To spend or to save? Assessing energetic growth-storage tradeoffs in native and invasive woody plants

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Abstract
Many non-native woody plants invade low-light forest understories but differ from native species in leaf phenology and seasonality of photosynthesis. It is unknown whether such differences in assimilation patterns are due to contrasting strategies of energy allocation. In a group of native and invasive species in Eastern North America, we hypothesized that invaders employ a grow-first strategy, prioritizing allocation to new structural biomass over carbon storage compared to native congeneres. We also hypothesized that species producing a single spring leaf flush exhibit a more conservative carbon storage strategy than species with continuous leaf production. We measured sugar and starch concentrations (non-structural carbohydrates; NSCs) in spring and fall in the stems and roots of 39 species of native and non-native shrubs in a common garden, and compared these to patterns of leaf production across species. Native species had higher soluble sugar concentrations than invaders, but invaders tended to store more root starch in spring. We found no difference in leaf production between natives and invaders. Determinate species had more soluble sugars than indeterminate species but had lower root starch. We found no relationship between aboveground productivity and carbon storage. Our results suggest that closely related species with contrasting evolutionary histories have different carbon storage strategies, although not necessarily in relation to their growth potential. The higher soluble sugar concentrations of native species may reflect their evolutionary response to historical disturbances, or different interactions with soil microbes, while increased spring root starch in invaders may support fine root or fruit production.

Keywords Carbon allocation · Invasions · Nonstructural carbohydrates · Survival · Seasonal

Introduction
Identifying resource-use strategies of invasive species, and whether they differ predictably from those of co-occurring natives, is a primary objective in invasion biology because it underlies how invasions occur and whether invaders impact ecosystems (Rejmanek and Richardson 1996; Daehler 2003; Funk and Vitousek 2007; Leishman et al. 2010; Funk 2013). Non-native, invasive plants are often more productive than co-occurring native species, even in low resource environments (Funk and Vitousek 2007; Liao et al. 2008; van Kleunen et al. 2010b). For example, in light-limited deciduous forest understories of Eastern North America (ENA), invasive woody species from East Asia (EAS) and Europe (EUR) maintain photosynthetically active leaves for nearly a month longer than native species, which affords them both higher annual carbon gain and higher resource-use efficiencies (Fridley 2012; Heberling and Fridley 2013; Jo et al. 2015; Gallinat et al. 2015; Heberling et al. 2016). Why do
co-occurring native species not share this high assimilation and growth strategy? One unexplored hypothesis is that native species have evolved a strategy of increased energy storage over growth allocation, which may be advantageous in environments subject to unpredictable disturbances such as extreme weather events (Philippi and Seger 1989; Chapin et al. 1990; Zohner et al. 2017). For example, Zohner et al. (2017) showed that ENA woody deciduous species have delayed spring leaf emergence compared to phylogenetically related species of EAS and EUR, which is associated with higher historical spring temperature variability in ENA. In this context, extreme weather events may have shaped a carbon allocation strategy in ENA lineages that is biased toward storage, constraining their growth phenology to greater extent than those of EAS and EUR (Chapin et al. 1990). Although such carbon stores could confer increased resistance (e.g., freezing protection) and recovery from disturbances (e.g., energy reserves) in native species, they may come at a cost of reduced growth potential if storage and growth are competitive processes (Wiley and Helliker 2012). Other carbon pools, like reproduction, belowground production or defense allocation, could mediate the growth-storage relationship. To our knowledge, the potential for different growth-storage strategies in native and invasive species has not yet been examined.

Soluble sugar and starch [collectively termed non-structural carbohydrates (NSCs)] have myriad roles in plant survival, reproduction, and growth (Dietze et al. 2014). Deciduous species retain large pools of NSCs in winter to support the onset of spring leaf production (Chapin et al. 1990). Following spring leaf production, most species also maintain storage pools to recover from tissue damage due to herbivory, pathogen attack, or extreme weather events (Kozlowski 1992; Kobe 1997). Additionally, NSCs are stored over short periods in roots as a supply to mycorrhizal fungi and/or symbiotic or free-living bacteria in exchange for limiting nutrients (Karst et al. 2016). Carbohydrates travel between plant organs as soluble sugars (Kozlowski 1992), which are also involved in stem freezing protection, both as osmotic solutes and as signaling molecules (Sakai and Yoshida 1968; Ruan 2014). When plant growth is limited, however, newly assimilated carbohydrates may passively accumulate in tissues, and plants may use these carbohydrates for survival when demand exceeds supply (Palacio et al. 2013). We hypothesize that the various roles of NSCs promoting survival suggest that their concentration should be higher in ENA-native lineages shaped by a greater degree of spring weather variability compared to EUR and EAS invaders (Zohner et al. 2017). Alternatively, the greater carbon gain observed in many invaders (Heberling and Fridley 2013) may promote more passive accumulation of NSCs if non-photosynthetic growth limitation (e.g., cold) affects neighboring species equally.

Because carbon in plant tissues accumulates as a function of both supply (photosynthesis) and demand (growth, respiration) processes, there are other woody plant attributes that influence seasonal and tissue-specific NSC concentrations. In particular, structural growth in many species is seasonally restricted: ‘determinate’ (flush-type) species produce their entire canopy over a brief period at the beginning of the growing season, while ‘indeterminate’ (continuously leafing) species produce their leaves sequentially or in multiple flushes throughout the growing season (Lechowicz 1984). The lack of midseason allocation to aboveground structural growth in determinate species suggests they should accumulate NSCs to a greater extent than indeterminate species, reaching a maximum in winter before spring leaf emergence. Interestingly, the determinate leafing strategy is relatively rare in invasive species compared to ENA natives (Fridley and Craddock 2015; Martinez and Fridley, unpublished) and is likely associated with an overall carbon allocation strategy biased toward fast growth (see also Iwasa and Cohen 1989). However, there are several widespread invaders in ENA with a determinate leafing habitat (e.g., Euonymus alatus), and, given the likely strong role of growth determinacy in NSC levels, it is important to control for such dynamics in native-invader NSC comparisons.

We measured leaf production and seasonal carbon storage in a group of woody species found in temperate deciduous forests of ENA to understand how carbon allocation strategies differ between native and non-native invasive species. We hypothesized that a tradeoff between growth and storage explains potential productivity differences between natives and invaders (Heberling and Fridley 2013). In particular, we hypothesized that ENA native lineages are better adapted to historical disturbance regimes, including extreme events such as late spring frosts, which is most apparent in stem and root soluble sugars following spring leaf production when storage levels in deciduous species are at their annual minimum (Martinez-Vilalta et al. 2016). Remaining stores are available for new leaf production following damage. Alternatively, allocation to reproduction, defenses, or belowground production could mask the relationship between leaf production and carbohydrate storage. Because native species begin leaf senescence on average 28 days earlier than invaders (Fridley 2012), we also hypothesized that they allocate more soluble sugars to stems in autumn for freezing protection. In addition, we hypothesized that, independent of nativity, determinate species store more soluble sugars and starch at the end of the growing season than indeterminate species, in which NSCs fuel new (current season) leaf production. We tested these hypotheses using common garden measurements of leaf production and shoot phenology, along with stem and root soluble sugar and starch samples from phylogenetically paired native and non-native invasive species.
Materials and methods

We studied 39 species of native and non-native woody shrubs in a common garden at Syracuse University, Syracuse, New York, USA (Table 1). The common garden was established in 2006 and is composed of three replicate blocks per species. To the extent possible, we selected congeneric native/non-native pairs from 13 plant genera. Of the 21 non-native species, 17 are considered invasive in ENA, that is, spreading quickly and having demonstrable impacts on native species or ecosystem properties (Fridley 2008). The remaining four are naturalized; i.e., they survive in natural habitats but have not yet been documented to spread. Because past studies of this group showed that naturalized species tend to exhibit similar traits as invaders (Fridley 2012; Heberling and Fridley 2013; Fridley and Craddock 2015; Yin et al. 2015), for simplicity we treat both naturalized and invasive species as 'invaders' throughout the manuscript.

Table 1  Focal species along with taxonomic family, nativity status (Fridley 2008), and leaf production habit

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Invasive status</th>
<th>Species acronym</th>
<th>Leaf determinacy</th>
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<td>VIPR</td>
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<td>RHCA</td>
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<td></td>
<td>Rhamnus davurica</td>
<td>Naturalized</td>
<td>RHDA</td>
<td>Determine</td>
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</tbody>
</table>
We examined leaf production and phenology across species in 2008–2010, prior to destructive tissue harvests for NSCs in 2013–2014 on the same individuals. We defined an individual’s productivity as the maximum number of leaves produced over the growing season in five randomly selected branches per plant across years (2008–2010), multiplied by its mean dry leaf mass. *Cornus racemosa* individuals were growing adjacent to the common garden and their measurements did not include productivity. Patterns of seasonal leaf production and senescence from 2008 to 2010 in the same individuals (Fridley 2012) were used to categorize species’ leafing behaviors as determinate or indeterminate. Species that produced 90% of their leaves prior to June 15 were considered determinate, and indeterminate otherwise.

We collected stem and root samples (total *N* = 639) from three individuals per species following leaf drop in November/December 2013 and following full leaf expansion in May/June 2014. We sampled new (2013) and year-old (2012) stems separately. At each sampling event, we collected three stems of each age from each individual, and two root samples from the root crown. Three native species without invasive congeners (*Cornus florida, Cornus racemosa,* and *Hydrangea arborescens*) were only sampled in the fall, and invaders *Elaeagnus angustifolia* and *Frangula alnus* had no spring stems sampled. Samples were placed in a cooler of dry ice and stored at −80 °C. We freeze-dried tissue samples for 48 h prior to grinding samples to fit through a 40-mesh screen (Thomas Scientific Mini Wiley Mill, Swedesboro, NJ, USA). Ground samples were stored at 4 °C until analysis.

Soluble sugar and starch concentrations were determined using a combination of near-infrared spectroscopy and colorimetric methods following Ramirez et al. (2015). All samples were run through a near-infrared spectrometer (Bruker MPA Multi-purpose FT-NIR analyzer, Ettlingen, Germany) and their absorbances measured between 1300 and 2650 nm (Curran 1989). A subset of 98 of the 639 samples was selected for NSC analysis using the Kennard-Stone algorithm (Kennard and Stone 1969) on NIR spectra. The Kennard-Stone algorithm composes a representative subset by first selecting the two most distant samples from one another in parameter space. It continues selecting additional samples based on their maximum distance from the closest sample already included in the subset. These samples were used to calibrate NSC concentrations determined by wet chemistry to the NIR spectra.

We measured soluble sugar and starch (NSC) concentrations in the calibration sample set using the colorimetric method of Chow and Landhausser (2004). Briefly, soluble sugars were extracted using ethanol and phenol–sulfuric acid and sample absorbance was measured at 490 nm on a microplate reader (BioTek Instruments, Inc, Winooski, VT). Starches were broken down to glucose equivalents using alpha-amylase and amyloglucosidase enzymes, and then treated with PGO color solution + o-dianisidine for spectral analysis at 525 nm. NSC concentrations determined colorimetrically were calibrated with the near-infrared spectra using partial least squares (PLS) regression. The number of components used in the PLS model was determined by the component axis with the minimum coefficient of variation (Ramirez et al. 2015). This calibration model (see Supplementary Materials) was used to estimate the soluble sugar and starch concentrations of the entire sample dataset. We ran 500 iterations of a bootstrapping algorithm that sampled the calibration dataset with replacement and used these values to fit the PLS model to our sample dataset. We then estimated the standard error for each sample and incorporated these values into our statistical models as observation error (see below).

We compared soluble sugar and starch concentrations across species, seasons, and tissues using hierarchical Bayesian regression models (Fridley and Craddock 2015). Because we found no significant differences in NSCs between new and year-old stems (analysis not shown), we took the mean starch and soluble sugar concentrations across stem ages (*N* = 423 samples). Models included a phylogenetic variance–covariance matrix to account for the correlation of observations due to common descent (de Vilmereuil et al. 2012), using the approach and phylogeny of Jo et al. (2016). Pagel’s λ was used to estimate phylogenetic signal, scaled from 0 (phylogenetic independence) to 1 (Brownian evolution). We first examined the main effect of nativity (0 = invasive, 1 = native) on leaf production, accounting for phylogenetic relatedness. We then used separate models predicting soluble sugars and starches using the same phylogenetic correction (see Supplementary Materials). One set of models compared the overall effect of nativity to the main effects of season (0 = fall, 1 = spring), tissue type (0 = root, 1 = stem), determinacy (0 = indeterminate, 1 = determinate), and productivity (continuous) on sugar and starch concentrations. We also separated sugar and starch concentrations by season and tissue type to test for nativity and determinancy differences in stem and root storage in specific seasons, resulting in eight additional models. The latter models included tissue diameter to account for differences in NSC concentrations by organ size. We scaled continuous variables to make their effect sizes comparable to categorical variables by subtracting the mean and dividing by two standard deviations (Gelman and Hill 2007). We included observation error as a normal random intercept of mean zero and known standard deviation from the bootstrapped standard error of each NSC observation. All models were run in R (R Core Team 2016) using the R2jags package (Su and Yajima 2015). We ran three Markov chain Monte Carlo (MCMC) chains for 10,000 iterations (after 3000 burn-in) in the productivity model, 30,000 iterations (after 5000 burn-in) in the overall models, and 10,000 iterations (after 3000 burn-in) in tissue...
and season-specific models (with the exception of the spring stem starch model, which required 50,000 iterations with 10,000 burn-in). Model convergence was determined by the Gelman–Rubin (1992) convergence diagnostic (Rhat < 1.1).

We performed a principal components analysis (PCA) to describe relationships between NSC concentrations, productivity, leaf determinacy, and nativity. We used a MANOVA of mean species PC scores from the first and second components to test for multivariate differences between natives and invaders. We used ‘prcomp’ and ‘manova’ from the base R package for these analyses (R Core Team 2016).

**Results**

Natives and invaders did not differ in leaf production (Fig. 1). In an overall model comparing main effects of nativity, season, tissue type, growth determinacy, and productivity, we found strong effects of all factors except productivity on plant soluble sugar and starch concentrations (Fig. 2). Native species overall had significantly higher concentrations of soluble sugars (Fig. 3), as did determinate species of both native and invasive groups (Fig. 4). Starch concentrations showed the opposite pattern with respect to nativity and determinacy (Fig. 2), although their effect sizes were small in relation to root-stem differences (Figs. 3, 4). Effect sizes of nativity and determinacy were similar in magnitude to the effects of season and tissue type on soluble sugar concentrations (Fig. 2), and leaf production was neither associated with sugar nor starch concentrations across species. Post-leafout (spring) NSC levels were lower than fall levels for all species (Figs. 3, 4).

Nativity and determinacy patterns of NSCs were similar when examined separately by season and tissue type (Figs. 3, 4). The bias of soluble sugars in natives did not depend on season and had similar effect sizes in roots and stems (Fig. 3), nor did the greater sugars in determinate species depend on season or tissue type (Fig. 4). Indeterminate species had substantially larger root starch concentrations in both spring and fall (Fig. 4), but the starch bias in invaders was only significant in spring (Fig. 3). We detected only weak phylogenetic signal in the relationships between seasonal storage, nativity, and determinacy (λ < 0.3).

Species-level NSC patterns are shown in Supplemental Fig. 1. Native species including *Rhamnus alnifolia* and *Euonymus obovatus* had the highest stem NSC concentrations across seasons, while natives *Sambucus racemosa* and *Viburnum lentago*, and invaders *Euonymus phellomanus* and *Lonicera japonica*, consistently had the lowest stem NSCs. *Sambucus racemosa* had the highest root NSCs across seasons. The native *Euonymus atropurpureus* also had very high root NSCs across seasons, but was intermediate for stem NSCs. With the exception of spring stem concentrations, the native N-fixer *Elaeagnus commutata* consistently ranked near the bottom in NSC concentrations. Spring stem rankings reflected leaf determinacy, with indeterminate

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**Fig. 1** Mean leaf production and total % NSC (stem + root) in native (white circles) and invasive (black circles) species in a spring and b fall. Error bars represent ± one standard error. Refer to Table 1 for species acronyms.
Fig. 2 95% (thin lines) and 80% (thick lines) credible intervals for posterior coefficients of nativity, season, tissue type, leaf determinacy, and productivity in a overall soluble sugar and b starch models. Season had the strongest effect on soluble sugars—spring concentrations were significantly lower than fall concentrations, while tissue type was the strongest determinant of starch concentration—stems had lower starch concentrations than roots. Native species and determinate species had higher soluble sugar concentrations than invaders and indeterminate species, respectively, but indeterminate species had higher starch concentrations.

Fig. 3 Mean soluble sugar and starch concentrations in native and invasive species in a spring stems (N=53 invaders, 41 natives), b fall stems (69, 49), c spring roots (60, 44), and d fall roots (68, 45). Error bars represent ± SEM. “*” indicates that 95% of the posterior distribution of the native-invader difference did not include zero.
species occurring primarily at the low end of the spectrum (Figure S1a), while fall stem and root rankings exhibited native dominance at the highest NSC concentrations (Figure S1 b, d).

In multivariate analysis, the first two principal components (PC1 and PC2) accounted for 23 and 17% of the variation in NSC concentrations, respectively, across species, season, and tissue type (Fig. 5). Native and invasive species occupied significantly different regions of PC1 and PC2 (MANOVA, Pillai’s number = 0.18, $F = 8.72$, $P < 0.0005$). Root starch and root sugars varied predominantly along PC1, while stem starch and fall stem sugars varied along PC2. Starch and sugar concentrations were negatively associated, particularly in stems.

**Discussion**

We found significant differences in stored carbon between native and non-native, invasive woody species in ENA, despite high variance in storage within some species (Fig. 1). In contrast to our hypothesis that increased storage in natives is related to their generally more conservative growth phenology, we found no evidence of a negative relationship between carbon invested in annual leaf growth and total NSCs across species. Moreover, our estimates of leaf production rates did not show an invader bias despite large differences in growing season duration (Fridley 2012), assimilation rate (Heberling and Fridley 2013), and estimated annual carbon gain (Fridley 2012). Although we did not measure whole plant carbon budgets in our study, our results point to two non-exclusive, novel contrasts between native and invasive species in ENA forests: (1) the greater carbon gain of invaders may support both growth and storage—that is, greater root starch reserves than natives after spring leaf out may translate to a more rapid response to defoliation (e.g., herbivory), without incurring a growth cost; and (2) natives consistently maintain more soluble sugars in stems and roots, with an effect size that rivals other plant attributes (e.g., determinacy) associated with NSC dynamics (Fig. 2a). We discuss the significance of these differences to forest invasions in turn.

After spring leaf out, invaders contained, on average, about 11% greater root starch concentration than native species, an effect that remained after controlling for both phylogeny and the tendency of invaders to exhibit indeterminate leaf growth (Fig. 3c). Although we did not investigate its potential function in the present study, the role of root starch in woody plants as an energy reserve that promotes resprouting in the event of defoliation is well established (Poorter et al. 2010; Dietze et al. 2014) and suggests that at least part of invaders’ enhanced annual carbon gain goes...
Fig. 5 Principal components analysis of soluble sugars and starches, nativity, and productivity values. Points represent species means, but all individual measurements from each species were used in the analysis. Black circles represent invasive species, while white circles represent native species.

Toward survival in addition to growth mechanisms. This is corroborated by studies documenting strong compensatory responses to herbivory in many invaders (Schierenbeck et al. 1994; Rogers and Siemann 2002; Callaway et al. 2006), although we note that, absent complete defoliation, compensatory responses can also be achieved by higher assimilation rates of surviving leaf tissue (Huang et al. 2010). As our estimates of annual leaf growth do not suggest an overall bias toward invaders, it is unclear why the native-invader root starch difference disappears by fall. One possibility is that energy stored as root starch in spring is allocated to fine roots later in the growing season, which Jo et al. (2015) showed to be greater overall for invaders using individuals from the same common garden. Another possibility is that invaders allocate more energy to fruit production in summer and fall. Although invasive species have generally been shown to produce more offspring than co-occurring native species (Mason et al. 2008; van Kleunen et al. 2010a), we are unaware of studies on reproductive allocation per se in forest invaders.

On the other hand, the higher concentration of soluble sugars in native species was consistent across seasons and tissues (22% greater in roots, and 11% greater in stems; Fig. 3). This difference is in addition to the independent contribution of a determinate leaf habit, which is more common in native ENA species than the overall invader pool (Fridley and Craddock 2015). There are several potential ramifications of this soluble sugar difference to understanding ENA forest invasions. First, these results support our hypothesis that native lineages may be better adapted to historical disturbance regimes than more recently arrived (invasive) lineages. For example, historic early-season freeze events in ENA may require woody species to maintain relatively high stem soluble sugar concentrations to reduce risk of embolism or cell lysis (Sakai and Yoshida 1968; Kozlowski 1992; Ashworth et al. 1993; Travert et al. 1997; Grant and Dami 2015; Zohner et al. 2017). These unpredictable damage events may promote bet-hedging behavior in native species, where plants maintain high soluble sugar in stem and root tissues to minimize variance in performance across years or seasons at the expense of other carbon pools (Philippi and Seger 1989; Philippi 1993; Fridley 2017). This may suggest that increases in unpredictable events that bring high risk of embolism or cell damage may limit the spread of invaders, if survival is promoted by soluble sugar reserves (Morin et al. 2007; Charrier and Améglio 2011; Grant and Dami 2015, 2014). Second, differences in root sugar concentrations between natives and invaders might also indicate a greater investment in soil microbial interactions in natives or differences in the timing of above/belowground carbon translocation patterns (Kozlowski 1992; Marler et al. 1999; Wolfe et al. 2008; Pringle et al. 2009; Karst et al. 2016). Jo et al.
(2015) found large differences in specific root length and fine root growth between this group of native and invasive species that could indicate a tradeoff in nutrient foraging, with nutrient uptake in natives biased toward microbial relationships (requiring carbohydrate transfer) and away from root structural investment. Current studies are underway in this group to document whether such nativity-based systematic differences in soil microbial relationships occur. Third, the greater concentration of soluble sugars in native species may result from passive accumulation due to a shorter period of leaf growth (Fridley 2012), as would be expected in fall NSCs. However, passive sugar accumulation is an unlikely explanation for native-invader sugar differences in spring, shortly after leaf out, particularly given such large differences in both roots and shoots. In this context, functional NSC studies are a clear next step in forest invasion research.

As hypothesized, species with determinate growth had higher soluble sugar concentrations in all tissues, but indeterminate species maintained higher root starch concentrations in spring and fall. Because determinate species do not reinvest photosynthates in additional leaf and stem structural tissue during the growing season, elevated fall sugar concentrations are a straightforward consequence of less overall tissue produced (but see Canham et al. 1999). What is less clear is why determinate species maintain higher soluble sugar concentrations following spring leaf out. One hypothesis is that, like native species overall, leaf determinacy is part of a syndrome of conservative behaviors, including elevated storage allocation. Many determinate species in deciduous forests are shade tolerant, produce long-lived leaves, and do not break bud until later in the spring than indeterminate species (Lechowicz 1984; Navas et al. 2003; Fridley and Craddock 2015). Indeterminate species may ultimately make the same investment in leaves as determinate species, but their relative leaf investment is lower in the first part of the growing season. Thus, we expect determinate species to have a greater incentive to protect their canopy via greater allocation to NSCs and anti-freeze protection (sugars). The large difference in root starch content between indeterminate and determinate species is surprising, and may suggest a direct link between late season carbon gain (through new leaf production in indeterminate species) and root energy storage. In particular, Smith et al. (2014) showed that root production occurred earlier in spring in two indeterminate Lonicera species compared to determinate shrubs in the Rhamnaceae. Thus, indeterminate species that allocate carbon to leaf growth in the summer may preferentially reserve root starch in the winter to promote root expansion before spring leaf display. Alternatively, indeterminate species may require greater starch reserves to produce multiple leaf cohorts throughout the growing season.

Despite overall differences in storage patterns between natives and invaders, both groups showed high variation in soluble sugar and starch concentrations (Supplemental Figure 1). Several factors likely contribute to this variation. First, species in the common garden occur across a large array of latitudes and light environments (e.g., forest edges vs. interiors), which differ in freezing risk and likely have strong influences on phenology, growth patterns, and storage (Lechowicz 1984; Morin et al. 2009; Panchen et al. 2014; Muffler et al. 2016). Second, because our focal species reach reproductive maturity at different ages and sizes, some individuals in our study showed high reproductive allocation and others none; additional measurements of flower and fruit abundance could shed additional light on growth-storage constraints in these species. Third, given the large taxonomic representation in our study, species likely differ in the chemical form of stored compounds, including lipids and oligosaccharides (Hoch et al. 2003) that we did not measure.

**Conclusion**

We found differences in carbon allocation to soluble sugars and starches in native and invasive woody plants of Eastern North American forests. Although the function of stored forms of carbon remains unclear, our study provides a foundation for comparative studies of natives and invaders that focuses on survival (e.g., freezing resistance, response to defoliation). In particular, high allocation to soluble sugars in natives may align with a bet-hedging strategy that confers resilience in an unpredictable environment: the benefit of protecting tissues against damage from environmental extremes (like spring freeze events) outweighs the cost of forgoing growth in stable conditions (Zohner et al. 2017). Alternatively, there may be a connection between high soluble sugar concentrations in native species and belowground interactions with microbial mutualists. Measuring carbohydrate mobility and fluxes in native and invasive species, particularly as it relates to frost damage prevention and survival from defoliation, is likely to improve our understanding of invasion mechanisms in a global change context.

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**Author contribution statement** EH and JF worked together to design this research project. EH carried out the data collection and statistical analysis. EH and JF wrote the manuscript.
References


trees: relations with carbohydrate storage and shade tolerance. Ecology 91(9):2613–2627


Smith MS, Fridley JD, Goebel M, Bauerle TL (2014) Links between belowground and aboveground resource-related traits reveal species growth strategies that promote invasive advantages. PLoS ONE 9(8):e104189

Su YS, Yajima M (2015) R2jags: Using R to run ‘JAGS’. R package version 0.5-7


Trischuk RG, Schilling BS, Low NH, Gray GR, Gusta LV (2014) Cold acclimation, de-acclimation and re-acclimation of spring canola, winter canola and winter wheat: the role of carbohydrates, cold-induced stress proteins and vernalization. Environ Exp Bot 106:156–163


