



Research article

Plant nutrient concentrations inform white-tailed deer diet limitations

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ABSTRACT

Management of large herbivores often involves increasing availability of forages sufficient in nutrient density to allow animals to meet dietary demands. Nutritional carrying capacity (NCC) models commonly are used to compare plant communities and management strategies, but failure to use the most limiting nutrient could result in overestimating NCC. Moreover, the relationship between limiting nutrients often is not considered, which may influence the utility of NCC models based on a single nutrient, especially when herbivores must simultaneously meet multiple constraints. We examined crude protein and phosphorus concentrations in 131 plant species commonly eaten by white-tailed deer (*Odocoileus virginianus*) to determine whether they would meet a minimum 14% crude protein and 0.3% phosphorus constraint for a lactating female. Crude protein and phosphorus demands were met in 43.9% and 18.8% of sampled forages, respectively. Concentrations of crude protein and phosphorus were greatest in young forb tissue, with an average of 18.6% crude protein and 0.28% phosphorus. Protein and phosphorus concentrations were positively correlated, but not all plants which met protein requirements simultaneously provided sufficient phosphorus. We created NCC models using crude protein and phosphorus and documented phosphorus tended to be more limiting, but variation existed among sites. Given that limiting nutrients may vary spatiotemporally, focusing conservation efforts on providing a diversity of plants, particularly to include forbs that simultaneously meet multiple nutritional demands, is likely the most practical management approach.

1. Introduction

Nutrient availability strongly influences diet selection by herbivores. Forages dense in limiting nutrients, such as crude protein (CP), phosphorus (P), sodium, cobalt, or soluble sugars, are selected by herbivores (Verheyden-Tixier et al., 2008; Ceacero et al., 2009; Lashley et al., 2015; Dykes et al., 2018, 2020). Herbivores must optimize forage intake to simultaneously meet multiple nutritional demands (Westoby, 1974; Hanley, 1997) while also avoiding potentially toxic concentrations of nutrients (Belovsky, 1978; Weckerly, 1994; Provenza et al., 2003; Ginane and Petit, 2005; Ceacero et al., 2015). For example, white-tailed deer (*Odocoileus virginianus*; hereafter, deer) select forages with greater digestibility and CP but lower sulfur concentrations (Dykes et al., 2020). Thus, foraging decisions likely depend on herbivores considering multiple plant nutrients simultaneously to meet requirements to support various life history processes. Lactation is the costliest nutritional

process for mammals, and diet quality during lactation often is used as a minimum benchmark when evaluating forage availability. Female deer commonly give birth to twins (Turner et al., 2019; Swartout et al., 2023), and lactation to support twin fawns requires 4.7 times greater energy and 1.4 times greater CP intake than maintenance (Hewitt, 2011). Males also require elevated energy and CP intake for antler growth (National Research Council, 2007; Hewitt, 2011). Forage quality and availability during costly life history processes strongly influence morphology and demography, with deer tending to be larger and more productive in areas with greater availability of high-quality forages (Pettorelli et al., 2001; Jones et al., 2010; Turner, 2024). Nutritional requirements peak in May–July for both sexes during lactation and antler growth (Hewitt, 2011), so management often focuses on providing increased high-quality forage availability at this time. Given the interest in deer morphology and productivity, identifying forage nutrient concentrations across a broad geographic range could inform

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managers attempting to provide high-quality forage for maximum productivity and antler growth.

Deer forage nutrient concentration varies by plant species, age of plant tissue, time since disturbance, and climatic conditions (Lashley and Harper, 2012; Lashley et al. 2014, 2022; Harper et al., 2025). Forbs tend to have greater nutrient concentrations than woody plants, but wide variation exists among different species (Mixon et al., 2010; Lashley et al., 2011; Nanney et al., 2018). Younger plant parts tend to have greater concentrations of most nutrients, and thus are selected by many herbivores, especially concentrate selectors such as deer (Lashley et al., 2014; Vera-Velez and Lamb, 2021). Climatic conditions, especially drought events, and disturbance such as fire, also influence nutrient availability (Lashley and Harper, 2012; Sittler et al., 2018; Lashley et al., 2022; Powell et al., 2022). Although the quality of different forages is important to consider, management often focuses on landscape-level forage availability with consideration for both forage quality and biomass, as providing increased availability of forages capable of supporting nutritional requirements across a property is necessary to have population-level demographic and morphometric changes to meet management objectives.

Nutritional carrying capacity (NCC) models are used to estimate forage availability for large herbivores. NCC models were proposed by Hobbs and Swift (1985), and they provide an estimated number of animals capable of being supported for a day at some minimum nutritional constraint by incorporating estimates of biomass and nutrient concentration for each forage in a given area. Previous research has considered CP as the most limited nutrient when evaluating nutrition for deer during the growing season (Edwards et al., 2004; Lashley et al., 2011; Nanney et al., 2018; Harper et al., 2021; Turner et al., 2024). CP likely is more limiting for white-tailed deer during spring and summer than digestible energy (Lashley et al., 2015), but previous research has indicated P also may limit morphometrics in many areas of the southeastern U.S. (Jacobson, 1984). Deer also often select plants with high P concentrations, indicating P is an important nutrient for diet selection and may be limiting on the landscape (Grasman and Hellgren, 1993; Lashley et al. 2015, 2022; Dykes et al., 2018; Nichols et al., 2021). Adequate CP, P, and many other nutrients, must be met simultaneously through selective foraging, and nutrients may cooccur at high levels within selected plants (Vangilder et al., 1982; Langvatn and Hanley, 1993). Thus, evaluating both the relationship between these nutrients in a given plant and determining which is most limiting across the landscape would improve our understanding of diet selection and nutritional limitations.

Despite the scope of research on herbivore forage availability and selection, there is limited information that directly quantifies nutrient concentrations among young and older tissue of various forbs, semi-woody, and woody plants across a wide geographic range. We evaluated which forages provide limiting nutrients to provide information to managers attempting to promote high-quality forages. We also sought to better understand the relationship among limiting nutrients at the plant and landscape level. Therefore, we considered the relationship between CP and P within a forage sample and also created NCC models using CP and P to determine which nutrient represented the most-limiting constraint on a variety of sites. We developed three hypotheses related to forage nutrients. First, we hypothesized there would be differences in nutrition among plant types, and predicted young forb tissue would provide the greatest average nutrient levels. Our prediction was based on how strongly forbs influence NCC estimates, though few studies have considered average quality by plant class across a broad geographic range (Nanney et al., 2018; Harper et al. 2021, 2025; Nichols et al., 2021). Second, we hypothesized CP and P would positively correlate within a plant species, allowing foraging decisions to balance intake of both nutrients simultaneously. Finally, we hypothesized CP and P NCC estimates using CP or P as the constraint would be positively correlated, and we predicted P would be more limiting at most sites than CP as suggested in Lashley et al. (2015). Understanding which nutrient is most

limited at the plant and site level should inform management to promote an array of plant species that provide adequate nutrition during the period of greatest nutritional need by deer.

2. Methods

2.1. Study area

We collected forages at 43 sites across 25 U.S. states (Fig. 1) to determine nutrient concentrations. We attempted to distribute sites across a wide geographic area to assess variation in forage availability and quality. Site size averaged 567 ha (range: 53–4553 ha) and latitude ranged from 28.10 to 44.24°N. Most sites were selected through collaboration with the National Deer Association (NDA) to identify cooperating members who would allow us to collect forage samples on their private property. We also added 1 site each in Illinois, Indiana, and Tennessee that were managed by government agencies when we were unable to locate a site within a particular area. Dominant landscape cover at our sites ranged from closed-canopy forest to frequently burned open-canopy woodlands to row-crop agriculture, representing a wide diversity of conditions present across the distribution of deer. We sampled a subset of sites across our latitude gradient and overall geographic range each year to minimize collection year effects.

2.2. Data collection

We collected selected deer forage plants at each site late May–early August 2021–2023, to assess forage availability across each property. We collected forages at ≥ 100 sample points at each site during a single visit over 1–2 days using a stratified sampling design. First, we delineated the following vegetation types based on management history and aerial images on each site: closed-canopy hardwood forest, closed-canopy softwood forest, open-canopy hardwood forest, open-canopy softwood forest, early succession, food plot, row crop, pasture/hay, and shrubland. Forested areas were assigned based on dominant tree coverage, and whether they were closed ($<30\%$ canopy openness) or open ($\geq 30\%$ canopy openness). Early succession were areas dominated primarily by native, shade-intolerant herbaceous plants. Food plots were areas planted with agronomic crops to provide forage and/or attraction for viewing and hunting. Pasture/hay included all areas dominated by grass which was regularly mowed, hayed, or grazed, and we considered areas dominated by shrubs as shrubland. We assigned one random sampling point within a vegetation type for each percentage point that vegetation type comprised at a site. For vegetation types with $<20\%$ coverage, we assigned 20 random points to ensure adequate sampling intensity. For example, if a site had 70% coverage of row crop, 23% coverage of pasture, and 7% coverage of early succession, we collected 70 random points in the row crop, 23 random points in the pasture, and 20 random points in the early succession. We did not place a buffer around sample sites during random point creation, but all sample points were at least 10 m apart because of the relatively large study areas.

We collected all forages inside a 0.5 m² frame placed at each random sampling point that were moderately to highly selected by deer based on previous literature reporting selection (Miller and Miller, 2005; Harper, 2019). Although the majority of samples were taken from plants evaluated in previous literature, we collected some plant species not referenced in the literature that were commonly browsed across a site based on sampler observation (Appendices 1, 2, 3). We collected all biomass of young and relatively older leaves separately to determine nutrient concentration by age of plant part. We considered young leaves those closest to the tips of twigs that tend to be more digestible and higher in concentration of several nutrients (Lashley et al., 2014). Older leaves were fully formed leaves on the plant occurring below the youngest leaves nearest the tip of a stem or twig. We did not collect the oldest leaves near the bottom of stems or twigs that had begun to turn yellow or otherwise discolored.

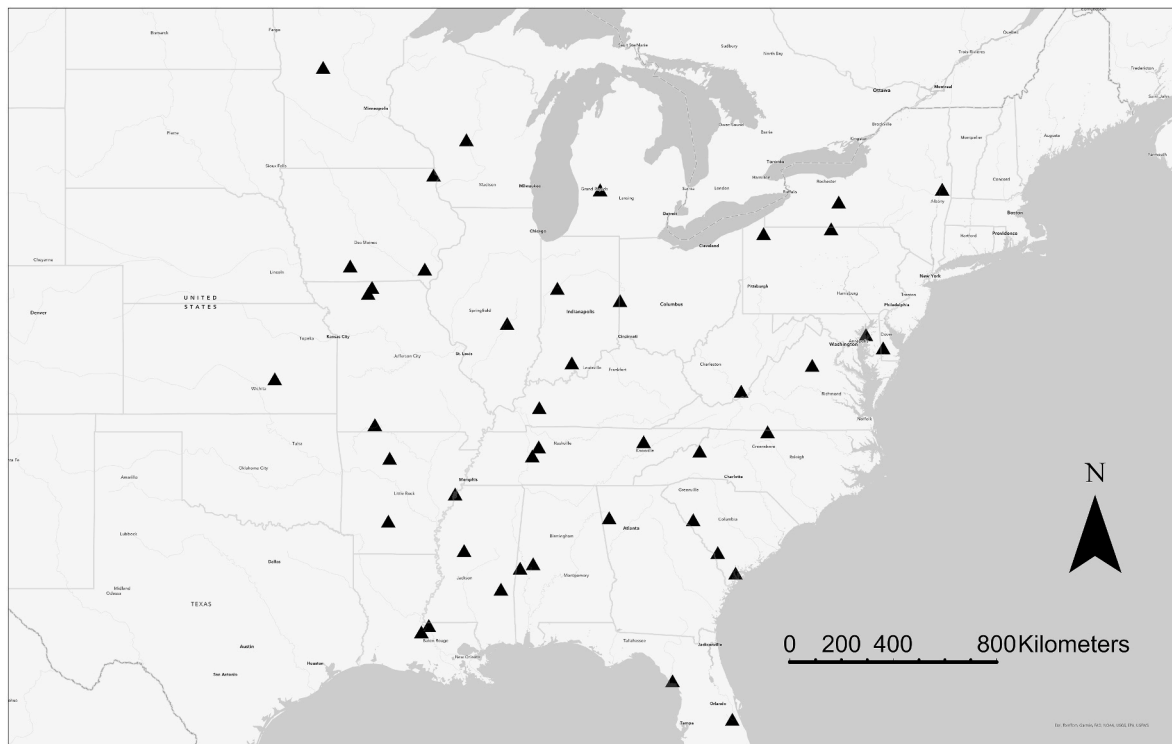


Fig. 1. Locations of sites across the eastern U.S. where deer forage samples were collected late May–early August 2021–2023.

We mixed subsamples collected across frames to produce a single sample for each plant species and age from each site to analyze nutrient concentrations. We classified forage samples into the following forage classes: young forb tissue, older forb tissue, young semiwoody, older semiwoody, young woody, and older woody. Semiwoody plants included brambles and vines, and woody plants included trees and shrubs. We dried forage samples to constant mass at 50 °C, weighed them, and sent them to either Custom Laboratory (3068 State Highway 37, Monett, MO) or the Clemson University Agriculture Service Laboratory for wet chemistry nutritional analysis of CP and P concentrations. In cases where we did not have sufficient biomass (>5 g dried) to submit a sample of both young and old tissue of a species for a site, we combined them into a composite sample. We used composite samples only in NCC estimation; we did not include them in analyses related to nutritional comparisons by plant class or tissue age.

Following nutrient analysis, we created NCC estimates for each site based on CP and P. We calculated mixed-diet NCC estimates based on CP and P constraints for each vegetation type at each site based on Hobbs and Swift (1985) using a 14% CP constraint, 0.3% P constraint, and 2.3 kg/day dry weight intake of a lactating female with twin fawns (Hewitt, 2011). We then calculated a NCC estimate for CP and P at each site by multiplying the NCC of each vegetation type by the proportion of a site in the vegetation type. These weighted estimates for each nutrient allowed us to compare whether CP or P tended to be more limiting across a variety of sites in the eastern U.S.

2.3. Data analysis

We compared concentrations of CP and P between our forage classes using ANOVA in Program R (R Core Team, 2021). Upon detecting significant differences between forage classes for a particular nutrient, we used Tukey's HSD multiple comparison test to determine which forage classes differed. Additionally, we considered forage values relative to the nutritional requirements of a lactating female to determine the proportion of forages within each class that would meet those requirements and used a chi-squared test to determine whether these

proportions differed among forage classes.

We also created a generalized least squares (GLS) model to evaluate correlation between CP and P concentrations. GLS modeling allows for nonconstant variance by weighing each observation based on a variance function, and we used the power of the variance covariate (VarPower) in package nlme (Pinheiro et al., 2023). We also regressed mixed-diet CP and P NCC estimates against each other to evaluate whether these estimates correlated. We square-root transformed NCC estimates based on both CP and P to meet normality assumptions. Neither of these models were designed to imply causation, but rather to evaluate relationships among forage nutrients and NCC estimates that may influence diet selection and nutrient availability.

3. Results

We collected 918 forage samples for nutritional analysis, representing 131 plant species. We collected a total of 63 species of forbs (Appendix 1), 16 species of semiwoody plants (Appendix 2), and 52 species of woody plants (Appendix 3). Of our samples, 497 were forbs, 202 were semiwoody, and 219 were woody plants. Young forb tissue provided the greatest nutrient concentrations, with an average of 18.6% CP ($p < 0.001$) and 0.28% P ($p < 0.001$). Older forb tissue had the second-greatest nutrient concentrations, with an average of 16% CP ($p < 0.001$) and 0.23% P ($p < 0.001$). Young and older tissue of semiwoody and woody plants provided similar, reduced nutrient concentrations, averaging 11.6–12.5% CP and 0.15–0.17% P (Table 1; Fig. 2).

The proportion of forages meeting CP ($\chi^2 = 230.1$, $df = 5$, $p < 0.001$), P ($\chi^2 = 143.3$, $df = 5$, $p < 0.001$), and both constraints simultaneously ($\chi^2 = 151.2$, $df = 5$, $p < 0.001$) varied among forage plant classes. Only 43.9% and 18.8% of all forages met the CP and P constraints, respectively. Only 29.2% of forbs met both the CP and P constraint, and only 2% of semiwoody, and 0.9% of woody plants simultaneously met both constraints (Table 2). Of the plants that met the CP constraint, only 37.5% also met the P constraint. Conversely, 87.3% of plants that met the P constraint simultaneously met the CP constraint. Our GLS model detected a positive relationship between CP and P levels in deer forage

Table 1

Mean and standard error (SE) for percent crude protein (CP) and phosphorus (P) for various forage classes collected across the eastern U.S., late May–early August 2021–2023. Different letters within a nutrient column represent significant differences in nutrient concentration among plant types.

	CP	SE	P	SE
Y Forbs	18.6 C	0.37	0.28 C	0.01
O Forbs	16.0 B	0.38	0.23 B	0.01
Y Semiwoody	12.5 A	0.32	0.17 A	0.01
O Semiwoody	12.2 A	0.19	0.15 A	0.004
Y Woody	11.7 A	0.41	0.15 A	0.01
O Woody	11.6 A	0.24	0.15 A	0.01

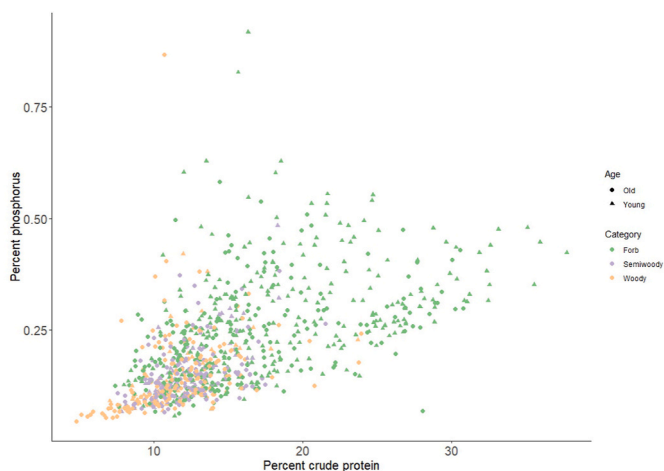


Fig. 2. Crude protein (CP) and phosphorus (P) concentration of young and old forb, semiwoody, and woody forage samples collected from 43 sites across the eastern U.S., late May–early August 2021–2023.

Table 2

Total sample size (N) and proportion of forages meeting crude protein (CP), phosphorus (P), and simultaneously meeting CP and P across various forage classes collected across the eastern U.S., late May–early August 2021–2023. Constraints are based on the minimum requirements of a lactating doe, with a 14% CP minimum and 0.3% P minimum.

	N	CP	P	CP and P
Y Forbs	282	73%	39.7%	36.2%
O Forbs	215	56.7%	20.9%	20%
Y Semiwoody	55	25.5%	3.6%	3.6%
O Semiwoody	147	17.7%	3.4%	1.4%
Y Woody	51	11.8%	3.9%	0%
O Woody	168	17.3%	4.2%	1.2%

plants, with CP concentration increasing by 3.6% ($p < 0.001$) for every 0.1% increase in P concentration.

Sitewide NCC estimates based on a 14% CP constraint averaged 33.5 (± 13.2) deer days/ha, and NCC estimates based on a 0.3% P constraint averaged 9.7 (± 2.2) deer days/ha. CP estimates were greater than P at 38 sites, whereas P estimates were greater than CP at 5 sites. Six sites did not have any sampled forages that met the minimum P requirement, whereas all sites had ≥ 1 sampled forage that met the minimum CP requirement. We found a positive correlation between site-specific NCC for CP and P, with CP NCC increasing by 0.29 (± 0.1) deer days/ha for every 1 deer day/ha increase in P NCC ($p = 0.039$; Fig. 3). Removing one outlier with values of 579.7 CP NCC and 5.9 P NCC improved model fit ($R^2 = 0.39$ versus $R^2 = 0.08$ in full model) but did not greatly influence the beta value or significance ($\beta = 0.288$ in reduced model; $p < 0.001$).

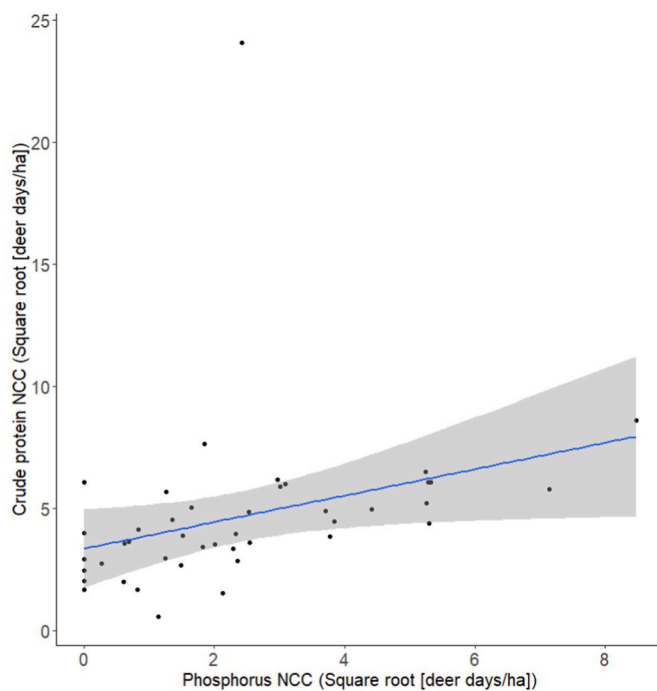


Fig. 3. Relationship between site-specific lactation-level nutritional carrying capacity (NCC) estimates derived based on crude protein (CP) and phosphorus (P) from 43 sites across the eastern U.S., late May–early August 2021–2023 ($p < 0.001$). NCC is given in deer days/ha, and square-root transformations were performed on data prior to analysis. CP estimates are based on 14% CP constraint and P estimates based on 0.3% P constraint. Bands represent a 95% confidence interval.

4. Discussion

Nutrient concentrations varied by plant class, with forbs having greater CP and P concentrations than semiwoody or woody plants. Our data support the separate collection and categorization of young and older plant tissue for forbs when estimating deer carrying capacity, as nutrient concentrations differed based on tissue age. We found positive correlation between CP and P concentrations within forages, but most plants did not meet both nutritional constraints simultaneously. Plants meeting the P constraint tended to also meet the CP constraint, whereas many plants that provided adequate CP concentrations did not simultaneously meet P constraints. Although we also found correlation between NCC estimates derived from CP and P, NCC estimates based on P generally were lower than those based on CP, and some sites had no plants meeting the minimum P requirements for a lactating female with twin fawns.

Forbs provided the greatest nutrient concentrations in our study, consistent with previous research (Mixon et al., 2010; Nanney et al., 2018; Harper et al., 2025). Young forb tissue provided the greatest levels of CP and P of any forage class, followed by older forb tissue. Deer generally select forbs over other plant classes when they are available (Vangilder et al., 1982; Henke et al., 1988; Nanney et al., 2018), but not all forbs met both CP and P requirements. Even if deer were to consume only plants meeting a minimum CP constraint, it is possible they would fail to meet P demands as less than a third of forbs met both nutrient constraints simultaneously. Diet selection must involve multiple nutrients to ensure herbivores fulfill their nutritional requirements, and consideration should be given to how selection for a particular nutrient may influence intake of another nutrient (Dykes et al., 2020). Nonetheless, several forbs met both requirements simultaneously more often than others. Horseweed (*Coryza canadensis*) met both requirements simultaneously in 80% of samples, alfalfa (*Medicago sativa*) in 78.6% of

samples, jewelweed (*Impatiens capensis*) in 66.7% of samples, soybeans (*Glycine max*) in 61.5% of samples, and pokeweed (*Phytolacca americana*) in 60% of samples. Meeting nutritional demands that allow for maximum productivity or body size depends upon providing plant communities with forbaceous species such as these which can simultaneously meet both CP and P requirements.

Correlation between CP and P in selected deer forages should allow deer to concomitantly select plants with greater concentrations of both nutrients. Our results build on the results of Vangilder et al. (1982), who found correlation among nutrients within 34 selected forages in the Missouri Ozarks. Similarly, Short et al. (1966) reported P was correlated with CP among nine mule deer (*Odocoileus hemionus*) forages. Although nutrient cooccurrence allows deer to select plants with greater concentrations of both nutrients, they may particularly select for plants with more P given fewer forages meet P requirements. Plants providing adequate P generally also met CP constraints, so diet selection for P likely would result in adequate CP intake. Strong selection of P has been documented in multiple systems (Lashley et al., 2015; Dykes et al., 2018), and several studies have noted P as a limiting mineral in deer forages (Blair et al., 1977; Barnes et al., 1990; Ramírez et al., 1996). Our results concur with previous studies and suggest P likely is more limiting than CP at most sites.

Consideration should be given to using NCC models with explicit nutritional constraints to not only estimate forage availability, but also to determine which nutrients may be most limiting. Previous research has noted P as a major nutrient limitation that influences populations and diet selection (Jacobson, 1984; Lashley et al., 2015; Dykes et al., 2018), and our results indicate CP is unlikely the most-limiting nutrient across the eastern U.S. However, our data also indicate nutrient limitations may vary among sites. It is important to note that estimated nutritional constraints, especially for P, vary by sex, age, and study design (French et al., 1956; Ullrey et al., 1975; Grasman and Hellgren, 1993). Actual P requirements for lactation may differ from our constraint of 0.3% (Shin et al., 2000), but NCC is still a valuable measure of relative forage quality and availability. Although the literature suggests P may be more limiting than CP in some areas, few have made direct comparisons of NCC estimates derived using P and CP constraints. NCC may respond differently to habitat management treatments based on the nutritional constraint used (Jones et al., 2009), and it may be appropriate to use the nutrient which results in the lowest NCC estimate for each site to provide the most-suitable measure of forage available to meet nutritional demands. Therefore, competing models of NCC based on multiple nutritional constraints could be developed with the lowest estimate used to represent forage availability when comparing treatments or sites to best represent nutritional availability capable of supporting a particular life-history process.

It may be useful for managers interested in improving forage availability to compare availability of plants meeting CP and P constraints on a property based on our nutrient results (Appendices 1, 2, and 3), previously published nutrient concentrations (i.e. Lashley et al., 2015; Nanney et al., 2018; Harper, 2019), or site-specific samples collected from a property. Evaluating the abundance of plants meeting nutritional requirements should help managers determine which nutrient is likely most-limiting and which plants already present they should aim to promote. As an example, our NCC data had a strong outlier at a site in New York dominated by agriculture. Soybeans provided abundant forage biomass that exceeded minimum CP requirement at 25.6% CP, but were slightly below minimum P requirement at 0.26% P at this particular site. Thus, the manager at this site could promote forbaceous species high in P that occur in early successional plant communities to allow deer to meet minimum P requirements with a mixed diet (Harper, 2017; Harper et al., 2021). Treatments such as growing-season fire and mechanical cutting in woodlands to promote stump-sprouting also could be used to promote greater mineral availability within semiwoody and woody plants at this site (Nichols, 2020; Nichols et al., 2021; Lashley et al., 2022).

Our site-wide estimates of NCC were relatively low and similar to unmanaged Control units from studies designed to increase deer forage availability. For example, our average CP NCC estimate of 33.5 was similar to estimates of closed-canopy hardwood forests (range: 1.1–67; Lashley et al., 2011; Nanney et al., 2018; Turner et al., 2024), nonnative grass fields (range: 19–66; Harper et al., 2021; Powell et al., 2022), and pine forests managed with infrequent disturbance (range: 1.6–35.9; Turner and Harper, 2024), all of which represent limited deer forage availability. Treatment units in manipulative studies have produced much greater NCC estimates, including canopy reduction and prescribed fire in hardwood forests (range: 84–591; Lashley et al., 2011; Turner et al., 2024), forest conversion to early succession using timber harvest, herbicide applications, and fire (range: 155–224; Nanney et al., 2018), and conversion of nonnative grass to native plant communities using herbicide applications and fire (range: 145–279; Harper et al., 2021; Powell et al., 2022). Therefore, managers have ample opportunities to significantly increase NCC for deer using various treatments on most properties.

Collecting and analyzing young and older plant tissue separately is important when working with higher-quality forages. Several previous studies have collected and analyzed all leaves together when evaluating forage quality and availability (Edwards et al., 2004; Jones et al., 2009; Glow et al., 2019), which may result in less precise NCC estimates when forbs comprise a large proportion of forages. As concentrate selectors, deer selectively forage on younger plant tissue of specific species when available (Lashley et al., 2014), which would tend to increase their diet quality compared to a whole-plant forage sample. Although we did not find support for differences in forage quality based on the age of woody and semiwoody samples, others have found such differences, especially among young tissue collected soon after disturbance (Schindler et al., 2004; Nichols et al., 2021; Lashley et al., 2022). Future work should collect young and older tissue separately for forbs and also for semiwoody and woody plants when disturbance, such as fire, stimulates resprouting young plant tissue.

Although there has been considerable work conducted over the past several decades investigating nutritional requirements for deer, we believe additional work is needed to refine estimates of NCC. Previous studies investigating nutritional demands have had relatively small sample sizes, and many involved only fawns/yearlings or a mixture of age classes, which may be a problem as nutritional requirements vary with age (French et al., 1956; Holter et al., 1979; Grasman and Hellgren, 1993; Asleson et al., 1996). Given the great amount of individual variation in nutrient use and requirements (Provenza, 2018), it is difficult to determine nutritional demands without a robust sample. Changes in nutrient absorption rates, retention, and resorption from bone during stress periods may allow deer to meet nutrient requirements without dietary changes (Grasman and Hellgren, 1993; Hewitt, 2011), further complicating the development of accurate nutritional constraints. Minimum P requirements for cervids are especially lacking in the literature (Shin et al., 2000), which may partially explain CP being a more commonly used constraint in NCC models. Future research should develop accurate estimates for multiple nutrients as required for maximum growth, milk production, and antler size to better understand the role of plant nutrients in deer morphology.

Other nutrients beyond CP and P also may influence diet selection and nutritional ecology of deer. Energy requirements for deer are well-established in the literature, but most herbaceous forages meet minimum nutritional requirements (Lashley et al., 2015; Turner, 2024). Calcium and potassium also are required for maintenance and growth, but these minerals are unlikely limiting given most forages meet or exceed estimated requirements (Barnes et al., 1990; Turner et al., 2021; Harper et al., 2025). Toxicity also plays a role in diet selection, as nutrient balancing requires avoidance of toxicity in addition to maximizing limiting nutrients. Sulfur may be particularly important, as several studies have documented strong avoidance of plants with high sulfur concentrations (Ceacero et al., 2015; Dykes et al., 2020).

Incorporating toxicity thresholds into NCC models would improve our estimates of nutrient availability, but we currently lack toxicity estimates for deer (Dykes et al., 2020). Developing toxicity constraints would benefit management of large herbivores, but providing a diversity of plants that meet the minimum requirements of limited nutrients likely is the best approach to allow animals to meet nutritional demands while avoiding toxicity given our current understanding of diet balancing.

5. Conclusions

We present data on average nutritional concentrations of young and older leaves of forbaceous, semiwoody, and woody deer forage species. We considered both the average nutrient levels, as well as whether various forages would meet the nutritional requirements for lactating females. We also considered whether NCC models using CP or P would result in different estimates of carrying capacity. Our findings indicate forbs provided the highest average nutritional quality, with young forb tissue having greater nutritional quality than older forb tissue. However, not all forbs met both the CP or P constraint simultaneously, indicating deer need to balance their diet with foraging selection. We also found correlation between CP and P in selected deer forages. Finally, NCC estimates tended to be lower when considering a nutritional constraint based on P versus CP, but this was not the case at all sites. Given variation in individual requirements and some uncertainty around nutritional constraints, managers should promote a diversity of forbs to provide deer sufficient availability of dietary CP and P.

Appendix 1. Common name, scientific name, number of sites collected (n), percentage that met 14% crude protein (CP) constraint, percentage that met a 0.3% phosphorus (P) constraint, and percentage that simultaneously met CP and P of forb samples collected on sites across the eastern U.S. during late May–early August 2021–2023 to evaluate deer forage availability and quality

Common name	Scientific name	n	% met CP	% met P	% met both
Alfalfa	<i>Medicago sativa</i>	14	100	78.6	78.6
Alyceclover	<i>Alysicarpus vaginalis</i>	1	100	0	0
American jointvetch	<i>Aeshynomene americana</i>	2	100	50	50
Arrowleaf clover	<i>Trifolium vesiculosum</i>	4	100	50	50
Asiatic dayflower	<i>Commelina communis</i>	1	0	0	0
Berseem clover	<i>Trifolium alexandrinum</i>	1	100	0	0
Bicolor lespedeza	<i>Lespedeza bicolor</i>	1	100	0	0
Birdsfoot trefoil	<i>Lotus corniculatus</i>	1	100	0	0
Black-eyed susan	<i>Rudbeckia hirta</i>	2	50	0	0
Black snakeroot	<i>Actaea racemosa</i>	2	100	100	100
Brazilian vervain	<i>Verbena brasiliensis</i>	4	100	100	100
Buckwheat	<i>Fagopyrum esculentum</i>	2	100	50	50
Butterfly pea	<i>Centrosema virginianum</i>	13	69.2	7.7	7.7
Canada goldenrod	<i>Solidago canadensis</i>	71	32.4	18.3	12.7
Chicory	<i>Cichorium intybus</i>	2	100	100	100
Cinquefoil	<i>Potentilla simplex</i>	1	0	0	0
Common lambsquarters	<i>Chenopodium album</i>	2	100	50	50
Common ragweed	<i>Ambrosia artemisiifolia</i>	30	100	36.7	36.7
Cowpea	<i>Vigna unguiculata</i>	4	100	50	50
Croton	<i>Croton capitatus</i>	1	100	0	0
Cutleaf coneflower	<i>Rudbeckia laciniata</i>	4	50	50	50
Daisy fleabane	<i>Erigeron annuus</i>	5	40	40	40
Flattop goldentop	<i>Euthamia graminifolia</i>	8	50	0	0
Florida pusley	<i>Richardia scabra</i>	1	0	0	0
Fragrant goldenrod	<i>Solidago odorata</i>	12	16.7	16.7	16.7
Giant ragweed	<i>Ambrosia trifida</i>	7	100	85.7	85.7
Hairy lespedeza	<i>Lespedeza hirta</i>	9	33.3	0	0
Hairy white old-field aster	<i>Symphyotrichum pilosum</i>	11	36.4	63.6	36.3
Hoary mountain mint	<i>Pycnanthemum incanum</i>	5	20	20	20
Hog peanut	<i>Amphicarpaea bracteata</i>	8	100	12.5	12.5
Horseweed	<i>Erigeron canadensis</i>	30	93.3	83.3	80
Jewelweed	<i>Impatiens capensis</i>	6	100	66.7	66.7
Joepyee weed	<i>Eutrochium purpureum</i>	4	25	0	0
Late-flowering thoroughwort	<i>Eupatorium sertorinum</i>	20	85	45	45
Many-flowered pennywort	<i>Hydrocotyle umellata</i>	1	0	100	0
Panicled ticktrefoil	<i>Desmodium paniculatum</i>	10	70	0	0

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CRedit authorship contribution statement

Mark A. Turner: Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Craig A. Harper:** Writing – review & editing, Resources, Project administration, Funding acquisition, Conceptualization. **Marcus A. Lashley:** Writing – review & editing, Methodology, Conceptualization. **Bronson K. Strickland:** Writing – review & editing, Methodology, Conceptualization. **Mark Q. Wilber:** Writing – review & editing, Methodology, Formal analysis.

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.

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Common name	Scientific name	n	% met CP	% met P	% met both
Partridge pea	<i>Chamaecrista fasciculata</i>	4	100	0	0
Pigeonwings	<i>Clitoria mariana</i>	1	100	0	0
Pointed-leaf ticktrefoil	<i>Desmodium glutinosum</i>	8	87.5	0	0
Pokeweed	<i>Phytolacca americana</i>	10	100	60	60
Prickly lettuce	<i>Lactuca serriola</i>	1	0	0	0
Prostrate ticktrefoil	<i>Desmodium rotundifolium</i>	2	100	0	0
Purple prairie-clover	<i>Dalea purpurea</i>	1	0	0	0
Red clover	<i>Trifolium pratense</i>	10	100	10	10
Rosinweed	<i>Silphium integrifolium</i>	3	0	0	0
Roundhead lespedeza	<i>Lespedeza capitata</i>	5	20	0	0
Roundleaf goldenrod	<i>Solidago patula</i>	2	0	0	0
Showy ticktrefoil	<i>Desmodium canadense</i>	1	100	0	0
Slender lespedeza	<i>Lespedeza virginica</i>	5	40	0	0
Soybean	<i>Glycine max</i>	26	100	61.5	61.5
Sticktight	<i>Bidens frondosa</i>	7	57.1	57.1	28.6
Stiff ticktrefoil	<i>Desmodium obtusum</i>	16	62.5	6.25	6.25
Stinging nettle	<i>Laportea canadensis</i>	9	100	55.6	55.6
Swamp agrimony	<i>Agrimonia parviflora</i>	8	12.5	0	0
Sweet white violet	<i>Viola blanda</i>	4	25	0	0
Tall ironweed	<i>Vernonia altissima</i>	5	60	0	0
Trailing lespedeza	<i>Lespedeza procumbens</i>	14	50	0	0
Virginia meadowbeauty	<i>Rhexia virginica</i>	1	0	0	0
White clover	<i>Trifolium repens</i>	29	100	41.4	41.4
White vervain	<i>Verbena urticifolia</i>	2	0	0	0
Woodland sunflower	<i>Helianthus divaricatus</i>	15	20	6.7	0
Wrinkleleaf goldenrod	<i>Solidago rugosa</i>	7	0	0	0
Yellow sweetclover	<i>Melilotus officinalis</i>	1	100	0	0

Appendix 2 Common name, scientific name, number of sites collected (n), percentage that met 14% crude protein (CP) constraint, percentage that met a 0.3% phosphorus (P) constraint, and percentage that simultaneously met CP and P of semiwoody plant samples collected on sites across the eastern U.S. during late May–early August 2021–2023 to evaluate deer forage availability and quality

Common name	Scientific name	n	% met CP	% met P	% met both
Alabama supplejack	<i>Berchemia scandens</i>	2	0	0	0
Black raspberry	<i>Rubus occidentalis</i>	18	44.4	16.7	5.6
Crossvine	<i>Bignonia capreolata</i>	1	0	0	0
Highbush blackberry	<i>Rubus argutus</i>	49	22.4	0	0
Japanese honeysuckle	<i>Lonicera japonica</i>	10	0	10	0
Lanceleaf greenbrier	<i>Smilax smallii</i>	1	0	0	0
Multiflora rose	<i>Rosa multiflora</i>	3	33.3	0	0
Muscadine	<i>Vitis rotundifolia</i>	26	3.8	0	0
Peppervine	<i>Ampelopsis arborea</i>	10	30	20	20
Roundleaf greenbrier	<i>Smilax rotundifolia</i>	29	31.0	0	0
Saw greenbrier	<i>Smilax bona-nox</i>	11	9.1	0	0
Southern dewberry	<i>Rubus trivialis</i>	3	33.3	0	0
Summer grape	<i>Vitis aestivalis</i>	7	0	0	0
Trumpet creeper	<i>Campsis radicans</i>	7	0	0	0
Virginia creeper	<i>Parthenocissus quinquefolia</i>	22	22.7	4.5	4.5
Yellow jessamine	<i>Gelsemium sempervirens</i>	3	0	0	0

Appendix 3. Common name, scientific name, number of sites collected (n), percentage that met 14% crude protein (CP) constraint, percentage that met a 0.3% phosphorus (P) constraint, and percentage that simultaneously met CP and P of woody plants collected on sites across the eastern U.S. during late May–early August 2021–2023 to evaluate deer forage availability and quality

Common name	Scientific name	n	% met CP	% met P	% met both
American beautyberry	<i>Callicarpa americana</i>	15	46.7	0	0
Autumn olive	<i>Elaeagnus umbellata</i>	1	100	0	0
Black cherry	<i>Prunus serotina</i>	2	0	0	0
Black locust	<i>Robinia pseudoacacia</i>	2	100	0	0
Black oak	<i>Quercus velutina</i>	1	100	0	0
Blackgum	<i>Nyssa sylvatica</i>	6	0	0	0
Boxelder	<i>Acer negundo</i>	1	100	0	0
Bush honeysuckle	<i>Lonicera tatarica</i>	11	0	0	0
Carolina buckthorn	<i>Rhamnus caroliniana</i>	2	50	0	0
Chestnut oak	<i>Quercus montana</i>	6	16.7	0	0
Chinese privet	<i>Ligustrum sinense</i>	7	28.6	28.6	14.3
Common persimmon	<i>Diospyros virginiana</i>	9	0	0	0
Common pricklyash	<i>Zanthoxylum americanum</i>	2	100	0	0

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Common name	Scientific name	n	% met CP	% met P	% met both
Coralberry	<i>Symphoricarpos orbiculatus</i>	8	12.5	12.5	0
Devil's walking stick	<i>Aralia spinosa</i>	5	20	0	0
Eastern redbud	<i>Cercis canadensis</i>	2	0	0	0
Elliot's blueberry	<i>Vaccinium elliotii</i>	1	0	0	0
Fetterbush lyonia	<i>Lyonia lucida</i>	5	0	0	0
Flowering dogwood	<i>Cornus florida</i>	2	0	0	0
Fragrant sumac	<i>Rhus aromatica</i>	1	0	0	0
Gallberry	<i>Ilex glabra</i>	3	0	0	0
Green ash	<i>Fraxinus pennsylvanica</i>	14	7.1	14.3	0
Hackberry	<i>Celtis occidentalis</i>	1	100	0	0
Highbush blueberry	<i>Vaccinium corymbosum</i>	12	0	0	0
Honeylocust	<i>Gleditsia triacanthos</i>	1	100	100	100
Live oak	<i>Quercus virginiana</i>	3	0	0	0
Mapleleaf viburnum	<i>Viburnum acerifolium</i>	2	0	50	0
Mockernut hickory	<i>Carya tomentosa</i>	5	40	0	0
Mulberry	<i>Morus alba</i>	2	50	0	0
Northern red oak	<i>Quercus rubra</i>	1	0	0	0
Post oak	<i>Quercus stellata</i>	2	50	0	0
Red maple	<i>Acer rubrum</i>	8	0	0	0
Sand laurel oak	<i>Quercus hemisphaerica</i>	2	0	0	0
Sassafras	<i>Sassafras albidum</i>	1	100	0	0
Scarlet oak	<i>Quercus coccinea</i>	1	0	0	0
Serviceberry	<i>Amelanchier arborea</i>	1	0	0	0
Shingle oak	<i>Quercus imbricaria</i>	1	0	0	0
Silky dogwood	<i>Cornus amomum</i>	2	0	0	0
Smooth sumac	<i>Rhus glabra</i>	1	0	0	0
Southern red oak	<i>Quercus falcata</i>	6	0	0	0
Sparkleberry	<i>Vaccinium arboreum</i>	3	0	0	0
St. Johnswort	<i>Hypericum hypericoides</i>	5	0	0	0
Sugar maple	<i>Acer saccharum</i>	2	0	0	0
Sweetleaf	<i>Symplocos tinctoria</i>	1	0	0	0
Yaupon	<i>Ilex vomitoria</i>	1	0	0	0
Water oak	<i>Quercus nigra</i>	8	0	0	0
White ash	<i>Fraxinus americana</i>	17	29.4	11.8	0
White oak	<i>Quercus alba</i>	8	25	0	0
Willow oak	<i>Quercus phellos</i>	1	0	0	0
Winged elm	<i>Ulmus alata</i>	3	0	0	0
Winged sumac	<i>Rhus copallinum</i>	4	0	0	0
Yellow poplar	<i>Liriodendron tulipifera</i>	6	16.7	0	0

Data availability

Data will be made available on request.

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