Deer Habitat Potential of Pine-Hardwood Forests in Louisiana

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SUMMARY

Responses of the understory and overstory plant community to selection tree harvest in an all-aged loblolly (*Pinus taeda* L.)-shortleaf pine (*Pinus echinata* Mill.) and mixed hardwood forest in Central Louisiana were studied along with nutrient-related attributes and seasonal utilization of forage to define the impact of forage dynamics on the habitat capability for white-tailed deer *(Odocoileus virginianus mucrourus* Rafinesque). Relationships were studied under three levels of controlled deer stocking.

Herbage and browse yields peaked within two years after logging and progressively declined as overstory competition increased. Browse comprised 75 percent or more of the annual forage production. For three to four years after logging, the habitat appeared capable of supporting one deer on each 12 to 18 acres. Capability declined rapidly thereafter as preferred foods diminished. Within seven years after timber harvest the capability was approaching 40 acres per animal. After 10 years over 40 acres were needed to support one deer yearlong.

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The response of understory vegetation to the management of loblolly (*Pinus taeda* L.)-shortleaf pine (*Pinus echinata* Mill.) forests for timber products largely determines the habitat's ability to support white-tailed deer (*Odocoileus virginianus macrourus* Rafinesque) and many other wildlife species. Periodic logging reduces overstory competition, and forbs and browse that are beneficial to deer temporarily proliferate. Early stages of succession in the understory are, however, short-lived because secondary plant succession progresses rapidly in southern forests (Blair and Brunett 1976). To maintain early stages of succession and a favorable habitat for deer, timber managers must consider the dynamics of understory vegetation.

This study assesses the floral and structural response of the understory and overstory plant community to a selection harvest in an all-aged loblolly-shortleaf pine and mixed hardwood stand in central Louisiana. Forage dynamics are related to the habitat's capacity to support deer. The research began in 1960 immediately after a selection timber harvest and continued through 1970. Understory dynamics were studied under three controlled levels of deer stocking.

Study results are applicable to the 58 million acres of loblolly-shortleaf pine cover type (U.S. Department of Agriculture 1965), particularly natural stands or plantations in the rolling uplands of east Texas, Louisiana, south Arkansas, Mississippi, Alabama, and Georgia.

STUDY AREA

The study was conducted within three 160-acre deer enclosures, each paired with a 20-acre exclosure. Enclosures were maintained at different levels of animal stocking, employing static populations of female white-tailed deer. Facilities were established on the Kisatchie National Forest in Winn Parish, central Louisiana.

The forest was an all-aged, second-growth pine-hardwood stand with a dense multitiered canopy. Loblolly and shortleaf pine were dominant. Prominent hardwoods were southern red oak (*Quercus falcata* Michx.), white oak (*Quercus alba* L.), sweetgum (*Liquidambar styraciflua* L.), American holly (*Ilex opaca* Ait.), blackgum (*Nyssa sylvatica* Marsh.), red maple (*Acer rubrum* L.), and eastern hophornbeam (*Ostrya uirginiana* [Mills.] K. Koch).

The understory plant community consisted primarily of tree reproduction, shrubs, and woody vines. Herbaceous flora was sparse. The density of understory vegetation was greatest beneath openings in the tree canopy where the light level was highest.

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Deer, cattle, and domestic hogs ranged the area before the study, but grazing was light. Livestock was excluded from the area during the study.

Before the study, pine and commercially valuable hardwoods were harvested approximately every ten years by the single tree or group selection system. From late 1958 to early 1960 about 18 ft^2 basal area per acre of mature and overmature pine and 10 ft^2 per acre of hardwoods were harvested. White and southern red oaks were the principal hardwood species removed.

The residual stand averaged 84.8 ft^2 basal area per acre in trees $\geq$ 0.55 inch dbh (table 1). Hardwoods comprised 49 percent of the residual basal area and 84 percent of the stocking per acre. The average pine, however, was nearly two and one-half times larger in diameter than the average hardwood.

Throughout the study at least 77 percent of the hardwoods and 42 percent of the pines were $<$ 3.55 inches dbh. Over 90 percent of the hardwoods and at least 57 percent of the pines were $<$ 6.55 inches dbh. Hardwoods dominated the stocking by a consistent hardwood:pine ratio of about 5.2:1 while pine averaged a little over half of the total basal area. From 1960 to 1970, pine basal area increased 17 percent and hardwood basal area increased 11 percent.

The terrain is essentially rolling hills dissected and well-drained by intermittent drainages. Soils were developed from fine textured Coastal Plain sediments (Pearson and Ensminger 1957). Because of high annual rainfall and excessive leaching, soils are predominantly acid in reaction and low in both organic matter and plant nutrients.

The climate in summer is hot and humid and winters are generally mild. The mean frost-free season is 240 days between March 19 and November 13. Average annual precipitation of 55.4 inches is well distributed throughout the year.

Table 1.—*Stand dynamics of pine and hardwood trees* $\geq$ 0.55 *inch dbh following a single-tree selection harvest*

Stand data		1960	1965	1970
Stocking-number/acre	Pine	75	87	89
	Hardwood	386	449	444
	Total	461	536	533
Basal area—ft^2/acre	Pine	43.4	45.0	50.7
	Hardwood	41.4	43.4	46.0
	Total	84.8	88.4	96.7
Mean dbh — in	Pine	10.3	9.8	10.2
	Hardwood	4.4	4.2	4.4

Spring growth of woody perennials begins in late March or early April and twig elongation and tissue maturation are nearly complete on most species by early summer (Kozlowski 1964, Halls and Alcaniz 1965, Blair and Halls 1968). Minor growth activity is common on some species after summer rains, and several broadleaved evergreens, such as Carolina jessamine (*Gelsemium semperuirens* [L.] Ait.), grow during intermittent warm periods in winter. Pines grow throughout most of the frost-free period.

METHODS

Deer Stocking Levels

After an initial inventory of the plant community in late summer 1960, the three 160-acre enclosures were stocked at rates of one deer per 20, 40, and 80 acres (high, medium, and low stocking). No deer were permitted in the exclosures. Enclosures were stocked with animals less than 2 years of age. Before release each doe was x-rayed to exclude pregnant animals, weighed, and equipped with a color-coded collar.

Animal Condition

A young population was maintained in each enclosure by systematically replacing older animals. Each deer removed was weighed and examined for both physical conformation and external parasites. Animals were necropsied for internal parasites, body fat, disease symptoms, and evidence of malnutrition as indicated by bone marrow fat.

Timber Stand

Beginning in winter 1960, timber within each unit (enclosure and exclosure) was sampled at 5-year intervals by the variable-plot-radius method of Bitterlich (Grosenbaugh 1952). The basal area and diameter of all pines and hardwoods $\geq$ 0.55 inch dbh were determined by species on 24 permanent sampling points established within each enclosure and 18 points within each exclosure. Basal area was sampled with a Relaskop?

Understory Plant Community

Forage Production

The net primary production of current leaves and stems of understory vegetation up to 5 feet

[1] Mention of a trade name is solely to identify the equipment and does not imply endorsement by the U.S. Department of Agriculture.

above ground was determined by the double-sampling technique (Wilm, and others 1944). Production was determined from 96 permanent and 24 temporary milacre quadrats established in a grid pattern within each enclosure and 64 permanent and **16** temporary quadrats within each exclosure (Blair and Brunett 1976). Current growth was sampled by species for woody flora and by five separate classes for herbaceous vegetation: grasses, grasslike plants, composites, legumes, and other forbs.

To express forage yield on a dry-weight basis, clipped plant material was dried to constant weight in a forced-draft oven at 65° C. Browse leaves were separated from stems. Leaves of evergreen species, both pines and hardwoods, and twigs from all species were used to estimate the woody forage available after autumnal leaf abscission. Net primary production was sampled in September 1960, 1961, and 1962 and in alternate years thereafter. Yield data excluded spring ephemerals, basal rosettes of leaves produced by some forbs and grasses in winter, and small growth flushes produced by some evergreen shrubs and woody vines during winter warm periods.

Forage Utilization

Systematic observations were made bimonthly to determine the species of herbage and parts of woody plants ingested. Each September before leaf abscission and again in early March immediately before spring green-up, deer utilization of forage plants was determined by visual estimate of the fresh weight of tissue removed by browsing. Utilization was estimated for browse species and for herbage classes on the permanent milacre quadrats within each enclosure. During the early autumn measurement the tips of all browsed twigs were dotted with orange paint to distinguish between summer and winter use.

Forage Nutrient Quality and Dry- Matter Digestibility

In 1964 and 1970, samples of dried current plant growth from clipped quadrats within each unit were used to determine nutrient-related attributes and dry-matter digestibility of summer forages. Plant tissues were grouped into grass and grasslike plants, forbs, browse leaves, and browse twigs for analyses.

Dried tissues were ground through a 2 mm screen in a Wiley mill and analyzed for percentage content of crude protein, phosphorus, and calcium by methods of the Association of Official Agricultural Chemists (1965). Amounts of cell wall constituents (CWC), acid detergent fiber (ADF), acid detergent lignin (ADL), and silica were determined by procedures of Goering and Van Soest (1970). Caloric values, expressed as gross energy, were assayed by oxygen bomb calorimetry (adiabatic calorimeter). 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. Apparent digestible energy (ADE) values were calculated from gross energy determinations using the regression $Y = -0.713 + 0.991X$ (Robbins and others 1975), where Y = % ADE and X=% dry matter digestibility.

In vivo dry-matter digestibility was determined for each forage class by the nylon bag procedure (Lowrey 1970) using ruminally cannulated domestic goats as a substitute for deer (Fowle and Church 1973, Short and others 1974). Trials were conducted on 1-gm samples of dry-milled tissue that passed through a 40-mesh screen but were retained by a 60-mesh screen. Nylon-bag dry-matter digestibility values reported herein are averages of the four determinations of each sample (duplicate samples in each of 2 goats).

Cannulated animals were maintained on a balanced commercial ration and native forage until two weeks before digestion trials. They were then placed on native forages only.

Oak Mast

The annual autumn production of acorns was sampled on an area basis using 204 trap points within each enclosure and 150 points within each exclosure, established in a grid pattern. A trap was set only at a sampling point that occurred beneath or within 10 feet of the crown of an oak ≥ 5.55 inches dbh. Grid points not sampled by a trap were regarded as zero yields.

Pine Regeneration

The stocking and distribution of pine seedlings up to 5 feet in height in enclosures and exclosures and browsing on seedlings by deer within enclosures were determined on the permanent milacre quadrats established for measuring understory vegetation. Regeneration was sampled in late summer. Browsing on pines and the degree of injury were recorded in late summer and late winter.

RESULTS

Overstory Dynamics

Selective logging of pines and hardwoods altered the physical structure of the timber stand but had little impact on species composition (Blair and Brunett 1976). Harvest of the large-diameter trees opened the canopy and increased the light, moisture, and nutrients for understory forage plants. Log skidding disturbed the heavy litter accumulation and provided an improved seedbed for plant establishment.

After the reduction in overstory competition, the growth of young trees, particularly hardwoods, increased the density of the multitiered midstory. Light penetration to the understory subsequently declined and forage growth was progressively suppressed or eliminated. Within six growing seasons the stocking of both pines and hardwoods increased 16 percent and stabilized over the next 5 years. Basal area increases were lessened by the loss of several large-diameter pines to bark beetles and the loss of several large oaks and hickories to decay and windthrow.

Pine Regeneration

The number of seedlings $\leq$ 5 feet in height increased for the first 2 years after logging at all levels of deer stocking but then progressively declined as competition increased from adjacent vegetation (table 2). Most seedlings were $\leq$ 2 feet in height, which included seedlings of the year. Seedlings tended to survive only beneath canopy openings; therefore, distribution was poor. Mortality was high since young loblolly pine seedlings do not survive long in dense shade after their secondary needles develop, and saplings or larger trees are even less tolerant of shade (Bormann 1956, Wahlenberg 1960).

The number of seedlings $>$ 2 feet in height increased until 1968, followed by a 57 percent decline. Below normal rainfall during summer 1969 seemed to be the principal cause of the excessive mortality. The drought effect was not reflected by the density of seedlings $<$ 2 feet due to the influx of new seedlings during spring 1970.

Forage Production

As expected, growth of forage plants began to decline soon after logging in response to the increasing competition from trees. Responses in the botanical composition and dry-matter yield of herbaceous and browse forage were similar for all deer stocking levels; hence, the results of forage yields reported herein are the average of all stocking regimes.

Herbage

Herbage was sparse within the dense timber stands and growth of forbs and grasses occurred primarily beneath openings in the canopy. The peak yield of dry matter was 100 pounds per acre in 1961, two growing seasons after logging (table 3). Herbage declined rapidly until 1966 when production stabilized at around 23 pounds per acre.

Grasses were the predominant herbage. In 1961 the stands yielded 89 pounds of grass per acre which was 89 percent of the herbage dry matter. Over the next 9 years production of grass declined 84 percent. Forbs declined 86 percent from a peak yield of 14 pounds per acre in 1960 to 2 pounds in 1966.

Uniolas (*Uniola sessiliflora* Poir and *Uniola laxa* [L.] BSP.), which are shade tolerant, contributed over 85 percent of the grass yield. Other common herbaceous species were small panic grasses (*Panicum* spp.), whip razorsedge (*Scleria triglomerata* Michx.), partridgeberry (*Mitchella repens* L.), horseweed (*Conyza canadensis* [L.] Cronquist), trailing lespedeza (*Lespedeza procumbens* Michx.), little tickclover (*Desmodium ciliare* [Muhl.] DC.), hyssop skullcap (*Scutellaria integrifolia* L.), hairy elephantfoot (*Elephantopus to-*

Table 2.—*Stocking of pine regeneration per acre and the percent distribution*[1] *of seedling following a selection harvest*

Height class	1960	1961	1962	1964	1966	1968	1970
O-2.0 ft	5042	6198	3160	2586	1059	712	1156
2.1-5.0 ft	94	137	234	413	606	862	370
Total	5136	6335	3394	2999	1665	1574	1526
Distribution %	61	77	53	56	38	39	41

[1] Based on percent of sample quadrats stocked in late summer with one or more seedlings.

Table 3.—*Net primary production of current forage in pounds dry matter per acre*

Class of vegetation	1960	1961	1962	1964	1966	1968	1970
Herbaceous							
Grass and grasslike plants	72	89	66	33	21	19	14
Forbs	14	11	12	4	2	6	5
Total	86	100	78	37	23	25	19
Browse							
Leaves	201	213	208	163	128	112	81
Twigs	82	79	66	46	34	31	23
Total	283	292	274	209	162	143	104
Browse leaf:twig ratio	2.5:1	2.7:1	3.2:1	3.5:1	3.8:1	3.6:1	3.5:1

mentosus L.), and wrinkled goldenrod (*Solidago rugosa* Ait.).

Browse

Browse, which consists of the current leaves and stems of trees, shrubs, and woody vines, contributed at least 75 percent of the total forage. As with herbage, the net primary production peaked 2 years after logging; the dry-matter yield was 292 pounds per acre (table 3). Yields then declined to a low of 104 pounds in 1970.

Leaves contributed at least 70 percent of the browse yield throughout the study. The leaf:twig ratio increased for about 7 years after logging, indicating an increase in leaf dry matter in response to increased shade. Although overstory competition intensified, the ratio varied little after 1966.

Woody species preferred by deer contributed 44 to 49 percent of the total dry-matter yield of browse (table 4). The peak yield of preferred browse was 140 pounds per acre in 1961, but yields declined 65 percent by 1970. The yield of nonpreferred browse declined 64 percent during this period.

Leaves contributed 64 percent of the dry matter from preferred browse in 1960 and 76 percent by 1970. The leaf:twig ratio of nonpreferred species was larger than that of preferred species due to the preponderance of large-leaved species such as sweetgum, southern red oak, and post oak (*Quercus stellata* Wangenh.) that are nonpalatable to deer.

With leaf abscission from deciduous browse species each autumn the availability of forage from preferred woody species declined greatly (table 5). The percentage loss in preferred browse from leaf fall increased yearly after timber harvest from 58 percent in 1960 to 69 percent in 1970. The growing loss reflected both an increasing leaf:twig ratio of summer growth and a relatively greater decline in the growth of broad-leaved evergreens than of deciduous species.

Table 4.—*Net primary production of preferred and nonpreferred browse in pounds dry matter per acre*

Class of browse	1960	1961	1962	1964	1966	1968	1970
Preferred							
Leaves	89	95	95	68	56	47	37
Twigs	50	45	37	25	20	16	12
Total	139	140	132	93	76	63	49
Leaf:twig ratio	1.8:1	2.1:1	2.6:1	2.7:1	2.8:1	2.9:1	3.1:1
Nonpreferred							
Leaves	112	118	113	95	72	65	44
Twigs	32	34	29	21	14	15	11
Total	144	152	142	116	86	80	55
Leaf: twig ratio	3.5:1	3.5:1	3.9:1	4.5:1	5.1:1	4.3:1	4.0:1
Preferred:nonpreferred browse	1.0:1	0.9:1	0.9:1	0.8:1	0.9:1	0.8:1	0.9:1

Table B.-*Preferred and nonpreferred browse dry matter available per acre in the late fall and winter seasons and the fraction contributed by leaves*

Class of browse	1960	1961	1962	1964	1966	1968	1970
Preferred-lb	59	56	50	33	25	21	15
Nonpreferred-lb	46	48	45	35	27	27	15
Total-lb	105	104	95	68	52	48	30
Preferred Leaf fraction-%	14.9	20.4	25.7	24.0	21.8	21.4	16.8
Nonpreferred Leaf fraction-%	29.8	28.6	36.0	41.0	46.2	44.0	29.1

Evergreen hardwoods contributed an average of 36 percent of the preferred browse from 1960 to 1970. Their yield declined 76 percent during this period.

Predominant species of preferred browse were the vines Carolina jessamine, common green brier (*Smilax rotundifolia* L.), saw greenbrier (*Smilax bona-nox* L.), and crossvine (*Bignonia capreolata* L.) and the shrubs and tree reproduction American beautyberry (*Callicarpa americana* L.), blackgum, brambles (*Rubus* spp.), red maple, flowering dogwood (*Cornus florida* L.), yaupon (*Ilex vomitoria* Ait.), arrowwood viburnum (*Viburnum dentatum* L.), haws (*Crataegus* spp.), sweetleaf (*Symplocos tinctoria* [L.] L'Her), and Elliott's blueberry (*Vaccinium elliottii* Chapm.). Prevalent species that were either low in preference or nonpreferred were American holly, sweetgum, southern red oak, loblolly and shortleaf pines, muscadine grape (*Vitis rotundifolia* Michx), winter huckleberry (*Vaccinum arboreum* Marsh), witch-hazel (*Hamamelis virginiana* L.), post oak, common deerberry (*Vaccinium stamineum* L.), and rabbit-eye blueberry (*Vaccinium virgatum* Ait.).

Acorn Yields

Lowest production of sound, mature acorns occurred in 1962; highest occurred in 1967. Relatively good crops were also produced in 1961, 1964, and 1968. White and southern red oaks were the primary producers. Yearly production by species of mature, sound acorns 'was as follows:

Forage Utilization

Although the estimated weight of forage utilized during both summer and winter was directly proportional to animal stocking, it was, at all stocking intensities, far below the amount necessary to maintain the animals. Less than 10 percent of the estimated dry-matter requirement for animal maintenance was accounted for from sample quadrats. This discrepancy could possibly be attributed to insufficient sampling intensity, difficulty in locating evidence of use, and the ingestion of foodstuffs not included in the utilization inventories such as fleshy fruits, acorns, ephemeral forbs and grasses, and mushrooms. Due to the magnitude of the discrepancies, data served only as indices of seasonal use patterns and of differences in species browsed between animal stocking levels.

In evaluating habitat capability, emphasis was given to the degree of browsing on specific indicator species, both preferred and nonpreferred.

Forbs, although relatively sparse, *were* consistently utilized in spring and summer. Use was particularly prevalent on readily accessible plants growing along roads and fences. Utilization on grasses and grasslike plants, while difficult to distinguish, appeared to be light and sporadic. Use in winter occurred primarily on new growth of panic grasses.

Leaves and twigs of browse were the major forage items ingested. Use of browse leaves appeared

Species of oak	Year 1961	1962	1963	1964	1965	1966	1967	1968	1969	1970
	pounds dry matter per acre									
White	11.2	1.1	2.1	0.5	4.4	0.0	22.8	7.5	6.9	6.2
Post	0.3	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Southern red	0.5	1.1	3.7	9.5	2.9	3.5	2.4	7.2	1.9	0.6
Water and willow	1.0	0.4	1.4	1.6	1.6	1.9	1.2	3.0	0.5	1.2
Total yield	13.0	2.6	7.2	11.7	8.9	5.4	26.4	17.7	9.3	8.0

to be considerably more prevalent than use of twigs, especially after twig fiber increased with maturity.

A variety of species was browsed during the different seasons. Even nonpreferred or low preference species were often browsed when they were next to a preferred species that was utilized. After autumnal leaf abscission the leaves of broadleaved evergreens such as yaupon, Carolina jessamine, and tardily deciduous dewberries were readily sought by deer.

Seasonal use patterns on browse species were similar between deer stocking levels and constant within an individual enclosure for about five years after logging. As the availability of preferred forage declined with increasing overstory competition, the impact of stocking intensity on the food supply became obvious. At the high level, browsing on nonpreferred pine reproduction increased from 31 seedlings per acre in 1964 to 146 in 1965 and remained high thereafter. The greatest use of pine seedlings occurred in 1969 and 1970 when preferred forage growth was lowest. With few exceptions young pines were browsed in late autumn and winter when green forage was sparse. Under the medium and low stocking levels seedlings were browsed only occasionally. Browsing was never observed on seedlings over 2 feet in height. There was little silvicultural damage as animals ingested only the terminal needles and usually a small portion of the stem. Most browsed seedlings formed a new terminal leader and continued growth.

By 1966, the distribution pattern of browsing at high and medium stocking had changed from scattered spots of concentrated use to area-wide use. Blackgum reproduction and yaupon were being severely hedged under these stocking levels. With high stocking southern waxmyrtle (*Myrica cerifera* L.), a nonpreferred species, received moderate use. In 1967 utilization of leaves and twigs of American beautyberry, a species of moderate to low preference, was increasing appreciably.

The availability of acorns did not noticeably affect the degree of forage utilization in autumn and winter.

Forage Nutrient Quality and Digestibility

Forage nutrient quality is at its peak during rapid spring growth when tissues are succulent (Blair and others, in press, Blair and Epps 1969, Blair and Halls 1968, Causey 1964). By early summer growth is nearly complete; nutrient levels decline rapidly and fiber levels elevate. Browse leaves were the most nutritious forage available in summer; grasses and current browse twigs were poorest in quality (table 6). With tissue mat-

Table B.--Mean summer nutrient composition and dry-matter digestibility of forages.

Forage class and year	Composition as Percent Oven-Dry Weight										Gross energy cal/g	Dry-matter digestibility percent	Apparent digestible energy cal/gm
	Crude protein	Phosphorus	Calcium	Cell solubles	Cell wall content	Acid detergent fiber	Hemicellulose	Acid detergent lignin	Cellulose	Silica			
Grass and grasslike plants													
1964	7.5	0.064	0.33	25.5	74.5	46.7	27.8	10.0	36.7	8.00	3964	31.6	1213
1970	6.2	0.060	0.22	21.4	78.6	47.2	31.4	10.7	36.5	5.41	4130	28.9	1153
Forbs													
1964	8.3	0.072	1.08	44.2	55.8	43.9	11.9	13.8	30.1	2.84	3975	47.4	1839
1970	8.0	0.077	1.16	44.5	55.5	47.3	8.2	13.1	34.2	2.80	4047	49.0	1936
Browse leaves													
1964	10.9	0.083	1.04	62.8	37.2	30.2	7.0	12.7	17.5	0.76	4365	71.7	3070
1970	10.1	0.086	1.09	63.6	36.4	30.7	5.7	12.7	18.0	0.65	4400	68.5	2956
Browse twigs													
1964	4.8	0.052	0.67	28.6	71.4	56.1	15.3	18.3	37.8	0.31	4262	26.6	1093
1970	4.4	0.054	0.55	25.7	74.3	58.1	16.2	19.4	38.7	0.14	4344	27.2	1140

uration fiber increases considerably less in browse leaves than in twigs and herbage (Blair and others, in press, Short, and others 1975).

In 1964 and 1970 over 71 percent of the summer dry matter of grasses and woody twigs and 55 percent of the forb dry matter consisted of poorly- or non-digestible cell wall constituents. In contrast, 63 percent of the leaf tissue in summer consisted of highly digestible cell solubles which include lipids, sugars, organic acids, nonprotein nitrogen, pectins, soluble protein, and other water soluble matter.

The crude protein level of leaves was higher than for other forages in summer and was above the estimated daily maintenance requirement for deer of 7 percent of the dry matter (Magruder and others 1957). Phosphorus levels in all forages, however, were well below the estimated minimum daily maintenance requirement of 0.25 to 0.30 percent. Nondigestible acid detergent lignin, which includes aliphatic cutin and silica, was comparatively high in leaves. Cutin is believed to be extremely resistant to microbial degradation; hence, along with silica and lignin, it adversely affects nutritive value (Van Soest 1970).

In summer 1961 forage yielded approximately 34.6 pounds of crude protein per acre (table 7). By 1970 forage production had declined 64 percent and the protein yield was 10.5 pounds. Phosphorus declined from about 0.283 to only 0.094 pounds per acre during this period and cell solubles declined 66 percent from 184.0 to 62.6 pounds per acre. In 1961 leaves contained about 67 percent of the crude protein, 63 percent of the phosphorus, 70 percent of the calcium, 73 percent of the cell solubles, and 75 percent of the estimated apparent digestible energy in summer forages. By 1970 leaves in summer contained about 78 percent of the crude protein, 74 percent of the phosphorus, 80 percent of the calcium, and 82 percent of the cell solubles and estimated apparent digestible energy.

Leaf tissues were the most digestible summer forage while the highly fibrous grasses, grasslike plants, and browse twigs were the least digestible (table 6). Dry-matter digestibility of forages varied little between 1964 and 1970.

Table 7.-Approximate summer nutrient *yields per acre by forage classes at 3, 5, and 11 years after a selection timber harvest*

Forage class and year	Crude Protein	Phos-phorus	Calcium	Cell Solubles	Cell Wall Content	Digestible Dry matter	Gross Energy	Apparent Digestible Energy
	pounds						MKcal	
Grass and grasslike plants								
1961'	6.7	0.057	0.29	22.7	66.3	28.1	160.03	49.00
1964	2.5	0.021	0.11	8.4	24.6	10.4	59.34	18.16
1970	0.9	0.008	0.03	3.0	11.0	4.0	26.23	7.33
Forbs								
1961'	0.9	0.008	0.12	4.9	6.1	5.2	19.83	9.17
1964	0.3	0.004	0.04	1.8	2.2	1.9	7.21	3.33
1970	0.4	0.004	0.06	2.2	2.8	2.4	9.18	4.39
Browse leaves								
1961'	23.2	0.177	2.22	133.8	79.2	152.7	421.73	296.65
1964	17.8	0.135	1.70	102.4	60.6	116.9	322.73	227.01
1970	a.2	0.070	0.88	51.5	29.5	55.5	161.66	108.59
Browse twigs								
1961'	3.8	0.041	0.53	22.6	56.4	21.0	152.73	39.17
1964	2.2	0.024	0.31	13.2	32.8	12.2	88.93	22.81
1970	1.0	0.012	0.13	5.9	17.1	6.3	45.32	11.89
TOTAL								
1961	34.6	0.283	3.16	184.0	208.0	206.9	754.32	393.99
1964	22.8	0.184	2.16	125.8	120.2	141.9	478.21	271.31
1970	10.5	0.094	1.10	62.6	60.4	68.2	242.39	132.20

'Estimates based on 1961 forage yields in conjunction with nutrient composition of forages derived in 1964.

Animal Condition

Malnutrition was never evident in study animals removed from enclosures from 1961 to 1971. Further, incidence of internal parasites was not related to the population density of deer. Live weights of animals removed from enclosures between 1966 and 1971, a period when browse use indicated excessive and increasing pressure on the food supply at both heavy and medium stocking levels, were not noticeably related to population density. Young deer at stocking time averaged 50.6 pounds and 7.6 months of age. At the time of removal, after at least 18 months confinement, weights in March and April averaged 87.7 pounds under heavy stocking, with individual weights ranging from 70 to 105 pounds. With medium stocking, spring weights averaged 81.6 pounds, ranging from 67 to 107 pounds and with light stocking the average was 93.2 pounds, ranging from 86 to 100 pounds.

DISCUSSION

The capability of all-aged loblolly-shortleaf pine-hardwood stands to sustain deer largely depends upon the intensity and frequency of timber cutting. With timber harvest and a reduction in competition, the forage-nutrient base peaks and then declines as overstory competition increases. To sustain an adequate nutrient base for the growth and maintenance of deer, timber stands must be thinned frequently and sufficiently to stimulate a diversified growth of palatable and nutritious forage.

The capability can be estimated by relating the seasonal metabolic needs of animals to the nutrients available in the food supply. The pattern of seasonal use on available forage species provides supporting evidence. The precision of capability estimates can be enhanced by specifically relating the seasonal metabolic needs of deer to animal sex, age, and physiologic activity. Cover and water are seldom deficient in the habitat.

For 3 or 4 years after harvest the habitat in this study appeared capable of sustaining one deer on about 12 to 18 acres during the warm season. With a stocking of one deer per 20 acres palatable species of browse were only lightly used, suggesting an even greater capability. Habitat capability estimated from an evaulation of the forage-nutrient supply and approximate metabolic needs of deer supported the capability indicated. by the pattern of forage utilization. For example, in 1961, the peak year of forage production, roughly 34.6 pounds of crude protein per acre were yielded in summer by forage dry matter (table 7). Considering only the protein available in forbs and half the leaves of palatable browse species (50 percent proper use assumed for browse leaves) and assuming a 75-pound deer might require between 0.35 and 0.43 pound of protein per day for proper growth performance (Magruder and others 1957), 14 to 17 acres would be needed to supply protein for one animal during the 240 day warm season. While forbs and browse leaves are principal forages for deer (Harlow and others 1975), added protein would undoubtedly be obtained from mushrooms and tender twig tips, thereby improving the estimate of capability.

Habitat capability indicated in 1961 by the relationship of energy supply to metabolic need was 10 acres per deer during the warm season, somewhat higher than that suggested by a protein evaluation. The daily gross energy requirement for growth of a 75 pound deer was assumed to be 4725 Kcal (Magruder and others 1957).

Phosphorus appeared to be a limiting factor in the nutrient supply. Low forage phosphorus, however, can be expected in these habitats since soil phosphates available for root absorption are readily leached by the high annual rainfall (Lytle 1960). During feeding, deer possibly selected forage tissues that were relatively high in phosphorus and supplemented this by consuming mushrooms which are a good source of phosphorus. Swift (1948) and Longhurst and others (1968) concluded that deer can apparently select plants and plant fractions higher in nutrients than those sampled by man,

From 1961 to 1964 the summer supply of crude protein in the dry matter of forbs and the leaves of palatable browse declined about 32 percent as competition intensified within the plant community. By 1970 it declined an additional 32 percent to only 4.1 pounds per acre. The gross energy potential in these summer forage fractions declined approximately 32 percent between 1961 and 1964, from an estimated 207,930 Kcal per acre to 141,850 Kcal. The energy potential was down an additional 28 percent by 1970, to a supply of 83,030 Kcal per acre.

Utilization of palatable browse as well as use of nonpreferred pine seedlings was increasing by 1964 at the high stocking level. By 1966, seven years after logging, deer at this stocking density were commonly browsing several nonpreferred species, such as southern waxmyrtle, sweetgum, American beech (*Fagus grandifolia* Ehrh.), and tree sparkleberry. Winter use on loblolly and shortleaf pine seedlings had increased substantially. Several species, such as blackgum and yaupon were now being hedged under both the high and medium levels. The pattern of browse use indicated excessive pressure on the food supply and a progressively declining habitat capability.

Forage use data indicated a capability in 1964 of a little over 20 acres per deer, approaching 40 acres by 1966 and exceeding 40 acres by 1970.

The declining capability was substantiated by relating nutrient supply to metabolic needs of deer. In 1964 the relationship between crude protein supplied by forbs and half the leaves of palatable browse and estimated requirements for growth of a 75-pound animal indicated that **21** to **26** acres might be needed for one deer during the frost-free period. The gross energy potential indicated a need of about 15 acres per animal. The capability indicated by crude protein appeared more realistic when compared to the pattern of forage use than did the somewhat higher potential suggested by gross energy. By 1970, habitat capability- estimated on the basis of protein relationships had diminished to a range of 38 to 47 acres per deer. Based on gross energy, the estimated capability was 25 acres per animal. Again, the estimates founded on protein relationships appeared to be better correlated with forage use than that based on the supply and animal needs of gross energy.

Habitat capability declines with the autumnal loss of nutrients contained in forbs and deciduous browse leaves. From 1960 to 1970 leaf dry matter of palatable browse declined an average of 89 percent with autumnal abscission although nutrient quality changed little from summer to winter (Blair and Epps 1969, Blair and others, in press). Both the leaves of broadleaved evergreens and twig tips were utilized by deer during the winter. Soft fruits (Hastings 1966), acorns, the green basal rosettes of forbs, and mushrooms undoubtedly contributed additional nutrients during the cold season stress period.

A productive habitat, capable of supporting one deer on less than 40 acres, can be sustained in pine-hardwood stands by shortening the cutting cycle on management units from the common practice of 10 or more years to a maximum of 7. A preferable system for maintaining a quality forage base can be achieved by dividing a management compartment into 40- to 50-acre units and cutting alternate units, in a checkerboard pattern, every five years. The latter system would provide a more favorable habitat diversity and a consistently higher nutrient base than less frequent logging over a larger area.

Timber harvest must be sufficiently heavy to provide a substantial increase in light energy reaching vegetation in the deer feeding zone. Therefore a higher habitat capability can be maintained by increasing the cutting intensity and/or frequency. Where cutting is delayed and the deer population exceeds the food base, damage not only to food plants but also to forest regeneration becomes increasingly substantial. The supply of forage nutrients can be increased by felling palatable hardwoods and shrubs that have grown beyond the deer feeding zone to stimulate resprouting (Blair and Feduccia, in press). Woody species that are nonpreferred as forage and have no food value as fruit producers or commercial value for wood products should be eliminated to reduce the competition to desirable forage.

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For three to four years after logging, an all-aged pine-hardwood forest in Central Louisiana appeared capable of supporting one deer on each 12 to 18 acres. Capability declined rapidly thereafter as overstory competition increased and preferred foods diminished. Within seven years after timber harvest the capability was approaching *40* acres per animal and after *10* years over *40* acres were needed to support one deer year-long.

Additional keywords: White-tailed deer, loblolly-shortleaf pine, secondary succession, forage yield, forage quality, nutrients, deer enclosures.

Metric Conversions

Basal Area	m^2 per hectare = 0.2296 (ft^2 per acre)
DBH	cm = 2.54 (in)
Height Class	m = 0.3048 (ft)
Nutrient Yields	MKcal per hectare = 2.471 (MKcal per acre)
Plot Size, Quadrats	0.0004 hectare = 1 milacre
Production	Kg per hectare = 1.1208 (lb per acre)
Stocking	number per hectare = 2.471 (number per acre)

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