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Research article

Species and physiographic factors drive Indian cucumber root and Canada mayflower plant chemistry: Implications for white-tailed deer forage quality

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ABSTRACT

Nutrition is fundamental to white-tailed deer (*Odocoileus virginianus*) management given its relationship to habitat carrying capacity and population productivity. Ecological Sites (ESs) are a United States federal landscape management unit of specific land potential due to unique soils, topography, climate, parent material, and perhaps deer forage nutritional value. We present results of a study that extends the use of ESs to inform white-tailed deer management by evaluating indicator plant chemistry in two spring forb species, Indian cucumber root (*Medeola virginiana)* and Canada mayflower (*Maianthemum canadense*), across the northcentral Appalachians. We sampled spring forbs and underlying soils across two ESs: *Dry, upland, oak–maple–hemlock hardwood forest* (OMH) and *Deep soil, high slope, northern hardwood forests* (NHF). Plant elemental content, soil pH, and site aspect, slope and elevation were measured. Our results show that forb chemistry differs between species and within a species geographically. Indian cucumber root, as compared to Canada mayflower, has significantly higher Mg, Na, Cu, Fe, and Zn, and lower Mn. Canada mayflower in the NHF ES, versus OMH ES, was found to have significantly higher K, Mn, and B. Indian cucumber root in the NHF ES, versus the OMH ES, was found to have significantly higher Mg, Al, Fe, and Ca:P ratio but lower K. Linear discriminant analysis shows that plant tissue Mn was the best discriminator between species, and between ESs, Canada mayflower plant tissue Mn and Indian cucumber plant tissue P, K, Ca, Mg and Mn were best discriminators. Given that nutrition determines habitat carrying capacity, differences in forage nutrition between ESs may have different potentials to support deer. Forage nutrition is an important aspect of deer habitat conditions and carrying capacity, thus ESs are likely to support deer populations with different growth potential, which means that even if the same plant species occur in different ESs their nutritional value to deer may differ.

1. Introduction

The United States Department of Agriculture (USDA), Natural Resources Conservation Service (NRCS) has led a national effort to develop a new type of land management unit, the Ecological Site (ES). Ecological Sites provide a framework for classifying and describing forestland soils and vegetation with the intention of delineating areas that should respond similarly to management activities or disturbance. Used in conjunction with state-and-transition models (Bestelmeyer, 2015; Bestelmeyer et al., 2017), ESs can help guide land management decisions that consider current and potential flora, fauna, soils, and commodities (USDA-NRCS, 2014). State-and-transition models used with ESs have been shown to predict the response of wildlife populations to habitat changes using a variety of ecological indicators (Holmes and Miller, 2010; Geaumont et al., 2016; Hendrickson et al., 2016; Sussman et al., 2010) and thus can act as a framework to inform wildlife and habitat management decision making (Sussman et al., 2010). Also, because ESs are delineated using environmental factors that influence vegetation, such as soil, they may represent areas of distinct habitat quality for wildlife.

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White-tailed deer (*Odocoileus virginianus*) are native to eastern North America, are socially and economically important (USFWS, 2018), and as herbivores are directly affected by the quantity and quality of vegetation available as forage. Furthermore, deer themselves can be a disturbance in forested ecosystems because at high densities they differentially consume plant species, which can alter current and future plant species composition (Tilghman, 1989; Horsley et al., 2003; Nuttle et al., 2014; Latham et al., 2005; Rawinski, 2008; DiTommaso et al., 2014). Consequently, managing forests and white-tailed deer are inextricably linked where it can be beneficial for natural resource agencies responsible for managing deer to consider forest habitat conditions (Rosenberry et al., 2009) and, similarly, for landowners and natural resource agencies managing forests to consider the effects of deer herbivory (White, 2012).

The quantity and quality of forest vegetation can influence the density of deer that a given ES can support and can influence population productivity (Fulbright and Ortega-Santos, 2013). Because deer are selective in the consumption of plant species, preferred species can serve as an indicator of browsing pressure on forest vegetation (Filazzola et al., 2014; Wam et al., 2021). However, understanding is limited in terms of how deer forage changes spatially and temporally (Ónodi et al., 2017), or how forage-specific nutrition varies seasonally. Forbs comprise 36–75% of U.S. white-tailed deer diet in the spring but forb consumption declines through the summer (Barnes et al., 1990; Crawford, 1982). Indian cucumber root (*Medeola virginiana*) and Canada mayflower (*Maianthemum canadense*) are two northern Appalachian spring forbs that are preferred by white-tailed deer. Canada mayflower can comprise 20–25% of the total spring diet of white-tailed deer in eastern North American forests, and >50% of total forbs in the summer (Crawford, 1982; Skinner and Telfer, 1974). These two forbs co-occur in northern Appalachian forests and the presence and growth of both species is negatively related to deer density due to herbivory (Goetsch et al., 2011; Rooney, 1997; Stout et al., 2013).

Deer utilize a number of food sources, but forbs, compared to other forages, are an important component of the diet of white-tailed deer because they generally have higher concentrations of P and K, essential nutrients for ungulates (McDowell, 1985; Vangilder et al., 1982). Because P plays a role in skeleton formation, protein formation, and nearly every aspect of metabolism (McDowell, 1985; Robbins, 1983), the needs of white-tailed deer vary seasonally and by age. For example, P requirements for mature males are 1600 mg kg^{-1} P (percent dry weight in diet) in the spring and 1100 mg kg^{-1} P in the summer (Grasman and Hellgren, 1993; Fulbright and Ortega-Santos, 2013). White-tailed deer fawns require greater levels of P in their diet (4600–5100 mg kg^{-1}; Fulbright and Ortega-Santos, 2013). Almost 50% of Na can be lost in white-tailed deer during lactation, so females require twice the amount of Na as male deer during the spring (Pletscher, 1987).

Not only are dietary concentrations of nutrients important, but the ratio of certain elements in the diet can be critical to white-tailed deer health. The Ca:P ratio is considered an important dietary metric for indicating adequate P metabolism (Fulbright and Ortega-Santos, 2013). A dietary Ca:P ratio of 1:1–7:1 is acceptable for white-tailed deer, but a lower ratio is important when P intake is low because relatively high Ca can exacerbate P deficiency (McDowell, 1985; Ullrey et al., 1973). Excess of Ca, P, or K can cause Mg deficiency and result in a disorder called grass tetany (McDowell, 1985).

Seasonality is a potentially important consideration in deer nutrition because plant nutrients can change over the growing season as plant tissues senesce. Nutrients associated with photosynthesis (P, K, and Cu) decrease with senescence and nutrients associated with plant structural components (e.g., Ca) increase with senescence (Oster et al., 2018). Magnesium and Mn also may decrease over the growing season (Suttle, 2010). Nutrient ratios affect diet quality because, for example, plant senescence could create increasingly inadequate Ca:P ratios for white-tailed deer. Given that the ultimate source of elements in plants is soil, soil plays an important role in deer health and behavior by influencing deer forage nutrient content and biomass. The spatial distribution of soils correlates with nutritional differences among deer forages in Mississippi (Jones et al., 2010). The mineral content of forages and soil, especially Na, has been shown to explain the movement and concentration of ungulates across North America, Europe, and Africa (Jones and Hanson, 1985; McNaughton, 1988, 1990).

The use of Indian cucumber root and Canada mayflower as indicator species of deer browse pressure or diet composition is well studied (Rooney, 1997; Huebner et al., 2010). However, the use of plant chemistry from these forbs for also assessing potential deer health differences across landscapes, or spatial occurrence differences, is not documented. How might spatial and temporal changes in plant chemistry affect the use of these forbs as an indicator? We couple forb chemistry assessment over the growing season with a spatial assessment, using ESs, to show the importance of accounting for plant chemistry and geographic extent when using these forb ecological indicators to manage deer populations. Two preliminary ESs in northern Appalachian forests are the northern hardwood forest (NHF) and oak-maple-hemlock forest (OMF; Ireland and Drohan, 2015; Drohan and Ireland, 2016). Our objective was to quantify differences in forage nutrient content between Indian cucumber root and Canada mayflower and test whether differences in nutrient content exist between ESs.

2. Methods

2.1. Site and sampling

We sampled 90 Indian cucumber root and Canada mayflower plants from May to August 2017, across 59 permanent plots in 2 preliminary ESs (*Deep soil, high slope, northern hardwood forests* (NHF) and *Dry, upland, oak–maple–hemlock hardwood forests* (OMH)) of the northcentral Appalachians (Fig. 1, Table 1; Ireland and Drohan, 2015; Drohan and Ireland, 2016).

The OMH ES occurs within the Ridge and Valley physiographic province (Berg et al., 1980; Shultz, 1999; Sevon, 2000). The Ridge and Valley Province is a series of parallel sandstone and shale ridges and dominantly shale or limestone valleys running approximately northeast to southwest. Plots in this ES site occur within Rothrock and Bald Eagle state forests, which overlay Silurian and Devonian-aged formations comprised largely of quartzite, sandstone, and shale with inclusions of siltstone (Dicken et al., 2005). Soils consist of sandy, low-clay Inceptisols, Spodosols, and Ultisols with an acidic pH (<5) (Ciolkosz et al., 1989) and the USDA-NRCS soil climate regime is Typic Udic (moisture regime) and Typic Mesic (temperature regime) or Typic Udic/Moist Udic (moisture regime) and Typic Mesic (temperature regime) (Waltman, 1997). Mean yearly (years 1981–2010) rainfall from nearby State College, Pennsylvania (USNWS, 2021a) is 100.6 cm and temperature is 10.0 °C.

The NHF ES occurs across the unglaciated Appalachian Plateau and has thick, horizontally bedded sedimentary formations with highly dissected landscapes, v-shaped valleys, and dendritic stream patterns (Berg et al., 1980; Shultz, 1999; Sevon, 2000). Plots occur within Susquehannock State Forest and overlie Mississippian, Devonian, and Pennsylvanian-aged formations comprised specifically of sandstone and minor inclusions of siltstone and conglomerate (Dicken et al., 2005). Soils in the unglaciated Appalachian Plateau include Inceptisols, Spodosols, and Ultisols (Ciolkosz et al., 1989), and the USDA-NRCS soil climate regime is Perudic Udic (moisture regime) and Cool Phase Mesic (temperature regime) or Perudic Udic (moisture regime) and Frigid (temperature regime) (Waltman, 1997). Mean yearly (years 1981–2010) rainfall from the nearby Coudersport 7SE, Pennsylvania National Weather Service weather station is 106.8 cm and temperature is 6.6 °C (USNWS, 2021b).

We sampled plants and soils from 50 of 200 independently chosen permanent monitoring plots, which are part of an existing study (Begley-Miller et al., 2018, 2019) designed to assess the role of deer,

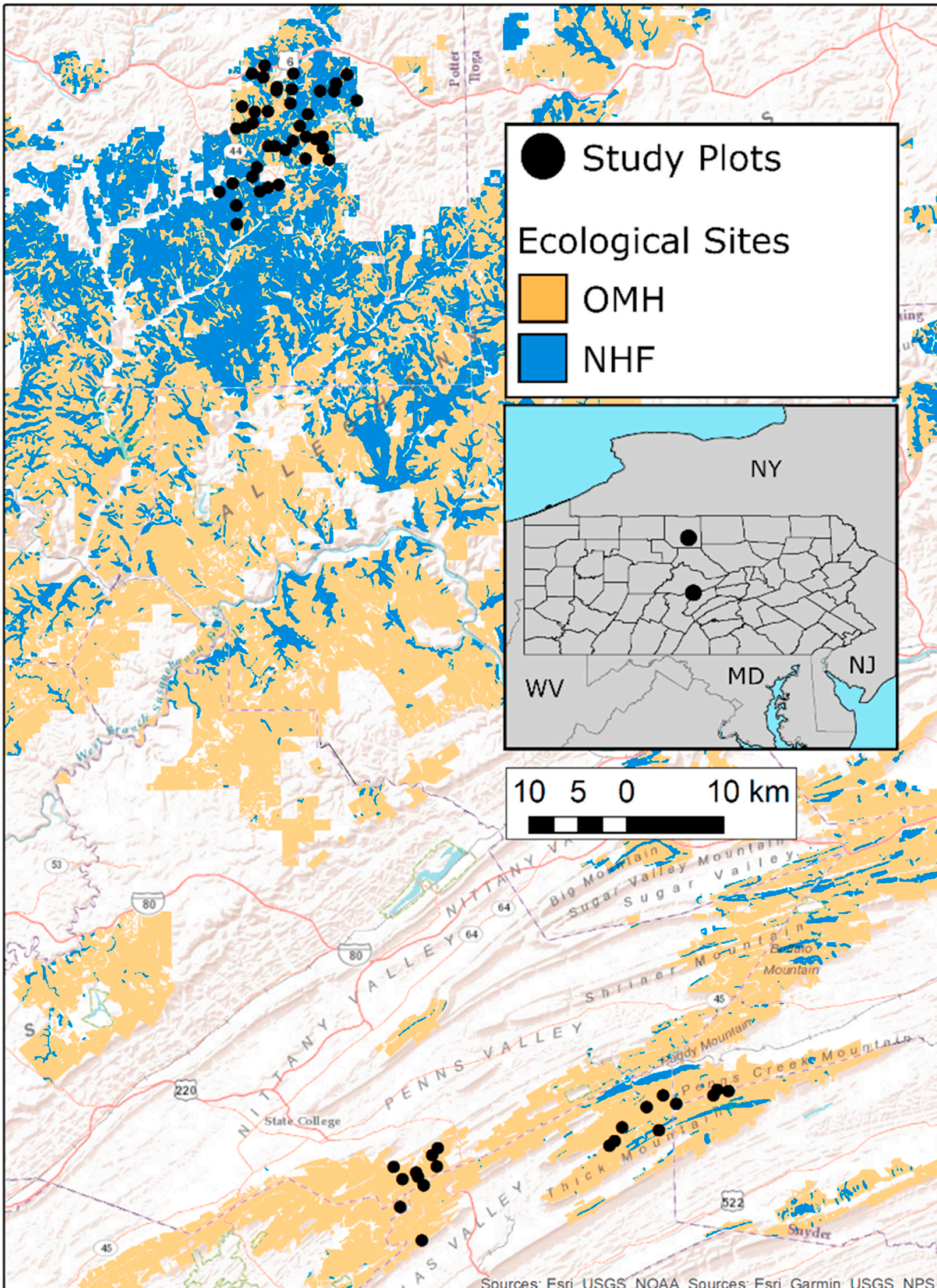

Fig. 1. Study area Ecological Sites are OMH (Dry, upland, oak-maple-hemlock hardwood forest) and NHF (Deep soil, high slope, northern hardwood forest). Pennsylvania county inset map with two black dots shows the general study area locations in the Mid-Atlantic United States (state name abbreviations included, WV = West Virginia, MD = Maryland, NJ = New Jersey; NY = New York).

Table 1
Means and standard errors of: A. species by aspect (percent of observations in parentheses); B. May–August growing species by elevation or slope); C. and D. soil pH differences between northcentral Pennsylvania Ecological Sites or where each species is growing.

	n plants	——— Aspect ———			
A. Species		*North*	*East*	*South*	*West*
Canada mayflower‡	33	12 (36%)	6 (18%)	10 (30%)	5 (15%)
Indian cucumber root	56	25 (45%)	10 (18%)	14 (25%)	7 (13%)
B.	**n plants**	**Elevation (m)**	**Slope (o)**		
Species					
Canada mayflower	33	650 (16)	11 (1.4)		
Indian cucumber root	56	620 (13)	10 (1.0)		
C.	**n plants**	**Elevation (m)**	**Slope (o)**		
Ecological Site/Species					
Northern hardwood					
Canada mayflower	28	667 (11)	11 (1.4)		
Indian cucumber root	37	674 (8)	12 (1.3)		
Oak hickory					
Canada mayflower	5	527 (179)	3 (4.9)		
Indian cucumber root	19	514 (85)	8 (1.4)		
D.		**Soil** pH **top horizon**	**Soil** pH **bottom horizon**		
Ecological Site					
Northern hardwood	65	3.2 (0.05)	3.8 (0.04)		
Oak hickory	24	3.1 (0.09)	3.7 (0.07)		
Species					
Canada mayflower	33	3.2 (0.07)	3.8 (0.06)		
Indian cucumber root	56	3.2 (0.06)	3.8 (0.05)		

*significant at an alpha = 0.05 using a Mood's median test.
†significant at alpha = 0.1 using a Mood's median test.
‡ICR: Indian cucumber root and CM: Canada mayflower; NHF: Deep soil, high slope, northern hardwood forest; OMH: Dry, upland, oak–maple–hemlock hardwood forest.

versus edaphic factors, in forest regeneration. We surveyed plots for each species, and if found, the aboveground forb biomass was sampled. In addition to plant sampling, we excavated a soil profile under the plant and sampled by morphologic horizon to at least 30 cm depth unless refusal was reached. If plants co-occurred within ~1.5 m of each other then we excavated only one soil profile. We described soils according to Schoeneberger et al. (2012), air dried, and sieved them through a 2-mm sieve. In three instances two plants were found on a plot. However, given plot-level differences are not the focus of our analysis, these plants were still treated as independent samples.

2.2. Chemical analysis

We oven dried plant material for 5 days at 45 °C and ground using a mill (Thomas Wiley Mill, USA) fitted with a 1 mm sieve. Plant samples underwent total elemental analysis at the Agricultural Analytical Services Laboratory at The Pennsylvania State University. We dry-ashed (Miller, 1988) and acid digested (Huang and Schulte, 1985) plant samples and extracts were analyzed for P, K, Ca, Mg, Mn, Fe, Cu, B, Al, Zn, Na, and S using a Varian 730-ES Inductively Coupled Plasma-Optical Emission Spectrometer (Palo Alto, CA).

Only pH data for the first and bottom horizons are reported in this study. We measured soil pH in 1 N KCl and 0.01 M $CaCl_2$ and mineral horizon soil pH samples were prepared in a 1:2 (weight:volume) solution (Blume et al., 1990). We measured soil pH using a VWR SympHony pH meter (Radnor, PA).

We extracted for each plot center in Fig. 1 topographic slope and aspect values (Deumlich et al. (2010) using a 10-m digital elevation model (USGS, 2019); aspect was recoded into four cardinal directions (north, east, south, west) (Schoeneberger et al., 2012).

2.3. Statistical analysis

We performed all analyses in RStudio (RStudio Team, 2016) or Minitab v21.1 (Minitab Statistical Software, 2022), and prior to parametric analyses, non-normal variables were transformed using a square root or log transformation; statistically significant relationships were noted using an $\alpha = 0.05$ and exploratory relationships using an $\alpha = 0.1$.

To account for the potential effects of seasonality in soil or plant chemistry sampling, we used ordinal date to adjust plant tissue chemistry data. The mid-point of the sampling period's ordinal date (180) was used to adjust the plant tissue chemical variable by multiplying its original value by the slope of a regression relationship between the values of the variable versus ordinal date; pooling both species (Appendix 1). If a site was sampled prior to the mid-point ordinal date the resulting adjustment was added to the original value, and if after, the adjusted value was subtracted (see Appendix 1 for regressions).

We used a 2-sample T-test (Minitab Statistical Software, 2022) to identify significant differences between ESs for each plant species' tissue element content and soil pH (surface mineral horizon and the horizon present at 30 cm).

We used Cross Tabulation with a Chi Square analysis to evaluate geographic aspect and species presence (counts). Within each ES, we applied linear discriminant analysis (Venables and Ripley, 2002) using variables that exhibited significant differences between ESs from the Mood median test. Linear discriminant analysis helped us determine if the plant nutrients were effective in predicting species membership within each ES.

While 90 plants were sampled, we removed one analysis because the sample mass was too small. We still used in analysis extraction ICP values that fell below the limit of quantitation (LOQ, the lowest concentration standard; 3 sulfur, 1 copper, 4 boron, and 39 sodium), but values used in analysis were derived by randomly selecting a calculated value between zero and one-half the detection limit.

3. Results

3.1. Edaphic differences

Between species, no significant difference was found in site aspect (Table 1A) or top or bottom horizon soil pH, elevation, or slope (Table 1B). Top horizon soil pH and elevation were significantly greater in ES NHF (Table 1C), while no difference was detected between ESs for bottom soil horizon pH or slope. Within each respective ES (Table 1D), no differences were detected between species in site top or bottom horizon soil pH, elevation, or slope.

3.2. Plant chemistry differences

Compared to Indian cucumber, Canada mayflower tissue Mg, Na, Al, Cu, Fe, and Zn was significantly lower and Mn was higher (Fig. 2). Canada mayflower tissue K, Mn, and B were significantly higher in ES NHF, versus OMH (Fig. 3). Indian cucumber tissue Ca:P, Mg, Mn, and Al was significantly higher in ES NHF while P and K were lower (Fig. 4). Tissue Mn was the best segregator of species as indicated by linear

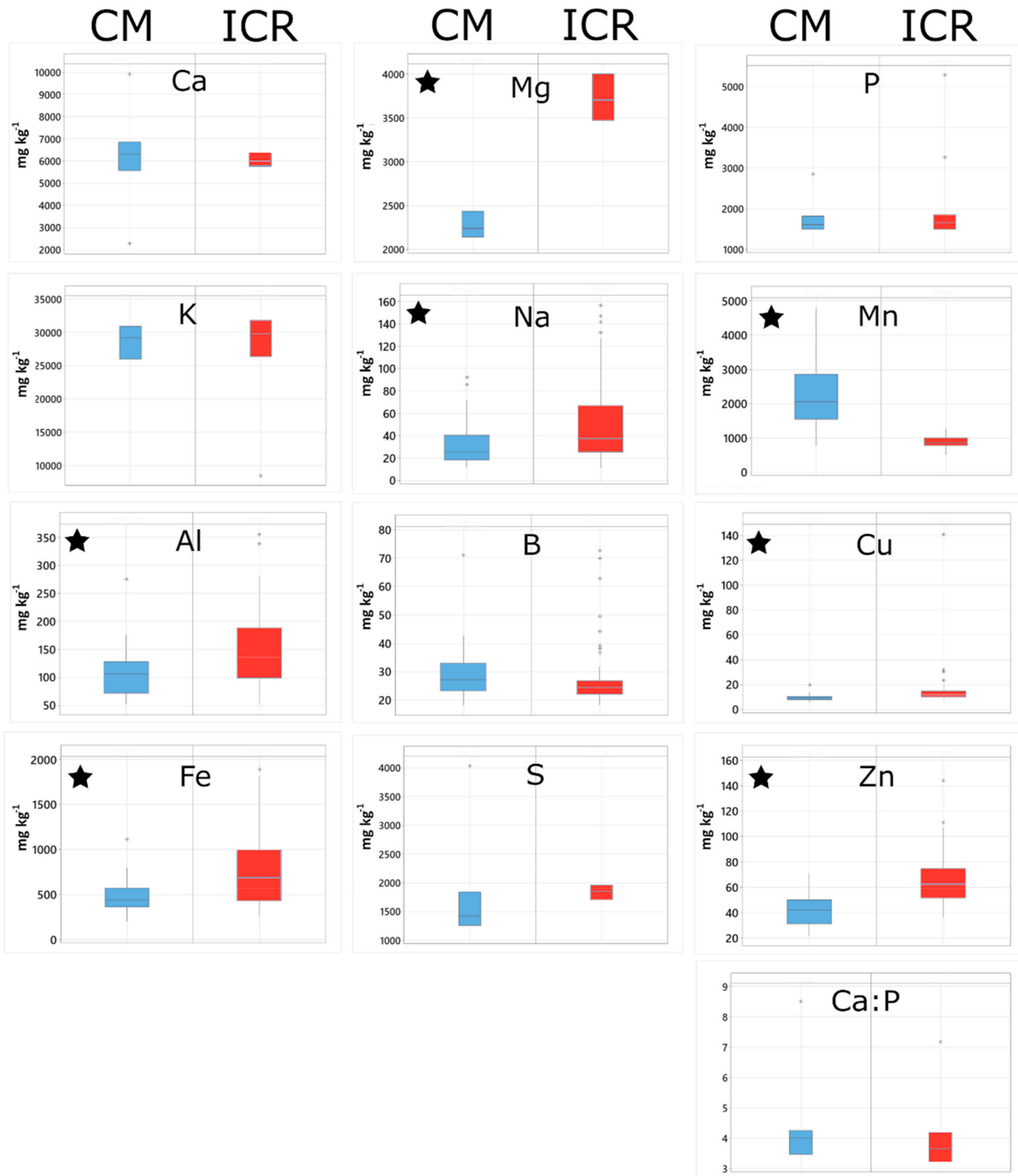

Fig. 2. T-Test (alpha = 0.05, stars indicate significant differences) results for May to August tissue chemistry (mg kg^{-1}) differences between Canada mayflower (CM) and Indian cucumber (ICR).

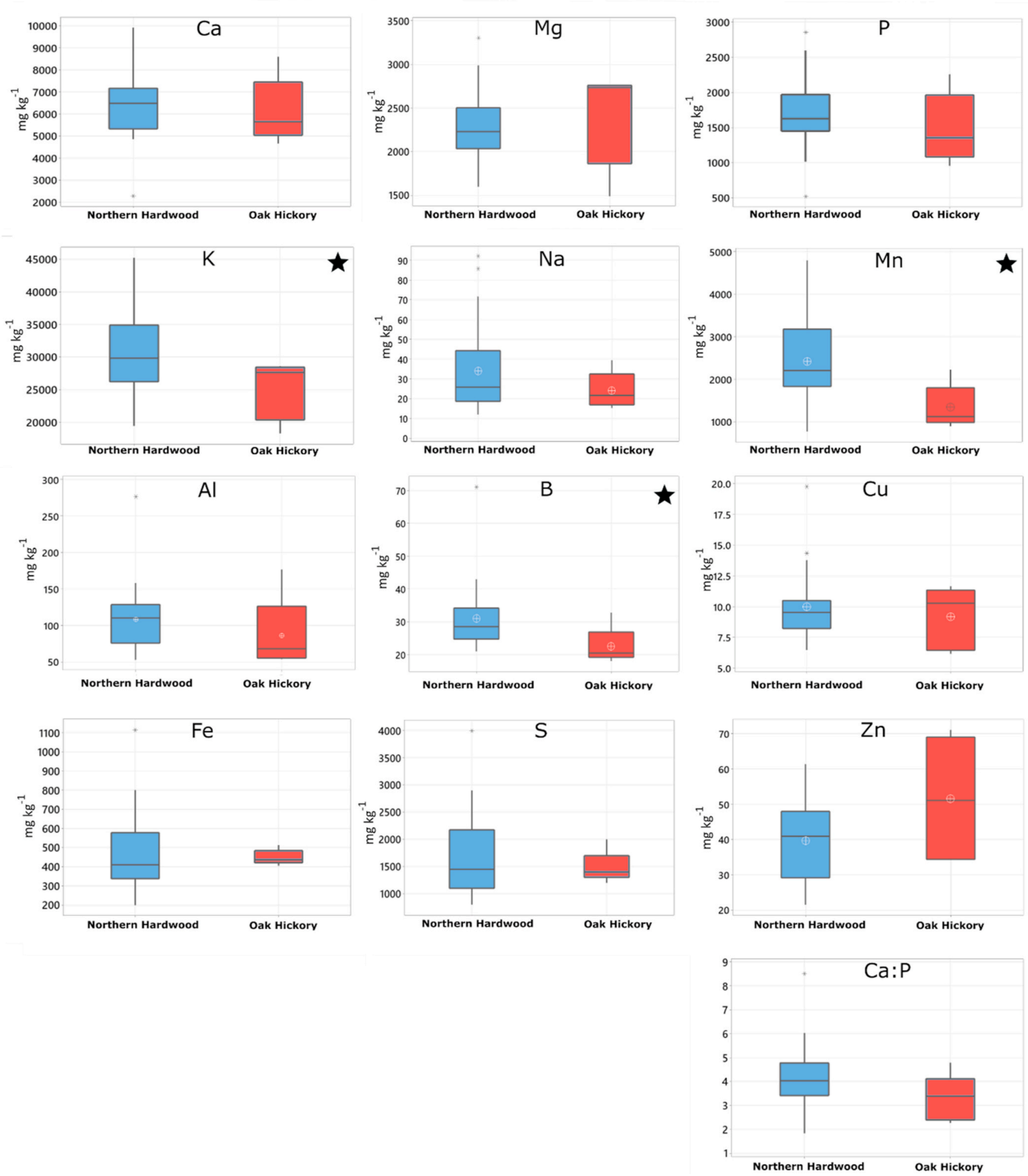

Fig. 3. Canada mayflower May to August tissue chemistry (mg kg^{-1}) T-Test results (alpha = 0.05, stars indicate significant differences) for differences between northcentral Pennsylvania Ecological Sites. Ecological Sites are Northern hardwood: Deep soil, high slope, northern hardwood forest; and Oak Hickory: Dry, upland, oak-maple-hemlock hardwood forest.

discriminant analysis with cross validation (91%; Table 2A). Tissue Mg was next best at discriminating between species (73%). Using a linear discriminant model with cross validation (Table 2B), Ecological Sites could be differentiated as well using plant chemistry. Canada mayflower tissue Mn was best at discriminating between ESs followed by P and Ca (76%, 73% and 73% respectively). Indian cucumber tissue P, K, Ca, and Mg were best at discriminating between ESs (97%, 86%, 73%, and 73% respectively). For both species, other plant chemistry elements could also segregate between ESs, but with a lower proportion of success (<70%).

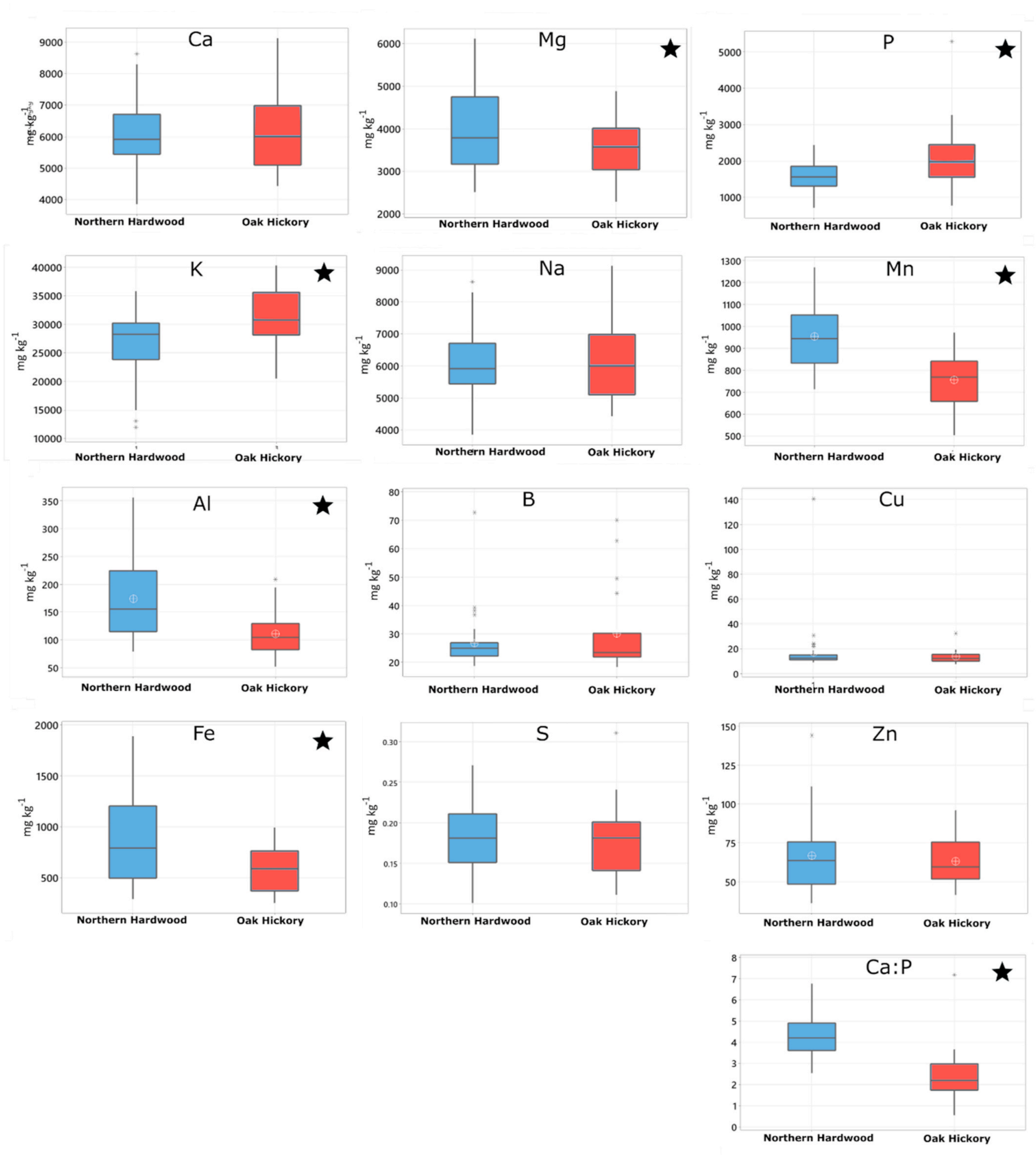

Fig. 4. Indian cucumber May to August tissue chemistry (mg kg^{-1}) T-Test results (alpha = 0.05, stars indicate significant differences) for differences between northcentral Pennsylvania Ecological Sites. Ecological Sites are Northern hardwood: Deep soil, high slope, northern hardwood forest; and Oak Hickory: Dry, upland, oak-maple-hemlock hardwood forest.

4. Discussion

4.1. *Forb chemistry differences: species-specific elemental signatures*

We found that forb chemistry differs between species and in some cases within a species between ESs. Forb chemistry differences could have implications for deer nutrition and health, especially given the concentrations of several elements was twice as high within and between species. For example, between forb species, Indian cucumber root Mg was nearly 2x higher while Mn was 2x lower. Canada mayflower in NHF had significantly higher K, Mn, and B. Indian Cucumber root in NHF had significantly higher Mg, Mn, Al, Fe, and a Ca:P ratio, but lower

Table 2
Discriminant analysis results using plant issue chemistry to differentiate between May–August growing species or northcentral Pennsylvania Ecological site.

A. Using plant issue chemistry to differentiate between species					
	Element	Proportion correct (%)			
	Mn	91			
	Mg	73			
	Fe	67			
	B	66			
	Al	63			
	Zn	63			
	Ca:P	61			
	Cu	60			
	Ca	59			
	S	59			
	Na	55			
	K	50			
	P	48			
B. Using CM or ICR plant tissue chemistry to differentiate between Ecological Sites					
Species[a]	Element	Proportion correct (%)	Species	Element	Proportion correct (%)
CM	Mn	76	ICR	P	97
	P	73		K	86
	Ca	73		Ca	73
	Mg	67		Mg	73
	Zn	67		Mn	71
	Al	61		Al	63
	K	61		B	63
	B	61		Fe	61
	S	52		Na	55
	Fe	46		Zn	48
	Cu	46		S	36
	Na	46		Cu	36
	C:P	21		C:P	23

[a] ICR: Indian cucumber root; CM: Canada mayflower.

P and K. White-tailed deer consuming these forbs, in different geographic areas, are potentially receiving different amounts of an element, which in turn could affect deer growth and body condition. Linear discriminant analysis indicated that Mn (91%) was by far the best forb chemistry variable discriminating between species followed by Mg (73%). Canada mayflower tissue manganese was also strong at differentiating between ESs (76%), followed by P and Ca (each 73%). Indian cucumber root P (97%) K, Ca, Mg, and Mn (86, 73, 73, and 71% respectively). Differences in forb chemistry between ESs are likely attributed to inherent differences in soils evolved in each ES via their unique soil forming factors (Ireland and Drohan, 2015).

Differences between forb species chemistry, between and within ESs, suggests that ranges in forb chemistry would be important to recognize given a plant in one ES could have differing plant chemistry from a plant in another ES. In addition, our results suggest that focusing on one or two elements of a forb's chemistry to ascertain, for example, the effect of forb chemistry on deer due to deer ingestion of the plant, could miss a broader suite of forb chemistry differences and their ultimate importance in deer health.

Coupled with species and regional differences in tissue chemistry, seasonal chemistry variability, especially nutrients associated with photosynthesis, could further alter forb tissue chemistry. For example, P, K, and Cu decrease to senescence and nutrients associated with plant structural components, notably Ca, increase to senescence (Oster et al., 2018). Magnesium and Mn may also decrease over the growing season but to a lesser extent (Suttle, 2010).

It is unknown if differences in forb abundance were due to geographic range or browse pressure. While the range of both our study species spans both ESs (Gleason and Cronquist, 1991; Kartesz, 2015 & 2018) we did find far fewer Canada mayflower plants in OMH (n = 5) as compared to NHF (n = 28). Given that Indian cucumber root declines in abundance as one moves north of our study area (Gleason and Cronquist, 1991; Kartesz, 2015 & 2018), we hypothesize that differences in our study species are tied to edaphic factors and less likely to browse pressure. Regardless, fewer plants of one species, with a better or worse forb chemistry for deer health, could affect deer health.

4.2. *What does forb chemistry tell us about potential deer health?*

Since Indian cucumber root and Canada mayflower are forbs that comprise a major portion of deer spring diet (Crawford, 1982; Skinner and Telfer, 1974; Stout et al., 2013), these species could have important implications for deer (e.g Ramírez et al., 1996), especially because of relatively high deer nutrient demand in spring months. Spring nutrient requirements for lactating females and weaned fawns are much higher than those of males (Fulbright and Ortega-Santos, 2013; Robbins, 1983). Lactating females can also lose more than 30% of P and significant amounts of Ca during lactation (Pletscher, 1987). Most fawns within the northcentral Appalachians are born during May–June, with half born by 1 June (Diefenbach et al., 2019). Weaned white-tailed deer require 4600–5100 mg kg^{-1} P compared to 1600 mg kg^{-1} for adult males (Fulbright and Ortega-Santos, 2013). Lactating females can also lose more than 30% of P and significant amounts of Ca during lactation (Pletscher, 1987).

Our results indicate that Indian cucumber root and Canada mayflower met the minimum Ca, Mg, and K dietary requirements in adult male deer or domestic ruminants across NHF and OMH (McDowell, 1985; Fulbright and Ortega-Santos, 2013). Dietary Na requirements for deer (400 mg kg^{-1}; McDowell, 1985; Robbins, 1983) were not met by either forb suggesting that deer must have some other source of Na for adequate nutrition but forages across the eastern U.S. (Pletscher, 1987) and Alaska (Oster et al., 2018) have consistently low Na content.

We found that the Ca:P ratio exceeded 2:1 [believed ideal for proper P metabolism in deer (Barnes, 1988; Barnes et al., 1990; Keegan et al., 1989)]. Canada mayflower mean P (1492 mg kg^{-1}) in OMH and Indian cucumber root mean P (1,586) in NHF was below the deer nutrient requirement (1600 mg kg^{-1}) (Figs. 3 and 4) (Fulbright and Ortega-Santos, 2013). Also, the P levels in both species was inadequate for weaned deer (4600–5100 mg kg^{-1}; Fulbright and Ortega-Santos, 2013); consumption of other food sources could make up low forb P.

Ecological Sites OMH and NHF may represent areas of distinct forage nutrition for Indian cucumber root and Canada mayflower, and thus require different approaches for addressing deer nutrition. Phosphorous is considered worldwide one of the most limiting nutrients for ungulates like deer (Grasman and Hellgren, 1993), so differences in forb P across ESs may be crucial for nutrition during the higher spring nutrient demand (Fulbright and Ortega-Santos, 2013). Future research could address seasonal differences in forb chemistry. Since Indian cucumber root and Canada mayflower are forbs that comprise a large portion of deer spring diet in the northeastern U.S. and Canada (Crawford, 1982; Skinner and Telfer, 1974; Stout et al., 2013), their ingestion, especially in different geographic areas given our results, could have important implications for deer condition. Few fawns get pregnant in NHF whereas about 20% do in the OMH (Diefenbach et al., 2019). Fawn pregnancy differences are likely related to nutrition because fawns need to attain a minimum body mass before they will come into estrus.

5. Conclusion

We paired forb chemistry assessment with a spatial assessment, using USDA ESs, to show the importance of accounting for plant chemistry and geographic extent when using these forb ecological indicators to assess the effects of deer herbivory. Our results show important, significant differences in forb chemistry between and within ESs. Given these identified differences in plant chemistry between geographic regions, we hypothesize that deer carrying capacity would also differ, and thus management of deer populations may need to adjust deer population objectives for individual management units.

Preliminary ESs NHF and OMH may represent areas of distinct white-tailed deer nutrition in spring forages such as Indian cucumber root and Canada mayflower, especially for low levels of P. While both species have adequate Ca:P, both forb species have low P levels and in some instances mean values drop below the overall deer nutrient requirement of 1600 mg kg^{-1} and well below the weaned deer nutritional requirement of 4600–5100 mg kg^{-1}. Given that nutrition determines habitat carrying capacity, differences in forage nutrition between ESs may have different potentials to support deer.

The nutritional quality of forage is important to deer management because it determines habitat carrying capacity and population productivity (Fulbright and Ortega-Santos, 2013). The Pennsylvania Department of Conservation and Natural Resources uses forest understory vegetation conditions to inform the number of hunting permits issued by management unit (DCNR, 2018). Given that forage nutrition is an important aspect of habitat conditions and carrying capacity, ESs are likely to support deer populations with different growth potential, which means that even if the same plant species occur in different ESs their nutritional value to deer may differ. In turn, this may mean that wildlife and forest managers could benefit from different levels of abundance of these indicator species to support similar deer densities.

Author contribution

Navarro contributed to conceptualization, Investigation, Methodology, Visualization, Writing – original draft; Drohan, Diefenbach and McDill contributed to funding acquisition, Supervision, Conceptualization, Investigation, Resources, Methodology, Visualization, Writing – original draft, Writing – review & editing; Rosenberry and Domato contributed to funding acquisition, Conceptualization, Investigation, Resources, Methodology, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2022.116545.

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