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Variation in Nutritional Quality of Plants for Deer in Relation to Sunny Versus Shady Environments

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Cover photos: Bunchberry dogwood (upper) and oval-leaf blueberry (lower) plants, growing in shady forest understory (left) and open sunny habitats (right).

All photos by Thomas Hanley.

Abstract

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Variation in nutritional quality of natural forages for black-tailed deer (*Odocoileus hemionus*) was studied in summer and winter in southeast Alaska. Freeze-dried samples of 17 summer forages collected in early July and 10 winter forages collected in February from three replicate sites each of shady forest understory and open, sunny habitat were analyzed and compared for their concentrations of digestible protein, digestible dry matter, and digestible energy. Data from each forage, ranging from forb and shrub leaves to woody twigs, were analyzed separately in a single-factor analysis of variance experimental design. Only five to seven of the summer forages differed significantly ($P < 0.05$) in values from sun and shade treatments: digestible protein was lower while digestible dry matter and digestible energy were higher in sun-grown than shade-grown forages. Differences in winter forages were fewer and inconsistent. However, despite general trends in patterns across all forages, variation both among and within forages was high at all scales of sampling: subsamples within a site, replicate sites of habitat types, and habitat types. Light intensity plays a major role in determining plant chemistry of some species, but the high degree of variation in plant response makes underlying patterns of variation especially important.

Keywords: *Odocoileus hemionus sitkensis*, *Vaccinium*, southeast Alaska, tannins, protein, energy, digestible, digestibility, plant defense, forage, forest.

Summary

Major forages for black-tailed deer were studied in summer and winter to compare differences in nutritional value related to their light environment: shady forest understory vs. open, sunny habitat in coastal forests of southeast Alaska. Nutritional value was quantified in terms of digestible protein, digestible dry matter, and digestible energy. Sun-grown forages in summer tended to have lower concentrations of digestible protein and higher concentrations of digestible dry matter and digestible energy than did shade-grown forages, while differences in winter were few, and responses differed among forages in both seasons. Variation in plant response was high among forages and at all scales of sampling. Principal implications of the results were the following:

Light plays an important role in the nutritional quality of some forages for deer and the diversity of their chemical and nutritional environment. However, understanding the variability in plant response to light, both among and within forages, is at least equally important as understanding the average, overall responses.

Summer nutritional values observed in this study tended to be higher than those reported in other studies within the region, principally because of slightly earlier phenology at the time of sampling and also because of explicitly accounting for sunny versus shady habitats.

The earlier sampling time in this study better corresponds with peak lactation requirements for deer in the region. The data will be important additions to current nutritional databases and also provide a basis for expanding databases to begin accounting for differences in sunny and shady habitats.

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Introduction

Knowledge of nutritional quality of foods for animals is central to an understanding of habitat quality for animals because food is fundamental to life and its processes. Nutritional quality of foods for herbivores varies considerably as forages differ in tissues, stage of growth, and nutrient and light environments. Large, generalist herbivores that consume a wide variety of plants have a continuous supply of potentially thousands of bites of food, yet relatively little of what is available for deer to consume may be of sufficient quality to meet their metabolic needs. Indeed, animal science for domestic herbivores has long been centered on understanding animal nutritional requirements and the nutritional quality of their forage resources. Wildlife biologists, too, have sought an understanding of the nutritional requirements of focal species and principal determinants of food quality (Moen 1973, Robbins 1983), although for species like black-tailed deer (*Odocoileus hemionus*) in natural forest environments, the diversity of their potential forage resources far exceeds that of domestics in cultivated pastures.

The enormous variation in chemical composition of wild plants has been of keen interest to ecologists for many decades, especially those interested in herbivore-plant interactions, because chemical variation has been seen as both affecting the nutritional quality of the plant for the herbivore and acting as a chemical defense against herbivory by the plant. The latter consideration was first heightened in importance when certain chemicals commonly occurring within plants were recognized as not being necessary for primary metabolic pathways involving growth and reproduction yet were detrimental to pathogens and herbivores. Those compounds were labeled "secondary" compounds or secondary metabolites and were considered chemical adaptations of plants to protect themselves from herbivory (Dethier 1954, Fraenkel 1959, Whittaker and Feeny 1971). Since then, much ecological theory has developed around the idea of plant defenses against herbivory, especially from an evolutionary point of view. The role of environmental variation in affecting or determining plant defense is central to all of that theory.

Plant defense theory has primarily evolved around four major hypotheses: (1) the "optimal defense" hypothesis, (2) the "carbon-nutrient balance" hypothesis, (3) the "growth rate" hypothesis, and (4) the "growth-differentiation balance" hypothesis (Stamp 2003). The optimal defense hypothesis (McKey 1974, 1979; Rhoades 1979; Rhoades and Cates 1976) identified a production cost with secondary compounds and viewed tradeoffs between growth, reproduction, and defense as an optimization problem within an evolutionary context. Environments differ in their soil nutrient availability, light, and intensity of herbivory; plants evolve to maximize their genetic fitness within those constraints. The carbon-nutrient balance

hypothesis (Bryant et al. 1983, Tuomi et al. 1988) explained adaptive plant defenses explicitly on the basis of relative availability of carbon and nutrients in the plant's environment: where soil nutrients are limiting to plant growth, surplus energy from light is invested in the production of carbon-rich (photosynthetic energy-expensive) defensive compounds, such as phenolics including tannins; but where the availability of light is limiting to plant growth, surplus nutrients (especially nitrogen) are invested in nitrogen-based defenses, such as alkaloids and other N-based toxins. The carbon-nutrient balance hypothesis has been especially useful in studying the **within**-species plasticity of plant responses to their environment. The growth rate hypothesis (Coley 1987a, 1987b; Coley et al. 1985) elaborated upon the carbon-nutrient balance hypothesis but in the context of **among**-species differences in plant defense. The growth-differentiation balance hypothesis (Herms and Mattson 1992), on the other hand, built upon the ideas of Loomis (1932, 1953) in viewing plant growth and differentiation of various tissues as an allocation process in relation to resource availability. Herms and Mattson (1992) put those ideas within the context of ecological and evolutionary tradeoffs involving resource availability, competition, and herbivory in the environment. For example, in a light-limited environment, production of additional leaf tissue should take priority over production of carbon-rich defensive compounds.

Although all four hypotheses have provided very useful constructs for viewing plant-herbivore-environment interactions, all have had only mixed success in being predictive instead of explanatory (Stamp 2003). The carbon-nutrient balance and growth-differentiation balance hypotheses are the most mechanistic and applicable to within-species response to environmental variation, but both have been found to work well for only certain species and kinds of secondary compounds (such as phenolics) and not at all well for others, leading some to argue their failure (Hamilton et al. 2001) and others to argue their need for modification (Massad et al. 2012) or more judicious application (Lerdau and Coley 2002).

Our interest in this study is in the nutritional quality of major forages commonly available to Sitka black-tailed deer (*O. h. sitkensis*) in natural forest environments of southeast Alaska. We were interested in plant species and tissues (leaf, twig) most commonly consumed in early summer (early July) at the time of peak nutritional requirements for lactating females and in mid winter (February) when deciduous forages are no longer available. Summer is a time of reproduction (fawn-rearing), growth, and accumulation of body reserves in deer, while winter is a time of depletion of body reserves and potential starvation (Moen 1973, Robbins 1993). Summer forages change rapidly in both nutritional quality and standing biomass (ovendry weight per unit area) with advancing plant phenology, while winter

forages change little in nutritional quality but greatly in their availability owing to burial by snow (Hanley and McKendrick 1983, 1985; Parker et al. 1999). Earlier investigations of nutritional quality of deer forages in forests of southeast Alaska indicated significant differences within species in relation to the light environment of their habitat, whether they were grown in the shade of forest understory or the open, "sunny" environment of young clearcuts, especially for nitrogen, phenolics (both tannin and nontannin), and digestible protein concentrations, tannin-binding capacity, and even relative palatability (Hanley et al. 1987, 1991; McArthur et al. 1993; Rose 1990; Van Horne et al. 1988). Those results were consistent with the carbon-nutrient balance and growth-differentiation balance hypotheses. However, they were heavily influenced by oval-leaf blueberry (*Vaccinium ovalifolium*[1]), which was the principal species studied and which also yielded very consistent results. Despite the high conformance of oval-leaf blueberry with theory, its closely related congeneric red huckleberry (*V. parvifolium*) and another major understory species, salmonberry (*Rubus spectabilis*), did not respond similarly in garden experiments in Washington state (Svendsen 1992), thereby casting some doubt on the generality of the hypotheses. As other tests of both hypotheses flooded the scientific literature, it became apparent that the results were highly species specific (Hamilton et al. 2001, Stamp 2003).

Therefore, we recognized that the nutritional quality of major forages consumed by deer in southeast Alaskan forests differs greatly among species and season and probably by the light environment of the habitat. However, we lacked confidence in plant defense theory to predict, a priori, species-specific differences for any species other than the well-studied oval-leaf blueberry. With deer as our focal herbivore species, we focused our measures of nutritional quality on digestible protein, digestible dry matter, and digestible energy concentrations because they are the most important and well-understood factors in the nutritional ecology of deer (Barboza et al. 2009, National Research Council 2007, Robbins 1993, Van Soest 1994). Mineral deficiencies in deer may be important locally but are not common, and secondary plant chemistry for nonphenolics is poorly understood for deer. All three measures of forage quality we used are affected by tannins in the digestive process: tannins binding with proteins reduce protein digestion and dry-matter digestion, which in turn reduces digestible energy (calculated as the product of gross energy and dry-matter digestibility).

[1] We include the very closely related *V. alaskaense* with *V. ovalifolium* because they hybridize and are mostly indistinguishable in the field. See appendix 1 for common and scientific nomenclature and authorities for all plants in this report.

Methods

Field Sampling

All forage samples were collected from field sites accessible from the Juneau, Alaska, road system. Because we needed sufficient sample material for multiple subsamples at each site, multiple sites for each type of habitat, and two types of habitat (shady and open), we were limited to only the most common major forages consumed by deer. By "forage" we mean both the plant species and its part (leaf, twig). Leaves and twigs (current year's woody growth) of the same species were considered as separate forages, because they differ so much in their physical and chemical composition and nutritional value. We studied 17 summer forages: leaves of fernleaf goldthread (*Coptis aspleniifolia*), bunchberry dogwood (*Cornus canadensis*), spreading woodfern (*Dryopteris expansa*), skunkcabbage (*Lysichiton americanus*), devilsclub (*Oplopanax horridus*), rusty menziesia (*Menziesia ferruginea*), five-leaved bramble (*Rubus pedatus*), salmonberry, threeleaf foamflower (*Tiarella trifoliata*), oval-leaf blueberry, red huckleberry, and the evergreen, sexually immature growth form of both blueberry and huckleberry (*Vaccinium* sp., species indistinguishable); twigs of salmonberry, oval-leaf blueberry, red huckleberry, and evergreen, sexually immature *Vaccinium* species; and current annual growth (both leaves and twigs together) of western hemlock (*Tsuga heterophylla*). In winter, we studied 10 forages: leaves of deer fern (*Blechnum spicant*), fernleaf goldthread, bunchberry dogwood, five-leaved bramble, threeleaf foamflower, and evergreen, sexually immature *Vaccinium* species; twigs of oval-leaf blueberry, red huckleberry, and sexually immature *Vaccinium* species; and current annual growth of western hemlock. Additionally, we collected samples of two other important forages for which we could obtain sufficient samples in only the open habitat and not from the shady forest: leaves of fireweed (*Chamerion angustifolium*) and current annual growth of Alaska cedar (*Callitropsis nootkatensis*). Because they came from only one habitat type, they were not included in our experimental design. Similarly, we collected leaf samples of deer fern in summer, too, but from only one open site, which excluded it from the experimental design.

The sampling design for each forage was to collect three subsamples (each being a composite collection of many leaves or twigs, usually from several to many different plants, sufficient to yield an ovendry weight of at least 8.0 g) from each of three independent sites representative of two distinctly different types of habitat—shady understory beneath a forest canopy and open, "sunny" habitat of a young clearcut (within 5 to 10 years of logging the forest overstory). The shady and sunny study sites were not paired or geographically related to one another; they were

simply six independent stands of forest vegetation (three shady, three sunny) scattered on the Juneau road system, although shady and sunny sites were within a few kilometers of each other. The three subsamples at each site were not stratified in any spatial context, either; they were three bags of the forage, collected from plants occurring more or less throughout the site. Therefore, each forage was to have a total of 18 subsamples of ≥8 g dry weight each (three subsamples × three sites × two habitat types). Sampling times were targeted at early July and February but actually ranged from 26 June through 19 July and from 17 January through 26 March (because of interference from snow), with the most intense effort in the middle of those ranges. Although both periods of sampling extended longer than we wished, we took care to obtain all three of a forage's subsamples from a given site within the same day and to obtain samples from shady and sunny sites within a couple of days of each other (i.e., there was no temporal clumping of samples for any forage during either season).

All samples were immediately stored on ice in a cooler during field collection, frozen at -18 °C at the end of the day, and freeze-dried and mill-ground within a week of harvest. Freeze-dried samples were sent to the Wildlife Habitat and Nutrition Laboratory at Washington State University, Pullman, Washington, for ovendry weight correction and analyses: total nitrogen by auto-analyzer, fiber composition by sequential detergent fiber analysis (Goering and Van Soest 1970, as modified by Mould and Robbins 1981 and Robbins et al. 1987b) without sodium sulfite, tannin astringency (protein-precipitating capacity) by the bovine serum albumin technique (Martin and Martin 1982, Robbins et al. 1987a), and gross energy by bomb calorimeter. Digestible protein (grams per 100 grams) and digestible dry matter (percentage) were calculated with the equations of Robbins et al. (1987a,1987b) and Hanley et al. (1992). Digestible energy (kilojoules per gram) was calculated as the product of gross energy and dry-matter digestibility.

Statistical Analyses

We quantified laboratory precision by calculating average coefficients of variation (CV = standard deviation divided by mean) across 13 blind-replicated samples (unidentified duplicates sent to the lab) for each of the laboratory analyses. Average CV, therefore, was the mean of 13 CV values, each being calculated from a pair of the replicated samples.

We examined patterns of variation in the data by calculating coefficients of variation for sampling at each of the three levels of stratification: among subsamples within study sites, among study sites within shady/sunny habitat types, and between the two habitat types. Average subsample CV for each forage was calculated by

averaging the six CV values calculated within each of the six sampling sites for the three subsamples per site. Average study site CV for each forage was calculated by averaging the two CV values calculated within each of the two habitat types for the three replicate sites per habitat type. The habitat-type CV for each forage was calculated from the mean and standard deviation of the two overall habitat-type means, one for shady habitats and the other for sunny habitats. We did no statistical testing of these data.

We were interested in statistically testing the shady versus sunny comparison of nutritional values of each of our forages, so each forage within each season was statistically analyzed independently. The experimental design was a standard completely randomized single factor analysis of variance with two treatments ("shade" and "sun" habitats), each replicated three times (sites) with three subsamples at each site. We used the SAS general linear model (GLM) procedure (SAS 2004) for the calculations and an alpha level of 0.05 (two-tailed test) for statistical significance. Preliminary examinations of the data indicated no need for transformation.

The analysis of variance tests (above) were used for each forage independently and should not be used for across-forage inferences, because multiple testing is likely to result in some "significant" differences simply by chance (e.g., at an alpha level of 0.05, we should expect 1 in 20 tests to indicate a significant difference when, in fact, no difference truly occurred). This must be kept in mind when considering the independent forage analyses as well. Therefore, in across-forage comparisons (e.g., results from shady versus sunny habitats with all forages considered together), we used the paired-sample t-test and an alpha level of 0.05 (two-tailed).

Results and Discussion

Laboratory Precision

The 13 blind samples analyzed in duplicate to provide estimates of laboratory error (variation) were selected to provide a wide range in values for digestible protein (1.7 to 21.1 g/100 g), digestible dry matter (36.1 to 79.1 percent), and digestible energy (7.9 to 16.1 kJ/g). Their coefficients of variation across all 13 samples averaged 0.143 (± 0.042 SE) for digestible protein, 0.018 (± 0.003) for digestible dry matter, and 0.019 (± 0.006) for digestible energy. The lower precision in digestible protein was primarily the result of relatively high variation in estimates of protein-precipitating capacity (mean CV = 0.269) rather than total nitrogen (mean CV = 0.072), which is commonly the case, as the protein-precipitation technique requires calculating a mean slope from five or more regression equations rather than just one analysis. Laboratory error was within the normal range of precision for digestible protein and was exceptionally low for digestible dry matter and digestible energy.

Patterns of Variation

Our sampling design of three subsamples per site, three sites per habitat type, and two habitat types enabled us to explore patterns of variation within our data by calculating the coefficient of variation for each forage at each of those three levels of sampling (table 1). Variation is important because high variation means that being selective among potential bites of the same forage (at the subsample level), among potential stands of similar vegetation (at the site level), and among types of environment (at the habitat-type level) can be rewarding to a forager. It also is important to forage-sampling researchers because it provides an indication of the relative sampling efforts required for estimating true population means at each of the three levels.

As would be expected, the variation among all the different forages ("Column CV" in table 1) was greater than the average variation among subsamples, replicate sites, and habitat types for all three nutritional variables and in both seasons. This simply means that different forages differ greatly in their nutritional value. However, there also are more interesting patterns evident in the data of table 1:

1. Among-sample variation ("Column mean" row) was substantially greater (up to about an order of magnitude greater) in digestible protein than in either digestible dry matter or digestible energy across all levels of sampling (subsamples, replicate sites, habitat types); and this was true in both summer and winter seasons;
2. Variation among forages ("Column CV") was almost twice as great in summer as in winter for digestible protein, but was similar in summer and winter for digestible dry matter and digestible energy.
3. Average sampling variation ("Column mean" row) in digestible protein and digestible energy was more or less similar across all three levels of stratification (subsamples, replicate sites, habitat types) in both seasons.[2] This last point is especially important in indicating that deer (and forage-sampling researchers) experience about the same amount of variation (and choices) in their foraging within a patch of vegetation (i.e., the subsamples within a site) as they do among various patches on the landscape, including even sunny versus shady patches for digestible protein and digestible energy. That is true both in summer and in winter, although it would be true in summer only for patches that are at about the same phenological stage of seasonal maturity. Within-site variation in nutritional quality, even within the same forage, is therefore very

[2] Average variation in digestible dry matter, on the other hand, was greater between habitat types than among subsamples and replicates in both seasons.

Table 1—Patterns of variation among samples at three levels of sampling and across all forages in two seasons (summer and winter) for digestible protein (g/100 g), digestible dry matter (percent), and digestible energy (kJ/g)[a]

Season and forage code	Digestible protein (g/100 g)				Digestible dry matter (%)				Digestible energy (kJ/g)			
	Overall mean	Mean coefficients of variation			Overall mean	Mean coefficients of variation			Overall mean	Mean coefficients of variation		
	DP (g/100 g)	Sub-sample	Repli-cates	Habitat types	DDM (%)	Sub-sample	Repli-cates	Habitat types	DE (kJ/g)	Sub-sample	Repli-cates	Habitat types
Summer:												
COAS	9.0	0.126	0.166	0.034	55.1	0.029	0.022	0.042	11.6	0.031	0.026	0.031
COCA	7.5	0.153	0.154	0.294	67.1	0.025	0.018	0.037	12.4	0.023	0.015	0.028
DREX	9.7	0.264	0.347	0.311	56.8	0.074	0.046	0.059	11.8	0.080	0.045	0.033
LYAM	22.3	0.070	0.121	0.149	71.5	0.036	0.038	0.015	14.3	0.066	0.069	0.008
MEFE_L	9.2	0.096	0.159	0.310	63.6	0.027	0.037	0.053	13.0	0.031	0.027	0.056
OPHO_L	15.2	0.111	0.071	0.230	73.1	0.037	0.030	0.076	15.1	0.032	0.030	0.076
RUPE	9.6	0.133	0.089	0.182	61.9	0.337	0.026	0.029	13.2	0.055	0.066	0.017
RUSP_L	13.2	0.216	0.118	0.256	64.0	0.048	0.052	0.092	12.6	0.046	0.066	0.084
RUSP_T	4.7	0.437	0.390	0.178	41.0	0.035	0.013	0.066	7.9	0.044	0.000	0.061
TITR	8.5	0.179	0.116	0.368	58.2	0.055	0.036	0.003	11.2	0.075	0.029	0.001
TSHE	5.7	0.236	0.331	0.189	60.3	0.032	0.050	0.045	13.5	0.034	0.068	0.026
VACCI_L	8.8	0.295	0.160	0.190	62.3	ISM	ISM	1.530	12.9	ISM	ISM	0.009
VAOV_L	10.4	0.233	0.168	0.320	63.2	0.026	0.017	0.064	13.5	0.022	0.029	0.054
VAOV_T	3.1	0.302	0.272	0.290	39.6	0.030	0.031	0.050	8.5	0.034	0.039	0.034
VAPA_L	11.8	0.109	0.132	0.315	60.1	0.063	0.082	0.168	13.2	0.070	0.088	0.157
VAPA_T	4.1	0.314	0.150	0.002	38.7	0.043	0.056	0.127	8.5	0.045	0.055	0.109
Column mean:	9.5	0.204	0.187	0.226	58.5	0.056	0.034	0.154	12.1	0.043	0.041	0.049
Column CV:	0.491				0.178				0.174			

Table 1—Patterns of variation among samples at three levels of sampling and across all forages in two seasons (summer and winter) for digestible protein (g/100 g), digestible dry matter (percent), and digestible energy (kJ/g)[a] (continued)

Season and forage code	Digestible protein (g/100 g)				Digestible dry matter (%)				Digestible energy (kJ/g)			
	Overall mean	Mean coefficients of variation			Overall mean	Mean coefficients of variation			Overall mean	Mean coefficients of variation		
	DP (g/100 g)	Sub-sample	Repli-cates	Habitat types	DDM (%)	Sub-sample	Repli-cates	Habitat types	DE (kJ/g)	Sub-sample	Repli-cates	Habitat types
Winter:												
BLSP	6.9	0.166	0.314	0.078	58.4	0.043	0.031	0.171	10.9	0.037	0.054	0.216
COAS	6.2	0.078	0.184	0.077	56.7	0.020	0.019	0.004	11.5	0.015	0.014	0.003
COCA	5.3	0.147	0.151	0.009	69.4	0.014	0.012	0.021	12.5	0.016	0.009	0.015
RUPE	7.3	0.169	0.087	0.071	63.9	0.043	0.030	0.021	12.3	0.036	0.028	0.005
TITR	7.8	0.215	0.245	0.371	64.0	0.026	0.019	0.101	11.9	0.014	0.009	0.090
TSHE	3.0	0.565	0.393	0.325	49.3	0.015	0.059	0.023	10.8	0.023	0.058	0.040
VACCI_L	7.7	0.201	0.128	0.048	63.3	0.016	0.027	0.710	13.0	0.023	0.015	0.015
VACCI_T	5.8	0.178	0.073	0.044	36.9	0.067	ISM	0.029	8.0	0.027	ISM	0.027
VAOV_T	3.1	0.220	0.187	0.076	39.8	0.047	0.029	0.048	8.4	0.041	0.037	0.028
VAPA_T	5.2	0.445	0.059	0.279	39.3	0.026	0.031	0.085	8.6	0.038	0.052	0.099
Column mean:	5.8	0.238	0.182	0.138	54.1	0.031	0.028	0.121	10.8	0.027	0.031	0.054
Column CV:	0.297				0.220				0.170			

ISM = insufficient sample material for calculating standard deviations. DP = digestible protein. DE = digestible energy. DDM = digestible dry matter.

[a] Average (mean) coefficients of variation (CV) were calculated at the level of subsamples within a study site (three subsamples per site), replicate study sites (target three study sites per habitat type), and habitat type (two types–sunny and shady). Mean CV across all forages within a season ("Column CV") was calculated for overall mean forage value after averaging all subsamples, sites, and both habitat types. See appendix 1 for common and scientific names of forage codes. See appendix 2 for actual numbers of replicate sites for each forage by habitat and nutritional variable.

important, regardless of what statistically significant differences might exist in overall mean values at broader spatial and environmental scales (the main focus of this study). Overall mean values provide information about general differences in patterns of plant response to environmental variation (e.g., sunny versus shady habitats) and a forager's mean encounter rates with forages of varying quality, but a forager can encounter substantial variation and opportunities for nutritional choice while foraging within even one patch of habitat.

The possible reasons for high variability, especially within subsamples, cannot be discerned from this study, but they might include at least four factors affecting plant-to-plant variation:

- Differences in age of tissues sampled during summer (i.e., slight differences in phenology among individual plants).
- Inherent variation among plants in their response to light, especially at the species level.
- Micro-environmental variation in light regimes at the level of individual leaves and soil variability at the level of individual plants.
- Micro-environmental variation in susceptibility to frost damage in winter.

However, regardless of reasons, what's important is that variation was so high at all levels of sampling, despite careful attention to collecting only what appeared to be similar material (i.e., same phenological stage in summer, lack of frost-damaged tissues in winter).

Moreover, keep in mind that our subsample variation is actually an underestimate of the variation encountered by a forager the size of a deer (or smaller), because each subsample was itself a composite collection of leaves (or twigs) from several to many plants rather than individual bites. These generalizations are being made at the level of all forages studied, however; they do not apply to each and every forage individually. Some forages exhibited significant departures from the overall generalizations, as evidenced by the values for individual forages within the body of the table, especially those forages that differed significantly in their values from sunny versus shady habitats (below).

One practical implication of these results is that it is reasonable to apply the same estimates of variation in forage quality (standard deviations) in the FRESH-Deer habitat evaluation model (Hanley et al. 2012) to both its stand-level and landscape-level applications.

Individual Forages

We were able to obtain adequate sample material for most forages in both seasons, but we were a little short with a few (see app. 2 for actual sample sizes), most notably for the diminutive, evergreen, sexually immature form of *Vaccinium* species in summer. Overall, results indicated 5 to 7 of the 17 summer forages differed in their nutritional values between shade versus sun habitat types, and 3 to 4 of the 10 winter forages did so (table 2). Three forages differed in all three nutritional variables in summer: leaves of bunchberry, devilsclub, and blueberry; none differed in digestible protein in winter.

Table 2—Forage-specific laboratory results for 17 summer forages and 10 winter forages from replicated shady forest understory (shade) and open sunny (sun) sites for digestible protein (g/100 g), digestible dry matter (percent), and digestible energy (kJ/g)[a]

Season and forage code	Digestible protein (g/100 g)		Digestible dry matter (percent)		Digestible energy (kJ/g)	
	Shade	Sun	Shade	Sun	Shade	Sun
Summer:						
COAS	9.3	8.8	**53.5***	**56.8***	11.4	11.9
COCA	**9.1***	**5.9***	**65.4***	**68.9***	**12.2***	**12.7***
DREX	11.8	9.8	59.1	54.4	12.1	11.5
LYAM	24.7	19.9	70.9	72.3	14.4	14.2
MEFE_L	**11.2***	**7.2***	61.2	66.0	**12.4***	**13.5***
OPHO_L	**17.6***	**12.8***	**69.2***	**76.9***	**14.3***	**15.9***
RUPE	**10.9***	**8.3***	60.6	63.2	13.1	13.4
RUSP_L	14.5	10.9	59.9	68.4	11.9	13.4
RUSP_T	5.3	3.8	39.1	43.0	7.6	8.3
TITR	**10.9***	**6.3***	58.0	58.3	11.2	11.2
TSHE	6.4	4.9	58.3	62.2	13.2	13.7
VACCI_L	10.7	7.7	ISM	ISM	ISM	ISM
VACCI_T	4.6	3.9	ISM	ISM	ISM	ISM
VAOV_L	**12.7***	**8.0***	**60.3***	**66.1***	**13.0***	**14.0***
VAOV_T	3.7	2.5	38.2	41.0	8.3	8.7
VAPA_L	**14.4***	**9.1***	**53.0***	**67.3***	11.7	14.6
VAPA_T	4.1	4.1	**35.2***	**42.2***	**7.9***	**9.2***
Winter:						
BLSP	6.6	7.3	**52.1***	**65.4***	9.3	12.6
COAS	6.5	5.9	56.9	56.6	11.4	11.5
COCA	5.2	5.4	**70.4***	**68.4***	**12.6***	**12.3***
RUPE	7.8	7.0	64.9	63.1	12.4	12.1
TITR	9.8	5.6	**68.1***	**59.7***	**12.6***	**11.1***
TSHE	2.4	3.6	47.1	50.3	10.5	11.1
VACCI_L	8.0	7.4	63.6	62.7	12.9	13.2
VACCI_T	5.6	6.0	36.2	37.7	7.9	8.2
VAOV_T	3.3	2.9	37.8	41.1	8.1	8.7
VAPA_T	6.2	4.3	**36.9***	**41.2***	**7.9***	**9.0***

ISM = insufficient sample material for means testing.

[a] Values are means calculated across replicate sites for each forage. Paired means highlighted in bold and asterisk differ significantly ($P < 0.05$, single factor analysis of variance). See appendix 1 for common and scientific names of forage codes. See appendix 2 for number of replicate sites, standard errors, and additional forages with insufficient sampling for means testing.

In summer, all forages that differed significantly between habitat types responded the same way: sun values were lower than shade values for digestible protein and greater than shade values for digestible dry matter and digestible energy. The reasons were the same for all species exhibiting that pattern. Digestible protein concentration was lowest in sun habitat because total nitrogen concentration was low and protein-precipitating capacity (reflecting tannin astringency) was high, thereby reducing digestible protein concentration in both its principal factors. Digestible dry matter concentration, on the other hand, was highest in sun habitat primarily because neutral detergent solubles concentration (mostly cellular cytoplasm) was high, and, to a lesser degree, because neutral detergent fiber digestibility (mostly cell wall) also was high, and the combined effects were easily high enough to outweigh the negative dry-matter digestibility effect of tannin-binding of proteins. Our data from oval-leaf blueberry provide a clear example. The following are the mean values calculated across all nine subsamples of blueberry from each habitat type, sun value first followed by shade value: 2.2 vs. 2.9 percent total nitrogen; 0.09 vs. 0.02 mg/mg protein-precipitating capacity; 72.8 vs. 64.9 percent neutral detergent solubles; 39.6 vs. 30.7 percent neutral detergent fiber digestibility; and 2.9 vs. 0.7 percent dry-matter loss to tannin binding. Although we did not measure specific leaf weight and readily digestible carbohydrates, Rose (1990) studied them in oval-leaf blueberry in both the field (Juneau, Alaska) and laboratory controlled-environment growth chambers: she found that the reduced total nitrogen concentration in sun-grown leaves (compared with shade grown) was primarily the result of a dilution effect from increased leaf thickness (specific leaf weight) and increased neutral detergent solubles largely consisting of sugars and starches in the leaf. The net effect in our study was the difference of 8.0 vs. 12.7 percent digestible protein and 66.1 vs. 60.3 percent digestible dry matter concentrations (sun vs. shade, respectively) (table 2). The corresponding difference in digestible energy concentration (14.0 vs. 13.0 kJ/g) simply follows from the large difference in dry-matter digestibility outweighing the insignificant difference in gross energy concentration (21.2 vs. 21.6 kJ/g, respectively).

The observed differences in digestible protein concentrations of summer leaves are consistent with both the carbon-nutrient balance and growth-differentiation balance hypotheses of plant chemical defense theory. However, the elevated dry-matter and energy digestibilities in the sun-grown leaves are not consistent with any sort of “defense” against a ruminant herbivore like deer, even though herbivory by deer can exert a profound influence on the physical structure, survival, and reproduction of plants and the composition and structure of plant communities in southeast Alaska (Gillingham et al. 2000, Hanley 1987, Klein 1965, Lewis 1992). The observed differences in plant responses to variation in their light environment

are more consistent with the early ideas of Loomis (1932, 1953) regarding growth and differentiation in relation to resource availability but without an emphasis on defense against herbivores, per se. Carbon-rich compounds of varied kinds (tannins, sugars, starches) increased with increased light and photosynthetic activity (Rose 1990). Moreover, it is important to recognize that 8 of the 17 summer forages did not differ in **any** of the three nutritional variables in this study (table 2).

In winter, none of the forages differed in digestible protein concentration in relation to sun versus shade habitats, and only 3 of the 10 differed in digestible energy concentrations, but in a mixed fashion: digestible energy concentration was greater in shade leaves than sun leaves (the opposite pattern from summer) of bunchberry and foamflower, but greater in sun twigs than shade twigs in red huckleberry (table 2). The difference in huckleberry twigs probably just carried across from the same pattern in the same twigs of the preceding summer. The opposite pattern in the evergreen forbs bunchberry and foamflower, however, may have reflected frost damage in the open-grown plants, as some winter mortality in open-grown plants of those species is commonly evident as dead leaves in the open but seldom under a forest canopy. High variability among replicate sites was responsible for the lack of statistical significance in the apparent large difference in mean digestible protein for foamflower.

Across Forages

The overall pattern of sun versus shade is evident when the forage-specific results are plotted graphically in comparison with a 1:1 relation (figs. 1 through 3). The basic trends identified for the statistically significant differences within individual forages (above) tend to apply broadly across summer forages despite the lack of statistical significance in many individual comparisons. Most summer values for sun-grown forages were lower in digestible protein and higher in digestible dry matter and digestible energy than their corresponding shade-grown values (figs. 1a, 2a, and 3a). Winter values, on the other hand, were not consistently over or under the 1:1 relation (figs. 1b, 2b, and 3b). Paired-sample t-tests of sun versus shade values across all summer forages indicated that the mean differences (sun minus shade) of -2.8, 4.3, and 0.8 percent for digestible protein, dry matter, and energy, respectively, were all highly significant ($P < 0.01$), whereas none of those for winter (-0.6, 1.2, and 0.4 percent, respectively), were statistically significant ($P > 0.20$ for all).

We suspect the patterns evident in figures 1 through 3 probably apply broadly across many, if not most, forages of southeast Alaskan forests, largely consistent with the Loomis (1932, 1953) ideas of growth-differentiation balance in relation to light availability. Light availability is a strongly controlling factor for growth and survival of plants in this region of dark forests and wet, coastal climate (Hanley and

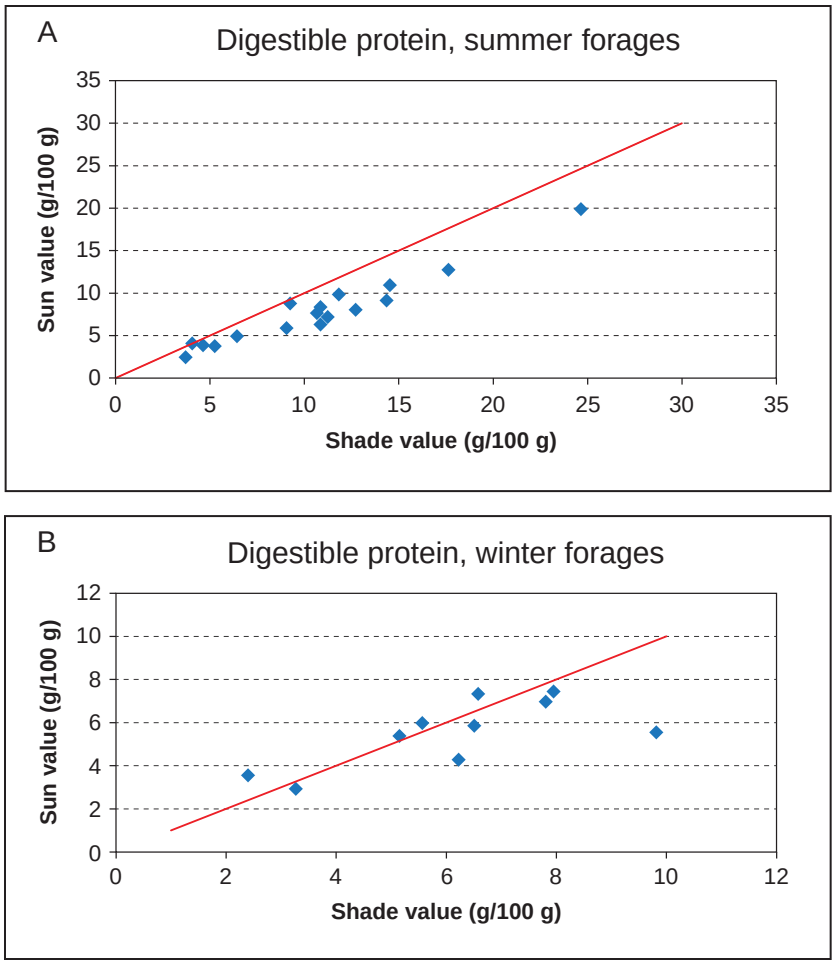

Figure 1—Digestible protein values (g/100 g) of forages from shady forest understories (shade value) and open, sunny habitats (sun value) for 17 forages in summer (A) and 10 forages in winter (B). Forages and values are those listed in table 2. The solid line in each figure indicates a 1:1 relation between shade and sun values.

Barnard 2014, Hanley et al. 2014a). The chemical effects are most evident in leaf tissue during the growing season, less evident in twig tissue, and least evident in winter when other canopy-influenced environmental factors may be more important than light. However, the effects of light, even in summer, are highly variable at all levels of scale (table 1), resulting in many statistically nonsignificant differences in overall means for individual forages (table 2). If we are correct in these conclusions, then light availability plays a major role in the nutritional quality of forages for deer and the diversity of their chemical and nutritional environment.

Comparison With Other Data From Southeast Alaska

The nutritional database for the FRESH-Deer habitat evaluation model (app. 2 of Hanley et al. 2012) provides a basis for comparison of our results for digestible protein and digestible dry matter with others from southeast Alaska; it is currently

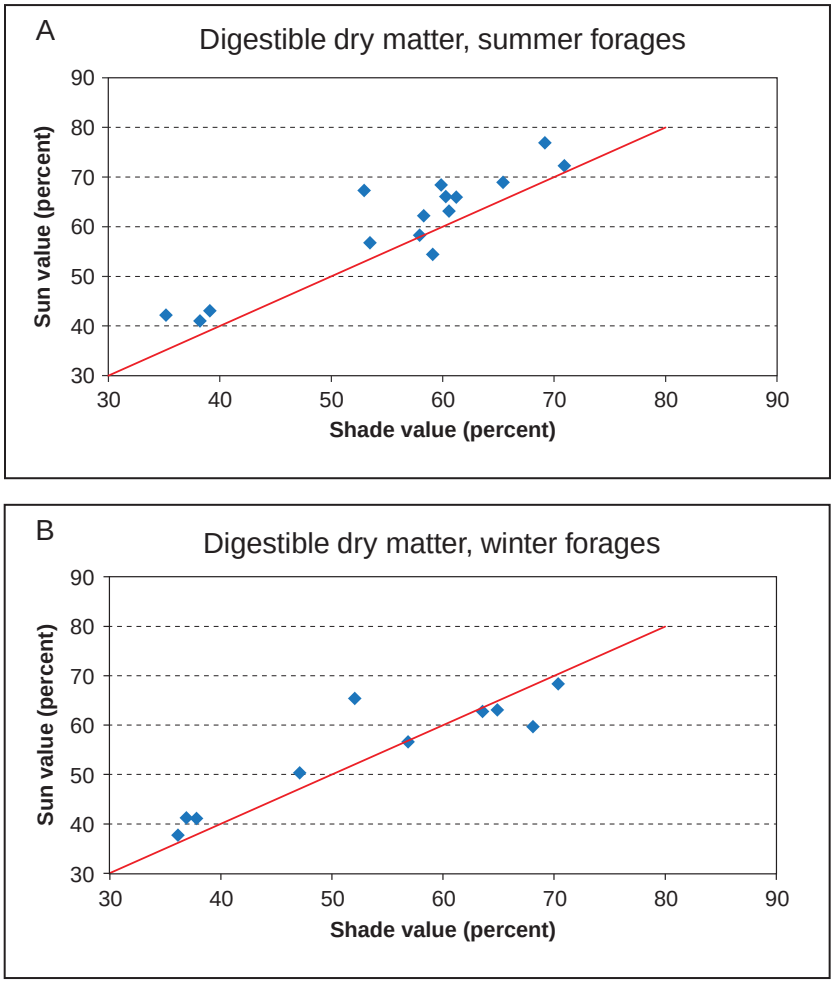

Figure 2—Digestible dry matter values (percentage) of forages from shady forest understories (shade value) and open, sunny habitats (sun value) for 15 forages in summer (A) and 10 forages in winter (B). Forages and values are those listed in table 2. The solid line in each figure indicates a 1:1 relation between shade and sun values.

based on data from four published studies (Hanley and McKendrick 1983, Hanley et al. 1992, McArthur et al. 1993, Parker et al. 1999) and unpublished data. In comparison with the values in the database, our summer results are significantly higher ($P < 0.05$, paired-sample t-test) for digestible dry matter in both sun- and shade-grown forages and digestible protein in shade-grown forages (figs. 4b, 5a, and 5b, respectively); they did not differ from the database values for digestible protein in sun-grown forages (fig. 4a). Our winter results did not differ from the database values for either sun- or shade-grown forages in either digestible protein or digestible dry matter. However, such overall comparison with mean values in the database overlooks the variation within individual forages (differences among studies) in the database. On a forage-specific basis including that variation, few values differed significantly ($P < 0.05$, two-tailed t-test) from database values: for summer

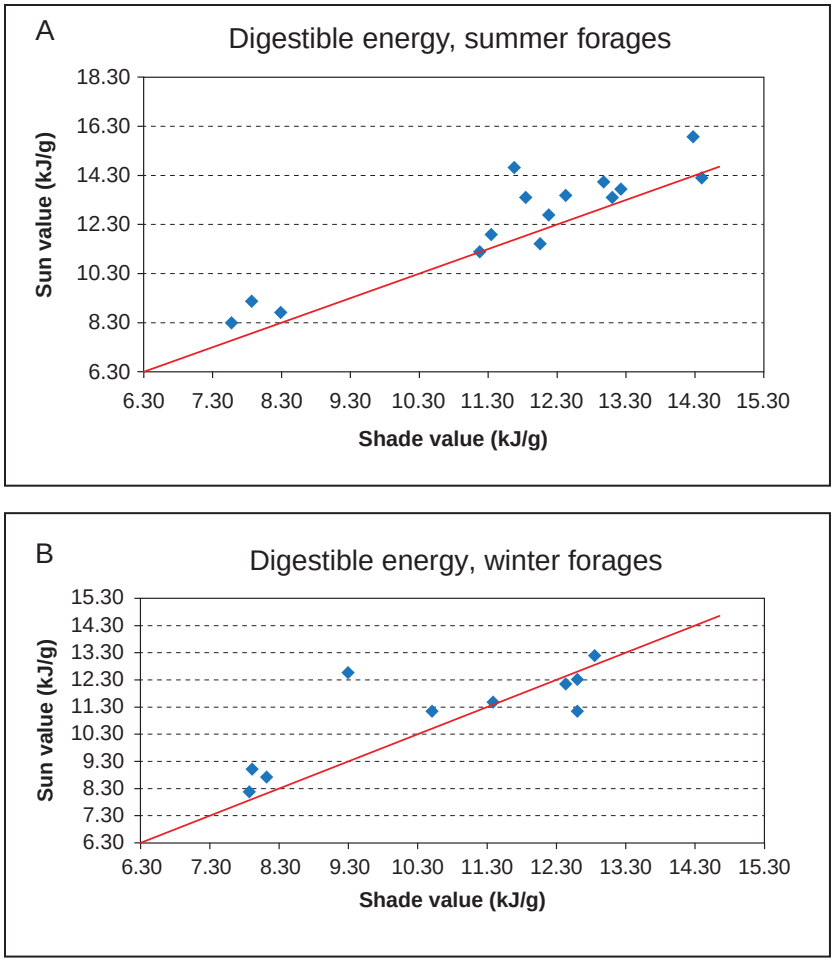

Figure 3—Digestible energy values (kJ/g) of forages from shady forest understories (shade value) and open, sunny habitats (sun value) for 15 forages in summer (A) and 10 forages in winter (B). Forages and values are those listed in table 2. The solid line in each figure indicates a 1:1 relation between shade and sun values.

forages, only leaves of fernleaf goldthread (both sun grown and shade grown) and five-leaved bramble (shade grown only) were higher in digestible protein, and only leaves of bunchberry and blueberry (both sun and shade grown) were higher for digestible dry matter. None of our summer values were significantly lower than database values, and none of our winter values differed significantly from database values in either direction.

There are two most likely explanations for this pattern of generally higher nutritional value (though highly variable) in our summer data compared with database values: (1) our sun-grown samples were all from open, "sunny" habitat, whereas most of the database samples were from forest understories, and (2) our samples were, on average, collected a couple of weeks earlier than most samples in the FRESH-Deer database. Blueberry leaves are the only forage in the current FRESH-Deer database that has unique values for shade-grown and sun-grown

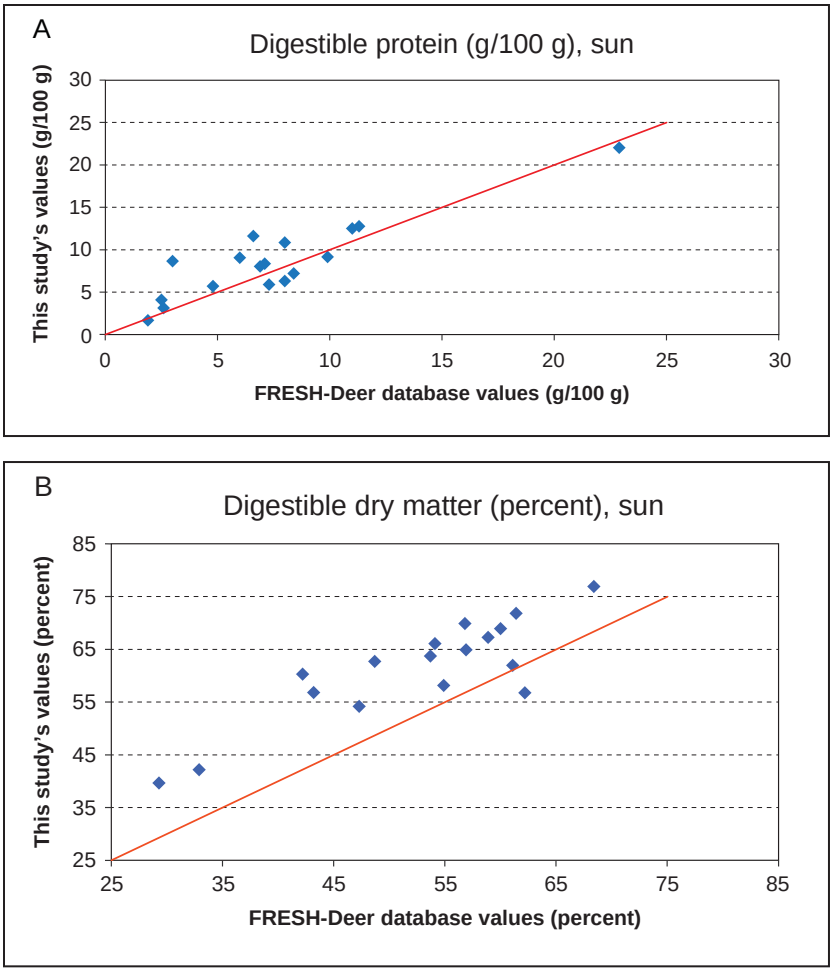

Figure 4—Forage-specific comparisons of mean values in current FRESH-Deer nutritional database with the values found in this study for individual forages in summer in terms of (A) digestible protein (g/100 g) and (B) digestible dry matter (percentage). The 17 forages are from those listed in appendix 2 that also have corresponding original values in the database, with this study's plotted value either that of the sun habitat (when significantly different from shade) or the pooled value (for no significant difference between sun and shade). Solid line indicates a 1:1 relation.

leaves. The relative lack of sun-grown forages in the database could largely account for the differences in digestible dry matter in our sun-grown samples. However, the difference in timing of sampling is very important, too, and would affect shade-grown forages as well as sun grown. We intentionally targeted early July for the peak of our sampling effort, because that is the time of peak lactation for deer in the region (data from Sadleir 1980, applied to southeast Alaska), whereas the samples in the database were simply "July" samples from anytime during that month. Nutritional quality changes greatly and rapidly with changes in plant phenology during the growing season (Hanley and McKendrick 1983, Parker et al. 1999), so the slightly earlier collection of our samples could account for much of the differences.

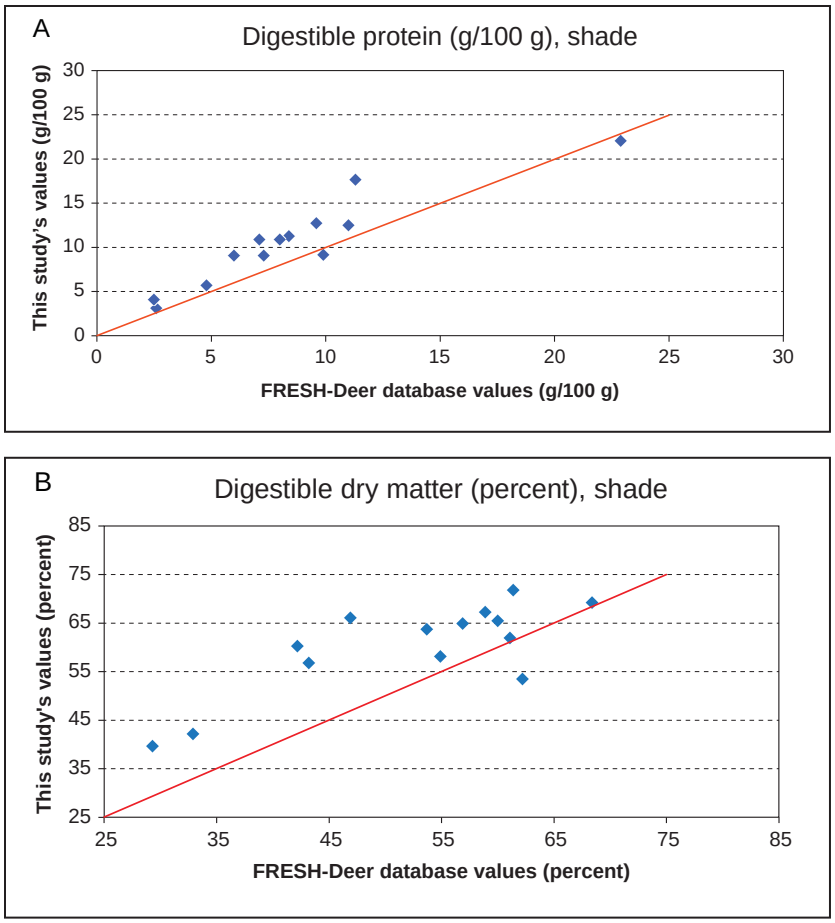

Figure 5—Forage-specific comparisons of mean values in current FRESH-Deer nutritional database with the values found in this study for individual forages in summer in terms of digestible protein (g/100 g) (A) and digestible dry matter (percentage) (B). The 14 forages are from those listed in appendix 2 that also have corresponding original values in the database, with this study's plotted value either that of the shade habitat (when significantly different from sun) or the pooled value (for no significant difference between sun and shade). Solid line indicates a 1:1 relation.

Furthermore, if plants are responding to their environment in a Loomis (1932, 1953) growth-differentiation fashion, carbon allocations within leaves might shift from highly mobile and digestible sugars and starches early in the growing season to digestion-reducing tannins later in the season. Indeed, intake of blueberry leaves by Sitka black-tailed deer shifts during the growing season, from relatively high levels of intake in early summer to very little intake in later summer (Hanley and McKendrick 1985, Hanley et al. 2014b), and palatability of blueberry leaves is greater for tannin-poor shade-grown leaves than for tannin-rich sun-grown leaves (Hanley et al. 1987, McArthur et al. 1993).

On the other hand, another factor could have played a role in slightly **underestimating** the dry-matter digestibility of our sun-grown leaves: we did not include

sodium sulfite in the detergent analysis. Omitting sodium sulfite tends to underestimate the digestibility of the neutral detergent fiber (NDF) in tannin-rich forages, but including it provides more accurate results for tannin-poor forages (Hanley et al. 1992). However, we did not know a priori which forages would be tannin-rich, and we wanted to apply the same laboratory methods to all forages. In the blueberry leaves used as an example earlier, the mean NDF concentration of the nine sun-grown (tannin-rich) subsamples was 27.2 percent with a mean NDF digestibility of 39.6 percent; thus, digestible NDF would have contributed about 10.8 percent dry matter of the total digestible dry matter of 66.1 percent for the forage. With an average lignin-cutin content of 18.8 percent of NDF, the omission of sodium sulfite probably underestimated the NDF digestibility by only a few percentage points at most (fig. 3 in Hanley et al. 1992). If the underestimate were 5 percent too little (i.e., true NDF digestibility of 44.6 percent), the net effect would have been a difference of 1.4 percent digestible dry matter (i.e., 67.5 instead of 66.1 percent).

Our winter values did not differ from database values because plants are not changing phenologically during winter, and differences between sun- and shade-grown forages are few in winter (above).

Implications

Our results from this study help to quantify the importance of light in affecting the chemical and nutritional environment, and therefore, habitat quality for black-tailed deer in Alaska. By studying a broad range of forages in both summer and winter, rather than just one or a few forages in one season, general patterns are evident in light's influence on plant chemistry, especially tannins and neutral detergent solubles, in determining digestible protein, digestible dry matter, and digestible energy concentrations of forages.

A large and important part of those patterns, however, is the high degree of variability inherent in them. Not only do different forages differ in their chemical composition, but they also differ in their response to light, some predictably according to resource allocation theory, but others apparently not at all. That within-species variation may be as great within a given patch of habitat as among patches and even among different kinds of habitat has important implications for foraging theory and habitat modeling. Within-habitat diversity should be especially important at low population densities of deer, because selectivity of bites could result in harvest of forage much better than average; however, that advantage would decrease with increasing population density. Forage researchers, too, need to be aware of both the overall importance of light and also the high degree of variability in plant response, because both factors strongly affect the results of their sampling.

In studies sharply constrained by the cost of laboratory analyses, compositing field samples from a variety of scales will be important for estimating true population means but will come at a cost of not understanding their underlying patterns of variation.

The higher dry matter digestibility in many summer forages observed in this study, compared with previous work, has direct implications for quantitative habitat evaluations for deer. The role of blueberry, especially, is significant because it is such a widespread and dominant species in forest understories of the region. The pattern of low nitrogen concentration combined with high tannin concentration in sun-grown leaves, observed decades ago, led to the idea that the vegetation of young, open clearcuts (1 to 15 years after logging) would likely be limiting in digestible protein for lactating deer because blueberry is such a dominant forage in the available biomass (Hanley et al. 1989, 1991). However, when extensive field data for such stands finally became available, nutritionally based analyses with the FRESH-Deer habitat evaluation model indicated that for all 51 stands of 9- to 13-year-old clearcuts, digestible dry matter, not digestible protein, was the limiting factor for lactating deer (Hanley et al. 2013). The principal reason why digestible protein was not limiting was because the vegetation was much more diverse with other species than just the dominant blueberry. However, substituting our new results for sun-grown forages into the nutritional database of the FRESH-Deer model (using sun values for forages differing significantly between sun and shade and pooled values for forages not differing significantly between sun and shade), the same 51 stands yield a different pattern in nutritional limitations for lactating deer: 45 stands limited by digestible dry matter, 4 stands limited by digestible protein, and 2 stands limited by total biomass (no nutritional limitation). The reason for the difference is because the digestible dry matter constraint is more easily satisfied with the higher digestible dry matter values from the current study; total capacity of the habitat (deer days per hectare) increases throughout, but nutritional limitations also shift relative to one another. Furthermore, specification of only a slightly higher requirement for digestible protein (e.g., for twins instead of singleton fawns) results in digestible protein being the limiting factor in many more of the stands.

Thus, the results from this study should be important additions to the nutritional database of the FRESH-Deer model, both in better matching the database's values with timing of peak lactation demands for deer and in providing a basis for expanding the database to account for differences in sunny and shady habitats. Although the difference between sunny and shady is likely a gradient response with

increasing light, the gradient may be nonlinear and may exhibit a sharp inflection point similar to that exhibited by major understory species in their growth rates in relation to light (Hanley et al. 2013a and unpublished data[3]). Rose, in her Alaska fieldwork with carbon-nutrient balance in oval-leaf blueberry (Rose 1990) found a threshold shift from "sun" to "shade" chemical composition occurring at about 60 to 75 percent overstory canopy coverage within low-volume noncommercial forests of the region; leaves in stands more open than that were characteristic of sunny habitat, while leaves in stands more closed than that were characteristic of shady habitat. She did not publish those results, but that idea could be field-tested easily, especially using oval-leaf blueberry as a model species. If field-testing, then it would be desirable to collect samples at least twice during the growing season, in both early summer (e.g., early July, like ours) and later summer (e.g., late August) to see if carbon stores shift from labile sugars and starches to tannins as the growing season progresses. Specific leaf weight (ovendry grams per square centimeter) also should be measured.

With better understanding of patterns of nutritional quality of plants in relation to environmental variation, combined with advances in quantifying nutritional value of forages in terms most directly relevant to deer and better tools for integrating measures of food quantity, quality, and deer nutritional requirements, we are now at a point where much progress can be made in better understanding habitat quality for deer in quantitatively meaningful terms. With better quantitative understanding of light in determining plant chemical composition, growth rate, and survival, we will be able to more effectively manage forests for desired outcomes.

Acknowledgments

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[3] Preliminary, unpublished data from greenhouse light-gradient trials with four species of understory plants indicate that concentrations of total nitrogen and digestible protein respond in a highly nonlinear, threshold-type relation to increasing intensity of light, while dry-matter digestibility and digestible energy responses are not so consistent (Hanley, T.A.; Barnard, J.C.; Bormann, B.T.; Nay, S.M.; Spalinger, D.E. On file at: USDA Forest Service, Forestry Sciences Laboratories, Juneau, Alaska, and Corvallis, Oregon).

English Equivalents

When you know:	Multiply by:	To get:
Centimeters (cm)	0.394	Inches
Meters (m)	3.28	Feet
Hectares (ha)	2.47	Acres
Square meters (m^2)	10.76	Square feet
Grams (g)	0.0352	Ounces
Kilograms (kg)	2.205	Pounds
Kilojoules (kJ)	0.2388	Kilocalories (kcal)
Kilojoules (kJ)	0.948	British thermal units (BTU)
Kilojoules per gram (kJ/g)	26.932	BTU/ounce

Literature Cited

Barboza, P.S.; Parker, K.L.; Hume, I.D. 2009. Integrative wildlife nutrition. New York: Springer. 342 p.

Bryant, J.P.; Chapin, F.S., III; Klein, D.R. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos. 40: 357–368.

Coley, P.D. 1987a. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. Oecologia. 74: 531–536.

Coley, P.D. 1987b. Interspecific variation in plant anti-herbivore properties: the role of habitat quality and rate of disturbance. New Phytologist. 106 (Supplement): 251–263.

Coley, P.D.; Bryant, J.P.; Chapin, F.S., III. 1985. Resource availability and plant antiherbivore defense. Science. 230: 895–899.

Dethier, V.G. 1954. Evolution of feeding preferences in phytophagous insects. Evolution. 8: 33–54.

Fraenkel, G.S. 1959. The raison d'être of secondary plant substances. Science. 129: 1466–1470.

Gillingham, M.P.; Parker, K.L.; Hanley, T.A. 2000. Partial consumption of shield fern, *Dryopteris dilatata*, rhizomes by black-tailed deer, *Odocoileus hemionus sitkensis*, and its potential implications. Canadian Field-Naturalist. 114: 21–25.

Goering, H.K.; Van Soest, P.J. 1970. Forage analyses (apparatus, reagents, procedures and some applications). Agric. Handb. 379. Washington, DC: U.S. Department of Agriculture. 20 p.

Hamilton, J.G.; Zangeri, A.R.; DeLucia, E.H.; Berenbaum, M.R. 2001. The carbon-nutrient balance hypothesis: its rise and fall. Ecology Letters. 4: 86–95.

Hanley, T.A. 1987. Physical and chemical response of understory vegetation to deer use in southeastern Alaska. Canadian Journal of Forest Research. 17: 195–199.

Hanley, T.A.; Barnard, J.C. 2014. Responses of southeast Alaska understory species to variation in light and simulated herbivory. Res. Pap. PNW-RP-599. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 22 p.

Hanley, T.A.; Bormann, B.T.; Barnard, J.C.; Nay, S.M. 2014a. Responses of southeast Alaska understory species to variation in light and soil environments. Res. Pap. PNW-RP-598. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 17 p.

Hanley, T.A.; Gillingham, M.P.; Parker, K.A. 2014b. Composition of diets selected by Sitka black-tailed deer on Channel Island, central southeast Alaska. Res. Note PNW-RN-570. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 21 p.

Hanley, T.A.; McClellan, M.H.; Barnard, J.C.; Friberg, M.A. 2013 Precommercial thinning: implications of early results from the Tongass-Wide Young-Growth Studies experiments for deer habitat in southeast Alaska. Res. Pap. PNW-RP-593. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 64 p.

Hanley, T.A.; Cates, R.G.; Van Horne, B.; McKendrick, J.D. 1987. Forest stand-age-related differences in apparent nutritional quality of forage for deer in southeastern Alaska. In: Provenza, F.D.; Flinders, J.T.; McArthur, E.D., comps. Proceedings—symposium on plant-herbivore interactions. Gen. Tech. Rep. INT-222. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 9–17.

Hanley, T.A.; McKendrick, J.D. 1983. Seasonal changes in chemical composition and nutritive value of native forages in a spruce-hemlock forest, southeastern Alaska. Res. Pap. PNW-312. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 41 p.

Hanley, T.A.; McKendrick, J.D. 1985. Potential nutritional limitations for black-tailed deer in a spruce-hemlock forest, southeastern Alaska. Journal of Wildlife Management. 49: 103–114.

Hanley, T.A.; Robbins, C.T.; Hagerman, A.E.; McArthur, C. 1992. Predicting digestible protein and digestible dry matter in tannin-containing forages consumed by ruminants. Ecology. 73: 537–541.

Hanley, T.A.; Robbins, C.T.; Spalinger, D.E. 1989. Forest habitats and the nutritional ecology of Sitka black-tailed deer: a research synthesis with implications for forest management. Gen. Tech. Rep. PNW-GTR-230. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 52 p.

Hanley, T.A.; Robbins, C.T.; Spalinger, D.E. 1991. Influence of the forest environment on nutritional ecology of black-tailed deer in Alaska. In: Bobek, B.; Perzanowski, K.; Reglan, W., eds. Global trends in wildlife management. Transactions of the 18th International Union of Game Biologists Congress. Krakow-Warsaw, Poland: Swiat Press: 357–361.

Hanley, T.A.; Spalinger, D.E.; Mock, K.J.; Weaver, O.L.; Harris, G.M. 2012. Forage Resource evaluation system for habitat—deer: an interactive deer habitat model. Gen. Tech. Rep. PNW-GTR-858. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 64 p.

Herms, D.A.; Mattson, W.J. 1992. The dilemma of plants: to grow or defend. Quarterly Review of Biology. 67: 283–335.

Klein, D.R. 1965. Ecology of deer range in Alaska. Ecological Monographs. 35: 259–284.

Lerdau, M.; Coley, P.D. 2002. Benefits of the carbon-nutrient balance hypothesis. Oikos. 98: 534–536.

Lewis, S.W. 1992. Relationships between deer and vegetation on Coronation Island, southeastern Alaska. Fairbanks, AK: University of Alaska Fairbanks. 103 p. M.S. thesis.

Loomis, W.E. 1932. Growth-differentiation balance vs. carbohydrate-nitrogen ratio. Proceedings of the American Society for Horticultural Science. 29: 240–245.

Loomis, W.E. 1953. Growth and differentiation—an introduction and summary. In: Loomis, W.E., ed. Growth and differentiation in plants. Ames, IA: Iowa State College Press: 1–17.

Martin, J.S.; Martin, M.M. 1982. Tannin assays in ecological studies: lack of correlation between phenolics, proanthocyanidins and protein-precipitating constituents in mature foliage of six oak species. Oecologia (Berlin). 54: 205–211.

Massad, T.J.; Dyer, L.A.; Vega C.G. 2012. Costs of defense and a test of the carbon-nutrient balance and growth-differentiation balance hypotheses for two co-occurring classes of plant defense. PLoS ONE. 7(10): e47554. doi: 10.1371/journal.pone.0047554.

McArthur, C.; Robbins, C.T.; Hagerman, A.E.; Hanley, T.A. 1993. Diet selection in a ruminant generalist browser in relation to plant chemistry. Canadian Journal of Zoology. 71: 2236–2243.

McKey, D. 1974. Adaptive patterns in alkaloid physiology. American Naturalist. 108: 305–320.

McKey, D. 1979. The distribution of secondary compounds within plants. In: Rosenthal, G.A.; Janzen, D.H., eds. Herbivores: their interactions with secondary plant metabolites. New York: Academic Press: 55–133.

Moen, A.N. 1973. Wildlife ecology: an analytical approach. San Francisco, CA: W.H. Freeman and Company. 458 p.

Mould, E.D.; Robbins, C.T. 1981. Evaluation of detergent analysis in estimating nutritional value of browse. Journal of Wildlife Management. 45: 937–947.

National Research Council. 2007. Nutrient requirements of small ruminants: sheep, goats, cervids, and New World camelids. Washington, DC: National Academies Press. 384 p.

Parker, K.L.; Gillingham, M.P.; Hanley, T.A.; Robbins, C.T. 1999. Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. Wildlife Monographs. 143: 1–48.

Rhoades, D.F. 1979. Evolution of plant chemical defense against herbivores. In: Rosenthal, G.A.; Janzen, D.H., eds. Herbivores: their interactions with secondary plant metabolites. New York: Academic Press: 1–55.

Rhoades, D.F.; Cates, R.G. 1976. Toward a general theory of plant antiherbivore chemistry. In: Wallace, J.W.; Mansell, R.L., eds. Recent advances in phytochemistry. New York: Plenum Press: 10: 168–213.

Robbins, C.T. 1983. Wildlife feeding and nutrition. New York: Academic Press. 343 p.

Robbins, C.T. 1993. Wildlife feeding and nutrition. 2nd ed. New York: Academic Press. 352 p.

Robbins, C.T.; Hanley, T.A.; Hagerman, A.E.; Hjeljord, O.; Baker, D.L.; Schwartz, C.C.; Mautz, W.W. 1987a. Role of tannins in defending plants against ruminants: reduction in protein availability. Ecology. 68: 98–107.

Robbins, C.T.; Mole, S.; Hagerman, A.E.; Hanley, T.A. 1987b. Role of tannins in defending plants against ruminants: reduction in dry matter digestion? Ecology. 68: 1606–1615.

Rose, C.L. 1990. Application of the carbon/nitrogen balance concept to predicting the nutritional quality of blueberry foliage to deer in southeastern Alaska. Corvallis, OR: Oregon State University. 150 p. Ph.D. thesis.

Sadleir, R.M.F.S. 1980. Energy and protein in relation to growth of suckling black-tailed deer fawns. Canadian Journal of Zoology. 58: 1347–1354.

SAS Institute Inc. 2004. SAS/STAT 9.1 user's guide. Carey, NC: SAS Institute Inc. 5121 p.

Stamp, N. 2003. Out of the quagmire of plant defense hypotheses. Quarterly Review of Biology. 78: 23–55.

Svendsen, C.R. 1992. Ecological relationships between elk and deer: behavior and plant-herbivore interactions. Seattle, WA: University of Washington. 171 p. Ph.D. dissertation.

Tuomi, J.; Niemelä, P.; Chapin, F.S., III; Bryant, J.P.; Sirén, S. 1988. Defensive responses of trees in relation to their carbon/nutrient balance. In: Mattson, W.J., ed. Mechanisms of woody plant defenses against insects: search for pattern. New York: Springer: 57–72.

Van Horne, B.; Hanley, T.A.; Cates, R.G.; McKendrick, J.D.; Horner, J.D. 1988. Influence of seral stage and season on leaf chemistry of southeastern Alaska deer forage. Canadian Journal of Forest Research. 18: 90–99.

Van Soest, P.J. 1994. Nutritional ecology of the ruminant. 2nd ed. Ithaca, NY: Comstock Publishing Associates. 488 p.

Whittaker, R.H.; Feeny, P.P. 1971. Allelochemics: chemical interactions between species. Science. 171: 757–770.

Appendix 1:

Table 3—Scientific and common names of plants and their forage codes[a]

Forage code	Scientific name	Common name
BLSP	*Blechnum spicant* (L.) Sm.	Deer fern fronds
CANO	*Callitropsis nootkatensis* (D. Don) Oerst. ex D.P. Little	Alaska cedar CAG[b]
COAS	*Coptis aspleniifolia* Salisb.	Fernleaf goldthread leaves
COCA	*Cornus canadensis* L.	Bunchberry dogwood leaves
CHAN	*Chamerion angustifolium* (L.) Holub ssp. *angustifolium*	Fireweed leaves
DREX	*Dryopteris expansa* (C. Presl) Fraser-Jenkins & Jermy	Spreading woodfern fronds
LYAM	*Lysichiton americanus* Hultén & H. St. John	Skunkcabbage leaves
MEFE_L	*Menziesia ferruginea* Sm.	Rusty menziesia leaves
OPHO_L	*Oplopanax horridus* (Sm.) Miq.	Devilsclub leaves
RUPE	*Rubus pedatus* Sm.	Five-leaved bramble leaves
RUSP_L	*Rubus spectabilis* Pursh	Salmonberry leaves
RUSP_T	*Rubus spectabilis* Pursh	Salmonberry twigs
TITR	*Tiarella trifoliata* L.	Threeleaf foamflower leaves
TSHE	*Tsuga heterophylla* (Raf.) Sarg.	Western hemlock CAG
VACCI_L	*Vaccinium* L. spp.[c]	Immature blueberry leaves
VACCI_T	*Vaccinium* L. spp.[c]	Immature blueberry twigs
VAOV_L	*Vaccinium ovalifolium* Sm.[d]	Oval-leaf blueberry leaves
VAOV_T	*Vaccinium ovalifolium* Sm.[d]	Oval-leaf blueberry twigs
VAPA_L	*Vaccinium parvifolium* Sm.	Red huckleberry leaves
VAPA_T	*Vaccinium parvifolium* Sm.	Red huckleberry twigs

[a] Source of nomenclature is PLANTS database, http://plants.usda.gov/java/.
[b] CAG = current annual growth (both leaves and twigs).
[c] Evergreen, decumbent, sexually immature form of several *Vaccinium* spp. (indistinguishable species when immature) including *V. ovalifolium*, *V. alaskaense*, and *V. parvifolium*.
[d] Includes Alaska blueberry, *V. alaskaense* Howell, which hybridizes with this species.

Appendix 2:

Table 4—Results from all species analyzed in this study, including those that were not replicated sufficiently for statistical analysis in the main report[a]

Season and forage code	Number of replicate sites		Digestible protein (g/100 g)					
			Shade		Sun		Pooled	
	Shade	Sun	Mean	SE	Mean	SE	Mean	SE
Summer:								
BLSP	0	1			11.6	3.3		
CANO	0	2			1.7	0.2		
COAS	3	3	9.3	0.9	8.8	0.8	9.1	0.4
COCA	3	3	9.1*	0.6	5.9*	0.6		
CHAN	0	3			8.6	0.6		
DREX	3	3	11.8	0.8	9.8	0.8	10.8	0.6
LYAM	3	3	24.7	1.7	19.9	1.6	22.0	1.0
MEFE_L	3	3	11.2*	0.8	7.2*	0.8		
OPHO_L	3	3	17.6*	0.9	12.8*	1.0		
RUPE	3	3	10.9*	0.6	8.3*	0.5		
RUSP_L	2	3	14.5	1.5	10.9	1.3	12.5	1.1
RUSP_T	2	3	5.26	1.51	3.75	1.19	3.94	0.67
TITR	3	3	10.9*	0.7	6.3*	0.7		
TSHE	3	3	6.4	1.1	4.9	1.1	5.7	0.5
VACCI_L	3	2	10.7	0.9	7.7	1.8	10.1	0.9
VACCI_T	3	1	4.6	0.9	3.9	2.3	4.6	0.8
VAOV_L	3	3	12.7*	1.0	8.0*	1.0		
VAOV_T	3	3	3.7	0.5	2.5	0.5	3.1	0.3
VAPA_L	2	3	14.4*	1.1	9.1*	0.9		
VAPA_T	2	3	4.1	0.6	4.1	0.5	4.1	0.4
Winter:								
BLSP	2	2	6.6	2.5	7.3	2.3	7.1	1.1
CANO	0	1			1.8	0.1		
COAS	3	3	6.5	0.8	5.9	0.8	6.3	0.3
COCA	3	3	5.2	0.6	5.4	0.6	5.2	0.3
RUPE	3	3	7.8	0.5	7.0	0.5	7.4	0.4
TITR	3	2	9.8	1.0	5.6	1.2	7.7	1.0
TSHE	3	3	2.4	0.5	3.6	0.5	3.0	0.4
VACCI_L	2	2	8.0	1.0	7.4	1.2	7.8	0.5
VACCI_T	2	2	5.6	0.5	6.0	0.6	5.7	0.4
VAOV_T	3	3	3.3	0.4	2.9	0.4	3.0	0.2
VAPA_T	3	3	6.2	0.8	4.3	0.9	5.4	0.6

Table 4—Results from all species analyzed in this study, including those that were not replicated sufficiently for statistical analysis in the main report[a] (continued)

Season and forage code	Number of replicate sites		Digestible dry matter (percent)					
			Shade		Sun		Pooled	
	Shade	Sun	Mean	SE	Mean	SE	Mean	SE
Summer:								
BLSP	0	1			62.7	3.9		
CANO	0	2			54.2	0.5		
COAS	3	3	53.5*	0.8	56.8*	0.8		
COCA	3	3	65.4**	0.7	68.9**	0.7		
CHAN	0	3			69.9	1.0		
DREX	3	3	59.1	1.7	54.4	1.7	56.8	1.3
LYAM	3	3	70.9	1.6	72.3	1.5	71.8	0.8
MEFE_L	3	3	61.2	1.5	66.0	1.5	63.7	0.9
OPHO_L	3	3	69.2*	1.3	76.9*	1.4		
RUPE	3	3	60.6	1.2	63.2	1.1	62.0	0.8
RUSP_L	2	3	59.9	2.2	68.4	1.8	64.9	1.6
RUSP_T	1	2	39.1	1.7	43.0	0.8	42.4	0.9
TITR	3	3	58.0	1.3	58.3	1.2	58.1	0.9
TSHE	3	3	58.3	1.9	62.2	1.9	60.3	0.9
VACCI_L	1	1					62.3	1.1
VACCI_T	1	0	33.7	ISM				
VAOV_L	3	3	60.3*	0.7	66.1*	0.7		
VAOV_T	3	3	38.2	0.7	41.0	0.7	39.6	0.5
VAPA_L	2	3	53.0*	3.3	67.3*	2.7		
VAPA_T	2	3	35.2*	1.5	42.2*	1.2		
Winter:								
BLSP	2	2	52.1*	1.6	65.4*	1.1		
CANO	0	1			50.8	0.4		
COAS	3	3	56.9	0.7	56.6	0.7	56.7	0.4
COCA	3	3			70.4*	0.5	68.4*	0.4
RUPE	3	3	64.9	1.3	63.1	1.3	64.0	0.8
TITR	2	2	68.1*	0.9	59.7*	0.8		
TSHE	3	3	47.1	1.7	50.3	1.7	49.5	0.8
VACCI_L	2	1	63.6	1.2	62.7	1.8	63.1	0.6
VACCI_T	1	1	36.2	0.8	37.7	0.6	37.1	0.6
VAOV_T	3	3	37.8	0.9	41.1	0.8	39.6	0.7
VAPA_T	3	3	36.9*	0.6	41.2*	0.7		

Table 4—Results from all species analyzed in this study, including those that were not replicated sufficiently for statistical analysis in the main report[a] (continued)

Season and forage code	Number of replicate sites		Digestible energy (KJ/g)					
			Shade		Sun		Pooled	
	Shade	Sun	Mean	SE	Mean	SE	Mean	SE
Summer:								
BLSP	0	1			12.4	0.4		
CANO	0	2			12.3	0.1		
COAS	3	3	11.4	0.2	11.9	0.2	11.6	0.1
COCA	3	3	12.2*	0.1	12.7*	0.1		
CHAN	0	3			13.5	0.2		
DREX	3	3	12.1	0.3	11.5	0.3	11.8	0.3
LYAM	3	3	14.4	0.6	14.2	0.6	14.3	0.3
MEFE_L	3	3	12.4*	0.2	13.5*	0.2		
OPHO_L	3	3	14.3*	0.3	15.9*	0.3		
RUPE	3	3	13.1	0.6	13.4	0.6	13.3	0.3
RUSP_L	2	3	11.9	0.6	13.4	0.5	12.8	0.3
RUSP_T	1	2	7.6	0.4	8.3	0.2	8.2	0.2
TITR	3	3	11.2	0.3	11.2	0.3	11.2	0.2
TSHE	3	3	13.2	0.5	13.7	0.5	13.5	0.2
VACCI_L	1	1					12.9	0.1
VACCI_T	1	0	7.5	ISM				
VAOV_L	3	3	13.0*	0.2	14.0*	0.2		
VAOV_T	3	3	8.3	0.2	8.7	0.2	8.5	0.1
VAPA_L	2	3	11.7	0.8	14.6	0.6	13.4	0.5
VAPA_T	2	3	7.9*	0.3	9.2*	0.3		
Winter:								
BLSP	2	2	9.3	0.6	12.6	0.5	11.5	0.6
CANO	0	1			11.3	0.9		
COAS	3	3	11.4	0.1	11.5	0.1	11.4	0.1
COCA	3	3	12.6*	0.1	12.3*	0.1		
RUPE	3	3	12.4	0.3	12.1	0.3	12.3	0.2
TITR	2	2	12.6*	0.1	11.1*	0.1		
TSHE	3	3	10.5	0.4	11.1	0.4	11.0	0.2
VACCI_L	2	1	12.9	0.1	13.2	0.3	12.9	0.1
VACCI_T	1	1	7.9	0.2	8.2	0.2	8.0	0.1
VAOV_T	3	3	8.1	0.2	8.7	0.2	8.4	0.1
VAPA_T	3	3	7.9*	0.2	9.0*	0.3		

ISM = insufficient sample material.

[a] Results are means and standard errors (SE) for digestible protein (g/100 g), digestible dry matter (percent), and digestible energy (kJ/g) for summer and winter forages collected in shady understory forest (Shade) or open, sunny habitats (Sun) as multiple subsamples obtained at each of several replicated sites (number of replicate sites shown). Means that differed statistically (single factor analysis of variance with alpha of 0.05) are indicated with an asterisk; their SE values are from the analysis of variance (reported in LS Means statement of SAS GLM procedure). When means did not differ significantly, all subsamples were pooled and their pooled mean and SE were calculated from the subsamples. For forages with insufficient material for statistical analysis, their reported mean and SE are from the pooling of all their subsamples. See appendix 1 for common and scientific names of forage codes.

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