

SEASONAL NUTRIENT YIELD AND DIGESTIBILITY OF DEER FORAGE FROM A YOUNG PINE PLANTATION

ROBERT M. BLAIR, Wildlife Habitat and Silviculture Laboratory, Southern Forest Experiment Station, Forest Service—USDA, Nacogdoches, Texas 75962¹

HENRY L. SHORT, Wildlife Habitat and Silviculture Laboratory, Southern Forest Experiment Station, Forest Service—USDA, Nacogdoches, Texas 75962²

E. A. EPPS, JR., Feed and Fertilizer Laboratory, Louisiana Agricultural Experiment Station, Louisiana State University, Baton Rouge 70803

Abstract: Six classes of current herbaceous and woody forage were collected seasonally from a 5-year-old mixed loblolly (*Pinus taeda*)-shortleaf pine (*Pinus echinata*) plantation (in Texas) and subjected to nutrient analyses and nylon bag dry-matter digestion trials. Forages were most nutritious and digestible in the spring when tissues were succulent and growing rapidly. Browse leaves and twig tips were the most abundant forage from spring to autumn and the most nutritious and digestible forage throughout the year. Pine and the residual twigs of browse were low in quality and digestibility at all seasons. Forbs were more nutritious than grasses but both declined seasonally in nutrient quality and digestibility as their fiber content increased with maturation. A low level of phosphorus in forage tissues at all seasons appeared to be a major limiting factor for deer in the young plantation.

J. WILDL. MANAGE. 41(4):667-676

For 3 to 5 years after a pine plantation is established, a wide assortment of grasses, forbs, and browse develops (Blair 1968). Between 5 and 8 years, crowns of the young pines are closing rapidly and forage growth declines with the diminishing light. Upon crown closure forage for deer remains sparse until trees are thinned or clearcut (Blair and Enghardt 1976).

The capacity of a young plantation to support deer can be estimated by considering the amount of palatable vegetation available during different seasons, the yield of plant nutrients, the metabolic usefulness of forages, and the nutrient requirements of the animals. Although forage often is abundant during summer and fall (Blair 1967, 1968), tissues may be deficient in nutrient quality except in spring (Short 1969). This paper evaluates the dry-matter yield, nutrient content, and dry-matter digestibility of

forage in a 5-year-old plantation of mixed loblolly and shortleaf pine. Forages were sampled at several different phenological periods and evaluated by specific classes of plants and plant tissues.

PROCEDURES

Study Plantation

The study was conducted during 1970 and early 1971 at the Stephen F. Austin Experimental Forest near Nacogdoches, Texas. The terrain of the area is relatively flat. The soils are fine sandy loams with heavy clay subsoils. In the fall of 1964, immediately before planting, the area was burned to reduce a heavy rough of dried grass. All shrubs and small hardwoods were mowed. The plantation was not burned or mowed thereafter.

Loblolly and shortleaf pine seedlings were planted in alternate rows. Seedlings were spaced 1.83 by 2.44 m apart, giving an initial density of 2,244 stems per ha. At plantation age 5, pine survival was 78 percent. Canopy coverage, delineated from a low-

¹ Laboratory maintained in cooperation with the School of Forestry, Stephen F. Austin State University.

² Present address: Western Energy and Land Use Team, Room 206 Federal Building, 301 South Howe St., Fort Collins, Colorado 80521.

level aerial photograph, averaged 68 percent.

The forage community was composed mainly of species common in open areas of high light intensity. Switchgrass (*Panicum virgatum*) contributed over 80 percent of the total grass yield. Low growing panicums (*Panicum* spp.), although abundant, were a small portion of the yield. Other common grasses were pinehill bluestem (*Andropogon scoparius* var. *divergens*), and broom-sedge bluestem (*Andropogon virginicus*). Forbs common in the plantation were hairy sunflower (*Helianthus hirsutus*), ragweed (*Ambrosia* spp.), camphorweed (*Heterotheca subaxillaris*), Maryland goldaster (*Heterotheca mariana*), eupatorims (*Eupatorium* spp.), and partridgepea (*Cassia fasciculata*). The principal species of browse were trumpetcreeper (*Campsis radicans*), peppervine (*Ampelopsis arborea*), dewberries and blackberries (*Rubus* spp.), sweetgum (*Liquidambar styraciflua*), common persimmon (*Diospyros virginiana*), flowering dogwood (*Cornus florida*), Japanese honeysuckle (*Lonicera japonica*), sassafras (*Sassafras albidum*), grapes (*Vitis* spp.), and saw greenbrier (*Smilax bona-nox*).

Forage Tissues

The plantation was divided into a 0.8-ha segment for sampling forage yields and nutrient composition and a fenced 0.6-ha segment for confining study animals during digestibility determinations.

Dry-matter yield.—Forage was sampled at midmonth of April, July, October and January by the ranked-set technique (Dell 1969). The October sample was taken before leaves dropped from deciduous browse. The current growth of vegetation was sampled up to a height of 1.52 m.

Clipped samples were separated into 6 forage classes: a) grasses and grasslike

plants, hereafter referred to as grass, b) forbs, c) the current leaves plus the terminal 2.5 cm or less of twig growth from all woody species except pine, d) the residual growth of current twigs from all woody species except pine, e) the current needle and twig growth of pine, and f) mushrooms and fruits. Fruits included those from browse and the large fruits (>0.32 cm diameter) of legumes and other forbs. Prominent fruiting species were partridgepea, nightshade (*Solanum* spp.), peppervine, Japanese honeysuckle, trumpet creeper, and smooth sumac (*Rhus glabra*). Pine was quantified separately as it was the commercial species involved and its tissues contain resins and volatile oils that are believed to influence ruminant digestion.

Plant tissue samples were dried to constant weight in a forced-draft oven at 55 C, and the weights then adjusted to an oven-dry base of 100 C.

Nutrient analysis.—At each sampling period the dried plant tissues were ground through a 2 mm screen in a Wiley mill and analyzed for crude protein and phosphorus (AOAC 1960), cell wall constituents (CWC), acid detergent fiber (ADF), acid detergent lignin (ADL), and silica (Goering and Van Soest 1970). Bomb calorimetry was used to determine caloric values, which were expressed as gross energy. Cell solubles were estimated as the difference between the total dry-matter sample and CWC, hemicellulose as the difference between CWC and ADF, and cellulose as the difference between ADF and ADL.

Caloric values were determined by Donald R. Dietz, Research Wildlife Biologist, formerly headquartered at the Rocky Mountain Forest and Range Experiment Station, U.S. Forest Service, Rapid City, South Dakota. Other nutrient analyses were conducted by the Feed and Fertilizer Lab-

Table 1. Seasonal dry-matter yields of current deer forage expressed in kilograms per hectare.

| Forage class | Spring | Summer | Fall | Winter |
|------------------------|--|------------------|--------------------|------------------|
| Herbaceous | | | | |
| Grasses | 133.3 <i>a</i> ¹ 2 ² | 178.0 <i>a</i> 3 | 239.6 <i>a</i> 2,3 | 220.8 <i>a</i> 1 |
| Forbs | 103.9 <i>a</i> 2 | 119.8 <i>a</i> 3 | 168.6 <i>a</i> 3,4 | 81.9 <i>a</i> 2 |
| Total herbaceous | 237.2 | 297.8 | 408.2 | 302.7 |
| Browse | | | | |
| Leaves and twig tips | 382.9 <i>b</i> 1 | 677.3 <i>a</i> 1 | 500.8 <i>b</i> 1 | 56.4 <i>c</i> 2 |
| Residual twig fraction | 79.2 <i>b</i> 2 | 319.6 <i>a</i> 2 | 311.6 <i>a</i> 2 | 308.1 <i>a</i> 1 |
| Pine needles and twigs | 11.0 <i>b</i> 3 | 94.5 <i>a</i> 3 | 91.7 <i>a</i> 4 | 88.8 <i>a</i> 2 |
| Total browse | 473.1 | 1,091.4 | 904.1 | 453.3 |
| Mushrooms and fruits | 1.8 | 2.2 | 2.2 | 2.0 |
| Total yield | 712.1 | 1,391.4 | 1,314.5 | 758.0 |

¹ Seasonal yields within a forage class (row) that are followed by a common letter do not differ significantly ($P > 0.05$).

² Forage class yields within a season (column) that are followed by a common number do not differ significantly ($P > 0.05$).

atory, Louisiana Agricultural Experiment Station, Baton Rouge.

Dry-matter digestion.—Within 10 days after plant collection, *in vivo* dry-matter digestion was determined for each forage class by the nylon bag procedure (Lowrey 1970) with ruminally cannulated goats (Short *et al.* 1974). Individual samples were duplicated in each of 2 goats, then averaged. When not in use for digestion trials, cannulated animals were maintained in a 2.0 ha fenced paddock of natural vegetation contiguous to the plantation.

Statistical Treatment

Dry-matter yields, nutrient composition, nutrient yields, and dry-matter digestibility for the different forage classes and seasons were examined by analyses of variance. When differences were significant, means were compared by Duncan's (1955) multiple range test. All tests were conducted at the 0.05 probability level. Because of their scarcity, mushrooms and fruits were excluded from the statistical treatment of forage data.

RESULTS AND DISCUSSION

Dry-Matter Yields

Woody species dominated the understory of the young plantation, and their yields were probably close to maximum because the pine canopy was closing rapidly (Table 1). Significant differences in seasonal dry-matter yields of forage were largely a reflection of growth stage. Grass and forb yields did not differ significantly between seasons, although average yields tended to be highest in the fall when most grass and forb growth was completed. Twig elongation on most woody species was virtually completed by early July (Blair and Halls 1968, Halls and Alcaniz 1965); thus, browse yields peaked in summer. From summer to fall the dry matter of browse leaves and twig tips declined 26 percent as leaves of many plants were prematurely dropped in response to high temperatures and drought. After leaves dropped from deciduous species in late autumn, the availability of evergreen browse leaves and twig

Table 2. Mean seasonal nutrient composition and dry matter digestibility of forage classes.

| Forage class and season | Composition as Percent Oven-Dry Weight | | | | | | | | | | |
|--------------------------------------|--|---------------|---------------|--------------------------|----------------------------|----------------|-----------------------------|---------------|---------------|----------------------|------------------------|
| | Crude protein | Phosphorus | Cell solubles | Cell wall contents (CWC) | Acid detergent fiber (ADF) | Hemicellulose | Acid detergent lignin (ADL) | Cellulose | Silica | Kcal/gm gross energy | Percent D.M. digestion |
| Grasses | | | | | | | | | | | |
| Spring | 11.1 <i>a</i> ¹ | 0.17 <i>a</i> | 29.1 <i>a</i> | 70.9 <i>d</i> | 39.6 <i>d</i> | 31.3 <i>b</i> | 5.7 <i>c</i> | 33.9 <i>c</i> | 3.85 <i>a</i> | 4.001 <i>c</i> | 49.4 <i>a</i> |
| Summer | 7.2 <i>b</i> | 0.13 <i>b</i> | 23.1 <i>b</i> | 76.9 <i>c</i> | 42.1 <i>c</i> | 34.8 <i>a</i> | 6.3 <i>c</i> | 35.8 <i>c</i> | 1.72 <i>b</i> | 4.185 <i>b</i> | 45.1 <i>b</i> |
| Fall | 6.6 <i>b</i> | 0.09 <i>c</i> | 20.8 <i>c</i> | 79.2 <i>b</i> | 47.4 <i>b</i> | 31.7 <i>b</i> | 8.3 <i>b</i> | 39.1 <i>b</i> | 2.15 <i>b</i> | 4.175 <i>b</i> | 33.7 <i>c</i> |
| Winter | 5.2 <i>c</i> | 0.07 <i>d</i> | 15.4 <i>d</i> | 84.6 <i>a</i> | 53.8 <i>a</i> | 30.9 <i>b</i> | 10.3 <i>a</i> | 43.5 <i>a</i> | 1.77 <i>b</i> | 4.369 <i>a</i> | 19.6 <i>d</i> |
| Forbs | | | | | | | | | | | |
| Spring | 13.3 <i>a</i> | 0.25 <i>a</i> | 56.2 <i>a</i> | 43.8 <i>d</i> | 35.6 <i>d</i> | 8.2 <i>c</i> | 8.8 <i>c</i> | 26.7 <i>d</i> | 4.08 <i>a</i> | 3.912 <i>b</i> | 68.2 <i>a</i> |
| Summer | 8.6 <i>b</i> | 0.13 <i>b</i> | 45.8 <i>b</i> | 54.2 <i>c</i> | 44.6 <i>c</i> | 9.6 <i>bc</i> | 10.9 <i>b</i> | 33.7 <i>c</i> | 1.36 <i>b</i> | 4.356 <i>a</i> | 51.5 <i>b</i> |
| Fall | 7.1 <i>c</i> | 0.10 <i>c</i> | 38.4 <i>c</i> | 61.6 <i>b</i> | 50.0 <i>b</i> | 11.6 <i>ab</i> | 11.8 <i>b</i> | 38.3 <i>b</i> | 0.98 <i>b</i> | 4.412 <i>a</i> | 42.1 <i>c</i> |
| Winter | 6.3 <i>c</i> | 0.07 <i>d</i> | 25.2 <i>d</i> | 74.8 <i>a</i> | 61.8 <i>a</i> | 13.1 <i>a</i> | 14.6 <i>a</i> | 47.2 <i>a</i> | 1.25 <i>b</i> | 4.302 <i>a</i> | 26.7 <i>d</i> |
| Browse—leaves & twig tips | | | | | | | | | | | |
| Spring | 16.4 <i>a</i> | 0.28 <i>a</i> | 64.1 <i>a</i> | 35.9 <i>a</i> | 25.5 <i>a</i> | 10.4 <i>a</i> | 10.1 <i>a</i> | 15.5 <i>b</i> | 0.38 <i>a</i> | 4.210 <i>ab</i> | 67.2 <i>a</i> |
| Summer | 10.5 <i>b</i> | 0.13 <i>b</i> | 66.0 <i>a</i> | 34.0 <i>a</i> | 27.5 <i>a</i> | 6.5 <i>a</i> | 11.8 <i>a</i> | 15.7 <i>b</i> | 0.48 <i>a</i> | 4.154 <i>b</i> | 58.1 <i>a</i> |
| Fall | 9.8 <i>b</i> | 0.12 <i>b</i> | 64.0 <i>a</i> | 36.0 <i>a</i> | 28.7 <i>a</i> | 7.3 <i>a</i> | 11.2 <i>a</i> | 17.5 <i>a</i> | 0.90 <i>a</i> | 4.287 <i>ab</i> | 60.4 <i>a</i> |
| Winter | 11.7 <i>b</i> | 0.15 <i>b</i> | 61.0 <i>a</i> | 39.0 <i>a</i> | 31.3 <i>a</i> | 7.7 <i>a</i> | 12.3 <i>a</i> | 19.0 <i>a</i> | 0.55 <i>a</i> | 4.445 <i>a</i> | 55.6 <i>a</i> |
| Browse—residual twigs | | | | | | | | | | | |
| Spring | 8.7 <i>a</i> | 0.22 <i>a</i> | 34.8 <i>a</i> | 65.2 <i>b</i> | 50.7 <i>b</i> | 14.5 <i>a</i> | 14.6 <i>b</i> | 36.0 <i>a</i> | 0.17 <i>a</i> | 4.149 <i>b</i> | 40.0 <i>a</i> |
| Summer | 5.3 <i>b</i> | 0.13 <i>b</i> | 30.0 <i>b</i> | 70.0 <i>a</i> | 56.3 <i>a</i> | 13.7 <i>a</i> | 18.1 <i>a</i> | 38.2 <i>a</i> | 0.36 <i>a</i> | 4.190 <i>b</i> | 26.6 <i>b</i> |
| Fall | 5.5 <i>b</i> | 0.09 <i>c</i> | 30.8 <i>b</i> | 69.2 <i>a</i> | 55.7 <i>a</i> | 13.6 <i>a</i> | 18.4 <i>a</i> | 37.3 <i>a</i> | 0.14 <i>a</i> | 4.305 <i>ab</i> | 29.1 <i>b</i> |
| Winter | 5.6 <i>b</i> | 0.09 <i>c</i> | 29.2 <i>b</i> | 70.8 <i>a</i> | 58.1 <i>a</i> | 12.8 <i>a</i> | 19.5 <i>a</i> | 38.5 <i>a</i> | 0.13 <i>a</i> | 4.557 <i>a</i> | 28.4 <i>b</i> |
| Pine—needles & twigs | | | | | | | | | | | |
| Spring | 8.3 <i>ab</i> | 0.19 <i>a</i> | 47.1 <i>b</i> | 52.9 <i>a</i> | 39.8 <i>a</i> | 13.1 <i>a</i> | 17.6 <i>a</i> | 22.1 <i>a</i> | 0.21 <i>b</i> | 4.327 <i>c</i> | 39.9 <i>a</i> |
| Summer | 7.0 <i>c</i> | 0.13 <i>b</i> | 51.2 <i>a</i> | 48.8 <i>b</i> | 41.3 <i>a</i> | 7.5 <i>b</i> | 18.4 <i>a</i> | 22.9 <i>a</i> | 0.56 <i>a</i> | 4.663 <i>b</i> | 33.5 <i>b</i> |
| Fall | 7.7 <i>b</i> | 0.11 <i>b</i> | 53.1 <i>a</i> | 46.9 <i>b</i> | 38.8 <i>a</i> | 8.0 <i>b</i> | 18.0 <i>a</i> | 20.9 <i>a</i> | 0.48 <i>a</i> | 4.422 <i>c</i> | 40.8 <i>a</i> |
| Winter | 8.7 <i>a</i> | 0.12 <i>b</i> | 55.1 <i>a</i> | 44.9 <i>b</i> | 38.4 <i>a</i> | 6.5 <i>b</i> | 17.1 <i>a</i> | 21.3 <i>a</i> | 0.58 <i>a</i> | 4.965 <i>a</i> | 44.1 <i>a</i> |
| Mushrooms & fruits | | | | | | | | | | | |
| Spring | 13.4 | 0.27 | 54.9 | 45.1 | 38.3 | 6.8 | 14.7 | 23.6 | 2.39 | 4.524 | 56.6 |
| Summer | 9.8 | 0.26 | 58.9 | 41.1 | 34.0 | 7.1 | 16.8 | 17.2 | 0.11 | 4.677 | 58.4 |
| Fall | 29.5 | 0.67 | 60.6 | 39.4 | 27.8 | 11.6 | 7.4 | 20.4 | 4.16 | 4.374 | 76.3 |
| Winter | 15.9 | 0.08 | 46.9 | 53.1 | 30.3 | 22.8 | 9.1 | 21.2 | 6.75 | 4.447 | 66.8 |

¹ Seasonal nutrient values, within a forage class, followed by a common letter are not significantly different ($P > 0.05$).

Table 3. Seasonal ranking¹ and statistical differences² of forage classes³ for important nutrient attributes.

| Season | Crude protein | Phosphorus | Cell solubles | Acid detergent fiber (ADF) | Acid detergent lignin (ADL) | Dry matter digestion |
|--------|---------------|---------------|---------------|----------------------------|-----------------------------|----------------------|
| Spring | BLT | BLT <i>a</i> | BLT | BRT | P | F <i>a</i> |
| | F | F <i>ab</i> | F | P <i>a</i> | BRT | BLT <i>a</i> |
| | G | BRT <i>bc</i> | P | G <i>a</i> | BLT <i>a</i> | G |
| | BRT <i>a</i> | P <i>cd</i> | BRT | F | F <i>a</i> | BRT <i>a</i> |
| | P <i>a</i> | G <i>d</i> | G | BLT | G | P <i>a</i> |
| Summer | BLT | BLT <i>a</i> | BLT | BRT | P <i>a</i> | BLT |
| | F | P <i>a</i> | P | F | BRT <i>a</i> | F |
| | G <i>a</i> | F <i>a</i> | F | G <i>a</i> | BLT <i>b</i> | G |
| | P <i>a</i> | G <i>a</i> | BRT | P <i>a</i> | F <i>b</i> | P |
| | BRT | BRT <i>a</i> | G | BLT | G | BRT |
| Fall | BLT | BLT <i>a</i> | BLT | BRT | BRT <i>a</i> | BLT |
| | P <i>a</i> | P <i>ab</i> | P | F <i>a</i> | P <i>a</i> | F <i>a</i> |
| | F <i>ab</i> | F <i>bc</i> | F | G <i>a</i> | F <i>b</i> | P <i>a</i> |
| | G <i>c</i> | G <i>bc</i> | BRT | P | BLT <i>b</i> | G |
| | BRT | BRT <i>c</i> | G | BLT | G | BRT |
| Winter | BLT | BLT <i>a</i> | BLT <i>a</i> | F <i>a</i> | BRT <i>a</i> | BLT |
| | P | P <i>a</i> | P <i>a</i> | BRT <i>ab</i> | P <i>ab</i> | P |
| | F <i>a</i> | BRT <i>b</i> | BRT <i>b</i> | G <i>b</i> | F <i>bc</i> | BRT <i>a</i> |
| | BRT <i>a</i> | F <i>b</i> | F <i>b</i> | P | BLT <i>cd</i> | F <i>a</i> |
| | G <i>a</i> | G <i>b</i> | G | BLT | G <i>d</i> | G <i>a</i> |

¹ Forage classes ranked by descending order of magnitude, based on values given in Table 2.

² Classes followed by a common letter are not statistically different ($P > 0.05$).

³ G—grasses; F—forbs; BLT—browse leaves and twig tips; BRT—browse residual twigs; P—Pine.

tips was only 8 percent of the summer yield.

From spring to fall, yields of browse leaves and twig tips were significantly greater than those of other forages. In winter, cured grasses and hardened residual twigs of browse were the most abundant forages. Leaves and twig tips comprised 54 percent of the dry matter in spring, 49 percent in summer, 38 percent in autumn, and only 7 percent in the winter. Forty-one percent of the winter yield was residual twigs.

Nutrient Composition and Yield

Nutrient levels were closely related to the stage of plant growth. With few exceptions, the highly digestible and nonfibrous cell solubles, crude protein, and phosphorus were at their highest seasonal level in the succulent spring growth (Table 2). As grasses, forbs, and browse twigs matured,

nonfibrous fractions declined and fibrous, poorly digestible cell wall constituents increased. In contrast, the cell solubles and cell wall constituents in browse leaves and twig tips varied little between seasons.

Leaves and twig tips of browse and mushrooms and fruits were seasonally higher than other forages in crude protein, phosphorus, and total cell solubles and lower in CWC, ADF, hemicellulose, and cellulose (Tables 2 and 3). High levels of cell solubles in relation to fiber constituents, such as occurred in these tissues at all seasons, are fundamental to deer sustenance. Deer possess a small rumen volume and have high metabolic requirements, indicating that they cannot digest fibrous growth rapidly enough to subsist on high-fiber forages (Short 1963).

Spring.—In the spring, 53 percent of the forage dry-matter was cell solubles (Table

Table 4. Seasonal nutrient yield by different forage classes.

| Season and forage class | Digestible dry matter | Cell solubles | Crude protein | Phosphorus | Cell wall contents (CWC) | Acid detergent fiber (ADF) | Acid detergent lignin (ADL) | Gross energy |
|---------------------------|----------------------------|----------------|----------------|----------------|--------------------------|----------------------------|-----------------------------|---------------------|
| Kg oven-dry matter/ha | | | | | | | | |
| Spring | | | | | | | | |
| Grass & grasslike plants | 65.8 <i>b</i> ¹ | 38.8 <i>bc</i> | 14.8 <i>b</i> | 0.23 <i>b</i> | 94.5 <i>ab</i> | 52.8 <i>b</i> | 7.6 <i>b</i> | 533,333 <i>b</i> |
| Forbs | 70.9 <i>b</i> | 58.4 <i>b</i> | 13.8 <i>b</i> | 0.26 <i>b</i> | 45.5 <i>bc</i> | 37.0 <i>b</i> | 9.1 <i>b</i> | 406,457 <i>b</i> |
| Browse—leaves & twig tips | 257.3 <i>a</i> | 245.4 <i>a</i> | 62.8 <i>a</i> | 1.07 <i>a</i> | 137.5 <i>a</i> | 97.6 <i>a</i> | 38.7 <i>a</i> | 1,612,009 <i>a</i> |
| Browse—residual twigs | 31.7 <i>bc</i> | 27.6 <i>cd</i> | 6.9 <i>bc</i> | 0.17 <i>bc</i> | 51.6 <i>bc</i> | 40.2 <i>b</i> | 11.6 <i>b</i> | 328,601 <i>bc</i> |
| Pine-needles & twigs | 4.4 <i>c</i> | 5.2 <i>d</i> | 0.9 <i>c</i> | 0.02 <i>c</i> | 5.8 <i>c</i> | 4.4 <i>c</i> | 1.9 <i>b</i> | 47,597 <i>c</i> |
| Mushrooms & fruits | 1.0 | 1.0 | 0.2 | T ² | 0.8 | 0.7 | 0.3 | 8,143 |
| Summer | | | | | | | | |
| Grass & grasslike plants | 80.3 <i>b</i> | 41.1 <i>b</i> | 12.8 <i>b</i> | 0.23 <i>bc</i> | 136.9 <i>b</i> | 74.9 <i>b</i> | 11.2 <i>c</i> | 744,930 <i>c</i> |
| Forbs | 61.7 <i>b</i> | 54.9 <i>b</i> | 10.3 <i>b</i> | 0.16 <i>c</i> | 64.9 <i>c</i> | 53.4 <i>b</i> | 13.1 <i>c</i> | 521,849 <i>c</i> |
| Browse—leaves & twig tips | 393.5 <i>a</i> | 447.0 <i>a</i> | 71.1 <i>a</i> | 0.88 <i>a</i> | 230.3 <i>a</i> | 186.3 <i>a</i> | 79.9 <i>a</i> | 2,813,504 <i>a</i> |
| Browse—residual twigs | 85.0 <i>b</i> | 95.9 <i>b</i> | 16.9 <i>b</i> | 0.42 <i>b</i> | 223.7 <i>a</i> | 179.9 <i>a</i> | 57.8 <i>b</i> | 1,339,124 <i>b</i> |
| Pine-needles & twigs | 31.7 <i>b</i> | 48.4 <i>b</i> | 6.6 <i>b</i> | 0.12 <i>c</i> | 46.1 <i>c</i> | 39.0 <i>b</i> | 17.4 <i>c</i> | 440,654 <i>c</i> |
| Mushrooms & fruits | 1.3 | 1.3 | 0.2 | 0.01 | 0.9 | 0.7 | 0.4 | 10,289 |
| Fall | | | | | | | | |
| Grass & grasslike plants | 80.7 <i>b</i> | 49.8 <i>b</i> | 15.8 <i>b</i> | 0.22 <i>b</i> | 189.8 <i>a</i> | 113.6 <i>ab</i> | 19.9 <i>b</i> | 1,000,330 <i>bc</i> |
| Forbs | 71.0 <i>b</i> | 64.7 <i>b</i> | 12.0 <i>b</i> | 0.17 <i>b</i> | 103.9 <i>ab</i> | 84.3 <i>bc</i> | 19.9 <i>b</i> | 743,863 <i>bc</i> |
| Browse—leaves & twig tips | 302.5 <i>a</i> | 320.5 <i>a</i> | 49.1 <i>a</i> | 0.60 <i>a</i> | 180.3 <i>a</i> | 143.7 <i>ab</i> | 56.1 <i>a</i> | 2,146,930 <i>a</i> |
| Browse—residual twigs | 90.7 <i>b</i> | 96.0 <i>b</i> | 17.1 <i>b</i> | 0.28 <i>b</i> | 215.6 <i>a</i> | 173.6 <i>a</i> | 57.3 <i>a</i> | 1,341,438 <i>b</i> |
| Pine-needles & twigs | 37.4 <i>b</i> | 48.7 <i>b</i> | 7.1 <i>b</i> | 0.10 <i>b</i> | 43.0 <i>b</i> | 35.6 <i>c</i> | 16.5 <i>b</i> | 405,497 <i>c</i> |
| Mushrooms & fruits | 1.7 | 1.3 | 0.6 | 0.01 | 0.9 | 0.6 | 0.2 | 9,623 |
| Winter | | | | | | | | |
| Grass & grasslike plants | 43.3 <i>b</i> | 34.0 <i>b</i> | 11.5 <i>ab</i> | 0.15 <i>b</i> | 186.8 <i>a</i> | 118.8 <i>a</i> | 22.7 <i>b</i> | 964,675 <i>b</i> |
| Forbs | 21.9 <i>b</i> | 20.6 <i>b</i> | 5.2 <i>b</i> | 0.06 <i>b</i> | 61.3 <i>b</i> | 50.6 <i>b</i> | 12.0 <i>b</i> | 352,334 <i>c</i> |
| Browse—leaves & twig tips | 31.4 <i>b</i> | 34.4 <i>b</i> | 6.6 <i>b</i> | 0.08 <i>b</i> | 22.0 <i>b</i> | 17.7 <i>b</i> | 6.9 <i>b</i> | 250,698 <i>c</i> |
| Browse—residual twigs | 87.5 <i>a</i> | 90.0 <i>a</i> | 17.3 <i>a</i> | 0.28 <i>a</i> | 218.1 <i>a</i> | 179.0 <i>a</i> | 60.1 <i>a</i> | 1,404,012 <i>a</i> |
| Pine-needles & twigs | 39.2 <i>b</i> | 48.9 <i>b</i> | 7.7 <i>b</i> | 0.11 <i>b</i> | 39.9 <i>b</i> | 34.1 <i>b</i> | 15.2 <i>b</i> | 440,892 <i>bc</i> |
| Mushrooms & fruits | 1.3 | 0.9 | 0.3 | T | 1.1 | 0.6 | 0.2 | 8,894 |

¹ Forage class values, within a season, followed by a common letter are not significantly different ($P > 0.05$).² Less than 0.005 kg per ha.

4) which consist of simple sugars, lipids, organic acids, pectin, starch, soluble protein, non-protein nitrogen, and other water soluble matter (Van Soest and Moore 1956). Browse leaves and twig tips contributed 65 percent of the cell solubles present in the total forage during this period. In spring growth the cell soluble:cell wall ratio was 1.78 for browse leaves and twig tips, 1.28 for forbs, 1.25 for mushrooms and fruits, 0.90 for pine, 0.53 for the residual twigs of browse, and 0.41 for grasses. Browse leaves and twig tips contributed proportionately less to the yield of ADF.

Of the 99.4 kg per ha of crude protein produced in spring (Table 4), 63 percent was from browse leaves and twig tips. These tissues contributed 61 percent of the phosphorus and 55 percent of the gross energy contained in spring forages.

Summer–Autumn.—Browse leaves and twig tips remained the principal source of highly digestible nutrients through summer and autumn. In summer they contributed 65 percent of the cell solubles, 60 percent of the crude protein, and 48 percent of the phosphorus and gross energy. By autumn, leaves and twig tips comprised 55 percent of the cell soluble output, 48 percent of the crude protein, 43 percent of the phosphorus, and 38 percent of the gross energy. The yield of these components from other classes of forage generally varied little from summer to fall (Table 4).

As browse tissues mature cell walls thicken and lignify and cell lumens diminish in volume (Leopold 1964). These anatomical changes undoubtedly account for the decline in cell solubles and increase in CWC that occurred in the residual twigs from spring to summer. The level of cell solubles and fibrous components varied little in leaves and twig tips as the seasons progressed because fiber deposition and

lignification are less in them than in residual twigs.

Cell solubles in pine were significantly greater in summer than in spring. Possibly some of the previous year's growth was mistakenly included in the spring sampling, or resins in the early growth interfered with analytical determination of CWC. The seasonal association of other nutrients in pine was similar to that of other woody tissues.

The crude protein and phosphorus yields from mushrooms and fruits were greatest in autumn because mushrooms, which tend to be higher in these nutrients than fruits (Hastings 1966, Miller and Halls 1969), were most abundant in the fall sample.

Winter.—During the late fall and winter period of minimal nutrient availability, leaves of evergreen browse and twig tips were the most nutritious forages (Tables 2 and 3). Before leaves dropped from deciduous species in late autumn, a portion of their protein and phosphorus was translocated to the twig tips (Kramer and Kozłowski 1960). Mushrooms, fruits, and the basal leaf growth on some forb and grass species were supplemental sources of winter nutrients. In most forage tissues, caloric values were highest in winter, which suggests fat levels were high during that season (Blair and Epps 1969, Short et al. 1966).

After leaf abscission in late fall the largest contributor of cell solubles, crude protein, and phosphorus was the residual twigs of browse. These tissues, however, were highly fibrous and poorly digestible. They contained 41 percent of the CWC, 45 percent of the ADF, and 52 percent of the non-digestible ADL. In winter the hardened twigs would provide little more than a starvation diet to ruminants.

Dry-Matter Digestibility

The in vivo nylon bag dry matter digestibility (NBDMD) of forages was closely

associated with the nutrient composition of tissues at different stages of plant development. Each season, forages that ranked high in cell solubles tended to rank high in digestible dry matter (Table 2).

Digestibility of grasses and forbs was highest in the spring when growth activity was greatest and CWC, ADF, ADL, and cellulose levels were lowest. The digestibility of these forages declined significantly each season as growth activity and nutrient quality diminished. In spring, forbs and the leaves and twig tips of browse had NBDMDs of 68.2 and 67.2 percent and were significantly more digestible than other forages. After spring, browse leaves and twig tips were significantly more digestible than any forage. The lowest NBDMD for leaves and twig tips of 55.6 percent in winter was not significantly different from the highest. That leaves and twigs were highly digestible all year further substantiates the importance of these tissues, especially leaves, to the dietary regime of herbivores such as deer. The mean NBDMD of mushrooms and fruits was comparable to the relatively high digestibility levels of browse leaves and twig tips.

By summer, the NBDMD of browse tissues, especially leaves and twig tips, fell below the percentage of cell solubles in these tissues. This suggests the presence of chemical and/or physical constituents that inhibit the microbial degradation of cell wall structures and digestion of cell solubles. Common inhibitors are cutin, tannin, waxes, volatile oils, silica, and lignin (Van Soest 1970, Robbins 1973).

Pine and the residual twigs of browse were among the least digestible forages from spring to autumn (Table 3). In winter, residual twigs and weathered grasses and forbs were least digestible. The association between digestibility and the nutritive composition of tissues was not clearcut in

pine. Digestibility was probably governed to a considerable extent by the adverse impact of resins and volatile oils on the microbial population inhabiting the rumen (Nagy 1970).

CONCLUSIONS

Many factors interact between deer and their habitat to govern carrying capacity. When habitat capacity for wild ruminants is evaluated solely on the basis of total available forage dry matter, as it commonly is, capacity is generally overestimated. More realistic estimates can be derived by relating the seasonal availability of nutrients to metabolic needs of the animals.

Table 5 presents various and comparable approximations of the seasonal deer carrying capacity per ha of the young pine plantation based on several quantitative and qualitative dietary attributes. Only forbs, browse leaves and twig tips, and mushrooms and fruits are included since these forages constitute the major portion of a deer's diet in the South (Harlow *et al.* 1974). The capacity estimates relate the seasonal yield of dry matter, pertinent nutrients, and digestible dry matter to the metabolic requirements of deer.

Based on the estimated daily needs for animal growth, each ha of the plantation provided sufficient digestible dry matter to support 4 45 kg deer for 61 days in spring, 70 days in summer, 68 days in autumn, and only 12 days in winter. Protein was adequate for about 45 days in both spring and summer, 37 days in autumn, and 8 days in winter. Of the dietary criteria considered, phosphorus appeared to be a major factor limiting the capacity of the plantation throughout the year. In contrast to protein, nearly twice the area would be needed seasonally to provide adequate phosphorus for animal growth. Low phosphorus content can be expected on many southern deer

Table 5. Estimated seasonal deer use capacity based on the availability of nutrient attributes¹ and the approximate requirements for animal growth.

| Season and forage class | Dry matter | Digestible dry matter | Crude protein | Phosphorus | Gross energy |
|---|--------------|-----------------------|---------------|-------------|---------------|
| | Deer days/ha | | | | |
| Spring | | | | | |
| Forbs | 63.7 | 86.5 | 55.2 | 37.1 | 64.5 |
| Browse—leaves & twig tips | 117.5 | 156.9 | 125.6 | 76.4 | 127.9 |
| Mushrooms & fruits | 1.1 | 1.2 | 0.8 | 0.6 | 1.3 |
| Total | 182.3 | 244.6 | 181.6 | 114.1 | 193.7 |
| Summer | | | | | |
| Forbs | 73.5 | 75.2 | 41.2 | 22.9 | 82.8 |
| Browse—leaves & twig tips | 207.8 | 239.9 | 142.2 | 62.9 | 223.3 |
| Mushrooms & fruits | 1.3 | 1.6 | 0.8 | 1.4 | 1.6 |
| Total | 282.6 | 316.7 | 184.2 | 87.2 | 307.7 |
| Fall | | | | | |
| Forbs | 103.4 | 86.6 | 48.0 | 24.3 | 118.1 |
| Browse—leaves & twig tips | 153.6 | 184.5 | 98.2 | 42.9 | 170.4 |
| Mushrooms & fruits | 1.3 | 2.1 | 2.4 | 1.4 | 1.5 |
| Total | 258.3 | 273.2 | 148.6 | 68.6 | 290.0 |
| Winter | | | | | |
| Forbs | 50.2 | 26.7 | 20.8 | 8.6 | 55.9 |
| Browse—leaves & twig tips | 17.3 | 19.1 | 13.2 | 5.7 | 19.9 |
| Mushrooms & fruits | 1.2 | 1.6 | 1.2 | 0.6 | 1.4 |
| Total | 68.7 | 47.4 | 35.2 | 14.9 | 77.2 |
| Daily requirements ² per 45 kg of deer body weight | kg 1.63 | kg 0.82 | kg 0.25 | kg 0.007 | Kcal 6,300 |

¹ Nutrient production of browse leaves and twig tips were reduced by 50% to account for proper utilization intensity of the photosynthetic tissues.

² From Dietz (1972) and Magruder et al. (1957). Oven-dry basis.

habitats because soil phosphates available for root absorption are leached by the high annual rainfall (Lytle 1960).

LITERATURE CITED

- ASSOCIATION OF OFFICIAL AGRICULTURAL CHEMISTS. 1960. Official methods of analysis. Ed. 9. Washington, D.C. 832pp.
- BLAIR, R. M. 1967. Deer forage in a loblolly pine plantation. *J. Wildl. Manage.* 31(3): 432-437.
- . 1968. Keep forage low to improve deer habitat. *For. Farmer* 27(11):8-9, 22-23.
- , AND H. G. ENGHARDT. 1976. Deer forage and overstory dynamics in a loblolly pine plantation. *J. Range Manage.* 29(2): 104-108.
- , AND E. A. EPPS, JR. 1969. Seasonal distribution of nutrients in plants of seven browse species in Louisiana. USDA For. Serv. Res. Pap. SO-51. South. For. Exp. Stn., New Orleans, LA: 35pp.
- , AND L. K. HALLS. 1968. Growth and forage quality of four southern browse species. Pages 57-62 in Proc. of the 21st Annu. Conf. of the Southeast. Assoc. of Game and Fish Comm. 1967, New Orleans, LA.
- DELL, T. R. 1969. The theory and some applications of ranked set sampling. Ph.D. Dissertation, Univ. of Georgia, Athens. 84pp.
- DIETZ, D. R. 1972. Nutritive value of shrubs. In *Wildland shrubs—their biology and utilization*. USDA Forest Serv. Gen. Tech. Report INT-1, pp. 289-302. Intermountain Forest and Range Exp. Stn. Ogden, Utah.
- DUNCAN, D. B. 1955. Multiple range and multiple *F* tests. *Biometrics* 11(1):1-42.
- GOERING, H. K., AND P. J. VAN SOEST. 1970. Forage fiber analyses (apparatus, reagents, procedures, and some applications). USDA Agric. Res. Serv. Agric. Handb. No. 379, 20pp.
- HALLS, L. K., AND R. ALCANIZ. 1965. Seasonal twig growth of southern browse plants. USDA For. Serv. Res. Note SO-23, South. For. Exp. Stn., New Orleans, LA. 5pp.
- HARLOW, R. F., H. S. CRAWFORD, AND D. F. URBSTON. 1974. Rumens contents of white-tailed deer: comparing local with regional samples. Pages 562-567 in Proc. of the 28th Annu. Conf. Southeast. Assoc. of Game and

- Fish Comm., White Sulphur Springs, West Virginia.
- HASTINGS, E. F. 1966. Yield and chemical analyses of fruit produced by selected deer-browse plants in a loblolly-shortleaf pine-hardwood forest. Ph.D. Dissertation, Louisiana State Univ., Baton Rouge. 230pp.
- KRAMER, P. J., AND T. T. KOZLOWSKI. 1960. Physiology of trees. McGraw-Hill Book Co., N.Y. 642pp.
- LEOPOLD, A. C. 1964. Plant growth and development. McGraw-Hill Book Co., N.Y. 466pp.
- LOWREY, R. S. 1970. The nylon bag technique for the estimation of forage quality. Pages 01-012 *In Proc. of the Natl. Conf. on Forage Qual. Eval. and Util.* 1969. Nebr. Cent. for Contin. Educ., Lincoln.
- LYTLE, S. A. 1960. Physiography and properties of southern forest soils. Pages 1-8 *in South. For. Soils*, 8th Annu. For. Symp. 1959, Louisiana State Univ., Baton Rouge.
- MAGRUDER, N. D., C. E. FRENCH, L. C. McEWEN, AND R. W. SWIFT. 1957. Nutritional requirements of white-tailed deer for growth and antler development. II. Experimental results of the third year. Penn. Agr. Exp. Sta. Bull. 628. 21pp.
- MILLER, H. A., AND L. K. HALLS. 1969. Fleshy fungi commonly eaten by southern wildlife. USDA For. Serv. Res. Pap. SO-49, South. For. Exp. Stn., New Orleans, LA. 28pp.
- NAGY, J. G. 1970. Biological relations of rumen flora and fauna. Pages 159-163 *in Range and Wildlife Habitat Evaluation—A Research Symposium*. USDA For. Serv. Misc. Publ. 1147.
- ROBBINS, C. T. 1973. The biological basis for the determination of carrying capacity. Ph.D. Dissertation, Cornell Univ., Ithaca, N.Y. 239pp.
- SHORT, H. L. 1963. Rumen fermentations and energy relationships in white-tailed deer. *J. Wildl. Manage.* 27(2):184-195.
- . 1969. Physiology and nutrition of deer in southern upland forests. Pages 14-18 *in White-tailed deer in the southern forest habitat*. Proc. of a Symp. at Nacogdoches, TX. USDA For. Serv., South. For. Exp. Stn., New Orleans, LA.
- SHORT, H. L., R. M. BLAIR, AND C. A. SEGELQUIST. 1974. Fiber composition and forage digestibility by small ruminants. *J. Wildl. Manage.* 38(1):197-209.
- , D. R. DIETZ, AND E. E. REMMENGA. 1966. Selected nutrients in mule deer browse plants. *Ecology* 47:222-229.
- VAN SOEST, P. J. 1970. The chemical basis for the nutritive evaluation of forages. Pages U1-U19 *in Proc. of the Natl. Conf. on Forage Qual. Eval. and Util.* 1969. Nebr. Cent. for Contin. Educ., Lincoln.
- , AND L. A. MOORE. 1966. New chemical methods for analysis of forage for the purpose of predicting nutritive value. Pages 783-789 *in Proc. IX Int. Grassland Congr.*, São Paulo, Brazil, 1965.

Received 28 May 1976.

Accepted 14 July 1977.