have investigated how these species respond to freezing temperatures (except Stewart et al. 2006; Friedman et al. 2008; McEwan et al. 2009).

To determine potential costs and benefits of extended leaf phenology in invasive woody plants at northern latitudes, we observed leaf phenology, modeled seasonal carbon gain, measured growth rates, and tested the susceptibility to freezing temperatures of four native and four invasive shrubs in a disturbed forest in Northern Minnesota, USA. Our study site is in the northern part of these invasive species' ranges (Fig. 1) and is further north than many previous studies (Harrington et al. 1989; Schierenbeck and Marshall 1993; Luken et al. 1997; Silander and Klepeis 1999; Xu et al. 2007; Cunard and Lee 2009; Fridley 2012; Lieurance and Landsbergen 2016; Heberling et al. 2018). At this latitude, freezing temperatures occur later in the spring and earlier in the fall, seasonal changes in daylength are more drastic,

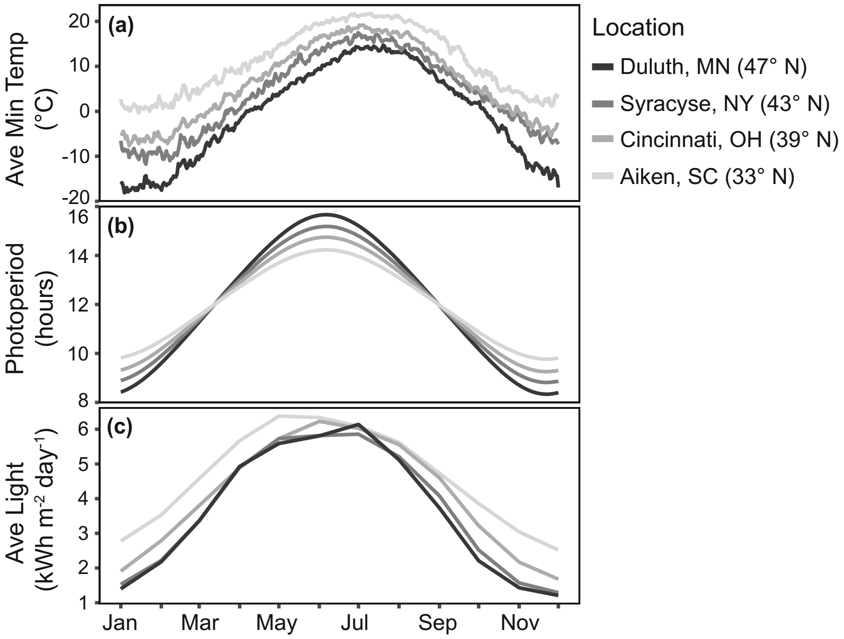

Fig. 1 Temperature and light conditions throughout the year for sites ranging from 33° N to 47° N latitude. Locations span the distribution of the invasive species included in this study and represent previous studies investigating invasive shrub physiology: Duluth, MN (black, this study), Syracuse, NY (dark grey, Fridley 2012), Cincinnati, OH (medium grey, Lieurance and Landsbergen 2016), Aiken, SC (light grey, Schierenbeck and Marshall 1993). **a** Daily minimum temperatures from the Global Historical Climatology Network (Menne et al. 2012a, b) averaged across 50 years (1968–2018). **b** Daily photoperiod (hours of daylight) for 2017 calculated with the R package insol (Corripio 2003). **c** Monthly averages of daily solar irradiance across each study site's corresponding county and over 11 years (1998–2009). Data are from the National Renewable Energy Laboratory (Perez-SUNY/NREL 2007) and represent the global horizontal irradiance, which is the sum of direct normal and diffuse irradiance components

and irradiance levels are lower overall than at more southern latitudes. This study addresses the questions: (1) Do invasive shrubs leaf out earlier and/or retain leaves later than their native associates, even when phenological events are condensed into shorter time frames at northern latitudes? (2) Does extended leaf phenology enable greater total carbon gain for invasive shrubs, as a result of higher carbon assimilation during the spring and fall? (3) Do invasive species exhibit lower susceptibility to freezing temperatures than native species because they have leaves later and/or early in the year? We predict that shorter springs and falls and lower light levels will reduce spring and fall carbon gain, while a brighter disturbed forest will increase the role of summer carbon gain. We also expect that invasive species require a lower susceptibility to freezing temperatures to help support the maintenance of leaf tissue during early spring and late fall. This research provides insight into the costs and benefits of extended leaf phenology at northern latitudes and helps us understand how freezing temperatures and light levels might limit invasive species' northern expansion in the future.

Materials and methods

Study site and species selection

Our study site, Bagley Nature Area, in Duluth, Minnesota, USA (46.81686427° N, 92.08800509° W), is located at the border between boreal and temperate forest ecotypes. Bagley Nature Area is a 22-hectare site with a 50-year-old mixed forest dominated by *Acer saccharum, Betula papyrifera, Populus tremuloides,* and *Abies balsamea.* Ten individuals of the four most invasive understory shrub species were selected to study at the site (Table 1). We surveyed the six closest native shrubs around each of these plants to determine the four most common associates (Table S1 from ESM). Our selection of invasive species was limited by growth form (3 shrubs and 1 sub-shrub) and replication was the same for native and invasive plants (10 individuals per species).

Leaf phenology

Beginning in mid-February 2017 and late March 2018, we visited the same ten plants per species weekly and estimated the percentage of buds at each of five phenophases (Lenz et al. 2013; Fridley and Craddock 2015): (0) dormant—bud inactive and tightly closed, (1) swelling—bud beginning to change color and expand, (2) bursting—green leaf tips visible, (3) leaf emergence—leaves present but still folded, and (4) leaf out—leaves reflexed and petiole extended (Fig. S1 from ESM). Bud burst and leaf out dates were determined by fitting self-starting gaussian models and self-starting nonlinear least squares logistic models in R (version 3.4.1, 2017), respectively, with date predicting the estimated percent of buds at budburst (Eq. S1 from ESM) or leaf out (Eq. S2 from ESM). A plant was considered to have reached a given phenophase when at least 30% of its buds qualified for that stage (Augspurger 2008). These models were selected to provide continuous daily estimates of phenology progression and more holistically represent phenological events, similar to Moussus et al. (2010). The percentage of full leaf expansion in 2017 was calculated based on weekly measurements of scanned leaf area on 6–15 leaves per plant.

We monitored weekly fall phenology by estimating the percentage of leaves on each plant that senesced from the beginning of September until mid-December in 2017 and late-November in 2018 similar to Panchen et al. (2015). Leaves were considered senesced when they dropped, changed color, and/or lost photosystem function. Loss of photosystem function was confirmed in mid-November 2017 by measuring chlorophyll fluorescence on dark-adapted leaves with a mini-PAM II (Heinz Walz GmbH, Effeltrich, Germany) on the three species that still had leaves (i.e., *Lonicera, Rhamnus,* and *Frangula*). Since *Rubus* is biennial, senescence of first- and second-year growth were averaged. Senescence estimates in *Cornus* may include damage from insect predation in both years. We fit sigmoidal curves to percent senescence as a function of date for each plant, with the self-starting nonlinear least squares logistic model in R (Eq. S2 from ESM). Using the resulting equation, the date of 50% and 75% senescence for each plant was interpolated.

Annual carbon assimilation model

Maximum total carbon acquisition of six plants per species was estimated during one growing season by measuring understory light availability, carbon dioxide assimilation rates, and leaf area over time, and then modelling carbon assimilation in R assuming only sunny days (Fig. 2).

Understory light availability (Box 1 in Fig. 2)

To quantify understory light, percent light transmittance on cloudy days was measured above 10 plants per species at four time points: May—open canopy, July—closed canopy and long daylength, September—closed canopy and short daylength, and October—open canopy. Each measurement is the ratio of

Table 1 Description of species in the study

Species	Family	Origin	Growth form	Life cycle
Berberis thunbergii D.C.	Berberidaceae	Invasive	Subshrub	Perennial
Frangula alnus Mill.	Rhamnaceae	Invasive	Tree-like shrub	Perennial
Lonicera × *bella* Zabel [*L. morrowii* × *L. tatarica*]	Caprifoliaceae	Invasive	Shrub	Perennial
Rhamnus cathartica L.	Rhamnaceae	Invasive	Tree-like shrub	Perennial
Cornus sericea L.	Cornaceae	Native	Shrub	Perennial
Corylus cornuta Marshall var. *cornuta*	Betulaceae	Native	Shrub	Perennial
Rubus idaeus L.	Rosaceae	Native	Subshrub	Biennial
Viburnum lentago L.	Caprifoliaceae	Native	Tree-like shrub	Perennial

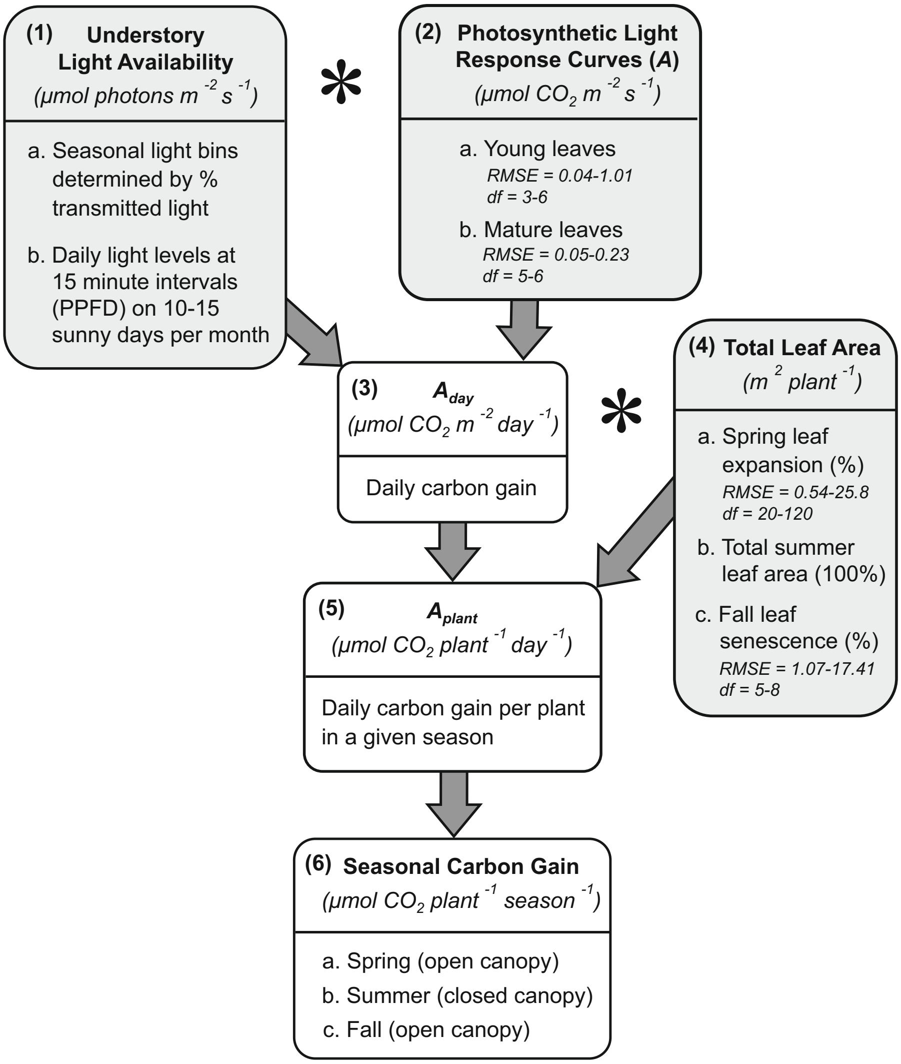

Fig. 2 Seasonal carbon gain model components. The model is comprised of three main inputs (shaded boxes): (1) understory light availability, (2) photosynthetic light response curves, and (4) total leaf area. Numbers specify order of steps and lowercase letters represent components of each parameter. Arrows indicate the workflow direction and * represents input multiplication. Model fits are provided as RSME and df ranges for inputs that were fit to curves within the model

the light level (lumens s^{-1}, 15-s average) above the plant to the light level recorded simultaneously in the open (Parent and Messier 1996). Using these data, we divided the plants into six bins during each time period (e.g. July: $< 20\%$, 21–31%, 32–43%, 44–54%, 55–66%, 67–78%, $> 79\%$ transmitted light) and selected six plants with the percent light transmittance closest to the bin averages (Box 1a in Fig. 2). Light was then measured at 15-min intervals on 10–15 sunny days per month using lux sensors (HOBO Pendant Temp/Light, 8 k, UA-002-08, Onset Computer Corporation, Bourne, Massachusetts USA) mounted at the top of the selected plants (Box 1b in Fig. 2). These data were converted from lux (lumens s^{-1}) to PPFD (µmol photons m^{-2} s^{-1}) based on seasonal calibrations in each month (Long et al. 2012; Table S2 from ESM) using a light meter (LI-250A, LI-COR, Lincoln, NE).

Photosynthetic light response curves (Box 2 in Fig. 2)

Plant photosynthetic rate changes with light levels. To estimate carbon assimilation rate (A), we measured light response curves of immature, expanding leaves (early June) and mature leaves (mid-August) on six plants per species (Box 2 in Fig. 2). Measurements were made on sun leaves between 8 a.m. and 2 p.m. during sunny days using a portable gas exchange system (6400, LI-COR, Lincoln, NE) with a red-blue light source (6400-02B). The auto program Light-Curve was used with 10 light levels between 0 and 2000 μmol photons m^{-2} s^{-1}. To standardize measurements, we set leaf temperature at 20 °C and CO_2 concentration at 400 μmol CO_2 mol^{-1} air. Water content and flow rate were kept in the range of 12–15 mmol H_2O mol air^{-1} and 50–200 μmol air s^{-1}, respectively. Light response curves were fit in R with a non-rectangular hyperbola using least squares regression (Marshall and Biscoe 1980; Heberling and Fridley 2013).

Light response curves were then used to determine total carbon assimilated (*A*) every 15-min from the daily PPFD measurements (multiplying Box 1 and Box 2 in Fig. 2). We used light response curves from immature leaves for spring (Box 2a in Fig. 2) and from mature leaves for summer and fall (Box 2b in Fig. 2) to account for seasonal changes in photosynthetic capacity. Although photosynthetic capacity also declines during the fall (Morecroft et al. 2003) and in older leaves (Wilson et al. 2001), our model assumes maximum carbon gain with sustained photosynthetic capacity throughout the fall. Total daily carbon assimilation (A_{day}) was calculated as the area under the curve of *A* over time (Box 3 in Fig. 2). On days that light levels were not measured, A_{day} was interpolated using a 5-parameter polynomial curve of A_{day} over the growing season. This interpolation indirectly included daylength because daily carbon assimilation decreases with photoperiod.

Total leaf area (Box 4 in Fig. 2)

To account for leaf area, the CO_2 assimilated each day (A_{day}, Box 3 in Fig. 2) was multiplied by the total leaf area per plant (Box 4 in Fig. 2) giving us total carbon gain per plant per day (A_{plant}; Box 5 in Fig. 2). To estimate total leaf area, we collected and scanned 6-15 fully expanded leaves per plant, measured individual leaf size using ImageJ (Rasband 1997–2018), counted the number of leaves per plant, and multiplied the average leaf size by the total leaf count. Leaf area was adjusted based on our estimates of percent expansion in the spring (Box 4a in Fig. 2) and senescence in the fall (Box 4c in Fig. 2).

Seasonal carbon gain (Box 6 in Fig. 2)

Total carbon assimilated per plant per season was estimated by adding A_{plant} (Box 5 in Fig. 2) over the complete growing season (Box 6 in Fig. 2). It is important to note that these calculations assume that there is no self-shading within the tree. As a result, our output is an overestimate of carbon assimilation and gives a maximum carbon assimilation per plant per year. To investigate how canopy openness impacted carbon gain, the growing season was divided into three time frames: spring (open canopy), summer (closed canopy), and fall (open canopy) based on hemispherical photographs of the overstory canopy taken above 80 plants 1–2 times a month (Frazer et al. 1997; Lopez et al. 2008). Photographs were processed with an ImageJ plugin created by Beckschäfer (2015). Hemispherical photos, rather than percent light transmittance, were used to partition understory carbon gain relative to overstory phenology because, while light transmittance is a useful metric for determining light levels, hemispherical photos more directly estimate overstory phenology.

To evaluate the best predictors of total seasonal carbon gain, multiple linear regression models were tested in R including variables representing the three main components of our carbon estimation model: seasonal light (logged spring, summer, and logged fall % PPFD), total leaf area (logged), and carbon assimilation rate (logged A_{max} in June and August), as well as additional traits potentially relating to carbon gain (square root of plant height, SLA, stem number, leaf out date, and 75% senescence date). Through an iterative selection process, predictor variables exhibiting collinearity were removed and only those correlated with total seasonal carbon gain were included in the final regression model.

Growth traits

We measured monthly (June, July, August, and November) branch elongation of six new branches on ten plants per species during the 2017 growing season and estimated the total rate of elongation from leaf emergence to 50% leaf senescence. Sun branches were selected when possible and the longest branch was measured when branch growth diverged. We fit asymptotic curves in R over the growing season and used the asymptote as the total branch length when calculating absolute branch elongation rate (AGR). Stems consumed by herbivores or otherwise damaged were excluded from analysis from the time of damage onward. Relative basal growth rate was calculated by measuring with calipers the basal diameter of 1-3 stems per plant in June and September 2018. Stems were measured in the widest direction and the three largest stems were selected for plants with more than three stems. Average basal area was multiplied by June stem counts to address differing growth forms and total basal area was used in the calculation of relative basal growth rate (RGR). We measured specific leaf area (SLA) for at least six expanded leaves per plant in mid-July 2017 because SLA has been shown to correlate with growth rate (Wright et al. 2004; Reich 2014). Light response curves (described above) were also used to estimate maximum photosynthetic capacity ($A_{\max}$) of immature and mature leaves, another metric often correlated with growth rate (Reich 2014).

Freezing damage

Sample collection and freezing cycles

Freezing tolerance is a complex trait that varies across seasons and among tissue types (Sakai and Larcher 1987; Savage and Cavender-Bares 2013). To characterize some of this variation, we examined the freezing damage of branches with young leaves (late May–June), mature leaves (mid-September–early October), and late fall buds (November) exposed to different temperature treatments. Plants that exhibited less damage in response to our treatments were considered more freezing tolerant.

Branches were cut underwater, and 5-cm segments were placed in water-filled rose tubes. The samples were then frozen at − 5 °C per hour in a controlled freezing chamber (Tenney TUJR, Thermal Product Solutions, White Deer, Pennsylvania USA) with a temperature ramping controller (Watlow F4S/D, Winona, Minnesota USA) and held at a minimum temperature for 3 h. Exothermic freezing events were recorded by attaching thermocouples (HOBO 4-channel thermocouple logger UX120-014 M, Onset Computer Corporation, Bourne, Massachusetts USA) to the buds and leaves and ambient temperature was measured with thermocouples placed in the freezer interior. Exotherms occurred at − 3.5 °C ± 1.9 SD, indicating that temperature treatments below − 8 °C induced freezing for all species. In all trials, one control from each individual remained at 7 °C in the refrigerator.

Quantifying freezing damage

We used two techniques to quantify freezing damage: electrolyte leakage to assess branch, bud, and young leaf freezing damage (Lenz et al. 2013; Vitasse et al. 2014b) and chlorophyll fluorescence to determine freezing damage of young and mature leaves (Boorse et al. 1998). With each metric, LT50, or the lethal temperature at which the tissue experienced 50% of maximum freezing damage was determined by measuring freezing damage at a range of temperatures and fitting a 3-parameter logistic curve in JMP or a self-starting nonlinear least squares logistic model in R (Eq. S3 from ESM), similar to Thalhammer et al. (2014). Measurements were standardized relative to the maximum measured damage (i.e., the asymptote value) for both chlorophyll fluorescence and electrolyte leakage (Friedman et al. 2008). For mature leaves and fall buds, we used values from samples frozen to − 20 °C and − 80 °C, respectively, as the maximum damage controls because tissue frozen to these temperatures exhibited maximum damage in the spring.

We compiled our data on freezing damage to estimate freezing tolerance using a principle component analyses (PCA) in JMP. In this analysis, we described freezing tolerance based on LT50 young leaf electrolyte leakage, LT50 young leaf chlorophyll fluorescence, LT50 mature leaf chlorophyll fluorescence, and autumn bud electrolyte leakage at − 30 °C. All metrics of freezing damage were scaled to one before conducting the PCA. To test for relationships between freezing tolerance, phenology, and native range temperature, linear regressions were performed in R with the freezing tolerance PCA two primary axes as predictors for leaf out date, 75% senescence date, and minimum temperature in each species' native range.

Electrolyte leakage and chlorophyll fluorescence measurements

In the spring (during leaf out), freezing damage was measured with electrolyte leakage at a range of temperatures and in the fall (dormant buds), all plants were compared at − 30 °C. After freezing, we excised 1-cm stem segments from the frozen and control samples and placed them in test tubes with 10 mL of Milli-Q water. After 22–26 h in a 22 °C water bath, we measured the conductivity of the frozen samples and non-frozen controls. To determine the maximum conductivity of a dead sample, all samples (except those frozen to − 80 °C) were autoclaved at 121 °C for 20 min, incubated in the water bath for 22–26 h, and remeasured. Freezing damage was estimated using the index of injury according to Flint et al. (1967).

We also assessed leaf freezing damage by measuring dark-adapted quantum efficiency using a mini-PAM II (Heinz Walz GmbH, Effeltrich, Germany). In late spring and early fall, leaves (22–30 samples per species) were frozen to − 2 °C, − 5 °C, − 8 °C and − 10 °C. In the spring, we also included − 15 °C and − 20 °C to guarantee maximum damage. After freezing, the leaves were held at 7 °C for 24 h and dark adapted for at least 2 h before measuring chlorophyll fluorescence (Badeck and Rizza 2015). The decline in photosystem function was determined by subtracting each measurement from the unfrozen control measured at the same time.

Species distribution models

Climatic suitability was modeled with Maxent (Version 3.4.1, Phillips 2018) based on the coldest temperatures in known locations for each species. We used bioclimatic data from WorldClim (WorldClim.org, Fick and Hijmans 2017) for the minimum temperature of the coldest month (code: BIO6) and occurrence data from the Global Biodiversity Information Facility website (GBIF.org 2018; Table S3 from ESM). For the native species, occurrences were limited to North America. For invasive species, native ranges were determined based on the Kew Botanical Gardens "Plants of the World Online" resources (plantsoftheworldonline.org; IPNI 2018; WCSP 2018) and their invasive ranges was determined based on their North American ranges. We found a minimum of 111 occurrence locations per species and used 75% of the occurrence data to train each model and the remaining 25% to test the model. Freezing tolerance was also compared to historic temperatures in Duluth over the past 50 years using data from the Daily Global Historical Climatology Network (Menne et al. 2012a, b).

Testing for differences by species' origin and species

Differences between native and invasive species were examined in traits relating to phenology, carbon gain, growth, and susceptibility to freezing temperatures using generalized linear models and ANOVA's ($\alpha = 0.05$) tested in JMP (pro 14.0.0, 2018). Most models included two fixed-effects: origin (native or invasive) and species nested within origin. We used ANOVA's for normally distributed data and generalized linear models with the best fit distribution for each trait (Table S4 from ESM). Leaf age (young or mature) effect was added in the ANOVA comparing maximum photosynthesis rates. Temperature effects (− 2 °C, − 5 °C, and − 8 °C) were also added in the generalized linear models of freezing damage, and tissue type and method combinations were tested separately. The interaction of additional effects with origin and species nested within origin was accounted for. Model fit was assessed with a Wald's test to determine whether the explanatory variables were significant.

Results

Leaf phenology

Spring occurred later and more rapidly in 2018 than in 2017, yet the overall order of budburst remained consistent for most species across both years (Fig. 3a). Native and invasive plants exhibited no significant difference in budburst date (Wald-$\chi^2_{1,6} = 0.28$, $p = 0.6$) nor in leaf out date (Wald-$\chi^2_{1,6} = 1.0$, $p = 0.3$) in spring 2017, as interpolated from 3-parameter nonlinear least squares logistic models (Table S5 in ESM; RMSE = 0.0–13.9 percent of buds at budburst, RMSE = 0.0–13.9 percent of buds at leaf out). Under- and overstory plants expanded their leaves nearly simultaneously, but at least 30% of understory leaves were unfolded before the canopy

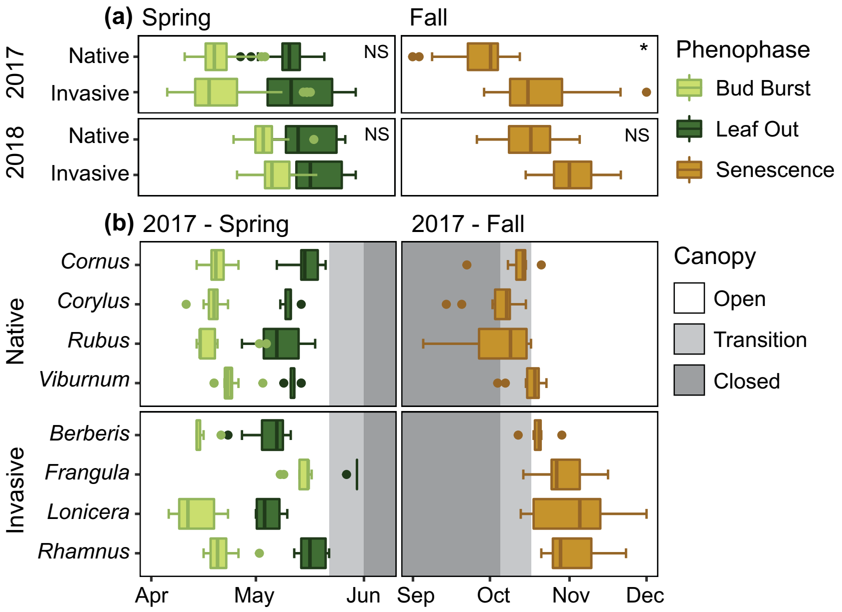

Fig. 3 Leaf phenology in 2017 and 2018 based on weekly observations of 10 plants per species. Boxplots represent phenophases: 30% bud burst date (light green), 30% leaf out date (dark green), and 75% senescence date (orange). **a** Leaf phenology by origin in both years ($\alpha = 0.05$; $*p < 0.05$, NS = no significant difference). **b** Leaf phenology by species in 2017. Background shading indicates canopy phenology calculated from hemispherical photographs: open canopy (white), closed canopy (dark grey), and transition period ranging from 25% canopy open to 25% canopy closed (light grey). All data were interpolated from fitted curves

was more than 75% closed (Fig. 3b). Bud burst dates and leaf out dates were more similar between native and invasive species in 2018 (Fig. S2 from ESM; bud burst: Wald-$\chi^2_{1,6} = 1.2$, $p = 0.3$; leaf out: Wald-$\chi^2_{1,6} = 1.9$, $p = 0.2$) based on fitted curves (Table S5 in ESM; RMSE = 0.0–9.8 percent of buds at budburst, RMSE = 0.0–29.8 percent of buds at leaf out) and all phenological stages occurred within a shorter time window.

In autumn 2017, invasive plants reached 75% leaf senescence 24 days later than native plants on average (Fig. 3; Wald-$\chi^2_{1,6} = 4.5$, $p = 0.03$), based on dates interpolated from 3-parameter nonlinear least squares logistic models (Table S5 in ESM; RMSE = 1.7–17.4 percent leaf senescence). Meaning that, contrary to the natives, invasive species retained green leaves after the canopy re-opened, thereby experiencing extended access to light and a lengthened growing season. Although invasive and native fall senescence dates were not significantly different in 2018 (Fig. 3a, Fig. S2 from ESM; Wald-$\chi^2_{1,6} = 2.7$, $p = 0.1$), autumn 2018 patterns were consistent with 2017 and invasive species reached 75% senescence 15 days on average after native species based on dates interpolated from fitted curves (Table S5 in ESM; RMSE = 0.1–34.6 percent leaf senescence).

Carbon assimilation

According to carbon gain estimates from our model, invasive and native species accumulated similar amounts of total carbon in one year (Wald-$\chi^2_{1,6} = 0.071$, $p = 0.8$), but their relative carbon gain differed within and across seasons (Fig. 4). Natives species gained a larger percentage of their total carbon in the spring (Wald-$\chi^2_{1,6} = 18.5$, $p = < 0.0001$) and summer (Wald-$\chi^2_{1,6} = 4.8$, $p = 0.03$). Although fall accounted for less than 17% total carbon gain, invasive species made up for their earlier season deficit with greater relative fall carbon gain than native species (Wald-$\chi^2_{1,6} = 19.8$, $p = 0.003$). This trend is especially notable for *Rhamnus* and *Frangula*, and less applicable for *Berberis* which relied heavily on spring carbon gain. Overall, summer was the most important season for carbon gain, with all species acquiring over 75% of their total annual carbon during the summer.

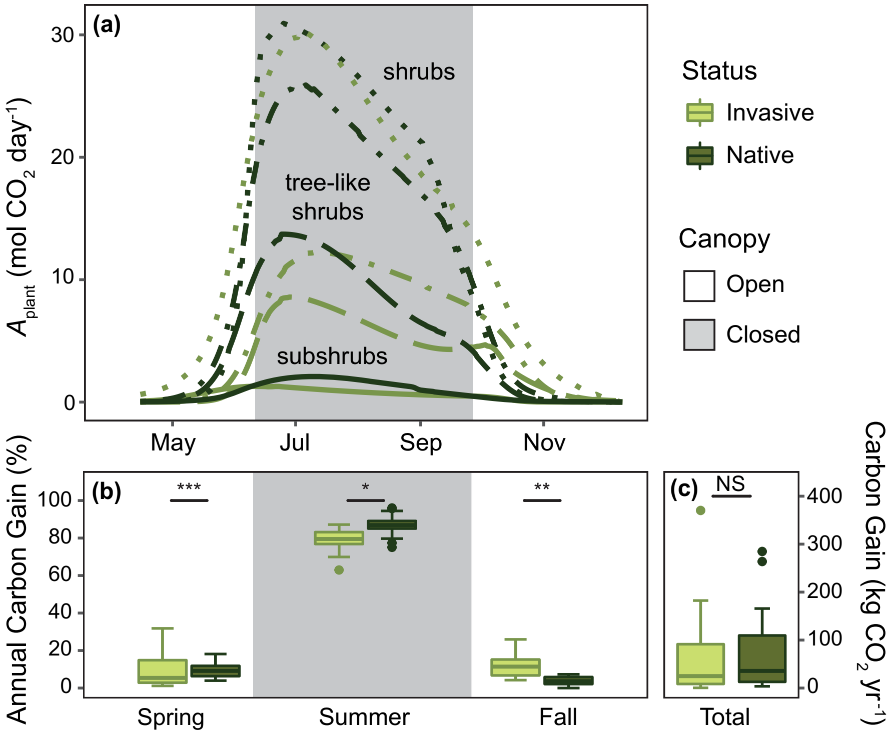

Fig. 4 **a** Modeled daily carbon gain for native (dark green) and invasive species (light green) for eight species: *Berberis* and *Rubus* (solid), *Lonicera* and *Corylus* (dotted), *Frangula* and *Viburnum* (long dash), *Rhamnus* and *Cornus* (dot dash). Background shading indicates when the canopy is > 95% closed. **b** Native species gained significantly greater proportions of their carbon in the spring and summer, while invaders made up the difference in the fall. **c** According to our model native and invasive species assimilated similar total amounts of carbon annually ($\alpha = 0.05$; ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, NS = no significant difference)

The light response curves within the carbon gain model were well represented by non-rectangular hyperbola least squares regression models (Table S6 in ESM; RMSE = 0.04–1.01 µmol CO$_2$ m^{-2} s^{-1} for young leaves, RMSE = 0.05–0.86 µmol CO$_2$ m^{-2} s^{-1} for mature leaves). Likewise, nonlinear least squares logistic models were a good fit for leaf area expansion over time (Table S7 in ESM; RMSE = 0.5–25.8 cm^2).

Of the three carbon model inputs (Fig. 2, Box 1: understory light availability, Box 2: photosynthetic light response curves, and Box 4: total leaf area), total leaf area was the best predictor of carbon gain (Table 2; leaf area total: partial F = 63.41, $p = < 0.0001$, partial $r^2 = 0.99$; A_{max} mature leaf: partial F = 8.51, $p = < 0.0001$, partial $r^2 = 0.02$). Removing leaf area from the model reduces the importance of summer carbon gain (Fig. S3 from ESM). Because total leaf area relates to growth form, species grouped by growth form in their summer daily carbon assimilation rates (Fig. 4a). The two subshrubs, *Berberis* and *Rubus*, had the smallest leaf area and the lowest daily carbon gain. Of the shrubs, *Lonicera, Cornus,* and *Corylus* exhibited the highest carbon assimilation rates due to their higher leaf counts and multi-stemmed growth form. Meanwhile, *Rhamnus, Frangula,* and *Viburnum* had fewer leaves, large single stems, and mid-level assimilation rates.

Growth traits

The invasive shrubs had similar growth rates (basal RGR and branch AGR), specific leaf area (SLA), and maximum carbon assimilation rate (A_{max}) as native species, but exhibited higher absolute branch growth rate (AGR) than native species (Fig. 5; basal RGR: $\chi^2_{1,6} = 1.9$, $p = 0.2$; branch AGR: Wald-$\chi^2_{1,6} = 5.9$, $p = 0.02$; A_{max} mature leaf: $F_{1,6} = 3.6$, $p = 0.06$; SLA: $\chi^2_{1,6} = 0.45$, $p = 0.5$).

Freezing damage

Native and invasive species had similar overall susceptibility to freezing damage (Fig. 6). The 3-parameter nonlinear least squares logistic models were well-fitted to freezing damage (Table S8 from ESM, Fig. S4 from ESM; young leaves measured with electrolyte leakage: RMSE = 14.4–21.9 percent damage; young leaves measured with chlorophyll fluorescence: RMSE = 0.08–0.17 decline in photosystem II function, Y(II); mature leaves measured with

Table 2 Multiple linear regression models for total carbon gain and freezing principle components predictors of minimum temperature

Model	Model no.	Independent variable	F-ratio	*df*	*p* value	adj. r^2	AIC
Carbon gain	1	log(total leaf area) + stem count + $\sqrt{}$plant height + spring PPFD + log(summer PPFD) + log(fall PPFD) + log(budburst date) + leaf out date + senescence date + log(A_{max} young leaf) + log(A_{max} mature leaf) + log(branch AGR) + log(SLA)	492.1	13, 26	< 0.0001	0.99	− 37.9
Carbon gain	2	log(total leaf area) + log(A_{max} mature leaf) + senescence date + log(summer PPFD)	1448	4, 42	< 0.0001	0.99	− 43.8
Carbon gain	3	log(total leaf area) + log(A_{max} mature leaf) + senescence date	1560	3, 43	< 0.0001	0.99	− 34.7
Carbon gain	4[a]	log(total leaf area) + log(A_{max} mature leaf)	2010	2, 44	< 0.0001	0.99	− 28.6
Carbon gain	5	log(total leaf area)	1525	1, 45	< 0.0001	0.97	15.2
Freezing	1	freeze PC1 + freeze PC2 + freeze PC3	6.436	3, 3	0.080	0.73	36.6
Freezing	2[a]	freeze PC1 + freeze PC2	12.18	2, 4	0.020	0.79	35.0
Freezing	3	freeze PC1	7.324	1, 5	0.042	0.51	40.4

[a] Best predictive models

chlorophyll fluorescence: RMSE = 0.13–1.49 decline in photosystem II function, Y(II)). Freezing damage was comparable between native and invasive species' young leaves assessed with electrolyte leakage ($\chi^2_{1,6} = 12$, $p = 0.07$) and chlorophyll fluorescence ($\chi^2_{1,6} = 2.1$, $p = 0.2$), and mature leaves assessed with chlorophyll fluorescence ($\chi^2_{1,6} = 3.6$, $p = 0.06$) at different temperatures. Furthermore, the temperatures at which the tissue experienced 50% of the maximum damage (LT50) did not differ between groups (young leaves measured with electrolyte leakage: $F_{1,6} = 4.5$, $p = 0.08$; young leaves measured with chlorophyll fluorescence: $F_{1,6} = 3.3$, $p = 0.1$; mature leaves measured with chlorophyll fluorescence: $F_{1,6} = 0.30$, $p = 0.6$). Average minimum temperatures at the study site during the last 50 years have not been cold enough to induce substantial freezing damage during the times of year that we measured freezing damage (Fig. 6).

The first two axes of the PCA analysis explained 71.9% of the variation in freezing tolerances (Fig. 7a). The two axes corresponded to freezing tolerance in different seasons, with PC1 and PC2 capturing variation in fall and spring freezing tolerance, respectively. The invasive and native species showed spatial separation along the second axis, which explains 26.5% of differences between species and was driven by spring freezing tolerance (young leaf electrolyte leakage and chlorophyll fluorescence). Electrolyte leakage and chlorophyll fluorescence were not correlated with each other in the spring ($t_{1,6} = -1.7$, $p = 0.9$, $r^2 = 0.005$) and exhibited opposite trends. One explanation for this pattern is that the native plants have a lower quantum efficiency because they exhibit a cold-induced photoprotective response and have sustained zeaxanthin concentrations at night (Adams et al. 1995). However, more research is needed to determine if this is the case. In the fall, freezing tolerance of mature leaves and dormant buds do show similar trends across species, though they are not correlated ($t_{1,6} = 1.6$, $p = 0.2$, $r^2 = 0.3$) and not related to invasiveness. Additionally, spring (young leaf) and fall (mature leaf and dormant bud) metrics of were not correlated across seasons.

Because the first two axes of the PCA separated out by season, we examined how phenological events and native range minimum temperatures related to freezing tolerance during each season. Leaf out date did not correlate with spring leaf freezing tolerance (PC2; $t_5 = -0.7$, $p = 0.5$, $r^2_{adj} = -0.08$) and the timing of 75% leaf senescence did not relate to fall freezing tolerance (PC1; $t_5 = -0.82$, $p = 0.4$, $r^2_{adj} = -0.05$). Instead, freezing tolerance correlated with minimum

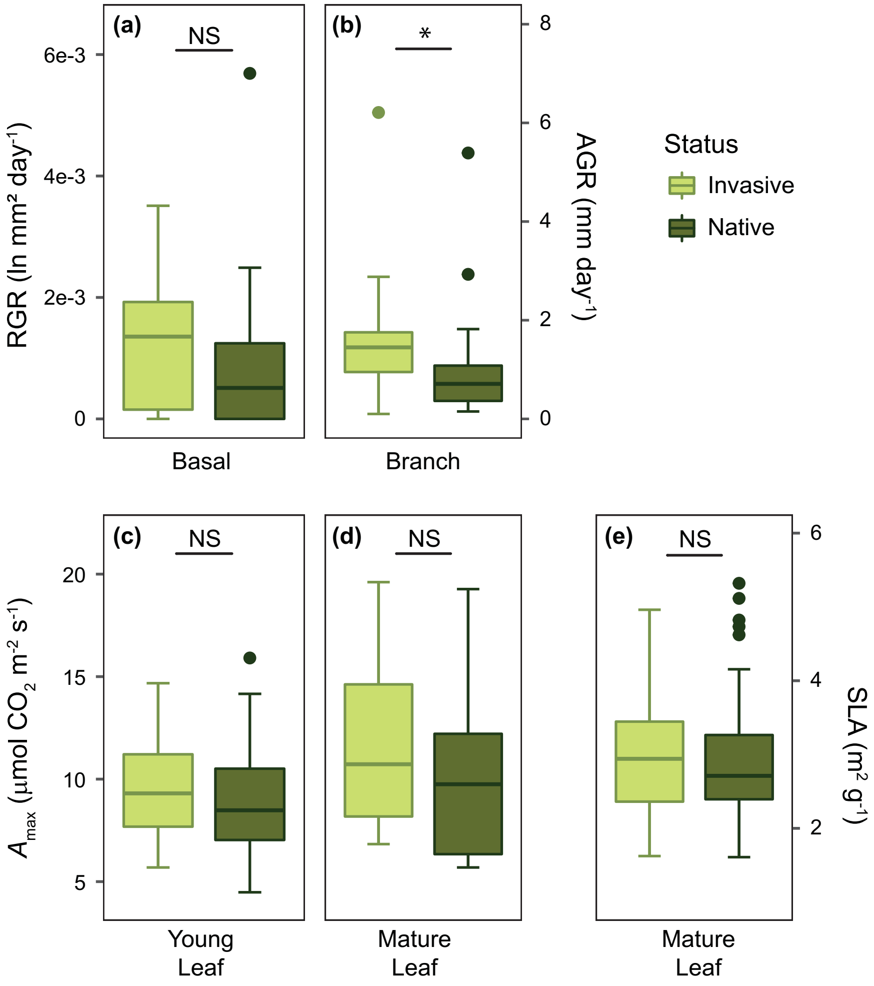

Fig. 5 Differences in growth traits between invasive (light green) and native shrubs (dark green). **b** Invasive shrubs have significantly faster branch absolute growth rate, AGR. There are no significant differences between native and invasive shrubs for **a** basal relative growth rate, RGR, maximum carbon assimilation for **c** young and **d** mature leaves, $A_{\max}$, and **e** specific leaf area of mature leaves, SLA ($\alpha = 0.05$, $*p < 0.05$, and NS = no significant difference)

temperatures in the species' native ranges. The best predictive regression model for the minimum temperature in the species' native ranges included the first two axes of the freezing tolerance PCA, though PC2 (a proxy for spring freezing tolerance) was not independently correlated with minimum temperature (Fig. 7b; Table 2; PC1: partial F = 3.20, $p = 0.03$, partial $r^2 = 0.72$; PC2: partial F = 2.7, $p = 0.05$, partial $r^2 = 0.65$). Our climate models also indicate that invasive species moved from warmer to colder climates during their invasion (Table S9 from ESM), and the occurrence data show that our study site is at the northern edge of their North American invaded ranges (Fig. S5 from ESM), while more central to the native species distributions (Fig. S6 from ESM). We excluded *Lonicera* from distribution analyses because this species resulted from a hybridization in its invasive range.

Discussion

Although invasive species retained leaves after the canopy reopened in the fall (Fig. 3), their extended leaf phenology did not result in greater total carbon gain, as compared to native associates (Fig. 4). We propose that extended leaf phenology provided no photosynthetic advantage at our site because of reduced light levels and shorter spring and fall length at the northern latitude. Instead, both groups relied on summer carbon gain, when light levels were highest in the disturbed forest of our study site (Table 3). Invasive and native species also had comparable susceptibility to freezing temperatures (Fig. 6), and we found no evidence that freezing temperatures limit the invasive species' northern distributions. In the end, the largest determinant of both susceptibility to freezing temperatures and

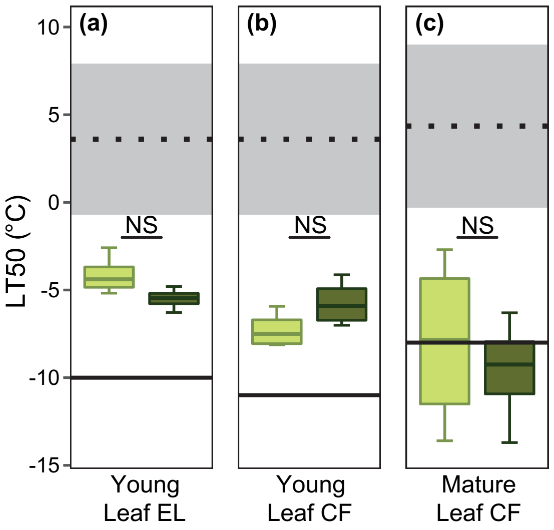

Fig. 6 The temperature at which **a**, **b** young and **c** mature leaves experienced 50% of maximum freezing damage assessed with electrolyte leakage (EL) and chlorophyll fluorescence (CF). Background shading indicates the average minimum temperatures (dashed black line, shaded area is SD) and record coldest temperature (solid black line) during the past 50 years. There was no significant difference between invasive (light green) and native (dark green) leaf freezing damage in the spring when measured with electrolyte leakage and chlorophyll fluorescence, nor in the fall, when measured with chlorophyll fluorescence ($\alpha = 0.05$ and NS = no significant difference)

phenology was geographic origin. All invasive species studied here are from Europe or Asia (or in the case of *Lonicera x bella,* their parental species), where growing seasons are inherently longer (Zohner and Renner 2017) and spring temperatures more consistent (Zohner et al. 2017). They also originated in warmer climates and their fall susceptibility to freezing temperatures correlated with the minimum temperature in their native range (Fig. 7b). These results suggest that light and geographic origin are critical to understanding the ability of invasive species to survive in northern habitats.

Extended leaf phenology may relate to geographic origin

In northern Minnesota, the four invasive shrub species we monitored only exhibited extended leaf phenology in the fall and not in the spring (Fig. 3). These results are contrary to previous observations at more southern latitudes that found early spring leaf out increased carbon gain for *Rhamnus cathartica, Lonicera x bella,* and *Berberis thunbergii* (Harrington et al. 1989; Xu et al. 2007). However, later warming at northern latitudes may force co-occurring species to leaf out within a shorter timeframe (Polgar and Primack 2011; Fahey 2016) and sometimes simultaneously with the canopy (Kwit et al. 2010). Our study is consistent with the findings of an investigation of differences in invasive species' leaf phenology across latitudes (Maynard-Bean 2019) and a comprehensive common garden study conducted in Syracuse, New York that found North American invasive species mainly extended their leaf phenology in the fall (Fridley 2012).

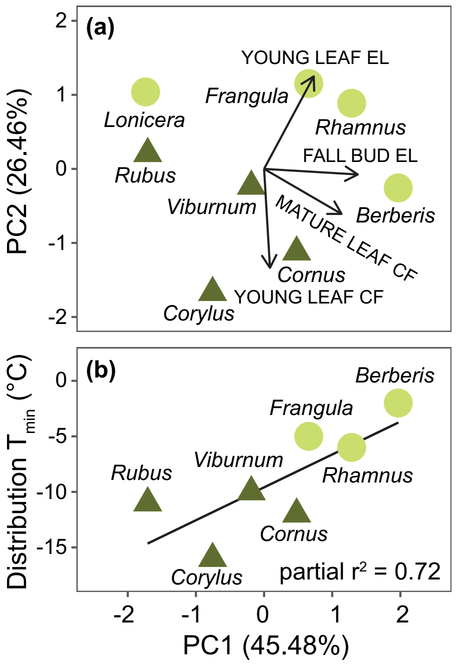

Fig. 7 **a** Principle components analysis of the lethal temperature at which the tissue experienced 50% maximum damage (LT50) of young leaves measured with electrolyte leakage (YOUNG LEAF EL), young leaves measured with chlorophyll fluorescence (YOUNG LEAF CF), mature leaves measured with chlorophyll fluorescence (MATURE LEAF CF), and dormant bud freezing damage at − 30 °C measured with electrolyte leakage (FALL BUD EL). Arrows point in the direction of greater freezing susceptibility. Invasive species (light green circles) and native species (dark green triangles) separate primarily along PC2. **b** The minimum temperature during the coldest month in each species' native distribution (Distribution T_{min}) relates to freezing tolerance (PC1). *Lonicera* was excluded because it is a hybrid and its parental species are from different native ranges (Europe and Japan)

Native geographic distributions are likely a major driver of differences in leaf phenology between native

Table 3 Understory light environment at Bagley Nature Area, Duluth, MN, USA

Understory light metric	Spring	Summer	Fall
Canopy phenology[a]	Open	Closed	Open
Canopy openness[b]	85% [47–97%]	26% [5–83%]	84% [41–100%]
Transmitted light[c]	59.3% [15.8–90.1%]	24.9% [1.37–100%]	30.03% [4.32–80.4%]
PPFD (μmol photons m^{-2} s^{-1})	265.9 [53.2–749.1]	73.38 [1.1–480.8]	33.7 [2.61–222.9]
Daily PPFD[d] (mol photons m^{-2} day^{-1})	18.4 [6.16–35.3]	16.4 [1.45–53.3]	7.2 [1.48–24.3]
Percent of total season light[e]	34%	61%	5%

[a] Canopy phenology is based on 95% of maximum canopy closure

[b] Canopy openness was calculated based on hemispherical photographs (ranges do not include transitional periods of canopy closing or opening)

[c] Transmitted light is the ratio of light (lumens s^{-1}) above the plant to light in the open, measured on cloudy days

[d] Daily PPFD measurements were taken on sunny days

[e] Total seasonal light percentages are between average budburst date and 75% senescence date. Average [min–max]

and non-native plants in this study. Plants native to North America tend to have shorter periods of seasonal growth than plants native to Europe or Asia, regardless of invasive classification (Zohner and Renner 2017). For example, *Rhamnus cathartica* exhibits similar leaf phenology to native European species where it originated (Knight et al. 2007). Because spring temperatures vary more in North America than Europe and Asia (Zohner et al. 2017), invasive plants in the United States are often more responsive to temperature cues than their native associates (Wolkovich and Cleland 2011). This plasticity could provide invasive plants with a fitness advantage under future climate conditions (Wolkovich and Cleland 2011; Cleland et al. 2012; Zohner and Renner 2014). The situation maybe be further exasperated because the invasive species in this study are native to warmer climates than their Minnesotan associates (Table S9 from ESM) and plants from southern latitudes often react more strongly to spring warming (Morin et al. 2007).

Invasive species shift the timing of their carbon assimilation

According to our carbon gain model, invasive and native species exhibited comparable total annual carbon gain but differed in their relative carbon gain during each season (Fig. 4). Invasive plants gained more carbon in the fall because they had larger leaf areas (e.g. greater number of leaves and/or larger leaves) when carbon assimilation rates were highest. Even when assuming maximum productivity (i.e., all sunny days, no self-shading within a plant, and no decline in photosystem function during the fall or at lower temperatures), extended leaf phenology did not confer much of an advantage to the invasive species in our study and only allowed them to stay competitive with the natives in terms of carbon gain. We propose these results are primarily a consequence of the short growing season and low light levels present at a northern latitude (Fig. 1). If this is the case, then invasive species with extended leaf phenology may only have a fitness advantage over native plants at more southern latitudes.

All species assimilated less than 20% of their total seasonal carbon during the spring and instead assimilated the majority (> 75%) of their carbon during the summer, when the canopy was closed (Fig. 4). This pattern is partly explained by higher light transmittance in the disturbed forest at our site than at sites with complete canopy closure (Baldocchi et al. 1984; Gill et al. 1998; Augspurger 2008; Lopez et al. 2008) or canopy closure simulated with shade cloth, such as the common garden at Syracuse (Fridley, 2012). The average light transmittance during the summer was 24.9% ± 26.7 SD because some plants were growing at the forest edge or in gaps (Table 3). Without complete canopy closure, seasonal light availability was more influenced by photoperiod and irradiance levels, rather than overstory phenology. Although our results appear contrary to studies emphasizing the importance of early spring carbon assimilation

(Harrington et al. 1989; Augspurger et al. 2005; Lopez et al. 2008; Heberling et al. 2018), we propose this discrepancy occurs partly because spring starts later and progresses more rapidly at northern latitudes, resulting in a shorter window for carbon gain prior to canopy closure (Fig. 3). In the fall, irradiance levels are lower because of rapid changes in daylength and light quality at northern latitudes (Fig. 1) and this could explain why invasive plants at our site had lower fall carbon assimilation than studies at slightly lower latitudes like Syracuse, NY (Fridley 2012).

Native and invasive species both exhibit low susceptibility to freezing temperatures

All species studied, regardless of invasive status, began to incur substantial freezing damage at temperatures lower than average observed minimum temperatures in the spring and fall (Fig. 6). We hypothesize that this pattern explains why we did not observe a relationship between spring leaf phenology and freezing damage as expected (Lenz et al. 2013; Vitasse et al. 2014a). Leaves required temperatures below − 2 °C to exhibit 50% damage (LT50) according to our electrolyte leakage and chlorophyll fluorescence measurements. In the spring these damaging temperatures are colder than temperature extremes at that time of year during the past 50 years (Fig. 6). In general, temperatures in northern Minnesota while plants have leaves are not cold enough to cause substantial damage to any of the species in our study. Instead, fall freezing tolerance across species appears to relate most strongly with the minimum temperature in their native ranges (Fig. 7b). Since all four invaders moved from warmer climates to colder climates during their North American invasion (Table S9 from ESM), they presumably evolved with weaker selective pressure for freezing tolerance. These results suggest freezing temperatures may not limit expansion north of the invasive species and could provide them with an advantage under future climatic conditions as earlier springs continue to have late freezing events.

Conclusions

To better understand invasive species' growth and physiology at the northern edge of their distributions, we investigated leaf phenology, carbon gain, growth, and freezing tolerance of invasive and native species in a disturbed forest in Northern Minnesota. The invasive species leafed out simultaneously with native species in the spring and demonstrated an equally high freezing tolerance, but retained their leaves later in the autumn. Since the invasive species assimilated less carbon during the summer than the native species, extended fall phenology in invaders was critical to maintaining competitive levels of carbon gain. However, with an extended leaf phenology and higher responsiveness to temperature changes, invaders may be able to take advantage of warming springs and longer autumns in the future (Wolkovich and Cleland 2011). This study demonstrates the importance of considering geography and latitude when studying invasive species phenology and physiology and suggests that seasonal light, and not climatic temperatures, may be more important in limiting invasive species' northern migrations. Going forward, it is critical the we consider the impact of latitude and forest structure when studying invaders' phenology and growth. Continued work in this area is needed to further elucidate what limits invasive species' northern expansion and how northern plant communities will continue to change in the future.

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Authors' contribution Study designed by EO and JS. Data collected and analyzed by EO. Manuscript written by EO and JS.

Data availability The data presented in this paper are now available online through the Data Repository for the University of Minnesota. The data can be found in Plant traits: https://doi.org/10.13020/5dp7-5a20; Understory light: https://doi.org/10.13020/mwhd-jy06; Carbon assimilation model: https://doi.org/10.13020/t9bg-vr86.

Compliance with ethical standards

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

References

Adams WI, Demmig-Adams B, Verhoeven A, Barker D (1995) "Photoinhibition" during winter stress: involvement of sustained xanthophyll cycle-dependent energy dissipation. Funct Plant Biol 22(2):261–276. https://doi.org/10.1071/PP9950261

Augspurger CK (2008) Early spring leaf out enhances growth and survival of saplings in a temperate deciduous forest. Oecologia 156(2):281–286. https://doi.org/10.1007/s00442-008-1000-7

Augspurger CK, Cheesemen JM, Salk CF (2005) Light gains and physiological capacity of understorey woody plants during phenological avoidance of canopy shade. Funct Ecol 19(4):537–546. https://doi.org/10.1111/j.1365-2435.2005.01027.x

Badeck FW, Rizza F (2015) A combined field/laboratory method for assessment of frost tolerance with freezing tests and chlorophyll fluorescence. Agronomy 5(1):71–88. https://doi.org/10.3390/agronomy5010071

Baldocchi D, Hutchison B, Matt D, McMillen R (1984) Seasonal variation in the radiation regime within an oak-hickory forest. Agric For Meteorol 33(2–3):177–191. https://doi.org/10.1016/0168-1923(84)90069-8

Beckschäfer P (2015) Hemispherical_2.0 Batch processing hemispherical and canopy photographs with ImageJ—user manual. https://doi.org/10.13140/rg.2.1.3059.4088

Boorse CG, Bosma TL, Meyer AC, Ewers FW, Davis SD (1998) Comparative methods of estimating freezing temperatures and freezing injury in leaves of chaparral shrubs. Int J Plant Sci 159(3):513–521. https://doi.org/10.1086/297568

Cleland EE, Allen JM, Crimmens TM, Dunne JA, Pau S, Travers SE, Zavaleta ES, Wolkovich EMW (2012) Phenological tracking enables positive species responses to climate change. Ecology 93(8):1765–1771. https://doi.org/10.1890/11-1912.1

Corripio JG (2003) Vectorial algebra algorithms for calculating terrain parameters from DEMs and the position of the sun for solar radiation modelling in mountainous terrain. Int J Geogr Inf Sci 17(1):1–23. https://doi.org/10.1080/713811744

Cunard C, Lee TD (2009) Is patience a virtue? Succession, light, and the death of invasive glossy buckthorn (*Frangula alnus*). Biol Invasions 11(3):577–586. https://doi.org/10.1007/s10530-008-9272-8

Davis SD, Sperry JS, Hacke UG (1999) The relationship between xylem conduit diameter and cavitation caused by freezing. Am J Bot 86(10):1367–1372. https://doi.org/10.2307/2656919

Dawson W, Fischer M, van Kleunen M (2011) The maximum relative growth rate of common UK plant species is positively associated with their global invasiveness. Glob Ecol Biogeogr 20(2):299–306. https://doi.org/10.1111/j.1466-8238.2010.00599.x

Fahey RT (2016) Variation in responsiveness of woody plant leaf out to anomalous spring onset. Ecosphere 7(2):1–15. https://doi.org/10.1002/ecs2.1209

Fan Z, Moser WK, Hansen MH, Nelson MD (2013) Regional patterns of major nonnative invasive plants and associated factors in upper midwest forests. For Sci 59(1):38–49. https://doi.org/10.5849/forsci.10-100

Fick SE, Hijmans RJ (2017) Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol 37(12):4302–4315. https://doi.org/10.1002/joc.5086

Flint HL, Boyce BR, Beattie DJ (1967) Index of injury: a useful expression of freezing injury to plant tissues as determined by the electrolytic method. Can J Plant Sci 47(2):229–230. https://doi.org/10.4141/cjps67-043

Frazer GW, Trofymow JA, Lertzman KP (1997) A method for estimating canopy openness, effective leaf area index, and photosynthetically active photon flux density using hemispherical photography and computerized image analysis techniques. Canadian Forest Service, Forest Ecosystem Processes Network. http://www.cfs.nrcan.gc.ca/pubwarehouse/pdfs/4867.pdf

Fridley JD (2012) Extended leaf phenology and the autumn niche in deciduous forest invasions. Nature 485:359–364. https://doi.org/10.1038/nature11056

Fridley JD, Craddock A (2015) Contrasting growth phenology of native and invasive forest shrubs mediated by genome size. New Phytol 207:659–668. https://doi.org/10.1111/nph.13384

Friedman JM, Roelle JE, Gaskin JF, Pepper AE, Manhart JR (2008) Latitudinal variation in cold hardiness in introduced *Tamarix* and native *Populus*. Evol Appl 1(4):598–607. https://doi.org/10.1111/j.1752-4571.2008.00044.x

GBIF.org (2018) GBIF Home Page. https://www.gbif.org. Accessed 8 Jun 2018

Gill DS, Amthor JS, Bormann FH (1998) Leaf phenology, photosynthesis, and the persistence of saplings and shrubs in a mature northern hardwood forest. Tree Physiol 18(5):281–289. https://doi.org/10.1093/treephys/18.5.281

Grotkopp E, Rejmánek M, Rost TL (2002) Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. Am Nat 159(4):396–419. https://doi.org/10.1086/338995

Harrington RA, Brown BJ, Reich PB (1989) Ecophysiology of exotic and native shrubs in Southern Wisconsin. Oecologia 80(3):356–367. https://doi.org/10.1007/BF00379037

Heberling JM, Fridley JD (2013) Resource-use strategies of native and invasive plants in Eastern North American forests. New Phytol 200(2):523–533. https://doi.org/10.1111/nph.12388

Heberling JM, Cassidy ST, Fridley JD, Kalisz S (2018) Carbon gain phenologies of spring-flowering perennials in a deciduous forest indicate a novel niche for a widespread invader. New Phytol 221(2):778–788. https://doi.org/10.1111/NPH.15404

IPNI (2018). International Plant Names Index. The Royal Botanic Gardens, Kew, Harvard University Herbaria & Libraries and Australian National Botanic Gardens. http://www.ipni.org. Retrieved 8 June 2018

Knight KS, Kurylo JS, Endress AG, Stewart JR, Reich PB (2007) Ecology and ecosystem impacts of common buckthorn (*Rhamnus cathartica*): a review. Biol Invasions 9(8):925–937. https://doi.org/10.1007/s10530-007-9091-3

Koehler K, Center A, Cavender-Bares J (2012) Evidence for a freezing tolerance-growth rate trade-off in the live oaks (*Quercus* series *Virentes*) across the tropical-temperate divide. New Phytol 193(3):730–744. https://doi.org/10.1111/j.1469-8137.2011.03992.x

Kurylo JS, Knight KS, Stewart JR, Endress AG (2007) *Rhamnus cathartica*: native and naturalized distribution and habitat preferences. J Torrey Bot Soc 134(3):420–430. https://doi.org/10.3159/1095-5674(2007)134%5b420:rcnand%5d2.0.co;2

Kwit MC, Rigg LS, Goldblum D (2010) Sugar maple seedlings carbon assimilation at the northern limit of its range: the importance of seasonal light. Can J For Res 40(2):385–393. https://doi.org/10.1139/X09-196

Lappi J, Stenberg P (1998) Joint effect of angular distribution of radiation and spatial pattern of trees on radiation interception. Ecol Model 112(1):45–51. https://doi.org/10.1016/S0304-3800(98)00112-4

Lenz A, Hoch G, Vitasse Y, Körner C (2013) European deciduous trees exhibit similar safety margins against damage by spring freeze events along elevational gradients. New Phytol 200(4):1166–1175. https://doi.org/10.1111/nph.12452

Lieurance D, Landsbergen K (2016) The influence of light habitat on the physiology, biomass allocation, and fecundity of the invasive shrub Amur honeysuckle (*Lonicera maackii*, Caprifoliaceae). J Torrey Bot Soc 143(4):415–426. https://doi.org/10.3159/TORREY-D-15-00056.1

Long MH, Rheuban JE, Berg P, Zieman JC (2012) A comparison and correction of light intensity loggers to photosynthetically active radiation sensors. Limnol Oceanogr Methods 10(6):416–424. https://doi.org/10.4319/lom.2012.10.416

Lopez OR, Farris-Lopez K, Montgomery RA, Givnish TJ (2008) Leaf phenology in relation to canopy closure in southern Appalachian trees. Am J Bot 95(11):1395–1407. https://doi.org/10.3732/ajb.0800104

Luken JO, Tholemeier TC, Kuddes LM, Kunkel BA (1995) Performance, plasticity, and acclimation of the nonindigenous shrub *Lonicera maackii* (Caprifoliaceae) in contrasting light environments. Can J Bot 73(12):1953–1961. https://doi.org/10.1139/b95-208

Luken JO, Kuddes LM, Tholemeier TC, Haller DM (1997) Comparative responses of *Lonicera maackii* (Amur honeysuckle) and *Lindera benzoin* (spicebush) to increased light. Am Midl Nat 138(2):331–343. https://doi.org/10.2307/2426826

Marshall B, Biscoe PV (1980) A model for C_3 leaves describing the dependence of net photosynthesis on irradiance. J Exp Bot 31(1):29–39. https://doi.org/10.1093/jxb/31.1.29

Martinez KA, Fridley JD (2018) Acclimation of leaf traits in seasonal light environments: are non-native species more plastic? J Ecol 106(5):2019–2030. https://doi.org/10.1111/1365-2745.12952

Maynard-Bean, E (2019) Shedding light on invasive shrubs in eastern deciduous forests of North America. Dissertation, Pennsylvania State University

McEwan RW, Birchfield MK, Schoergendorfer A, Arthur MA (2009) Leaf phenology and freeze tolerance of the invasive shrub Amur honeysuckle and potential native competitors. J Torrey Bot Soc 136(2):212–220. https://doi.org/10.3159/08-RA-109.1

Meiners SJ, Pickett STA, Cadenasso ML (2002) Exotic plant invasions over 40 years of old field successions: community patterns and associations. Ecography 25(2):215–223. https://doi.org/10.1034/j.1600-0587.2002.250209.x

Menne MJ, Durre I, Korzeniewski B, McNeal S, Thomas K, Yin X, Anthony S, Ray R, Vose RS, Gleason BE, Houston TG (2012) Global historical climatology network - daily (Version 3.24). NOAA National Climatic Data Center. https://doi.org/10.7289/v5d21vhz. Retrieved 15 Nov 2018

Menne MJ, Durre I, Vose RS, Gleason BE, Houston TG (2012b) An overview of the global historical climatology network-daily database. J Atmos Ocean Technol 29:897–910. https://doi.org/10.1175/JTECH-D-11-00103.1

Merow C, Treaner Bois S, Allen JM, Xei Y, Silander JA Jr (2017) Climate change both facilitates and inhibits invasive plant ranges in New England. Proc Natl Acad Sci USA 114(16):E3276–E3284. https://doi.org/10.1073/pnas.1609633114

Miyashita A, Sugiura D, Sawakami K, Ichihashi R, Tani T, Tateno M (2012) Long-term, short-interval measurements of the frequency distributions of the photosynthetically active photon flux density and net assimilation rate of leaves in a cool-temperate forest. Agric For Meteorol 152:1–10. https://doi.org/10.1016/j.agrformet.2011.08.001

Morecroft MD, Stokes VJ, Morison JIL (2003) Seasonal changes in the photosynthetic capacity of canopy oak (*Quercus robur*) leaves: the impact of slow development on annual carbon uptake. Int J Biometeorol 47:221–226. https://doi.org/10.1007/s00484-003-0173-3

Morin X, Augspurger C, Chuine I (2007) Process-based modeling of species' distributions: what limits temperate tree species' range boundaries? Ecology 88(9):2280–2291. https://doi.org/10.1890/06-1591.1

Moussus JP, Julliard R, Jiguet F (2010) Featuring 10 phenological estimators using simulated data. Methods Ecol Evol 1(2):140–150. https://doi.org/10.1111/j.2041-210x.2010.00020.x

Panchen ZA, Primack RB, Nordt B, Ellwood ER, Stevens AD, Renner SS, Willis CG, Fahey R, Whittemore A, Yanjun D, Davis CC (2014) Leaf out times of temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy. New Phytol 203(4):1208–1219. https://doi.org/10.1111/nph.12892

Panchen ZA, Primack RB, Gallinat AS, Nordt B, Stevens AD, Du Y, Fahey R (2015) Substantial variation in leaf senescence times among 1360 temperate woody plant species: implications for phenology and ecosystem processes. AoB Plants 116(6):865–873. https://doi.org/10.1093/aob/mcv015

Parent S, Messier C (1996) A simple and efficient method to estimate microsite light availability under a forest canopy. Can J For Res 26(1):151–154. https://doi.org/10.1139/x26-017

Perez R (2007) National solar radiation database 1991–2005 update: user's manual

Phillips SJ, Dudík M, Schapire RE. Maxent software for modeling species niches and distributions (Version 3.4.1) http://biodiversityinformatics.amnh.org/open_source/maxent/. Retrieved 8 Jun 2018

Polgar CA, Primack RB (2011) Leaf-out phenology of temperate woody plants: from trees to ecosystems. New Phytol

191(4):926–941. https://doi.org/10.1111/j.1469-8137.2011.03803.x

Pretorius A (2015) Role of leafing phenology in the invasion of forest ecosystems by *Rhamnus cathartica*. Master thesis, University of Minnesota, Minneapolis, Minnesota, USA. Retrieved from https://conservancy.umn.edu/handle/11299/172621

Reich PB (2014) The world-wide "fast-slow" plant economics spectrum: a traits manifesto. J Ecol 102(2):275–301. https://doi.org/10.1111/1365-2745.12211

Sakai A, Larcher W (1987) Ecological studies, frost survival of plants: responses and adaptation to freezing stress, 1st edn, vol 62. Springer, Berlin. https://doi.org/10.1007/bf02854542

Sanford NL, Harrington RA, Fownes JH (2003) Survival and growth of native and alien woody seedlings in open and understory environments. For Ecol Manage 183(1–3):377–385. https://doi.org/10.1016/S0378-1127(03)00141-5

Savage JA, Cavender-Bares J (2013) Phenological cues drive an apparent trade-off between freezing tolerance and growth in the family Salicaceae. Ecology 94(8):1708–1717. https://doi.org/10.1890/12-1779.1

Schierenbeck KA, Marshall JD (1993) Seasonal and diurnal patterns of photosynthetic gas exchange for *Lonicera sempervirens*. Appl Plant Sci 80(11):1292–1299. https://doi.org/10.1002/j.1537-2197.1993.tb15367.x

Silander JA, Klepeis DM (1999) The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape. Biol Invasions 1(2–3):189–201. https://doi.org/10.1023/A:1010024202294

Smith LM (2013) Extended leaf phenology in deciduous forest invaders: mechanisms of impact on native communities. J Veg Sci 24(6):979–987. https://doi.org/10.1111/jvs.12087

Smith MS, Fridley JD, Yin J, Bauerle TL (2013) Contrasting xylem vessel constraints on hydraulic conductivity between native and non-native woody understory species. Front Plant Sci 4:486. https://doi.org/10.3389/fpls.2013.00486

Stewart JR, Graves WR, Landes RD (2006) Cold hardiness and vernal budbreak of *Rhamnus caroliniana* and the nvasive *Rhamnus cathartica*. J Am Soc Hortic Sci 131(3):345–351. https://doi.org/10.21273/JASHS.131.3.345

Thalhammer A, Hincha DK, Zuther E (2014) Measuring freezing tolerance: electrolyte leakage and chlorophyll fluorescence assays. Methods Mol Biol 1166:15–24. https://doi.org/10.1007/978-1-4939-0844-8_3

Vitasse Y, Baslzr D, Way D (2014a) Is the use of cuttings a good proxy to explore phenological responses of temperate forests in warming and photoperiod experiments? Tree Physiol 34(2):174–183. https://doi.org/10.1093/treephys/tpt116

Vitasse Y, Lenz A, Körner C, Wisniewski M, Arora R (2014b) The interaction between freezing tolerance and phenology in temperate deciduous trees. Front Plant Sci 5:1–12. https://doi.org/10.3389/fpls.2014.00541

WCSP (2018) World checklist of selected plant families. Facilitated by the Royal Botanic Gardens, Kew. http://apps.kew.org/wcsp/. Retrieved 8 June 2018

Wilson KB, Baldocchi DD, Hanson PJ (2001) Leaf age affects the seasonal pattern of photosynthetic capacity and net ecosystem exchange of carbon in a deciduous forest. Plant, Cell Environ 24(6):571–583. https://doi.org/10.1046/j.0016-8025.2001.00706.x

With KA (2002) The landscape ecology of invasive spread. Conserv Biol 16(5):1192–1203. https://doi.org/10.1046/j.1523-1739.2002.01064.x

Wolkovich EM, Cleland EE (2011) The phenology of plant invasions: a community ecology perspective. Front Ecol Environ 9(5):287–294. https://doi.org/10.1890/100033

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulia J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Olesksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov V, Roumet C, Thomas SC, Tjoelker M, Veneklaas E, Villar R (2004) The worldwide leaf economics spectrum. Nature 428(6985):821–827. https://doi.org/10.1038/nature02403

Xu CY, Griffin KL, Schuster WSF (2007) Leaf phenology and seasonal variation of photosynthesis of invasive *Berberis thunbergii* (Japanese barberry) and two co-occurring native understory shrubs in a northeastern United States deciduous forest. Oecologia 154(1):11–21. https://doi.org/10.1007/s00442-007-0807-y

Yin J, Fridley JD, Smith MS, Bauerle TL (2016) Xylem vessel traits predict the leaf phenology of native and non-native understorey species of temperate deciduous forests. Funct Ecol 30:206–214. https://doi.org/10.1111/1365-2435.12476

Zohner CM, Renner SS (2014) Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change. Ecol Lett 17(8):1016–1025. https://doi.org/10.1111/ele.12308

Zohner CM, Renner SS (2017) Innately shorter vegetation periods in North American species explain native–non-native phenological asymmetries. Nat Ecol Evol 1(11):1655–1660. https://doi.org/10.1038/s41559-017-0307-3

Zohner CM, Benito BM, Fridley JD, Svenning JC, Renner SS (2017) Spring predictability explains different leaf-out strategies in the woody floras of North America, Europe and East Asia. Ecol Lett 20(4):452–460. https://doi.org/10.1111/ele.12746