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Composition and Digestibility of Deer Browse in Southern Forests

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COMPOSITION AND DIGESTIBILITY OF DEER BROWSE IN SOUTHERN FORESTS

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Leaves and twigs from browse plants important as deer foods in the loblolly-shortleaf pine forests of the South were subjected to nutrient analyses and in vivo ***microdigestion by the nylon bag technique. Twigs were most succulent, nutritious, and digestible during spring while growing rapidly. After they matured, usually in early summer, they were of increased fiber content and reduced digestibility. Quality and digestibility of mature twigs declined as distance from the twig tip increased. Browse leaves from evergreen species retained their good forage quality and digestibility throughout the year. Leaves of deciduous species usually lost their quality*** and ***digestibility after abscission.***

Additional keywords: Forage quality, nutrients, ruminants, in vivo microdigestion, woody twigs, wildlife foods.

The characteristic growth pattern of woody browse plants in the South is accompanied by major changes in nutrient composition and digestibility. Growth generally is rapid for a short time after buds burst in early spring. Initially the woody shoot is succulent and has characteristics not unlike those of herbaceous vegetation (Cushwa *et al.* 1970). This state is transitory, however, because shoot growth proceeds rapidly and may be essentially completed by late spring or early summer (Halls and Alcaniz 1972). As the rate of twig elongation slows, cell walls thicken and lignify (Isenberg 1963), and cellular protoplasm is lost (Wort 1962). Coincident with the slowing and hardening of twig growth is a decrease in digestibility (Short *et al.* 1972).

This paper describes seasonal changes in nutrient composition and digestibility for leaves and twigs of browse species common in southern forests where shortleaf and loblolly pines grow in mixture with hardwoods. The species are identified in table 1. While general seasonal trends in browse quality are well known, the data published here are more specific and detailed than any other on record for this forest type.

METHODS

Browse tissue was collected from the Stephen F. Austin Experimental Forest near Nacogdoches, Texas, during spring (April), summer (August), and autumn (October) of 1970, and during the winter of 1971 (January) (table 1). Samples were taken within the 5-foot deer feeding zone on an area that had been prescribe-burned during January 1970. Each sample was a composite from the current growth of several plants.

Four-inch terminal twigs were taken from species or species groups: Alabama supplejack, common and saw greenbriers, grapes, common trumpetcreeper, and peppervine. Two-inch terminals were collected from the other species. Leaves, when present, were separated from the twigs. Dried and fallen leaves of deciduous species were collected from the ground during winter.

Tissues were dried at 40°C, ground in a Wiley mill, and analyzed for silica, neutral detergent

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Table I.-Composition *and digestibility of twigs from* 20 *browse species collected in east Texas at the four seasons*

Species	Season collected	Dry matter	Crude protein	Crude fiber	Phosphorus	CWC[1]	ADF	ADL	Silica	Hemicellulose	Cellulose	Digestibility NBDMD	Digestibility ETDMD
		Percent *of green weight*	*Percent of ovendry weight*										
Loblolly and shortleaf pine, ***Pinus*** taeda L. and ***P.*** echinata Mill.	Spring	28.2	8.2	30.5	0.18	51.1	35.8	16.8	0.14	15.3	19.0	60.3	55.8
	Summer	45.0	3.7	43.8	.08	66.8	55.4	27.5	.17	11.4	27.9	42.2	41.6
	Autumn	45.3	5.2	40.4	.12	61.3	51.0	25.0	.03	10.3	26.0	42.6	46.5
	Winter	49.5	6.2	36.6	.09	56.5	46.4	23.0	.22	10.1	23.4	49.3	50.3
Common and saw greenbriers, ***Smilax rotundifolia*** L. and S. ***bona-nox*** L.	Spring	12.7	31.7	16.0	.69	30.7	18.7	5.6	.09	12.0	13.1	87.5	77.4
	Summer	40.4	6.9	57.9	.13	77.5	62.4	24.7	.06	15.1	37.7	18.0	38.5
	Autumn	44.2	7.0	59.0	.11	78.7	61.3	23.9	.08	17.4	37.4	18.2	38.0
	Winter	42.3	8.1	55.0	.13	76.0	55.7	22.0	1.05	20.3	33.7	20.9	36.6
Willow oak, Quercus ***phellos*** L.	Spring	32.5	10.7	37.4	.25	56.3	42.2	13.5	.25	14.1	28.7	51.9	58.9
	Summer	53.8	4.6	43.6	.12	62.5	52.6	18.5	.17	9.9	34.1	37.4	52.6
	Autumn	63.1	4.9	41.0	.08	68.5	50.6	20.1	.02	17.9	30.5	35.8	45.3
	Winter	61.9	6.6	40.9	.11	65.3	50.6	19.9	.19	14.7	30.7	37.9	48.0
Water oak, ***Q.*** nigra L.	Spring	26.7	10.4	33.4	.24	50.8	37.7	10.0	.08	13.1	27.7	55.3	66.0
	Summer	56.5	4.2	41.7	.13	64.3	53.2	19.1	.11	11.1	34.1	38.6	50.8
	Autumn	56.6	4.9	41.5	.09	67.5	50.7	19.5	.03	16.8	31.2	35.3	46.9
	Winter	58.5	5.9	41.0	.09	63.9	48.1	18.7	.21	15.8	29.4	40.2	49.4
Winged elm, ***Ulmus alata*** Michx.	Spring	30.8	18.2	25.3	.35	38.9	30.8	7.9	.48	8.1	22.9	78.3	73.9
	Summer	59.0	5.4	41.9	.10	64.5	55.4	22.8	.84	9.1	32.6	44.9	47.6
	Autumn	61.1	5.8	38.0	.11	62.3	52.9	22.7	.81	9.4	30.2	42.0	48.5
	Winter	60.8	7.7	39.6	.08	62.4	53.2	22.9	1.16	9.2	30.3	47.0	44.8
Common sassafras, Sassafras ***albidum*** (Nutt.) Nees	Spring	15.8	28.6	15.9	.71	39.1	33.1	16.0	.09	6.0	17.1	53.7	65.3
	Summer	47.1	4.2	42.8	.08	62.0	50.1	16.6	.03	11.9	33.5	43.8	54.2
	Autumn	55.1	6.2	36.0	.08	62.7	42.6	14.2	.03	20.1	28.4	45.3	53.6
	Winter	56.3	6.0	39.5	.07	58.9	44.8	15.7	.04	14.1	29.1	50.7	55.3
American sweetgum, ***Liquidambar styraciflua*** L.	Spring	19.6	14.5	14.6	.39	28.3	27.6	11.5	.12	.7	16.1	77.6	75.8
	Summer	38.8	3.7	27.5	.08	48.7	41.7	12.4	.23	7.0	29.3	54.2	65.4
	Autumn	43.0	5.6	26.4	.10	45.8	37.3	13.7	.30	8.5	23.6	56.3	64.0
	Winter	43.0	6.6	34.1	.10	51.9	42.7	15.5	.47	9.2	27.2	51.3	59.7
Hawthorns, Crataegus spp.	Spring	33.1	13.6	15.8	.34	26.3	20.9	6.1	.08	5.4	14.8	84.2	80.6
	Summer	61.4	4.3	34.9	.08	57.5	46.3	20.2	.04	11.2	26.1	39.7	52.0
	Autumn	58.4	5.4	31.4	.09	59.6	45.3	19.7	.05	14.3	25.6	41.9	50.3
	Winter	54.4	7.5	32.3	.16	60.0	44.5	20.3	.23	15.5	24.2	45.1	49.0
American and flatwoods plum, ***Prunus americana*** Marsh. and ***P. umbellata*** EII.	Spring	21.9	24.1	10.8	.17	19.2	15.7	5.3	.11	3.5	10.4	89.2	84.3
	Summer	61.2	5.0	36.8	.07	59.2	50.4	20.0	.08	8.8	30.4	38.1	52.5
	Autumn	61.8	5.7	32.6	.07	63.3	49.6	22.9	.02	13.7	26.7	39.0	46.1
	Winter	58.6	7.4	32.7	.12	61.2	52.5	26.1	4.71	8.7	26.4	37.6	32.1
Blackberry, ***Rubus*** spp.	Spring	19.9	20.5	14.2	.47	21.5	16.8	3.5	.27	4.7	13.3	86.7	86.2
	Summer	42.6	6.1	36.2	.13	53.4	44.0	14.2	.13	9.4	29.8	36.1	60.8
	Autumn	47.5	6.9	36.4	.14	54.8	42.4	14.1	.02	12.4	28.3	39.9	59.2
	Winter	52.7	8.3	36.1	.12	52.2	40.1	13.2	.11	12.1	26.9	49.9	61.2
Yaupon, ***Ilex vomitoria*** Ait.	Spring	26.9	12.1	24.1	.18	37.1	31.5	11.4	.14	5.6	20.1	71.0	70.7
	Summer	57.2	4.1	48.9	.08	71.4	63.4	18.1	.15	8.0	45.3	26.5	51.2
	Autumn	55.1	4.5	48.8	.08	70.3	57.4	17.0	.07	12.9	40.4	32.1	51.0
	Winter	59.0	4.8	43.8	.06	69.0	53.2	16.0	.17	15.8	37.2	31.5	51.5
Alabama supplejack, ***Berchemia scandens*** (Hill) K. Koch	Spring	23.8	9.7	31.7	.18	47.3	39.9	14.5	.11	7.4	25.4	64.3	63.1
	Summer	49.8	4.0	42.2	.08	59.0	54.1	20.8	.09	4.9	33.3	31.8	53.3
	Autumn	60.8	4.8	41.3	.06	70.6	51.5	24.0	.04	19.1	27.5	29.0	39.9
	Winter	56.8	5.6	42.8	.07	63.6	51.6	27.4	.03	12.0	24.2	26.4	42.8
Peppervine, ***Ampelopsis arborea*** (L.) Koehne	Spring	18.3	16.1	16.6	.59	26.1	22.6	5.6	.17	3.5	17.0	80.9	82.2
	Summer	34.0	5.1	30.4	.11	47.7	40.3	12.9	.11	7.4	27.4	51.1	64.9
	Autumn	35.6	5.2	34.9	.12	54.1	46.4	16.1	.03	7.7	30.3	43.6	58.9
	Winter	52.7	5.0	43.8	.08	64.8	54.1	21.6	.04	10.7	32.5	30.8	48.1
Grapes, ***Vitis*** spp.	Spring	12.8	21.2	15.7	.59	33.4	28.6	12.1	.20	4.8	16.5	72.0	71.6
	Summer	27.0	4.6	38.8	.14	56.2	47.5	11.9	.23	8.7	35.6	52.5	63.7
	Autumn	32.7	3.9	40.8	.11	60.7	52.9	14.9	.20	7.8	38.0	48.0	58.5
	Winter	62.5	4.7	48.4	.09	71.7	59.9	22.3	.42	11.8	37.6	27.5	44.5

Table 1.—*Composition and digestibility of twigs from 20 browse species collected in east Texas at the four seasons* (Continued)

Species	Season collected	Dry matter	Crude protein	Crude fiber	Phos-phorus	CWC[1]	ADF	ADL	Silica	Hemicel-lulose	Cellu-lose	Digestibility NBDMD	Digestibility ETDMD
		Percent of green weight	— — — —			— — *Percent of ovendry weight* — — — — — — — —							
Flowering dogwood, *Cornus florida* L.	Spring	23.8	11.0	19.9	.21	28.6	24.8	7.0	.08	3.8	17.8	78.6	79.4
	Summer	36.4	4.1	29.1	.08	40.3	35.6	12.1	.10	4.7	23.5	64.1	69.2
	Autumn	43.2	f.4	26.4	.10	38.5	33.0	10.9	.02	5.5	22.1	66.3	70.8
	Winter	44.2	7.4	26.5	.11	40.9	33.9	11.9	.92	7.0	22.0	66.2	68.3
Black tupelo, *Nyssa sylvatica* Marsh.	Spring	15.4	10.0	20.5	.22	37.1	26.9	5.2	.31	10.2	21.7	83.1	78.6
	Summer	48.3	3.8	35.2	.07	61.2	48.2	16.2	.08	13.0	32.0	43.1	54.5
	Autumn	54.9	4.9	36.5	.06	63.4	46.4	16.5	.06	17.0	29.9	38.6	51.7
	Winter	47.2	5.5	38.7	.12	60.0	48.6	11.0	.09	11.4	31.6	44.4	54.5
American beautyberry, *Callicarpa americana* L.	Spring	15.3	24.5	16.8	.39	39.7	30.0	10.4	1.42	9.7	19.6	84.8	65.1
	Summer	44.2	6.3	41.8	.12	66.7	53.0	13.1	.23	13.7	39.9	36.4	57.6
	Autumn	52.8	7.7	37.2	.10	61.4	46.4	13.3	.14	15.0	33.1	42.5	57.7
	Winter	60.0	8.3	35.2	.10	56.9	43.9	26.1	.26	13.0	17.8	41.6	46.4
Common trumpetcreeper, *Campsis radicans* (L.) Seem.	Spring	14.6	21.8	18.5	.59	35.5	27.2	7.7	.11	8.3	19.5	79.4	74.8
	Summer	47.2	4.3	47.9	.09	68.0	54.6	16.4	.25	13.4	38.2	35.1	52.2
	Autumn	47.6	5.3	43.5	.10	nn.5	49.8	17.8	.16	16.7	32.0	33.3	49.3
	Winter	56.3	5.8	44.5	.12	69.6	54.1	20.2	.04	15.5	33.9	32.7	46.0
Japanese honeysuckle, *Lonicera japonica* Thunb.	Spring	17.1	10.6	26.3	.32	41.2	29.6	8.3	.12	11.6	21.3	70.6	71.2
	Summer	46.4	4.8	41.7	.13	66.4	48.2	15.0	.13	18.2	33.2	35.0	52.5
	Autumn	43.0	4.7	45.4	.08	72.0	52.9	18.5	.21	19.1	34.4	29.6	45.8
	Winter	52.4	5.5	44.9	.09	70.3	50.7	18.7	.15	19.6	32.0	31.1	45.8
Rusty blackhaw, *Viburnum rufidulum* Raf.	Spring	20.1	12.7	15.8	.35	27.2	21.9	6.0	.08	5.3	15.9	88.3	80.6
	Summer	56.7	3.1	46.0	.07	68.0	54.2	15.2	.06	13.8	39.0	32.8	53.8
	Autumn	56.6	4.4	40.0	.10	63.0	50.0	17.0	.09	13.0	33.0	42.2	52.9
	Winter	52.7	5.2	39.7	.12	63.6	48.3	16.7	.02	15.3	31.6	46.0	52.1

[1] Cell contents can be calculated as 100 minus CWC.

fiber or cell wall components (CWC), acid detergent fiber (ADF), and acid detergent lignin (ADL) by the procedures of Goering and Van Soest (1970). Crude protein, crude fat, crude fiber, calcium, and phosphorus were assayed by methods of the Association of Official Agricultural Chemists (1965).

Nylon-bag dry matter digestion (NBDMD) values were determined with ruminally cannulated goats (Short *et al. 1974).* Estimated true dry matter digestibility (ETDMD) was computed, by the equation described in Goering and Van Soest (1970), from CWC, the proportion of ADL in the ADF component, and the silica content.

Data on composition and digestibility were subjected to variance analyses (0.05 level of probability) to determine if seasonal differences occurred. In browse twigs the analysis for each nutrient took the form of a one-way classification contrasting the four seasons; the 20 species were viewed as replications. For leaves, the values obtained for each of the species during spring, summer, and autumn again served as replications, but two sample classes were recognized during winter. Thus, the format was that of a one-way analysis of variance with five levels. One winter sample class included the seven evergreen and tardily deciduous species or species groups: Japanese honeysuckle, blackberries, willow oak, common and saw greenbriers, water oak, yaupon, and loblolly and shortleaf pine. The second sample class included the other species, whose dry leaves were recovered from the ground. Duncan's multiple range test was used to further describe seasonal differences in nutrient quality. Correlation matrices were developed for both twigs and leaves.

Nutrient composition and digestibility of consecutive l-inch twig segments were determined from common sassafras twigs collected in September. Values from three replicate collections of the terminal 6 inches were subjected to variance analyses and multiple range tests.

TWIG ANALYSES

Spring

At the time of the April collection shoot growth of all species was well established but was incomplete and succulent. In half the species, twig dry matter was less than 20 percent of green tissue weight (table 1). The more succulent twigs tended to have lower fiber contents than average, but greater protein and phosphorus values. Protein contents varied from more than 30 percent in greenbriers to less than 10 in Alabama supplejack and pine twigs. Phosphorus varied from 0.17 percent in American and flatwoods plum to 0.71 in sassafras.

Cell contents representing the nonfibrous constituents of twigs ranged from 44 percent in willow oak to 81 in plum (values calculated as 100 minus CWC; see table 1). Half of the spring twigs had less than 40 percent CWC, less than 30 percent ADF, less than 20 percent cellulose and crude fiber, and less than 10 percent lignin. Pine, oaks, and Alabama supplejack had some of the highest fiber values.

Cell wall contents and other measures of fiber were significantly and negatively correlated with digestibility (table 2).

Spring twigs varied substantially in ETDMD -from 56 percent for pine to 86 percent for blackberry. Twigs with high digestibility had low CWC, ADF, and ADL content. Sufficient silica to appreciably reduce ETDMD was present only in American beautyberry.

NBDMD ranged from 52 percent for willow oak to 89 for plum. For 70 percent of the spring twigs the two digestibility estimates did not vary by more than 5 percentage points, and they varied by more than 10 percentage points only for greenbrier, sassafras, American beautyberry, and water oak.

Summer, Autumn, and Winter

Many woody twigs elongate rapidly during a brief portion of the growing season. Mean ending date of growth for Alabama supplejack and some grapes is in June. Sassafras, greenbriers, and rusty blackhaw end in July, and American beautyberry, common trumpetcreeper, and black tupelo end in August (Halls and Alcaniz 1972). As elongation ceases and twigs harden, dry matter and fiber content increase to levels which are maintained until regrowth begins the following year, while protein and digestibility diminish (Short *et al.* 1972). Mean composition and digestibility of twigs did not differ significantly in the summer, autumn, and winter samples, and therefore these data are lumped in table 2.

Crude protein in mature twigs did not exceed 8.3 percent for any of the species during summer, autumn, and winter (table 1), and some twigs had less than 4 percent. Phosphorus never exceeded 0.16 percent and dropped as low as 0.06 percent of dry matter. These values are clearly

Table 2.-*Correlation matrix for* characteristics *of browse twigs. Significant values* (0.05 level) *only* are *listed for immature twigs of* 20 *browse species collected during spring and for* mature *twigs collected during* summer, *autumn,* and *winter (N = 60)*

Characteristic	Season	ETDMD	Cellulose	Hemicellulose	NBDMD	Silica	ADL	ADF	CWC[1]	Phosphorus	Crude fiber	Protein
Dry matter	Spring	...	...	...	...	...	...	...	...	−0.62	0.56	-0.56
	Summer-autumn-winter	−0.50	...	0.32	-0.32	...	0.47	0.28	0.36	−.38	...	...
Protein	Spring	...	−0.56	...	...	...	...	−.45	...	.75	−.63	
	Summer-autumn-winter	...	−.40	...	...	0.33	...	...	...	.43	...	
Crude fiber	Spring	−.75	.90	...	−.75	...	.52	.86	.91	−.50		
	Summer-autumn-winter	−.64	.73	.48	−.84	...	.42	.87	.88	...		
CWC[1]	Spring	−.93	.88	...	−.83		.72	.94				
	Summer-autumn-winter	−.81	.66	.69	−.89	:::	.54	.89				
ADF	Spring	−.91	.88	...	−.88	...	.82					
	Summer-autumn-winter	−.74	.75	.29	−.83	...	.59					
ADL	Spring	−.90	.45	...	−.82	...						
	Summer-autumn-winter	−.88	...	...	−.55	.26						
Silica	Summer-autumn-winter	−.33	...	...	...							
NBDMD	Spring	.83	−.69	...								
	Summer-autumn-winter	.76	−.57	−.56								
Hemicellulose	Summer-autumn-winter	−.54	...									
Cellulose	Spring	−.68										

[1] Correlation coefficients for cell contents are the same, except for sign, as those for cell wall contents.

less than the minimal standards for wildlife suggested by Halls (1970).

Only six samples of mature twigs-flowering dogwood at the three seasons, peppervine in summer, and sweetgum in summer and autumn-had cell content values greater than 50 percent of dry matter. These samples comprised most of the instances when NBDMD also exceeded 50 percent. In contrast, ETDMD was greater than 50 percent for 36 of the 60 samples of mature woody twigs. Discrepancies between NBDMD and ETDMD were major, averaging over 10 units (table 3). NBDMD of mature woody twigs was closely associated with cell content and could be predicted from the equation $\hat{Y}$ = 106.73-1.08 CWC; r =-0.89 and the significant F value = 227.0. Clearly the very fibrous nature of mature woody twigs reduces their usefulness to herbivores.

The composition of a developing browse twig during spring usually did not bear a predictable relationship to the composition of the mature twig sampled at the other seasons. Except for protein, phosphorus, dry matter, and hemicellulose content during summer and autumn there were no significant relationships between the relative ranking of a nutrient in spring twigs and the relative nutrient content of twigs at other seasons. Mature twigs of a particular species, on the other hand, tended to have similarly high or low levels of nutrients during summer, autumn, and winter. Exceptions to this generalization are labile constituents such as phosphorus, which may be increased in twig tissues during winter because of translocation from leaves during autumn (Kramer and Kozlowski 1960). For mature woody twigs of a particular species, therefore, the measurements made during summer will still be a reasonable estimate of nutrient content during the subsequent autumn and winter.

Digestibility of Twig Segments

Quality and usefulness of mature twigs decrease with increasing distance from the meristematic bud tissues, more or less in proportion as dry matter and fiber increase. In sassafras twigs, crude protein, cell contents, phosphorus, and NBDMD of the l-inch segment closest to the twig tip were significantly greater than in more distal segments (fig. 1). Few differences were noted after the fourth inch. ETDMD did not change after the second twig segment, apparently because ADL did not vary significantly between twig segments.

The difference in nutrient composition between twig segments may be related to the quantity of mature wood cell walls, the quantity of meristematic and bark tissues, and the lignin-carbohydrate associations in wood and bark. Composition of bark differs markedly from that of wood. For example, Short *et al.* (1972) de-

Table *3.-Mean composition and estimated digestibility of twigs and leaves of 20 browse* species

Plant part and season	Dry matter	Crude protein	Crude fiber	Phosphorus	Cell contents	CWC	ADF	ADL	Silica	Hemicellulose	Cellulose	NBDMD	ETDMD
	Percent of green weight	*- - - - - - - - - - - - - Percent*	*of ovendry*	*weight - - - - - - - - - - - - -*									
TWIGS													
Spring	21.5[a1]	16.5”	21.0”	0.37”	64.2')	35.8”	28.1”	9.2[a]	0.22[a]	7.7[a]	18.9[a]	74.9”	73.1[b]
Summer	47.7”	4.7[a]	40.5”	.10[a]	38.9[a]	61.1”	50.5[b]	17.4[b]	.16[a]	10.5[a,b]	33.2”	40.1[a]	54.5”
Autumn	50.9”	5.5[a]	38.9”	.10[a]	37.8[a]	62.2”	48.5”	18.1”	.12[a]	13.7[b]	30.4”	40.1[a]	51.8[a]
Winter	54.1”	6.4[a]	39.8”	.10[a]	38.1[a]	61.9”	48.9”	19.8”	.53[a]	13.1[b]	29.1[b]	40.4[a]	49.3”
LEAVES													
Spring	28.2”	22.1[c]	13.2[a]	.42[b]	73.9[c]	26.1[a]	20.78	9.0[a]	.37[a]	5.7[b]	11.7[a]	78.6[b]	77.1[b]
Summer	42.6”	10.3”	17.8”	.12[a]	65.0”	35.0”	26.6[b]	10.4[a]	.62[a]	8.4[b]	16.2”	67.4”	70.6[b]
Autumn	45.1”	10.1”	17.0”	.12[a]	68.1[b,c]	31.9[a,b]	24.8[a,b]	10.0”	.51[a]	7.4[b]	14.8[a,b]	68.0[b]	72.6[b]
Winter													
— Evergreen?	48.0”	11.3”	20.7”	.13[a]	64.6[b]	35.4”	25.8[a,b]	10.8[a]	.50[a]	9.6[b]	15.0[a,b]	65.0[b]	69.9”
— Deciduous”. [4]		7.3”	20.3[b]	.08[a]	51.4[a]	48.6[c]	50.9[c]	27.5”	2.18”	2.3”	23.3~	44.9[a]	49.6[a]

For twig or for leaf samples, the seasonal values within a column are significantly different if they bear different superscript letters.
Values are for seven evergreen and tardily deciduous species.
Values are for 13 deciduous species.
As leaves of deciduous species were picked from the ground in winter, dry matter could not be measured reliably.

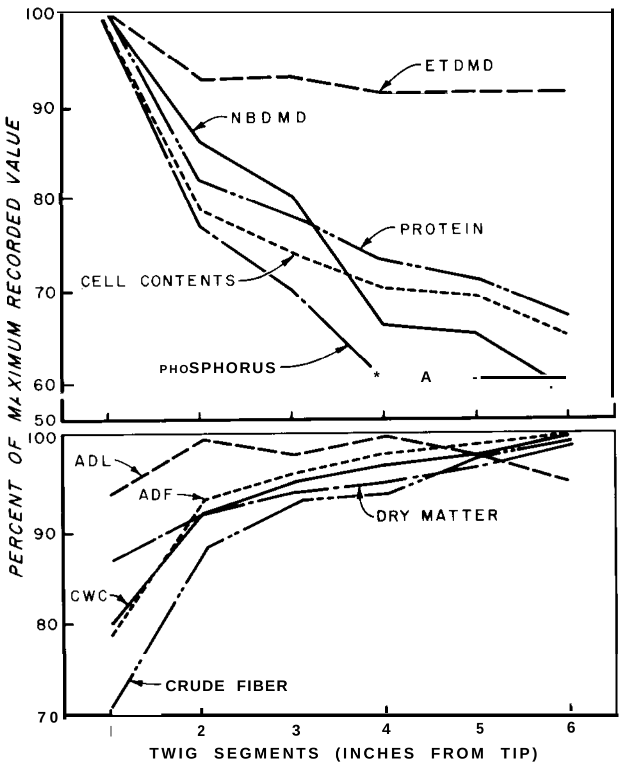

Figure 1.-Nutritional *composition and digestibility of l-inch segments of* **sassafras** *twigs collected in September in east Texas.*

termined that bark of sassafras twigs contained more ash and benzene-alcohol and cold-water extractives (representing fats, fatty acids, resins and waxes, organic salts, simple sugars, cyclitols, gums, and pectin-like materials) than did wood. Also, lignin apparently limits digestibility less in bark than in wood, and digestible dry matter was three times greater in bark, although the two tissues were about equally digestible after delignification.

LEAF ANALYSES

Spring

Dry matter content of leaves (table 4) collected in spring was not significantly correlated with other leaf values (table 5). Crude protein averaged 22 percent in spring leaves and ranged from less than 11 percent for pine to greater than 30 percent for greenbriers, trumpetcreeper, and American beautyberry. Leaves with high protein contents also tended to have high phosphorus values (r = 0.76). Phosphorus averaged 0.42 percent and varied from more than 0.70 percent in trumpetcreeper and peppervine to 0.20 percent in Alabama supplejack. Cell contents exceeded 80 percent of dry matter for leaves of flowering dogwood, peppervine, blackberry, hawthorn, and plum, but amounted to only 46 percent in pine needles.

For all species combined, spring leaves averaged 13 percent crude fiber, 26 percent CWC, 21 percent ADF, 9 percent ADL, and 12 percent cellulose (table 3). The 2.9 percent silica content of American beautyberry leaves lowered ETDMD (spring twigs of this species also had high silica values).

ETDMD and NBDMD values were not so highly correlated (r = 0.65) for spring leaves as for spring twigs (r = 0.83, table 2). Perhaps the reduced correlation is due to the presence of waxes, oils, resins, or other leaf components that affect either NBDMD values or reliability of the detergent fiber analyses, or both.

Summer and Autumn

Leaves of few species had as much as 13 percent protein or 0.20 percent phosphorus during summer and autumn. Still, cell contents and NBDMD averaged more than 65 percent during these seasons (table 3). Dry matter and crude fiber were significantly higher, and protein and phosphorus lower, during summer and autumn than during spring. ADL, hemicellulose, silica, and leaf digestibility changed little from spring through summer.

Winter

Leaves of the evergreen and tardily deciduous species-Japanese honeysuckle, blackberry, willow oak, greenbriers, water oak, yaupon, and pine-were lumped for the analysis (table 3), since their nutrient contents did not vary much from summer to winter.

The other species are deciduous. Leaves were collected from the ground during winter, and no dry matter determinations were made. Protein, cell contents, NBDMD, and ETDMD of these weathered leaves usually were sharply diminished from summer-autumn values, and most fiber contents were sharply increased. Translocation from the leaf before fall and leaching of nutrients afterwards probably account for the differences. Detergent analyses of weathered leaves collected during winter were imprecise as ADF measures of these tissues frequently exceeded CWC levels.

Table I.-*Composition and digestibility of leaves from 20 browse species collected in east Texas at the four seasons*

Species	Season collected	Dry matter	Crude protein	Crude fiber	Phosphorus	CWC[1]	ADF	ADL	Silica	Hemicellulose	Cellulose	Digestibility NBDMD	Digestibility ETDMD
		Percent of green weight	*Percent of ovendry weight*										
Loblolly and shortleaf pine	Spring	34.7	10.8	33.3	0.22	53.8	39.1	14.7	0.19	14.7	24.4	44.8	57.7
	Summer	36.5	7.9	35.1	.11	49.8	43.9	16.5	.98	5.9	27.4	38.9	60.7
	Autumn	39.7	9.1	30.3	.13	45.1	37.0	15.4	.59	8.1	21.6	39.0	62.6
	Winter	41.4	9.9	27.4	.13	40.6	33.8	15.0	.69	6.8	18.8	49.8	65.3
Common and saw greenbriers	Spring	17.6	30.9	9.7	.63	22.8	13.6	5.8	.30	9.2	7.8	91.2	79.9
	Summer	35.2	11.7	27.6	.11	43.9	34.1	12.3	.08	9.8	21.8	65.7	65.7
	Autumn	41.0	11.1	25.2	.11	40.6	30.3	10.2	.21	10.3	20.1	66.5	69.1
	Winter	42.3	12.3	23.3	.13	38.5	26.8	8.8	.05	11.7	18.0	73.3	70.9
Willow oak	Spring	30.0	18.5	18.3	.48	38.4	24.3	11.7	.22	14.1	12.6	43.4	66.0
	Summer	50.2	11.1	25.2	.11	44.9	32.1	14.0	.25	12.8	18.1	37.3	62.1
	Autumn	54.7	12.1	22.0	.12	43.3	31.7	14.7	.29	11.6	17.0	41.5	62.4
	Winter	56.9	10.3	23.2	.13	41.5	29.9	12.7	.10	11.6	17.2	48.4	65.1
Water oak	Spring	29.9	19.1	16.7	.32	34.6	20.1	8.3	.09	14.5	11.8	59.0	70.9
	Summer	52.3	10.3	25.9	.09	49.0	35.4	14.2	.31	13.6	21.2	41.2	60.2
	Autumn	57.5	12.2	27.1	.12	46.2	32.8	14.1	.28	13.4	18.7	40.3	61.2
	Winter	57.4	10.5	24.6	.11	42.5	30.6	13.1	.43	11.9	17.5	50.9	64.2
Winged elm	Spring	34.5	27.6	11.5	.46	21.7	16.1	5.8	.34	5.6	10.3	89.7	82.0
	Summer	55.2	11.2	20.6	.12	37.9	31.3	12.3	5.17	6.6	19.0	54.4	53.5
	Autumn	55.0	8.8	20.7	.12	38.0	31.9	11.6	1.30	6.1	20.3	51.4	66.0
	Winer	(2)	7.3	25.8	.07	61.4	55.9	30.8	2.54	5.5	25.1	26.6	36.3
Common sassafras	Spring	23.9	28.3	16.4	.46	29.6	23.1	9.3	.27	6.5	13.8	79.2	75.1
	Summer	36.0	12.3	18.2	.14	45.3	29.5	13.1	.18	15.8	16.4	69.4	61.5
	Autumn	37.3	9.6	15.3	.10	36.0	22.8	10.0	.03	13.2	12.8	77.4	69.1
	Winter	(2)	5.5	27.5	.07	65.2	58.7	37.5	.04	6.5	21.2	22.7	37.3
American sweetgum	Spring	25.8	16.9	9.4	.30	21.1	18.3	7.0	.47	2.8	11.3	71.5	82.1
	Summer	35.6	9.8	11.2	.11	35.9	30.9	10.7	1.03	5.0	20.2	54.2	69.0
	Autumn	37.9	9.9	9.4	.13	20.4	21.7	7.9	2.27	0.0	13.8	61.7	76.1
	Winter	(2)	5.3	17.3	.06	40.5	65.2	36.6	G.12	0.0	28.6	39.1	43.7
Hawthorns	Spring	35.8	19.0	9.8	.34	18.9	17.3	8.G	.11	1.6	8.7	90.0	82.0
	Summer	58.1	7.6	14.2	.09	26.7	21.0	9.8	.27	5.7	11.2	72.8	76.0
	Autumn	67.7	7.1	12.9	.08	29.5	26.0	13.4	.23	3.5	12.6	53.1	72.7
	Winter	(2)	7.4	18.3	.07	45.9	49.4	31.8	1.18	0.0	17.6	34.4	51.6
American and flatwoods plum	Spring	34.8	26.2	6.5	.57	12.2	10.3	4.3	.25	1.9	6.0	91.8	88.4
	Summer	50.7	11.1	12.2	.12	23.2	18.3	10.2	.29	4.9	8.1	85.0	77.5
	Autumn	53.0	13.1	9.6	.14	17.0	12.4	6.2	.09	4.6	6.2	89.4	83.6
	Winter	(2)	9.0	13.8	.08	40.2	41.0	26.4	4.02	0.0	14.6	58.8	48.4
Blackberry	Spring	32.6	24.3	13.0	.44	19.9	16.8	4.2	.22	3.1	12.6	82.2	85.9
	Summer	41.0	10.0	15.6	.12	31.1	22.7	7.7	.25	8.4	15.0	58.9	75.8
	Autumn	45.4	13.4	14.2	.15	28.0	19.8	6.9	.14	8.2	12.9	62.9	77.7
	Winter	52.3	11.7	14.9	.14	27.7	18.5	5.6	.26	9.2	12.9	70.3	79.3
Yaupon	Spring	31.2	18.4	12.5	.26	35.1	43.1	29.6	.08	0.0	13.5	80.9	64.4
	Summer	47.9	11.3	22.0	.08	40.0	31.6	15.0	.09	8.4	16.6	74.2	64.8
	Autumn	47.1	12.2	20.8	.12	35.2	26.9	12.7	.63	8.3	14.2	76.2	68.9
	Winter	50.5	11.6	17.7	.10	30.9	23.3	10.5	7.12	7.6	12.8	77.4	69.6
Alabama supplejack	Spring	33.5	16.2	8.9	.20	20.7	14.1	5.3	.13	6.6	8.8	92.6	82.5
	Summer	46.5	9.3	12.0	.07	30.5	18.6	6.6	.33	11.9	12.0	85.0	75.7
	Autumn	47.5	8.6	12.3	.08	23.5	17.9	8.3	.08	5.6	9.6	85.2	78.7
	Winter	(2)	8.3	17.4	.07	51.2	53.9	36.3	2.31	0.0	17.6	31.5	42.5
Peppervine	Spring	27.2	25.3	9.0	.72	14.0	13.1	5.7	.41	0.9	7.4	70.1	86.8
	Summer	38.6	13.8	8.7	.18	17.3	16.8	6.4	.32	0.5	10.4	65.0	85.0
	Autumn	43.2	13.5	9.7	.21	17.9	21.0	7.3	.16	0.0	13.7	78.3	85.1
	Winter	(2)	6.6	15.8	.13	42.5	65.1	40.6	2.28	0.0	24.5	29.7	51.9
Grapes	Spring	21.0	24.2	22.4	.60	37.9	33.6	12.3	.40	4.3	21.3	75.4	69.9
	Summer	33.3	12.1	13.3	.15	32.5	21.8	6.7	.86	10.7	15.1	86.5	75.9
	Autumn	39.2	8.0	13.5	.14	28.4	24.7	8.3	1.85	3.7	16.4	81.1	72.2
	Winter	(2)	6.9	23.8	.07	51.0	51.6	27.6	.11	0.0	24.0	53.3	53.6

Table I.-Composition and digestibility of leaves from 20 browse species collected in east Texas at the four seasons (Continued)

Species	Season collected	Dry matter	Crude protein	Crude fiber	Phos-phorus	CWC[1]	ADF	ADL	Silica	Hemicel-lulose	Cellu-lose	Digestibility NBDMD	ETDMD
		Percent of green weight	*Percent of ovendry weight*										
Flowering dogwood	Spring	31.7	20.7	13.8	.26	19.7	17.5	7.3	.12	2.2	10.2	82.8	82.5
	Summer	39.7	8.3	13.9	.09	20.6	20.0	4.8	.22	0.6	15.2	79.4	85.7
	Autumn	43.5	7.4	11.5	.08	19.4	18.2	5.0	.14	1.2	13.2	79.5	85.5
	Winter	(2)	5.9	17.8	.06	30.4	32.6	9.7	.09	0.0	22.9	85.5	77.6
Black tupelo	Spring	20.3	15.1	10.8	.22	27.2	17.8	6.4	.10	9.4	11.4	80.9	78.0
	Summer	39.4	8.8	14.8	.10	34.8	19.0	6.5	.14	15.8	12.5	54.7	73.0
	Autumn	41.4	6.8	17.9	.07	40.3	20.4	7.6	.06	19.9	12.8	56.7	67.9
	Winter	(2)	6.4	22.8	.11	43.5	35.5	16.4	1.85	8.0	19.1	56.7	56.8
American beautyberry	Spring	22.4	33.5	11.4	.46	28.5	21.3	8.3	2.89	7.2	13.0	84.4	67.6
	Summer	30.9	13.7	18.5	.19	41.0	33.4	10.6	.23	7.6	22.8	76.4	69.6
	Autumn	31.8	10.1	18.2	.15	34.2	27.1	9.0	.51	7.1	18.1	80.7	73.8
	Winter	(2)	9.0	22.3	.08	55.1	49.6	18.2	3.75	5.5	31.4	46.7	45.9
Common trumpetcreeper	Spring	22.3	30.2	10.2	.71	24.5	20.3	8.8	.33	4.2	11.5	84.6	78.4
	Summer	44.0	9.6	19.2	.12	36.9	25.6	9.3	.38	11.3	16.3	79.1	70.8
	Autumn	42.0	6.9	21.6	.10	38.5	28.0	10.1	.47	10.5	17.9	73.9	69.7
	Winter	(2)	11.3	20.6	.14	56.0	51.9	23.1	2.74	4.1	28.8	30.4	44.6
Japanese honeysuckle	Spring	28.0	16.2	10.9	.39	20.7	15.9	7.3	.19	4.8	8.6	86.5	81.1
	Summer	38.0	9.0	13.5	.20	30.2	24.3	15.6	.57	5.9	8.7	84.3	69.8
	Autumn	32.7	13.4	14.7	.18	28.6	20.2	12.0	.46	8.4	8.2	84.7	72.1
	Winter	35.5	12.6	13.9	.18	26.0	17.8	9.8	.86	8.2	8.0	84.9	75.1
Rusty blackhaw	Spring	26.8	20.7	9.6	.38	21.1	18.0	8.9	.19	3.1	9.1	91.2	80.2
	Summer	43.0	7.0	13.9	.08	27.8	22.1	6.1	.38	5.7	16.0	84.7	80.1
	Autumn	43.7	7.7	13.4	.09	28.6	24.8	8.2	.40	3.8	16.6	80.3	77.8
	Winter	(2)	6.2	20.8	.07	48.6	49.7	22.8	1.29	0.0	26.9	67.6	54.4

[1] Cell contents can be calculated as 100 minus CWC.
[2] No dry matter measurements were made on winter leaves picked from the ground.

Leaves of a species with relatively high or low levels of a nutrient during spring tended to have proportionally high or low levels of that nutrient during summer and autumn (table 4). Summer values were related to those observed in autumn and, for evergreen and tardily deciduous species, to winter values also. Nutrient levels in fallen leaves bore no significant resemblance to those in living leaf tissues.

DISCUSSION

During spring, rapidly growing twigs are a quality forage and are digested by ruminants about as efficiently as are quality herbages (Short *et al.* 1974). Dry matter and fiber content are low, and protein, phosphorus, cell content, and digestibility are higher than at any other season. ETDMD of succulent twigs (table 3) suggests that most of the cell contents and about 25 percent of the CWC are digested.

Twigs are generally mature by summer, at which time their protein, cell content, and digestibility values are less than in spring, and fiber and dry matter contents a r egreater. NBDMD of mature browse twigs about equaled cell contents; these values were less than the ETDMD estimates. Presumably, the equation for ETDMD does not adequately weigh the efficiency with which lignins in cell walls of mature wood reduce digestibility (Short *et al.* 1973). CWC, the largest plant fraction in mature woody twigs, essentially is metabolically unavailable to small ruminants like deer (Short and Reagor 1970). Mature woody twigs thus are of less value than would be suggested by a simple comparison of their composition with that of other foodstuffs like herbages.

Because major and rapid changes in nutrient content occur throughout the brief period of rapid twig growth, it is necessary to sample twigs frequently during springtime (Short 1967). By summer, elongation has ceased and twigs have matured so that sampling intensity can be reduced.

Browse leaves had more protein, phosphorus, and cell contents in spring than at other seasons.

Table 5.-*Correlation matrix for leaf components and digestion indices for browse leaves collected in spring, summer-autumn, and winter from east Texas. Only significant values are listed*

Characteristic	Season and plant type[1]	ETDMD	Cellulose	Hemicellulose	NBDMD	Silica	ADL	ADF	CWC[2]	Phosphorus
Dry matter	Summer-autumn	...	...	...	...	...	...	...	...	−0.40
Protein	Spring	...	...	...	...	0.52	...	...	...	.76
	Summer-autumn	...	...	...	...	...	...	...	...	.66
	Winter									
	Evergreen	0.77	...	...	0.95	...	−0.77	−0.83	...	...
Crude Fiber	Spring	−.77	0.92	0.58	−.74	...	...	.72	0.90	...
	Summer-autumn	−.71	.79	.40	−.52	...	.64	.85	.83	...
	Winter									
	Evergreen	−.86	.94	...	−.81	...	.76	.99	.96	...
	Deciduous	...	...	.72	...	...	...	...	.76	...
CWC[2]	Spring	−.95	.88	.67	−.73	...	.60	.84		
	Summer-autumn	−.91	.74	.71	−.63	...	.73	.86		
	Winter									
	Evergreen	−.89	.92	...	−.86	...	...	.95		
	Deciduous	−.79	...	.58	−.69	...	...	...		
ADF	Spring	−.86	.82	...	−.49	...	.89			
	Summer-autumn	−.82	.90	...	−.66	...	.80			
	Winter									
	Evergreen	−.92	.90	...	−.86	...	.84			
	Deciduous	−.68	...	...	−.76	...	.86			
ADL	Spring	−.71	.47	...	...	...				
	Summer-autumn	−.82	.45	...	−.55	...				
	Winter									
	Evergreen	−.92	...	...	...	...				
	Deciduous	−.67	...	...	−.79	...				
Silica	Summer-autumn	−.36	...	...	...					
	Winter									
	Evergreen	...	...	−.79	...					
NBDMD	Spring	.65	−.59	−.65						
	Summer-autumn	.64	−.57	...						
	Winter									
	Evergreen	.76	−.80	...						
	Deciduous	.85	...	...						
Hemicellulose	Spring	−.59	...	...						
	Summer-autumn	−.58								
Cellulose	Spring	−.78								
	Summer-autumn	−.61								

[1] Winter values were determined for leaves of 7 evergreen and tardily deciduous species and 13 deciduous species.
[2] Correlation coefficients for cell contents are the same, except for sign, as those for cell wall contents.

Their dry matter and crude fiber contents increased during summer-autumn, at which times phosphorus and protein declined. Nutrient quality and digestibility of fallen and weathered leaves were much diminished, but leaves of evergreen and tardily deciduous species changed little during winter. Whereas growing and maturing leaves should be frequently sampled to describe their changing nutrient content, a single collection of mature leaves might be adequate during summer-autumn and for nondeciduous leaves also during winter.

As living leaves of browse plants characteristically have a high ADL:ADF proportion (Short et al. 1974), their limited CWC fraction may be of little utility to herbivores. Still, the digestibility is high because cell contents are abundant.

LITERATURE CITED

Association of Official Agricultural Chemists. 1965. Official methods of analysis. 10th ed., 957 p. Wash., D.C.

Cushwa, C. T., R. L. Downing, R. F. Harlow, and D. R. Urbston. 1970. The importance of woody twig ends to deer in the Southeast. USDA For.

Serv. Res. Pap. SE-67, 12 p. Southeast. For. Exp. Stn., Asheville, N. C.

Goering, H. K., and P. J. Van Soest.
1970. Forage fiber analyses (apparatus, reagents, procedures, and some applications). USDA Agric. Handb. 379, 20 p.

Halls, L. K.
1970. Nutrient requirements of livestock and game. P. 10-18 in Range and Wildlfe Habitat Evaluation-A Research Symposium. USDA Misc. Publ. 1147.

Halls, L. K., and R. Alcaniz.
1972. Growth patterns of deer-browse plants in southern forests. USDA For. Serv. Res. Pap. SO-75, 14 p. South. For. Exp. Stn., New Orleans, La.

Isenberg, I. H.
1963. The structure of wood. P. 7-55 in B. L. Browning, ed. The Chemistry of Wood. Interscience Publ. Co., N.Y.

Kramer, P. J., and T. T. Kozlowski.
1960. Physiology of trees. 642 p. McGraw-Hill Book Co., N.Y.

Short, H. L.
1967. Forage analyses for deer management studies. Proc. Southeast. Assoc. Game and Fish Comm. Conf. 20: 15-18.

Short, H. L., and J. C. Reagor.
1970. Cell wall digestibility affects forage value of woody twigs. J. Wildl. Manage. 34: 964-967.

Short, H. L., R. M. Blair, and L. Burkart.
1972. Factors affecting nutritive values. P. 311-318 in Wildland Shrubs—Their Biology and Utilization. USDA For. Serv. Gen. Tech. Rep. INT-1. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Short, H. L., R. M. Blair, and E. A. Epps, Jr.
1973. Estimated digestibility of some southern browse tissues. J. Anim. Sci. 36: 792-796.

Short, H. L., R. M. Blair, and C. A. Segelquist.
1974. Fiber composition and forage digestibility by small ruminants. J. Wildl. Manage. 38: 197-209.

Wort, D. J.
1962. Physiology of cambial activity. P. 89-95 in T. T. Kozlowski, ed. Tree Growth. 442 p. Ronald Press Co., N.Y.

Short, Henry L., Robert M. Blair, and E. A. Epps, Jr.

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