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BLACK ROCK FOREST PAPERS

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DIFFERENTIAL BROWSING BY DEER ON PLOTS VARIOUSLY FERTILIZED

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During the course of fertilization experiments in a forty-year-old stand of mixed hardwoods on the Black Rock Forest it was observed that the preference of deer for plants of the same species varied widely with the quantity and type of fertilizer that had been applied to the soil. Quarter-acre sample plots fertilized with varying amounts of either rock phosphate or muriate of potash showed no unusual deer browsing. But some striking differences were noted between control areas and plots fertilized with varying amounts of nitrogen. The several fertilizer series offered excellent material to study the chemical or physical reasons for differential browsing. This is a subject of considerable interest, for of the many scientific food-habits researches that have been conducted, all include data as to what plant species are browsed, but usually no information as to the underlying causes for the observed preferences. The data presented in this report are discussed with special reference to the reasons why deer apparently relish browse of a certain type on one site but almost completely ignore the same species growing on others.

Plots of the several fertilizer series were laid out along a uniform slope on the Black Rock Forest. Soil, forest type and other physical and chemical characteristics have been previously described (Mitchell, 1935; Mitchell and Finn, 1935). The nitrogen series, which is the most interesting from the deer browsing standpoint, consisted of four quarter-acre plots separated from each other and from plots of the other series by generous isolation strips. One plot, the N 0 (zero), was left untreated as a control and the others were supplied varying amounts of nitrogen as an equal mixture of commercial nitrate of soda (16% N) and sulphate of ammonia (20% N). The treated plots are numbered according to the "units of N mix" applied, on an acre basis, *i.e.*, N 0, N 1, N 2, and N 3. This is an arbitrary unit equivalent to 1,600 lbs. of the mixture.

Fertilizer was applied May 14, 1935, and the effects of abruptly increased nitrogen supply were, as is usually the case, soon apparent in the various plants. The high soil nitrogen concentrations resulted in the defoliation or killing (probably due to plasmolysis) of many of the ground cover plants and shrubs on the N 1 plot, and practically all of those on the N 2 and N 3 plots. About a month later the plants on the N 1, 2 and 3 plots began to revive. Either leaching caused the nitrogen concentration in the upper soil horizons to be reduced to a favorable level or the plants became accustomed to the high nitrogen supplies. In any event the contrast between the control areas and the nitrogen fertilized plots soon became very striking. The stimulating effect of nitrogen was apparent in the dark green color of the luxuriant foliage produced by shrubs and herbaceous plants of the treated plots. Boundaries of these plots could be easily picked out on the basis of leaf color and size (Figs. 1 and 2; Table 1, col. 11). About this time a herd of white-tailed deer (*Odocoileus virginianus*) began using the foliage of the nitrogen treated plots as a source of food. Browsing was heavy and the ground was littered with droppings. At the borders of these plots browsing practically ceased as though an invisible fence were present. The control plot (N 0), isolation areas, and plots of the potassium and phosphorus series showed no unusual browsing.

In early September a tally was made of the amount (frequency) and intensity of browsing on the nitrogen series plots and the bordering isolation strips. The most abundant species heavily browsed was the flowering dogwood (*Cornus florida*) so this species was used for comparing browsing on the various plots. The results of this tally are shown in Fig. 1 (data from Table 1, cols. 2-7). Frequency of browsing is expressed as a percentage of the total number of dogwoods examined on each plot. Intensity of browsing (light, medium or heavy, according to an estimate of the number of tips removed) is also expressed as a percentage of the number examined.

It will be observed (Fig. 1) that the frequency of browsing increased from 3.6% on the control areas to 80.7% on the N 1 plot. This increase is sufficiently great to be considered highly significant. But it is apparent that the amount of browsing did not continue to increase with further nitrogen applications. In fact both the frequency and intensity of browsing were less on the N 2 plot than on either the N 1 or the N 3 plot. But these variations in the frequency and intensity of browsing on the fertilized plots are relatively small, show no consistent trends and may have been due to chance, or to insufficient sampling. For this reason the observed differences are of questionable significance. It is quite possible that deer consumed foliage from all fertilized plots with equal relish.

Why deer preferred to graze this particular set of plots was not easy to guess. There were several possibilities: leaves of plants on the nitrogen fertilized plots were larger, greener, and had a higher reducing sugar [2]

[1] Joint contribution from the Black Rock Forest and the Harvard Forest.

[2] Leaf samples were dried at a temperature of + 70° C. immediately after collection, and were kept in the oven until analyzed. Thus it is exceedingly doubtful if the sugars were altered by enzymatic action during the storage period before analysis. Most enzymes, if in solution (as in a fresh leaf) are inactivated or "killed" at temperatures of + 60° C. or over. Even though a temperature of + 70° C. may not inactivate all enzymes, a dry environment precludes their action (Gortner, 1929, p. 712).

The procedure given in Official and Tentative Methods of Analysis (A. O. A. C., 1930, p. 112) was used to determine reducing sugars. Because of the aldehyde or ketone group the monosaccharides and some other sugars are reducing agents. The hexose sugars, glucose and fructose, since they are common as such in plants, are probably the most important, and make up the greatest bulk of the monosaccharides included in the analyses. The disaccharide, maltose, since it also is a reducing sugar, would be included in the determinations. This sugar is found widely distributed in plant tissues although in small amounts. But sucrose, the most common and widely distributed disaccharide, would not be included because, like most disaccharides, it has no reducing properties. In the method of analysis followed, the disaccharides and polysaccharides (pentosans, hexosans, etc.) were not hydrolyzed to form their component monosaccharides,

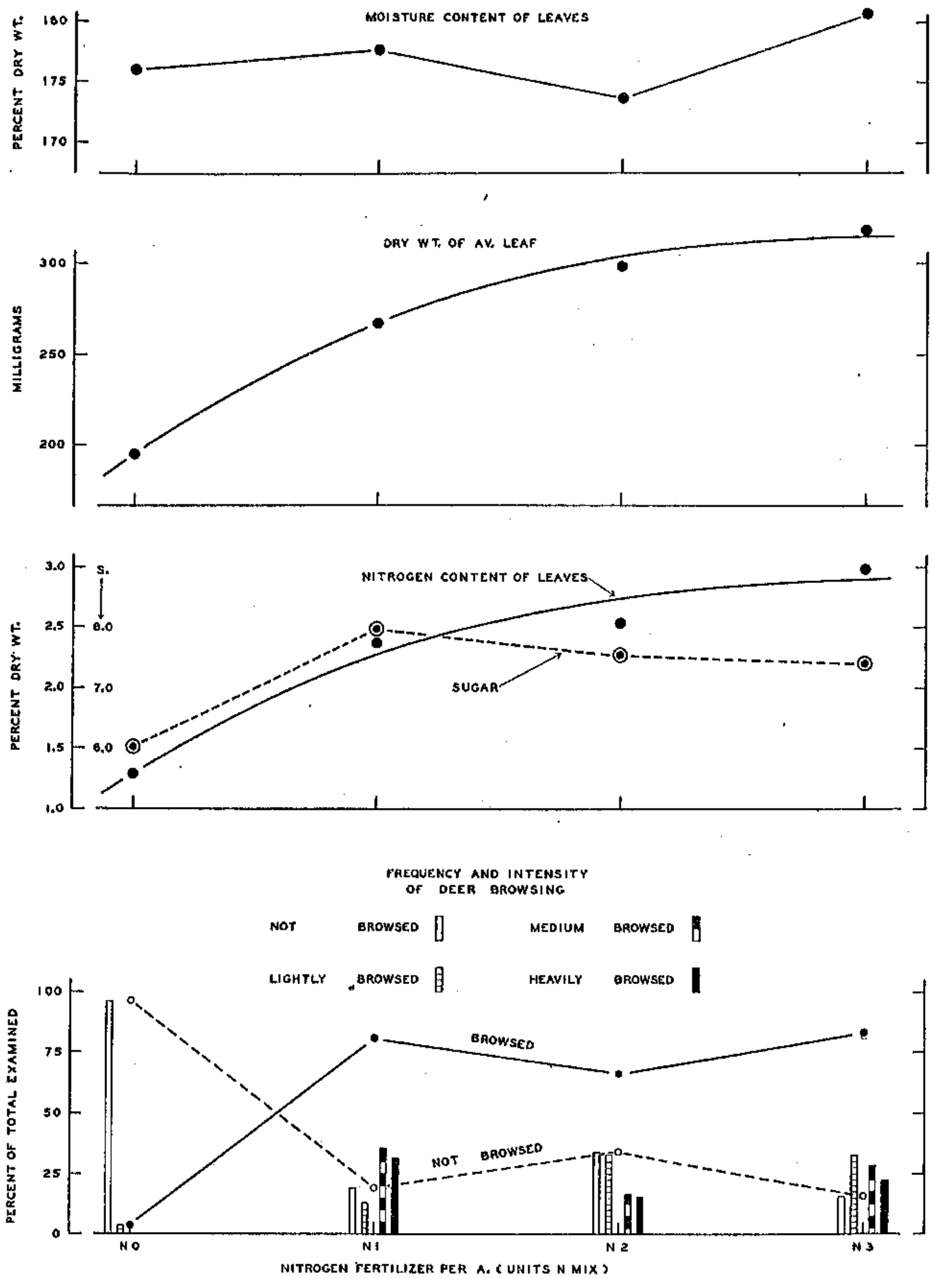

FIG. 1.—Frequency and intensity of deer browsing compared with trends in the dry weight, moisture, nitrogen and reducing sugar content of the leaves of dogwoods supplied various quantities of nitrogen fertilizer.

and nitrogen content than those of the control areas. They also appeared more succulent. However, the factor of succulence was soon eliminated, as a moisture analysis (Fig. 1; Table 1, col. 8) showed no significant differences in the water content of leaves from the various plots.

The individual leaves obviously increased in dry matter (Fig. 1) and surface area (silhouettes in Fig. 2) with increments in nitrogen supply. However, if either of these factors is important, the amount of browsing should have been significantly greater on the N 3 plot. But, according to the tally, such was not the case. There remains, though, another way to evaluate browsing. Due to the difference in size of individual leaves it is possible that a greater total mass of foliage was consumed from the N 3 plot than from either of the other treated areas. This suggests that the deer preferred large leaves—provided, of course, that the weight of foliage consumed can be considered an index to preference. But, if leaf size were the chief attraction, one would expect the frequency of browsing, as well as the total leaf weight consumed, to be greater on the plots with the higher N supplies. As pointed out above, this was not true. And if the deer were searching out large leaves, it is difficult to account for the fact that on the N 3 plot, which had the largest leaves, 16.3% of the dogwoods examined were untouched. The percentage of unbrowsed dogwoods on the N 1 and N 2 plots was not significantly higher. Deer were probably attracted to foliage of the fertilized plots by some factor other than leaf size.

Color is another factor that must be considered. The work along this line with birds, small animals, and particularly bees, indicates that some species distinguish various colors and show marked preferences. The color of dogwood leaves varied from a light yellow-green on the control plot to a deep blue-green on the N 3 plot. Although the change was most abrupt between the N 0 and N 1 plots, there was a gradual increase in deepness of blue-green leaf color between the N 1 and N 3 plots. However, since the leaf color variations on the fertilized plots were unaccompanied by differences in the frequency of browsing, the correlation is doubtful.

The application of one unit of nitrogen fertilizer resulted in a marked increase in the nitrogen content of the leaves and in the amount of browsing. But, as with leaf area and weight, the correlation does not seem to hold true for the entire fertilizer series. Further increments in N supply, and therefore the N content of the

which are reducing agents. However, Chandler and Mason (1933) have shown that sucrose usually makes up only a small part of the total sugar content of leaves. Pentosans, since they are found chiefly in the stems and seed coats of plants, are of no significance to this study. As the problem of differential browsing probably involves palatability, starches and cellulose, common in the leaves of all plants, are of doubtful importance.

leaves, were not accompanied by proportionate increases in the frequency or intensity of browsing.

It is true that, because of increased leaf weight, a larger total mass of foliage may have been removed from the N 3 plot. This, of course, suggests a correlation between browsing and the concentration of nitrogen, reducing sugars or some other substance in the leaves. But the existence of any such relation is difficult to either prove or disprove, since no data are available on the quantity of leaves consumed on the various plots. However, even if such data were available, it is believed that estimates of the total foliage consumed by deer are doubtful indicators of preference. If deer were attracted by the odor or taste of some substance, it is quite reasonable to believe that their preference would vary with the concentration, in the leaves, of the attracting substance, and that the size or weight of the leaves—assuming they tasted and smelled the same—would be incidental. For this reason a measure such as browsing frequency (percentage of the number of dogwoods browsed), is probably a better index to preference than the weight of foliage consumed. As pointed out above, there were no significant differences or consistent trends in the frequency or intensity of browsing on the fertilized plots. Thus it is exceedingly doubtful if deer preferred foliage of the nitrogen treated plots because of either the taste or odor of increased amounts of nitrogenous substances.

Trends in the reducing sugar content of the leaves seemed to follow very closely variations in the amount of browsing and, to some extent, the intensity of browsing (Fig. 1). On the basis of the data presented it appears that relatively high internal (leaf) nitrogen concentrations affect, either directly or indirectly, the metabolism of leaves in such a way as to stimulate sugar synthesis. An external supply of nitrogen, equivalent, in effect, to one unit of the "N mix," plus the unknown amount of this element supplied by the soil, apparently produced in dogwood leaves an internal N concentration of about 2.36% (on a dry wt. basis). This internal N concentration seems to be at or near the optimum for sugar synthesis per unit of leaf mass, since, as the data suggest, further increments of N resulted in somewhat lower sugar concentrations.

It will be observed that the intensity of browsing was, according to the tally, greatest on the plot (N 1) with the highest reducing sugar concentration. However, since the differences are relatively small, this may or may not be significant. But it is quite apparent that the frequency of browsing—probably the best index to preference—is more closely correlated with the reducing sugar concentration of the dogwood leaves than with the nitrogen content or any of the physical factors studied.

Why a wild animal shows a preference for a certain food is a question about which little is known. The higher mammals undoubtedly have a good sense of taste, but any ideas on the reasons for preferences are apt to be falsely colored by the tendency to assign human characteristics to other species. The danger in this and and the need for study of each species is evidenced by the fondness of the black bear (*Ursus americanus*) for the root of the Indian turnip (*Arisaema triphyllum*) which contains acid crystals that cause a violent burning sensation in the human mouth. Of course, cases of use of a plant by one species which is poisonous to others are common. The white-tailed deer eats the leaves and twigs of poison ivy (*Rhus toxicodendron*) with no apparent ill effects. As Leopold (1933, p. 253) says, "Experience, however, tells us little or nothing about WHY certain foods are eaten or rejected, or what rôle the various foods play in sustenance or reproduction of the species. Even the most scientific food-habits research tells us WHAT has been eaten, but not always how much, and never for what reason." However, when, as in this case, a mammal rejects the browse of a single species where the plants have been untreated or treated with either phosphorus or potassium and especially relishes that where the plants were fed nitrogen, it seems logical to suppose that either the nitrogen content or the content of some other compound influenced by increasing available nitrogen must be the cause.

Since the reducing sugar concentration of the leaves increased with increasing nitrogen supply up to a cer-

Table 1

The dry weight, moisture, nitrogen and reducing sugar content, and the frequency and intensity of deer browsing, of the leaves of dogwoods supplied various quantities of nitrogen fertilizer.

Plot No.[1]	Number of Dogwoods Examined	Amount of Browsing (Per Cent): Not Browsed	Browsed: Lightly	Browsed: Medium	Browsed: Heavily	Browsed: Total	Moisture[2] Content of Leaves as % Dry Wt.	Nitrogen[2] Content of Leaves as % Dry Wt.	Reducing Sugars[2] in Leaves as % Dry Wt.	Dry Wt.[2] of Av. Leaf in Mg.
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
N 0	84	96.4	3.6	....	....	3.6	176.6	1.288	6.03	194.0
N 1	31	19.3	12.9	35.5	32.3	80.7	177.7	2.362	7.96	267.0
N 2	100	34.0	33.0	17.0	16.0	66.0	173.5	2.521	7.52	298.0
N 3	49	16.3	32.7	28.6	22.4	83.7	181.9	2.983	7.40	318.0

[1] Plots are numbered according to the units of "N mix." applied (*on an acre basis*). These are arbitrary units of an equal mixture (by weight) of commercial nitrate of soda (16% N) and sulphate of ammonia (20% N). One unit is equivalent to 1,600 lbs. of this mixture.

[2] Leaf samples were taken from a majority of the dogwoods on each plot. Dry weights, nitrogen, sugar and moisture content values presented in the table are means of individual determinations.

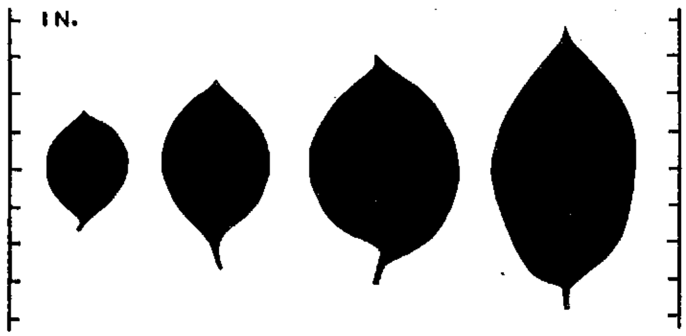

FIG. 2.—Silhouettes showing increases in the surface area of leaves from dogwoods fertilized with (left to right) 0, 1, 2 and 3 units of the nitrogen mixture.

tain point, above which the frequency and intensity of browsing appeared to follow the sugar content more closely than that of nitrogen, reducing sugars are suggested as the cause of the preference. This agrees with the experiments of Rensch (1925) who found that birds were attracted to cane sugar solutions and repelled by sour, salt and, to a lesser extent, bitter ones. The present experiment tends to explain the strong liking exhibited by deer for the browse on recent cuttings. There the nitrogen availability, due largely to the stimulating effect of increased temperature on microbiological activity, has been shown (Griffith, Hartwell and Shaw, 1930) to be considerably greater than in a growing forest.

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