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Effect of Fertilization on Woody Plant Chemistry: The Role in Diet Selection by Goats

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EFFECT OF FERTILIZATION

ON WOODY PLANT CHEMISTRY:

THE ROLE IN DIET SELECTION BY GOATS

by

Amanuel Gobena

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of the requirements for the degree

of

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DEDICATION

I take the opportunity to dedicate this work to my parents. In the midst of poverty they allowed me to leave my herdsman's life to go to school. My brother, who on the death of my father adopted me, sacrificed his own education to raise me and provided for my education. My mother, who ungrudgingly sacrified the necessities of her life, provided me with the kerosene to light the lamp for my study at night in that small hut.

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Amanuel Gobena

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Effect of Fertilization on Woody Plant Chemistry:

The Role in Diet Selection by Goats

by

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Department: Range Science

Lack of forage quantity and quality limit livestock production during the dry season in northeast Brazil. Coppice produced following cutting of tree species in this area has the potential to increase forage quantity and quality during the dry season, because trees that coppice retain green foliage throughout most of the dry season. However, the palatability of coppice is often low.

From a theoretical standpoint, woody plants with inherently slow growth rate should be less palatable to herbivores than plants with inherently fast growth rates, because plants that grow slowly allocate more carbon to compounds such as tannins and resins that reduce palatability. I tested this hypothesis with four tree species (*Mimosa caesalpiniaefolia*, *Croton sonderianus*, *Auxemma oncocalyx*, and *Caesalpinia bracteosa*) growing on both fertile (non-calcic brown) and infertile (lithic) soils. Inherent plant growth rates were determined by growing young plants of all species on both soil types in a greenhouse. Plants were fertilized with NPK (150 or 300 kg/ha) and watered to field capacity. Urea ($(NH_2)_2CO$), diammonium phosphate $(NH_4)_2$ Po_4 and KCL were used as sources of fertilizer. On fertile soils, Mimosa had the highest inherent growth rate, followed by Auxemma, Croton, and Caesalpinia. In pen and field trials, Mimosa was preferred by goats, followed by Auxemma, Croton, and Caesalpinia. Results were similar on infertile soils, but Croton had a higher growth rate than Auxemma, and Croton was preferred to Auxemma by goats. Fertilization with 150 or 300 kg/ha of NPK increased palatability of coppice of all plant species to goats on both fertile (non-calcic brown) and infertile (lithic) soils.

Fertilization affected the chemical and physical characteristics of the four plant species. Concentrations of tannins and lignins decreased as did leaf toughness, while nitrogen, phosphorus, and calcium increased. In vitro organic matter and neutral detergent fiber digestibilities did not change. The prediction that fertilized plants would be lower in carbon based compounds than the unfertilized plants was supported by the results of my study.

(98 pages)

CHAPTER I

INTRODUCTION

Goat and sheep production is one of the dominant economic pursuits for small farmers of northeast Brazil. Productivity of these species remains rudimentary, due to environmental stress, to availability of forages, and to the low palatability and nutritional quality of forages, particularly during the dry season. Pfister (1983) and Kirmse (1984) found nutritional limitations during the dry season; protein (Kirmse 1984), and probably energy, are limiting. They also indicted that leaf litter from trees constitutes a large part of the diets of goats and sheep during the dry season.

Manipulation of woody plant species for increased understory production and increased forage quality has recently received attention (Kirmse et al. 1987a, b, c, Hardesty 1987). Kirmse et al. (1987 a,b,c) indicate that understory production can be enhanced, and that the growth of green forage on trees can be extended throughout the dry season by cutting the woody species. The green forage was produced by trees that coppiced after being cut. However, the palatability of many of the woody species that coppice is low. A concern, therefore, is to improve the palatability of coppice to alleviate nutritional stress and increase livestock production during the dry season.

Ecological studies indicate that during the juvenile stage (e.g. trees that coppice), many woody plants contain high concentrations of compounds such as resins, tannins, and alkaloids that may lower palatability and in a sense defend plants against browsing by herbivores (Bryant et al. 1983). Differences in such metabolites within and among plants may also be due to soil fertility, environmental stress (e.g. lack of nutrients or moisture) and responses to herbivory (Bryant et al. 1983, Gershenzon 1984). Avoidance by herbivores of plants or plant parts caused by such compounds has been observed by several workers (Freeland and Janzen 1974, Levin 1976, Bryant and Kuropat 1980, Provenza and Malechek 1984). It is unclear in many cases, however, which plant substances affect palatability and quality.

Plant palatability is also related to inherent plant growth rate (Bryant et al. 1983, Coley et al. 1985, Grime 1977). Slow growing species that evolved in resource limited environments experience lower levels of herbivory than fast-growing species that occur in resource rich environments. Low resource availability favors slow-growth rates which do not put a high demand on limited resources. Plant species with inherently slow growth rates cannot adequately replace material lost to herbivory, and therefore have a large investment in anti-herbivore defense. For example, species growing in a nutrient-poor environment were less palatable to browsing ruminants such as domestic goats, kudus and impalas, as compared to species growing in a nutrient-rich environment (Cooper and Owen-Smith 1985, Owen-Smith and Cooper 1987a,b). Plants growing in the nutrient-poor environment had higher lignin and condensed tannin concentrations that apparently deterred the herbivores from browsing.

Contemporary ecological theory states that the energetic cost of producing large quantities of carbon-based defensive substances, such as tannins and resins, limits growth of woody plants in infertile soils (Janzen 1974) such as those in northeast Brazil (i.e. production of chemical defenses causes reduced growth rates). However, Bryant et al. (1983) propose an alternative explanation. Carbon-based defenses are relatively inexpensive to produce by plants growing in infertile soils. Rather, nutrients such as nitrogen and phosphorus limit growth. As a result, slow growth rates are the cause rather than the consequence of allocating carbon to defensive chemicals by plants growing on infertile soils.

These alternative hypotheses imply different responses by plants to enhanced mineral nutrition: (1) fertilization will not increase growth at the expense of carbon-based defenses if allocation of carbon to chemical defenses limits plant growth; and (2) fertilization will increase growth rates at the expense of defense if growth is limited by nutrient availability. Fertilizing woody plants growing in nutrient deficient soils, such as those in northeast Brazil, may increase productivity, extend the growth period and reduce levels of secondary metabolites, thereby improving palatability.

This research was designed to study the effects of inherent plant growth rate and fertilization on the productivity and palatability of coppice from four dominant woody species [sabia, (*Mimosa caesalpiniaefolia*), catingueira (*Caesalpinia bracteosa*), pau branco (Auxemma oncocalyx), and marmeleiro (Croton sonderianus)] in northeast Brazil. The primary objectives of this research were:

1. To determine the relative growth rates of these four woody plants.
2. To determine the relative palatability to goats of fertilized and unfertilized plants of each species.
3. To quantify some changes in chemical and physical characteristics of the four species as a result of fertilization.

This dissertation is divided into five interrelated chapters. The first chapter is a general introduction and literature review. Chapter II deals with the relative growth rates of the four woody plants and their relative palatabilities to goats. The focus of Chapter III is to determine the effects of fertilization on production and utilization by goats of each species (Objectives 1, 2 and part of 3). In Chapter IV, leaf chemistry and toughness for the four woody plants are discussed. Chapter V summarizes the results of the research project and provides some recommendations for further research and management of the four woody plant species to increase small ruminant production in caatinga woodlands.

Literature Review

Theoretical Considerations

Woody plant defense strategies may be integrally related to plant adaptation to disturbance and nutrient availability (Janzen 1974, Grime 1977, 1979; Bryant et al. 1983; Coley 1981, 1983; Coley et al. 1985). Woody plants that are adapted to grow on nutrient deficient sites have inherently slow growth rates and should be strongly selected for high levels of chemical defense. This has been observed in arctic tundra (Batzli and Jung 1980; MacLean and Jensen 1985), boreal forests (Bryant and Kuropat 1980; Bryant et al. 1983), neotropical rainforests (Janzen 1974; Coley 1983), African rainforests (McKey et al. 1978; Gartlan et al. 1980) and southern African Savanna (Cooper and Owen-Smith 1985; Owen-Smith and Cooper 1987a, b) and may occur in the semi-arid caatinga of Brazil.

Concentrations of secondary metabolites increase at certain times of the year and under environmental conditions when carbon is present in excess of growth and maintenance requirements (Bryant et al. 1983). Thus, carbon which cannot be invested in growth may be diverted to production of secondary metabolites, which in turn influences patterns of herbivory.

Bryant et al. (1983) predicted that increased feeding by herbivores upon plants fertilized with growth limiting nutrients is a consequence of reduced synthesis of carbon-based secondary plant metabolites such as phenolics or terpenes. Fertilization stimulates both growth (Chapin 1980) and photosynthesis (Mooney and Gulmon 1982). However, the increase in growth is greater than the increase in photosynthesis so that growth demands for carbohydrate exceed carbohydrate supplies (reserves and recent photosynthate) (Chapin 1980). This difference in supply and demand is paid for at the expense of chemical defense, i.e. synthesis of carbon-based chemical defenses declines because of substrate limitation (Bryant et al.

1983). This decline in concentrations of substances such as phenolics or terpenes is presumed to be the primary cause of increased feeding by herbivores upon fertilized woody plants. Results of several studies of plant herbivore interactions in boreal forests (e.g. Bryant and Chapin 1982; Waring et al. 1985; Larsson et al. 1986; Bryant et al. 1987a, b) including use of coppice by mammals such as hares (Bryant 1987) support this hypothesis.

Evidence

The application of fertilizer for increased plant production has been practiced since biblical times (Tisdale et al. 1985), but use has mainly been with agronomic and horticultural crops. The objectives have been mainly limited to increasing production, rather than improving the palatability and nutritional quality of plants. Studies of fertilization on native rangelands suggest that the nutrient content of plants, plant palatability to grazing and browsing animals, and vegetation composition could be improved (Wood and Lindsey 1967, McGinnies 1968, Freyman and Van Ryswyk 1969, Goetz 1969, Carpenter 1971, Dwyer 1971, Anderson 1972, Pieper et al. 1973, Harry and Duncan 1984).

Several authors (Curlin 1962, Gibbens and Pieper 1962, Wood and Lindsey 1967) have summarized the benefits derived from fertilizing browse species on native rangelands: (1) increased cover for game animals, (2) increased nutritive value and palatability of browse species, (3) better distribution of animals, (4) increased reproductive levels and (5) increased quantity and quality of browse species. In spite of the potential importance of fertilization, its routine use on rangelands to increase forage yields and nutritive value is no longer considered economically justifiable. However, fertilization of shrubs and forage trees may have economic potential under tropical conditions, where forage is limited during the dry season (Malechek et al. 1986, Bryant et al. 1987c).

Fertilization increases barking and browsing of lodgepole pine (Pinus contorta) and red pine (Pinus resinosa) by snowshoe hares (Lepus americanus) in North America (Heiberg and White 1951; Sullivan and Sullivan 1982), and Scots pine (P. sylvestris) by mountain hares (Lepus timidus) in Finland (Rousi 1983; Rousi et al. 1987). Loyttyniemi (1982) fertilized young stands of Pinus sylvestris and compared the results to the unfertilized plants. The fertilized trees were browsed more often and browsing was concentrated almost exclusively on current shoots during the two years of investigation. His findings confirmed that nitrogen fertilization can significantly increase the susceptibility of pine plantations to browsing.

There are numerous other reports confirming that nitrogen and phosphorus fertilization increase palatability of plants to herbivores (Miller 1968, Behrend 1973, Ellison 1976, Hewson 1977, Connolly et al. 1980). Schultz et al. (1958) found that crude protein concentrations and palatability of seedlings of wedgeleaf ceanothus (Ceanothus cuneatus), deerbush (Ceanthus integerrimus), chamise (Pandenoslema fasciculatum) and western mountain mahogany (Cercocarpus betuloides) increased as a result of nitrogen fertilization under rangeland conditions. Bayoumi (1975) also found that palatability of sagebrush (Artemisia tridentata) and bitterbrush

(Purshia tridentata) to mule deer (Odocoileus hemionus) increased as a result of fertilizing with nitrogen and phosphorus.

Plant Nutrition

The nutritive value of forage is a consequence of the conditions of plant growth (Van Soest and Wine 1982). These conditions may be grouped into two broad groups: climatic and edaphic factors (McNaughton and Georgiadis 1987). Although we have little control of climate, edaphic factors can be manipulated with existing technology to overcome shortage of feed to increase livestock production. The amount of micro and macro nutrients in the soil has a significant effect on production and chemical composition of plants, which in turn affects animal production.

Nitrogen absorbed by plants in the form of NO_3^- and NH_4^+ plays a role in the formation of proteins and is also an integral part of the chlorophyll molecule (Tisdale et al. 1985). The proper abundance of nitrogen helps the plant to grow vigorously with a dark green color. Its absence can retard the growth rate of plants. Nitrogen also enhances utilization of carbohydrates by plants and the formation of proteins from carbohydrates.

Phosphorus is absorbed by plants in the form of $H_2PO_4^-$ or HPO_4^{2-}, depending upon soil pH (Tisdale et al. 1985). It is one of the macronutrients available in plants, with concentrations of approximately 1000 to 4000 ppm. It's primary role is energy storage and transfer. Energy created from photosynthesis is stored in the phosphate (ATP and ADP) compounds for subsequent use by plants for growth (Glass et al. 1980). In addition, it also plays a role by forming an important structural component of a wide variety of biochemicals: nucleic acids, coenzymes, nucleotides, phosphoproteins, phospholipids and sugar phosphates (Wallingford 1978). Phosphorus is one of the major limiting nutrients in tropical soils. When present, it is often below the rooting zone (Sanchez 1976).

Potassium is another macronutrient needed by plants for growth. Its concentration ranges from 40,000 to 50,000 ppm in plants. Potassium is mainly involved in activation of plant enzymes (Kilmer et al. 1968), osmotic regulation (Brag 1963, Mengel and Kirby 1982), production of high energy phosphate molecules (ATP) (Kilmer et al. 1968), transportation of sugars (Wallingford 1980), nitrogen uptake and protein synthesis (Adams 1961, Smid and Peaslee 1976) and in the synthesis of starch (Wallingford 1980).

Calcium and magnesium are also essential macronutrients absorbed by plants in the form of Ca^{++} and Mg^{++}. Their concentrations in plants usually range between 10,000 to 20,000 ppm and 100,000 to 400,000 ppm, respectively. Calcium helps in cell elongation, division and in the structure and permeability of cell membranes (Jackson and Evans 1962). Magnesium provides the structural component for ribosomes, and activates the formation of polypetide chains of amino acids. It is also important for the synthesis of oils in plants (Sherman 1969).

Sodium is one of the micronutrients needed by C_4 plants. The lack of Na^+ can shift plants from the C_4 to C_3 photosynthetic pathway (Brownell and Crossland 1972). It can partially substitute for K.

Organic matter imparts many important physical and chemical properties to the soil, but it is used in the process. Thus, organic matter must be continually added to the soil. Soil organic matter comes to an equilibrium with the addition and decomposition of vegetation (Pritchett and Fisher 1987).

Study Site

General

The study was conducted in the semi-arid region of northeast Brazil, state of Ceara, about 10 km from the city of Sobral at the Brazilian Federal Agricultural Research Agency, CNPC (Centro National Pesquisa de Caprinos) (Figure 1). It is located at approximately 3.5° south latitude and 41° west longitude. The mean altitude is about 80 m and the landscape is flat to slightly undulating.

The climate of the region is characterized by distinct wet and dry seasons. The rain generally starts in December or January and stops in May or June. The long term average precipitation is about 750 mm. Precipitation on the study sites (2 km apart) was about 1500 mm during the year of this experiment (Table 1).

The mean daily (average of day and night) temperature during the rainy season is about 22°C and during the dry season is about 25°C (Anuario Estatistico do Brazil 1972). Evapotranspiration is higher than precipitation for most months (Queiroz 1985). There is also great variability in relative humidity within a day, from 90 percent in the morning to 25 percent in the afternoon during the dry season.

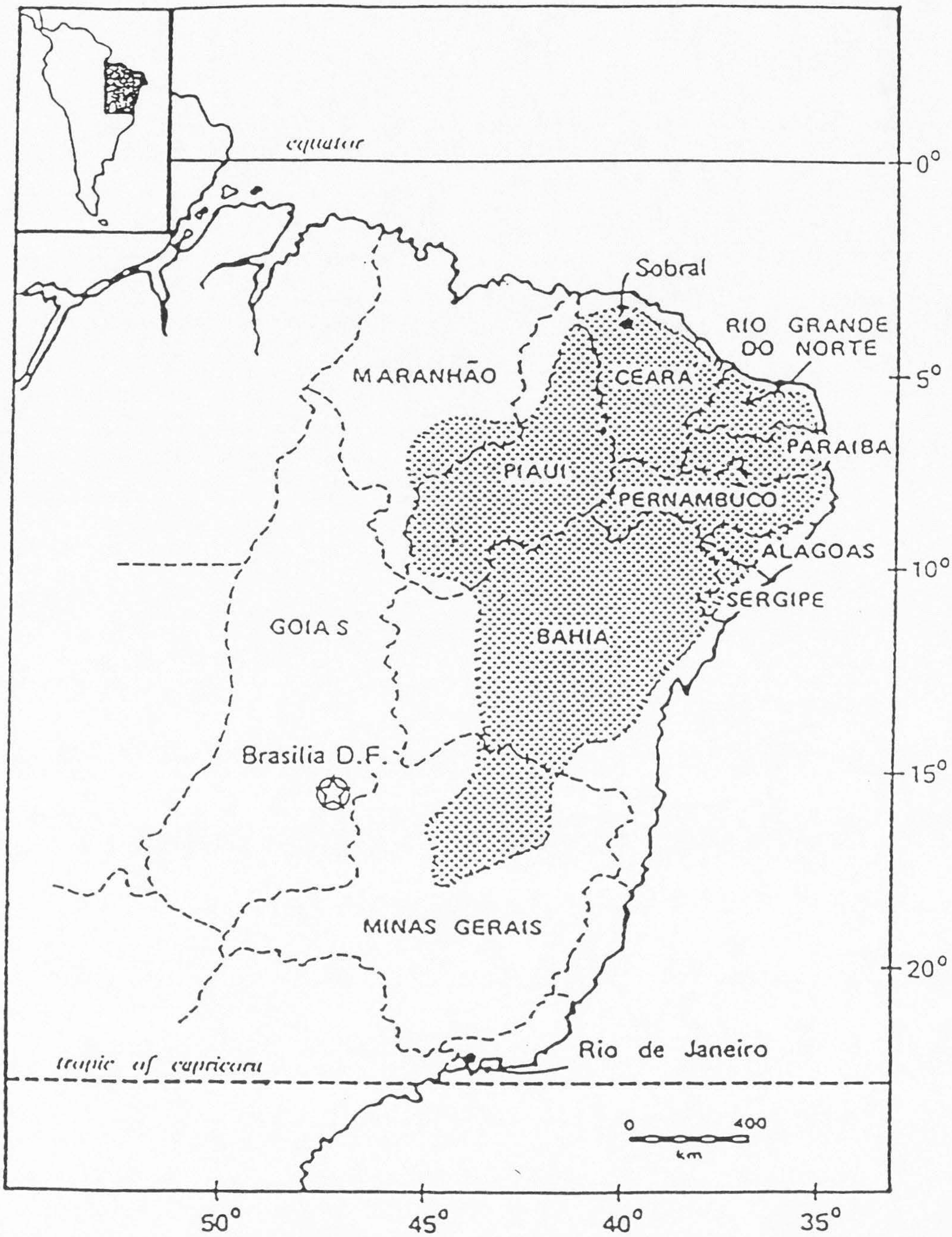


Figure 1. The caatinga vegetation zone (stipled area) of northeastern Brazil (adapted from Mason 1980).

Table 1. Monthly precipitation during 1986 on the non-calcic brown and lithosol study areas in northeast Brazil.

Month	Precipitation (mm)	
	non-calcic brown	lithosol
January	155	141
February	273	294
March	417	376
April	355	348
May	114	111
June	56	61
July	19	19
August	10	8
September	0	0
October	0	0
November	0	0
December	133	130
Total	1532	1488

The two major soil types on the study area are lithosol and non-calcic brown. Lithosols are shallow soils lacking well-expressed pedogenic horizons. Their morphological characteristics are generally related to the kind of parent material. This class of soil is subdivided into two subclasses: eutrophic and dystrophic. These are differentiated by the percent base saturation of the A and AC horizons. The eutrophic lithosol is characterized by base saturation values in excess of 50 percent whereas the dystrophic subclass has values less than 50 percent (Queiroz 1985). The non-calcic brown soil is characterized by having more than 24 cmol (+) kg^{-1} of clay and has more than 50 percent base saturation. It is usually deeper and is often used for cultivation of crops. These two soils can also be differentiated by the kind and amount of vegetation: non-calcic brown soils usually support a more dense and diverse mix of woody species (Queiroz 1985).

Vegetation of the study area is predominantly caatinga (a native word meaning white forest) woodland composed of many plant species (Eiten and Goodland 1979, Ferri 1980, Bucher 1982, Kirmse et al. 1983, Kirmse et al. 1987a,b,c) (Table 2). It includes a wide spectrum of vegetation types from savannah-like to dry deciduous forest intermingled with vines. The understory is primarily annual herbs (Appendix Table 1).

Caatinga vegetation has been classified in several ways based on density and height of the woody strata and understory characteristics (Hayashi and Numata 1976). Queiroz (1985) used cluster analysis and ordination techniques to classify caatinga

Table 2. Major tree species (including seedlings) and their densities in the two types of soils near Sobral, Ceara, Northeast Brazil.

Common Name	Scientific Name	Number per hectare	
		Lithosol	Non-calcic
Paubranco	Auxemma oncocalyx	2979	7722
Marmeleiro	Croton sonderianus	8097	2972
Catinguiera	Caesalpinia bracteosa	1479	542
Sabia	Mimosa caesalpiniaefolia	382	216
Manicoba	Manihot glaziovii	195	35
Juazeiro	Zizyphus joazeiro	49	70
Jurema preta	Mimosa achitistipula	97	0
Pereira	Aspidosperma pirifolian	90	125
Cipor (many spp).	Euphorbia phosphorea	90	570
Pau Darco	Tecoma sp.	7	0
Mofumbu	Combretum leprosum	146	1938
Imburana	Burseara leptophloeus	21	0
Jucazeiro	Caesalpinia ferrea	35	132
Mororo	Bauhinia aculeata	0	389
Freigorge	Cordia alliodora	28	340
Jurema branca	Pithecolobium dumosum	0	21
Aroeira	Astronium urundeura	42	28
Angico	Piptadenia macrocarpa	0	118

woodlands. Several researchers (Schacht 1986, Kirmse et al. 1983, Hayashi and Numata 1976) have described the important woody species and indicate that very few of these species dominate aboveground biomass production (Kirmse et al. 1983, Hayashi and Numata 1976, Schacht 1986).

Plant Species Studied

Auxemma oncocalyx belongs to the Boraginaceae family and is one of the dominant plant species in northeast Brazil. It is used for fuelwood, construction and furniture making (Hardesty 1987). Construction firms depend on this species to a great extent. Small ruminants in the area use it as forage but it is less palatable than other herbaceous and tree species. Coppice stumps produce abundant foliage that usually persists through the dry season. Cattle also use this species to a great extent, especially after other forage species are utilized (Braga 1960).

Mimosa caesalpiniaefolia is a leguminous tree that is economically important for fence posts, construction of buildings and houses, and firewood for bakeries. It is shallow rooted and produces coppice. It is palatable to sheep, goats and cattle.

Caesalpinia bracteosa is a leguminous plant of low economic importance. It is usually hollow in the center. After cutting it also produces epicormic shoots, but is rarely browsed by any class of livestock (Hardesty 1987). However, once the leaves fall, goats utilize them to some extent.

Croton sonderianus belongs to the Euphorbiaceae family. Some people refer to it as a tree and some as a shrub. It rarely attains a height of 6-8 m. It has a pungent smell but is browsed moderately by goats. It is the first plant to shed leaves in the dry season. Marmeleiro usually grows at high densities in less fertile, disturbed areas. It is one of the principal tree species used by the apiculture industry.

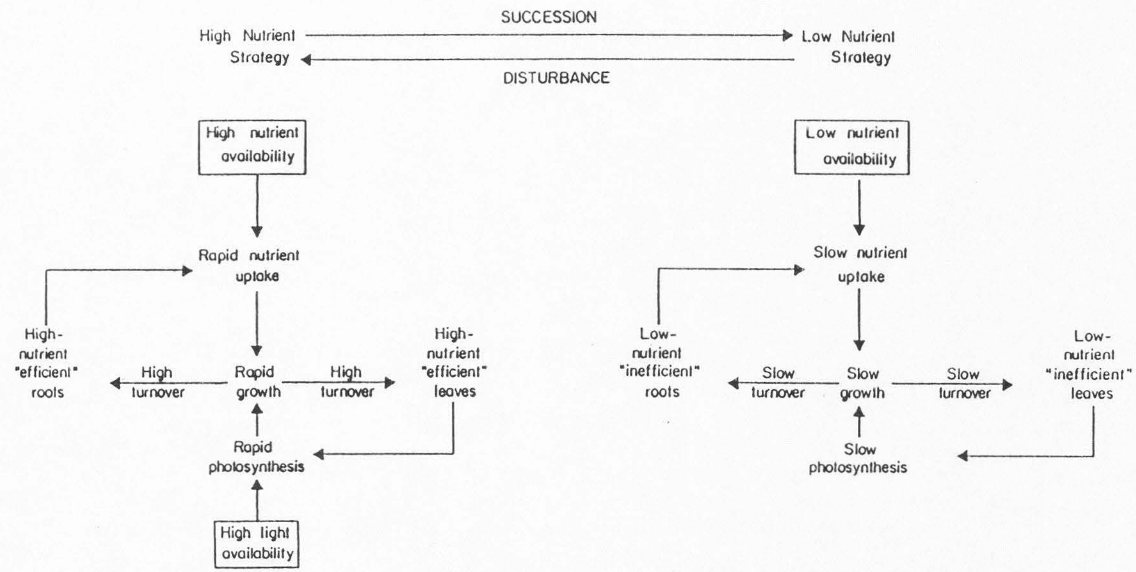
CHAPTER II

RELATIONSHIP BETWEEN PLANT MEAN RELATIVE GROWTH RATE AND FOLIAGE PALATABILITY TO GOATS

Introduction

A significant recent advance in plant antiherbivore defense theory is the recognition that the availability of resources such as mineral nutrients, sunlight and water may play a major role in the evolution and phenotypic expression of plant resistance to herbivory (Janzen 1974, Bryant et al. 1983, Coley et al. 1985). On an evolutionary scale, genetic adaptation to low resource environments favors selection for phytochemical defenses whereas adaptation to high resource environments does not (Bryant and Kuropat 1980, Bryant et al. 1983, Coley et al. 1985). On an ecological scale, phenotypic responses of plants to nutrient or carbon limitation control the expression of a plant's genetic potential to express antiherbivore defense (Bryant et al. 1983).

Plants that evolved in environments of low resource availability should have inherently slow growth rates and should contain high concentrations of compounds that reduce palatability and nutritional value of their tissues to herbivores. Inherently slow growth is a consequence of interdependent traits that limit the capacity of plants to acquire resources such as mineral nutrients and carbon (Figure 2). Plants with inherently slow growth rates have relatively



<u>Growth Characteristics</u>

High Inherent Growth Rates
High Photosynthetic Rates
High Leaf Protein Contents
High Dark Respiration Rates
Short Leaf Lifetimes

<u>Antiherbivore Characteristics</u>

High Rates of Herbivory
High Tolerance of Herbivory
Low Levels of Defense Metabolites
Mobile (Qualitative) Defenses
High Turnover Rates of Defenses

<u>Growth Characteristics</u>

Low Inherent Growth Rates
Low Photosynthetic Rates
Low Leaf Protein Contents
Low Dark Respiration Rates
Long Leaf Lifetimes

<u>Antiherbivore Characteristics</u>

Low Rates of Herbivory
Low Tolerance of Herbivory
High Levels of Defense Metabolites
Immobile (Qualitative) Defenses
Low Turnover Rates of Defenses

Figure 2. Plant strategies that are adaptive under conditions of high- and low-resource availability, and changes in these strategies that occur as consequences of disturbance and succession (modified from Bryant et al. 1983 and Coley et al. 1985).

low nutrient absorption capacities (Chapin 1980, Chapin et al. 1983) and photosynthetic rates (Mooney 1972). Thus, these plants grow slowly even in the most productive environments (Grime 1977, 1979, Chapin 1980, Bryant et al. 1983, Coley et al. 1985, Sarmiento et al. 1985). A limited capacity to acquire resources reduces a plant's ability to compensate for herbivory through regrowth. Thus, as inherent growth rate declines the detrimental impact of herbivory on plant fitness increases which should increase selection for phytochemical defenses (Bryant et al. 1983, Coley et al. 1985).

Conversely, woody plants that evolved in environments with abundant resources have been selected for rapid growth (Grime 1977). These species grow rapidly to outcompete their neighbors and thus dominate the available light and mineral resources. They also regrow quickly following disturbance such as fire or browsing (Kozlowski and Algren 1974, Chapin and Van Cleve 1981, Bryant et al. 1987c). Thus, species with inherently fast growth rates should allocate resources to growth rather than chemical defense (Bryant et al. 1983, Coley et al. 1985).

Although limited, the available evidence from tropical rainforests (Janzen 1974, McKey et al. 1978, Gartlan et al. 1980, Coley 1983), subtropical savannas (Cooper and Owen-Smith 1985, Owen-Smith and Cooper 1987a,b), boreal forests (Bryant and Kuropat 1980, Bryant et al. 1983), and arctic shrub tundra (Batzli and Jung 1980, Maclean and Jensen 1984) suggests that plants with slow inherent growth rates are of low palatability to herbivores (Bryant et al. 1987c). However, little research has been conducted to quantify inherent plant growth rates and to determine whether or not they are related to plant palatability to herbivores. The objective of this study was to determine whether or not the inherent growth rates of four trees that commonly occur in caatinga woodlands of northeast Brazil were related to their palatability to goats.

Methods

Inherent Plant Growth Rate

The study was conducted in a greenhouse (March to August 1986) at a Brazilian goat research center (EMBRAPA/CNPC) near Sobral, Ceara. Two soil types, infertile (lithic) and fertile (non-calcic brown) were utilized. Physical and chemical characteristics of these soils are indicated in Chapter I. Four plant species were utilized: sabia (Mimosa caesalpiniaefolia), catingueira (Caesalpinia bracteosa), marmeleiro (Croton sonderianus) and pau branco (Auxemma oncocalyx).

Four-hundred thirty-two current year's seedlings (108 from each plant species) were collected from each soil type and were planted in large pots of approximately .8 m^3 volume. Approximately 5 kg of soil from each soil type was placed in 864 cement pots. Once the seedlings were established, one of the three fertilizer levels (0, 150, or 300 kg/ha NPK) was randomly applied to plants within 3 replications of the 2 soil types. Urea, diammonium phosphate and potassium chloride were used as sources of fertilizer and were applied three times at two week intervals. Seedlings were watered to field capacity every two days throughout the experiment. There were 4 harvest periods, at monthly intervals.

At every harvest, 3 plants were sampled from each treatment (i.e. 2 soil types x 3 replications x 4 plant species x 3 fertilizer levels x 4 harvest periods x 3 plants sampled = 864 plants). Plants were divided into roots, leaves and stems. Leaves were dried in an oven for 48 hours at 72°C while roots and stems were dried for 72 hours at 72°C. Total biomass was obtained by summing the different plant parts. Mean values were calculated for the three plant subsamples. Mean relative growth rates ($\bar{R}$) were calculated using the formula of Hunt (1978).

$$\bar{R} = \frac{\ln W_{22} - \ln W_{11}}{\ln W_{11}} \cdot \frac{1}{t_2 - t_1}$$

where R = mean relative growth rate, W_{11} = mean dry weight at t_1, W_{22} = mean dry weight at t_2.

The experimental design for the analysis was a split plot with three replications. The following model was used to analyze the data:

$$\text{Model Y (RPFH)} = R(R) + P(P) + F(F) + H(H) + PF + PH + FH + PFH + \text{Error}$$

where R = replications, P = plant species, F = fertilizer level, and H = harvest periods. Data analysis was conducted using the statistical package Rummage (Bryce et al. 1980). Least squares analysis was performed and the protected LSD procedure was used to determine differences among means. Probability levels <.05 were considered significant. Significant interactions are discussed in the text. Moreover, I presented significant differences with letter superscripts. The analysis of variance tables indicated in the appendix have mean square errors associated with each source of variation. The varianc statistics can be calculated using an ** level of 0.05 with an appropriate degrees of freedom and $\sqrt{\frac{2MSE}{n}}$ where n = is the sample size and MSE is the mean square error.

Goat Utilization and Preference

Leaves from unfertilized plants of each plant species were collected in the field and fed to 8 goats held in separate pens. Goats were fed ad libitum a basal ration of pellets made from corn stubble, manihot, soybean meal, premix, minerals, salt and chopped dried cunha (Centrosema sp.) hay. Goats were fed the basal ration at 1000 and 1500 hours daily. Goats were not fed in the morning before trials. Fresh leaves from each plant species were offered to each goat for 3 minutes. Each goat received 75 g of leaves from one of the four plant species on each of 4 days. The order in which animals received each plant species was randomized for each goat. The amount of each plant species ingested was recorded and utilization was calculated as the percentage of the total amount of leaves consumed to the total amount of leaves offered for each plant species.

Goats clearly differentiated between the most (sabia) and least palatable (catingueira) species but did not differentiate as clearly between the two moderately palatable species (pau branco and marmeleiro). Therefore, an additional experiment was conducted to determine relative palatability of these species. Fifty grams of fresh leaves from these two species were offered to the same 8 goats for 3 minutes. This experiment was repeated for 4 consecutive days and percent utilization was calculated.

The analysis of variance for both experiments used a randomized block design with the following model:

Y(ASD) = A(A) + S(S) + D(D) + AS(error A) + D + DS + Error B

where A = animals, S = plant species and D = days.

Results

Inherent Plant Growth Rate

Similar results were observed by using roots, leaves, stems, leaves and stems and total (roots plus leaves and stems) biomass data. Therefore, I will only present data on total biomass. Sabia grew fastest and catingueira slowest on both soil types at least during the first harvest period (Table 3, Appendix Table 2). No consistent differences were observed between pau branco and marmeleiro. As harvest periods increased these two species tended to alternate. By the last harvest period, seedlings were senescing and therefore comparisons of mean inherent growth rates are not meaningful.

As fertilizer level increased mean relative growth rates in both types of soils tended to increase during the first harvest period (Table 4). However, there was generally no significant difference between the 150 and 300 kg/ha fertilizer levels but an increase in growth rate as fertilizer level increased to 300 kg/ha was recorded only in the first period on the non-calcic brown soil.

Table 3. Mean relative growth rates ($g\ g^{-1}\ d^{-1}$) of four plant species in (A) lithosol and (B) non-calcic brown areas.

A. Lithic Soil

Plant Species	Harvest Periods 1	2	3
Sabia	.084[a]	.024[a]	.042[a]
Paubranco	.054[b]	.021[a]	.001[b]
Marmeleiro	.043[b]	.009[b]	.022[c]
Catingueira	.026[c]	.008[b]	.023[c]

B. Non-calcic Brown

Plant Species	Harvest Periods 1	2	3
Sabia	.073[a]	.034[a]	.005[a]
Paubranco	.044[b]	.077[b]	.001[b]
Marmeleiro	.049[b]	.041[a]	.000[b]
Catingueira	.027[c]	.021[b]	.001[b]

[abc]Means with different superscripts within harvest periods are different ($P \leq 0.05$) using Fisher's LSD.

Table 4. Mean relative growth rates (g g^{-1} d^{-1}) of fertilized plants in (A) lithic soil and (B) non-calcic brown soil.

A. Lithic Soil

Fertilizer Level (NPK kg/ha)	Harvest Period		
	1	2	3
0	.042^{a}	.021^{a}	.010^{a}
150	.061^{b}	.023^{a}	.030^{b}
300	.063^{b}	.031^{a}	.012^{a}

B. Non-calcic Soil

Fertilizer Level (NPK kg/ha)	Harvest Period		
	1	2	3
0	.036^{a}	.031^{a}	.001^{a}
150	.045^{a}	.030^{a}	.010^{a}
300	.064^{b}	.032^{a}	.000^{a}

^{abc}Means with different superscripts are different ($P \leq 0.05$) using Fisher's LSD.

As fertilizer level increased there was an increase in mean relative growth rates for almost all plant species (except pau branco). The increase for catingueira was about 48 percent in the lithic soil and 120 percent in the non-calcic brown soil while that for sabia was 83 percent in the lithic soil and 59 percent in the non-calcic brown soil (Table 5).

Goat Preference

Goats preferred sabia to the other three species throughout the experiment (Figure 3, Appendix Table 3). The overall utilization of sabia leaves was 60 percent as compared to catingueira with approximately 2 percent. On the other hand, no significant ($P \leq 0.05$) differences were observed between pau branco and marmeleiro. However, when these two species were offered exclusively to goats, they preferred pau branco ($P<0.05$) to marmeleiro (56 and 44 percent utilization respectively). Therefore, preferences for these species were sabia > pau branco > marmeleiro > catingueira.

Discussion

My experiments support the hypothesis that inherent growth rate is positively related to plant palatability to herbivores. Similar relationships have been documented in other ecosystems (Bryant et al. 1983, Coley et al. 1985, Bryant et al. 1987c). Plant species like sabia with inherently fast growth rates have been selected for rapid growth to outcompete neighbors and dominate the uptake of available resources such as nutrients and light. The high absorption of nutrients may result in increased photosynthetic rates, accumulation

Table 5. Mean relative growth rates (g g^{-1} d^{-1}) of four plant species as influenced by fertilization in (A) lithic soil and (B) non-calcic brown soil.

A. Lithic Soil

Fertilizer Level (NPK kg/ha)	Plant Species			
	Sabia	Paubranco	Catinguiera	Marmelerio
0	.040[a]	.031[a]	.021[a]	.011[a]
150	.042[a]	.032[a]	.044[b]	.021[a]
300	.073[b]	.044[a]	.031[a]	.034[b]

B. Non-calcic Brown Soil

Fertilizer Level (NPK kg/ha)	Plant Species			
	Sabia	Paubranco	Catinguiera	Marmelerio
0	.034[a]	.021[a]	.020[a]	.010[a]
150	.036[a]	.031[a]	.031[a]	.020[a]
300	.054[b]	.031[a]	.044[b]	.034[b]

[ab]Means with different suprescripts within plant species significantly differ at $P \leq 0.05$ using Fisher's LSD.

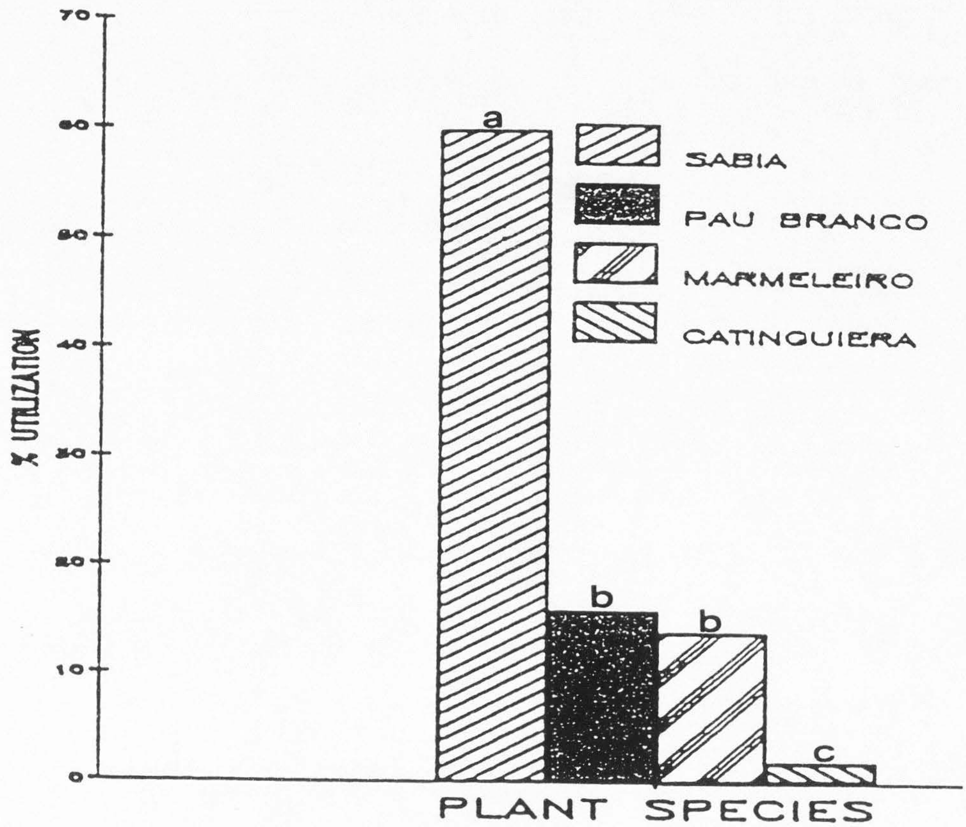


Figure 3. Percent utilization by goats in pens of foliage from four woody plants. Bars with different letters are different ($P \leq .05$) using Fisher's LSD.

of dry matter and apparently improved quality of forages through reduced concentrations of deterrent phytochemicals. On the other hand, plants that have a genetically limited capacity to acquire resources and an inherently slow growth rate, like catingueira, have increased concentrations of compounds that deter goats. Plants growing in nutrient rich soils in acacia woodlands of South Africa had lower concentrations of condensed tannins and lignin as compared to plants growing in nutrient poor soils (Cooper and Owen-Smith 1985, Owen-Smith and Cooper 1987a, b).

The most noticeable feature in this study was the consistent preference that goats showed for the four plant species. Sabia was consistently preferred and catingueira was consistently rejected. Results of the mean utilization levels of these species under field conditions were also consistent with the pen studies (see Chapter III). Hence, mean relative growth rates and palatabilities of the four woody plant species both under pen conditions and in field trials are in agreement.

After four centuries of disturbance, it is difficult to visualize the original condition and extent of caatinga species. Many researchers have suggested that caatinga species are of recent origin, having evolved from dry forest in response to increasing aridity (Axelrod 1979), and this has lead to the expansion of its territory (Sarmiento 1975). Furthermore, Lima (1965) indicated that caatinga may be a disclimax on degraded forest land, a seral stage in the regeneration of disturbed forest, or the climax vegetation, depending on environmental factors and the history of the site.

Therefore, documentation and placement of the plant species I studied along a gradient of resource availability, from an evolutionary standpoint, is difficult. Catingueira and marmeleiro may have evolved in resource poor environments while sabia and pau branco may have evolved in resource rich environments, but no data are available upon which to base a conclusion.

Irrespective of plants species evolutionary history, relative growth rates may still be positively correlated with plant palatability to herbivores. Hilbert et al. (1981) believes that relative growth rate is a useful measure which integrates a large number of plant physiological responses to the environment, one of which is utilization by herbivores. Mean relative growth rate may also change on an evolutionary scale depending on the intensity of herbivore use. Therefore a change in this ecologically significant parameter may change the chemical characteristics of plant species.

CHAPTER III

EFFECT OF FERTILIZATION ON PRODUCTION AND PALATABILITY TO GOATS OF COPPICE FROM TREES GROWING IN FERTILE AND INFERTILE SOILS IN NORTHEAST BRAZIL

Introduction

Lack of nutritionally adequate forage limits production of livestock during the dry season in northeast Brazil (Pfister 1983; Schacht 1986; Kirmse et al. 1987a,b,c). Clearing of woody plant species in northeast Brazil, practiced primarily for the production of charcoal, fence posts, and construction materials, causes trees to coppice. The coppice produced by most species remains green throughout most of the dry season and could serve as an important source of forage. However, the palatability of coppice from many species is low. A question of concern, therefore, is can the palatability of coppice be increased?

Increasing the palatability of coppice through fertilization is feasible theoretically (Bryant et al. 1987c). Fertilization can increase palatability of forage to livestock by reducing metabolites within plant tissues that deter herbivores (see Chapter IV).

Fertilization generally has not been tested experimentally under rangeland conditions within tropical regions for economic reasons. However, fertilization, when forage value is coupled with other uses such as charcoal, fence post, and lumber production of caatinga species, may be economically feasible. The intent of this study was to investigate the effect of fertilization on coppice production by four important caatinga species and their subsequent utilization by goats.

Methods

Fertilization

Using existing soil maps (Ramos 1981), I identified two soil types, non-calcic brown (fertile) and lithic (infertile). I established a 3 ha study area on each soil type (2 km apart). There were three replications of 1 ha each within each soil type. Each replication was fenced to allow for control of goat browsing.

Within each soil type, two leguminous (*Mimosa caesalpinieafolia* and *Caesalpinia bracteosa*) and two non-leguminous (*Croton sonderianus* and *Auxemma oncocalynx*) tree species were selected for study. Twelve plants of each species were randomly selected for study within each replication. An additional three plants of each species were selected as reserve plants within each replication. All trees were cut at 30 cm stump height two weeks prior to the rainy season. Before cutting on 30 December 1985, the height, diameter at breast height, and rooting characteristics of each tree species were measured (Table 6). The density of each species was also measured in 12, 4 X 10 m quadrats within each replication (Table 2).

One level of NPK (0, 150, or 300 kg/ha) was applied per four trees (within 2 meters radius) of each plant species in each replication on each soil type (i.e. 3 levels of fertilizer x 4 plant

Table 6. Above and below ground characteristics of four common caatinga species prior to cutting.

Species	Root intercepts at 1 meters distance from plant[1]	Meters of root in 0.5m strip (cm)	Mean diameter at breast height (cm)	Mean tree height (m)
Auxemma oncocalyx	29	16	37	13
Mimosa caesalpiniaefolia	15	6	22	10
Caesalpinia bracteosa	15	7	27	9
Croton sonderianus	8	5	12	5

[1]Data from Queiroz (1985).

species x 4 sample trees per plant species x 3 replications per soil type x 2 soil types = 288 sample plants). One-third of the determined rate of fertilizer was applied once prior to the onset of the rainy season on 13 January 1986, once on 13 February 1986, and once on 13 March, about the middle of the rainy season. Soil pH was determined one week after each fertilizer application.

In addition, four soil profiles were dug (30 x 30 x 40 cm) within a 2 m radius of each test plant before imposing the treatments. The soil profiles were divided into two soil depths (0-15 cm, 15-30 cm). Samples were composited by soil depth (i.e. 2 samples per test plant), tightly bagged and sent to the Soil Science Department at the Federal University of Ceara. Soil samples were mixed, sieved and analyzed for N, P, K^+, Na^+, Ca^{++}, Mg^{++}, Al^{+++}, organic matter (OM), and pH (Veltori 1969). Soil analysis were repeated at the end of the rainy season after fertilizer applications.

Standing Crop

Coppice and Herbs

Foliage standing crop for coppice sample plants was determined at the end of the rainy season in May by collecting the following data: (1) the number and height of epicormic shoots per plant; (2) the average number of leaves per epicormic shoot on three sample shoots per plant; (3) the average oven-dry (65^0 for 48 h) leaf weight of 50 leaves per plant. In addition, standing crop of herbs was measured on two 0.3 m^2 quadrats within 2 m of each coppice sample plant.

Utilization

One-hundred and eight goats of mixed age, sex,and breed were obtained from the research center near the end of the rainy season. They were allowed to forage on caatinga woodlands for 2 weeks prior to being placed on the experimental pastures.

Following the adjustment period goats were divided equally, based on metabolic body weight, into six groups. Each group was placed on a separate replication and body weight of goats was monitored weekly. When the weight of the animals began to decline significantly from their original weights, they were removed from the pastures.

Utilization of foliage from three sample epicormic shoots permanently marked per coppice plant was monitored bi-weekly by counting the number of leaves. The amount utilized was converted to a weight basis by multiplying the number of leaves removed by average leaf weight. Herbaceous standing crop was also monitored on a bi-weekly basis by sampling 40 quadrats of 0.3 m^2.

Preference

Fresh leaves from each plant species were harvested, sorted and combined by treatment groups. Six different combinations of these treatment groups (0 vs. 150 vs. 300 kg/ha NPK) were considered for each plant species: 0 and 0, 0 and 150, 0 and 300, 150 and 150, 150 and 300, 300 and 300 kg/ha of NPK. Fifty grams of fresh leaves from each fertilizer level were randomly placed in 2 feed boxes and fed for three minutes to each of 8 goats held in separate pens. Goats were not fed before the trials. The amount ingested of each plant species was recorded. The treatment combinations were randomized. These two choice preference tests were conducted for each of the plant species in each replication on each soil type (i.e., 4 plant species x 3 replications x 2 soil types). Preference indices were according to Bell (1959) for two choice tests.

Experimental Design

The experimental designs for the analyses were split plots. The following models were used to analyze the data.

Soils

Y(RFPDTA) = R(R) + F(F) + P(P) + FP + A(FPA) + D(D) + DF + DP+ DFP + DA + T(T) + TF + TP + TD + TFP + TFD + TPD + TFPD + TA + E

Coppice

Y(RFP) = R(R) + F(F) +P(P) + FP + E

Herbs

Y(RF) = R(R) + F(F) + E

Utilization in the field

Y (RFPAT) = R(R)+ F(F)+ P(P) + FP+ A(RFP)+ T(T)+ FT+ PT + FPT + E

Where Y = response variable, R = replications, F = fertilizer or treatment level, P = Plant species, D = soil depth, T = time, A, DA, TA are error terms involving animals and E is subsampling.

The following model was used to analyze goat preference for foliage from fertilized plants:

$$Y(ARSPF) = A(A) + R(R) + S(S) + P(P) + F(F) + SP + SF + PF + SPF + E$$

where A = goats, R = Replication, S = soil type, P = plant species, and F = the 6 fertilizer combinations.

Data analysis was conducted using the statistical package Rummage (Bryce et al., 1980). Significant interaction means were reported. Least squares analysis was performed and the protected LSD procedure was used to detect differences among means. Probability levels < .05 were considered significant.

Results

Utilization in the Field

Coppice. Foliage utilization (g/plant/browsing period) by goats increased as a result of fertilization (Tables 7A, B; Appendix Tables 4 and 5). In both types of soil, goats preferred sabia the most and catingueira the least. Fertilization increased utilization two- to three-fold. Because sabia is highly palatable and less abundant than pau branco, it was nearly all consumed by goats during the first week of browsing. Therefore, as time increased there was low availability and consequently low utilization of this species. However, utilization of pau branco, catingueira and marmeleiro increased with time.

Herbs. Of approximately 3500 kg/ha of herbaceous biomass produced in both types of soils there was very little left after a

Table 7. Mean foliage utilization (g dry wt/plant/browsing period) on the lithosol and non-calcic brown study areas. Goat browsing began on 25 June 1986 and ended on 25 August 1986. Utilization was measured on 11 July 1986 for sabia and on 31 July and 14 August for pau branco, catingueira and marmeleiro.

A. Lithosol

Plant Species	NPK (kg/ha) 0	150	300
Sabia			
11 July	63[a]	213[b]	162[b]
08 August	30[c]	28[c]	33[c]
Pau branco			
31 July	23[ab]	42[b]	71[c]
14 August	107[d]	169[e]	201[f]
Catingueira			
31 July	12[ab]	15[b]	19[b]
14 August	13[c]	66[d]	69[e]
Marmeleiro			
31 July	16[a]	26[a]	38[a]
14 August	70[b]	97[c]	123[d]

B. Non-calcic brown

Plant Species	NPK (kg/ha) 0	150	300
Sabia			
11 July	102[a]	212[b]	162[c]
08 August	69[d]	52[d]	58[d]
Pau branco			
31 July	63[a]	126[b]	170[c]
14 August	25[d]	133[b]	144[b]
Catingueira			
31 July	13[a]	59[b]	59[b]
14 August	11[a]	163[c]	86[d]
Marmeleiro			
31 July	15[a]	56[b]	62[c]
14 August	34[d]	123[e]	115[f]

[abcdef] Means with different superscripts, within a species by fertilizer by utilization differ ($P \leq 0.05$) using Fisher's LSD.

month of utilization (Table 8). The herbaceous material left was primarily unpalatable stems.

Goat Preference under Pen Condition

Under pen conditions, fertilization increased the palatability of all four plant species (Figure 4, Appendix Table 6 and 7). There was no interaction between plant species and fertilizer level. When the same levels of fertilizer (i.e. 0-0, 150-150, 300-300) were compared the preference indices were about .5 as expected. As the fertilizer level increased from 0 to 150, 0 to 300 or 150-300 kg/ha of NPK, goats preferred plants with the highest level of fertilizer.

Standing Crop

Coppice. Pau branco produced the most foliar biomass and marmeleiro the least of the four woody plant species studied. As fertilizer level increased, foliar biomass, number of epicormic shoots produced per plant, and height of epicormic shoots generally increased for all species (Tables 9, 10, 11 and Appendix Table 8). However, differences in height were significantly different at 300 kg/ha of NPK fertilizer. This trend was the same for both soil types, but production was generally lower for the infertile lithosol area.

Herbs. Application of fertilizer increased herbaceous standing crop on both soil types (Table 12 and Appendix Table 9). However, the increase was not significantly different between 150 and 300 kg/ha of NPK fertilizer.

Table 8. Herbaceous standing crop (kg/ha) before and after 4 weeks of goat browsing.

Standing Crop (kg/ha)	Soil Type	
	Lithosol	Non-calcic brown
before goat grazing	3680[a]	3374[a]
after goat grazing	145[b]	183[b]

[ab]Means differ within soil type at $P \leq .05$ using Fisher's LSD.

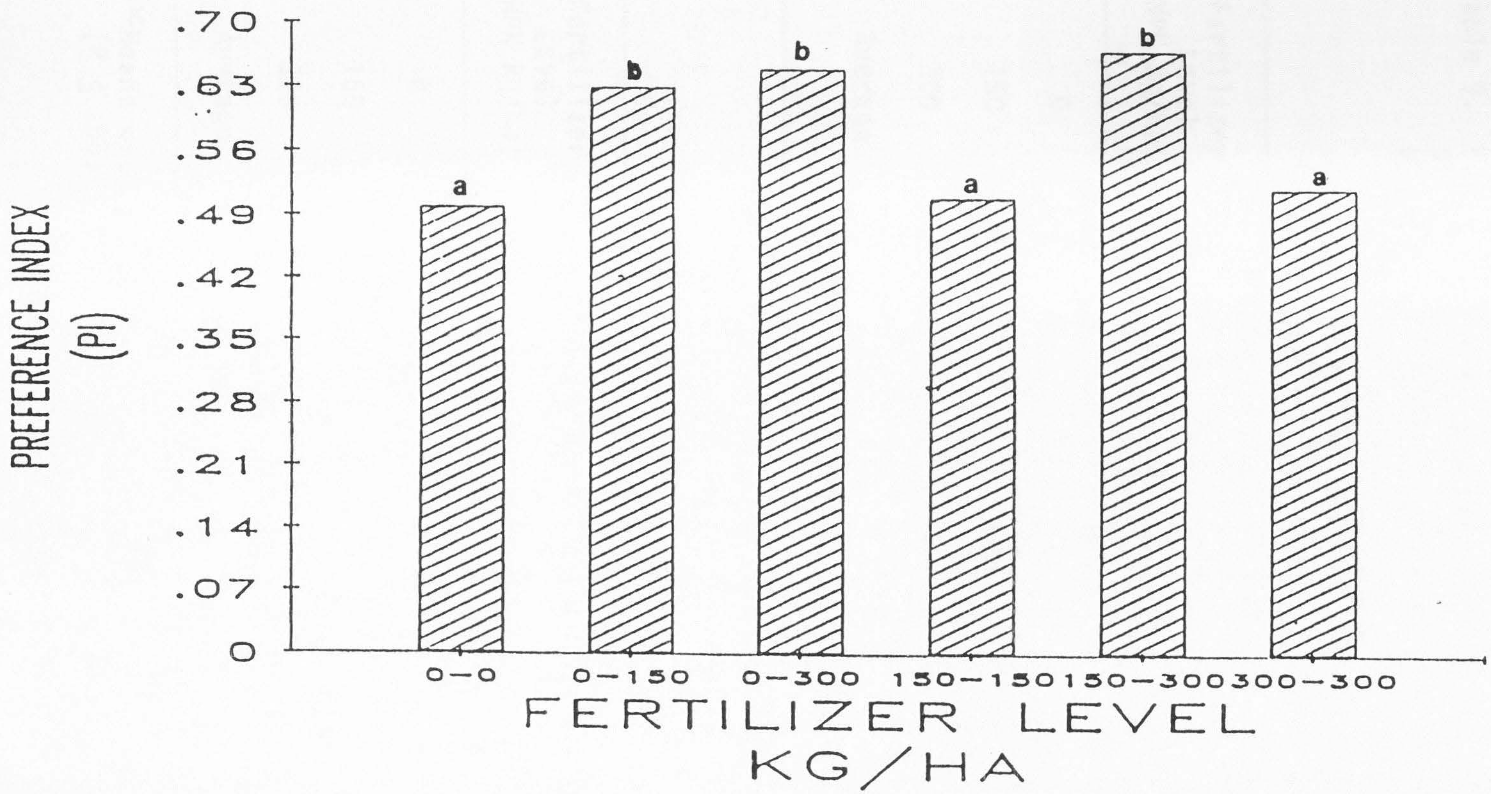


Figure 4. Effect of fertilization on the palatabilities of all four woody plant species. Numbers below each bar represent fertilizer level in each two-choice test. Fertilization (0-150, 0-300, 150-300) increased palatability above control levels (0-0, 150-150, 300-300) in every case. No interaction existed between fertilizer level and plant species.

Table 9. Production of foliar biomass (g/plant) by epicormic shoots of coppice plants in (A) lithosol and (B) non-calcic brown study areas.

A. Lithosol

Fertilizer Level (NPK kg/ha)	Plant Species				Average
	Sabia	Pau branco	Catingueira	Marmelerio	
0	444[a]	4011[a]	285[a]	137[a]	1219
150	576[b]	5057[b]	299[a]	373[a]	1576
300	657[c]	6181[c]	398[b]	377[a]	1903
Average	559	5083	327	296	

B. Non-calcic brown

Fertilizer Level (NPK kg/ha)	Plant Species				Average
	Sabia	Pau branco	Catingueira	Marmelerio	
0	584[a]	4368[a]	228[a]	156[a]	1334
150	784[b]	4848[a]	356[a]	168[a]	1539
300	812[c]	5128[b]	392[b]	224[b]	1639
Average	727	4781	249	183	

[abc]Means with different superscripts within a species are different ($P \leq .05$) using Fisher's LSD.

Table 10. Number of epicormic shoots produced per coppice plant in the (A) lithosol and (B) non-calcic brown study areas.

A. Lithosol Soil

Fertilizer Level (NPK kg/ha)	Plant Species				Average
	Sabia	Paubranco	Catingueira	Marmelerio	
0	9^{a}	29^{a}	4^{a}	6^{a}	12
150	12^{b}	31^{b}	5^{b}	7^{b}	14
300	13^{b}	33^{c}	8^{c}	8^{b}	16
Average	11	31	6	7	

B. Non-calcic brown

Fertilizer Level (NPK kg/ha)	Plant Species				Average
	Sabia	Paubranco	Catingueira	Marmelerio	
0	15^{a}	43^{a}	12^{a}	10^{a}	20
150	15^{a}	44^{a}	14^{b}	11^{a}	21
300	18^{b}	47^{b}	17^{c}	14^{b}	24
Average	16	45	14	12	

[abc]Means with different superscripts within a species are different ($P \leq .05$) using Fisher's LSD.

Table 11. Height (cm) of epicormic shoots for coppice plants in the (A) lithosol and (B) non-calcic brown study areas.

A. Lithosol Soil

Fertilizer Level (NPK kg/ha)	Plant Species				
	Sabia	Paubranco	Catingueira	Marmelerio	Average
0	204^{a}	207^{a}	97^{a}	150^{a}	165
150	205^{a}	208^{a}	110^{b}	158^{a}	170
300	220^{b}	216^{b}	111^{b}	204^{b}	188
Average	210	210	106	171	

B. Non-calcic brown

Fertilizer Level (NPK kg/ha)	Plant Species				
	Sabia	Paubranco	Catingueira	Marmelerio	Average
0	235^{c}	244^{a}	110^{a}	157^{a}	187
150	259^{a}	249^{a}	122^{b}	174^{b}	201
300	265^{b}	264^{b}	135^{b}	206^{c}	188
Average	253	252	122	179	

^{abc}Means with different superscripts within a species are different ($P \leq .05$) using Fisher's LSD.

Table 12. Effect of fertilization on herbaceous biomass production in lithic and non-calcic brown areas.

Fertilizer (kg/ha)	Production (kg/ha)	
	Lithosol	Non-calcic brown
0	3158[a]	2640[a]
150	3689[b]	3508[b]
300	4194[b]	3972[b]

[ab]Means within a soil type are different $P \leq .05$ using Fisher's LSD.

Soil Analysis

Differences in replications for both types of soil show that there were microsite differences for most of the soil variables measured (Appendix Tables 10, 11). Changes resulting from fertilization varied by soil type and element.

The increase in P may have been due to the release of P from decomposing plant material (Tables 13, 14, 15). Moreover, by the end of the rainy season the application of 150 kg/ha of NPK had increased the concentration of phosphorus by about two fold (2.44 to 4.46 ppm), but the application of 300 kg/ha was not significantly different from 150 kg/ha.

The concentration of K in the soil solution on both soil types increased by about nine-fold over the rainy season (Tables 13 and 14). The increase is probably due primarily to plant decomposition and the recycling of nutrients and secondarily to fertilization.

Concentration of N decreased significantly over the rainy season in both soil types. Application of fertilizer did not increase N. This may be associated with the addition of a small concentration of N to a large pool existing in both soil types. The decrease may also be related to microbial activity.

In the lithosol area the acidity of the soil was lower at the end of the rainy season than at the beginning (Table 13), while no difference was observed in the non-calcic brown area (Table 14). The change in pH may be attributed primarily to the increase in concentration of H and secondarily to low concentration of Al.

Table 13. Chemical characteristics of soils at the beginning and at the end of the rainy season on the lithosol area.

Rainy Season	Soil Variables							
	P (ppm)	K^+ (ppm)	TN (ppm)	Na^+ (ppm)	$Ca^{++}Mg^{++}$ (ppm)	Al^{+++} (ppm)	OM	pH
Beginning	1.57^a	28.91^a	0.13^a	8.41^a	9.99^a	0.20^a	1.51^a	5.90^a
End	3.76^b	247.99^b	0.07^b	32.63^b	6.98^a	0.03^b	1.46^b	5.21^b

[ab]Means followed by different superscripts within the same column are different ($P \leq .05$) using Fisher's LSD.

Table 14. Chemical characteristics of soils at the beginning and at the end of the rainy season on the non-calcic brown area.

	Soil Variables							
Rainy Season	P (ppm)	K^+ (ppm)	Total Nitrogen (ppm)	Na^+ (ppm)	$Ca^{++}Mg^{++}$ (ppm)	Al^{+++} (ppm)	OM (%)	pH
Beginning	2.17^{a}	42.10^{a}	0.076^{a}	6.21^{a}	12.98^{a}	$.043^{a}$	1.45^{a}	6.19^{a}
End	3.81^{b}	379.08^{b}	0.068^{b}	22.86^{b}	11.52^{b}	$.002^{b}$	1.22^{b}	5.84^{b}

^{ab}Means followed by different superscripts within the same column are different ($P \leq .05$) using Fisher's LSD.

Fertilization increased the concentration of P in the lithosol area and decreased N in the non-calcic brown area, but the decrease was not significantly different at 300 kg/ha NPK (Table 15). Moreover, acidity decreased significantly ($P<0.05$) as the level of fertilizer increased.

Analysis of soil variables by soil depth is indicated in Appendix Tables 12, 13, 14. As expected there was a decrease in concentrations of mineral nutrients as soil depth increased.

Discussion

Utilization

The results of this research indicate that fertilization of coppice plants with NPK increased their palatability to goats in pens and generally increased their utilization in the field. This is important because it will increase the amount of green forage available during the dry season (quantity and maybe quality, Chapter IV). Occasionally, no differences in utilization were observed between 150 and 300 kg/ha of NPK. Therefore, additional research is needed to determine optimum levels of fertilizer application for these two soil types. However, its cost effectiveness is subject to further research. Not all fertilizer elements that were added were limiting. For example, K was abundantly available and, therefore, its addition was not justified.

Fertilization resulted in increased growth (Table 5). In general this increase was associated with an increase in the utilization of all species (Fig. 4, Table 7). Similar results have

Table 15. Mean (ppm) interaction effect of treatments by time for phosphorus, potassium and pH in the lithosol and total nitrogen in the non-calcic brown area.

	Fertilizer Level (NPK kg/ha)		
	0	150	300
Phosphorus			
beginning	1.61[a]	1.48[a]	1.60[a]
end	2.44[a]	4.46[c]	4.39[c]
Potassium			
beginning	30.47[a]	28.55[a]	27.22[a]
end	228.40[b]	256.00[c]	259.60[d]
pH			
beginning	5.90[a]	5.90[a]	5.90[a]
end	5.37[b]	5.17[c]	5.08[d]
Nitrogen			
beginning	0.76[a]	0.79[a]	0.73[a]
end	0.67[b]	0.66[b]	0.72[a]

[abcd]Means with different superscripts differ ($P \leq 0.05$) within elements using Fisher's LSD.

been reported in other studies of the effects of fertilization upon use of woody plants as food by mammals (e.g. Behrend 1973; Bryant and Chapin 1982; Rousi 1983; Loyttyniemi 1982; Bryant 1987; Bryant et al. 1987a; Rousi et al. 1987). These results may be a consequence of decreased concentrations of carbon-based secondary metabolites in coppice resulting from increased carbon demands of growth (Bryant et al. 1983).

Coppice Production

The application of NPK fertilizer increased the number and foliage production of epicormic shoots for all species. The addition of 300 kg/ha of NPK generally increased biomass production above the 150 kg/ha level. Further studies are needed to determine at the optimum rate and combination of fertilizer application.

Enhanced mineral nutrition apparently stimulated the growth and development of epicormic shoots. The increased height and foliage mass might be related to the application of N because its main function is in the development, differentiation and elongation of cells. However, the interaction of other nutrients cannot be ruled out.

Herbaceous Production

Results of this study also reveal that fertilization along with clearing of caatinga increased herbaceous biomass production. Increased herbaceous production resulting from clearcutting has been reported by other researchers (Kirmse et al. 1987a, Schacht 1986, Hardesty 1987, Scifres et al. 1976, Scifres et al. 1982). None of these studies, however, have coupled clearing with the application of NPK fertilizer. At no fertilizer application my results are similar to those of Kirmse et al (1987a) for cleared areas (3600 and 3500 kg/ha, respectively).

Soils

My results indicate that soil nutrients vary according to soil type, depth and time. Soil parent material greatly determines the inherent fertility status of soils. Lithic soils were developed from gneiss, schist, migmatite and sandstone while the non-calcic brown soil was developed from metamorphic rock and granite on andesite landforms (Queiroz 1985). Due to these differences and other management practices, there were clear differences in the fertility of these soils. The non-calcic brown soil is slightly higher in P, Ca, Mg and K at both depths and time and, in general, both types of soil are very low in the concentration of available P, which is the macro-nutrient most limiting to plants at least in tropical regions (Sanchez 1976, Pritchett and Fisher 1987). Therefore, the application of phosphorus fertilizer probably had a significant effect.

Caatinga vegetation is moderately effective in transferring nutrients from the subhorizon(s) to the surface horizon(s). The presence of relatively high P, K, OM, total N and higher pH in the upper soil horizons is a good indicator of the deposition and recycling of nutrients in both types of soils. The low concentration of N at the end of the rainy season could be attributed to the inherent characteristic of N in the ecosystem. It is usually very mobile and is lost through leaching or captured by soil microorganisms or by undecomposed OM or absorbed by plants for synthesis.

Moss (1968) pointed out that recycling of nutrients from subsurface to surface horizons is more important for K than for P. The presence of high levels of K in the upper 0 to 15 cm of both soils is probably a result of recycling rather than the addition of K fertilizer. In addition, high presence of K in the top soil could be because it is more mobile than P. Moreover, OM decomposition may have been responsible for the high K concentrations in the soil solution. The presence of low Na may also have been related to increased K concentrations. The increased presence of K may also parallel the accelerated microbial activity during the rainy season. The presence of high microbial activity and/or arthropods may have enhanced the rate of decomposition (Kirmse et al. 1987b). The low and high total N concentration parallel the presence of low and high organic matter in both types of soil.

The presence of minerals in the first 15 cm of soil may have lead to acidification of the soil solution toward the end of the rainy season. The decrease in pH could have been associated with the application of fertilizer and interaction of fertilizer elements with other nutrients (e.g. Al^{+++} with phosphate groups, increased H concentrations). Results from other experiments suggest that among the plant nutrients, carriers of nitrogen decrease both soil pH and the loss of cations by leaching. Diammonium phosphate usually tends to increase pH initially, but the effect is relatively short-lived.

The low pH of the soil may reduce the availability of phosphorus. On the other hand, leaching might have caused lower horizons to contain higher Ca, Mg, Na and Al ion concentrations. Specifically the high presence of Na in the lower soil horizons (> 10 ppm) can cause severe problems to the normal functioning of the plants. It may impair the soil's permeability to air, water and root penetration. The shallow rooting systems of most caatinga species may be caused in part by high Na concentrations in lower soil horizons (Queiroz 1985).

CHAPTER IV

EFFECTS OF FERTILIZATION ON PLANT CHEMISTRY

Introduction

Fertilization often increases the palatability of woody plant species to herbivores (Oh et al. 1970, Anderson 1972, Matteson 1980, Loyttyniemi 1982, Sullivan and Sullivan 1982, Bryant et al. 1983, 1987a, b, Rousi 1983, Rousi et al. 1987). However, there are cases where fertilization had no effect (Haukioja and Neuvonen 1985), or even decreased the palatability of shrubs and trees to herbivores (Simonds and Marten 1971, Gershenzon 1984). Only recently has a theoretical basis developed to explain such observations (Bryant et al. 1983, Gershenzon 1984, Tuomi et al. 1984, Haukioja and Neuvonen 1985).

The palatability of woody plants to browsing mammals is sensitive to plant carbon/nutrient balance (Figure 5). When nutrients are less available, nutrient uptake is low and tissue concentrations decline. Nutrient limitation reduces photosynthetic rate directly by reducing RuBP carboxylase, chlorophyll, and phospholipid contents, and indirectly by increasing leaf longevity because older leaves tend to have reduced photosynthetic rates (Mooney 1972, Chapin 1980, Mooney and Gulmon 1982). The decline in growth with nutrient stress is generally greater than the decline in photosynthesis (Chapin 1980), so that carbon-based defensive

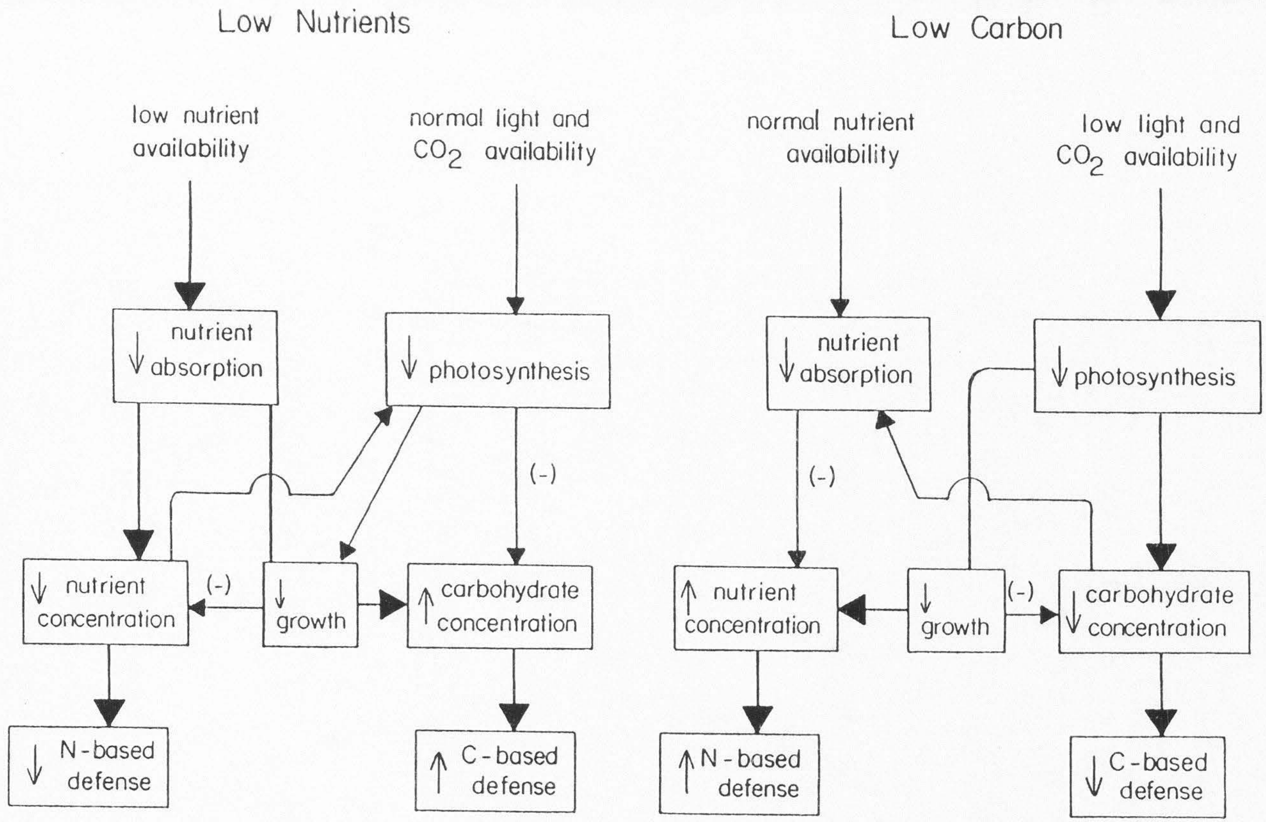


Figure 5. Effects of suboptimal nutrient or light availability upon carbon/nutrient relationships of plants and concentrations of plant chemical defenses. Vertical arrows within boxes indicate positive effects unless otherwise indicated (-). Thickness of arrow indicates magnitude of effect (modified from Bryant et al. 1983).

metabolites such as phenolics, resins, and terpenes accumulate (Wilde et al. 1948, Wong 1973, Gershenzon 1984). The phenotypic response to carbon stress due to insufficient light is essentially the reverse of that described for nutrient stress. Photosynthesis and carbohydrate concentrations decline. Growth rate is reduced more severely than is nutrient absorption, so that tissue nutrient concentrations accumulate above levels necessary to support growth. Under such circumstances, carbon-based defenses decline while nitrogen-based defenses such as alkaloids increase (Bryant et al. 1983, Gershenzon 1984, Waring et al. 1985, Bryant 1987, Bryant et al. 1987a, b, c).

The objective of this study was to assess the effects of fertilization on the chemical and physical characteristics of Auxemma oncocalyx, Mimosa caesalpiniaefolia, Caesalpinia bracteosa and Croton sonderianus. Because the palatability of these species increased as a result of fertilization (see Chapter III), I predicted that carbon-based metabolites such as tannins and lignins would be lower in fertilized than in unfertilized plants.

Methods

I established a 3 ha study area on each two soil types, lithic (infertile) and non-calcic (fertile). Within each soil type were 3 replications of 1 ha each. Within each replication, twelve plants of each of the two leguminous (Mimosa caesalpiniaefolia and Caesalpinia bracteosa) and two non-leguminous (Croton sonderianus and Auxemma oncocalyx) tree species were selected for study. All trees were cut on the same day at 30 cm aboveground at the beginning of the rainy season (December 1985). One level of NPK was applied per 4 trees (0, 150, or 300 kg/ha NPK). Foliage from three epicormic shoots per stump was harvested for chemical analysis, leaf toughness determinations, preference and bioassay studies as described below.

Chemical Analysis

In May 1986, leaves were harvested from three epicormic shoots from each of the 4 sample plants for each plant species, promptly frozen at -40^{0} C, freeze dried and ground in a Wiley Mill to pass a 1 mm screen. Samples were analyzed sequentially for neutral detergent fiber (NDF) and permanganate lignin (Van Soest and Wine 1968, Goering and Van Soest 1970). Samples were also analyzed for nitrogen (AOAC 1970) and in vitro organic matter digestibility (IVOMD) using the Moore modification of the Tilley and Terry technique (Harris 1970). Rumen fluid used for the inoculation of the fermentation tubes was taken from rumenally fistulated goats ranging freely in pastures of caatinga vegetation. The standards used were described by Schacht (1986).

Samples from the 3 epicormic shoots on the 4 sample plants were pooled for each plant species and analyzed for potassium, phosphorus, calcium, magnesium and tannins (i.e. 3 replications x 3 levels of fertilizer x 4 plant species = 72 samples per soil type). Proanthocyanidin tannins were analyzed using techniques described by Bullard et al. (1981) and Martin and Martin (1983). The proanthocyanidin analysis measures condensed tannins but also measures non tannin monomeric flavenoids (Martin and Martin 1983). The standard used in this assay was quebracho tannin. Tannins were expressed as percent dry weight in quebrecho tannin equivalents. Although use of quebracho tannin as a standard does not allow exact measurement of the concentration of condensed tannin in plant tissue (Wisdom et al. 1987), it provides a reliable index of tissue condensed tannin. Calcium and magnesium cation levels were determined by the direct current plasma (DCP) method on a Beckman Spectrascan VI spectrometer (Parsons et al. 1983). Potassium cation levels were determined by the atomic absorption spectrophotometer model 5000. Cation levels were determined on both percent of dry matter and ppm basis.

The experimental design was a split plot. The following model was used to analyze the data:

$$Y\ (RFPD) = R(R) + F(F) + P(P) + FP + D(FPD) + E$$

where R is replication, F is fertilizer level, P is plant species, D was the error term, and E is a subsampling term. Data analysis was conducted using the statistical package Rummage (Bryce et al. 1980). Probability levels < .05 were considered significant.

Preference Trials

As a preliminary step to identifying the compound(s) that deter goats from feeding on catingueira, I conducted a short series of bioassays. I lacked the methanol and ether necessary for extracting the other two plant species (pau branco and marmeleiro). Therefore, extractions were conducted with the least palatable plant species (catingueira). Bioassays were conducted using ether and methanol/water extracts. Five goats were kept in each of 5 pens (i.e. one goat per pen) with 2 feed boxes. Goats were offered a pelleted basal ration made from corn stubble, manihot, soybean meal, premix, minerals and salt for one week prior to the bioassays and daily intake was recorded. The bioassys were conducted by placing 150 g of control pellets, to which the carrier solvent was applied the previous night, and 150 g of treated pellets, to which the carrier solvent and the extract had been applied the previous night in adjacent feed boxes. Each of the goats was offered food containing each fraction on three consecutive days. Preference indices (Bell 1959) were calculated for each fraction as follows:

$$PI = \frac{C}{C + P}$$

PI is a preference index, C is the basal ration to which the carrier solvent (diethyl ether or methanol/water) and the extractable compound were added and P is the basal ration to which the carrier solvent only was applied. Preference indices range from 0 to 1 where .5 indicates equal preference of goats for C or P, less than .5 indicates goats preferred P and greater than .5 indicates goats preferred C.

To determine preference of green versus dry catingueira leaves from coppice plants (Chapters II and III), 20 g each of dry and green leaves were randomly placed in pairs of feeding boxes. Goats were allowed to feed for 3 minutes on 3 different days. Preference (Bell 1959) was calculated for each goat on each day as:

$$PI = \frac{D}{D + G}$$

where PI is preference index, D is dry leaves, and G is green leaves.

Leaf Toughness

Leaf toughness was measured for all plant species as described by Coley (1983). Fifty-four punch holes (i.e., 3 holes in each of 6 young and old leaves for each of 3 epicormic shoots from each plant species) were made using a punch meter (Feeny 1970). The meter measured the force in newtons necessary to punch a rod 5 mm in diameter through the leaf (veins were avoided).

The experimental design was a split plot. The following model was used to analyze the data:

$$Y\ (RFP) = R(R) + F(F) + P(P) + FP + E$$

R is replication, F is fertilizer level, P is plant species, and E is an error term. Data analysis was conducted using the statistical package Rummage (Bryce et al. 1980). Probability levels $< .05$ were considered significant.

Results

Effect of Fertilization on Plant Chemistry and Leaf Toughness

The concentration of condensed tannins was high ($P < 0.05$) in sabia and marmeleiro and low in catingueira and pau branco (Table 16). Lignin concentrations were high in sabia and catingueira, somewhat lower in marmeleiro, and lowest in pau branco. As fertilizer level increased there was a significant reduction in the concentrations of condensed tannins and lignins for all plant species on both soil types with one exception, lignin in sabia on the lithic soil. The percentage decrease was greater for non-leguminous plant species, pau branco and marmeleiro, than for the leguminous plant

Table 16. Effect of fertilization on leaf chemistry and nutritional characteristics of four woody plant species in (A) Lithic and (B) Non-calcic soils.

A. Lithic Soil.

Plant Species	NPK Fertilizer Level (Kg/ha)	NDF (%)	Lignin (%)	IVOMD (%)	Condensed Tannin (QET*)	Leaf Toughness (newtons)		% N	% P	% K	% Ca	% Mg
						Old	Young					
Sabia	0	45.3^{a}	17.2^{a}	91.0^{a}	36.1^{a}	115^{a}	110^{a}	2.31^{a}	$.10^{a}$	0.77^{a}	$.72^{a}$	1.60^{a}
	150	45.1^{a}	16.5^{a}	90.7^{a}	33.0^{b}	102^{b}	92^{b}	2.32^{a}	$.14^{b}$	0.84^{b}	$.76^{b}$	1.74^{b}
	300	45.0^{b}	17.3^{a}	91.0^{a}	31.2^{c}	88^{c}	73^{c}	2.48^{b}	$.14^{b}$	0.70^{c}	$.83^{c}$	1.94^{c}
Pau branco	0	39.5^{a}	8.3^{a}	81.5^{a}	3.8^{a}	90^{a}	75^{a}	2.63^{a}	$.14^{a}$	1.74^{a}	1.49^{a}	3.17^{a}
	150	37.5^{a}	7.5^{b}	78.3^{a}	1.4^{b}	66^{b}	67^{b}	2.67^{a}	$.15^{a}$	2.00^{b}	1.75^{b}	3.55^{b}
	300	37.2^{a}	7.1^{b}	81.6^{a}	1.4^{b}	77^{c}	61^{c}	2.71^{a}	$.17^{b}$	1.97^{b}	1.45^{a}	3.49^{b}
Catingueira	0	64.7^{a}	18.0^{a}	51.9^{a}	2.3^{a}	193^{a}	167^{a}	2.18^{a}	$.18^{a}$	0.55^{a}	1.03^{a}	0.77^{a}
	150	59.6^{a}	16.2^{b}	51.6^{a}	1.9^{a}	130^{b}	99^{b}	2.16^{a}	$.25^{b}$	0.80^{b}	0.85^{b}	0.55^{b}
	300	60.0^{a}	15.9^{b}	50.4^{a}	1.7^{b}	133^{c}	89^{b}	2.25^{b}	$.26^{b}$	0.86^{b}	0.88^{b}	0.65^{b}
Marmeleiro	0	47.5^{a}	14.5^{a}	80.6^{a}	32.3^{a}	148^{a}	134^{a}	1.97^{a}	$.14^{a}$	1.12^{a}	1.13^{a}	3.47^{a}
	150	43.6^{a}	12.0^{b}	80.9^{a}	26.2^{b}	136^{b}	123^{b}	2.25^{b}	$.20^{b}$	1.33^{b}	0.77^{b}	3.17^{b}
	300	43.4^{a}	11.3^{b}	78.2^{a}	30.8^{a}	129^{c}	126^{b}	2.27^{b}	$.25^{c}$	0.66^{c}	0.63^{c}	3.03^{c}

Table 16. Continued.

B. Non-Calcic Soil.

Plant Species	NPK Fertilizer Level	NDF (%)	Lignin (%) (Kg/ha)	IVOMD (%)	Condensed Tannin (QET*)	Leaf Toughness (newtons) Old	Leaf Toughness (newtons) Young	% N	% P	% K	% Ca	% Mg
Sabia	0	45.7^{a}	14.9^{a}	92.3^{a}	34.7^{a}	108^{a}	84^{a}	2.44^{a}	.13^{a}	0.83^{a}	.69^{a}	1.26^{a}
	150	45.0^{a}	14.0^{a}	93.0^{a}	30.4^{b}	100^{b}	81^{a}	2.56^{b}	.16^{b}	0.36^{b}	.64^{b}	1.68^{b}
	300	41.1^{a}	12.1^{b}	90.3^{a}	29.0^{b}	100^{b}	81^{a}	2.61^{b}	.16^{b}	0.38^{b}	.72^{a}	1.37^{c}
Pau branco	0	38.2^{a}	8.0^{a}	82.9^{a}	1.53^{a}	96^{a}	88^{a}	2.25^{a}	.17^{a}	1.89^{a}	.35^{a}	3.30^{a}
	150	37.1^{a}	7.1^{b}	83.5^{a}	1.30^{b}	90^{a}	82^{b}	2.69^{b}	.20^{b}	1.82^{a}	1.16^{b}	4.94^{b}
	300	37.0^{a}	7.0^{b}	84.4^{a}	1.20^{b}	82^{b}	72^{b}	2.67^{b}	.23^{c}	1.48^{b}	1.17^{b}	4.95^{b}
Catingueira	0	64.2^{a}	19.6^{a}	54.1^{a}	2.2^{a}	229^{a}	161^{a}	2.21^{a}	.20^{a}	0.80^{a}	.94^{a}	0.71^{a}
	150	63.2^{a}	18.1^{b}	55.7^{b}	1.4^{b}	221^{a}	150^{b}	2.26^{a}	.20^{a}	0.54^{b}	.76^{b}	0.60^{b}
	300	62.3^{a}	17.4^{b}	53.8^{a}	1.7^{b}	199^{b}	146^{b}	2.31^{a}	.20^{a}	0.82^{a}	.79^{b}	0.72^{a}
Marmeleiro	0	48.1^{a}	14.0^{a}	78.9^{a}	27.0^{a}	170^{a}	167^{a}	1.77^{a}	.17^{a}	1.02^{a}	.89^{a}	3.69^{a}
	150	46.0^{a}	13.5^{a}	74.6^{a}	25.2^{a}	154^{b}	140^{b}	2.23^{b}	.20^{b}	1.09^{a}	.82^{a}	4.11^{b}
	300	40.7^{b}	10.9^{b}	83.0^{a}	16.3^{b}	148^{b}	133^{c}	2.22^{b}	.20^{b}	0.72^{b}	.70^{b}	3.19^{c}

^{abc}Means with different superscripts within a species are different ($P \leq 0.05$) using Fisher's LSD.
*QET = quebracho tannin equivalents.

species, sabia and catingueira. In both types of soil, as fertilizer level increased there was an increase in plant tissue concentrations of nitrogen, phosphorus, potassium and calcium, but the rate varied among plant species. Nitrogen concentrations were highest at 300 kg/ha of NPK for nearly all plant species (except for pau branco on lithic soil and catingueira on non-calcic soil). Marmeleiro had the lowest concentration of nitrogen as compared to the other 3 plant species. Concentrations of phosphorus were comparable for all 4 plants but sabia tended to be lowest. Calcium, potassium and magnesium concentrations were comparable for all plant species but catingueira and sabia tend to have lower concentrations of these nutrients.

Unfertilized catingueira had high and pau branco had low percentages of fiber (NDF) as compared to the other two plant species. No significant differences were observed in NDF and in vitro organic matter digestibility as a result of fertilizer application. Generally, in vitro organic matter digestibilities of the three plant species were very high in both types of soils but catingueira had consistently low digestibility.

Catingueira had high toughness as both old and young leaves in both types of soils while pau branco had low toughness values. Marmeleiro and sabia had relatively moderate values. Fertilization decreased leaf toughness and the rate of decrease was comparable for all plant species for a level of fertilizer application. The decrease, with the exception of sabia on lithic soil, corresponds to the decrease of lignin and NDF.

Bioassay

The methanol fraction of green catingueira leaves was more active (PI = .05±.15) than the ether fraction (PI = 0.44±.09). Goats preferred ($P < .05$) dry leaves to green leaves of catingueira (PI = .61±.20 and .39±.20, respectively).

Discussion

The chemical changes in leaves of these 4 woody plant species resulting from fertilization are generally consistent with predictions of the carbon/nutrient balance hypothesis (Bryant et al. 1983, Gershenzon 1984). Generally, fertilization resulted in increased nutrient concentrations and growth (Chapter II) and, with one exception (marmeleiro on lithic soil), a decrease in leaf condensed tannin. Palatability increased (Chapter III) in response to fertilization thereby suggesting that high concentrations of carbon-based secondary metabolites may have decreased in palatability. However, as pointed out in Chapter III, heavy fertilization of sabin, catingueira and marmeleiro, especially plants growing on the already fertile non-calcic brown soil, decreased in palatability. Thus, the presence of nitrogen containing secondary metabolites such as alkaloids that reduce palatability to livestock (Ralphs and Olsen 1987) cannot be discounted in these species.

Whether or not fertilization increased the nutritional value of these plant species to goats is uncertain. Lignin, condensed tannin and leaf toughness generally decreased, while nitrogen, phosphorus, potassium, calcium and magnesium generally increased as a result of fertilization. However, neutral detergent fiber and in vitro organic matter digestibility generally were not affected by fertilization. The generally high lignin values may have been due to the presence of cutin. Additional research is needed to determine the effects of fertilization on the nutritional quality of these plant species for goats.

Additional research is also needed to explain why goats prefer some plant species that are high in condensed tannins (Burritt et al. 1987), but reject other plant species equally high in condensed tannins (Provenza and Malechek 1984, Cooper and Owen-Smith 1985). In my study, sabia, despite its high concentration of condensed tannins, was highly preferred by goats (Chapter II). Conversely, catingueira had the lowest concentration of condensed tannins, but was the least preferred by goats of the plant species studied. The chemical characteristics of condensed tannins may vary for different plant species, thus leading to differences in palatability of different plant species to goats. As Reichardt et al. (1987) point out plant chemical defenses are a property of individual compounds, unpalatability is closely tied to exact molecular structure, and no broad class of secondary metabolites contains individual compounds that are uniformly deterrent. In addition, goats may adapt to plant species high in condensed tannins through physiological mechanisms (Kumar and Singh 1984, Robbins et al. 1987) and learning (Provenza and Balph 1988).

The bioassays with catingueira showed that the methanol fraction strongly deterred goats. However, it is unlikely that condensed tannins, which would be extracted in methanol, were responsible for this deterrence because of their low concentrations in the relatively unpalatable catingueira. In addition, dry catingueira leaves were more palatable to goats than green leaves suggesting that the compound(s) that deter goats change or are removed from leaves just prior to or after leaf abscission or on drying, as would be expected of a mobile (sensu Coley et al. 1985) defense rather than an immobile defense such as condensed tannin. Additional research is needed to identify the compounds in catingueira that deters goats.

CHAPTER V

SUMMARY AND CONCLUSIONS

This research was designed to study the effects of inherent plant growth rate and fertilization on the productivity, palatability and subsequent changes in chemical and physical characteristics of coppice from four dominant woody plant species, sabia (Mimosa caesalpiniaefolia), catingueira (Caesalpinia bracteosa), pau branco (Auxemma oncocalyx) and marmeleiro (Croton sonderianus), of northeast Brazil. The major objectives of the study were to determine: (a) the relative growth rates, (b) the relative palatabilities to goats, and (c) to quantify some changes in chemical and physical characteristics of the four species as a result of fertilization. The results of this research project lead to the following conclusions.

1. Sabia had the fastest inherent growth rate while catingueira had the slowest. Pau branco and marmeleiro had comparable and moderate inherent growth rates. Fertilization did not change the order of their inherent growth rates.
2. Fertilization increased palatabilities of these plant species to goats. Palatability studies with goats indicated that goats preferred plant species with high inherent growth rates as compared to plants with low inherent growth rates.

3. Fertilization increased utilization of all four plant species. The least palatable plant specie was utilized more by goats after fertilization. In addition, fertilization increased production of epicormic shoots from coppice plants, and increased herbaceous biomass production.
4. Fertilization generally increased concentrations of primary nutrients such as phosphorus, nitrogen, potassium, and calcium.
5. Fertilization decreased condensed tannins and lignins and leaf toughness. However, no changes were observed in the in vitro dry matter digestibility or neutral detergent fiber.
6. The prediction that fertilized plants would be lower in carbon-based compounds than the unfertilized plants was supported by this study.

Recommendations for Future Research

Several research ideas can be brought forward within the framework of this research project.

1. Many fertilizers have long term residual effects. Therefore, I recommend that the concentrations of secondary compounds within tissue of plants be monitored for several years.

2. Studies are needed to determine nutrients that are limiting plant palatability and growth in different soil types and to develop fertilizer applications for each soil type.
3. Research is needed to determine chemical characteristics of other plants that are abundant in the region, but are unpalatable to livestock, and to determine the effect of fertilization on their palatability and nutritional quality to livestock.
4. Goats utilized less palatable plant species during the dry season. Increased utilization of the less palatable plant species could be attributed to the lack of availability of other forages or to the decline in concentrations of secondary metabolites in plant tissues. Therefore, investigation into the seasonal variation of these compounds within different plant parts is needed because palatabilities of the less palatable plant species varied at the onset and the end of the dry season.
5. The year that I conducted this experiment was exceptionally wet, about twice the average 30 years precipitation of the area. The response of the four plant species to fertilization and their use by goats may be different under lower soil moisture regimes. Therefore, a few years of studies are required before any management practice is defined.

6. Research is needed to understand the physiological mechanisms by which goats or sheep can tolerate plants high in plant secondary compounds.
7. Manage the two soil types, lithosols and non-calcic brown, differently if higher forage production and livestock production is sought. Soils nutrient status especially phosphorus in the two soil types studied is at its low level. Therefore, soils like the lithosols low in phosphorus should be managed for increased forage production and utilization differently as compared to the non-calcic brown soils.

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APPENDIX

Appendix Table 1. Some common herbaceous species in the study area.

Common Name	Family	Scientific Name
Gergelim cavalo (Brava)	Leguminoceae	_Crotolania anagyroide_ M. B. K.
		Crotalaria juncea Linn.
		Grotalaria mucronata Desv.
		Crotalaria stipularia Desv.
		Crotalaria vitellina Kerr.
Lingua de vaca	Compositeae	_Chaptalia integrifolic_ Bak.
		Chaptalia nutans Hemsl.
Fava de boi	Leguminoceae	_Canavalia obtusifolia_ Dc.
Cuandu	Leguminoceae	_Cuandu_ (?)
Manicoba do ceara (Verda diera)	Euforbiaceae	_Glaziovii_ Muell.
Matapasto	Leguminoceae	_Caissia sericea_ Swartz.
Melosa	Acataceau	_Ruellia asperula_ Lindau.
Cara	Dioscoreaceaes	_Dioscorea amazonum_ Griseb.
Milha Vermelha	Graminoideae	_Aristida_ (?) Capillacea Lam.
Capimbarba de Bode	Graminoideae	_Andropogon virginicus_ Linn.
		Aristida pullens Cav.
		Sporobulus aerieus Kunth.
		Sporobulus orrgutus Kunth.
		Sporobulus virginicus Kunth.
Fedegoso	Borraginaceae	_Heliotropium_ spp.
Fedegoso bravo	Borraginaceae	_Heliotropium angiospormum_ Murr.
Fedegoso do mato	Borraginaceae	_Heliotropium elogatum_ Willd.

Appendix Table 1. (continued)

Common Name	Family	Scientific Name
Fedegosso mindo	Borraginaceae	Tiaridium filiforme M. B. K.
Quebra panela	Amarantaceae	Gomphrena demissa mart.
Quebra Pedra	Euforbiaceas	Phyllanthus lathroides H. B. K.
Cipo de fogo	Euforbiaceae	Europhia phosphorea Mart.
Cipo de fogo	Vitaceae	Vitis erosa Bak.
Cipo de fogo	Bignoriaceae	Pyrostegia ignea Presl.
Capin rabo de raposa	Graminoideae	Andropogon bicornis Linn.
Azedinha	Polygonaceae	Rumex acetosa Linn.
Azedinha	Polygonaceae	Rumex brasiliense Link.
Capim rastecio	Graminoideae	Bouteloa americana scribn. (Aristida)
Malicia vermilha	Leguminoceae	Mimosa sensitiva Linn.
Malicia vermilha	Leguminoceae	Mimosa camporum Benth.
Malva paco-paco	Malvaceae	Malva e cae spp.
Melosa brava	Leguminoceae	Cassia hispiduhe (?)
Malva relogio	Malvaceae	Side rhombifolia (?)
Modubim	Leguminoceae	Arachis pusjilla (?)
Mirosol	Compositeae	Zexmenia rudis (?)
Mariana	Comelinaceae	Commelina nudiflora (?)
Mariana	Comelinacceae	Commelina deficiens (?)
Maracuja rasterio	Passiflonaceae	Passiflora foetida (?)
Pepide galinha	Gramineae	Echinochola elusine (?)
Urtiga verde	Urticaceae	Ureara baccifera (?)
Jitirana	Convolvulaceae	Ipomea spp.

Appendix Table 2. Analysis of variance for the mean relative growth rates in lithic and non-calcic brown soil.

Source of variation	Degrees of Freedom	Lithic	Non-Calcic Brown
Replications (R)	2	NS	NS
Species (P)	3	NS	**
Fertilizer (F)	2	NS	*
Harvest (H)	2	**	**
PF	6	*	*
PH	6	*	**
FH	4	NS	**
PFH	12	NS	NS
Error	70		

NS = Not significant

* = Significant at $P \leq 0.05$

** = Highly significant at $P \leq 0.01$

Appendix Table 3. Analysis of variance for goats preferences of two plant species (Pau branco and marmeleiro).

Source of variation	Degrees of Freedom	Mean Square	F - Ratio
Goats (G)	7	0.10	1.74
Species (S)	2	0.20	3.44*
Days (D)	3	0.10	1.62
D x S	6	0.08	1.34
Error	77	0.06	

*Significantly different at $P \leq 0.05$.

Appendix Table 4. Analysis of variance table for the mean utilization levels (g/plant browsing period) by goats for the four plant species treated at different fertilizer levels in the lithosol area.

Source of Variation	Degrees of Freedom	Mean Square	F Ratio	Probability Level of Significance
Replications (R)	2	6147	5.67	.010 **
Fertilizer (F)	2	62182	57.36	.000 **
Species (P)	3	68838	63.51	.000 **
FP	6	5752	5.31	.002 **
Error(a)	22	1084	22.34	
Time (T)	1	47812	22.34	.000 **
FT	2	1946	0.91	.416 NS
PT	3	177697	83.05	.000 **
FPT	6	14966	6.99	.000 **
Error (b)	24	2140		

*Significantly different at $P \leq 0.05$.

Appendix Table 5. Analysis of variance table for the mean utilization levels (g/plant browsing period) by goats for the four plant species treated at different fertilizer levels in the non-calcic brown area.

Source of Variation	Degrees of Freedom	Mean Square	F Ratio	Probability Level of Significance
Replications (R)	2	6140	1.17	0.330 NS
Fertilizer (F)	2	173291	32.90	0.000 **
Species (P)	3	80420	15.27	0.000 **
FP	6	4233	0.80	0.578 NS
Time (T)	1	23194	8.90	0.006 **
FT	2	2839	1.09	0.353 NS
PT	3	112284	43.07	0.000 **
FPT	6	15492	5.94	0.001 **

*Significantly different at $P \leq 0.05$.

Appendix Table 6. Analysis of variance table for goats preference test of the four woody plant species fertilized with three different levels of NPK in two soil types under pen condition.

Source of Variation	Degrees of Freedom	Mean Square	F Ratio
Animals (A)	7	.0940	3.00
Replications (R)	2	.0650	2.08
Soil (S)	1	.0004	0.01
Species (P)	3	.2706	8.61*
Fertilizer (F)	5	.7162	22.79*
SP	3	.0049	0.16
SF	5	.0236	0.75
PF	15	.0413	1.31
SPF	14	.0261	0.83
Error (E)	860	.0314	

*Significantly different at $P \leq 0.05$.

Appendix Table 7. Mean preference values for the interaction of plant species by fertilizer level under pen condition. Numbers within the fertilizer column represent fertilizer levels used in each two-choice test.

Fertilizer Level	Plant Species			
	Sabia	Paubranco	Catingueira	Marmeleiro
0 - 0	.50	.53	.52	.46
150 - 150	.48	.48	.57	.49
300 - 300	.47	.47	.53	.55
0 - 150	.58	.60	.69	.68
0 - 300	.57	.61	.72	.68
150 - 300	.60	.60	.70	.71

*No significant differences were observed ($P \geq 0.05$) using Fisher's LSD.

Appendix Table 8. Analysis of variance for foliar biomass production, coppice production, and height growth in lithic and non-calcic brown soils.

		Production		Coppice		Height	
		Soil Type					
Source of Variation	Degrees of Freedom	Lithic	Non-calcic brown	Lithic	Non-calcic brown	Lithic	Non-calcic brown
Replications (R)	2	**	NS	**	NS	**	NS
Treatment (F)	2	**	NS	**	NS	*	NS
Species (P)	3	**	**	**	**	**	**
FP	6	*	*	*	*	*	*
Error	130						

**Highly significant at $P \leq 0.01$
*Significant at $P \leq 0.05$
*NS = not significant

Appendix Table 9. Analysis of variance table for the herbaceous production (A) in the lithic soil (B) in the non-calcic brown.

A. Lithic soil.

Source of Variation	Degrees of Freedom	Mean Square	F Ratio	Probability Level of Significance
Replications	2	8309205	1.75	0.176
Fertilizer	2	16124156	3.40*	0.04
Error	175	4736860		

B. Non-calcic brown.

Source of Variation	Degrees of Freedom	Mean Square	F Ratio	Probability Level of Significance
Replications	2	57993317	9.20**	00
Fertilizer	2	27404713	4.4**	.014
Error	175	6307096		

*Significantly different at $P \leq 0.05$.

Appendix Table 10. Analysis of variance table for soil variables in the lithosol area.

Source of Variation	Degrees of Freedom	P	K^+	TN	Na^+	$Ca^{++}Mg^{++}$	Al^{+++}	OM	pH
Replications (R)	2	NS	**	**	**	**	*	*	**
Fertilizer (F)	2	**	NS	NS	NS	NS	NS	NS	*
Species (P)	3	NS	*	NS	NS	*	NS	*	NS
FP	6	NS	NS	NS	NS	NS	NS	NS	NS
Depth (D)	L	**	**	**	**	*	**	**	**
FD	2	NS	NS	NS	NS	NS	NS	NS	NS
PD	3	NS	NS	NS	NS	NS	NS	NS	NS
FPD	6	NS	NS	NS	NS	NS	NS	NS	NS
Time (T)	1	**	**	**	**	**	**	**	**
FT	2	**	NS	NS	NS	NS	NS	NS	*
PT	3	NS	NS	NS	NS	NS	NS	NS	NS
DT	1	NS	NS	**	NS	NS	**	**	**
FPT	6	NS	NS	NS	NS	NS	NS	NS	NS
PDT	3	NS	NS	NS	NS	NS	NS	NS	NS
FDPT	6	NS	NS	NS	NS	NS	NS	NS	NS

* Means are significantly different at $P \leq 0.05$.
** Means are highly significant at $P \leq 0.01$.
NS Means are not significantly different at $P = 0.05$.

Appendix Table 11. Analysis of variance table for soil variables in the non-calcic brown area.

Source of Variation	Degrees of Freedom	P	K^+	TN	Na^+	$Ca^{++}Mg^{++}$	Al^{+++}	OM	pH
Replications (R)	2	*	NS	**	**	**	NS	**	**
Fertilizer (F)	2	*	NS	NS	NS	NS	NS	NS	NS
Species (P)	3	NS	NS	NS	*	NS	NS	**	NS
FP	6	NS	NS	NS	NS	NS	NS	NS	NS
Depth (D)	L	**	*	**	**	**	**	**	**
FD	a	NS	NS	NS	NS	NS	NS	NS	NS
PD	3	NS	NS	NS	NS	NS	NS	*	NS
FPD	6	NS	NS	NS	NS	NS	NS	NS	NS
Time (T)	1	**	**	**	**	**	**	**	**
FT	2	NS	NS	*	NS	NS	NS	NS	NS
PT	3	NS	NS	NS	NS	NS	NS	NS	NS
DT	1	NS	NS	**	NS	*	**	**	**
FPT	6	NS	NS	NS	NS	NS	NS	NS	NS
PDT	3	NS	NS	NS	NS	NS	NS	NS	NS
FDPT	6	NS	NS	NS	NS	NS	NS	NS	NS

* Means are significantly different at $P \leq 0.05$.
** Means are highly significant at $P \leq 0.01$.
NS Means are not significantly different at $P = 0.05$.

Appendix Table 12. Chemical characteristics of soils at two depths (0-15 and 15-30 cm) on the lithosol area.

Depth (cm)	P (ppm)	K^+ (ppm)	Total (ppm)	Na^+ (ppm)	$Ca^{++}Mg^{++}$ (ppm)	Al^{+++} (ppm)	% OM	pH
0-15	2.82^{a}	149.40^{a}	$.147^{a}$	17.63^{a}	8.16^{a}	0.036^{a}	1.89^{a}	5.59^{a}
15-30	2.50^{a}	127.50^{a}	$.060^{b}$	23.41^{b}	8.81^{a}	0.20^{b}	1.08^{b}	5.52^{a}

[a]Means followed by different superscripts within the same column are significantly different ($P \leq 0.05$).

Appendix Table 13. Chemical characteristics of soils at two depths (0-15 and 15-30 cm) on the non-calcic brown area.

Depth (cms)	P (ppm)	K^{+} (ppm)	Total (ppm)	Na^{+} (ppm)	$Ca^{++}Mg^{++}$ (ppm)	Al^{+++} (ppm)	% OM	pH
0-15	3.35^{a}	224.23^{a}	$.088^{a}$	13.74^{a}	11.69^{a}	$.005^{a}$	1.62^{a}	6.10^{a}
15-30	2.65^{b}	196.65^{a}	$.057^{b}$	15.33^{f}	12.81^{b}	$.040^{b}$	1.04^{b}	5.94^{a}

[a]Means followed by different superscripts within the same column are significantly different ($P \leq 0.05$).

Appendix Table 14. Means for assays (ppm) for depth by time interaction on the lithosol and non-calcic brown area.

(soil depth cm)	Soil Type			
	Lithosol		Non-calcic brown	
	Beginning of Rainy Season	End of Rainy Season	Beginning of Rainy Season	End of Rainy Season
Nitrogen				
0-15	$.210^{a}$	$.085^{b}$	$.097^{a}$	$.079^{b}$
15-30	$.056^{c}$	$.065^{b}$	$.055^{c}$	$.058^{b}$
Aluminum				
0-15	$.05^{a}$	$.02^{a}$	$.009^{a}$	$.001^{a}$
15-30	$.06^{a}$	$.05^{c}$	.007b	$.004^{a}$
Calcium/Magnesium				
0-15	9.59^{a}	6.73^{b}	12.13^{a}	11.15^{a}
15-30	10.38^{a}	7.24^{b}	13.82^{b}	11.80^{a}
Organic Matter				
0-15	2.07^{a}	1.71^{c}	1.85^{a}	1.39^{b}
15-30	0.95^{b}	1.22^{d}	1.04^{c}	1.05^{b}
pH				
0-15	6.00^{a}	5.18^{b}	6.34^{a}	5.87^{b}
15-30	3.80^{a}	5.24^{b}	6.04^{c}	5.82^{b}

^{abcd}Means within a soil type with different superscripts are different ($P \leq 0.05$).

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