

## Deer browsing overwhelms extended leaf phenology benefits: A test case with *Rubus allegheniensis* and a recalcitrant hay-scented fern layer

Alejandro A. Royo<sup>a,\*</sup>, John S. Stanovick<sup>b</sup>

<sup>a</sup> USDA Forest Service, Northern Research Station, 335 National Forge Road, P.O. Box 267, Irvine, PA 16329, USA

<sup>b</sup> USDA Forest Service, Northern Research Station, 1549 Long Pond Road, Long Pond, PA 18334, USA



### ARTICLE INFO

#### Keywords:

*Odocoileus virginianus*

Phenology

Competition

Allegheny hardwoods

### ABSTRACT

Plant species coexistence can be promoted by multiple tradeoffs including temporal niche separation via differences in phenology. Namely, if phenological differences afford longer leaf life-spans that confer species the opportunity to exploit light and fix carbon during periods relatively free of other competitors, then coexistence, or even competitive superiority, may arise. Phenological niche separation explanations, including the Extended Leaf Phenology (ELP) hypothesis, have garnered considerable support as a mechanistic explanation for both exotic invasive species success and maintenance of native plant species. The benefits conferred by a phenological advantage, however, can be nullified if tissue losses from browsing are coincident with this phenological window of opportunity. This study experimentally tests the role of phenological advantage and white-tailed deer (*Odocoileus virginianus*) browsing, alone and in concert, in structuring coexistence between the native forest shrub *Rubus allegheniensis*, which possesses an extended phenological window, and the native invasive fern *Dennstaedtia punctilobula*. Browsing treatments (ambient versus excluded) were factorially crossed with shading treatments (none versus shading timed to eliminate phenological advantage). The results demonstrate the phenological advantage is an essential growth mechanism for *Rubus* as seedlings deprived of the ELP advantage were, on average, 50% shorter than those not treated with shade. However, this benefit was largely dependent on herbivory pressure, as deer browsing largely nullified the growth benefits provided by the phenological advantage. This experiment is the first experimental study documenting how browsing impacts affect a plant species by curtailing a phenological coexistence advantage. The results suggest elucidating the interacting roles of the ELP and browsing is critical, particularly as the phenological niche advantage does not necessarily constitute a fitness advantage where browsing pressure is high. Results from this work also provide broader insight into how exotic plant species invasions that are assumed to be aided by a phenological (ELP) advantage, may be modulated through their browse susceptibility. Overall, these results suggest understanding the co-occurring roles of phenology and browsing may guide management decisions to maintain or promote understory plant diversity.

### 1. Introduction

Competition for light is universally recognized among the pre-eminent mechanisms structuring plant communities (Canham et al., 1990; Farrior et al., 2016; Kobe et al., 1995; McCarthy, 2001). Given the unidirectional nature of light competition, the dynamic is highly asymmetric wherein taller or denser species preempt a disproportionate amount of light (Schwinning and Weiner, 1998; Weiner, 1990). Thus, competitive outcomes and species coexistence in light-structured systems should be effectively predicted by resource preemption and attenuation (Banta et al., 2008; Dybziński and Tilman, 2007). This straightforward outcome, however, is often prevented by tradeoffs

between light attenuation and shade tolerance which allow suppressed shade tolerant species to persist, grow and potentially displace overtopping vegetation (shade tolerance paradigm; Engelhardt and Anderson, 2011; Harrington et al., 1989; Lienard et al., 2015; Valladares and Niinemets, 2008; Walters and Reich, 1996).

Aside from shade tolerance, coexistence in light-structured, highly asymmetric systems can be mediated via other traits (reviewed by Aschehoug et al., 2016; Barot, 2004) including temporal niche separation via differences in phenology (Huang et al., 2018; Sapijanskas et al., 2014). Namely, if phenological differences afford longer leaf life-spans that confer species the opportunity to exploit light and fix carbon during periods relatively free of other competitors, then coexistence, or

\* Corresponding author.

E-mail address: [alejandroyosedas@usda.gov](mailto:alejandroyosedas@usda.gov) (A.A. Royo).

even competitive superiority, may arise. This Extended Leaf Phenology (ELP) hypothesis has garnered considerable support as an explanation for exotic invasive species success (Fridley, 2012; Smith, 2013; Wolkovich and Cleland, 2011) as well as a mechanism promoting diversity among native plant species.

The advantages conferred by variation in shade-tolerance, phenology and other key traits mediating light competition (e.g., relative growth rate) are often significantly altered by trophic interactions, including herbivory (Louda et al., 1990; Maron and Crone, 2006). Variation among species in susceptibility to tissue loss from herbivory can reinforce or reverse competitive outcomes (Grover and Holt, 1998; Tilman, 1997). Thus, the effect of herbivory on coexistence may ultimately be determined by how plant species tradeoff between competitive ability and herbivore vulnerability (e.g., Krueger et al., 2009). Under this framework, species that can tolerate, defend, or avoid herbivore pressure may magnify benefits gained from ELP. In contrast, herbivore susceptibility may weaken or even nullify any gains from ELP (Martinod and Gorchoy, 2017).

In this study, both ELP and herbivory are examined in an integrated effort to ascertain how both forces structure competitive dynamics between the native early-successional perennial shrub *Rubus allegheniensis* Porter (hereafter *Rubus*) and the perennial fern *Dennstaedtia punctilobula* (Michx.) T. Moore (hereafter hay-scented fern). Co-existence between *Rubus* and hay-scented fern offers an ideal test case of the role of ELP and herbivory. Hay-scented fern commonly forms a dense recalcitrant layer in heavily browsed forests of the northeastern United States that strongly attenuates light thereby strongly impeding plant species recruitment (George and Bazzaz, 1999; Royo and Carson, 2006). Despite these inimical conditions, *Rubus* seedlings are often found under and occasionally even grow through the fern layer (de la Cretaz and Kely, 2002; Horsley and Marquis, 1983). This ability of a putatively inferior competitor to persist and grow in these conditions may be explained by the ELP hypothesis. Hay-scented fern fiddleheads emerge and unfurl between mid-April and May, forming a mature canopy of 30 to 74 cm tall fronds by mid-June that lasts until early October when fronds senesce (Cody et al., 1977; Mahall and Bormann, 1978). Thus, it is only during the summer months that hay-scented fern strongly reduces light (de la Cretaz and Kely, 2002). In contrast, *Rubus* exhibits an ELP strategy wherein bud-break occurs in mid-April and leaves remain photosynthetically active through much of November (Caplan et al., 2018; de la Cretaz and Kely, 2002). This ELP strategy provides *Rubus* approximately 3 months (~45+ days in both spring and autumn) during which it can potentially capitalize on a higher light availability early and late in the season when the fern canopy is either waxing or waning. Nonetheless, although ELP may provide *Rubus* a growth advantage, the species is also strongly limited by white-tailed deer (*Odocoileus virginianus*, Zimmermann) browsing, particularly when deer are at high abundance (Healy, 1971; Horsley et al., 2003). In contrast, hay-scented fern lacks the ELP strategy but is rarely browsed by deer (Averill et al., 2016).

Given the contrasting phenological (ELP) and browsing vulnerability traits of these two species, this study tests three specific predictions: 1) The ELP hypothesis predicts that experimentally eliminating the phenological advantage afforded to *Rubus* will diminish *Rubus* survival and growth. 2) Similarly, the browsing hypothesis predicts that preferential deer browsing on *Rubus*, relative to hay-scented fern, will restrict *Rubus* seedling survival and growth. 3) Both mechanisms may operate concurrently with the expectation that *Rubus* seedling survival and growth will be most limited when the ELP niche is eliminated and browsing is present and, conversely, *Rubus* survival and growth will be greatest where ELP can provide a phenological advantage and browsing is eliminated.

## 2. Methods

This study was conducted at three, 80–100 year old Allegheny

hardwood forest sites in northwestern Pennsylvania, USA that originated from clearcutting in the early 20th century. The major tree species include *Prunus serotina*, *Acer saccharum*, *A. rubrum*, *Betula lenta*, and *B. allegheniensis* (see Stout et al., 2013). Two of the sites were on the Allegheny National Forest and a third was located on private land. Sites spanned a distance of 35 km. All sites had moderately open canopies resulting from past harvesting and natural disturbances. Light readings at two of the sites using an AccuPAR ceptometer (Decagon Devices, Inc<sup>1</sup>) showed understory light levels averaged  $26.7\% \pm 0.04$  (SE) and  $6.8\% \pm 0.01$  (SE) of full sunlight at 100 cm and 20 cm from the forest floor, respectively. Overstory basal area estimated using a 10-factor prism (Grosenbaugh, 1952) averaged  $19.1 \text{ m}^2$  per hectare and the understory was dominated by hay-scented fern, a common signature of chronic deer overabundance in forests of this region (Royo and Carson, 2006). Regional deer populations during the period of study ranged from 3.74 to 6.9 deer per  $\text{km}^2$  (Royo et al., 2017; Stout et al., 2013). At each of the three sites, we installed a  $2 \times 2$  factorial experiment with deer browsing (ambient vs. absent) and phenological niche manipulations (present vs. eliminated) on  $2.32 \text{ m}^2$  ( $1.52 \times 1.52 \text{ m}$ ) experimental plots. Deer browsing was manipulated by randomly assigning half of the plots a plastic deer fence treatment (Deerbusters, Inc<sup>1</sup>). The phenological window was manipulated using 90% knitted black polypropylene shade cloth (DeWitt Company<sup>1</sup>) erected randomly over half of all the plots in both deer browsing treatments. Shading was deployed for a period of approximately 60 days beginning in early-April corresponding to the period of time between bud-break in *Rubus* and before maturing hay-scented-fern fronds begin to strongly suppress light (de la Cretaz and Kely, 2002; Mahall and Bormann, 1978). Shade cloth was removed from June through early October, to allow the fully expanded hay-scented fern access to light during its active growing season. Shade cloth was redeployed beginning in October and maintained through November, a period of time in which hay-scented fern completely senesces, but *Rubus* remains photosynthetically active (Caplan et al., 2018). Shading level approximated the percent of light attenuation ( $93.2\% \pm 0.01$  [SE]) experienced at 20 cm at these sites during mid-summer. The use of shade cloth may alter a number of unwanted microclimatic variables, including temperature, precipitation, wind speed and red:far-red ratio (Fridley, 2012; Le Roux et al., 2005). To mitigate some of these effect, shade cloth was erected horizontally at 150 cm above ground surface and draped down along sides of the plot to approximately 50 cm above the ground surface. Moreover, changes in red:far-red ratio under hay-scented fern cover increase in the same direction as under shade cloth (Horsley, 1993). Thus, the experiment consisted of four distinct treatments: (i) control, (ii) no browsing, (iii) no phenological niche (i.e., extended shade), and (iv) no browsing and no phenological niche. Each treatment was replicated six times within a site resulting in a total of 24 plots per stand with the exception of one site (FR318) in which two extra fenced plots were established by error, one with and one without shade, resulting in a total of 74 plots.

On May 4, 2009 we transplanted three naturally established *Rubus* individuals (5–10 cm in height) into the center of each experimental plot. Transplanted individuals were not first year germinants, but rather established (1+ year old) seedlings. Seedlings were planted in the corners of a triangular array, 15 cm from each other and marked with flags and a colored binder ring. We revisited plots on May 28 and replanted any missing seedlings that had died from transplant shock. Each experimental plot was visited in late August from 2009 to 2014 to record survival and longest stem length of *Rubus* seedlings. Additionally, hay-scented fern frond densities in the central square meter of the experimental plots were assessed in 2009, 2010, and 2014. When all planted *Rubus* seedlings in a plot were missing or dead, the plot was no

<sup>1</sup> The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

longer censused. The experiment was terminated following summer 2014 as only 21 plots contained seedlings and one site (FR173HA) had no active plots remaining.

The analyses proceeded as a multi-location, repeated measures, completely randomized factorial design using PROC GLIMMIX (SAS Institute Inc., 2013). For the analyses, fence, shade, year and the associated interactions were fixed effects in the model. Site and fence × shade × site were random effects. Average *Rubus* seedling stem length for each experimental plot was calculated, rather than length of individual seedlings, so as to account for the imbalance in number of plants alive throughout the temporal extent of the study. To verify the robustness of these results given potential complications with ANOVAs of unequal size (Sokal and Rohlf, 1995), we also ran stem length analysis using a single randomly drawn seedling from each plot and year. This approach yielded similar results, hence we present analyses using averages of all seedlings so as to not underutilize the data. Stem length was best modelled with a gamma distribution and log link function.

Seedling survival was examined in two ways. The first approach modelled how survival varied over time and across treatments by examining the proportion of seedlings surviving the original three planted seedlings within each experimental plot and year. These analyses used the binomial distribution with the logit link function. Additionally, whole-plot survival was modelled using a logistic regression model where the outcomes are whether plots contained any transplanted *Rubus* seedlings (event = 1) or all seedlings were dead/missing (event = 0). These analyses used a binary distribution with the logit link function. Correlations between years was modelled using an autoregressive first-order covariance structure, except in the case of stem length for which we used the heterogeneous extension of the autoregressive first order structure in order to adjust for heterogeneous residuals among years. Models used the Kenward-Rogers denominator degrees of freedom adjustment method (Littell et al., 2006). Pairwise comparisons among fixed effects were evaluated using least squares means (LSMEANS). In addition, residuals were statistically tested for normality and homogeneity of variance via the Shapiro-Wilk and Levene’s test respectively. Further models were adjusted accordingly to rectify assumption violations.

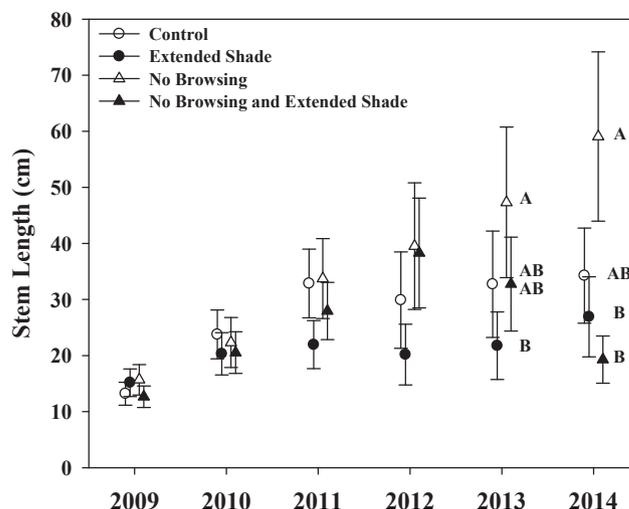
### 3. Results

Transplanted *Rubus* seedling growth differed among treatments. The ELP advantage was essential for *Rubus* growth, as seedlings in unshaded plots attained the largest size (Table 1, Fig. 1). After five years of treatment, seedlings deprived of the ELP advantage were, on average, 50% shorter than those not shaded (Mean ± SE: 44.9 ± 8.6 cm versus 22.8 ± 4.2 cm). Moreover, surviving *Rubus* seedlings grew tallest when they were protected from browsing and unshaded (significant fence × shade × year interaction; Table 1, Fig. 1). By the end of the experiment, these seedlings averaged 59.1 ± 15.1 cm, two- and three-fold taller than seedlings in either treatment lacking ELP. Additionally,

**Table 1**

Mixed effects model results testing change in *Rubus allegheniensis* seedling growth (i.e., stem length) and proportion of seedlings surviving over time, and the logistic regression approach modelling whole plot survival (i.e., all seedlings dead in a plot (1/0). Fence refers to browsing effect (ambient versus absent) and Shade refers to the manipulation of the Extended Leaf Phenology (ELP) window (present versus absent).

Effect	Height		Proportion Surviving		Whole-Plot Survival	
	F-value	P value	F-value	P value	F-value	P value
Fence	F <sub>1, 16.21</sub> = 1.14	0.30	F <sub>1, 67.2</sub> = 1.01	0.32	F <sub>1, 62.7</sub> = 0.05	0.82
Shade	F <sub>1, 16.121</sub> = 2.96	0.10	F <sub>1, 66.9</sub> = 1.22	0.27	F <sub>1, 62.7</sub> = 0.05	0.82
Fence × Shade	F <sub>1, 16.21</sub> = 0.08	0.78	F <sub>1, 66.9</sub> = 0.02	0.88	F <sub>1, 62.7</sub> = 0.07	0.79
Year	F <sub>5, 72.1</sub> = 21.87	< 0.0001	F <sub>4,147.1</sub> = 2.86	0.03	F <sub>4, 186.4</sub> = 7.54	< 0.0001
Fence × Year	F <sub>5, 72.1</sub> = 1.42	0.23	F <sub>4,146.5</sub> = 0.42	0.42	F <sub>4, 186.3</sub> = 0.16	0.96
Shade × Year	F <sub>5, 72.1</sub> = 2.43	0.04	F <sub>4,146.5</sub> = 0.23	0.26	F <sub>4, 186.8</sub> = 0.82	0.51
Fence × Shade × Year	F <sub>5, 72.1</sub> = 2.71	0.03	F <sub>4,146.5</sub> = 0.66	0.61	F <sub>4, 186.2</sub> = 0.35	0.85



**Fig. 1.** Effect of manipulations of browsing and the extended phenology window (i.e., extended shade) on *Rubus allegheniensis* stem length (cm) over time. Values plotted denote the back-transformed means and standard error of the mean. Superscripts denote significant least-squares means differences among treatments within a census period.

browsing ultimately curtailed growth gains of seedlings with ELP as these seedlings were 44% shorter than seedlings with ELP and protected from deer herbivory (pair-wise comparison: t-value = -1.74, P = 0.09). Overall, stem length of surviving *R. allegheniensis* seedlings protected from browsing continued to increase over time whereas that of the other three treatments levelled off.

Transplanted *R. allegheniensis* seedling survival was poor across all treatments. By the end of the experiment only 21 plots (27% of original) had any seedlings left and 82% of the all the transplanted seedlings had died (Fig. 2). Seedling survival was unaffected by any treatment as assessed by either the seedling survival probabilities or the whole-plot survival probability (Table 1).

Finally, hay-scented fern frond densities were not affected by shading or fencing treatments over time (Tables 2 and 3). Across treatments and year, frond densities averaged 94.1 ± 2.9 fronds per meter squared.

### 4. Discussion

This work experimentally demonstrated ELP is an essential phenological trait for seedlings of the native forest shrub *Rubus*, particularly when grown under a dense canopy of the co-occurring hay-scented fern. This finding is consistent with the observation that seedlings of this early-successional, shade-intolerant shrub can continue to grow even when in a dense fern layer (de la Cretaz and Kelty, 2002). In fact, experimentally eliminating the ELP advantage through early and late

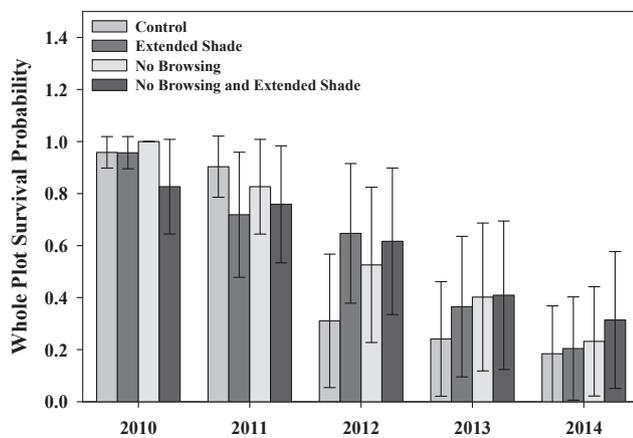


Fig. 2. Effect of manipulations of browsing and the extended phenology window (i.e., extended shade) on transplanted *Rubus allegheniensis* seedling survival (i.e., whole-plot survival) over time.

Table 2

Mixed effects model testing change in hay-scented fern frond densities (fronds/m<sup>2</sup>) over time. Fence refers to browsing effect (ambient versus absent) and Shade refers to the manipulation of the Extended Leaf Phenology (ELP) window (present versus absent).

Effect	F-value	P value
Fence	F <sub>1, 19.5</sub> = 0.62	0.44
Shade	F <sub>1, 19.5</sub> = 1.06	0.31
Fence × Shade	F <sub>1, 19.4</sub> = 0.78	0.39
Year	F <sub>2, 33.5</sub> = 1.63	0.21
Fence × Year	F <sub>2, 34.2</sub> = 0.14	0.87
Shade × Year	F <sub>2, 34.3</sub> = 1.59	0.22
Fence × Shade × Year	F <sub>2, 34.3</sub> = 0.28	0.76

Table 3

Hay-scented fern frond densities (Mean ± SE; fronds/m<sup>2</sup>) over time.

Treatment	2009	2010	2014
Control	96.36 ± 12.21	93.69 ± 11.64	93.29 ± 18.58
No ELP	102.15 ± 13.55	85.92 ± 13.10	99.26 ± 19.40
No Browsing	95.78 ± 13.28	95.18 ± 12.75	89.91 ± 19.85
No Browsing, No ELP	110.35 ± 13.29	96.17 ± 12.83	125.79 ± 18.69

seasonal shade treatment caused growth stagnation in transplanted seedlings. Nevertheless, the ELP benefit was largely dependent on herbivory pressure, as white-tailed deer browsing overwhelmed the growth benefits provided by this phenological advantage. Indeed, the impact of browsing is conservative as the presence of shade cloth for a portion of the growing season likely reduced cumulative browse pressure on seedlings. These findings support the hypothesis that tradeoffs between competitive ability and herbivore vulnerability are often key to coexistence. Although it has long been known that *Rubus allegheniensis* is a highly preferred browse species (Healy, 1971) and even moderate deer densities can reduce its abundance by 60% or more (Horsley et al., 2003; Royo et al., 2010), this is the first experimental study documenting how browsing impacts disproportionately affect a plant species by curtailing a phenological coexistence advantage.

While speculative, the findings support observational evidence that *Rubus* seedlings may establish, grow through, and potentially displace the hay-scented fern canopy (de la Cretaz and Kelty, 2002; Horsley and Marquis, 1983; Nuttle et al., 2014), provided browse pressure is low. This observed dynamic is of interest to managers as a longer-term, successional approach to fern control (Engelman and Nyland, 2006) as an alternative to current options which are generally limited to herbicide applications (Ristau et al., 2011; but see de la Cretaz and Kelty,

2006). It is important to note this work was not designed to test *in situ* competitive outcomes. Rather, it examined the growth and survival dynamics of *Rubus* seedlings planted at very low densities. In fact, fern densities in the plots remained stable and comparable to reported densities in other studies (de la Cretaz and Kelty, 2006) providing evidence that frond dynamics were not directly affected by either the shading or browsing treatments or indirectly by changes in *Rubus* stem length. In contrast, *R. allegheniensis* survival was poor regardless of treatment, indicating that the relatively low-light conditions resulting from a partially open overstory canopy and a recalcitrant fern layer largely limit the survival of this shade intolerant species (Donoso and Nyland, 2006). Moreover, although care was taken to determine whether observed ramet mortality represented genet mortality by examining whether any new stems were emerging from the root stock, it is possible *R. allegheniensis* survival was underestimated (see Schnitzer et al., 2002). Nevertheless, given that *Rubus* seedlings in this and other studies (e.g., *R. glandulosus*; Laskurain et al., 2004) exhibit the high mortality rates, competitive displacement, if possible, would require seedling densities orders of magnitude greater than the ones in this study, as is commonly observed in early-successional forest understories (20–200 seedlings per m<sup>2</sup>; Elliott et al., 2002; Peterson and Carson, 1996).

Perhaps more importantly, these results suggest *R. allegheniensis* and their congeners may buffer forest understories against exotic plant invaders provided these species compete for the same phenological niche. Indeed, Fridley (2012) found many exotic invaders of the northeastern United States exhibit extended leaf phenologies that broadly overlap with *Rubus* (i.e., mid-April through mid-November). As with competitive control over hay-scented fern, however, resistance against invasives by a resident *Rubus* layer may be possible only if seedling densities are high and deer pressure is low. This mechanism of resistance to invasion merits further investigation.

The ELP hypothesis has garnered widespread attention as a mechanism explaining plant invasions (Wolkovich and Cleland, 2011). However, as this study demonstrates, ELP can play a role in promoting coexistence in native understory species (see also *Viburnum alnifolium*; Gill et al., 1998). Fundamentally, the key mechanism operating is not extended leaf longevity *per se*. Rather, persistence or success arises from a phenological niche differentiation (*sensu* Fargione and Tilman, 2005) that provides ‘windows of opportunity’ to exploit resources and fix carbon during periods that are relatively free of competitors. Viewed through this lens, phenological niche differentiation is the same mechanism invoked to explain the persistence of spring herbs (Rathcke and Lacey, 1985), despite exhibiting relatively short leaf longevities (i.e., < 60 days for true spring ephemerals; Lapointe, 2001) or the coexistence of tree seedlings and saplings that often leaf out just a few days before their conspecific adult canopies (e.g., Augspurger and Bartlett, 2003; Gill et al., 1998; Martinod and Gorchov, 2017).

Regardless of plant taxa, results demonstrate that phenological niche differentiation does not necessarily constitute a fitness advantage if browsing pressure is high. This herbivory-driven nullification of phenological niche advantages may be why Webster et al. (2005) and others often find browsing disproportionately affects spring ephemerals as tissue losses from browsing are coincident with the critical period of resource acquisition afforded by the phenological niche (e.g., Knight, 2007). Similarly, Canham and colleagues (1994) found spring and early summer tissue loss to hardwood seedlings exerted disproportionately greater reductions to growth and survival than tissue loss at other times of the year. Thus, as Fridley (2012) points out, the phenological niche may not be advantageous, even for exotic invaders, if other critical tradeoffs exist. This contention is critical as invasive plant species in the eastern U.S. vary widely in their susceptibility to deer from highly preferred (e.g., *Celastrus orbiculatus*) to generally avoided (*Alliaria petiolata*; Averill et al., 2016). These results suggest understanding the interacting roles of phenological niche and browsing may help elucidate invasive success, rate or spread, and possibly control. Given that

deer population numbers are generally high across much of the eastern United States (Walters et al., 2016), it is imperative that invasion ecology research account for the role deer browsing may play in promoting (e.g. *A. petiolata*; Kalisz et al., 2014) or diminishing (e.g., *Lonicera maackii*; Peebles-Spencer et al., 2018) plant invasions in exotic species possessing a phenological niche advantage.

Overall, these results emphasize the importance of capitalizing on temporal windows of greater resource availability via phenological niche differentiation. Lacking physiological measurements, this work cannot assess, for example, the contribution of these temporal niches to the overall carbon gain budget of *Rubus* (e.g., Engelhardt and Anderson, 2011; Harrington et al., 1989). Moreover, shade cloth manipulations often cannot completely decouple shading effects from additional microclimatic effects wrought by the treatment. Finally, it is important to note that the shade treatments preclude access to light during critical periods rather than representing a true manipulation of ELP. Direct ELP tests could experimentally alter the timing of bud break and leaf senescence through environmental cues, hormones, or molecular techniques (e.g., Gan and Amasino, 1997) and thereby mitigate the confounding effects of shade. Nevertheless, these experimental results demonstrate a clear cost, in terms of growth reduction, when the phenological advantage is eliminated. Although others have manipulated the phenological window via shading (Augsburger, 2008; Engelhardt and Anderson, 2011) or examined physiological impacts of browsing to understory plants throughout their growing season (Heberling et al., 2017), this research represents an initial step in addressing knowledge gaps identified by Smith (2013) who concluded existing ELP research as generally anecdotal and pressed for multi-factor experiments testing how phenological advantages in resource competition interact with other factors. Moreover, this work tests the role of ELP on native plant species, as opposed to exotic invasives, which is the focus the majority of ELP studies.

## Acknowledgements

Financial support for the work came from the Pennsylvania Department of Conservation and Natural Resources, Bureau of Forestry and the USDA-FS Northern Research Station. I thank the Allegheny National Forest and Landvest, Inc. for access to field sites. Patricia Raymond, Scott Stoleson, Mason Heberling and two anonymous reviewers provided valuable editorial suggestions.

## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.06.019>.

## References

- Aschehoug, E.T., Brooker, R., Atwater, D.Z., Maron, J.L., Callaway, R.M., 2016. The mechanisms and consequences of interspecific competition among plants. *Annu. Rev. Ecol. Syst.* 47 (1), 263–281.
- Augsburger, C.K., 2008. Early spring leaf out enhances growth and survival of saplings in a temperate deciduous forest. *Oecologia* 156 (2), 281–286.
- Augsburger, C.K., Bartlett, E.A., 2003. Differences in leaf phenology between juvenile and adult trees in a temperate deciduous forest. *Tree Physiol.* 23 (8), 517–525.
- Averill, K.M., Mortensen, D.A., Smithwick, E.A.H., Post, E., 2016. Deer feeding selectivity for invasive plants. *Biol. Invasions* 18 (5), 1247–1263.
- Banta, J.A., Stark, S.C., Stevens, M.H.H., Pendergast, T.H., Baumert, A., Carson, W.P., 2008. Light reduction predicts widespread patterns of dominance between asters and goldenrods. *Plant Ecol.* 199 (1), 65–76.
- Barot, S., 2004. Mechanisms promoting plant coexistence: can all the proposed processes be reconciled? *Oikos* 106 (1), 185–192.
- Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. Jour. For. Res.* 20, 620–631.
- Canham, C.D., McAninch, J.B., Wood, D.M., 1994. Effects of the frequency, timing, and intensity of simulated browsing on growth and mortality of tree seedlings. *Can. J. For. Res.* 24 (4), 817–825.
- Caplan, J.S., Whitehead, R.D., Gover, A.E., Grabosky, J.C., 2018. Extended leaf phenology presents an opportunity for herbicidal control of invasive forest shrubs. *Weed Res.* 58 (4), 244–249.

- Cody, W.J., Hall, I.V., Crompton, C.W., 1977. The biology of Canadian weeds. 26. *Dennstaedtia punctilobula* (Michx.) Moore. *Can. Jour. Plant Sci.* 57, 1159–1168.
- de la Cretaz, A.L., Kelty, M.J., 2002. Development of tree regeneration in fern-dominated forest understories after reduction of deer browsing. *Restor. Ecol.* 10 (2), 416–426.
- de la Cretaz, A.L., Kelty, M.J., 2006. Control of hay-scented fern by mowing. *N. Jour. Appl. For.* 23 (3), 149–154.
- Donoso, P.J., Nyland, R.D., 2006. Interference to hardwood regeneration in northeastern North America: The effects of raspberries (*Rubus* spp.) following clearcutting and shelterwood methods. *N. Jour. Appl. For.* 23 (4), 288–296.
- Dybzinski, R., Tilman, D., 2007. Resource use patterns predict long-term outcomes of plant competition for nutrients and light. *Am. Nat.* 170 (3), 305–318.
- Elliott, K.J., Hitchcock, S.L., Krueger, L., 2002. Vegetation response to large scale disturbance in a southern Appalachian forest: Hurricane Opal and salvage logging. *J. Torrey Bot. Soc.* 129 (1), 48–59.
- Engelhardt, M.J., Anderson, R.C., 2011. Phenological niche separation from native species increases reproductive success of an invasive species: *Alliaria petiolata* (Brassicaceae)-garlic mustard. *J. Torrey Botanical Soc.* 138 (4), 418–433.
- Engelman, H.M., Nyland, R.D., 2006. Interference to hardwood regeneration in north-eastern North America: Assessing and countering ferns in northern hardwood forests. *N. Jour. Appl. For.* 23 (3), 166–175.
- Fargione, J., Tilman, D., 2005. Niche differences in phenology and rooting depth promote coexistence with a dominant C4 bunchgrass. *Oecologia* 143 (4), 598–606.
- Farrion, C.E., Bohlman, S.A., Hubbell, S., Pacala, S.W., 2016. Dominance of the suppressed: Power-law size structure in tropical forests. *Science* 351 (6269), 155–157.
- Fridley, J.D., 2012. Extended leaf phenology and the autumn niche in deciduous forest invasions. *Nature* 485 (7398), 359.
- Gan, S., Amasino, R.M., 1997. Making sense of senescence (molecular genetic regulation and manipulation of leaf senescence). *Plant Physiol.* 113 (2), 313.
- George, L.O., Bazzaz, F.A., 1999. The fern understory as an ecological filter: Emergence and establishment of canopy-tree seedlings. *Ecology* 80 (3), 833–845.
- Gill, D.S., Amthor, J.S., Bormann, F.H., 1998. Leaf phenology, photosynthesis, and the persistence of saplings and shrubs in a mature northern hardwood forest. *Tree Physiol.* 18 (5), 281–289.
- Grosenbaugh, L.R., 1952. Plotless timber estimates - new, fast, easy. *J. For.* 50 (1), 32–37.
- Grover, J.P., Holt, R.D., 1998. Disentangling resource and apparent competition: realistic models for plant-herbivore communities. *J. Theor. Biol.* 191 (4), 353–376.
- Harrington, R.A., Brown, B.J., Reich, P.B., 1989. Ecophysiology of exotic and native shrubs in Southern Wisconsin. I. Relationship of leaf characteristics, resource availability, and phenology to seasonal patterns of carbon gain. *Oecologia* 80, 356–367.
- Healy, W.M., 1971. Forage preferences of tame deer in a Northwest Pennsylvania clear-cutting. *J. Wildl. Manage.* 35 (4), 717–723.
- Heberling, J.M., Brouwer, N.L., Kalisz, S., 2017. Effects of deer on the photosynthetic performance of invasive and native forest herbs. *AoB PLANTS* 9 (2).
- Horsley, S.B., 1993. Mechanisms of interference between hay-scented fern and black cherry. *Can. J. For. Res.* 23 (10), 2059–2069.
- Horsley, S.B., Marquis, D.A., 1983. Interference by weeds and deer with Allegheny hardwood reproduction. *Can. J. For. Res.* 13 (1), 61–69.
- Horsley, S.B., Stout, S.L., deCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecol. Appl.* 13 (1), 98–118.
- Huang, L., Koubek, T., Weiser, M., Herben, T., 2018. Environmental drivers and phylogenetic constraints of growth phenologies across a large set of herbaceous species. *J. Ecol.* 106 (4), 1621–1633.
- Kalisz, S., Spigler, R.B., Horvitz, C.C., 2014. In a long-term experimental demography study, excluding ungulates reversed invader's explosive population growth rate and restored natives. *Proc. Natl. Acad. Sci.* 111 (12), 4501–4506.
- Knight, T.M., 2007. Population-level consequences of herbivory timing in *Trillium grandiflorum*. *Am. Midl. Nat.* 157 (1), 27–38.
- Kobe, R.K., Pacala, S.W., Silander, J.A., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* 5, 517–532.
- Krueger, L.M., Peterson, C.J., Royo, A., Carson, W.P., 2009. Evaluating relationships among tree growth rate, shade tolerance, and browse tolerance following disturbance in an eastern deciduous forest. *Can. J. For. Res.* 39 (12), 2460–2469.
- Lapointe, L., 2001. How phenology influences physiology in deciduous forest spring ephemerals. *Physiol. Plant.* 113 (2), 151–157.
- Laskurain, N., Escudero, A., Olano, J., Loidi, J., 2004. Seedling dynamics of shrubs in a fully closed temperate forest: greater than expected. *Ecography* 27 (5), 650–658.
- Le Roux, P.C., McGeoch, M.A., Nyakatya, M.J., Chown, S.L., 2005. Effects of a short-term climate change experiment on a sub-Antarctic keystone plant species. *Global Change Biol.* 11 (10), 1628–1639.
- Lienard, J., Florescu, I., Strigul, N., 2015. An appraisal of the classic forest succession paradigm with the shade tolerance index. *PLoS One* 10 (2).
- Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., Schabenberger, O., 2006. SAS for Mixed Models, second ed. SAS Institute, Inc., Cary, NC.
- Louda, S.M., Keeler, K.H., Holt, R.D., 1990. Herbivore influences on plant performance and competitive interactions. In: Grace, J.B., Tilman, D. (Eds.), *Perspectives on Plant Competition*. Academic Press, San Diego, pp. 413–444.
- Mahall, B.E., Bormann, F.H., 1978. A quantitative description of the vegetative phenology of herbs in a northern hardwood forest. *Bot. Gaz.* 139 (4), 467–481.
- Maron, J.L., Crone, E., 2006. Herbivory: effects on plant abundance, distribution and population growth. *Proc. Roy. Soc. B: Biol. Sci.* 273 (1601), 2575–2584.
- Martinod, K.L., Gorchov, D.L., 2017. White-tailed deer browse on an invasive shrub with extended leaf phenology meets assumptions of an apparent competition hypothesis. *AoB PLANTS* 9 (2).
- McCarthy, J., 2001. Gap dynamics of forest trees: A review with particular attention to boreal forests. *Environ. Rev.* 9 (1), 1–59.

- Nuttle, T., Ristau, T.E., Royo, A.A., 2014. Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years. *J. Ecol.* 102 (1), 221–228.
- Peebles-Spencer, J.R., Haffey, C.M., Gorchoy, D.L., 2018. Browse by white-tailed deer decreases cover and growth of the invasive shrub *Lonicera maackii*. *Am. Midland Natural.* 179 (1), 68–78.
- Peterson, C.J., Carson, W.P., 1996. Generalizing forest regeneration models: the dependence of propagule availability on disturbance history and stand size. *Can. J. For. Res.* 26 (1), 45–52.
- Rathcke, B., Lacey, E.P., 1985. Phenological patterns of terrestrial plants. *Annu. Rev. Ecol. Syst.* 16 (1), 179–214.
- Ristau, T.E., Stoleson, S.H., Horsley, S.B., deCalesta, D.S., 2011. Ten-year response of the herbaceous layer to an operational herbicide-shelterwood treatment in a northern hardwood forest. *For. Ecol. Manage.* 262 (6), 970–979.
- Royo, A.A., Carson, W.P., 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Can. J. For. Res.* 36 (6), 1345–1362.
- Royo, A.A., Collins, R., Adams, M.B., Kirschbaum, C., Carson, W.P., 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. *Ecology* 91 (1), 93–105.
- Royo, A.A., Kramer, D.W., Miller, K.V., Nibbelink, N.P., Stout, S.L., 2017. Spatio-temporal variation in foodscapes modifies deer browsing impact on vegetation. *Landscape Ecol.*
- Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N., Loreau, M., 2014. Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology* 95 (9), 2479–2492.
- SAS Institute Inc, 2013. SAS System for Windows. SAS Institute, Inc., Cary, NC.
- Schnitzer, S.A., Reich, P.B., Bergner, B., Carson, W.P., 2002. Herbivore and pathogen damage on grassland and woodland plants: a test of the herbivore uncertainty principle. *Ecol. Lett.* 5 (4), 531–539.
- Schwinning, S., Weiner, J., 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113 (4), 447–455.
- Smith, L., 2013. Extended leaf phenology in deciduous forest invaders: mechanisms of impact on native communities. *J. Veg. Sci.* 24 (6), 979–987.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry: the Principles and Practice of Statistics in Biological Research*, third ed. W.H. Freeman Company, New York.
- Stout, S.L., Royo, A.A., deCalesta, D.S., McAleese, K., Finley, J.C., 2013. The Kinzua Quality Deer Cooperative: can adaptive management and local stakeholder engagement sustain reduced impact of ungulate browsers in forest systems? *Boreal Environ. Res.* 18, 50–64.
- Tilman, D., 1997. Mechanisms of plant competition. In: Crawley, M. (Ed.), *Plant Ecology*. Blackwell Science, Oxford, England, pp. 239–261.
- Valladares, F., Niinemets, Ü., 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annu. Rev. Ecol. Evol. Syst.* 39 (1), 237–257.
- Walters, B.F., Woodall, C.W., Russell, M.B., 2016. (dataset) White-tailed deer density estimates across the eastern United States, 2008. Retrieved from the Data Repository for the University of Minnesota, <https://dx.doi.org/10.13020/D6G014>. [accessed 2/8/2019 2019].
- Walters, M.B., Reich, P.B., 1996. Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology* 77 (3), 841–853.
- Webster, C.R., Jenkins, M.A., Rock, J.H., 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park. *USA. Biol. Conserv.* 125 (3), 297–307.
- Weiner, J., 1990. Asymmetric competition in plant populations. *Trends Ecol. Evol.* 5 (11), 360–364.
- Wolkovich, E.M., Cleland, E.E., 2011. The phenology of plant invasions: a community ecology perspective. *Front. Ecol. Environ.* 9 (5), 287–294.