Growth and Nonstructural Carbohydrate Content of Southern Browse Species as Influenced by Light Intensity

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Abstract

Three species of palatable deer browse (flowering dogwood, yaupon, and Japanese honeysuckle) were grown under 3 levels of light intensity: 100, 45, and 8% of full sunlight. After 4 growing seasons, dogwood and yaupon under 45% light were significantly taller, contained more growing points, and produced a larger foliar, stem, and root biomass than plants under other light regimes. Twig growth and biomass were generally poorest in full sunlight, whereas foliar and root biomass were poorest in deep shade. Leaves of all species were smallest on plants in full sunlight. The dry weight per unit of leaf area and the concentration of total nonstructural carbohydrates in leaves declined for all species as light intensity declined.

Of the environmental parameters affecting the growth of deer and livestock forage in the understory of forest stands, light is generally recognized as the most influential. With sufficient understanding of the influence of light on the survival, growth, and regeneration of palatable forages, silvicultural guidelines can be developed for objectively sustaining desirable light intensities in the understory with the least infringement on wood production. Currently, the production of forage is little more than a chance by-product of stand silvics.

The research reported here explored the effects of 3 levels of light intensity on the leaf, stem, and root growth and the total nonstructural carbohydrate levels in the leaves of 3 species of palatable deer browse that commonly occur in the understory of southern pine-hardwood forests. Data were collected from 1974 through 1977 in conjunction with a study evaluating the influence of light intensity on the nutrient quality and digestibility of browse leaves (Blair et al. 1982, unpublished manuscript).

Study Area and Methods

The study was conducted within the loblolly-shortleaf pine forest type on the Stephen F. Austin Experimental Forest near Nacogdoches, Texas. The principal tree species in the forest type are loblolly pine *(Pinus taeda)* and shortleaf pine *(Pinus echinata)* in association with assorted hardwoods. Characteristically, stands consist of a multitiered midstory of pines, hardwoods, and shrubs beneath a pine-hardwood overstory. The stand structure and composition generally result in heavy shading in the forage stratum.

The open and relatively flat study site supports well-drained sandy loam soils with a heavy clay subsoil. The soils are acid in reaction and contain moderate amounts of organic matter and natural plant nutrients.

Summers are hot and humid and winters are generally mild. The frost-free season averages about 243 days from mid-March to mid-November. A mean annual precipitation of 122 cm is generally well distributed throughout the year.

Spring growth of woody plants begins in late March or early April and twig elongation is nearly completed on most species in June (Halls and Alcaniz 1965). Limited growth also occurs on some species following summer rains, particularly after a prolonged dry spell, and on some broadleaf evergreens during warm winter periods.

The study site was plowed and leveled to reduce competing vegetation and 127.3- by 26.5-m plots were established in a 3 treatment by 4 replication design, each separated by a 15-m buffer.

Light intensities of 100, 45, and 8% of full sunlight were randomly assigned to treatment plots. Each intensity was replicated 4 times in a completely randomized design. For treatments designated as less than full sun, polypropylene fabric, woven to provide the prescribed light reduction was placed over a 2.4-m high wood frame covering each treatment plot. The bottom 0.3 m on the sides and the top 1.0 m on the end walls were left open to facilitate air movement. Light entry at the upper end-wall openings was controlled by a fabric-covered overhang. Shading was placed over the frames immediately before planting.

Browse species studied were flowering dogwood *(Cornus florida)*, a deciduous small tree, and yaupon *(Ilex vomitoria)*, a broadleaf evergreen shrub, both endemic, and Japanese honeysuckle *(Lonicera japonica)*, a common and widespread vine of Asiatic origin that is generally evergreen in the Gulf Coast Plain. These species are considered moderate in shade tolerance, with flowering dogwood the most tolerant. Dogwood and yaupon plants were 2-year-old container-grown nursery stock and honeysuckle plants consisted of young rooted leaders lifted from an extensive open area adjacent to the study site.

In February 1974, 1 16-plant row of each species was outplanted on each treatment plot. Species row assignments were random. Plants were spaced 1.5 m within a row and 2.4 m between rows. The long axes of plots were oriented northeast by southwest so all plants would receive approximately equal exposure to solar radiation. Honeysuckle growth was supported on 1-m high woven-wire trellises extending the full length of each row.

To eliminate gross differences in soil moisture, gypsum soil blocks were buried on each plot and water needs were monitored by periodic readings with a Bouyoucos soil moisture meter. Water was applied when a meter readout dropped to 45% available soil moisture at either a 6- or 12-inch depth. More frequent water was needed on plots in full sunlight and under 45% light than on plots under 8% light.

Plants used for growth measurements and chemical determinations were randomly selected. Beginning in the spring of 1976, after plants had grown 2 years under their prescribed light regime, and again in 1977, leaf samples were collected at mid-month of April, May, June, July, August, September, and December, to evaluate differences in the content of total nonstructural carbohydrates. Current leaf tissues were collected only from the terminal 10.2 cm or less of dogwood and yaupon twigs and 20.4 cm or less of honeysuckle leaders. Each month the leaf sample was obtained

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from 1 plant within a species row and individual plants were sampled only once yearly. Samples were collected between 10:00 a.m. and 2:00 p.m. to minimize diurnal fluctuations in sugar content of the cell sap.

Excised samples were immediately dried to a constant weight in a forced-draft oven at 60° C, ground in a Wiley mill to pass a 1 mm screen, and temporarily stored in a freezer. All leaf tissues were analyzed for total nonstructural carbohydrate (TNC) by the Agronomy Department, Virginia Polytechnic Institute and State University, Blacksburg. Determinations were according to procedures described by Wolf and Ellmore (1975). Reported TNC values are averages of the 1976 and 1977 measurements.

In September 1976 and 1977, 10 leaves of flowering dogwood, 15 of honeysuckle, and 20 of yaupon were collected from 1 plant per species on each treatment plot to determine the area and weight of the average size leaf. Selection of sample leaves was based on what appeared to be the typical size for the plant. Excised leaves were temporarily affixed, by species, to a paper backing then photocopied to obtain leaf imprints. The area of each imprinted leaf blade was determined by a polar planimeter. After imprinting, leaf samples were dried at 100° C in weighing bottles, desiccated until cool, then weighed to the nearest 0.1 mg. Leaf area and weight data were averaged for the 2 years.

In September 1974, 1975, and 1977, after 1, 2, and 4 growing seasons, respectively, under the prescribed light regimes the total height growth and the number of growing points (twig tips) were determined on 3 plants of dogwood and yaupon on each treatment plot. In addition, the total linear growth of current twigs was measured on these plants in 1977. In late October 1977, prior to leaf abscission, all leaves were collected from 1 plant of dogwood and 1 of yaupon on 1 random plot of each light treatment. Leaves were oven-dried to constant weight at 100° C to derive total leaf biomass. During early December 1977 the root systems of these 3 plants of each species were extracted from the ground using a hydrolic water procedure. The maximum diameter of the crown and root system was determined for each extracted plant, after which plants were fractioned into current stems, old wood, and roots. Each root system was dried at 60° C, and ground through the 1-mm screen of a Wiley mill, after which a weighed subsampled was removed for a total nonstructural carbohydrate determination. The remaining root and wood fractions were oven-dried to constant weight at 100° C.

For honeysuckle only total leaf growth was collected from 1 plant of each treatment as the intertwining leaders could not be removed from the wire trellises and the linear growth measured.

From mid-March through mid-November during measurement years, the maximum, minimum, and ambient air temperatures, soil temperature, and relative humidity were determined biweekly on 1 random plot of each light regime. Air temperatures were taken at 76 cm and relative humidity was taken at about 122 cm above ground. Soil temperature was measured by a probe thermometer inserted 7.6 cm below the surface at 2 points per plot.

Growth and nonstructural carbohydrate data were subjected to variance analyses to evaluate differences due to light intensity and to test changes in carbohydrate content of leaves across time. When significant differences among treatments occurred, means were compared by Duncan's multiple range test. Testing was at the $P<0.05$ level.

Results

Environment

Except for differences in light intensity, the microclimate and phenological development of species varied little between treatments. The average maximum and ambient air temperatures increased slightly with an increase in light intensity. Minimum temperatures tended to be inverse to the light level. The mean differential, however, for maximum and minimum temperatures between treatments did not exceed 3.5° C while ambient temperature did not differ more than 2° C. Differences in mid-day relative humidity between plots in full sun and those with only 8% light averaged less than 5 percentage units.

Soil temperature at a depth of 7.6 cm averaged 3.6° C cooler under 45% light and 4.8° C cooler under 8% light than soils exposed to full sunlight. The retention of soil moisture following rain or manual watering was inverse to light intensity.

Plant Growth

The phenological development of species varied little between light regimes. Twig elongation and refoliation began in the open and under 45% light at about the same time in late March, but was initiated 5 to 7 days later under 8% light. Tissue maturation and the cessation of twig growth was nearly completed in late May on plants in the open and under moderate light, whereas, growth continued an additional 7 to 10 days under low light.

In late autumn, dogwoods growing in 45% light retained at least half their leaf biomass up to 2 weeks after open-grown plants lost all leaves. Plants growing in only 8% light retained about half their leaves up to 3 1/2 weeks after leaves abscised from plants in the open. Some fresh leaves persisted to midwinter.

Plant growth form and vigor of all species differed noticeably between light treatments. Under 45% light, plants were more robust in growth form and appeared more vigorous than those in full sunlight or under 8% light. Honeysuckle plants appeared to be severely stressed after about 2 years growth under the low light level. Even though new leaders were initiated each spring a portion of the current leaf crop would turn yellow and abscise as the growth flush matured. Leaders would subsequently die back several cm. At the low level of light, plants were apparently unable to produce

Table 1. Variation[1] in the growth characteristics of plants grown under 3 levels of light for 4 years.

		1974			1975			1977		
		Light intensity			Light intensity			Light intensity		
Growth character	Species	100%	45%	8%	100%	45%	8%	100%	45%	8%
Plant height[2] (cm)	Flowering dogwood	79 a	86 a	94 a	132 b	208 a	180 a	173 c	267 a	229 b
	Yaupon	97 a	114 a	117 a	130 b	224 a	211 a	160 c	254 a	234 b
Growing points[2] (no.)	Flowering dogwood	60 a	54 a	57 a	145 b	232 a	195 a	243 c	539 a	319 b
	Yaupon	76 a	80 a	80 a	137 b	240 a	182 a	374 b	1,081 a	434 b
Current stem growth[2] (cm)	Flowering dogwood	—	—	—	—	—	—	1,615 c	6,251 a	3,012 b
	Yaupon	—	—	—	—	—	—	1,011 c	6,424 a	3,076 b
Maximum crown diameter[3] (cm)	Flowering dogwood	—	—	—	—	—	—	79	198	229
	Yaupon	—	—	—	—	—	—	86	218	190
Maximum root diameter[3] (cm)	Flowering dogwood	—	—	—	—	—	—	236	183	99
	Yaupon	—	—	—	—	—	—	163	135	81

[1]Growth values (row) for each year and species followed by a common letter are not significantly different.
[2]Mean of 9 random plants for each light treatment.
[3]One random plant of each species for each light treatment.

Table 2. Size and weight[1] of mature leaves grown under 3 levels of light[2]. Means of leaves collected in 1976 and 1977.

	Flowering dogwood[1]			Yaupon			Japanese honeysuckle		
Light intensity	Area/leaf (cm^2)	Wt/leaf (mg)	Wt/area (mg/cm^2)	Area/leaf (cm^2)	Wt/leaf (mg)	Wt/area (mg/cm^2)	Area/leaf (cm^2)	Wt/leaf (mg)	Wt/area (mg/cm^2)
100%	40.7c	377.1b	9.4a	1.0c	14.2c	13.6a	9.8c	90.2b	9.2a
45%	89.6a	575.8a	6.4b	2.4b	25.4b	10.7b	21.7a	114.5a	5.3b
8%	66.6b	235.6c	3.6c	4.9a	28.6a	5.8c	14.8b	43.5c	3.0c

[1]Oven-dry weight.
[2]Values between light regimes (within a column) followed by the same letter are not statistically different.

sufficient photosynthate for growth and maintenance, hence, above-ground biomass progressively deteriorated.

Changes in the height growth of dogwood and yaupon plants and the number of growing points after 1, 2, and 4 growing seasons under the prescribed light treatments are shown in Table 1. Differences in plant growth between light regimes began to appear the second growing season (1975). Shaded plants were significantly taller and contained more growing points than those in full sun. By the fourth growing season (1977) both dogwood and yaupon plants growing under 45% light were significantly taller and contained a considerably larger number of growing points and more growth of current twigs than plants under other light regimes. Plants in full sun generally displayed the poorest trends in growth response except in 1977 when yaupon plants in full sunlight contained about the same number of growing points as those in 8% light.

In earlier research employing controlled levels of solar radiation, Logan (1965) reported growth responses for white and yellow birch *(Betula papyrifera* and *B. alleghaniensis)* and sugar and silver maple *(Acer saccharum* and *A. saccharinum)* that are closely similar to findings reported here. Phares (1971) also found that the height growth of red oak *(Quercus rubra)* seedlings was greater under a median light intensity (30%) than under full sun or low light (10%).

In this study the maximum crown diameter of plants in reduced light was over twice that of plants in full sun (Table 1). In contrast, the maximum diameter of root systems was larger on open-grown plants than on those in the shade.

Dogwood and honeysuckle leaves were largest on plants grown under 45% light and smallest on plants in full sunlight (Table 2). For example, the area of dogwood leaves was 120% greater in 45% light and 64% greater in 8% light than that of leaves grown in full sunlight. The relationship between the area of dogwood leaves and light intensity was closely similar for honeysuckle leaves. Yaupon leaf area was inverse to light intensity. Leaves which developed in 45% light were 2.4 times greater, and those in 8% light were 4.9 times greater in area than those in the open.

The dry weight per unit of leaf area declined significantly in all species as light intensity declined (Table 2). This illustrated the characteristic tendency for shaded leaves to be larger in size but thinner than those in the sun (Kozlowski 1971). However, shade-adapted leaves usually absorb light more efficiently than sun leaves, which influences their photosynthetic efficiency and their production of photosynthates (Kramer and Kozlowski 1960).

Foliar, stem, and root biomass tended to be substantially greater for dogwood and yaupon plants grown under 45% light than for plants grown at other light levels (Table 3). Plants in low light produced the least dry-matter weight of current leaves and roots while plants in full sunlight produced the least weight of current and old stem tissues. Leaf biomass on honeysuckle grown in full sunlight was 63% greater than that in 45% light and 1,517% greater than in 8% light.

Both the root/leaf and root/stem ratios were higher for dogwood plants in full sunlight than those in reduced light (Table 3). Ratios were similar for yaupon plants growing in the open and under 45% light but higher than for plants in 8% light.

Total Nonstructural Carbohydrates

The TNC concentration in leaves provides a comparative measure between light regimes of the products of current photosynthesis. When newly expanded leaves begin to produce carbohydrates they first use the products for their own growth and eventually export carbohydrates for growth to subtending internodes and other tissues (Kozlowski 1971).

From April to December TNC levels were highest for all species in leaves grown in full sunlight (Table 4). The concentration declined significantly as the intensity of light declined. With the maturing of tissues between mid-May and mid-June, TNC declined considerably in open-grown leaves. In leaves grown under reduced light the levels generally changed little during this period. The second sizeable change in TNC concentration occurred from late summer (September) to winter (December). The evergreen leaves of yaupon and honeysuckle contained substantially more TNC in winter than they did in late summer, whereas, the abscised and weathered leaves of dogwood contained considerably less TNC in winter than did the fresh leaves in late summer.

Table 3. Oven-dry biomass (g) of plant fractions[1] and the weight ratios between fractions after 4 growing seasons under different levels of light.

	Species and light intensity								
	Flowering dogwood			Yaupon			Japanese honeysuckle		
Plant fraction	100%	45%	8%	100%	45%	8%	100%	45%	8%
Current leaves	271	821	209	82	275	64	776	476	48
Previous year's leaves	—	—	—	17	149	132	—	—	—
Current stems	77	264	86	32	104	47	—	—	—
Old wood	736	1,892	870	327	1,512	698	—	—	—
Total above ground biomass	1,084	2,977	1,165	458	2,040	941	—	—	—
Roots	928	1,334	303	136	605	112	—	—	—
Root/leaf[2] ratio	3.4	1.6	1.4	1.4	1.4	0.6	—	—	—
Root/stem[3] ratio	12.1	5.1	3.5	4.2	5.8	2.4	—	—	—

[1]Based on 1 random plant of each species from each light treatment collected in 1977.
[2]Total leaves present on each plant.
[3]Current stems.

Table 4. Variations in the total nonstructural carbohydrate content (% of oven-dry tissue) of browse leaves grown under 3 levels of light in east Texas[1].

Species	% Light	Apr.	May	June	July	Aug.	Sept.	Dec.
Flowering dogwood	100	24.1 a	24.4 a	21.9 a	23.8 a	20.8 a	20.0 a	17.8 a
	45	18.2 b	18.9 b	18.2 b	17.2 b	15.5 b	16.4 b	14.9 b
	8	7.3 c	9.0 c	8.0 c	8.8 c	10.1 c	12.5 c	9.9 c
Yaupon	100	20.3 a	21.2 a	17.9 a	18.4 a	17.2 a	19.0 a	26.0 a
	45	15.7 b	15.4 b	13.8 b	16.2 b	15.4 b	14.9 b	23.0 b
	8	6.8 c	6.6 c	7.6 c	12.7 c	10.6 c	10.1 c	18.7 c
Japanese honeysuckle	100	25.0 a	23.6 a	20.6 a	18.4 a	18.6 a	21.4 a	25.0 a
	45	16.0 b	17.2 b	15.4 b	13.3. b	14.7 b	14.4 b	20.9 b
	8	10.7 c	11.4 c	11.6 c	10.3 c	10.4 c	9.4 c	15.7 c

[1]Values for each species and month combination (column) followed by a common letter do not differ statistically.

Based on one random plant from each light treatment in December, the TNC concentration in roots of dogwood and yaupon tended to decline as light intensity declined. Dogwood roots contained 16.0%, 15.5%, and 11.7% TNC under the respective light regimes of 100, 45, and 8% of full sunlight and yaupon roots contained 14.3%, 13.2%, and 11.7% for the respective light intensities.

Discussion

If a vigorous community of palatable deer browse is to be sustained beneath a forest stand, the stand must be managed in a manner that provides moderate to high light transmission to the understory. At best, average light intensity beneath an established stand would probably be no higher than 40 to 50% of full sunlight. Kramer and Kozlowski (1979) note that light transmission to the forest floor decreases rapidly as tree crown cover increases up to about 35%, but with further increase in crown cover light transmission decreases more slowly. Obviously, light available to the understory forage community would vary considerably with the age, structure, and botanical composition of the stand; illumination stands it may be as low as 1 to 5% of that in the open. Light levels of Light penetration is generally less in hardwood than in pine stands and decreases in pine stands as the hardwood component increases. For illustration, Kramer and Kozlowski (1979) noted that under open crowned, even-aged pine stands illumination at the forest floor may be only 10 to 15% of full sun and in hardwood stands it may as low as 1 to 5% of that in the open. Light levels of this low magnitude are not conducive to the sustained growth of palatable forage for deer and other herbivores. Shirley (1929) concluded that low light intensities in forests, which often do not exceed 20% of full sun, could support growth for a limited period but illumination is too low to ensure survival because root development is poor, and food reserves are inadequately assimilated. Vegetation beneath a forest canopy tends to disappear at light intensities below 4% of full sunlight (Shirley 1945).

After 4 growing seasons in deep shade, where the light intensity was only 8%, the height and twig growth of both dogwood and yaupon generally exceeded that of plants in the open, yet root biomass was comparatively low. Of further significance, the production of nonstructural carbohydrates was substantially less throughout the year in deep shaded leaves than in leaves grown under 45% to 100% full sunlight.

Total nonstructural carbohydrates, often referred to as total available carbohydrates, include all carbohydrates that can be used either directly or indirectly as a source of energy or as building material in the plant once they are broken down by enzymes. In most higher green plants the greater part of the TNC fraction is composed of sugars, fructosans, dextrin, and starch (Weinmann 1947). These water soluble carbohydrates are the primary source of energy readily available to plants for maintenance of vigor for survival, and for the production of new tissues.

The limited root systems that occurred on plants in deep shade were probably due to the fact that plants were unable to manufacture enough food to grow sufficiently extensive root systems for the absorption of adequate water and minerals during periods of deficient soil moisture (Kramer and Decker 1944). Adequate soil moisture was provided in this study and this undoubtedly minimized the stress of an unbalanced low root/shoot ratio in 8% light. In a natural and competitive forest community many plants with such low root/shoot ratios would probably die back, in part or in total, during periods of low soil moisture in the summer. Further, with the low root/shoot ratios evident for dogwood and yaupon growing in only 8% light, one can question how long the plants could have sustained growth even with adequate water. Honeysuckle was unable to sustain current growth after only 2 years in the low light intensity. Concurrent with tissue maturation in early summer a portion of the leaf biomass turned yellow and abscised, after which several inches of current leader growth died back each year.

The ratio between the water- and mineral-absorbing surface (roots) and the transpiring and photosynthetic surface (leaves) of a plant is an important factor in the growth of woody forages. A small root system limits shoot and leaf growth by curtailing the supply of water and minerals to the top, while reduction in the photosynthetic surface limits growth of roots by curtailing their supply of carbohydrates (Kramer and Kozlowski 1979). In general, this interaction, when in balance, tends to maintain a reasonably efficient ratio of roots to shoots, but desirable ratios can be disturbed by unfavorable factors such as the progressive loss of understory light in a forest stand.

Not only is a moderate to high intensity beneficial to the sustained growth of palatable browse forages in the understory, but, of equal importance, high light transmission appears to significantly enhance many of the desirable nutrient characteristics of forages. Leaf tissues of flowering dogwood, yaupon, and Japanese honeysuckle plants grown under 45% and 100% of full sunlight contained substantially higher levels of highly digestible cell solubles, digestible energy, and digestible dry matter in conjunction with lower levels of fibrous cell wall fractions than plants grown under 8% light (Blair et al. 1982, unpublished manuscript). Reduced light transmission, however, favored increases in the content of crude protein and phosphorus.

It is hoped that further studies will be undertaken to evaluate the influence of light on the growth and nutrient quality of other important forages in southern forests and to determine the light intensity that is associated with timber stands of different structure and composition. From the amassed findings, prediction equations can be developed by resource managers for estimating the quantity and quality of forages that can be sustained in the understory of different forest communities.

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