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Soil quality does not predict plant nutrition available to white-tailed deer

Craig A. Harper[1] | Bronson K. Strickland[2] | Marcus A. Lashley[3] |
Mark A. Turner[1] | Jordan S. Nanney[1] | M. Colter Chitwood[4] |
Christopher E. Moorman[5] | Natasha Ellison-Neary[2] |
Jarred M. Brooke[6] | Garrett M. Street[2]

[1]School of Natural Resources, University of Tennessee, 401 Agriculture and Natural Resources Building, Knoxville, TN 37996-4563, USA

[2]Department of Wildlife, Fisheries and Aquaculture, Mississippi State University, 100 Thompson Hall, MS State, MS 39762, USA

[3]Department of Wildlife Ecology and Conservation, University of Florida, 322 Newins-Ziegler Hall, Gainesville, FL 32611, USA

[4]Department of Natural Resource Ecology and Management, Oklahoma State University, 008C Agricultural Hall, Stillwater, OK 74078, USA

[5]Department of Forestry and Environmental Resources, North Carolina State University, 3225 Jordan Hall, Raleigh, NC 27607, USA

[6]Department of Forestry and Natural Resources, Purdue University, Forestry Building Room 202, West Lafayette, IN 47907, USA

Correspondence
Craig A. Harper, School of Natural Resources, University of Tennessee, 401 Agriculture and Natural Resources Building, 2431 Joe Johnson Drive, Knoxville, TN 37996-4563, USA.
Email: charper@utk.edu

Present addresses
Mark A. Turner, Department of Natural Resource Ecology and Management, Oklahoma State University, 008C Agricultural Hall, Stillwater, OK 74078, USA.

Abstract

Morphometric variation of white-tailed deer (*Odocoileus virginianus*; hereafter, deer) is caused by multiple environmental factors, including temperature, precipitation, soil quality, and forage availability. The effects of temperature and precipitation on plant growth are well documented, but it is unclear how soil mineral concentration affects deer morphometrics. Although it is recognized that deer have larger morphology and greater productivity in areas of the United States with mineral-rich soils, the question remains as to whether this trend is driven by increased food availability in areas with mineral-rich soils because of land use (i.e., agriculture) or if nutrient concentration of plants is greater in soils with greater mineral concentration. We collected plant tissue from 40 species commonly selected as forage by deer at 36 sites in 16 states across the eastern United States, representing a wide range of soil quality conditions over a broad geographical area. We categorized plant sampling locations into 5 soil quality classes based on a soil productivity index and analyzed plant nutrients to assess if soil productivity index classifications could be used to predict deer forage quality. We then made direct soil-plant comparisons by pairing each plant sample with a soil sample collected around the base of the plant to determine if soil nutrient concentration explained variation in plant nutrient concentration. We tested soil samples for phosphorus, potassium, and calcium. We analyzed plant samples for crude

Jordan S. Nanney, Compass South, Inc., 452 Upchurch Lane, Walterboro, SC 29488, USA.

protein, phosphorus, potassium, and calcium for the soil productivity classification comparisons, and we analyzed phosphorus, potassium, and calcium for the direct site-specific analyses, as these macronutrients are critical to deer body mass, productivity, and antler growth. We analyzed forages by plant type (i.e., forb, semi-woody, shrub, or tree) and plant tissue age (i.e., young or older tissue). Nutrient concentration varied by plant type and tissue age. Plant type explained the majority of variation in plant nutrients, with forbs containing greater concentrations of all nutrients than the other plant types. Young plant material contained more crude protein and phosphorus, whereas older plant material contained more calcium. The soil productivity index was a poor predictor of deer forage quality. Calcium was the only mineral that differed by soil productivity class, but calcium was not limiting for deer at any site, as plant calcium levels exceeded maximum requirements for deer across all soil productivity classes. Site-specific soil phosphorus, potassium, and calcium explained little variation in plant mineral concentration (partial $R^2 = 0.00$). Our results provide evidence that naturally occurring plants, especially forbs, can provide nutrition sufficient for maximum deer body weight, reproduction, and antler size, within a given area, across the eastern United States regardless of the dominant soil type. As such, the availability of naturally occurring native forbs may be a primary limiting factor regulating age-specific deer body mass and antler size, not limitations in plant nutrients resulting from soil mineral concentration. Land managers should be encouraged to influence plant composition toward greater forb coverage where increased forage quality for deer is desired, even in areas with soils low in mineral concentration.

KEYWORDS
deer forage, forbs, nutritional carrying capacity, *Odocoileus virginianus*, plant nutrients, soil nutrients, soil productivity index

Cervids exhibit variation in body mass, antler size, and reproduction based on a variety of factors. Moose (*Alces alces*), caribou (*Rangifer tarandus*), elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), red deer (*Cervus elaphus*), and white-tailed deer (*O. virginianus*) all vary in body and antler size in response to environmental conditions and availability of food resources (Robinette et al. 1973, Geist 1986, Skogland 1986, Sand et al. 1995, Bender et al. 2003, Jones et al. 2010b). Morphometrics of white-tailed deer (hereafter deer) vary greatly, with average

mature male body weights ranging from 110 kg in south-central Canada and north-central United States (Kline 1965, Fuller et al. 1989) to 65 kg in Gulf coastal populations (Strickland and Demarais 2000), and down to 34 kg in Key deer (*O. v. clavium*; Dickson 1955). Morphological requirements for heat dissipation (Speakman and Król 2010) coupled with spatial variability in net primary production (Huston and Wolverton 2011) are considered the primary cause of extreme variation in body size. Deer reproduction also is influenced by diet quality; maternal age and reproductive rate of deer vary with nutrient availability and a higher percentage of female fawns and yearlings breed when on a high nutritional plane (Morton and Cheatum 1946, Nixon 1971, Hansen et al. 1996, Green et al. 2017). Population density can affect body size at the local level (Kie et al. 1983, McCullough 1984, Ashley et al. 1998, Lashley et al. 2015), and more recent research has indicated chronic nutritional conditions over generations of deer may be responsible for much of the variation observed within the center of their distribution (Monteith et al. 2009, Michel et al. 2016).

Soils are considered a limiting factor because it is assumed that soil mineral content regulates nutrient availability in plants accessible to deer, and morphometrics and reproduction for deer and other species positively correlate with soil productivity across a soil-quality gradient (Crawford 1950, Jacobson 1984, Strickland and Demarais 2000, Jones et al. 2008, Jones 2010a, Lehoczki et al. 2011). However, the causative mechanism behind this correlation has not been established through scientific study. One hypothesis is that plants growing in nutrient-poor soils are deficient in minerals because those minerals are lacking in the soil; hence, nutrient-rich foods are not available for deer where those soils occur (Thorsland 1966, Shea et al. 1992, Shea and Osborne 1995, Keyser et al. 2005). Empirical data that support this hypothesis are lacking. Another hypothesis is that nutrient-poor soils limit plant growth (biomass) and yield, which reduces the amount of high-quality food available per deer (Geist 1987, 1998; Huston and Wolverton 2011). Lashley et al. (2015) reported various plant species in an area with mineral-poor soils contained minerals at levels sufficient to support deer during the period of greatest nutritional demand (lactation), deer selected those plants while foraging, and deer body mass increased as deer density decreased, refuting the first but supporting the second hypothesis. However, their study did not compare nutrient availability across a soil-quality gradient but simply demonstrated that nutritional quality of plants was maintained at the extreme low end of soil mineral content.

The relationship between soil minerals and plant minerals has been studied globally, but contrasting results from different regions and among different plant species indicate this relationship is not consistent among sites, minerals, or plant species (Chapin 1980, Aerts and Chapin 2000, Ordoñez et al. 2009, Zhang et al. 2017, Lin et al. 2019). Most of the research investigating the relationship between soil and plant nutrients has involved woody plant species, and relatively little work has been conducted in the United States involving native forbs and semi-woody plants, especially those selected by deer (Thorsland 1966, Dyess et al. 1994, Gilliam et al. 2018). Plants growing in nutrient-poor soils develop adaptations or traits that allow them to acquire sufficient nutrition for growth and development (Rorison 1968, White 1972, Chapin 1980, Aerts and Chapin 2000). For example, leaves may be reduced in number and size under stressful conditions, nutrients from older leaves may be moved to younger leaves, and plants may store nutrients through luxury consumption (Chapin 1980). Thus, plants may maintain greater tissue nutrient concentrations and show no macronutrient deficiency symptoms. As a concentrate selector, deer select younger plant parts that are more digestible and provide necessary nutrients (Hesselton and Hesselton 1982, Hoffman et al. 1989, Demarais et al. 2000, Lashley et al. 2015). Therefore, deer may be able to obtain sufficient nutrition for a large body and antler size and maintain productivity even on nutrient-poor soils if plant composition and deer density are not limiting forage availability.

Predominant land use may confound understanding of the influence of soils on nutrient availability for deer. For example, greater numbers of large-antlered deer are present in areas with greater variation in soil quality (Cain et al. 2019), and conversion of cropland to grassland has led to reduced deer body mass (Hefley et al. 2013). Soil fertility variation leads to differential land use, as agriculture is common in areas with greater soil fertility and forests dominate landscapes with less-productive soils (Roseberry and Woolf 1998, Schaetzl et al. 2012). Jones et al. (2010b) reported the presence of agriculture and the associated superior forage quality in the Delta region of Mississippi, USA, prevented modeling deer body mass or antler size as related to variation in forage quality in that

region because there was insufficient variation in both soil and plant quality throughout the region. Agriculture may increase nutrition for deer in 3 ways: many of the agricultural plants themselves (e.g., soybeans, alfalfa, and wheat) provide high-quality food for deer (Lashley et al. 2011, Hefley et al. 2013, Harper 2019, Turner et al. 2024b); agricultural landscapes are open, supporting more early successional nutrient-rich forbs than available in shaded forested environments (Lashley et al. 2011, Nanney et al. 2018, Turner et al. 2020, Powell et al. 2022); and deer density typically is less in open landscapes than forested landscapes, allowing more food per deer in open land-scapes (Roseberry and Woolf 1998, Hanberry 2021). Thus, it is not clear whether the influence of soils on deer morphometrics is a result of nutrient-rich soils elevating nutrient levels in the naturally occurring plants growing on those sites, increased biomass of naturally occurring plants growing on those sites, or if land-use practices (e.g., agriculture) supplement the existing native forage plants thereby providing a greater abundance of high-quality food in areas with nutrient-rich soils.

Understanding the environmental factors that cause spatial disparities in morphometrics may be important not only for conservation of deer but also other wildlife species. For example, if nutrition of individual plants is not the limiting factor in areas of nutrient-poor soils, then those areas could be managed such that naturally occurring plant communities provide adequate nutrition for deer without planting or providing supplemental food (Harper et al. 2021), thereby increasing habitat for many species that require early successional plant communities and open woodland communities (Harper 2007, GeFellers et al. 2020), while also ameliorating browsing pressure in adjacent forested communities that often are over-browsed and fail to provide habitat for various forest-dwelling species (McShea 1997, Waller and Alverson 1997, Rooney and Waller 2003, Côté et al. 2004). Furthermore, hunter participation is strongly linked with expectations and satisfaction levels (Brunke and Hunt 2008, Harper et al. 2012, Nanney et al. 2015, Quehl et al. 2024). If naturally occurring plant communities can be managed to positively influence deer body weights and antler size in areas with nutrient-poor soils, then hunters may be more likely to support managing deer density within nutritional carrying capacity and implementing habitat management that would benefit deer and many other wildlife species linked to early successional and open woodland plant communities (Harper et al. 2021; Lashley et al. 2015, 2022; Powell et al. 2022; Turner et al. 2024a).

We investigated the relationship between soil minerals and plant nutrients using a large-scale, multi-state field study. We collected tissue samples from commonly selected deer forages along with paired soil samples at 36 sites across 16 states encompassing a complete range of soil-quality index conditions to determine if soil minerals influence plant nutrition for deer. Based on data indicating nutrient-rich plants may occur in mineral-poor soils (Lashley et al. 2015, 2022), we hypothesized nutrient and mineral concentration for a given plant genus or species would be similar in mineral-rich and mineral-poor soils. We examined this hypothesis at 2 levels. First, we compared plant quality among broad groups of soils based on a soil productivity index classification (large spatial scale; Schaetzel et al. 2012) because the index positively relates to crop yields, and we were interested to see if such an index could be used to predict plant nutrient concentration. Second, we related plant mineral concentration to soil mineral concentration at the site where the plants were sampled (fine spatial scale; Lashley et al. 2015) to determine if soil nutrient concentration is related to plant nutrient concentration. We predicted plant nutrient concentration would be greatest for herbaceous species (forbs) and less for semi-woody (briars and brambles) and woody species (shrubs and trees), which are higher in lignin concentration and typically less digestible (Short et al. 1974, Vangilder et al. 1982, Nanney et al. 2018). We also predicted that a soil productivity index would not accurately predict plant nutrition available for deer, and site-specific soil mineral concentration would not be related to plant tissue mineral concentration.

STUDY AREA

We selected 36 study sites within the geographic distribution of white-tailed deer across the eastern United States (Figure 1) for sampling in 2015–2020. These sites had a mixture of ownership: 24 were privately owned and 12 were public properties, including Wildlife Management Areas managed by state wildlife agencies and federal
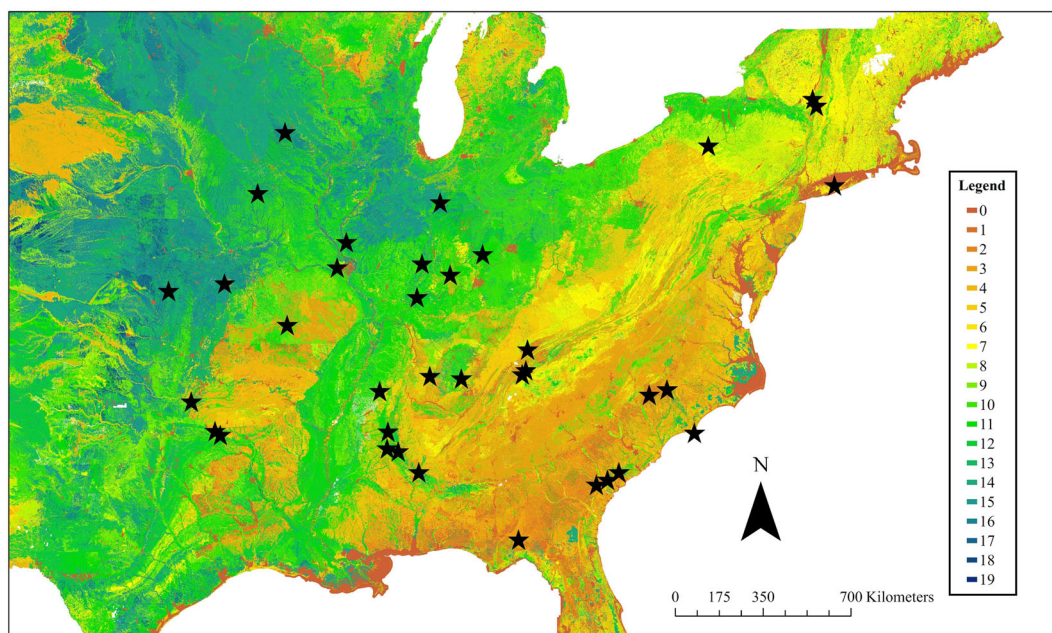
FIGURE 1 Locations of 36 sites across 16 states in the United States where we collected white-tailed deer forages and soil samples in June and July 2015, 2016, 2017, and 2020. Colors represent a soil productivity index ranging from 0 (least productive) to 19 (most productive).

military installations. Vegetation types, climate, land use, elevation, soil types, and geology varied widely across study sites in 16 states, representing considerable diversity across the study area. For example, dominant soil types ranged from silt loams in Iowa to cherty, channery, and gravelly loams in Pennsylvania, New York, and Tennessee to sand in eastern North Carolina (Natural Resources Conservation Service 2024). Dominant plant communities included longleaf pine (*Pinus palustris*) savanna in Florida, Blackland Prairie in Mississippi and Alabama, tallgrass prairie in Kansas, oak (*Quercus* spp.)-hickory (*Carya* spp.) forests and woodlands in Tennessee, and northern hardwood forest types in Pennsylvania and New York. Annual mean precipitation ranged from 84.6–145.5 cm/year (National Oceanic and Atmospheric Administration 2024).

METHODS

Forage and soil quality

We selected study sites based on the soil productivity index developed by Schaetzl et al. (2012), which considered family-level soil taxonomy information to rank soils and verified classifications using crop growth, yield, and production data along with land use and other productivity indices. The soil productivity index ranged from 0 (least productive) to 19 (most productive). Because of logistical difficulty and the cost associated with sampling multiple sites within all 20 soil index values, we condensed the range of index values into 5 groups whereby soil index values 0 to 3 were grouped into soil productivity classification 1 (SPC 1), soil index values 4 to 7 were grouped into SPC 2, soil index values 8 to 11 were grouped into SPC 3, soil index values 12 to 15 were grouped into SPC 4, and soil index values 16 to 19 were grouped into SPC 5. We located at least 6 sampling sites for each SPC group. We identified general locations for sampling using a map developed by Schaetzl et al. (2012), and we distributed

sampling sites within each SPC group over a wide geographical area (Figure 1). Once we determined general locations, we used personal contacts and contacts provided by the National Deer Association to identify land-owners who would be willing to provide access to properties for sampling.

We collected leaf tissue from plants commonly selected by deer (Miller and Miller 2005, Gee et al. 2011, Harper 2019; Table S1, available in Supporting Information). We attempted to collect the same plant species from all SPCs, but some species did not occur over the entire geographical range we sampled, so we included other species from the same genera (e.g., *Ambrosia*, *Rubus*, and *Cornus*). We grouped plant species into 4 plant types: forbs (broadleaf herbaceous plants), semi-woody (i.e., including species in the genera *Rubus* and *Smilax*), shrubs, and trees. We sampled plants from both forested and open areas, but we did not collect plant or soil samples from agricultural fields or other sites that may have received soil amendments, and we consistently sampled various plant species and genera in similar environments as related to sunlight availability (McKinney et al. 2023). We collected forage samples once per site during June and July 2015, 2016, 2017, and 2020. We restricted our sampling to June and July because that is the most nutritionally demanding period of the year for white-tailed deer, coinciding with gestation, lactation, and antler growth. Forage availability during the growing season has been suggested as the most important factor explaining morphology, as differences in forage availability during periods of growth may best explain size distribution in animals (Geist 1986, Wolverton et al. 2009, Huston and Wolverton 2011). We collected young and older plant leaf tissue samples separately for each species because digestibility and deer selectivity decline as plant tissue matures (Short et al. 1971; Ball et al. 2015; Dykes et al. 2020; Lashley et al. 2014, 2022). Young plant samples were characterized as the most recent growth available on the plant, including the youngest leaves and succulent stem tips of forbs and semi-woody plants. Older plant leaf samples were characterized as growth from earlier in the growing season, consisting of mature leaves and petioles. We bagged and labeled each forage sample according to site, species, and age. We refrigerated forages in a cooler between collection and drying based on recommendations from Lashley et al. (2014).

We dried all forage samples to constant mass in an air-flow drier at 50°C, then packaged and submitted dried forage samples for nutrient analysis of nitrogen (N), phosphorus (P), potassium (K), and calcium (Ca). We focused our analysis on the macronutrients because they are the main growth-limiting nutrients for naturally occurring plants in the eastern United States (Aerts and Chapin 2000). Forage nutrient concentration was determined using a wet chemistry nitrogen combustion technique at the Agricultural Service Laboratory at Clemson University (Clemson, SC, USA). We multiplied nitrogen concentration by 6.25 to estimate crude protein (CP; Robbins et al. 1987).

We collected corresponding soil samples to a depth of 25 cm at the base of each sampled forage plant using a soil probe for the site-specific, fine-scale analysis. Each soil sample consisted of a minimum of 10 subsamples collected in the vicinity of the plant. In some cases, we used individual soil samples for multiple plant samples if the plants were located in the vicinity of the soil sample collections (within approximately 2 m). Soil samples were analyzed at the University of Tennessee Soil, Plant, and Pest Center for P, K, and Ca.

Data analysis

To assess forage quality by plant type, we analyzed CP, P, K, and Ca of each plant type, plant age, and plant type-age combination (young forb tissue, older forb tissue, young semi-woody tissue, older semi-woody tissue, young shrub tissue, older shrub tissue, young tree tissue, older tree tissue). We used the MIXED procedure in SAS (Littell et al. 2006) to conduct a mixed-effect analysis of variance (ANOVA) with plant CP, P, K, and Ca as response variables and plant type as the fixed effect. We first analyzed plant type, then plant age, then combinations of both as ANOVA models. We evaluated year, SPC, site, and species as random effects in the models. We used the Kenward-Roger degrees of freedom approximation because we included random effects (Littell et al. 2006). We ensured all models converged and the G matrix was positive definite. If either condition failed, we removed random effects until both conditions were satisfied. We ensured data met the assumptions of ANOVA and concluded moderate to strong evidence of an effect at $P \leq 0.05$.

We determined if predictive indices of soil quality (i.e., the soil productivity index) based on soil taxonomic information were associated with variation in plant forage quality for deer. We examined relationships between soil productivity index values (SPC 1–5; Schaetzl et al. 2012) and corresponding deer-forage plant samples to determine if these soil productivity classification values could be used to predict plant-nutrient quality. We included plant type in our models because previous research has determined that plant types vary in nutrient concentration (Mixon et al. 2010; Nanney et al. 2018; Lashley et al. 2014, 2022). We used the MIXED procedure in SAS (Littell et al. 2006) to conduct mixed-effects ANOVAs with plant CP, P, K, and Ca as response variables, SPC value, plant type, and the interaction as fixed effects, and year, site, and species as random effects. As above, we used the Kenward-Roger degrees of freedom approximation, ensured all models converged and the G matrix was positive definite, ensured data met the assumptions of ANOVA, and concluded moderate to strong evidence of an effect at $P \leq 0.05$.

We designed a fine-scale, site-specific analysis to compare the actual soil mineral concentrations at the exact site where each plant was sampled to mineral levels in the plant tissue. We first used linear regression to investigate a potential relationship between plant and soil concentrations of P, K, and Ca. We fit a mixed-effects linear regression model for each of the nutrients, grouped by plant type as a categorical fixed effect. The response variable for each model was plant mineral concentration, and fixed effects were soil mineral concentration, plant type, and their interaction. Including the interaction between the numeric and categorical variables essentially splits the model into submodels for each level of the categorical variable (i.e., an ANCOVA), which modeled the relationship between plant and soil mineral concentration for each plant type. Species nested within the site served as a random effect in the models.

RESULTS

Forage quality by plant type

We collected 224 soil samples and 509 tissue samples from 40 plant species in 28 genera across 36 sites (Figure 1). Crude protein and mineral concentration in plant tissue varied by plant type (Table 1). Crude protein in plant tissue was influenced by plant type ($P = 0.009$) with forb leaves containing the greatest amount of CP and tree and shrub leaves containing the least (Table 1). Crude protein levels were greater in young plant tissue than older plant tissue ($P < 0.001$; Table 2). Crude protein also differed by plant type and age of plant tissue and was greatest in young forb tissue ($P < 0.001$; Table 3).

Phosphorus concentration was affected by plant type ($P = 0.018$) with forbs containing the most (Table 1). Young plant tissue contained more P than older plant tissue ($P < 0.001$; Table 2). When plant type and age variables were combined, young forb tissue contained the greatest concentration of P ($P < 0.001$; Table 3).

Potassium concentration also was influenced by plant type ($P = 0.002$). Forbs contained greater amounts of K than shrubs, semi-woody, or trees (Table 1). Potassium level was greater in young plant tissue than older plant tissue ($P < 0.001$; Table 2). Older forb tissue contained the greatest concentration of K and older tree leaves contained the least ($P < 0.001$; Table 3).

Calcium concentration also was influenced by plant type ($P = 0.040$) with the greatest concentration in forbs (Table 1). Unlike other minerals, older plant tissue contained greater concentrations of Ca than young plant tissue ($P < 0.001$; Table 2). Older forb tissue contained the greatest concentration of Ca and young shrub leaves contained the least ($P < 0.001$; Table 3).

Predicted soil productivity and forage quality

The soil productivity index was a poor predictor of plant quality, as only Ca differed by SPC ($P < 0.001$; Table 4). Plant type influenced each plant nutrient and interacted with SPC for CP ($P = 0.013$) and K ($P = 0.046$; Table 4). The interaction between SPC and plant type for CP was caused by elevated levels of CP in young semi-woody plants in

TABLE 1 Linear mixed effects models relating plant nutrient content (%) to plant type with year, soil productivity class, site, and species as random effects. We collected plant leaf tissue samples from 36 sites across 16 states in the United States, 2015, 2016, 2017, and 2020.

Nutrient	Plant type	Estimate[a]	SE	df	F	t	P
Crude protein[b]				3, 16.9	5.42		0.009
	Forb	21.66	2.071	10.5		10.46	<0.001
	Semi-woody	15.68	2.166	12.4		7.24	<0.001
	Shrub	13.75	2.120	12.0		6.49	<0.001
	Tree	14.67	1.891	8.50		7.76	<0.001
Phosphorus[c]				3, 7.5	6.37		0.018
	Forb	0.35	0.045	4.1		7.85	0.001
	Semi-woody	0.25	0.046	4.6		5.33	0.004
	Shrub	0.24	0.047	4.7		5.09	0.005
	Tree	0.24	0.044	3.8		5.46	0.006
Potassium[d]				3, 33.3	5.88		0.002
	Forb	2.92	0.338	30.6		8.65	<0.001
	Semi-woody	1.57	0.355	36.4		4.41	<0.001
	Shrub	1.84	0.334	38.3		5.52	<0.001
	Tree	1.16	0.273	37.1		4.25	0.001
Calcium[e]				3, 27.6	3.16		0.040
	Forb	1.72	0.266	27.8		6.46	<0.001
	Semi-woody	0.96	0.272	30.5		3.53	0.001
	Shrub	0.66	0.256	31.2		2.58	0.015
	Tree	0.94	0.211	31.6		4.45	<0.001

[a]Least squares means for plant types.
[b]Random effects included year, site, and species.
[c]Random effects included year, site, and species.
[d]Random effects included site and species.
[e]Random effects included year, soil productivity class, and species.

SPC 5, whereas CP values for young and older semi-woody plants were lower than the average in SPC 3 (Figure 2). The interaction between SPC and plant type for K was caused by greater values for older forb tissue in SPC 3 and shrubs in SPC 2 and SPC 3 than the other plant types (Figure 2).

Site-specific soil and forage quality

The relationship between soil mineral concentration and plant tissue mineral concentration was subtle and varied. In the P mixed-effects model, the fixed effects of plant type and soil P generated a marginal $R^2 = 0.25$. The inclusion of the random effects provided more explanatory power with a conditional $R^2 = 0.85$, demonstrating that the variance in plant tissue P concentration was somewhat explained by plant type, but most was explained by plant species nested in site. When we partitioned the explanatory power of the marginal effects, soil P alone explained little variation in

TABLE 2 Linear mixed effects models relating plant nutrient content (%) to plant age with year, soil productivity class, site, and species as random effects. We collected plant leaf tissue samples from 36 sites across 16 states in the United States, 2015, 2016, 2017, and 2020.

Nutrient	Plant age[a]	Estimate	SE	df	F	t	P
Crude protein[b]				1, 447	53.09		<0.001
	Young leaf tissue	17.41	1.581	6.39		11.01	<0.001
	Older leaf tissue	14.90	1.587	6.49		9.39	<0.001
Phosphorus[c]				1, 449	182.48		<0.001
	Young leaf tissue	0.31	0.041	3.67		7.52	0.001
	Older leaf tissue	0.22	0.041	3.69		5.28	<0.001
Potassium[d]				1, 455	14.01		<0.001
	Young leaf tissue	1.86	0.202	47.0		9.23	<0.001
	Older leaf tissue	1.65	0.203	48.3		8.13	<0.001
Calcium[e]				1, 471	122.84		<0.001
	Young leaf tissue	0.91	0.146	34.2		6.25	<0.001
	Older leaf tissue	1.26	0.147	34.9		8.56	<0.001

[a]Least squares means for plant ages.
[b]Random effects included year, site, and species.
[c]Random effects included year, site, and species.
[d]Random effects included site and species.
[e]Random effects included year, soil productivity class, and species.

plant P (partial R^2 = 0.00), whereas plant type explained more (partial R^2 = 0.17 for both plant type and the soil × plant type interaction). The variance of P in older and young tree leaves was influenced by soil P concentration, as indicated by the slopes of the fixed effects (Figure 3). However, the effect was minimal when compared with the effect of plant type. For example, at sites with the lowest soil P concentration (10th percentile), young forb P concentration (0.38%) was as high as young tree P concentration (0.38%) at sites with the highest soil P concentration (90th percentile).

The K model produced a similar result to the P model. Plant type and soil K produced a marginal R^2 = 0.38. Adding the random effects of plant genus nested within site improved model fit with a conditional R^2 = 0.87. Again, soil K explained little variation in plant K (partial R^2 = 0.00), whereas plant type explained most of the variation attributed to the main effect and covariate (partial R^2 = 0.34).

Plant type and soil Ca explained less variation in plant Ca than in the K model (marginal R^2 = 0.28), but including the random effects of plant genus nested within site improved model fit considerably (conditional R^2 = 0.91). As with the P and K models, soil Ca concentration explained little variation in plant Ca concentration (partial R^2 = 0.00), whereas plant type explained most of the variation in plant Ca concentration (partial R^2 = 0.23). Older shrub leaf tissue showed the greatest response to soil Ca concentration (Figure 3).

DISCUSSION

We assessed the influence of soil mineral concentration on plant nutrient concentration in 40 plant species collected across a wide range of soil productivity classifications over a broad geographical area of the eastern United States. At the site-specific level, soil P, K, and Ca concentration had little influence on plant P, K, and Ca

TABLE 3 Linear mixed effects models relating plant nutrient content (%) to plant type and age with year, soil productivity class, site, and species as random effects. We collected plant leaf tissue samples from 36 sites across 16 states in the United States, 2015, 2016, 2017, and 2020.

Nutrient	Plant type and age[a]	Estimate	SE	df	F	t	P
Crude protein[b]				7, 72.9	15.36		<0.001
	Young forb	23.57	2.058	14.1		11.5	<0.001
	Older forb	18.20	2.081	14.7		8.8	<0.001
	Young semi-woody	17.02	2.152	16.8		7.9	<0.001
	Older semi-woody	14.24	2.151	16.8		6.6	<0.001
	Young shrub	13.81	2.106	16.7		6.6	<0.001
	Old shrub	14.03	2.112	17		6.6	<0.001
	Young tree	15.31	1.827	11.1		8.4	<0.001
	Older tree	14.39	1.859	11.8		7.7	<0.001
Phosphorus[c]				7, 49.4	30.58		<0.001
	Young forb	0.39	0.049	6.6		8.0	<0.001
	Older forb	0.26	0.049	6.8		5.3	0.001
	Young semi-woody	0.30	0.050	7.5		6.1	<0.001
	Older semi-woody	0.20	0.050	7.5		3.9	0.005
	Young shrub	0.27	0.050	7.3		5.5	0.001
	Older shrub	0.21	0.050	7.4		4.2	0.003
	Young tree	0.28	0.045	5.4		6.1	0.001
	Older tree	0.22	0.046	5.6		4.8	0.004
Potassium[d]				7, 117	8.10		<0.001
	Young forb	2.87	0.343	32.6		8.4	<0.001
	Older forb	3.08	0.347	34.1		8.9	<0.001
	Young semi-woody	1.79	0.361	38.9		5.0	<0.001
	Older semi-woody	1.37	0.361	38.9		3.8	<0.001
	Young shrub	2.04	0.344	42.3		5.9	<0.001
	Older shrub	1.71	0.345	43.0		5.0	<0.001
	Young tree	1.29	0.279	39.4		4.6	<0.001
	Older tree	0.93	0.285	41.9		3.3	0.002
Calcium[e]				7, 104.0	19.67		<0.001
	Young forb	1.58	0.269	29.7		5.9	<0.001
	Older forb	1.99	0.270	30.4		7.4	<0.001
	Young semi-woody	0.76	0.274	32.3		2.8	0.010
	Older semi-woody	1.16	0.274	32.3		4.2	<0.001
	Young shrub	0.48	0.260	33.7		1.8	0.076

TABLE 3 (Continued)

Nutrient	Plant type and age[a]	Estimate	SE	df	F	t	P
	Older shrub	0.82	0.260	33.8		3.2	0.003
	Young tree	0.86	0.214	33.2		4.0	<0.001
	Older tree	1.09	0.217	35.0		5.0	<0.001

[a]Least squares means for plant type and age category.
[b]Random effects included year, site, and species.
[c]Random effects included year, site, and species.
[d]Random effects included soil productivity class, site, and species.
[e]Random effects included year, soil productivity class, and species.

TABLE 4 Linear mixed models relating plant nutrient content (%) to soil productivity classification (SPC, 1–5) and plant type with year, site, and species as random effects. We collected plant leaf tissue samples from 36 sites across 16 states in the United States, 2015, 2016, 2017, and 2020.

Nutrient	Effect[a]	df	F	P
Crude protein	SPC	4, 38.3	0.82	0.519
	Plant type	7, 28.3	5.68	<0.001
	Interaction	28, 407.0	1.73	0.013
Phosphorus	SPC	4, 47.8	0.74	0.570
	Plant type	7, 13.1	4.72	0.008
	Interaction	28, 396.0	1.35	0.112
Calcium[b]	SPC	4, 424.0	5.87	<0.001
	Plant type	7, 42.1	2.71	0.021
	Interaction	28, 431.0	0.85	0.693
Potassium[c]	SPC	4, 48.9	1.52	0.210
	Plant type	7, 43.1	4.88	<0.001
	Interaction	28, 413.0	1.52	0.046

[a]Plant types: young forb tissue, older forb tissue, young semi-woody leaf tissue, older semi-woody leaf tissue, young shrub leaf tissue, older shrub leaf tissue, young tree leaf tissue, older tree leaf tissue.
[b]Only year and species were used for random effects.
[c]Only site and species were used for random effects.

concentration, supporting our hypothesis that nutrient concentration for a given plant type would be similar in mineral-poor and mineral-rich soils. Plant type was far more influential in explaining variation of all plant nutrients than soil mineral concentration, indicating that managing plant composition has greater potential to improve deer forage quality. Following our prediction, all plant nutrients were greatest in forbs. The importance of plant type over soil mineral concentration can be illustrated using the estimated concentration of each mineral in the plant tissue when there was extremely low concentrations of each mineral in the soil (Figure 3). For example, plant P concentration in young forb tissue in areas with the lowest concentrations of soil P was equal or greater than plant P concentration in young tissue of all other plant types in areas with the highest concentrations of soil P. The high mineral content in forbs and young plant tissue growing on sites with the lowest soil mineral content clearly
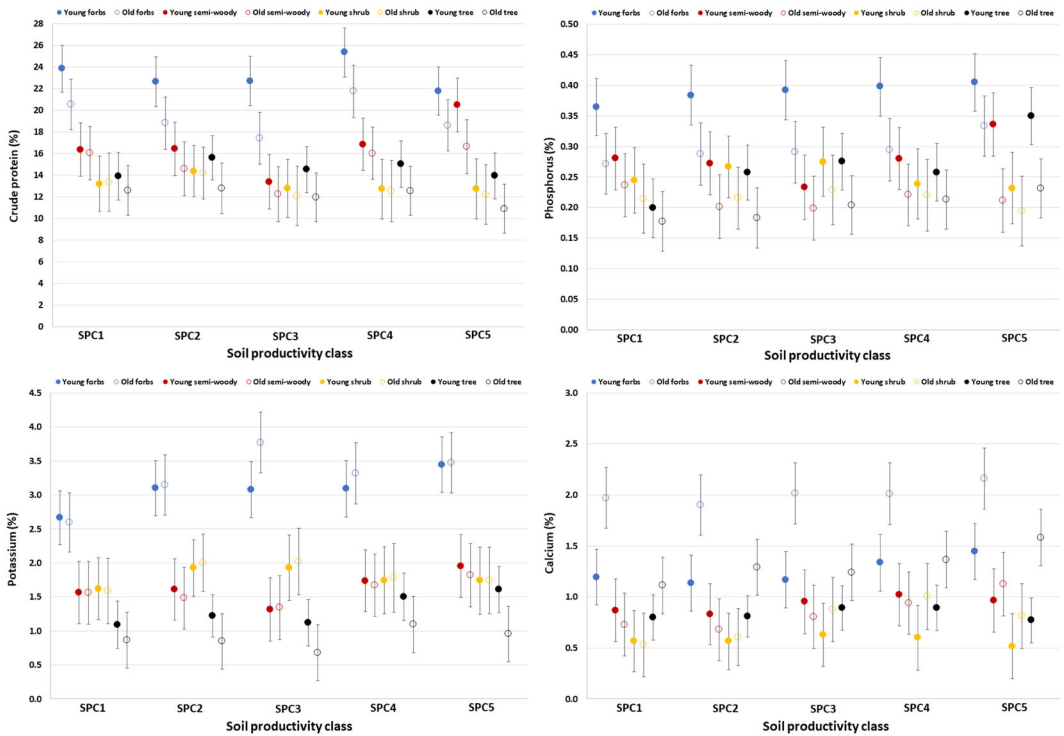
FIGURE 2 Least-squared means of nutrient (crude protein) and mineral concentration (% phosphorus [P], potassium [K], calcium [Ca]) in young and old tissue of plants commonly consumed by white-tailed deer for 5 soil productivity classes. We collected samples from 36 sites across 16 states in the United States, 2015, 2016, 2017, and 2020.

illustrates how plant type is more influential than soil mineral content for improving deer forage quality in the eastern United States.

In general, plant nutrition decreased from forbs to semi-woody plants to woody plants, which is not surprising as forbs are more digestible with fewer structural carbohydrates that reduce digestibility (Short et al. 1974, Vangilder et al. 1982, Ball et al. 2015). Forbs native to the eastern United States typically provide greater rates of digestible protein, energy, and other nutrients than other plant types at a similar stage of maturity, during both the growing and dormant seasons (Marten and Andersen 1975, Bosworth et al. 1980, Windels and Jordan 2008, Timmons et al. 2010). When considering the minimum requirements of a lactating female, Turner (2024) reported forbs were >15 times more likely to meet both CP and P requirements than semi-woody and woody plant species. Thus, our results support previous research related to nutritional quality in common deer forages and reinforce the need to provide greater coverage of forbs to improve deer diet quality.

Most of the plant types, regardless of soil quality, met the minimum maintenance requirements of deer, but some did not meet CP or P levels required during specific life stages. For example, only forbs and young semi-woody plant tissue contained the 16% CP level necessary for maximum antler growth (Ullrey 1982, Harmel et al. 1989). On average, all plant types, except shrubs (Table 1), provided adequate CP levels necessary to meet requirements for a lactating female with twin fawns (14%; National Research Council 2007, Hewitt 2011). The P requirement for a lactating female (0.31%; National Research Council 2007, Hewitt 2011) was met consistently only with young forbs. The P requirement for maximum antler growth is not well established in the literature, but likely is approximately 0.26% (Ullrey et al. 1975, Reitz 1981, Davis and Johnson 1984). If accurate, average plant P in young leaf tissue of all plant types we sampled would meet the P requirement for maximum antler growth
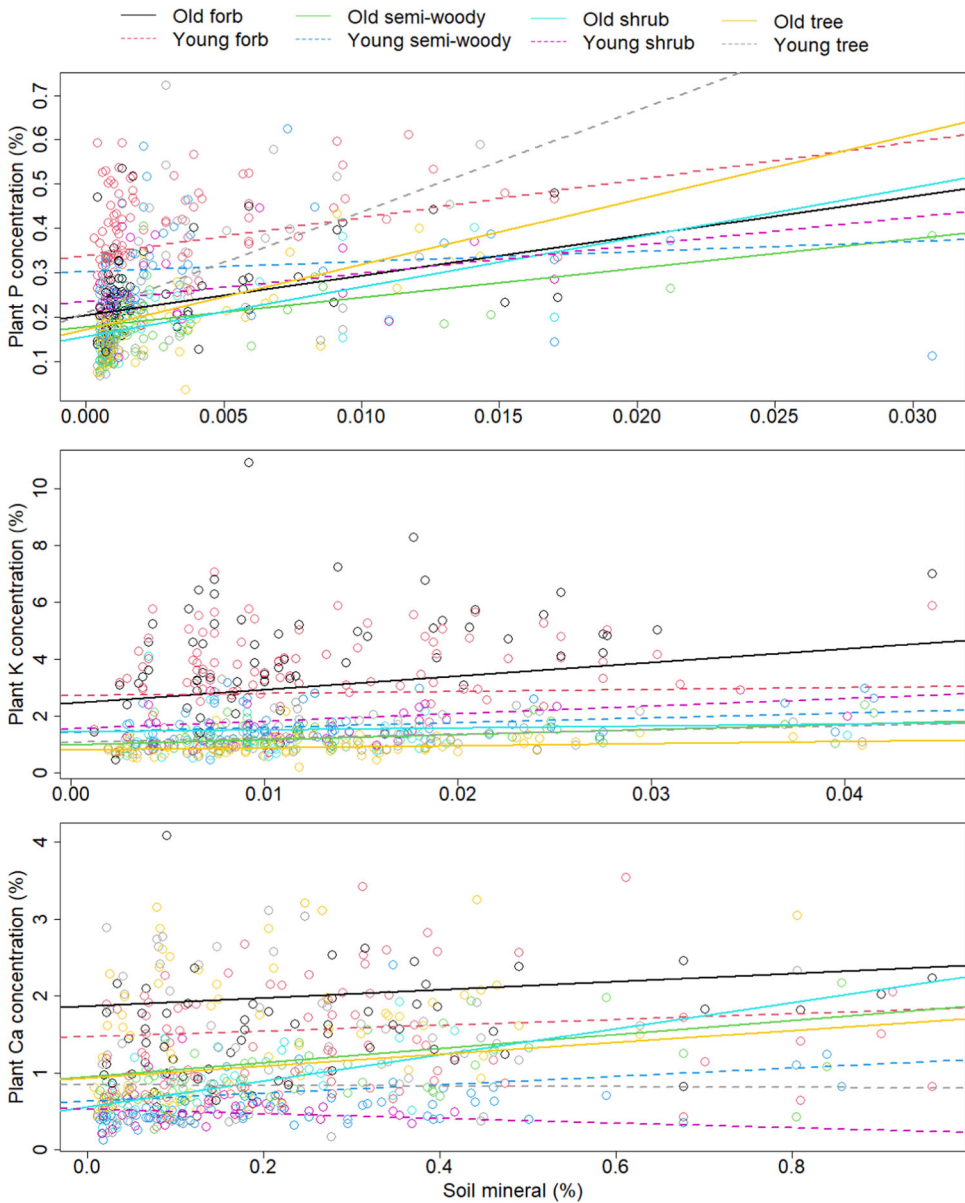
FIGURE 3 Linear regression lines relating soil mineral concentration (% phosphorus [P], potassium [K], calcium [K]) to the same mineral in young and old tissue of plants commonly consumed by white-tailed deer. We collected samples from 36 sites across 16 states in the United States, 2015, 2016, 2017, and 2020.

(Table 3). Phosphorus levels were greater in young leaves than older leaves for all plant types, whereas Ca levels were greater in older leaf tissue of all plant types. As a concentrate selector, deer would be able to meet their P requirements by foraging on select plants and select plant parts, if a diversity of plants is available (Lashley et al. 2015, Dykes et al. 2020) or if recent disturbance has stimulated an increase in quality associated with young, actively growing plant tissue (Nichols et al. 2021, Lashley et al. 2022). Calcium concentration in all plant types and ages exceeded the levels necessary for maximum antler development and lactation (0.17% and 0.34%, respectively; National Research Council 2007, Hewitt 2011), indicating Ca is not a limiting factor for deer in the eastern United

States. Potassium concentration was greater in forbs than all other plant types, but K also is not considered a limiting factor in the eastern United States for either lactation or antler growth for deer (Barnes et al. 1990). Nonetheless, our data indicate the presence of forbs greatly increases dietary quality for deer, and limited forb availability could lead to a reduction in milk production, body weight, and antler size (DeYoung et al. 2019, Lashley et al. 2022).

The soil productivity index poorly predicted plant nutrients and should not be used to predict deer morphometrics or productivity based on plant nutrient quality. However, there may be correlation in some areas between deer morphometrics and a soil productivity index because land use typically is dominated by agriculture in areas with productive soils (e.g., Strickland and Demarais 2000), thus providing more high-quality forage for deer. Agricultural areas may increase forage availability through the crops themselves and via the increased coverage of naturally occurring early successional forbs in open landscapes compared to forested landscapes (Lashley et al. 2011, Hefley et al. 2013, Nanney et al. 2018, Harper et al. 2021).

Previous work has reported mixed results when predicting or analyzing plant nutrients across a soil resource gradient. Ferwerda et al. (2006) reported a weak relationship between foliar P of mopane (*Colophospermum mopane*) and parent material using a geological map of southern Africa. Thompson et al. (1997) reported plant Ca was increased in plants on landforms where soil Ca was available in excess but not with other macronutrients, and they concluded plant N and P concentrations should be considered a plant species trait or attribute, irrespective of site. Although average plant Ca tended to increase from SPC 1 to SPC 5 in our study, plant Ca was far in excess of the maximum requirement for lactating female deer or male deer growing antlers for all plant types and should not be considered a limiting factor for the species in the broad geographical area we sampled. Jones et al. (2008) reported differences in plant CP using 8 common deer forages across a regional soil resource gradient in Mississippi, but there was not a consistent trend among all regions for predicted soil quality and deer forage CP levels. Navarro et al. (2023) documented slight differences in plant P for Indian cucumber root (*Mediola virginiana*) between 2 ecological sites, but they did not correlate soil P with plant P.

Because soil nutrients at the landscape and site level predicted little of the variation in plant nutrients, managers should focus on plant composition to influence deer forage quality, as the species of plants present was the strongest predictor of plant nutrient availability. Others have similarly reported no correlation between leaf and soil P concentrations, further supporting the premise that soil nutrients may not control nutrient accumulation in leaf tissue (Marler and Lawrence 2015, Miatto et al. 2016, Zhang et al. 2017, Lin et al. 2019). Our data contrast with Thorsland (1966), who reported a relationship between soil P and plant P for Japanese honeysuckle (*Lonicera japonica*) in South Carolina but not for other plants, and no native forbs were included in their study. Naturally occurring plant species may adapt to nutrient-poor sites by exhibiting traits and responses that differ from plant species adapted to fertile conditions or from typical agricultural crop plants. Specific adaptations may include a greater root-to-shoot ratio, a low root absorption rate, longer specific root length, development of lateral roots and root hairs, and allocation of more nutrients to roots than shoot growth, which may limit growth aboveground and lead to fewer and smaller leaves but still maintain sufficient photosynthesis and meristematic activity to sustain the plant (Rorison 1968, White 1972, Chapin 1980, Aerts and Chapin 2000). These traits and responses typically lead to reduced aboveground biomass of the plant, but nutritional quality is maintained (Bieleski 1973, Chapin 1980). Our results support the hypothesis that nutrient-poor soils can support nutrient-rich plants, but production or biomass of those plants can be expected to be less than in nutrient-rich soils, which results in a lower nutritional carrying capacity for deer.

Soil nutrients commonly are amended by liming and fertilization to increase plant biomass or crop yield, but effects of liming and fertilization on plant nutrients also have been mixed (Segelquist and Rogers 1975, Wood 1986, Dyess et al. 1994, Shaw et al. 2010, Turner et al. 2021). Increases have been noted for a nonnative vine (Segelquist and Rogers 1975), and a few native plant species exhibit luxury consumption, storing excess nutrients when available (Chapin 1980, Tripler et al. 2002, de Mazancourt and Schwartz 2012). Schreeg et al. (2014) reported some nutrient concentrations in relatively old leaves, stems, and roots increased following fertilization, but relatively

young leaves were less-sensitive indicators of soil nutrient availability. Dykes et al. (2018) reported greater levels of P in the tissue of 2 agronomic plants and deer selection for those plants when soil was supplemented with P fertilizer and lime to neutralize soil pH. Alternatively, Turner et al. (2021) reported a general lack of change in plant nutrient concentration following fertilization of native forbs common in fallow fields on the Cumberland Plateau, but plant height increased an average of 71%, which is consistent with plant growth and yield increases reported for both crop and wild plants following fertilization (Kunishi 1982, Wilson and Shure 1993, Osborne and Riedel 2006, Berg et al. 2007, Warren 2017).

Our data provide empirical evidence that naturally occurring wild plants, especially native forbs, can provide nutrition sufficient for maximum deer body weight and antler growth, within a given area, across the eastern United States regardless of the dominant soil types and without soil amendment. Soil nutrients had little influence on plant nutrient concentrations, whereas coverage of forbs has been documented as an important indicator of the nutritional carrying capacity for deer (Harper et al. 2021, Turner and Harper 2024). We assert that the availability of select plants, especially naturally occurring native forbs, while deer are gestating, lactating, and growing antlers, may be a primary limiting factor regulating age-specific deer body mass, reproduction, and antler size, not soil mineral concentration. Previous work has documented how improved nutrition leads to increased deer body mass and antler size (French et al. 1956, Ullrey 1982, Harmel et al. 1989, Brown 1990, Michel et al. 2016), which can strongly influence hunter satisfaction (Harper et al. 2012, Nanney et al. 2015). Proper management of deer habitat and deer density may enable managers to realize an increase in deer morphometrics, even in areas with nutrient-poor soils. More holistic deer habitat management that converts an appropriate amount of forest to open woodland and early successional communities, and converts fields dominated by grasses to forbs, not only will increase nutritional carrying capacity for deer (Lashley et al. 2011, Nanney et al. 2018, Harper et al. 2021) but also increase and enhance habitat for conservation-priority species, including northern bobwhite (*Colinus virginianus*), American bumble bee (*Bombus pensylvanicus*), and various other pollinators (Greene et al. 2019, GeFellers et al. 2020, Novotny et al. 2021).

MANAGEMENT IMPLICATIONS

Deer managers should be encouraged that nutrient-poor soils can support nutrient-rich forage for deer. Although the nutritional carrying capacity for deer is lower on average on nutrient-poor soils than on nutrient-rich soils, increased deer morphometrics may be possible by transitioning from a plant community dominated by semi-woody and woody species to one dominated by naturally occurring forbs while concurrently managing deer density. Our data indicate land use and plant composition affect diet quality for deer more than soil nutrients. We do not recommend use of a soil productivity index to predict plant nutrient quality or deer management potential as related to the influence of nutrient availability on deer productivity or morphometrics. Habitat management that creates and maintains various early seral plant communities and open woodlands that provide an abundance of forbs will increase deer diet quality, and may subsequently influence deer morphometrics and productivity, far more than soil mineral concentration.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This study did not involve handling of animals.

DATA AVAILABILITY STATEMENT

Analyzed data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Craig A. Harper 🅳 http://orcid.org/0000-0003-0577-6804

Mark A. Turner 🅳 http://orcid.org/0000-0003-1990-7422

M. Colter Chitwood 🅳 http://orcid.org/0000-0001-7240-7430

Jarred M. Brooke 🅳 http://orcid.org/0009-0001-1778-4548

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