INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

Bell & Howell Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA

UMI®
800-521-0600

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

DISSERTATION

SOIL-PLANT-HERBIVORE INTERACTIONS AND NUTRIENT DYNAMICS IN SEMI-ARID GRAZING SYSTEMS IN NORTHEASTERN BRAZIL AND WESTERN USA

Submitted by

Rômulo Simões Cezar Menezes

Soil and Crop Sciences Department

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Fall 1999

UMI Number: 9950901

UMI®

UMI Microform 9950901

Bell & Howell Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

COLORADO STATE UNIVERSITY

November 10, 1999

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY ROMULO SIMOES CEZAR MENEZES ENTITLED "SOIL-PLANT-HERBIVORE INTERACTIONS AND NUTRIENT DYNAMICS IN SEMI-ARID GRAZING SYSTEMS IN NORTHEASTERN BRAZIL AND WESTERN USA" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHIILOSOPHY.

Committee on Graduate Work

Michael B. Coughenour

Keith Paustian

Edward T. Elliott

Adviser

Gary A. Peterson

Co-Adviser

Department Head

ABSTRACT OF DISSERTATION

SOIL-PLANT-HERBIVORE INTERACTIONS AND NUTRIENT DYNAMICS IN SEMI-ARID GRAZING SYSTEMS IN NORTHEASTERN BRAZIL AND WESTERN USA

Nutrient cycling, availability, and use efficiency are key issues of sustainability and control important aspects of ecosystem function. In the series of studies in this dissertation, we evaluate how human-induced disturbances and interactions between soil, plants, and herbivores influence nutrient cycling, productivity, and ecosystem structure in semi-arid grazing systems in northeastern Brazil and Colorado, USA. We found that the presence of tree species within pastures of *C. ciliaris* in northeastern Brazil led to increases in soil nutrient levels, cycling rates, and availability in comparison to areas where all trees were removed. In Rocky Mountain National Park (RMNP), Colorado, we found that herbivores had a significant influence on nutrient pools, fluxes between pools, and also on ecosystem structure by possibly reducing the ability of *Salix* shrubs to take up N from the groundwater, which may affect the regeneration of *Salix* communities in that site. Overall, our findings indicate that the presence and preservation of trees or shrubs in the semi-arid grazing systems in northeastern Brazil and RMNP contributed to the maintenance of ecosystem function by increasing the capture, retention, and availability of nutrients and plant productivity in comparison to disturbed systems where the density of trees or shrubs was reduced.

Rômulo Simões Cezar Menezes
Soil and Crop Sciences Department
Colorado State University
Fort Collins, CO 80523
Fall 1999

ACKNOWLEDGEMENTS

I wish to express my sincere gratitude to a group of people that provided guidance, help, and support throughout my Ph.D. Graduate Program: Ted Elliott was a true mentor, and I am immensely grateful to his genuine efforts, throughout the whole period we worked together, to carefully provide guidance, stimulation, and encouragement, which greatly benefited my development as a researcher; Ignacio Salcedo, as an informal co-advisor, has also been an important mentor and friend, and provided inestimable support through countless discussions, and also by allowing me to have access to the laboratory, technical support, and resources at UFPE; Keith Paustian provided valuable inputs to my research work through several discussions throughout my graduate studies; Gary Peterson and Mike Coughenour served as members of my Graduate Committee, and always gladly provided help whenever I requested; Everardo Sampaio provided major collaboration in the preparation of the first manuscript of the dissertation and has been an important motivator throughout my graduate studies.

Steve Williams provided unvaluable technical support for my research in the Willow Project, such was the help of Dan Reuss in the laboratory analyses - without his help some jobs would have been much more difficult, and other jobs would have been impossible to accomplish. Priceless technical support was also provided by Clarindo C.

Pontes, Pedro A. da Silva Filho, Gilberto E. do Nascimento, Claudenice E. Santos, Nivaldo M. de Araujo, Jennifer Williams, and Tricia Wotan.

I am extremely grateful to the Brazilian Council for Research Development (CNPq), for providing full financial support to my Graduate Studies. CNPq has, for decades, brought great progress to the fields of science and technology in Brazil. I would not have been able to conduct these studies without the financial support for my experimental research work provided by WWF-Brasil, Fundação para o Amparo da Ciência e Tecnologia do Estado de Pernambuco (FACEPE), United States National Park Service, and Biological Resources Division of the USGS. I also thank the Agropecuária Jaçanã for allowing me to conduct studies in their land and for providing lodging and logistical support during the sampling trips.

Finally, I thank my family for their love and support; Karin Wirthlin for everything; and all other friends in Fort Collins for their companionship and joy throughout the last three years.

TABLE OF CONTENTS

INTRODUCTION

Human-induced disturbances are significantly altering Earth's ecosystems, and the management of an ever-increasing human population requires an understanding of how terrestrial ecosystems function (Aber and Melillo 1991, Schlesinger 1997). Nutrient cycling and availability are key issues of sustainability and control important aspects of ecosystem function (Elliott et al. 1993, Lugo et al. 1999). The study of multiple elements, particularly those that have the potential to limit ecosystem processes, gives a more complete understanding of how nutrient cycling may influence ecosystem sustainability (Hunt et al. 1983, Stewart et al. 1983, Aber and Melillo 1991, Elliott et al. 1993, Lugo et al. 1999). Among the elements of interest, nitrogen is usually one of the most limiting in terrestrial ecosystems (Aber et al. 1989, Nadelhoffer et al. 1999), but the availability of P, and other nutrients may also often limit ecosystem processes, particularly in tropical ecosystems (Aber and Melillo 1991, Hunt et al. 1993, Stewart et al. 1993, Sampaio 1995, Schlesinger 1997, Nandwa and Bekunda 1998, Wortmann and Kaizzi 1998, Lugo et al. 1999).

Vegetation plays an important role in controlling soil formation and development (Jenny 1941), and significantly affects ecosystem nutrient dynamics and productivity (Vitousek 1984, Young 1989, Sanchez 1995, Rhoades 1997, Schlesinger 1997). At the forest stand or individual stem scale, trees alter chemical, physical, and biological soil properties through their impact on nutrient fluxes within ecosystems (Rhoades 1997), and the knowledge of the influence of different tree species on ecological processes is fundamental to the understanding of ecosystem functioning (Garcia Montiel and Binkley 1998). Several studies have demonstrated the effects of some species of trees and shrubs on silvopastoral systems and savannas, which often correspond to improvements in soil nutrient, soil moisture, and increases in herbaceous understory biomass production in comparison to open grass areas (Tiedemann and Klemmedson 1973, Farrel 1990, Weltzin and Coughenour 1990, Belsky et al. 1993, Rhoades 1997). These resource-rich areas beneath tree canopies are known as resource islands (Reynolds et al., 1990), isles of fertility (West, 1981), or fertile islands (Halvorson et al., 1995).

Similarly, grazing affects many ecosystem constituents and may play a significant role in regulating ecosystem nutrient flow (Holland et al. 1992), mostly by influencing plant community structure and biogeochemical cycles within the soil-plant system (Frank et al. 1994, Frank and Groffman 1998, Hamilton et al. 1998, Schuman et al. 1999, Wijnen 1999). Herbivores can influence nutrient cycling by removing plant biomass and returning more readily available nutrients to the soil (McNaughton et al. 1988, Frank et al. 1994, Hamilton et al. 1998), increasing soil N mineralization rates and plant N uptake (Frank and Groffman 1998, Wijnen et al.1999), and spatially redistributing nutrients within the landscape (McNaughton 1985, Afzal and Adams 1992, Russelle 1992). Whether herbivory has a positive or negative influence on ecosystem structure and function depends in part on the specific characteristics of each system (Georgiadis et al. 1989, Hamilton et al. 1998, Mazancourt et al. 1998, Alstad et al. 1999).

In the series of studies included in this dissertation, we evaluate how human-induced disturbances and interactions between soil, plants, and herbivores influence nutrient cycling, productivity, and ecosystem structure in semi-arid grazing systems in northeastern Brazil and Colorado, USA. These two systems differ significantly in certain characteristics, such as climate and the nature and dynamics of major disturbances. For instance, in the tropical semi-arid region of northeastern Brazil, native and exotic trees are sometimes preserved or introduced within artificial pastures that are established after the slash and burn of the native dry forest called 'Caatinga' (Sampaio 1995). On the other hand, the temperate natural grazing system in Rocky Mountain National Park (RMNP), Colorado, have reportedly been affected by increasing elk (*Cervus elaphus*) numbers, due to previous human-induced disturbances to the Park's ecosystems and on-going alterations of surrounding areas (Singer et al. 1998b).

The first three chapters of the dissertation correspond to studies related to the sustainability of land use systems in semi-arid northeastern Brazil. Chapter I describes the current land use systems in the region and includes a discussion about potentially sustainable alternative systems. Among these alternative systems, silvopastoral systems present great potential to increase the sustainability of land use systems in semi-arid northeastern Brazil. Previous studies conducted in the region have reported that silvopastoral systems contribute to increases in livestock productivity and biodiversity of plant communities (Araujo Filho 1990, Silva et al. 1995). Based on these previous studies, we established several working questions with the objective of increasing our understanding of the influences of tree species on ecosystem processes in silvopastoral systems in northeastern Brazil: (1) Do trees have a significant influence on the patterns of soil nutrient levels and herbaceous productivity within silvopastoral systems in semi-arid northeastern Brazil? (2) Do different tree species influence these characteristics in different ways? (3) How do tree species affect microclimatic conditions and nutrient cycling and availability in silvopastoral systems in northeastern Brazil? Based on questions (1) and (2), we conducted an observational study (Chapter II) to investigate the influence of different tree species on the patterns of soil nutrient levels and herbaceous biomass productivity in a silvopastoral system in semi-arid northeastern Brazil. Subsequently, question (3) was approached by conducting an experimental study (Chapter III) in which we investigated the effects of tree species on microclimate conditions and nutrient dynamics in that silvopastoral system.

The fourth and fifth chapters of the dissertation correspond to studies conducted in RMNP. These studies were based on the concerns by park managers and the public that the recent increases in elk herbivory and changes in hydrology have contributed to declines in willow (*Salix* spp.) communities in RMNP. We addressed these concerns by conducting field experiments to investigate: (1) the effects of elk herbivory and changes in hydrology on the dynamics of C and N in these ecosystems (Chapter IV), and (2) how elk herbivory and changes in hydrology may affect the availability of different N sources for plants (Chapter V). Based on this research work, we present the management implications from our findings, which give support to park managers during the formulation of policies that may help to preserve ecosystem structure and function in the winter ranges for elk in RMNP.

Despite some of the differences between the two grazing systems in semi-arid northeastern Brazil and Colorado, we expected that the interactions between soils, plants, and herbivores are going to influence nutrient cycling and ecosystem structure in a similar way in both systems. Overall, we expect that the presence and preservation of trees or shrubs in both grazing systems will contribute to the maintenance of ecosystem production by increasing the capture, retention, and availability of nutrients in comparison to heavily disturbed systems where trees or shrubs are absent.

CHAPTER I

Sustainable land use systems for semi-arid northeastern Brazil[1]

Rômulo S.C. Menezes [2] and Everardo V.S.B. Sampaio [3]

---

[1] Manuscript submited for publication in the proceedings of the workshop 'Sustainable Cropping Systems for the Semi-arid Region of Brazil', XII Brazilian Meetings on Soil and Water Management and Conservation, Fortaleza, July 12 to17, 1998. In Press.

[2] Research Fellow of Brazilian CNPq. Soil and Crop Sciences Department and Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, USA. E-mail: romulo@nrel.colostate.edu

[3] Professor, Departamento de Energia Nuclear, UFPE, Av. Prof. Luis Freire 1000, Recife, PE, Brasil, 50740-540. E-mail: sampaio@npd.ufpe.br

Table of Contents

1 - Abstract

The semi-arid region of northeastern Brazil covers an estimated area of 6 to 9 x 10^5 km^{-2}, which corresponds to nearly 10% of the Brazilian territory. Rainfall precipitation, which ranges from 300 to 1000 mm y^{-1} in different areas of the region, is

concentrated in 3 to 5 months, but drought years are common and severe drought periods lasting 3 to 5 years have occurred every 3 or 4 decades. Irrigation is not feasible in at least 95% of the total area of the region, due to the lack of water and/or poor water quality. For this reason, dryland systems are the only alternative for most farmers, but the high climatic variability characteristic of the region significantly affects productivity of dryland systems and leads to socio-economic and environmental degradation. In this paper we present a brief discussion about adaptations of plants to arid environments, followed by a description of the current dryland land-use systems in semi-arid northeastern Brazil, and an analysis of the influences of management techniques and abiotic factors on the sustainability of these systems. We describe and discuss the sustainability of the three main land use practices in semi-arid northeastern Brazil: (1) agriculture; (2) pastoralism; and (3) gathering systems. These three land use activities are generally integrated and practiced simultaneously within each farm, but each may generate a different proportion of the farm income across the four main landscape patch types within the region: (1) hillslopes and plateaus of volcanic origin; (2) hillslopes and plateaus of sedimentary origin; (3) valleys; and (4) high altitude microclimates. Throughout the paper, we suggest alternative management practices and point the need for future studies that could help on the development of sustainable land use systems in semi-arid northeastern Brazil.

2 – Introduction

Both 'sustainable' and 'semi-arid northeastern Brazil' are terms that define a broad range of ideas and that have been widely used in the scientific literature in Brazil. A recent review on sustainable management of soils in northeastern Brazil (Sampaio and Salcedo 1997) summarized the basic concepts around these terms. Among the many definitions of sustainable systems, the authors chose '*systems that maximize the socio-economic benefits for the current generation, while preserving natural resources and the production potential for future generations*'. Furthermore, the semi-arid region of northeastern Brazil, which comprises hundreds of thousands of km^2, is defined primarily by the condition of water stress for plant growth during part of the year. Several parameters are used as indicators to define the boundaries of the region, such as rainfall averages and/or evapotranspiration and temperature averages (Reddy 1993). Regardless of the indicator chosen, it is implicit that the potential evapotranspiration (PET) exceeds rainfall precipitation during most months in a year and for the overall annual average. For this paper, we will consider as the semi-arid region the area defined in SUDENE (1997) as the "Drought Polygon", which includes portions of the nine states of the northeastern region and from the state of Minas Gerais.

Considering the temporal scale, the concepts of 'sustainability' and 'semi-arid region' may appear to be mutually exclusive within land use systems: sustainability implies stability in production and semi-aridity is closely associated with climatic variability and instability. However, the productivity of landuse systems in semi-arid regions may need to be evaluated using longer time scales, preferably based on mechanisms that aim to increase the resilience of production to climatic variability. Based on this rational, in this paper we present a detailed analysis of the development of sustainable land use systems in semi-arid northeastern Brazil, including a discussion on aspects of water availability for plants, plant adaptability to water stress, and the implications of these factors on biomass production. Following this analysis, we relate this discussion to the current production systems in semi-arid northeastern Brazil and suggest alternative practices that may lead to more sustainable landuse systems.

2.1 - Water availability

Optimum plant production requires a steady water supply throughout the growing period, in order to replace plant water losses through transpiration. Water availability will depend on water supply to the soil-plant system and the soil water storage capacity (Hillel 1998). In natural systems, water is supplied by rainfall, which is a phenomenon of stochastic pattern, during events that may last minutes to hours reoccurring at a time scale of minutes to months within annual cycles. Within each system, there may be spatial transferences along slope gradients with water moving from higher to lower landscape positions. Water storage in soil helps to reduce the temporal variability of rainfall patterns, extending the water availability for the plants, and depends mostly on the rooting depth and soil water holding capacity, which is closely related to soil texture.

Values of daily rainfall and temperature for several decades are available for hundreds of counties throughout the semi-arid northeastern Brazil, and regional precipitation and temperature maps are available (FIBGE 1985). These detailed data sets have been used often for climate studies, but very little for studies related to agricultural production in a regional scale. A limited amount of work on the identification of soil water storage capacity at a regional scale has been done to the present day. There have been a few localized studies, but no generalization is possible from this work. Therefore, it is not possible to overlay rainfall and soil water storage capacity maps for the region and, consequently, there are no regional maps of soil water availability for plant production. Research and survey work with the objective of constructing such maps should be prioritized and established as a long-term goal, in order to support decisions on regional land use planning.

One of the simplest soil water availability indicators is the relationship between rainfall precipitation and PET. Because PET does not vary much across the semi-arid region, (1500-2000 mm year^{-1}), rainfall averages have been used as an indicator of soil water availability and were also used to define the boundaries of the semi-arid region. Rainfall averages range from 300 mm per year, at the driest areas of the region, to 1000 mm per year, which is considered the upper limit of the rainfall for the semi-arid region. The majority of the semi-arid region (54% of the area) receives between 500 and 750 mm of rainfall per year, while 29% receive between 750 and 1000 mm per year, and the remaining 17% receive less than 500 mm per year. Soil water stress is not uniform throughout the year, because rainfall precipitation generally occurs for only 2 to 4 months per year (FIBGE 1985), which leads to 6 to 10 months of soil water stress (FIBGE 1977).

Therefore, considering the losses due to evapotranspiration and without taking into account water redistribution within the landscape, plant growth is limited by soil moisture for most of the year, which limits both agricultural and livestock production.

Water availability is not limited only by low levels of rainfall precipitation and high PET, but also by the high spatial and temporal variability of the rainfall events within the region, and this variability may strongly affect the dynamics of ecosystem processes. Caughley et al. (1987), working on arid and semi-arid environments in eastern Australia, identified the coefficient of inter-annual variation (CV) as a good indicator of ecosystem dynamics. Environments that had CV's higher or near 30 %, were dominated by variability rather than by average conditions, whereas in areas with CV's bellow 20 %, animal populations were relatively stable and developed a strong feedback with plant productivity (Ellis, 1994). In certain areas of semi-arid northeastern Brazil, the CV's for annual rainfall averages are greater then 50% (FIBGE 1977). However, despite the high variability in most of the region, there are no studies in semi-arid northeastern Brazil that relate rainfall variability with agricultural or livestock productivity.

Water availability is also affected by the redistribution of water within landscapes. Runoff from upper landscape positions flows to lower landscape areas and eventually escapes through drainage channels. The partition between runoff and infiltration will depend on the intensity of the rainfall events, infiltration rates, and topography. There are available data on the infiltration rates of the soil types within the northeastern Brazil, and also on the intensity of rainfall patterns across the region (FIBGE 1977). The combination of these data sets with topography maps could yield maps of the susceptibility of soils to rainfall erosion (Leprun 1983). In general, the water infiltration rate in soils of semi-arid northeastern Brazil is fairly high, with the exception of Non-Calcic Brown soils (Ustalf), Vertisols (high content of shrink and swell clays), and Solonetz-Solodizados (high sodium content), which have average infiltration rates of 32, 24, 8 mm h^{-1}, respectively. For this reason, runoff rates are usually low, as demonstrated by the data from the main watersheds of the semi-arid northeastern Brazil, in which surface runoff ranges from 3 to 13% and sub-surface runoff ranges from 1 to 5% of total rainfall precipitation (Gondim Filho 1994). Therefore, more than 80% of the rainfall precipitation returns to the atmosphere through evapotranspiration, and less than 20% could be diverted to increase the water inputs in other areas through irrigation. However, because the runoff data cited above corresponds to data from major rivers within the region, the redistribution within landscapes is not included. Therefore, the availability of water in hillslopes will certainly be limited by surface runoff losses, which diminishes water availability and the potential for agricultural production in the hillslopes.

Due to runoff and water redistribution within landscapes, the valleys are the patches of landscape that receive the most water. Mainly for this reason, but also because the soils in the valleys are often deeper than in the hillslopes, the valleys are the prime land for agriculture in the semi-arid northeastern Brazil (Sampaio and Salcedo 1997). It is estimated that the area of valleys within the semi-arid northeastern Brazil should correspond to approximately 15% of the total area of the region (Sampaio and Salcedo

1997). However, to this day, there are no available maps describing the extent of the area and distribution of valleys within the semi-arid northeastern Brazil, even though all the necessary information (such as topography and land-use maps) is available in the government institutions responsible for remote sensing operations. These maps are essential for supporting land-use planning and agricultural operation within the region, therefore every county should be mapped at a scale of at least 1:50,000 or 1:100,000.

A portion of the water lost through runoff eventually accumulates in artificial reservoirs or infiltrates to the groundwater table at different depths, and the remaining water eventually reaches the ocean. The reservoirs can be used to support the water supply to crop plants through irrigation. Large irrigation project sponsored by government agencies can be found next to the major rivers and reservoirs within the semi-arid northeastern Brazil. Currently, these large projects cover an area of approximately 1 % of the total area of the region. Even if all potential areas are put under irrigation, only 5% of the area of semi-arid northeastern Brazil can be irrigated, due to soil and/or water quality limitations (Sampaio and Salcedo 1997). In all the areas where irrigation projects were implemented, agricultural productivity is extremely high and the overall quality of life of the population has increased (Gomes and Vergolino 1995). For these reasons, most government resources towards agriculture have been allocated to these small areas. However, because these systems are not characteristic of the majority of the area of the semi-arid region, we will not further discuss it in this paper.

Redistribution of water within a field or between adjacent fields also has potential to increase water availability for crops. Such systems are utilized in arid and semi-arid regions around the world, and the proportion between the area that captures and area that receives water depends on the water demand and soil infiltration rates (Silva and Porto 1982, Reij et al. 1988). The estimation of the amount of runoff to be redistributed within the landscape must take into account the probabilities of different intensities of rainfall events, water infiltration rates for the soil, and topography. Water infiltration rates will depend on several aspects, such as soil texture, the presence and type of crop residue or cover crop, soil moisture content, and the occurrence, or not, of crusting at the soil surface. The length and degree of the slopes are the main variables related to topography and, within the semi-arid northeastern Brazil, these variables are used to divide hillslopes into two categories: 'short' and 'long' hillslopes (Reij et al. 1988). Short hillslope systems (also called microcapture watersheds) vary between 25 and 100 m in length, according to different authors, and are usually easier and less costly to build. They include structures such as small holes dug with a hoe at the time of sowing, wider trenches or walls built in "V" or "W" shape that direct runoff water to the plants, or contour walls and terraces. Long hillslope systems (macrocapture watersheds) generally include a hillslope for water capture and a lower area (valley) that receives the captured water. These systems require the construction of walls using soil, bricks, or stones, and often also include contour walls and terraces. Generally, long hillslope systems are built in areas with slopes less than 5%. All these systems have a relatively simple design, but may require a considerable amount of labor for construction and maintenance, therefore there has not been much acceptance by the farmers. One of the problems with the government extension programs that promoted such systems, was the lack of incentives for the maintenance of the structures, which did not encourage farmers to keep the systems functioning properly long enough to experience the long-term benefits of these systems. The choice of crops is critical for the success of these systems, and usually better results have been obtained with trees and shrubs rather than with annual crops.

Systems for capture of water in the subsoil of riverbeds can be found in some semi-arid regions around the world (Reij et al. 1988), and are commonly found in semi-arid northeastern Brazil. Also know as "dry reservoirs" these systems have underground dams, with variable permeability to water, that retain the underground flow of water in confined areas. Usually, the area of the reservoirs silts up and forms sites with reasonably deep soils that retain water for long periods, due to the considerably low evaporation rates, when compared to reservoirs that store water above the soil surface. Deep-rooted crops can usually develop well and produce good yields even in years of lower rainfall levels. These systems, most of the time, require a relatively high initial investment but last long and are potentially profitable. In semi-arid northeastern Brazil, the work by Padilha (1994) has demonstrated the viability of such systems.

2.2 – Plant adaptations to arid environments

Most of the dry matter of plants is formed from fixation of atmospheric CO_2 through photosynthesis. The photosynthetic process only works when the plant tissues present a relatively high degree of hydration. Therefore, terrestrial plants, specially those developed in water limited environments, usually present structures to avoid dehydration in the form of external tissues or waxes that reduce water losses. However, the necessary uptake of CO_2 uptake through the stomata is also coupled with water losses. Whenever water availability to the plants is reduced, the stomata close to avoid further water losses, but in the same process CO_2 uptake stops. For this reason, plant productivity in semi-arid regions is usually lower than in more mesic areas (Schlesinger 1997).

In semi-arid environments, plants usually present adaptive mechanisms to coup with water stress. These mechanisms, according to Boyer (1996), are of three main types: (1) rapid growth during the wet season, avoiding water stress; (2) increase in the ability to take up soil water; and (3) tolerance to water stress. We can also add: (4) reduction of water losses during non-photosynthesizing periods; and (5) increase in water use efficiency during photosynthesis. In this paper, we do not intend to discuss in detail any of these processes, but we will briefly comment and give examples of each of these mechanisms by plants found in semi-arid northeastern Brazil.

Even when plants are not photosynthesizing and the stomata are closed, a small amount of water is lost due to the incomplete closure of stomata or by diffusion through the external plant tissues. In the case of plants from mesic environments (some found in irrigated areas in semi-arid northeastern Brazil), these losses could be considerably high and dehydration may occur if water is not replenished constantly. In plants from drier environments these losses are reduced, and could be substantially small, such as for some Cactaceae (*Opuntia ficus-indica*), Bromeliaceae (*Ananas comosus*), and Agavaceae (*Agave* spp). These plants present modifications in the external tissues (waxes, hairs, and position of stomata) that reduce water losses at low metabolic costs.

The reduction of water losses during the process of photosynthesis is characteristic of plants that utilize the crassulacean acid metabolism (CAM) for CO_2 fixation, such as the three families cited above. Essentially all CAM plants evolved in water-limited environments such as in deserts or tree canopies without access to large volumes of soil (Mizrahi et al. 1997). The photosynthesis process of CAM plants is divided in two stages: CO_2 fixation at night, when temperatures are lower and relative humidity is higher, and conversion of CO_2 into carbohydrates during the day. This mechanism has high water use efficiency (WUE), in some case allowing the production of 1 g of dry biomass per 50 g of water used (Boyer 1996). Even though the separation of the two processes may lead to an overall low net primary production, which is generally 3 to 5 times lower than C_3 or C_4 plants, it may allow for survival under water limiting conditions.

Plants that develop exclusively during the wet season are usually annual herbaceous plants that avoid water stress by finishing the cycle within 2 to 4 months. Usually, these plants allocate a great portion of their resources to reproductive structures and very little in mechanisms to coup with water stress. In semi-arid northeastern Brazil these plants are represented by some annual crops and several native species.

The ability to increase the uptake of water from the soil usually involves the development of rooting systems deep into the soil, such as *Ziziphus joazeiro*, or well developed laterally, which is the case of *O. ficus-indica*. Well developed rooting systems do not imply high WUE, but allows the exploration of larger volumes of soil and the utilization of soil water outside the rooting depth of many other plant species growing in the same site. In general, plants from drier environments present a higher proportion of belowground biomass when compared to plants from mesic areas (Holbrook et al. 1995). This mechanism can be observed in plant species with annual cycles, such as pearl millet (*Pennisetum glaucum* (R.) Br.), but it is more commonly found in perennial species, since it requires a high allocation of biomass into the rooting system. Deep rooting systems will only be viable in soils with deep profiles, and it will be more efficient in lower landscape areas with accessible groundwater tables.

Tolerance to dehydration can involve mechanisms such as leaf abscission during the dry season. Some non-deciduous plants can be found in semi-arid northeastern Brazil, but generally the leaves of these species can be shed if water stress becomes more intense (Holbrook et al. 1995). Non-deciduous plants usually have leaves that are adapted to water stress, low osmotic potential in the vacuole, low nutrient concentration, and high weight (Medina 1995).

2.3 – Land use systems in highly variable environments

All the mechanisms of plant adaptation to tropical semi-arid environments indicate a great evolutionary diversity of vegetation in these regions. Tropical semi-arid environments present a greater diversity of life forms than vegetation in tropical humid environments, even though the species diversity is higher in humid regions (Medina 1995). This diversity of life forms allows for the use of resources in different niches, under varied scales of time and space, and leads to a greater stability than in less diverse systems, such as agricultural fields (Chapin et al. 1997, Coughenour et al. 1985). Generally, the greater the functional diversity of a system, the greater the energy flux and the resilience to environmental disturbances (McNaughton 1977). Coughenour et al. (1985) studied energy extraction and use by the Ngisonyoka, a group of nomadic pastoralists of Kenya, and found that the pastoralists could persist in a droughty environment through the diversification of primary and secondary producers. The Ngisonyoka harvested solar energy from a relatively diverse assemblage of energy flow channels, and this diversity allowed them to tolerate abiotic variability and stabilize energy flow during severe droughts, even though energy utilization and conversion efficiencies were generally low. However, because that is a maintenance-oriented rather than a production-oriented system, it promoted ecological stability.

The data on water availability and plant WUE available in the literature for semi-arid northeastern Brazil allow us to perform a gross estimation of the maximum production in the region. In plateaus and hillslopes, rainfall levels minus the losses due to runoff define the water inputs. The greater portion of these areas receives less than 750 mm of rainfall precipitation per year and loses 10 to 20% of this amount as surface runoff. Therefore, only 650 mm or less would be available for evapotranspiration, which corresponds to 6500 Mg ha^{-1} $year^{-1}$. Assuming an average WUE of 1 g of biomass to 1,000 g of water, in order to account for evaporation and other losses, the maximum production in these areas would be around 6.5 Mg ha^{-1} $year^{-1}$, including belowground biomass. There is little data on the productivity of agricultural and natural systems in the region, but the published studies report productivities ranging from 0.5 to 5.0 Mg ha^{-1} $year^{-1}$ (Sampaio 1995).

In the valleys and lower landscape areas, water availability would be higher due to transfers of water within the landscape, therefore the productivity in these patches would range from at least the same productivity of the slopes to the productivity of areas with no water limitation. There is no available data to describe the range of productivities in these areas, therefore we will estimate the amount of water that would be necessary to irrigate a patch of land in a valley for the whole year. If we want to deliver water at the same rate as the PET by collecting runoff water from adjacent fields, the runoff from approximately 10 ha would be required to permanently irrigate an area of 1 ha, which means that approximately 10% or less of the total area of semi-arid northeastern Brazil could be irrigated using runoff from rainfall events. In these irrigated areas, the production of biomass using C_4 plants (sugarcane, for instance) could reach 50 Mg ha^{-1} $year^{-1}$. These very rough estimates may be useful for the establishment of minimum and maximum limits of productivity in systems within semi-arid northeastern Brazil. They are supported by previous estimates that the total area that can be irrigated is under 10% of the area (Sampaio and Salcedo, 1997; Silva Filho, 1988) and that maximum productivity in the non-irrigated areas will be around 5 Mg ha^{-1} $year^{-1}$.

The levels of productivity mentioned above refer to the total net primary productivity. Most agricultural products represent just a portion of the net primary production, generally the reproductive structures (maize, beans, cotton), roots (cassava), or leaves (*Agave*). The ratio between the biomass harvested and the total biomass produced is the harvest index (HI). This index may be higher in herbaceous forage plants and can be 0 (zero) when water stress keeps grain crops from finishing the cycle. The so-called "green-droughts" are common in semi-arid northeastern Brazil, in which grain crops produce a considerable amount of biomass, but end-up with an HI of zero due to severe water stress at a critical period of the reproductive stage. Sampaio and Salcedo (1997) reported HI's of 0.3 for maize and beans in the sub-region of the "Cariris-Velhos", PB. However, as mentioned above, environmental variability can significantly affect the HI's of agricultural crops in semi-arid northeastern Brazil.

In fact, high environmental variability must be accepted as an intrinsic characteristic of semi-arid northeastern Brazil. Until recently, views of community and ecosystem patterns were based on the assumption that these systems were at or close to equilibrium, that is, were stable and had the ability to return to some previous state following perturbation (Wiens, 1984). This view was, in part, a legacy from the ideas of the “balance of nature” from the ancient Greeks (Boecklen and Price, 1990). However, several recent studies have identified non-equilibrium conditions in many ecological systems throughout the globe (Wiens, 1977; Ellis and Swift, 1988; Boecklen and Price, 1990; Strange et al., 1992; Ellis, 1994). As a consequence, the dominant paradigm of stability may lead to the failure of equilibrium-based land use management in systems that are rather dominated by stochastic events (Ellis and Swift, 1988).

For the farmers in semi-arid northeastern Brazil, a relative regularity in agricultural production and economic return is desirable but it is unlikely to be achieved based on the current land use systems. Irrigation may provide such stability, but only in a small area of the region where irrigation systems can be implemented. In the areas where dryland agriculture is the only alternative, the management of cropping systems will only ameliorate the fluctuations caused by environmental variability.

3 – Current land use systems

Currently, most land use systems in semi-arid northeastern Brazil are based on three main activities, which most of the times occur simultaneously within farms: (1) agriculture, based on a few subsistence crops; (2) pastoralism, based mostly on cattle, but also on goats, sheep, and small amounts of other animals; and (3) gathering systems, based mostly on wood gathering for fuel. These activities can be classified into more detailed production systems, according to the scale of production within different areas of semi-arid northeastern Brazil, as described by Sampaio et al. (1987). Each activity may occur within four main types of landscape patches that can be found across semi-arid northeastern Brazil (Silva et al. 1993), namely: (1) hillslopes and plateaus of volcanic origin; (2) hillslopes and plateaus of sedimentary origin; (3) valleys; and (4) high altitude humid microclimates or "Serras"(Sampaio et al. 1997).

Agricultural fields in the valleys and Serras are permanent or semi-permanent, while in the hillslopes and plateaus, slash and burn and shifting cultivation is the main type of agriculture. The classification of fields as permanent or not, is based on the frequency of cultivation. Fields that are cultivated for at least 70% of the time and are left fallow for 30% or less of the time are considered to be permanent (Norman et al. 1984). The main crops that are grown in the region are maize (*Zea mays*), beans (*Phaseolus vulgaris*), cassava (*Manihot esculenta*), and cotton (*Gossypium* spp.) (SUDENE 1997). In the Serras, sugarcane and vegetables are also common. No official survey of the area currently occupied by agriculture in the semi-arid northeastern Brazil has been done, but estimates usually report that less than 10% of the total area is used for agriculture (Sampaio and Salcedo 1997). Since the economic return of agricultural operations is very low, the area planted with crops seems to be decreasing in the less productive landscape patches, such as the hillslopes and plateaus, during the last decades. Pastoralism is one of the main activities in most farms and is ubiquitous to the whole region. Generally, livestock operations are extensive, with low animal density per area and low productivity. A few areas, mostly in the transition from the semi-arid to the more humid regions that surround it, present more favorable conditions for livestock operations and are responsible for most of the milk production within the region. In addition, a few relatively more intensive dairy operations can be found around the cities. A small but growing area of artificial pastures can be found, even though livestock grazes mostly on native vegetation. The use of cultivated *O. ficus-indica* as a dry-season forage is very common. In the valleys and some areas of hillslopes, cultivated forage grasses and *Prosopis juliflora* can be found, and crop residues are almost always used as animal fodder.

The gathering of wood for fuel used to be integrated with the shifting cultivation cycle. The wood from slashed trees was sold at the beginning of the cultivation cycle to help paying for the cost of slashing and planting. However, due to the increase in population and lack of new areas to slash, in combination with a decrease in the time left for fallow, agriculture and wood production are becoming increasingly disconnected. Even though it does not currently happen in a large scale, the slash of forests for the sole purpose of wood gathering (without subsequent cultivation of crops) is expected to increase, as a way to obtain some economic return from the areas in which agriculture is not economically viable. The extraction of waxes from some native trees and fruit production by *Spondias tuberosa* also represent gathering operations within the region that are of relative economic importance.

4 – Sustainability of agricultural systems

4.1 – Agriculture in the hillslopes and plateaus of volcanic origin

Among the three main economic activities within the semi-arid northeastern Brazil (agriculture, pastoralism, and gathering systems), agriculture is the least sustainable, based on the current techniques of production. The total area used for shifting cultivation in the hillslopes and plateaus is likely to decrease in the near future. Agricultural pressure in the past has degraded large portions of these areas, especially those that are unsuitable for cropping but were put under cultivation. Therefore, we may observe an increase in the areas left for fallow, allowing regrowth of native vegetation. Water availability in the hillslopes and plateaus is generally low, which limits crop yields. Since no animals or tractors are used in most of these fields, the economic return per capita is also low, and this low inherent productivities is worsened by the periodic droughts. The productivity of maize and beans, the main crops grown, averages 800 and 390 kg ha^{-1}, respectively, in non-drought years, and small farmers generally do not cultivate more than 2 or 3 ha. Cotton used to be a traditional crop for the hillslopes and plateaus, but decreases in productivity due to soil erosion, and the arrival of boll weevil has lead to a significant reduction in the area planted with cotton. There used to be significantly large areas planted with *Agave* for fiber production, but the low productivities associated with the competition by synthetic fibers has practically eliminated the cultivation of this Cactaceae (Sampaio et al. 1987).

Therefore, unless innovative techniques or crops are introduced into the region, agricultural productivity and economic return in the hillslopes and plateaus will remain low. Consequently, cultivation of subsistence crops may decrease sharply in these areas, because (1) the improvement of roads and transportation in the region will guarantee the supply of low cost, government subsidized subsistence food products; (2) improvements in education opens new opportunities for young people in the cities stimulating migration to the urban centers; and (3) the increasing number of rural workers under government welfare programs will tend to be less likely to venture into the high-risk and labor demanding subsistence cropping operation. In many cases, subsistence cropping in hillslopes and plateaus is only maintained due to the need to secure land tenure by leaving some family members living in the farm, while the others, generally the young men, migrate to the cities to find jobs.

Very little can be done to increase the sustainability of the current agricultural systems in the hillslopes and plateaus. Most of the cultivated crops, especially maize and beans, are not adapted to the environmental conditions of semi-arid northeastern Brazil. Maize is particularly sensitive to water stress during the flowering period (Norman et al. 1984), and not much can be expected from any genetic improvement to improve its resistance to water stress (Boyer 1996). Cultivation of sorghum (*Sorghum bicolor*) and/or pearl millet or at least the rotation of maize and beans with these and other crops such as pigeon pea (*Cajanus cajan*), could increase agricultural productivities. The main problems in the cultivation of sorghum are the higher susceptibility to diseases and insects within the region and the low acceptance by farmers.

Intercropping of alternative crops would increase the diversity of agricultural systems, which could lead to more stability, but no data in semi-arid northeastern Brazil is available regarding such effects. In general, more diverse systems are less likely to be susceptible to diseases and insects. Agrosilvopastoral systems could also have potential for increasing the sustainability and economic return of these systems (Sanchez 1995). However, when intercropping trees with food crops and pastures, it is important to assess if the effects of competition do not overcome the advantages of the presence of the trees (Rhoades 1997). Since most soils in the hillslopes and plateaus are quite shallow, it is likely that agrosilvopastoral systems in semi-arid northeastern Brazil would work best in the valleys.

Increases in the use of tractors could allow the cultivation of large areas per capita and maybe bring increases in the economic return of the operations, but the depth of the soils and the presence of stones in the soil surface limits the area where tractors could be used. In addition, mechanization in these shallow soils could lead to serious erosion problems (Leprun and Silva 1985, Sampaio and Salcedo 1997). The construction of stone walls and contour terraces could help reduce runoff and soil erosion (Reijntjes et al. 1994). However, these structures require intensive labor and may break under the high intensity rainfall events that are common in the region.

Losses of P during the burning of the native vegetation at the beginning of the cropping cycle (Kauffmann et al. 1993) is a problem that may not be noticed in a short term scale, but could significantly affect the sustainability of these systems (Sampaio et al. (1997).

4.2 – Agriculture in the hillslopes and plateaus of sedimentary origin

A great portion of the area of the hillslopes and plateaus of sedimentary origin has sandy soils, which generally have low water retention capacity and low fertility. In the areas with lower rainfall precipitation, agriculture has never been very significant due to the lack of adequate amounts of water for annual crops. In the more mesic areas, cassava and cashew (*Anacardium occidentale*, L.) are commonly found and, on average, produce 10,500 and 250 kg ha^{-1} year^{-1}, respectively. The soils in these areas are generally P deficient, but fertilizers are not used either because of the ignorance of their existence or because of the perception that they do not bring any benefit (Sampaio et al. 1995). Considering the residual effects of the application of chemical fertilizers, the application of small amounts could potentially be profitable, but long-term field trials are still need to determine the extent of these benefits (Sampaio et al. 1995). Application of animal manure generally improves soil fertility and water retention. However, due to the limited availability of manure, usually only small gardens next to the homes receive significant amounts of manure. Areas with flat relief are predominant and are adequate for the use of tractors. In the more hilly areas, the construction of terraces may help reduce runoff and soil erosion (Reijntjes et al. 1994).

The choice of crops to be adopted will depend on the combination of soil fertility and rainfall precipitation of each specific site. In areas of lower soil fertility, such as the Chapada do Araripe, for instance, low soil fertility levels make it impossible to grow successful crops of maize and beans. In these areas, the main crop is cassava, which can produce well in conditions of low soil fertility and moderate water (Norman et al. 1984). Cassava has several characteristics that make it a suitable crop for that area, such as a well developed rooting system, and the option to delay the harvest without deterioration of the roots. Even though cassava grows well in low fertility soils, it responds well to fertilization and removes a significant amount of potassium. Pigeon pea and pumpkin are also grown during the first year after the slash of the native vegetation, when soil fertility levels are still high. Intercropping sorghum or, more importantly, pearl millet with maize and beans could increase the productivity of these systems, due to the higher ability of these plants to grown on dry, low fertility soils (Norman et al. 1984).

Cashew trees are grown in the more mesic areas of sedimentary origin, mostly in the zones of transition to more humid regions. It is grown as a monoculture or intercropped with some grain crops or in association with livestock. Cashew nuts are a valuable commodity, but the cost of transportation and price fluctuations in the international market can be serious obstacle to the profitability of this crop.

Some patches within the areas of sedimentary origin are originated from calcareous parent material and present soils with good fertility and moderate water retention capacity. One example of these patches is the region of Irecê, in the state of Bahia, where beans are the dominant crop. Productivities could possibly be increased by the application of chemical fertilizers or by an improvement in the efficiency of N_2 fixation by the main cultivars utilized.

4.3 – Agriculture in the valleys

The suitability of dryland agriculture in the valleys depends on the amount of water transferred from the slopes and retained in the soils in the valleys within each watershed. There are no official numbers on the total area or distribution of valleys within semi-arid northeastern Brazil, even though these represent the best soils for agriculture. Despite the higher availability of soil water, agriculture is generally performed in the valleys mostly during the wet season. However, a small portion of the valleys may present the necessary conditions for continuous agriculture.

Usually, a relatively high diversity of crops may be found in the valleys, but the main crops are maize and beans, and also dwarf cotton, which has an average yield of 480 kg ha^{-1}. Further increases in the diversity of crops could increase the sustainability of these systems, if competition for soil moisture is not very intense between the intercropped plants, and the introduction of N fixers may increase soil fertility. Maybe the introduction of sorghum or millet could increase yields, because of the relatively high productivity of these crops under conditions of water stress. The diversification of functional groups with the introduction of trees or shrubs could also increase the productivity of these systems, by increasing the capture of water and nutrients from deeper soil layers (Rhoades 1997, Sanchez 1995). Moderate densities of trees and a regular pruning regime could allow for the increase of soil organic mater levels in these systems (Menezes and Salcedo 1999, Sanchez 1995). Trees should always be preserved along the river and streams, in order to reduce the risks of soil erosion. Oiticica (*Licania* *rigida*, Benth.) trees were, in the past, preserved along the rivers, mainly in the states of Ceara and Rio Grande do Norte, but nowadays are being eliminated from the landscape.

An alternative to increase water availability could be the adoption of techniques to redistribute the intercepted rainfall within the fields (Silva and Porto 1982, Reij et al. 1988, Reijntjes et al. 1994). Some of these techniques are: (1) deeper and wider sowing pits; (2) clearing and impermeabilization of the soil in the areas of water capture; (3) construction of large ridges with a "V" or "W" shape to direct water to the sowing pits; and (4) construction of "dry" reservoirs, as discuss previously in this paper. In addition, soil cover usually helps preventing water evaporation. Several materials may be used as soil cover, such as crop residues, plastic, or stones. Usually, farmers do not apply any soil cover, mostly because of the high value of crop residues as animal fodder and the high labor intensity or cost required by other materials.

The soils of the valleys are usually moderately fertile, but can be limited by the availability of N and P, especially under continuous cultivation (Sampaio et al. 1995). The levels of soil organic matter are generally low, and practices such as the utilization of crop residues as animal fodder and the failure to return animal manure to the fields contribute to further decreases in soil organic matter levels. The use of fire to eliminate regrowth of native vegetation should be avoided, in order to preserve the C and N in the aboveground material within the system, and the use of residues as soil cover, or cover crops should be encouraged.

Tractors are used, but only rarely and in a limited number of farms. Increases in mechanization could increase productivity per capita but would likely decrease the demand for hired labor within farms and increase unemployment in some areas of the region.

An important factor related to the sustainability of agriculture in the valleys is the integration of crops and livestock and the 'competition' between forage or crop production. The partitioning of the area used for food crops or for forage production depends on the size of the total area of valley available within a farm. Small valleys in large farms are usually used for forage production, while valleys in small farms are primarily dedicated to agricultural crops. Large valleys in large farms usually have both food crops and forages, but the partition between these depends on the water availability and the main type of activity within the farm (agriculture or livestock production).

4.4 – Agriculture in the high altitude humid microclimates

High altitude humid microclimates (Serras) receive significantly higher amounts of rainfall precipitation than the surrounding areas. Agriculture is usually practiced continuously or semi-continuously and population densities are quite higher than the remaining areas of semi-arid northeastern Brazil. The Serras are usually located in the areas of transition between the semi-arid region and more mesic areas of other regions, in areas of sedimentary as well as volcanic origin. However, there has not been yet a precise demarcation of all these areas in the maps of the semi-arid northeastern region.

These areas tend to be hilly and, because soils are generally shallow, soil erosion may become a serious problem (Sampaio and Salcedo 1997). The use of soil conservation practices is not common, but there have been reports of farms that used large stone walls to contain soil erosion. Fruit trees, which provide permanent soil cover, and vegetables grown with intensive labor in small plots, have demonstrated to decrease erosion rates in those areas (Freitas et al. 1981). Policy makers, through market incentives, should encourage increases in the area grown with these crops.

5 – Sustainability of pastoral systems

Livestock production was the basis for the colonization of semi-arid northeastern Brazil by Europeans, and to this day it continues to be the most significant economic activity. Livestock production is less affected by water stress than agriculture, being primarily dependent only on the amount of water necessary for the animals to drink. Forage production also depends on water availability, but several mechanisms contribute to increase the resilience of livestock operations to water stress: (1) the reduction in the availability of forage may lead to animal weight loss, but weight gain may compensate these losses with the arrival of rains; (2) the harvest index of forage crops is usually high, and biomass production by these plants do not depend on water availability during any specific developmental stage; (3) at any given time when rain stops, the forage biomass produced can be used, therefore droughts may reduce forage yields but not as dramatically as for grain production; (4) a great diversity of plants may be used for forage production in semi-arid northeastern Brazil, including several genetically improved herbaceous or woody native species, which allows for a more efficient use of the available resources; and (5) forage can be imported or animals can be exported to other areas in the years of very severe droughts.

Mostly for these reasons, livestock production is a more sustainable system than agriculture in semi-arid northeastern Brazil. The stability of livestock operations in this region is usually increased by the presence of more than one species of animal, such as cattle, goats, sheep, horses, and donkeys. In addition, pigs and poultry are also commonly raised in farms in the region, but generally only in a small scale, next to the house, to serve as a supplement to the diet of the family. Livestock production is the main activity in the hillslopes and plateaus of volcanic and sedimentary origin. The majority of the non-cultivated area within the semi-arid northeastern covered with native vegetation, which corresponds to 90% of the total area, is used as rangeland. Stocking rates are low, due to low production of forage biomass by the native vegetation. Forage production can be increased in the native vegetation by selective thinning and pruning, as demonstrated by the studies of Araújo Filho and Carvalho (1996). The implementation of artificial pastures after the slash of the native vegetation is common, since it can be easily done with tractors. However, areas that have been completely cleared of trees for pasture implementation may have severe decreases in productivity after a few years after the clearing, due to sharp decreases in soil organic matter and nutrients (Tiessen et al. 1994).

In addition to forage grasses, *O. ficus-indica* is also cultivated in slopes and plateaus of volcanic origin to be used as a forage reserve during the dry-season. The use of *O. ficus-indica* significantly increases the resilience of livestock operations to fluctuations in water availability, and can produce relatively high amounts of biomass (Mizrahi et al. 1997). The cultivation of *O. ficus-indica* in large scale will depend on the creation of a permanent market for this forage, which could be supported by companies that produce animal feed in search of an alternative cheaper than corn.

Chemical fertilization of artificial pastures is not common, and native pastures never receive any type of fertilization. It is likely that, similar to the response of crop plants, pastures could respond to the application of P in the areas of sedimentary origin with low soil fertility. Usually, the animals need to receive supplements of P and Ca, otherwise severe deficiencies of these elements may occur.

Crop residues from valleys or other areas are used as animal fodder in the farms that carry both livestock and agricultural production and, in the exclusively agricultural farms, they are sold to pastoralists. The removal of crop residues may lead to a reduction on the levels of soil organic matter, but there are no studies on the dynamics of soil organic matter under different land-use types in semi-arid northeastern Brazil.

6 – Sustainability of gathering systems

The harvest of wood for fuel is usually not as affected by the inter-annual rainfall variability characteristic of semi-arid northeastern Brazil, since it integrates the growth of plants during several years. The ability of the native vegetation to alternate periods of growth and stagnation depending on water availability, and to withstand long periods of water stress, allows the constant production of biomass under severely stressful conditions. The vigorous resprouting after the slash of native vegetation contributes to the rapid regrowth after a cropping cycle (Sampaio et al. 1998). The sale of wood as fuel corresponds to the second most profitable use of the native vegetation, after the use of the vegetation as forage for cattle. In the past, wood extraction was associated with the shifting cultivation cycle, and was an important income to help paying the initial costs of planting. However, in the last few years, the demand for fuel wood by cement and brick factories, along with other types of industry, has led to an increase in the rates of wood extraction from native forests. Shorter fallow periods have led to decreases in wood productivity in the last few years. In several states, studies about the extent of the use of wood as fuel have been conducted and this data is available (PNUD - FAO - IBAMA - SUDENE 1993).

After most of the wood is removed from a site, the small branches and litter are burned if agriculture or the implementation of pastures will follow. The fire facilitates the operations of planting, but may lead to significant losses of C, N, and P from the above ground biomass (Kauffman et al. 1993). Vegetation regrowth and input from N fixation can replenish losses of C and N, but the losses of P are less reversible. Short-term effects of P losses are difficult to detect within the few cropping cycles during the lifetime of a farmer, but in the long-term these losses may affect the sustainability of these systems.

Controls on the frequency and intensity of wood harvesting and burning should be imposed through policy regulation. The frequency of fires and wood gathering should be determined based not only on the subsequent biomass production or the preservation of soil P during the fire, but should also allow the full regeneration of the native plant communities to a late succession stage in some areas, as a way to guarantee the maintenance of the biodiversity of plant species. Late succession vegetation patches present plant communities with varied phenological states throughout the year (Machado et al. 1997), which may benefit faunal diversity and ecosystem structure and function in the region.

7 – Conclusions

Due to the extremely high variability of inter-annual rainfall precipitation levels, the productivity of dryland agriculture and livestock production systems in semi-arid northeastern Brazil is characterized by sharp fluctuations. These fluctuations negatively affect the sustainability of those systems, leading to decreases in human development levels and environmental degradation. Alternative land-use systems should aim at the increase in the resilience of the production systems, reducing the impacts of abiotic disturbances on the productivity of such systems.

In a general way, the first steps toward the development of alternative systems, should aim at the implementation of techniques to increase water capture and reduce water losses, in order to increase water availability for plants. Productivities may also be increase by the adoption of crops with high water use efficiency, and that are tolerant of water stress periods within the growing season that are common in semi-arid northeastern Brazil. Increases in the functional diversity of plant and animals communities may also contribute to increase the resilience of land use systems to abiotic disturbances, by allowing an optimization in the use of resources available at different points in time and space.

In a more detailed analysis, the specific techniques that could increase the sustainability of the three main economic activities in semi-arid northeastern Brazil (agriculture, pastoralism, and gathering systems) may vary within the four main landscape types (valleys, hillslopes and plateaus of volcanic or sedimentary origin, and high altitude microclimates), depending on the socio-economic and environmental characteristics of each landscape type.

The current dryland agricultural systems represent the least sustainable economic activity within semi-arid northeastern Brazil, mostly due to the susceptibility of the currently grown subsistence crops to rainfall variability. Very little can be done to increase the sustainability of such systems, but the adoption of crops more adapted to conditions of water stress, such as sorghum, pearl millet, or pigeon pea, may improve yields. Increases in the diversity of crop plants through intercropping of drought resistant plants and traditional crop plants may be a viable option in terms of acceptance by the farmers.

Agrosilvopastoral systems may also contribute to increases in economic return to the farmers and help to preserve soil organic matter and fertility in production systems in the region. However, additional studies are needed to determine the effects of complementarity and competition by different tree species when intercropped with pastures or food crops.

Usually, pastoral systems are not as affected by the inter-annual variability of rainfall precipitation. Because of this characteristic, pastoralism is the main economic activity in the hillslopes and plateaus of volcanic and sedimentary origin, which correspond to the driest patches within semi-arid northeastern Brazil. The majority of the 90% of the area of semi-arid northeastern Brazil that is not cultivated with food crops each year are utilized as range for livestock. Due to current declines in the area destined to shifting cultivation every year, the area used as rangeland may increase even further in the future. The establishment of artificial pastures is common, as well as the cultivation of *Opuntia*. This Cactaceae has good potential as a reserve forage crop to be used during the dry-season, due to relatively high productivity and quality of the cladodes as animal feed.

Wood gathering from native vegetation also represents an economic activity that is fairly resilient to the high rainfall variability, since it integrates the vegetation growth of many years. It is based on the ability of the native plants to stop growing during periods of water stress and recuperate quickly and grow fast when conditions are favorable. However, the sustainability of wood gathering systems will depend on the environmental characteristics and management practices within each specific landscape patch of semi-arid northeastern Brazil. Policy controls should be implemented in order to guarantee the appropriate regeneration of the vegetation during fallow, in order to allow the maintenance of ecosystem structure and function.

Policy-making will play an important role in the implementation and control of more sustainable land use systems in semi-arid northeastern Brazil. However, a tight integration between farmers, extensionists, scientists, and policy makers is essential for the success and adoption of alternative techniques. Different mechanisms, such as incentives to the creation of markets for new products, along with price controls for new and traditional products, and the establishment of environmentally sound rules for controlling land use practices, will positively influence the sustainability of land use systems in semi-arid northeastern Brazil.

8 – References

Araújo Filho, J.A. and F.C. Carvalho. 1996. Desenvolvimento sustentado da caatinga. pp.125-133. In: Alvarez V.H., L.E.F. Fontes, and M.P.F. Fontes. O solo nos grandes domínios morfoclimáticos do Brasil e o desenvolvimento sustentado. Viçosa. SBCS - UFV.

Boecklen, W.J. and P.W. Price. 1990. Nonequilibrial community structure of sawflies on Arroyo Willow. Oecologia 85:483-491.

Boyer, J.S. 1996. Advances in drought tolerance in plants. Adv. Agron. 56:187-218.

Caughley, G., N. Shepherd, and J. Short. 1987. Kangaroos: their ecology and management in sheep rangelands of Australia. Cambridge University Press, New York.

Chapin, F.S., B.H. Walker, R.J. Hobbs, D.U. Hooper, J.H. Lawton, O.E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science 277:500-504.

Coughenor, M.B., J.E. Ellis, D.M. Swift, D.L. Coppock, K.A. Galvin, J.T. McCabe, and T.C. Hart. 1985. Energy extraction and use in a nomadic pastoral ecosystem. Science 230:619-625.

Ellis, J. and K.A. Galvin. 1994. Climate patterns and land-use practices in the dry zones of Africa. Bioscience 44:340-349.

Ellis, J. 1994. Climate variability and complex ecosystem dynamics: implications for pastoral development. In: Scoones, I. (ed). Living with uncertainty: new directions in the pastoral development in Africa. Intermediate Technology Publications, Northern Yorkshire.

Ellis, J.E. and D.M. Swift. 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. J. Range Manag. 41:450-459.

FIBGE. 1977. Geografia do Brasil. Região Nordeste. Fundação Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

FIBGE. 1985. Atlas Nacional do Brasil. Região Nordeste. Fundação Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

Freitas, M.B., E.N. Choudhury, and C.M.B. Faria. 1981. Manejo e conservação de solo no agreste pernambucano. Boletim de pesquisa 6. Petrolina, CPATSA-EMBRAPA. 44 p.

Gomes, G.M. and J.R. Vergolino. 1995. A macroeconomia do desenvolvimento nordestino: 1960/1994. Recife, Instituto Economistas de Pernambuco. p.6-160.

Gondim Filho, J.G.C. 1994. Sustentabilidade do desenvolvimento do semi-árido sob o ponto de vista dos recursos hídricos. Uma estratégia de desenvolvimento sustentável para o Nordeste. Projeto Áridas, Brasília. 126 p.

Hillel, D. 1998. Environmental soil physics. Academic Press, London, pp. 771.

Holbrook, N.M., J.L. Whitebeck, and H.A. Mooney. 1995. Drought responses of neotropical dry forests. pp. 243-276. In: Bullock, S.H., H.A. Mooney, and E. Medina (eds.) Seasonally dry tropical forests. Cambridge University Press, Cambridge.

Kauffman J. B., R.L. Sanford, D.L. Cummings, I.H. Salcedo, and E.V.S.B. Sampaio. 1993. Biomass and nutrient dynamics associated with slash fires in neotropical dry forests. Ecology 74: 140-151.

Leprun, J.C. and F.B.R. Silva. 1995. Les degradations des sols en régions semi-arides au Brésil et en Afrique de l'Ouest. Compaison et conséquences. Suggestions sur leurs réhabilitations respectives. In: Pontanier, R.; M'Hiri, A.; Akrimi, N.; Aronson, J.; Le Floc'h, E. L'homme peut-il refaire ce qu'il a defait? Paris, John Libbey Eurotext. p. 267-291.

Leprun, J.C. 1983. Relatório de fim de convênio de manejo e conservação do solo no nordeste brasileiro (1982-1983). Recife, SUDENE. 290p.

Machado, I.C., L.M. Barros, and E.V.S.B. Sampaio. 1997. Phenology of caatinga species at Serra Talhada, PE, Northeastern Brazil. Biotropica 29:57-68.

McNaughton, S.J. 1977. Diversity and Stability of ecological communities – comment on the role of empiricism in ecology. Am. Nat. 111:515-525.

Medina, E. 1995. Diversity of life forms of higher plants in neotropical dry forests. pp. 221-242. In: Bullock, S.H., H.A. Mooney, and E. Medina (eds.) Seasonally dry tropical forests. Cambridge University Press, Cambridge.

Menezes, R.S.C. and I.H. Salcedo. 1999. Influence of tree species on the herbaceous understory and soil chemical characteristics in a silvopastoral system in semi-arid Northeastern Brazil. Revista Brasileira de Ciência do Solo. In Press.

Mizrahi, Y., A. Nerd, and P.S. Nobel. 1997. Cacti as crops. Horticultural Reviews 18: 291-320.

Norman, M.J.T., C.J. Pearson, and P.G.E. Searle. 1984. The ecology of tropical food crops. Cambridge University Press, Cambridge. 369 p.

Padilha, J.A. 1994. Programa "Base zero" do estado da Paraíba. pp.470-493. In: Anais da Conferência Nacional de Desertificação, Fortaleza, 1994. Brasília, Fundação Grupo Esquel Brasil.

PNUD-FAO-IBAMA-SUDENE. 1993. Documentos e relatório final. I Reunião sobre o Desenvolvimento do Setor Florestal do Nordeste. PNUD-FAO-IBAMA-SUDENE, Recife.

Reddy, S.J. 1983. Climatic classification: the semi-arid tropics and its environment - a review. Pesp. agropec. bras. 18:823-847.

Reij, C., P. Mulder, and L. Begemann. 1988. Water harvesting for plant production. Technical Paper 91. The World Bank, Washington. 123 p.

Reijntjes, C., B. Haverkort, and A. Walters-Bayer. 1994. Agricultura para o futuro: uma introdução à agricultura sustentável e de baixos insumos externos. Rio de Janeiro, ES-PTA. 324 p.

Rhoades, C.C. 1997. Single tree influences on soil properties in agroforestry: lessons from natural forest and savanna ecosystems. Agrofor. Syst. 35: 71-94.

Sampaio, E.V.S.B. and I.H. Salcedo. 1997. Diretrizes para o manejo sustentável dos solos brasileiros: região semi-árida. Congresso Brasileiro de Ciência de Solo, 26, Rio de Janeiro, 1997. Anais dos Simpósios, CD-ROM, 33 p.

Sampaio, E.V.S.B. Overview of the Brazilian caatinga. 1995. pp. 35-63. In: Bullock, S.H., H.A. Mooney, and E. Medina (eds.) Seasonally dry tropical forests. Cambridge University Press, Cambridge.

Sampaio, E.V.S.B., A.C.D. Antonino, H. Tiessen, and I.H. Salcedo. 1997. Utilização de fertilizante nitrogenado (^{15}N) em cultura de subsistência no semiárido nordestino.

IV Encontro Nacional de Aplicações Nucleares, Poços de Caldas, 1997. Anais, vol. 2, p.803-808. CD-ROM.

Sampaio, E.V.S.B., E.L. Araújo, I.H. Salcedo, and H. Tiessen. 1998. Regeneração da vegetação de caatinga após corte e queima, em Serra Talhada, PE. Pesq. Agropec. Brasil., 33: 621-632.

Sampaio, E.V.S.B., I.H. Salcedo, and F.B.R. Silva. 1995. Fertilidade de solos do semi-árido do Nordeste. Reunião Brasileira de Fertilidade dos Solos e Nutrição das Plantas, 21, Petrolina, 1994. pp.51-71. In: Anais do Simpósio: Fertilizantes: insumo básico para a agricultura e combate à fome. Petrolina, EMBRAPA-CPATSA/SBCS.

Sampaio, Y, E.V.S.B. Sampaio, and E. Bastos. 1987. Parâmetros para a determinação de prioridades de pesquisas agropecuárias no Nordeste semi-árido. Recife, Departamento de Economia -PIMES/UFPE. 224 p.

Sanchez, P.A. 1995. Science in agroforestry. Agrofor. Syst. 30:5-55.

Schlesinger, W.H. 1997. Biogeochemistry: An analysis of global change. Academic Press, San Diego, USA. 588 p.

Silva, A.S. and E.R. Porto. 1982. Utilização e conservação dos recursos hídricos em áreas rurais do trópico semi-árido do Brasil. Tecnologias de baixo custo. Documento 14. Petrolina, EMBRAPA-CPATSA. 128 p.

Silva, F.B.R., G.R. Riché, J.P. Tonneau, N.C. Souza Neto, L.T.L. Brito, R.C. Correia, A.C. Cavalcanti, F.H.B.B. Silva, A.B. Silva, J.C. Araújo Filho, and A.P. Leite.

1993. Zoneamento agroecológico do nordeste: diagnóstico do quadro natural e agrossocioeconômico. Petrolina, EMBRAPA - CPATSA/CNPS. 2v.

Silva Filho, J.C. de. 1988. Tecnologia agrícola para o semi-árido brasileiro. Recife, FUNDAJ, Editora Massangana. 102 p.

Strange, E.M., P.B. Moyle, and T.C. Foin. 1992. Interactions between stochastic and deterministic processes in stream fish community assembly. Environm. Biol. Fishes 36:1-15.

SUDENE. 1997. Região Nordeste em números. Recife, SUDENE. 62 p.

Tiessen, H., I.H. Salcedo, and E.V.S.B. Sampaio. 1992. Nutrient and soil organic matter dynamics under shifting cultivation in semi-arid northeatern Brazil. Agriculture, Ecosystems and Environment 38:139-151.

Wiens, J.A. 1977. On competition and variable environments. Am. Sci. 65:590-597.

CHAPTER II

Influence of tree species on the herbaceous understory and soil chemical characteristics in a silvopastoral system in semi-arid northeastern Brazil[1]

Rômulo S.C. Menezes[2] and Ignácio H. Salcedo[3]

---

[1] Manuscript submitted to Revista Brasileira de Ciência do Solo (Brazilian Journal of Soil Science). In Press.

[2] Research Fellow of the Brazilian CNPq, Soil and Crop Sciences Department and Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, 80523, USA. Phone: 970-491-2162, fax: 970-491-1965. E-mail: romulo@nrel.colostate.edu

[3] Professor Titular, Departamento de Energia Nuclear, Universidade Federal de Pernambuco, Av. Prof. Luís Freire, 1000, Cidade Universitária, Recife, PE, Brasil. Phone: 081-271-8252. E-mail: salcedo@npd.ufpe.br.

Abstract

Studies from some semi-arid regions of the world have shown that trees promote the formation of resource islands and increase the sustainability of silvopastoral systems. No data is available in this respect for tree species of common occurrence in semi-arid NE Brazil. In the present study, three tree species (*Ziziphus joazeiro*, *Spondias tuberosa*, and *Prosopis juliflora*) found within *Cenchrus ciliaris* pastures were selected to evaluate differences on herbaceous understory and soil chemical characteristics between samples collected beneath tree canopies and in open grass areas. Transects extending from the tree trunk to open grass areas were established, and soil (0-15 cm) and herbaceous understory (standing live biomass in 1 m^{-2} plots) samples were taken at 0, 25, 50, 100, 150, and 200% of the canopy radius. Higher levels of soil C, N, P, Ca, Mg, K, and Na were found under the canopies of *Z. joazeiro* and *P. juliflora* trees compared to open grass areas. Only soil Mg and organic P were higher under the canopies of *S. tuberosa* trees, in comparison to open grass areas. Herbaceous understory biomass was significantly lower under the canopy of *S. tuberosa* and *P. juliflora* trees (107 and 96 g m^{-2}, respectively), relatively to open grass areas (145 and 194 g m^{-2}). No herbaceous biomass differences were found between *Z. joazeiro* canopies and open grass areas (107 and 87 g m^{-2}, respectively). Among the three tree species studied, *Z. joazeiro* was the one that presented the greatest potential for the establishment of sustainable silvopastoral systems in our study site, since it promoted nutrient accumulation in the soil without negatively affecting herbaceous understory biomass, relatively to open grass areas.

Index terms: *Prosopis juliflora, Zyziphus joazeiro, Cenchrus ciliaris, Spondias tuberosa.*

Introduction

The semi-arid region of northeastern Brazil covers an estimated area of 6 to 9 x 10^5 km^2 (Sampaio et al., 1995), which represents nearly 10% of the Brazilian territory. The main vegetation type is deciduous thorn forest or thorn bush savanna known as caatinga. Rainfall precipitation, which ranges from 300 to 1000 mm y^{-1} in different areas of the region, is concentrated in 3 to 5 months, but drought years are common and severe drought periods lasting 3 to 5 years have occurred every 3 or 4 decades (Sampaio et al., 1995). The most common land use practices are based on shifting cultivation, establishment of livestock pastures, and fuel wood harvest (Kauffman et al., 1993), but productivity is usually very low (Sampaio et al., 1995).

Low agricultural productivities are mostly a consequence of practices such as the slash and burn of the native vegetation, applied by the majority of the farmers in the region. The use of fire to eliminate vegetation residues leads to significant decrease in soil nutrients (Salcedo et al., 1997). As a consequence of these nutrient losses, after two or three years the depletion of yields forces the farmers to abandon the land and clear another area to keep farming. The area left to fallow eventually recovers its natural fertility after several years (Tiessen et al., 1992). However, due to the increase in population and reduction of land availability, several farmers return to the cultivated areas before allowing enough time of bush fallow. This fact helps to increase environmental degradation, because crop development is poor and the soil gradually loses its capacity to support vegetation growth.

The preservation of trees during the slash of the native vegetation may lead to more sustainable dryland cropping systems for the semi-arid northeastern Brazil, where "sustainability" is used to define systems capable of supporting the local population while maintaining biodiversity and soil productivity for future generations. Based on studies from other semi-arid regions of the world, it seems that agrosilvopastoral systems have potential to fulfill these requirements. These studies have shown the beneficial effects of trees on agropastoral systems, represented by an improvement in soil nutrient and moisture levels, which resulted in an increased herbaceous understory biomass production under trees in comparison to open areas. These differentiated areas are known as resource islands (Reynolds et al., 1990), isles of fertility (West, 1981), or fertile islands (Halvorson et al., 1995). Several mechanisms are involved in the formation of these differentiated zones, including increased litterfall, reduction of soil temperature, and inputs via animals (Rhoades, 1995; Belsky et al., 1993; Weltzin & Coughenour, 1990; Farrel, 1990; Tiedemann & Klemmedson, 1973). However, in some cases, trees do not have any significant effect on soil and herbs (Belsky et al., 1993), due to either the characteristics of the tree species, which is related to aspects such as the ability to associate with nitrogen fixing organisms, or the characteristics of the environment, such as amount of rainfall.

In the last few years, some studies in the semi-arid region of Brazil have been conducted in order to determine optimum tree density when thinning the caatinga to establish pastures for livestock (Araújo Filho, 1990; Silva et al., 1995). Higher plant biomass production was observed with a tree density corresponding to 30% of ground cover, resulting in significant increases in meat production of goats, cattle and sheep. The questions addressed in these studies brought a significant contribution to the development of alternative dryland agricultural systems in the semi-arid, particularly regarding the role of trees in these systems. However, there are no available data on the dynamics of soil characteristics after tree density reduction, which is a crucial aspect to be considered in the assessment of sustainability.

The objective of this work was to quantify the differences in herbaceous understory characteristics and concentrations of soil nutrients between open grass areas and areas under the canopies of Z. *joazeiro*, P. *juliflora*, and S. *tuberosa*, in sites where: 1) native tree species were preserved during slash of the native vegetation for the establishment of buffel grass pastures, and 2) native vegetation was completely eliminated and buffel grass pastures were established intercropped with *P. juliflora* trees.

Material and methods

Three tree species were selected for the study: 1) *Spondias tuberosa* Arruda, a deciduous native species, which is always preserved during the slashing of the caatinga; 2) *Ziziphus joazeiro* Mart., a non-deciduous native species, also preserved during slashing; and 3) *Prosopis juliflora* (SW.) DC., an introduced leguminous species intensively cultivated in the region, whose pods are a forage source for animals during the dry season.

Description of Study Area

The study was conducted in 1996 in a beef cattle ranch at Custódia, PE (8° 14'S and 37°45'W). Average rainfall precipitation at the site is 740 mm year^{-1} (data from the records of the ranch) generally occurring from December to May. The area of the ranch was originally covered with native vegetation, which was slashed with tractors in 1984, followed by manual removal of the remaining bushes and tree stumps. The ranch has a total of three thousand hectares of *P. juliflora* orchards planted with a spacing of 10 x 10 m, intercropped with buffel grass (*Cenchrus ciliaris*), which is a perennial, drought resistant forage grass native to Africa. There were other large areas of established buffel grass pastures not planted with *P. juliflora* where some native tree species, such as *Z. joazeiro* and *S. tuberosa*, had been spared during the slash of the caatinga and left with an average distance of around 30 to 40 m between trees. The *P. juliflora* orchards were 12 years old, and all the native tree species selected were over 50 years old, according to the locals. The orchard area and that with native tree species represent different situations in terms of potential differences in soil and herbaceous characteristics within each system, since *P. juliflora* trees were planted at the same time of the pastures while the native trees were already present when the pasture was established.

The pastures never received any chemical fertilization and were mowed with tractors every two years at the end of the dry season for controlling invasion by woody species. No fire is used in the management of the pastures. Animal density in the farm fluctuates around 0.17 animal ha^{-1}, which is a relatively low density for buffel grass pastures in the region. Low animal density associated with high tree density in the pastures helped to reduce potential animal effects on the formation of fertility islands under the trees. The dominant soil type in the area is Bruno não-cálcico (Ustalf), with extensive patches of Regossolo (Orthent) in the lower parts of the landscape. Both soil types have a sandy loam texture in the top layer. The sampling areas were predominantly flat, with slopes ranging from 0 to 3%.

Soil and herbaceous understory sampling

Seven trees of each species were selected, giving preference to isolated mature trees. The selected individuals of *P. juliflora* were all located in areas of Bruno não-cálcico, while those of *Z. joazeiro* were in areas of Regossolo. Individuals of *S. tuberosa* are usually found in areas with both soil types, so four trees were selected in areas of Regossolo and three in Bruno não-cálcico areas. In each tree, canopy radius was determined by averaging the distance measured from the trunk to the canopy edge in four different directions. Soil samples were collected with a pickaxe and a shovel to a depth of 15 cm, and herbaceous understory samples were collected by clipping all standing live biomass in $1 m^2$ plots. Both soil and plant samples were collected in a transect oriented to the north at distances which corresponded to 0, 25, 50, 100, 150, and 200% of the canopy radius, starting from the trunk. Mean canopy radius was 6.6 ± 0.5, 4.5 ± 0.5, and 5.3 ± 0.8 m for *Z. joazeiro*, *P. juliflora*, and *S. tuberosa* trees, respectively.

Herbaceous understory samples were taken at each sampling position of the transects in $1 m^2$ (1,4 x 0,7 m) plots positioned transversely in relation to the transect. All standing live biomass was clipped to ground level and placed in paper bags. Following an oven-dry period of 48 h at 60 °C, forbs and grasses were separated and their individual dry matter weights recorded.

Soil and plant tissue analysis

Soil samples were air-dried and passed through a 2 mm sieve. Organic P was estimated from the 0.5 mol L^{-1} H_2SO_4 extractable P in a soil sample ignited at 550 °C and an unignited sample (Olsen and Sommers, 1982). Inorganic P was extracted using resin bags (Sibbesen, 1977) and determined colorimetrically (Murphy and Riley, 1962). Exchangeable bases were extracted with 1 mol L^{-1} NH_4Cl. Calcium, Mg, and K in the filtered extracts were determined by atomic absorption and Na by flame emission spectrophotometry. Soil pH was measured in a 2.5:1 (water:soil) suspension. The sand content was determined by passing a dispersed sample through a 0.053 mm sieve, after pretreatment with sodium hexametaphosphate solution. In a subsample ground to pass through a 0.25 mm sieve, total C was determined by wet oxidation-diffusion (Snyder and Trofymow, 1984) and total N by Kjeldahl digestion (Bremner and Mulvaney, 1982). In four trees of each species, soil bulk density was measured by taking two additional soil cores from both under canopy and open grass areas. The cores were 7.5 cm in diameter and 10 cm in height, and were taken from the 2 to 12 cm soil layer. Bulk densities of total soil and of soil fines (< 2 mm) were calculated for each soil type and sampling position in relation to the tree.

Plant samples were ground and subsamples digested with a sulfuric acid-hydrogen peroxide mixture (Thomas et al., 1967). The digests were analyzed for N and P by autoanalysis (Thomas et al., 1967), and for Ca, Mg, and K by atomic absorption spectrophotometry.

Statistical analysis

Statistical analyses were performed using the SAS Statistical Package (SAS, Version 6.12, SAS Institute Inc., Cary, NC). Within each transect, samples collected at 0, 25, and 50 % sampling positions were considered as "under canopy", while those at 100, 150, and 200% were defined as "open grass". Comparisons of soil and plant characteristics between "under canopy" and "open grass" positions were performed by tree species through orthogonal contrasts. The dry matter and nutrient stock of the herbaceous understory had a log-normal distribution and, for this reason, statistical analyses were performed on the log-normally transformed data. Forbs were found mostly under the canopies, being almost absent in the open grass areas around the three tree species. For this reason, there were many missing points for forbs in the open grass areas, and statistical analyses plant for nutrient content were done only for grass samples.

Results and discussion

Soil characteristics

For the three species, there were no differences in soil bulk density or sand content between canopy and open grass areas. Average bulk densities for total soil (including gravel) were 1.12, 1.1, and 1.07 g cm^{-3} in the areas of *Z. joazeiro*, *S. tuberosa*, and *P. juliflora*, while bulk densities for fines only (<2 mm) were 1.08, 0.85, 0.93 g cm^{-3}, respectively. Sand content averaged 709, 753, and 597 g kg^{-1} soil in areas of *Z. joazeiro*, *S. tuberosa*, and *P. juliflora* trees, respectively. This lack of differences allowed for the comparison of soil nutrient levels between canopy and open grass areas without the need for soil texture and bulk density adjustments.

The concentration of all soil nutrients was higher under the canopies of *Z. joazeiro* and *P. juliflora* trees in comparison to open grass areas surrounding these trees (Table 1). Only the levels of soil organic P and of exchangeable Mg were significantly higher under the canopies of *S. tuberosa* than in the correspondent open grass areas (Table 1). Higher soil nutrient content is commonly observed under trees within tree-grass systems (Rhoades, 1997). This pattern likely originates from increased nutrient uptake by tree roots at both greater depths under the tree and in the surrounding soil, followed by the recycling of these nutrients to the area beneath the tree through litterfall and root turnover (Rhoades, 1997).

Concentrations of soil organic P and total C and N were very low in the Regossolo soil type, where *Z. joazeiro* trees were located, independent of the sampling position (Table 1). The Bruno não-cálcico (BNC) soil type, which corresponds to the areas of *P. juliflora* trees, has higher values of organic matter and exchangeable bases than the sandier Regossolo, but has very low concentrations of extractable Pi. The values for the *S. tuberosa* area are intermediate, since these trees were found in areas of both Regossolo and BNC. In general, the low values of total N and organic P observed in this study agree with reviews about the fertility status of soils in the semi-arid region of NE Brazil, that have indicated generalized deficiencies in N (Sampaio & Salcedo, 1997), as well as in P and K (Sampaio et al., 1995).

The differences in soil nutrient content under and outside the canopies were converted to a hectare basis according to the soil bulk density of each area, and these values were adjusted to a 60% ground cover by the canopies, which was the average value observed in the *P. juliflora* orchards. Under the assumption of similar tree densities for the three species, the differences in soil nutrient concentrations led to a relatively high net nutrient accretion under the canopies of *Z. joazeiro* and *P. juliflora* trees, in comparison to buffel grass areas without trees (Table 1).

Characteristics such as tree species, age, gender (Rhoades et al., 1994; Rhoades, 1995; Rhoades, 1997), or soil type (Campbell et al., 1994) may lead to a lack of tree effects on soil properties. In the present study, differences in average soil properties between samples under the canopy of *S. tuberosa* trees and open grass areas were very small (Table 1). One of the reasons for this lack of differences is the fact that *S. tuberosa* trees were located both in BNC and Regossolo soil types. The collection of samples from the two soil types led to a significant increase in the variability within each sampling position, and resulted in no significant differences between canopy and open grass areas. After analyzing the results of the trees located in the patches of BNC and Regossolo separately, we found evidence of the influence of soil type on the effect of *S. tuberosa* trees on soil nutrients. Under the canopy of the four *S. tuberosa* trees growing in the Regossolo, there was significantly more soil total N and organic P than in the open grass areas, but no such differences were observed with the three trees located in the patches of BNC (Figure 1). The lack of differences in areas of BNC may be a result of the finer texture of this soil type, which did not allow for the detection of any eventual tree influence, as opposed to the areas of Regossolo. Sand content in the top soil layer (0-15 cm) in areas of Regossolo was 25% higher than the areas of BNC, and this proportion may be even higher at greater soil depths due to the presence of the argillic horizon characteristic of BNC soils. Campbell et al. (1994) found that, in sandier soils, even a moderate increase in soil organic matter beneath the tree crowns greatly increased the soil exchange complex and lead to a significant tree effect on soil nutrients. Those authors also found that, in finer-textured soils, where the exchange complex is dominated by the mineral component, rather than by organic matter, trees had a minor effect on soil nutrients.

The differences in soil nutrient concentrations found between the areas under the canopies of *P. juliflora* trees and open grass developed in a relatively short period of time (12 years) after tree planting. Since the trees and grasses were planted immediately after the removal of the native vegetation, it is possible that the observed patterns were resultant from both an increase in soil nutrient concentration under the canopy and a simultaneous decrease in soil nutrient concentration in the grass areas during that period. This could also have been the case in the areas of *Z. joazeiro* and *S. tuberosa*, with the difference that the individuals of these two native species were much older (> 50 years) and were preserved during the slash of the native vegetation and the implementation of *C. ciliaris*. However, due to the absence of a control area, no inferences regarding the dynamics of the system can be made.

Concentrations of labile forms of soil nutrients in dry tropical forests are characterized by strong seasonal patterns (Roy and Singh, 1995) due to the fluctuations in soil moisture throughout the year. A strong pulse of available nutrients, such as available

P or mineral N, may occur early in the rainy season due to mineralization after the rain or the release of nutrients mineralized during the dry season (Campo et al. 1998). In the present study, because the soil samples were taken in one single occasion, it could be possible that soil sampling at different times of the year could have yielded different results in the concentrations of mineral N, inorganic P, or exchangeable cations, such as K, Ca, Mg, and Na. However, the pools of organic C, N, and P make up the bulk of the amount of the three elements in those soils and, under conventional management practices, usually do not vary significantly within a year. The patterns observed for exchangeable cations were fairly consistent with the patterns of the nutrients in the organic forms. Therefore, it is likely that the observed differences in concentration of exchangeable cations between under-canopy and open-grass positions would still be present in samples taken at different times of the year.

The two soil types and the three tree species selected for this study are representative of large areas in the northeastern semi-arid region. Since the area selected for the study was not experimentally manipulated and is under commercial management, it seems reasonable to expect that the observed trends will also be present in similar soil-tree species combinations. It remains to be determined that the fertility islands observed around these trees could potentially benefit the crop or pasture intercropped with them, given an adequate tree density is established.

Herbaceous understory characteristics

There were no significant differences in herbaceous aboveground biomass

(AGB) between canopy and open grass areas for *Z. joazeiro* trees (Table 2). However, there was significantly less herbaceous AGB under the canopies of *S. tuberosa* and *P. juliflora* trees (Table 2). No animals were allowed in the pastures during the period between the first rains of the season and the period of sampling, which was performed at the beginning of grass seed production. Therefore, herbaceous AGB results should express the values for potential peak standing AGB in the open grass areas and under the canopies of the three tree species.

Herbaceous species composition was not identified in this study, but it was visually evident that there was more diversity of species under the canopies of the trees than in the *C. ciliaris* dominated open grass areas. AGB of *C. ciliaris* corresponded to 58% to 75% of total herbaceous AGB under the canopies, and 94 to 99% in the open areas (Table 2). The lower levels of *C. ciliaris* AGB under the canopy of *S. tuberosa* and *P. juliflora* were responsible for the significant differences in total herbaceous AGB between canopy and open areas for these species, since AGB of forbs was significantly higher under the canopies of all three species (Table 2). It is likely that understory microclimatic conditions or competition between the trees and the herbaceous understory for resources such as soil moisture and/or light may have led to the lower levels of *C. ciliaris* AGB under the canopies. The absence of significant differences between grass AGB levels under the canopy of *Z. joazeiro* and open areas suggest that competition for those resources may be less intense under the canopies of *Z. joazeiro*, when compared to the other two tree species.

Forbs were almost absent in the open grass areas, when compared to areas under trees, especially in the case of *Z. joazeiro* and *S. tuberosa* (Table 2), which indicates that these trees provided an understory environment favorable for the growth of forbs in the study site. Therefore, even without increasing soil nutrients or herbaceous AGB, which was the case of *S. tuberosa*, these native trees promoted the establishment of areas with increased biodiversity, compared to the low species diversity of *C. ciliaris* stands surrounding each tree.

Higher concentrations of *C. ciliaris* tissue N were observed under the canopy of *Z. joazeiro* trees in comparison to open grass areas (Table 3). Similarly, higher *C. ciliaris* tissue Ca was found under *Z. joazeiro* and *S. tuberosa* trees. Levels of Ca in *C. ciliaris* tissue were slightly lower under the canopies of *P. juliflora*, but no differences were observed for the other nutrients analyzed. The range of values for *C. ciliaris* tissue nutrient concentration observed in this study is consistent with values from previous studies with this species (Pandeya & Lieth, 1993; Esechie, 1992; Havard-Duclos, 1967) and other tropical grass species (Malavolta et al., 1986).

Overall, *C. ciliaris* tissue nutrient concentrations were higher in areas of Regossolo, when compared to areas of BNC (Table 3), even though the areas of Regossolo had lower soil N, Ca, and Mg levels (Table 1). Individuals of *S. tuberosa* were selected from both areas (Regossolo and BNC) and the tissue nutrient concentration values of *C. ciliaris* found under and around these trees are consistently in between those for *C. ciliaris* found in areas of Regossolo and BNC (Table 3). In the semi-arid region of NE Brazil, farmers generally prefer to establish agricultural fields in areas of Regossolo, even though these soils are usually sandy and have low concentration of nutrients in organic forms. This preference by the farmers is usually a result of the higher soil moisture availability for the crops found in these sandy soils, due to higher water infiltration and lower evaporation rates as compared to finer textured soils (Oliveira et al., 1992). According to the inverse texture hypothesis (Noy-Meir, 1973), in arid and semi-arid regions sandy soils usually store higher amounts of plant available water and, for this reason, are considered more fertile than fine textured, nutrient richer soils. As a consequence, the higher availability of soil water in sandier soils may also lead to higher nutrient availability due to increased soil organic matter mineralization. Salcedo and Menezes (1999) conducted a soil N mineralization field study at the same site of the present work. The authors found higher amounts of N mineralized in field incubation cores in areas of Regossolo than in areas of BNC, even though total soil N was 55 to 246% higher in BNC areas. These results may explain in part the higher tissue nutrient concentration in *C. ciliaris* from Regossolo areas in comparison to BNC areas (Table 3).

Outside the canopies, forbs were either absent or the AGB was in most cases too low to allow the analysis of tissue nutrient content. For this reason, no statistical comparisons between canopy and open grass areas were performed (Table 4). Median rather than mean values are shown to avoid the influence of extreme values observed in some samples. The overall trend in tissue nutrient content of forbs is very similar to the trend observed for grasses. With no exceptions, tissue nutrient content of forbs under the canopies of *Z. joazeiro* was higher than under the canopies of *P. juliflora*, while those under the canopies of *S. tuberosa* were intermediate.

There were no differences in the amount of nutrients immobilized in the herbaceous AGB under the canopies and open grass areas in the case of *Z. joazeiro* trees, with the exception of significantly higher levels of Ca under the trees (Table 5). A lower amount of nutrients was immobilized in the herbaceous AGB under *P. juliflora* canopies, with the exception of Ca, when compared to open grass areas. This was primarily a consequence of the lower levels of herbaceous AGB under the canopies, since there were no differences in *C. ciliaris* tissue nutrient concentration for this species (Table 3). Interestingly, in the case of *S. tuberosa* trees, even though significantly lower levels of herbaceous AGB were found under the canopy in comparison to open areas (Table 2), there were no significant differences in the amount of nutrients immobilized in herbaceous AGB between the two areas. This pattern was a result of the higher tissue nutrient content of forbs in comparison to *C. ciliaris* (Table 3 and 4), since forbs made up a higher proportion of the herbaceous AGB under the canopy (42%) as compared to open areas (6%) (Table 2).

In our study site, similar to most of the semi-arid northeastern Brazil (Sampaio 1995), soil moisture seems to be the most limiting resource for plant growth. For this reason, we suggest that the lower levels of peak standing herbaceous AGB under the canopy of *P. juliflora* and *S. tuberosa* trees were a result of competition between these tree species and the herbaceous plants for soil moisture. Recent studies have suggested this competitive interaction varies according to the level of rainfall precipitation, and competition is stronger at low rainfall sites (Belsky, 1994). There is no available information in the literature about *S. tuberosa* competitive interactions with the herbaceous understory, but Parker and Martin (1952) identified a significant decrease in soil moisture under the canopies of *P. juliflora* trees. This could be the case of the present study, where these two tree species may be decreasing the availability of soil moisture under the canopy. If soil moisture levels are lower under the canopies, the positive effects of soil nutrient enrichment may be canceled out, specially in environments where soil water is a highly limiting factor, such as in the semi-arid region of NE Brazil. Additional work in our study site is necessary for testing this hypothesis.

Conclusions

1. The soil under the canopies of *Z. joazeiro* and *P. juliflora* trees had higher nutrient content than the soil within open grass areas, but little difference in soil nutrient levels were observed between areas beneath *S. tuberosa* trees and open grass areas.
2. Herbaceous aboveground biomass was lower under the canopies of *P. juliflora* and *S. tuberosa* in comparison to open grass areas, but biomass levels were similar between areas under *Z. joazeiro* trees and surrounding open grass areas.
3. Under the canopies of the three tree species, aboveground biomass of *C. ciliaris* was lower than in the open areas, but aboveground biomass of forbs was significantly higher. The more favorable understory environment for the growth of native forbs may contribute to increase the biodiversity of these systems.
4. Significantly higher concentrations of *C. ciliaris* tissue N were found under the canopy of *Z. joazeiro* trees in comparison to open grass areas, and of Ca under both *Z. joazeiro* and *S. tuberosa* trees. Concentration of nutrients in *C. ciliaris* tissue was higher in areas of Regossolo, in comparison to areas of BNC, although soil N, Ca, and

Mg was lower in the Regossolo.

5. These results indicate the potential of certain tree species, such as *Z. joazeiro,* for maintaining soil fertility without negatively affecting herbaceous productivity. However, there is need for an improved understanding of the tree-herb-soil interactions in semi-arid Northeastern Brazil in order to support the development of sustainable silvopastoral systems in the region.

Acknowledgements

The authors would like to acknowledge the Fundação para o Amparo da Ciência e Tecnologia do Estado de Pernambuco (FACEPE) and the Brazilian Council for Research Development (CNPq) for the financial support to this research. We thank the Agropecuária Jaçanã for allowing us to conduct the study in their ranch and for providing lodging and logistical support during the sampling trips. Special thanks to Clarindo C. Pontes, Pedro A. da Silva Filho, Gilberto E. do Nascimento, Claudenice E. Santos, and Everaldo N. dos Santos for their technical support.

References

ARAÚJO FILHO, J.A. Manipulação da vegetação lenhosa da caatinga para fins pastoris. Sobral: EMBRAPA-CNPC, 1990. 18P. (EMBRAPA-CNPC. Circular Técnica, 11).

BELSKY, A.J. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. Ecology, 75: 922-932, 1994.

BELSKY, A.J.; MWONGA, S.M. & DUXBURY, J.M.. Effects of widely spaced trees and livestock grazing on understory environments in tropical savannas. Agrofor. Syst. 24:1-20, 1993.

BREMNER, J.M. & MULVANEY, C.S. Nitrogen-Total. In: PAGE, A.L.; MILLER, R.H. & KEENEY, D.R. eds. Methods of soil analysis. Chemical and microbiological properties. Part 2. Madison, ASA-SSSA, 1982. p. 595-624. (Agronomy Monograph, 9).

CAMPBELL, B.M.; FROST, P.; KING, J.A.; MAWANZA, M.; & MHLANGA, L. The influence of trees on soil fertility on two contrasting semi-arid soil types at Matopos, Zimbabwe. Agrofor. Syst., 28: 159-172, 1994.

CAMPO, J.; JARAMILLO, V.J. & MAASS, J.M. Pulses of soil phosphorus availability in a Mexican tropical dry forest: effects of seasonality and level of wetting. Oecologia, 115:167-172, 1998.

ESECHIE, H. A. Distribution of chemical constituents in the plant parts of six tropical origin forage grasses at early anthesis. J. Sci. Food Agric., 58:435-438, 1992.

FARREL, J. The influence of trees in selected agroecosystems in Mexico. In: GLIESSMAN, S.R. ed. Agroecology: Researching the ecological basis for sustainable agriculture, 1990. p. 167-183.

HALVORSON, J.J.; SMITH, J.L.; BOLTON jr., H.; & ROSSI, R.E. Evaluating shrub-associated patterns of soil properties in a shrub-steppe ecossystem using multiple-variable geostatistics. Soil Sci. Soc. Am. J., 59:1476-1487, 1995.

HAVARD-DUCLOS, B. Les plantes fourragères tropicales. Paris, G.-P. Maisonneuve & Larose, 1967. 397 p.

KAUFFMAN, J.B.; SANFORD, jr., R.L.; CUMMINGS, D.L.; SALCEDO, I.H.; & SAMPAIO, E.V.S.B. Biomass and nutrient dynamics associated with slash fires in neotropical dry forests. Ecology, 74: 140-151, 1993.

MALAVOLTA, E.; LIEM, T.H.; PRIMAVESI, A.C.P.A. Exigências nutricionais das plantas forrageiras. In: MATTO, H.B.; WERNER, J.C.; YAMADA, T.; MALAVOLTA E. (eds.), Calagem e adubação de pastagens. Assoc. Bras. Para Pesquisa da Potassa e do Fosfato, Piracicaba (SP), 1986, p. 31-76.

MURPHY, J. & RILEY, J.P. A modified simple solution method for the determination of phosphate in natural waters. Anal. Chim. Acta, 27: 31-36, 1962.

NOY-MEIR, I. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics, 4:25-51, 1973.

OLIVEIRA, J. B. DE, P.K.T. JACOMINE & M.N. CAMARGO. Classes gerais de solos do Brasil. Jaboticabal, FUNEP, 1992. 201 p.

OLSEN, S.R. & SOMMERS, L.E. Phosphorus. In: PAGE, A.L.; MILLER, R.H. & KEENEY, D.R., eds. Methods of soil analysis. Chemical and Microbiological Properties. Part 2. Madison, ASA-SSSA, 1982. p. 403-430.

PANDEYA, S.C. & H. LIETH. Ecology of Cenchrus grass complex. Dordrecht, Kluwer Academic Publishers, 1993. 234 p.

PARKER, K.W. & MARTIN, S.C. The mesquite problem on southern Arizona ranges. Washington, USDA Circ. 908, 1952. 70p.

REYNOLDS, J.F.; VIRGINIA, R.A.; & CORNELIUS, J.M. Resource island formation associated with desert shrubs, creosote bush (Larrea tridentata) and mesquite (Prosopis glandulosa) and its role in the stability of desert ecossystems: a simulation analysis. Bull. Ecol. Soc. Am. 70:299-300, 1990. Supplement 2.

RHOADES, C. C. Seasonal pattern of nitrogen mineralization and soil moisture Faidherbia albida (syn Acacia albida) in central Malawi. Agrofor. Syst. 29:133-145, 1995.

RHOADES, C.C. Single tree influences on soil properties in agroforestry: lessons from natural forest and savanna ecosystems. Agrofor. Syst. 35: 71-94, 1997.

RHOADES, C.C.; SANFORD jr., R.L.; & CLARK, D.B. Gender dependent influences on soil phosphorus by the deciduous lowland tropical tree *Simarouba amara*. Biotropica, 26: 362-368, 1994.

ROY, S. & SINGH, J.S. Seasonal and spatial dynamics of plant-available N and P pools and N-mineralization in relation to fine roots in a dry tropical forest habitat. Soil Biol. Biochem., 27: 33-40, 1995.

SALCEDO, I.H. & MENEZES, R. Mineralização comparativa de nitrogênio do solo, *in situ*, sob pastagem artificial e sob estrato arbóreo, no semi-árido de Pernambuco. Congresso Bras. Ci. Solo, 27. Brasília, Resumos, 1999.

SALCEDO, I.H.; TIESSEN, H.; & SAMPAIO, E.V.S.B. Nutrient availability in soil samples from shifiting cultivation sites in the semi-arid Caatinga of NE Brazil. Agric. Ecosys. Environ., 65:177-186, 1997.

SAMPAIO, E.V.S.B. Overview of the Brazilian caatinga. In: Bullock, S.H., H.A.

Mooney, and E. Medina, eds., Seasonally dry tropical forests. Cambridge University Press, pp. 35-63, 1995.

SAMPAIO, E.V.S.B. & SALCEDO, I.H. Diretrizes para o manejo sustentável dos solos brasileiros: região semi-árida. In: CONGRESSO BRASILEIRO DE CIÊNCIA DO SOLO, 26., Rio de Janeiro, 1997. Anais. 30p. CD-ROM.

SAMPAIO, E.V.S.B.; SALCEDO, I.H.; & SILVA, F.B.R. Fertilidade dos solos do semi-árido. In: PEREIRA, J.R. & FARIA, C.M.B. eds. Fertilizantes: Insumo básico para a agricultura e combate à fome. Petrolina, EMBRAPA-CPATSA/SBCS. 1995. 273p.

SIBBESEN, E. A simple ion-exchange resin procedure for extracting plant available elements from soil. Plant Soil, 46: 665-669, 1977.

SILVA, V.M.; ARAÚJO FILHO, J.A.; LEITE, E.R.; PEREIRA, V.L.A.; & UGIETTE, S.A. Manipulação da caatinga e seu efeito sobre parâmetros fitossociógicos e de produção, em Serra Talhada, Pernambuco. In: REUNIÃO DA SOCIEDADE BRASILEIRA DE ZOOTECNIA, 32., Brasília, 1995. Anais. Brasília, SBZ, 1995. P. 17-21.

SNYDER, J.D. & TROFYMOW, J.A. A rapid accurate wet oxidation diffusion procedure for determining organic and inorganic carbon in plant and soil analysis. Comm. Soil Sci. Plant Anal., 15:587:597, 1984.

THOMAS, R.L.; SHEARD, R.W.; & MOYER, J.R. Comparisson of conventional and automated procedures for N, P and K analysis of plant material using a single digestion. Agron. J., 59:240-243, 1967.

TIEDEMANN, A.R. & KLEMMEDSON, J.O. Effect of mesquite on physical and chemical properties of the soil. J. Range Manag., 26:27-29, 1973.

TIESSEN, H.; SALCEDO, I.H.; & SAMPAIO, E.V.S.B. Nutrient and soil organic matter dynamics under shifting cultivation in semi-arid northeatern Brazil. Agric. Ecosys. Environ., 38:139-151, 1992.

WELTZIN, J.F. & COUGHENOUR, M.B. Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. J. Veg. Sci., 1: 325-334, 1990.

WEST, N.E. Nutrient cycling in desert ecosystems. In: GOODALL, D.W. & PERRY, R.A. eds. Arid land ecosystems: structure, function, and management. Cambridge, University Press. 1981. p. 301-324.

Table 1. Mean values (n=21) of various soil characteristics (0-15 cm) under the canopy of *Z. joazeiro*, *P. juliflora*, and *S. tuberosa* trees and in open grass areas next to the trees.

Position	C	N	Po(1)	Pi(2)	Ca	Mg	K	Na	pH$_w$
	g kg^{-1}	-------- mg kg^{-1}--------			-------mmol (+) kg^{-1}---------				(1:2.5 w:v)
					Z. joazeiro				
Under canopy	8.3	917	81	26	45	14	10.5	1.5	6.8
Open grass	6.1	673	56	14	31	10	6.6	1.0	6.2
P-value	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Difference(3) (kg ha^{-1})	2138	237	24	12	272	47	148	11	-
					P. juliflora				
Under canopy	16.8	1552	146	6	83	22	8.7	1.6	6.8
Open grass	12.1	1206	123	3	66	17	5.3	1.1	6.7
P-value	<0.01	<0.01	<0.01	0.02	0.03	0.01	<0.01	<0.01	n.s.(4)
Difference (kg ha^{-1})	3934	290	19	3	285	50	111	10	-
					S. tuberosa				
Under canopy	11.4	1118	109	10	53	18	7.62	1.1	6.1
Open grass	11.8	1117	86	6	56	15	7.68	1.1	6.5
P-value	n.s.	n.s.	0.01	n.s.	n.s.	0.02	n.s.	n.s.	0.04
Difference (kg ha^{-1})	-	-	18	-	-	28	-	-	-

(1) Organic P. (2) Inorganic P. (3) Difference in soil nutrient concentrations between under canopy and open grass positions, expressed in an area basis (bulk densities for < 2mm soil = 1.08, 0.93 and 0.85 g cm^{-3} for *Z. joazeiro*, *P. juliflora* and *S. tuberosa* areas, respectively) and with an assumption of 60% ground cover by tree canopies. (4) Non-significant at $P < 0.10$.

Table 2. Dry matter of herbaceous plants under the canopies of *Z. joazeiro*, *P. juliflora* and *S. tuberosa* trees and in open grass areas next to the trees. Values represent means (n=7) and standard errors within parentheses.

	Understory vegetation		
Position	Forbs	Grasses	Total herbs
	---------- $g\ m^{-2}$ ----------		
		Z. joazeiro	
Under canopy	27.5 (6.7)	79.7 (18.9)	107.2 (19.2)
Open grass	0.99 (0.52)	86.2 (7.3)	87.2 (7.4)
P-value	<0.01	ns(1)	ns
		P. juliflora	
Under canopy	24.3 (7.2)	71.6 (19.2)	95.9 (17.5)
Open grass	0.38 (0.24)	193.2 (28.9)	193.6 (29.1)
P-value	<0.01	<0.01	0.011
		S. tuberosa	
Under canopy	44.6 (9.3)	61.9 (28.0)	106.5 (26.3)
Open grass	9.2 (5.0)	136.1 (23.1)	145.3 (22.0)
P-value	<0.01	<0.01	0.09

(1) Non-significant at $P < 0.10$

Table 3. Nutrient content of grasses under the canopies area of *Z. joazeiro*, *P. juliflora*, and *S. tuberosa* trees and in open grass areas next to the trees. Values represent means (n=7) with standard errors within parentheses.

Position	N	P	Ca	Mg	K
	g kg^{-1}				
Z. joazeiro					
Under canopy	15.1	1.73	7.77	2.46	39.2
Open grass	12.5	1.99	6.18	2.19	35.7
P-value	0.023	ns(1)	0.094	ns	ns
P. juliflora					
Under canopy	10.7	0.90	4.22	1.76	21.8
Open grass	9.0	1.16	4.59	1.91	23.6
P-value	ns	ns	0.080	ns	ns
S. tuberosa					
Under canopy	12.3	1.18	6.99	2.45	32.7
Open grass	11.3	1.17	5.62	2.75	29.1
P-value	ns	ns	0.039	ns	ns

(1) Non-significant at $P < 0.10$

Table 4. Nutrient concentrations of forb tissue under the canopies of *Z. joazeiro*, *P. juliflora*, and *S. tuberosa* trees and in open grass areas next to the trees. Values represent sample medians followed by ranges within parentheses (1).

Position	N	P	Ca	Mg	K
	---------- g kg^{-1} ----------				
			Z. joazeiro		
Under canopy (n=16)(2)	23 (13-33)	2.3 (1.2-3.5)	29 (12-43)	5.7 (3-14)	36 (14-59)
Open grass (n=4)	18 (17-20)	1.8 (1.1-1.9)	26 (16-29)	7.7 (4.8-7.7)	26 (11-30)
			P. juliflora		
Under canopy (n=14)	13 (10-19)	0.95 (0.6-1.9)	18 (9-37)	3.5 (1-17)	17 (8-35)
Open grass (n=3)	18 (16-19)	1.1 (1.06-1.12)	21 (15-26)	5.8 (3.2-8.5)	25 (11-38)
			S. tuberosa		
Under canopy (n=19)	19 (13-25)	1.7 (1.3-2.5)	20 (11-33)	3.9 (2-12)	29 (13-54)
Open grass (n=7)	29 (21-35)	2.2 (1.7-2.5)	25 (19-30)	7.9 (6-10)	37 (19-65)

(1) Statistical comparisons between positions were not performed due to the small sample sizes for open-grass areas. (2) The letter 'n' indicates the number of sampling sites where forbs were found from a total of 21sites within 7 experimental replications.

Table 5. Mean values of nutrient stock in the herbaceous layer under the canopy of *Z. joazeiro*, *P. juliflora*, and *S. tuberosa* trees and in open grass areas next to the trees.

Position	N	P	K	Ca	Mg
			---------- mg m^{-2} ----------		
			Z. joazeiro		
Under canopy	1287	146	2751	884	246
Open grass	991	155	2821	484	175
P-value	ns[(1)]	ns	ns	0.01	ns
			P. juliflora		
Under canopy	689	61	1250	454	157
Open grass	1287	161	3507	669	280
P-value	0.04	<0.01	<0.01	ns	0.04
			S. tuberosa		
Under canopy	1053	101	1913	866	249
Open grass	1365	137	3040	726	318
P-value	ns	ns	ns	ns	ns

[(1)] Non-significant at $P < 0.10$

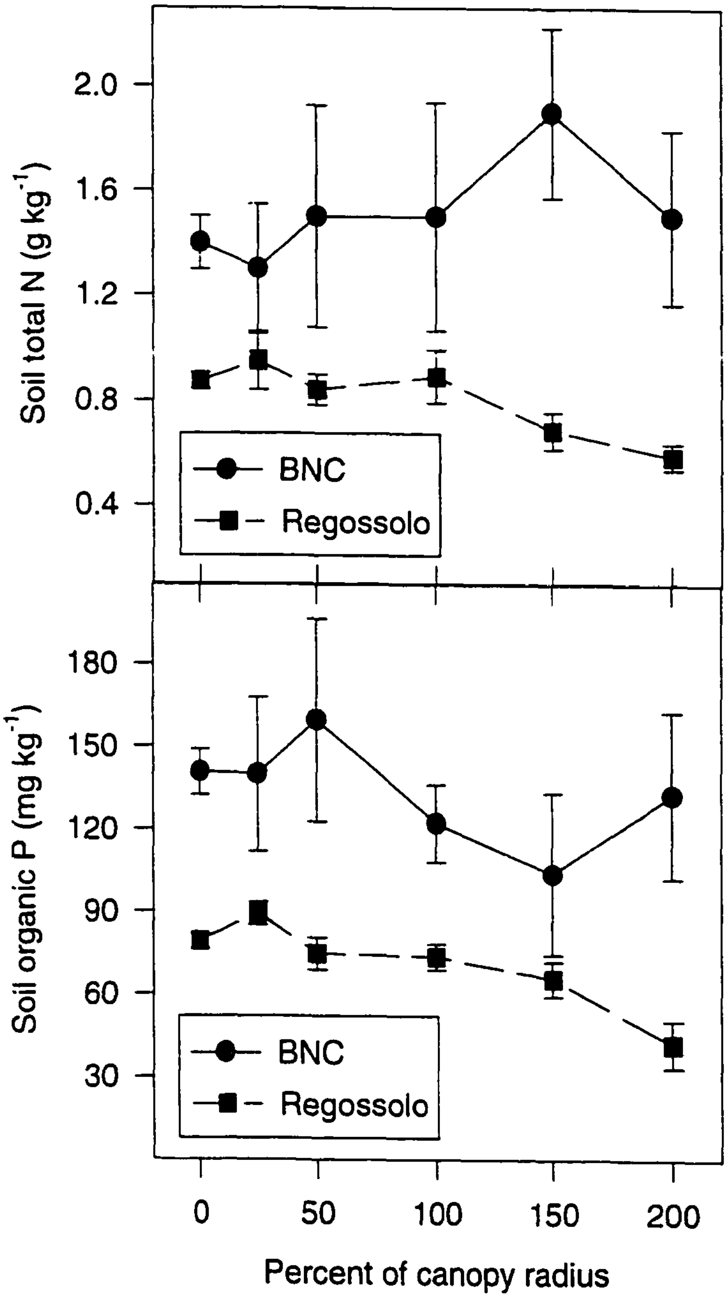

Figure 1. Soil total N and organic P under and outside the canopies of *S. tuberosa* trees in areas of Bruno nao-calcico (BNC) and Regossolo soil types. Error bars represent standard errors of means.

CHAPTER III

Influences of tree species on microclimate, litter, and soil nutrient dynamics in a silvopastoral system of semi-arid northeastern Brazil [1]

Rômulo S.C. Menezes [2,3], Ignácio H. Salcedo [4], and Edward T. Elliott [3]

---

[1] Manuscript submitted to Agroforestry Systems

[2] Corresponding author. Research Fellow of Brazilian CNPq. Soil and Crop Sciences Department, Colorado State University, Fort Collins, CO, 80521. Fax: 970-491-1965, E-mail: romulo@nrel.colostate.edu

[3] Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, 80521

[4] Departmento de Energia Nuclear, Universidade Federal de Pernambuco, Recife, PE, 50000, Brazil

Abstract

There is little available information on nutrient cycling and the controls of ecosystem processes in land use systems of dry neotropical regions. In this study, we conducted field and greenhouse experiments to investigate the influences of *Ziziphus joazeiro* and *Prosopis juliflora* trees on microclimatic conditions and nutrient dynamics in pastures of *Cenchrus ciliaris* in semi-arid northeastern Brazil. Soil moisture was lower under the canopies of *P. juliflora* trees during early season, when compared to open grass areas, but *Z. joazeiro* had no effect on soil moisture. Soil and air temperatures were lower under *Z. joazeiro* trees but *P. juliflora* trees had little effect on temperature. Differences in soil type between sites seemed to affect the influences of tree species on microclimatic conditions. Losses of P from all litter types were lower under the canopies of *Z. joazeiro* trees, but losses of biomass and N from litter were not consistently affected by the presence of trees. Soil N mineralization was greater under trees, in comparison to patches of *C. ciliaris*. Similarly, in the greenhouse study, plant biomass production and plant nutrient uptake was greater in soil samples collected under the canopies of the two tree species, in comparison to soil from patches of *C. ciliaris*. Our results indicate that the preservation of native trees or introduction of exotic tree species in *C. ciliaris* pastures in semi-arid northeastern Brazil significantly affects microclimatic conditions and the dynamics of litter and soil nutrients, and contributes to increases in the capture, retention, and cycling rates of nutrients in these systems.

Index terms: *Prosopis juliflora*, *Ziziphus joazeiro*, *Cenchrus ciliaris*, caatinga.

Introduction

Agricultural activities in the semi-arid region of northeastern Brazil are based primarily on slash and burn of the native vegetation, followed by shifting cultivation of subsistence crops, establishment of livestock pastures, and fuel wood harvest (Kauffman et al., 1993). Rainfall, which ranges from 300 to 1000 mm y^{-1} in different areas of the region, is concentrated in 3 to 5 months, but drought years are common and severe drought periods lasting 3 to 5 years have occurred every 3 or 4 decades (Sampaio et al., 1995). Only 3 to 7% of the land in the region can be irrigated, because of limitations due to soil characteristics and/or water quality and availability (Silva Filho, 1988; Sampaio and Salcedo, 1997). Due to the irregular rainfall distribution, the use of chemical fertilizers in the region is not economical (Sampaio et al., 1995), therefore, the management of soil fertility by farmers depends mostly on soil organic matter management (Tiessen et al., 1994).

Intercropping trees with pastures or food crops in areas of erratic rainfall, low soil fertility, and where farmers have limited land and capital resources may enhance the capture and retention of nutrients and increase the productivity and sustainability of such areas (Sanchez, 1995). Usually, the presence of single trees in agrosilvopastoral systems or savannas may lead to the formation of patches with higher levels of soil organic matter and soil moisture, which are called resource islands (Reynolds et al., 1990), isles of fertility (West, 1981), or fertile islands (Halvorson et al., 1995). Several mechanisms are involved in the formation of these differentiated zones, including increased capture of nutrients and litterfall inputs, reduction of soil and air temperatures, and inputs via animals (Tiedemann and Klemmedson, 1973; Farrel, 1990; Weltzin and Coughenour, 1990; Belsky et al., 1993; Rhoades, 1997).

Previous studies conducted in silvopastoral systems in semi-arid northeastern Brazil demonstrated that preserving trees during the slash of native vegetation to achieve a 30 % ground cover by canopies increased forage and meat production in comparison to areas where all trees were removed (Araújo Filho, 1990; Silva et al., 1995). Menezes and Salcedo (1999) found that the levels of soil organic matter and nutrients (N, P, K, Ca, and Mg) were significantly higher under the canopies of *Ziziphus joazeiro* Mart. and *Prosopis juliflora* (SW.) DC. trees in a silvopastoral system in semi-arid northeastern Brazil, when compared to open grass patches. In addition, those authors found that peak standing herbaceous biomass was not affected by the presence of *Z. joazeiro* trees, but was significantly lower under the canopies of *P. juliflora* and *Spondias tuberosa* trees. The results from these studies demonstrated that the preservation of trees during the slashing of native vegetation might lead to more sustainable land use systems in semi-arid northeastern Brazil. However, additional studies are needed to investigate the productivity and cycling of nutrients in systems with different soil-tree-herbaceous combinations.

The understanding of soil organic matter and nutrient dynamics in dry neotropical forest systems, as well as the controls over these processes, may contribute to increase the long-term productivity of these systems, and may also help to reduce emissions of C and N to the atmosphere (Kauffman et al., 1993; Jaramillo and Stanford, 1995). Of the nutrients that may influence and limit plant growth, N is of primary interest as it constitutes a large part of the photosynthetic apparatus of higher plants and it is usually the most limiting elements in terrestrial ecosystems (Aber et al., 1989; Nadelhoffer et al., 1999). In addition, the sustainability of land use systems in semi-arid northeastern Brazil and in other semi-arid tropical systems may often be limited by the availability of P (Sampaio 1995) and other nutrients (Nandwa and Bekunda, 1998; Wortmann and Kaizzi, 1998).

The influences of tree species on litter and soil organic matter dynamics and on microclimatic conditions in land use systems in semi-arid northeastern Brazil remain largely unknown. Based on the available information, we hypothesize that rates of litter and soil organic matter mineralization and nutrient availability to plants are greater under the canopies of Z. *joazeiro* and *P. juliflora* trees, due to higher litter inputs, higher soil moisture levels, and lower soil and air temperatures. In order to test our hypotheses, we conducted field and greenhouse studies and investigated the influences of Z. *joazeiro* and *P. juliflora* on soil moisture, soil and air temperature, litter decomposition, soil N mineralization, and potential soil nutrient supply in a silvopastoral system in semi-arid northeastern Brazil.

Materials and methods

Description of the Study Area

The study was conducted during the growing season of 1998 (January to June) in a beef cattle ranch at Custódia, PE (8° 14'S and 37°45'W). Average rainfall precipitation at the site is 740 mm year^{-1} (data from the records of the ranch) generally occurring from December to May. The vegetation within the area of the ranch, which originally consisted of primary growth deciduous dry woodland known as 'caatinga', was slashed with tractors in 1984. The slash was followed by manual removal of the remaining bushes and tree stumps by field workers. The ranch has a total of three thousand hectares of *P. juliflora* orchards planted with a spacing of 10 by 10 m, intercropped with buffel grass (*Cenchrus ciliaris*), which is a perennial, drought resistant forage grass native to Africa. Within the ranch, there were other large areas of buffel grass pastures not planted with *P. juliflora* and where *Z. joazeiro* and other native trees had been spared during the slash of the caatinga and left with an average distance of around 30 to 40 m between trees. The *P. juliflora* orchards were 14 years old at the time of this study, and all *Z. joazeiro* trees selected were over 50 years old, according to the locals.

The pastures never received any chemical fertilization and were mowed with tractors at the end of the dry season to control invasion by woody species every two years. No fire is used in the management of the pastures. Animal density in the ranch fluctuates around 0.17 animal ha^{-1}, which is a relatively low density for buffel grass pastures in the region. The combination of low animal densities and high tree density within the pastures helped to reduce potential effects of animals on the formation of fertility islands under the trees as a result of nutrient inputs in excrements. The predominant soil type in the areas of *P. juliflora* is Alfisol (Ustalf), while all the selected *Z. joazeiro* trees were located in patches of Entisol (Orthent). Sand content in top soil layer (15 cm) averaged 71 and 60 % in the areas of Entisol and Alfisol, respectively (Menezes and Salcedo, 1999). The sampling areas are predominantly flat, with slopes ranging from 0 to 3%.

Tree Selection and Sampling Design

Within the study area, we selected five individuals of *Z. joazeiro* and *P. juliflora*. All selected trees were isolated from other trees within the *C. ciliaris* matrix. The average canopy radius of each tree was calculated by measuring the distance between the tree bole to the edge of the canopy in four different directions. For each tree, we established a north-oriented transect extending from the tree bole to the open patches of *C. ciliaris* up to a distance equivalent to 300 % of the average canopy radius. In each transect, we defined three sampling positions: (1) 50 % of canopy radius (under canopy), (2) 150 % of canopy radius (intermediate position), and (3) 300 % of canopy radius (*C. ciliaris* patches).

Microclimatic Conditions

Soil moisture (0 to 28 cm) was determined by Time Dimension Reflectometry (TDR) using the Trase System model 6050x1. Measurements were performed every two or three weeks from January to May under the canopies of the trees and in patches of *C. ciliaris* along the transects of the five selected *Z. joazeiro* and *P. juliflora* trees.

Soil temperature was determined using HOBO data loggers buried in a vertical position between 1 and 6 cm of depth. The loggers were wrapped with a thin plastic film in order to avoid damage by soil moisture, and were placed under the canopies and in patches of *C. ciliaris* along the transects of four *Z. joazeiro* or *P. juliflora* trees.

Temperature measurements were recorded every 15 minutes for a period of 300 hours.

Simultaneously to the soil temperature measurements, we recorded air temperature under the canopies of the two tree species and in patches of *C. ciliaris* using HOBO loggers placed next (1 m of distance) to the soil temperature loggers. In order to avoid damage by rain, the loggers were placed inside a small and well-ventilated wooden box attached to a metal pole 1 m above the soil surface. We also measured total solar radiation under the canopy of one individual of each tree species and in patches of *C. ciliaris* for a period of 24 hours. Solar radiation sensors recorded total solar radiation in Watts m^{-2} every 20 seconds, integrating the measurements every 30 minutes.

Litter Decomposition

During the dry season of 1997, leaf litter from *Z. joazeiro* and *P. juliflora* was collected by placing nylon cloth traps under the canopies of these tree species, and *C. ciliaris* litter was collected by clipping the standing dead plants from pastures within the study area. All litter material was oven-dried at 40 °C and the litter from each plant species was homogenized. Litter decomposition bags were prepared by placing four grams of litter into nylon cloth (1 mm mesh) bags approximately 10 by 10 cm in size. Three litter bags of each litter type (*Z. joazeiro*, *P. juliflora*, and *C. ciliaris*) were placed in each of the three sampling positions (under canopy, intermediate position, and *C. ciliaris* patches) along the transect in each of the five selected *Z. joazeiro* and *P. juliflora* trees. One bag of each litter type was collected from each transect position at 30, 60, and 100 days after the bags were placed in the field. After each bag collection, each litter bag was oven dried at 40 °C, weighed, and ground to a fine powder. The concentration of N and P in the initial litter material and decomposed litter was analyzed by auto-analysis after digestion with a sulfuric acid-hydrogen peroxide mixture (Thomas et al., 1967). Final results of losses of biomass, N, and P from litter material throughout the growing season were corrected for moisture and ash content.

Soil Nitrogen Mineralization

Soil organic matter net nitrogen mineralization was measured with *in situ* field soil incubations using open-top aluminum cores. The cores were 15 cm long and 5 cm in diameter and were placed both under the canopies of the five selected individuals of *Z. joazeiro* and *P. juliflora* and in the patches of *C. ciliaris* associated with each tree. The soil was extremely dry and hard, which made it impossible to drive the cores into the soil. For this reason, we used a pick-ax to collect soil samples from the area of the canopy and the patches of *C. ciliaris*. The soil samples collected within each position were homogenized in a bucket and used to fill four aluminum cores for each treatment replicate. In the bottom of the aluminum cores, we placed ion-exchange resin-bags containing 15 cm^3 of a mixture of cation and anion resins, as described in Kolberg et al. (1997). We dug small trenches (120 cm long, 20 cm wide, and 15 cm deep) under the canopies and in the patches of *C. ciliaris*, placed the four cores inside the trench with a spacing of 30 cm between cores, and filled the trench again with soil. The cores were left in the field from 28 February 1998 until 20 April 1998. During this period, there was only one rainfall event of 36 mm in 14 March. After collection, the cores were kept refrigerated, taken to the laboratory, weighed, and inorganic N in sub-samples was extracted with 1 M KCl. The resin bags were sequentially extracted with five 30 ml aliquots of 1 M KCl. The extracts from soil samples and resin-bags were analyzed for inorganic N by spectrometry. Total soil C was determined by wet oxidation-diffusion (Snyder and Trofymow, 1984) and total soil N by Kjeldahl digestion (Bremner and Mulvaney, 1982) in sub-samples ground to pass through a 0.25 mm sieve.

Potential Soil Nutrient Supply - Green House Study

During early February 1998, soil samples (0-15 cm) were randomly collected with a pick-ax and a shovel from areas under the canopies of the five selected individuals of *Z. joazeiro* and *P. juliflora* and from the patches of *C. ciliaris* associated with each tree. For each canopy area or grass patch, a total of approximately 10 kg of soil was collected, homogenized, taken to the laboratory, air dried, and passed through a 2 mm sieve. The water holding capacity of the samples from each soil type (Entisol and Alfisol) was calculated by adding 10 ml of water to cylinders containing 200 g of soil, covering the cylinders with saran wrap, and allowing the wetting front to move for 48 hours, after which c. 10-g soil sub-samples from the surface of the cylinder were collected, oven-dried at 105 °C, and soil water content calculated on a weight basis. Subsequently, three 500-g sub-samples of each soil sample were placed into three PVC pots (15 cm of height and 7.5 cm of diameter). Pearl millet (*Pennisetum glaucum* (R.) Br. cv. 'IPA Bulk 1') was sown at a rate of 0.5 g of seeds per pot and the soil was irrigated to reach the water holding capacity. The moisture content of the soil in each pot was maintained near water holding capacity by weighing and adding water two times each day during the period of the experiment. The plants were harvested 30 days after planting, separated into aboveground and belowground tissue, and oven dried at 45 °C. For each pot, the weight of aboveground and belowground biomass was recorded and the two samples were combined and ground to a fine powder for determination of plant tissue nutrient concentration of the total plant biomass in each pot.

Soil and Plant Tissue Chemical Analysis

Soil NO_3^--N and NH_4^+-N were extracted with 1 M KCl, and the extracts were analyzed by spectrometry. Soil inorganic P was determined by extractions with both resin bags (Sibbesen, 1977) and dilute acid (Olsen and Sommers, 1982), followed by a colorimetric determination (Murphy and Riley, 1962). Exchangeable bases were extracted with 1 M NH_4Cl, and concentrations of Ca^{+2}, Mg^{+2}, and K^+ in the filtered extracts were determined by atomic absorption and Na^+ by flame emission spectrophotometry. Soil pH was measured in a 2.5:1 (water:soil) suspension. In a subsample ground to pass through a 0.25 mm sieve, total soil C was determined by wet oxidation-diffusion (Snyder and Trofymow, 1984) and total soil N by Kjeldahl digestion (Bremner and Mulvaney, 1982).

Plant samples were ground and subsamples were digested with a sulfuric acid-hydrogen peroxide mixture (Thomas et al., 1967). The digests were analyzed for N and P by autoanalysis (Thomas et al., 1967) and for Ca, Mg, and K by atomic absorption spectrophotometry.

Statistical Analyses

Statistical analyses were performed using the SAS Statistical Package (SAS, Version 6.12, 1995, SAS Institute Inc., Cary, NC). Litter decomposition and soil moisture were analyzed by tree species and sampling date using a randomized complete block design with three treatments (canopy, intermediate position, and *C. ciliaris* patch) and five replications. Comparisons of plant biomass and nutrient content from the green house study and soil chemical characteristics under the canopy or in patches of *C. ciliaris* were analyzed by tree species using paired t-tests. Results were considered significant at $P < 0.10$.

Results

Microclimatic conditions

Different from what we hypothesized, *Z. joazeiro* trees had no significant influence on soil (0 to 28 cm) moisture levels throughout the growing season. In contrast, soil moisture levels were lower ($P < 0.05$) under the canopies of *P. juliflora* trees early in the growing season, in comparison to patches of *C. ciliaris*, but no significant differences were observed during mid or late season. (Figure 1). The water holding capacity of the soils in the two areas, determined in the samples collected for the greenhouse study, was 0.13 and 0.10 g g soil^{-1} for the Alfisol and Entisol, respectively.

Daily minimum soil temperatures were similar between canopy areas and patches of *C. ciliaris*, but maximum temperatures were higher in *C. ciliaris* patches compared to areas under Z. *joazeiro* canopies (Figure 2). Daily maximum soil temperature was, on average, 16 ± 0.6°C lower under the canopies of Z. *joazeiro* trees, in comparison to C. *ciliaris* patches throughout the period of measurements. In contrast, P. *juliflora* trees had no significant effect on soil temperatures, as indicated by the overlap of the mean soil temperatures under the canopies of this species and patches of C. *ciliaris* (Figure 2). The canopy of Z. *joazeiro* intercepted an average of 65 to 70% of the total solar radiation between 10 a.m. and 2 p.m., in comparison to the radiation in C. *ciliaris* patches, while the canopy of P. *juliflora* intercepted only 20 to 30% of total solar radiation during the same period (Figure 3).

During the 10 days in which air temperature measurements were performed, minimum and maximum air temperatures in the study area averaged 20.2 ± 0.5 and 36.1 ± 0.8 °C, respectively. Maximum daily air temperatures were, on average, 2.8 ± 0.11 lower under the canopies of Z. *joazeiro* and 1.4 ± 0.10 °C lower under canopies of P. *juliflora* trees, in comparison to patches of C. *ciliaris*.

Litter Decomposition

Initial litter concentrations of N were 24.6, 23.2, and 12.0 mg g^{-1} and of P were 1.31, 0.95, and 1.27 mg g^{-1} for P. *juliflora* leaf litter, Z. *joazeiro* leaf litter, and C. *ciliaris* tissue litter, respectively. Initial C to N ratios of P. *juliflora*, Z. *joazeiro*, and C. *ciliaris* litter were 17.6, 18.5, and 35.8, respectively, and initial C to P ratios were 328, 452, 338, respectively.

Losses of P from the three litter types (P. *juliflora*, Z. *joazeiro*, and C. *ciliaris*) were consistently lower ($P < 0.05$) under the canopies of *Z. joazeiro* trees in comparison to intermediate positions and patches of *C. ciliaris* throughout the entire period of the experiment (Table 1). Within the areas of *Z. joazeiro* trees, a herd of cattle was transferred to the area of the experiment one week prior to the last sampling date, and most of the remaining litter bags were damaged by animal trampling. For this reason, there is no data for the last sampling date (100 days) in the areas of *Z. joazeiro* (Table 1). In addition, concentrations of P in the three litter types under the canopies of *Z. joazeiro* trees at 60 DAP were higher ($P < 0.05$) than litter P concentration in patches of *C. ciliaris* (data not shown). The presence of *Z. joazeiro* trees had no effect on losses of N from litter, with the exception of *Z. joazeiro* litter bags collected 30 days after placement (DAP) of the litter bags in the field. Different from what we expected, litter biomass losses were lower ($P < 0.05$) under the canopies of *Z. joazeiro* trees 30 DAP, but no significant differences were observed 60 DAP (Table 1).

The presence of *P. juliflora* trees had no significant influence on the losses of N and P from litter bags (Table 2). Losses of litter biomass for *C. ciliaris* and *Z. joazeiro* litter were lower ($P < 0.05$) under the canopies of *P. juliflora* trees 60 DAP, but no differences were observed 100 DAP (Table 2).

Overall, the order of the rates of biomass loss from litter was *P. juliflora* > *C. ciliaris* > *Z. joazeiro*; for N loss it was *P. juliflora* = *C. ciliaris* > *Z. joazeiro*; and for P loss it was *C. ciliaris* > *P. juliflora* > *Z. joazeiro*. In general, litter decomposition was greater between 30 and 60 DAP, probably because of the only rainfall event that occurred during the length of the experiment, which happened within that period, in 14 March.

Soil Nitrogen Mineralization

Soil nitrogen mineralization was higher ($P < 0.10$) under the canopies of *Z. joazeiro* and *P. juliflora* trees in comparison to patches of *C. ciliaris* (Table 3), mostly due to net increases in the amounts of NO_3^--N in both the soil and exchange resins. Total soil C and N were higher under the canopies of the two tree species, but the levels of significance between canopy and *C. ciliaris* patches were lower in the areas of *Z. joazeiro* ($P = 0.007$) as opposed to the areas of *P. juliflora* ($P < 0.10$) (Table 3).

Interestingly, we found no significant differences between the amounts of soil net N mineralized per gram of total soil N under *Z. joazeiro* canopies and in *C. ciliaris* patches, which averaged 16.3 and 12.4 μg g soil N^{-1}, respectively. In contrast, soil net N mineralized per gram of total soil N in the soil was higher ($P = 0.067$) under the canopies of *P. juliflora* trees compared to patches of *C. ciliaris*, averaging 9.6 and 5.4 μg g soil N^{-1}, respectively.

Potential Soil Nutrient Supply - Green House Study

Under the canopies of *Z. joazeiro* and *P. juliflora*, soil nutrient concentrations of samples were higher ($P < 0.10$) than those of samples from *C. ciliaris* patches, with the exception of resin- and extractable-P (Table 4). As expected, biomass production and nutrient uptake by pearl millet were significantly higher in plants grown in soils from areas under the canopies of the two tree species (Table 5). The concentrations of N, Ca, and Mg in pearl millet tissue were significantly higher in plants grown in soils from Z.

joazeiro canopies (15.6, 10.7, and 3.7 mg g^{-1}, respectively), as opposed to plants grown in *C. ciliaris* soil (13.5, 7.7, and 2.8 mg g^{-1}, respectively). There were no differences in pearl millet tissue P and K concentrations between plants grown in *Z. joazeiro* canopy soil and from *C. ciliaris* patches. Across these two treatments, tissue P and K concentrations averaged 3.8 and 49.8 mg g^{-1}, respectively. In the case of pearl millet plants grown in soil samples from *P. juliflora* canopies, the concentration of plant tissue N was significantly higher (18.0 mg g^{-1}) in comparison to plants grown in *C. ciliaris* soil (13.3 mg g^{-1}), but no treatment differences were observed for the concentrations of P, K, Ca, and Mg in plant tissue, which averaged 1.4, 9.4, 3.5, and 53.2 mg g^{-1}, respectively.

Discussion

Microclimatic conditions

Menezes and Salcedo (1999) reported that herbaceous biomass production is not affected by the presence of *Z. joazeiro* trees but, in contrast, herbaceous biomass is significantly lower under the canopies of *P. juliflora* trees at our study sites. In the present study, we found evidence that competition for soil moisture may be reducing herbaceous biomass production under the canopies of *P. juliflora* trees, since soil moisture levels were lower under the canopies of *P. juliflora* trees during early season ($P < 0.05$), when compared to patches of *C. ciliaris*. Interestingly, no differences in soil moisture were observed between areas under the canopies of *Z. joazeiro* and patches *of C. ciliaris*.

The different effects of *Z. joazeiro* and *P. juliflora* trees on soil moisture, relatively to adjacent *C. ciliaris* patches, could be a result of differences in the rooting pattern of these two tree species. In semi-arid northeastern Brazil, *Z. joazeiro* trees are commonly found in the lowest landscape positions (Machado et al., 1997) and usually develop a deep rooting system to capture water and nutrients from the water table (E.V.S.B. Sampaio, pers. comm., 1998). If *Z. joazeiro* trees take up a significant amount of water from depths inaccessible to the herbaceous plants, the competition for soil water in upper soil layers between these two life forms could be reduced.

In contrast, local farmers usually say that herbaceous plants do not grow well under the canopies of *P. juliflora* because this tree species may develop a shallow and extensive rooting system and 'dry up the upper soil layer'. Previous studies have reported lower soil moisture levels under *P. juliflora* canopies in comparison to areas outside the canopy (Parker and Martin, 1952). In our study site, the Alfisol characteristic of the areas where *P. juliflora* trees were found, are usually not deeper than 1 m (Oliveira et al., 1992), which contributes to restricting root growth to the upper soil layers. In addition, the relatively lower interception of solar radiation by *P. juliflora* canopies (Figure 3), seems to have little effect on the reduction of soil and air temperatures (Figure 2), when compared to *Z. joazeiro* canopies, and may not contribute much to reductions in water losses by evaporation beneath the canopies.

We suggest that the uptake of water from the water table by *Z. joazeiro* trees could even benefit the herbaceous plants due to transfers of water from the water table to upper soil layers. Several studies have demonstrated that certain plant species can move water from relatively moist to dry soil layers using the root systems as conduits in a process know as 'hydraulic lift' or 'hydraulic redistribution', and these transfers may benefit herbaceous neighboring species (Richard and Caldwell 1987, Dawson 1993, Caldwell et al. 1998, Burgess et al. 1998). However, additional studies in our sites are necessary to test this hypothesis.

Overall, soil moisture levels were lower in areas of *Z. joazeiro* when compared to areas of *P. juliflora*, likely because of differences in soil type between the sites where these tree species were found. The sand content in the top layer (0-15 cm) of the Entisol in the areas of *Z. joazeiro* was 20% higher than in the Alfisol in the areas of *P. juliflora* (Menezes and Salcedo 1999). This difference in sand content between the two soils is likely to be greater at deeper soil layers due to the presence of the argillic horizon characteristic of Alfisols (Oliveira et al. 1992). Differences in texture between soil types could play a significant role in the control of soil water availability for plants. In arid and semi-arid regions, soils with coarser texture tend to hold more available water when compared to finer textured soils, due to the higher infiltration rates, lower evaporation losses, and lower matric potential of sandier soils (Noy-Meir, 1973). In our sites, we found that the water holding capacity of soil samples from the upper soil layer (0-15 cm) of the Entisol is 30% lower than that of the Alfisol, due to the sandier texture of the Entisol. Maybe for this reason, the increase in soil moisture content in the areas of Entisol after the rainfall in 14 March was not as high as the increase observed in the areas of Alfisol (Figure 1).

The effects of different tree species on soil and air temperature is an important parameter for the design of agroforestry systems, since the photosynthesis-respiration relationship, which depends largely on ambient temperature, plays a vital role in the accumulation of carbohydrates and in the control of the survival of crops in those systems (Sanchez, 1995). Lower temperatures beneath tree canopies may reduce water stress and increase biomass of below-crown species (Amundson et al., 1995), if competition for light (Kessler, 1992) or soil moisture does not overcome the benefits of reduced temperature to the species beneath the tree canopy. We found that soil and air temperatures were, on average, 15.6 and 2.8 °C cooler under the canopies of *Z. joazeiro* trees, respectively, when compared to patches of *C. ciliaris*. In contrast, the presence of *P. juliflora* trees had no significant effect on soil temperatures and contributed to a decrease of only 1.4 °C in below-crown air temperatures. The different effects on temperature by these two tree species may explain in part the different patterns of herbaceous biomass found under and around the canopies of these trees reported by Menezes and Salcedo (1999). Similar to our results, previous studies have shown that soil temperatures were 5 to 12 °C lower under the canopies of *Acacia tortilis* and *Adansonia digitata* trees in Kenyan savannas (Rhoades, 1997). In addition, Singh et al. (1998) showed that air temperatures beneath tree canopies in a 7-year old *A. tortilis* plantation during a monsoon season were 0.1 to 2 °C lower than temperatures recorded in the open. The different effects of *Z. joazeiro* and *P. juliflora* on soil and air temperatures in our study probably result from the differences in canopy structure between these two tree species. We observed that the canopies of *Z. joazeiro* trees may intercept an average of 65 to 70% of total solar radiation between 10 a.m. and 2 p.m., while the canopies of *P. juliflora* may intercept only 20 to 30% of the total solar radiation during the same period in the day when the measurements were performed (Figure 3).

Litter decomposition

Surface litter decomposition may be one of the major pathways for nutrient cycling in dry forest ecosystems (Jaramillo and Sanford, 1995), and may contribute with up to 43 and 46 % of the N and P taken up by plants annually in some tropical dry forests (Singh, 1975; Lugo and Murphy, 1986). Several studies available in the literature describe the dynamics of C and N in decomposing litter but few studies describe the dynamics of P (McLaughlin et al., 1988a, b, and c; Sharpley and Smith, 1989; Buchanan and King, 1993; Schomberg and Steiner, 1999).

In our study, we found that the presence of *Z. joazeiro* and *P. juliflora* trees had a significant effect on the nutrient dynamics of surface litter throughout the growing season. Losses of P from all litter types were consistently lower under the canopies of *Z. joazeiro* trees than P losses in *C. ciliaris* patches, indicating that transfers of P by microbes from soil to litter may be greater under the canopy of this tree species than in *C. ciliaris* patches. Transfers of nutrients from soil to surface litter may occur through hyphal bridges between soil and residues to allow the use of nutrients from the soil and C from litter (Holland and Coleman, 1987; Schomberg and Steiner, 1999). In this study, we found that resin P levels were not significantly different (the *P* value for this comparison was equal to 0.12) between soil samples collected under the canopies of *Z. joazeiro* and in patches of *C. ciliaris* (Table 4). However, previous studies conducted in the same location as our study site, reported greater soil P availability ($P < 0.05$) under the canopies of Z. *jouzeiro* trees, in comparison to patches of *C. ciliaris* (Menezes and Salcedo, 1999; Wick et al., 1999). We suggest that, in our study, losses of P from surface litter were lower under the canopies of Z. *joazeiro* trees maybe because of greater soil P availability and/or more favorable conditions for microbial activity (lower temperature) under the canopy of this species throughout the growing season.

Usually, litter decomposition rates are faster at the beginning of the decomposition period, due to the initial losses of soluble C and other components that serve as sources of energy for the breakdown of more complex compounds (Schomberg and Steiner, 1999). However, since moisture is usually the main control of decomposition processes in dry tropical systems, losses of mass and nutrients from litter in our study were generally greater during the 30 to 60 day period because of the rainfall event that occurred during that period. Different from what we expected, losses of litter mass were lower under the canopies of both tree species early in the season, but these losses became non-significant toward the end of the season (Tables 1 and 2). The observed slower rates of litter decomposition under the canopies of *P. juliflora* trees at 60 DAP, when compared to patches of *C. ciliaris*, could be due to the significantly lower levels of soil moisture observed under these trees early in the season (Figure 1). In general, losses of litter biomass were greater for *P. juliflora* litter, compared to litter from *Z. joazeiro* and *C. ciliaris*, maybe due to the higher litter quality (lower C to N and C to P ratios, and considerably smaller leaf size) of *P. juliflora* compared to the other two litter types.

Soil nutrient availability

In agreement with our hypothesis, we found that average net N mineralized in the top 15 cm soil layer was higher under the canopies of *Z. joazeiro* and *P. juliflora* trees (218 and 129 %, respectively) than in the associated *C. ciliaris* patches. These results are supported by a previous study, which found higher tissue N concentrations in *C. ciliaris* plants growing under the canopies of *Z. joazeiro* trees, as opposed to *C. ciliaris* plants growing in open areas outside the canopy (Menezes and Salcedo 1999). Interestingly, there were no differences in the amount of N mineralized per gram of total soil N between canopies of *Z. joazeiro* and *C. ciliaris* patches, which indicates that the greater amounts of N mineralized may not be derived from faster N cycling, but rather from higher soil N concentration due to greater leaf litter nutrient inputs under the canopies of this tree species, when compared to patches of *C. ciliaris* (Wick et al. 1999). In contrast, the amount of net N mineralized per gram of total soil N was 77 % greater ($P = 0.067$) under the canopy of *P. juliflora* trees, indicating that the cycling of N may be faster under the canopy of this tree species due to higher litter quality (lower C to N, C to P, and smaller leaf size). *P. juliflora* is a potentially N-fixing tree (Babos and Cumana, 1992), and this fact may contribute to increases in N availability under the canopy of this tree species. Similar to our findings, Garcia-Montiel and Binkley (1998) reported that N cycling under the N-fixing *Albizia* was faster when compared to non N-fixing species, maybe due to higher litter quality. Our findings demonstrated a significant effect of *P. juliflora* trees on soil N availability and cycling rate only 14 years after the orchards were established.

In the soil samples collected for the green house study, nutrient concentrations were significantly higher under the canopies of the two tree species, when compared to open grass patches, with the exception of resin-P or extractable P (Table 4). Similar to our findings, previous studies have reported higher concentrations of soil nutrients in soil samples collected under the canopies of *P. juliflora* and *Z. joazeiro* trees, in comparison to adjacent open areas (Tiedemann and Klemendson, 1973; Menezes and Salcedo, 1999; Wick et al., 1999). Interestingly, the levels of available P were generally lower in the areas of Alfisol, when compared to the areas of Entisol, even though organic P levels are significantly higher in the areas of Alfisol in our sites (Menezes and Salcedo 1999). The lower P availability in the areas of Alfisol in our study site may be due to higher amounts of oxy-hydroxides of Fe and Al in these soils, when compared to the Entisol (Oliveira et al. 1992), which may lead to greater rates of P-sorption (Frossard et al. 1995).

Plant biomass and uptake of N, K, Ca, and Mg in our green house study were greater in plants grown in soils collected under the canopies of the two tree species than in plants grown in soil from *C. ciliaris* patches, but no differences in plant P uptake were observed (Table 5). In agreement with our field N mineralization study, plant tissue N concentrations in this green house assay were significantly higher for plants grown in soil from under the canopies of the two tree species, indicating that N availability under field conditions may be higher in canopy soil when compared to soil from *C. ciliaris* patches. In Kenyan savannas, fertilizer experiments demonstrated that plants grown in open sites were more nutrient limited than plants grown under tree canopies (Rhoades, 1997; Belsky, 1994). As expected, tissue P concentration and P uptake were generally lower in plants grown in samples from the Alfisol, when compared to plants grown in samples from the Entisol, due to the lower levels of available P in the Alfisol. Since nutrient levels were higher under tree canopies, we suggest that, in our study site, herbaceous plants could benefit from the increased nutrient supply under the canopies of *Z. joazeiro* trees, since soil moisture is not affected by the presence of this tree species. However, the effect of competition for other resources, such as light, still remains unknown.

In conclusion, our findings indicate that the preservation of native tree species or the introduction of exotic tree species in *C. ciliaris* pastures in semi-arid northeastern Brazil may affect microclimatic conditions and the dynamics of litter and soil nutrients, and contribute to an increase in the capture, retention, and cycling rates of nutrients in these systems.

Acknowledgements

The authors would like to acknowledge the World Wildlife Fund - Brasil (WWF-Brasil) and the Brazilian Council for Research Development (CNPq) for the financial support to this research. We thank the Agropecuária Jaçanã for allowing us to conduct the study in their ranch and for providing lodging and logistical support during the sampling trips. Special thanks to Clarindo C. Pontes, Gilberto E. do Nascimento, Claudenice E. Santos, and Pedro A. da Silva Filho for their technical support. We also acknowledge Dr. Victor J. Jaramillo, who provided helpful comments to the manuscript.

References

Aber, JD, Nadelhoffer KJ, Studler P, and Melillo JM (1989) Nitrogen saturation in northern forest ecosystems. Bioscience 39: 378-385

Amundson, RG, Ali RA, and Belsky AJ (1995) Stomatal responsiveness to changing light intensity increases rain-use efficiency of below-crown vegetation in tropical savannas. J Arid Environments 29: 139-153

Araujo Filho JA (1990) Manipulação da vegetação lenhosa da caatinga para fins pastoris. Sobral, EMBRAPA-CNPC (EMBRAPA-CNPC. Circular Técnica, 11), 18 pp

Babos K and Cumana LJC (1992) Xylotomical study of some Venezuelan tree species (Mimosaceae I-IV). Acta Botanica Hungarica 37: 183-238

Belsky AJ (1994) Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. Ecology 75: 922-932

Belsky AJ, Mwonga SM, and Duxbury JM (1993) Effects of widely spaced trees and livestock grazing on understory environments in tropical savannas. Agrofor Syst 24:1-20

Bremner JM and Mulvaney CS (1982) Nitrogen-Total. In: Page AL, Miller RH, and Keeney DR (eds), Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties, Agronomy Monograph no. 9, (2nd Edition), pp 595-624. ASA-SSSA, Madison, USA

Buchanan M and King LD (1993) Carbon and phosphorus losses from decomposing crop residues in no-till and conventional till agroecosystems. Agron J 85: 631-

638

Burgess SSO, Adams MA, Turner NC, and Ong CK (1998) The redistribution of water by tree root systems. Oecologia 115: 306-311

Caldwell MM, Dawson TE, and Richards JH (1998) Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113: 151-161

Dawson TE (1993) Hydraulic lift and water use by plants: implications for water balance, performance and plant interactions. Oecologia 95: 565-574

Farrel J (1990) The influence of trees in selected agroecosystems in Mexico. In Gliessman, SR (ed) Agroecology: Researching the Ecological Basis for Sustainable Agriculture, pp 167-183. Springer-Verlag, New York

Frossard E. Brossard M, Hedley MJ, Metherell A (1995) Reactions controlling the cycling of P in soils. pp. 107-137. In: Tiessen H (ed) Phosphorus in the global environment: transfers, cycle, and management. John Willey and Sons, England

Garcia-Montiel DC and Binkley D (1998) Effect of Eucalyptus saligna and Albizia falcataria on soil processes and nitrogen supply in Hawaii. Oecologia 113: 547-556

Halvorson JJ, Smith JL, Bolton Jr. H, and Rossi RE (1995) Evaluating shrub-associated patterns of soil properties in a shrub-steppe ecosystem using multiple-variable geostatistics. Soil Sci Soc Am J 59:1476-1487

Holland EA and Colleman DC (1987) Litter placement effects on microbial and organic matter dynamics in an agroecosystem. Ecology: 68: 425-433

Jaramillo VJ and Sanford RL (1995) Nutrient cycling in tropical deciduous forests. In:

Bullock, S.H.; Mooney, H.A.; Medina, E. (ed.). Seasonally dry tropical forests, pp 346-361. Cambridge University Press, Cambridge

Kauffman JB, Sanford RL, Cummings DL, Salcedo IH, and Sampaio EVSB (1993) Biomass and nutrient dynamics associated with slash fires in neotropical dry forests. Ecology 74(1): 140-151

Kessler JJ (1992) The influence of karite (*Vitellaria paradoxa*) and nere (*Parkia biglobosa*) trees on sorghum production in Burkina Faso. Agrofor Syst 17: 97-118

Kolberg RL, Rouppet B, Westfall DG, and Peterson GA (1997) Evaluation of an in situ net soil nitrogen mineralization method in dryland agroecosystems. Soil Sci. Soc. Am. J. 61: 504-508

Lugo AE and Murphy PG (1986) Nutrient dynamics of a Puerto Rican subtropical dry forest. J. Trop Ecol 2: 55-72

McLaughlin MJ, Alston AM, and Martin JK (1988a) Phosphorus cycling in wheat-pasture rotations. I. The source of phosphorus taken up by wheat. Aust J Soil Res 26: 323-331

McLaughlin MJ, Alston AM, and Martin JK (1988b) Phosphorus cycling in wheat-pasture rotations. II. The role of the microbial biomass in phosphorus cycling. Aust J Soil Res 26: 333-341

McLaughlin MJ, Alston AM, and Martin JK (1988a) Phosphorus cycling in wheat-pasture rotations. III. Organic phosphorus turnover and phosphorus cycling. Aust J Soil Res 26: 343-355

Menezes RSC and Salcedo IH (1999) Influence of tree species on the herbaceous understory and soil chemical characteristics in a silvopastoral system in semi-arid Northeastern Brazil. Revista Brasileira de Ciência do Solo (in press)

Murphy J and Riley JP (1962) A modified simple solution method for the determination of phosphate in natural waters. Anal Chim Acta 27: 31-36

Nadelhoffer KJ, Emmett BA, Gundersen P, Kjonaas OJ, Koopmans CJ, Scheleppi P, Tietema A, and Wright RF (1999) Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. Nature 398: 145-148

Nandwa SM and Bekunda MA (1998) Research on nutrient flows and balances in West Africa: state-of-the-art. Agriculture, Ecosystems and Environment 71: 1-4

Noy-Meir I (1973) Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25-51

Oliveira JB de, Jacomine PKT, and Camargo MN (1992) Classes gerais de solos do Brasil. FUNEP, Jaboticabal, 201 pp

Olsen SR and Sommers LE (1982) Phosphorus. In: Page AL, Miller RH, and Keeney DR (eds), Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties, Agronomy Monograph no. 9, (2nd Edition), pp 403-430. ASA-SSSA, Madison

Parker KW and Martin SC (1952) The mesquite problem on southern Arizona ranges. U.S. Dep Agr Circ No 908, 70 pp

Reynolds JF, Virginia RA, and Cornelius JM (1990) Resource island formation associated with desert shrubs, creosote bush (*Larrea tridentata*) and mesquite

(*Prosopis glandulosa*) and its role in the stability of desert ecosystems: A simulation analysis. Suppl Bull Ecol Soc Am 70(2):299-300

Rhoades CC (1995) Seasonal pattern of nitrogen mineralization and soil *moisture Faidherbia albida* (syn *Acacia albida*) in central Malawi. Agrof Syst 29:133-145

Richards JH and Caldwell MM (1987) Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia 73: 486-489

Sampaio EVSB (1995) Overview of the Brazilian caatinga. In: Bullock, S.H.; Mooney, H.A.; Medina, E. (Ed.). Seasonally dry tropical forests. pp 35-63. Cambridge University Press, Cambridge

Sampaio EVSB and Salcedo IH (1997) Diretrizes para o manejo sustentável dos solos brasileiros: região semi-árida. In: Anais do Congresso Brasileiro de Ciencia do Solo, 26. Rio de Janeiro, RJ

Sampaio EVSB, Salcedo IH, and Silva FBR (1995) Fertilidade dos solos do semi-árido. In: J.R. Pereira e C.M.B. de Faria (eds.) Fertilizantes: Insumo básico para a agricultura e combate à fome. EMBRAPA-CPATSA/SBCS. Petrolina, PE, 273 pp

Sanchez PA (1995) Science in agroforestry. Agrofor Syst 30:5-55

SAS Institute (1995) SAS User's Guide, Release 6.12. SAS Institute Inc., Cary, NC

Schomberg HH and Steiner JL (1999) Nutrient dynamics of crop residues decomposing on a fallow no-till soil surface. Soil Sci Soc Am J 63: 607-613

Sharpley AN and Smith SJ (1989) Mineralization of phosphorus from soil incubated with surface-applied and incorporated crop residue. J Environ Qual 18: 101-105

Sibbesen E (1977) A simple ion-exchange procedure for extracting plant available elements from soil. Plant Soil 46: 665-669

Singh RP (1975) Biomass, nutrient, and productivity structure of a stand of dry deciduous forest of Varanasi. Trop Ecol 37: 104-109

Singh M, Arrawatia ML, and Tewari VP (1998) Agroforestry for sustainable development in arid zones of Rajasthan. International Tree Crops Journal 9:203-212

Silva Filho JC de (1988) Tecnologia agrícola para o semi-árido brasileiro. FUNDAJ, Editora Massangana, Recife, Brasil, 102 pp

Silva VM, Araujo Filho JA, Leite ER, Pereira VLA, and Ugiette SA (1995) Manipulação da caatinga e seu efeito sobre parâmetros fitossociógicos e de produção, em Serra Talhada, Pernambuco. In: Reuniao da Sociedade Brasileira de Zootecnia, Brasília, Anais, pp 17-21. SBZ, Brasília, Brasil

Snyder JD and Trofymow JA (1984) A rapid accurate wet oxidation diffusion procedure for determining organic and inorganic carbon in plant and soil analysis. Commun in Soil Sci and Plant Anal 15:587-597

Thomas RL, Sheard RW, and Moyer JR (1967) Comparisson of conventional and automated procedures for N, P and K analysis of plant material using a single digestion. Agron J 59:240-243

Tiedemann AR and Klemmedson JO (1973) Effect of mesquite on physical and chemical properties of the soil. J Range Manag 26:27-29

Tiessen H, Cuevas E, and Chacon P (1994) The role of soil organic matter in sustaining soil fertility. Nature 371:783-785

Weltzin JF and Coughenour MB (1990) Savanna tree influence on understory vegetation and soil nutrients in northwetern Kenya. J Veg Sci 1: 325-334

West NE (1981) Nutrient cycling in desert ecossystems. In: Goodall DW and Perry RA (eds) Arid land ecossystems: Structure, function, and management, pp 301-324. Cambridge Univ. Press, Cambridge, England

Wick B, Tiessen H, and Menezes RSC (1999) Land quality changes following the conversion of the natural vegetation into silvo-pastoral systems in semi-arid NE Brazil. Plant and Soil (submitted)

Wortmann CS and Kaizzi CK (1998) Nutrient balances and expected effects of alternative practices in farming systems of Uganda. Agriculture, Ecosystems and Environment 71: 115-129

Table 1. Losses of total biomass, nitrogen, and phosphorous from litter decomposition bags containing litter from *P. juliflora*, *Z. joazeiro*, or *C. ciliaris*. The bags were placed under the canopies of *Z. joazeiro* trees, in intermediate positions right outside the canopies, or in open patches of *C. ciliares*, and collected at 30, 60, or 100 days after placement in the field. Values represent means (n = 5) followed by standard errors within parentheses. Soil moisture was higher during the 30-60 day period.

	Biomass loss (%)			Nitrogen loss (%)			Phosphorous loss (%)		
	0-30 days	30-60 days	60-100days	0-30 days	30-60 days	60-100 days	0-30 days	30-60 days	60-100 days
P. juliflora leaf litter									
Z. joazeiro canopy	11.1 (2.1)	37.5 (1.7)	n/a [‡]	6.7 (2.8)	28.6 (8.2)	n/a	**7.8 (2.8) b**[†]	**28.1 (3.8) b**	n/a
Intermediate	14.4 (1.4)	40.1 (5.0)	n/a	12.2 (2.0)	40.6 (7.3)	n/a	**21.4 (3.0) a**	**52.2 (6.4) a**	n/a
C. ciliaris patch	15.6 (0.9)	48.0 (3.9)	n/a	8.7 (2.1)	44.9 (3.9)	n/a	**19.6 (2.2) a**	**55.0 (4.4) a**	n/a
Z. joazeiro leaf litter									
Z. joazeiro canopy	**6.4 (0.4) b**	14.5 (0.7)	n/a	**15.5 (0.9) b**	21.8 (2.6)	n/a	**- 0.9 (1.9) b**	**5.6 (2.6) a**	n/a
Intermediate	**7.2 (0.3) ab**	21.2 (1.1)	n/a	**23.4 (1.8) a**	32.3 (2.4)	n/a	**13.6 (2.2) a**	**28.2 (1.8) b**	n/a
C. ciliaris patch	**8.5 (0.5) a**	17.7 (3.9)	n/a	**20.3 (2.8) ab**	29.3 (4.8)	n/a	**11.0 (2.0) a**	**33.1 (7.0) b**	n/a
C. ciliaris tissue litter									
Z. joazeiro canopy	4.3 (0.7)	22.1 (0.8)	n/a	27.8 (8.4)	34.5 (5.1)	n/a	**18.7 (6.8) b**	**49.0 (2.5) b**	n/a
Intermediate	3.1 (0.8)	29.3 (4.3)	n/a	25.8 (4.5)	46.7 (5.4)	n/a	**35.5 (3.6) a**	**63.5 (3.1) a**	n/a
C. ciliaris patch	5.6 (1.1)	21.4 (3.3)	n/a	34.2 (4.0)	45.4 (2.0)	n/a	**40.8 (3.3) a**	**60.7 (2.9) a**	n/a

[†] Means followed by different letters are significantly different at $P < 0.05$.

[‡] Data not available because of litter bag losses due to animal trampling.

Table 2. Losses of total biomass, nitrogen, and phosphorous from litter decomposition bags containing litter from *P. juliflora*, *Z. joazeiro*, or *C. ciliaris*. The bags were placed under the canopies of *P. juliflora* trees, in intermediate positions right outside the canopies, or in open patches of *C. ciliares*, and collected at 30, 60, or 100 days after placement in the field. Values represent means (n = 5) followed by standard errors within parentheses. Soil moisture was higher during the 30-60 day period.

	Biomass loss (%)			Nitrogen loss (%)			Phosphorous loss (%)		
	0-30 days	30-60 days	60-100 days	0-30 days	30-60 days	60-100 days	0-30 days	30-60 days	60-100 days
				P. juliflora leaf litter					
P. juliflora canopy	**8.3 (0.7) b** [†]	45.7 (1.1)	48.2 (0.8)	0.9 (1.4)	32.9 (2.7)	43.5 (3.7)	18.0 (4.8)	37.4 (4.3)	36.6 (5.7)
Intermediate	**10.4 (1.6) ab**	46.5 (0.8)	49.7 (1.2)	0.2 (1.1)	31.3 (1.5)	37.0 (2.6)	20.3 (5.9)	34.2 (1.8)	42.0 (3.0)
C. ciliaris patch	**11.3 (0.9) a**	38.7 (3.5)	45.6 (4.6)	3.7 (3.3)	24.9 (4.0)	34.9 (6.0)	18.6 (5.3)	18.9 (9.9)	36.9 (6.2)
				Z. joazeiro leaf litter					
P. juliflora canopy	5.5 (0.1)	**17.8 (1.6) b**	23.3 (1.2)	9.0 (3.2)	23.8 (1.8)	27.9 (4.8)	1.7 (1.8)	8.1 (3.8)	23.1 (9.4)
Intermediate	6.8 (1.5)	**22.0 (1.1) a**	24.2 (1.1)	9.2 (2.2)	25.7 (1.3)	25.6 (6.0)	1.7 (3.5)	14.8 (2.6)	32.9 (9.9)
C. ciliaris patch	7.1 (0.8)	**22.8 (1.5) a**	23.9 (2.0)	14.5 (2.1)	30.1 (2.3)	19.6 (6.4)	2.6 (2.4)	11.5 (6.0)	29.3 (10.9)
				C. ciliaris tissue litter					
P. juliflora canopy	3.9 (0.7)	**27.2 (2.9) b**	28.3 (3.8)	16.7 (5.1)	25.2 (3.7)	27.2 (9.2)	27.8 (2.0)	41.3 (3.0)	44.5 (2.4)
Intermediate	6.2 (0.8)	**29.1 (1.1) b**	30.6 (3.6)	11.0 (7.1)	38.7 (2.6)	40.3 (7.7)	21.4 (3.2)	47.9 (2.5)	53.9 (4.0)
C. ciliaris patch	4.9 (0.7)	**36.8 (1.6) a**	32.4 (2.6)	9.1 (3.7)	36.1 (5.0)	28.3 (4.5)	18.7 (6.4)	53.1 (4.0)	44.0 (8.4)

[†] Means followed by different letters are significantly different at $P < 0.05$.

Table 3. Soil (0 to 15 cm) net nitrogen mineralized in a seven-week field incubation and total soil C and N concentrations under the canopies of *Z. joazeiro* and *P. juliflora* and in *C. ciliaris* patches in a silvopastoral system in semi-arid northeastern Brazil. Values represent means (n = 5) with standard errors within parentheses.

	NH_4^+-N soil	NH_4^+-N resin	NO_3^--N soil	NO_3^--N resin	Total net N mineralized	Total soil C	Total soil N
			μg g soil^{-1}			mg g soil^{-1}	
				Z. joazeiro			
Under Canopies	0.75 (4.2)	0.50 (0.11)	13.3 (4.7)	3.60 (0.74)	18.1 (8.3)	12.8 (2.3)	1.12 (0.19)
C. ciliaris patches	-0.83 (0.3)	0.37 (0.04)	5.1 (1.1)	1.10 (0.22)	5.7 (1.2)	5.2 (0.7)	0.50 (0.05)
P-value	NS†	NS	0.064	0.006	0.089	0.007	0.007
				P. juliflora			
Under Canopies	-3.75 (1.1)	0.85 (0.12)	13.8 (3.7)	4.06 (0.78)	14.9 (4.5)	15.1 (1.3)	1.53 (0.15)
C. ciliaris patches	-1.31 (0.4)	0.76 (0.13)	5.9 (1.0)	1.14 (0.22)	6.5 (1.1)	12.7 (0.8)	1.20 (0.12)
P-value	0.035	NS	0.037	0.003	0.051	0.088	0.069

† Not significant at $P < 0.10$.

Table 4. Nutrient concentrations of soil samples (0-15 cm) collected from areas under the canopies of *Z joazeiro* and *P. juliflora* trees and from *C. ciliaris* patches next to the trees in a silvopastoral system in semi-arid Northeastern Brazil. Values represent means (n = 5) with standard errors within parentheses.

	Total C	Total N	NH_4^+-N	NO_3^--N	Resin P	Extr. P[†]	K^+	Ca^{+2}	Mg^{+2}
	g kg $soil^{-1}$		µg g $soil^{-1}$		µg g $soil^{-1}$		mmol (+) kg $soil^{-1}$		
					Z. joazeiro				
Under Canopies	14.6 (1.5)	1.43 (0.15)	10.8 (1.5)	4.06 (0.61)	41.1(13.4)	37.0 (12.8)	15.7 (1.7)	23.3 (1.8)	6.68 (1.11)
C. ciliaris patches	5.1 (0.7)	0.49 (0.05)	5.8 (0.3)	1.89 (0.52)	19.1 (3.6)	30.5 (11.1)	6.3 (0.5)	9.3 (1.2)	1.56 (0.18)
P-value	0.004	0.004	0.029	0.023	NS[‡]	NS	0.002	0.003	0.011
					P. juliflora				
Under Canopies	16.1 (0.8)	1.69 (0.14)	12.9 (0.9)	5.30 (1.13)	18.9 (8.2)	24.5 (18.5)	16.9 (2.3)	30.6 (1.8)	12.74 (2.1)
C. ciliaris patches	12.8 (0.8)	1.21 (0.12)	9.3 (0.2)	1.22 (0.22)	12.7 (5.7)	5.1 (0.9)	10.6 (1.2)	22.8 (2.5)	9.53 (1.2)
P-value	0.063	0.055	0.019	0.018	NS	NS	0.090	0.006	0.094

[†] Extractable P (dilute acid).

[‡] Not significant at $P < 0.10$.

Table 5. Biomass production and nutrient uptake by pearl millet (*Pennisetum glaucum* (R.) Br. cv. 'IPA Bulk 1') plants grown for 30 days in soil samples collected from areas under the canopies of *Z. joazeiro* and *P. juliflora* trees and from *C. ciliaris* patches next to the trees in a silvopastoral system in semi-arid northeastern Brazil. Values represent means (n = 5) with standard errors between parentheses.

	Plant biomass (g dry matter pot^{-1})			Nutrient uptake (mg pot^{-1})				
	Aboveground	Belowground	Total biomass	N	P	K	Ca	Mg
				Z. joazeiro				
Under canopies	1.80 (0.11)	0.75 (0.05)	2.55 (0.14)	39.8 (2.72)	9.40 (0.77)	135.4 (13.7)	27.2 (2.0)	9.44 (0.76)
C. ciliaris patches	1.29 (0.05)	0.75 (0.06)	2.04 (0.10)	27.3 (1.03)	7.81 (2.14)	93.9 (18.8)	15.6 (4.5)	5.42 (2.51)
P-value	0.003	NS[†]	0.039	0.018	NS	0.009	0.006	0.004
				P. juliflora				
Under canopies	1.38 (0.05)	0.63 (0.06)	2.01 (0.09)	36.5 (3.36)	2.60 (0.38)	111.8 (11.5)	20.2 (2.6)	7.68 (1.5)
C. ciliaris patches	1.11 (0.03)	0.52 (0.05)	1.63 (0.06)	21.6 (2.04)	2.54 (0.28)	83.2 (7.8)	14.7 (1.8)	5.24 (1.1)
P-value	0.001	NS	0.012	0.013	NS	0.009	0.046	0.060

[†] Not significant at $P < 0.10$.

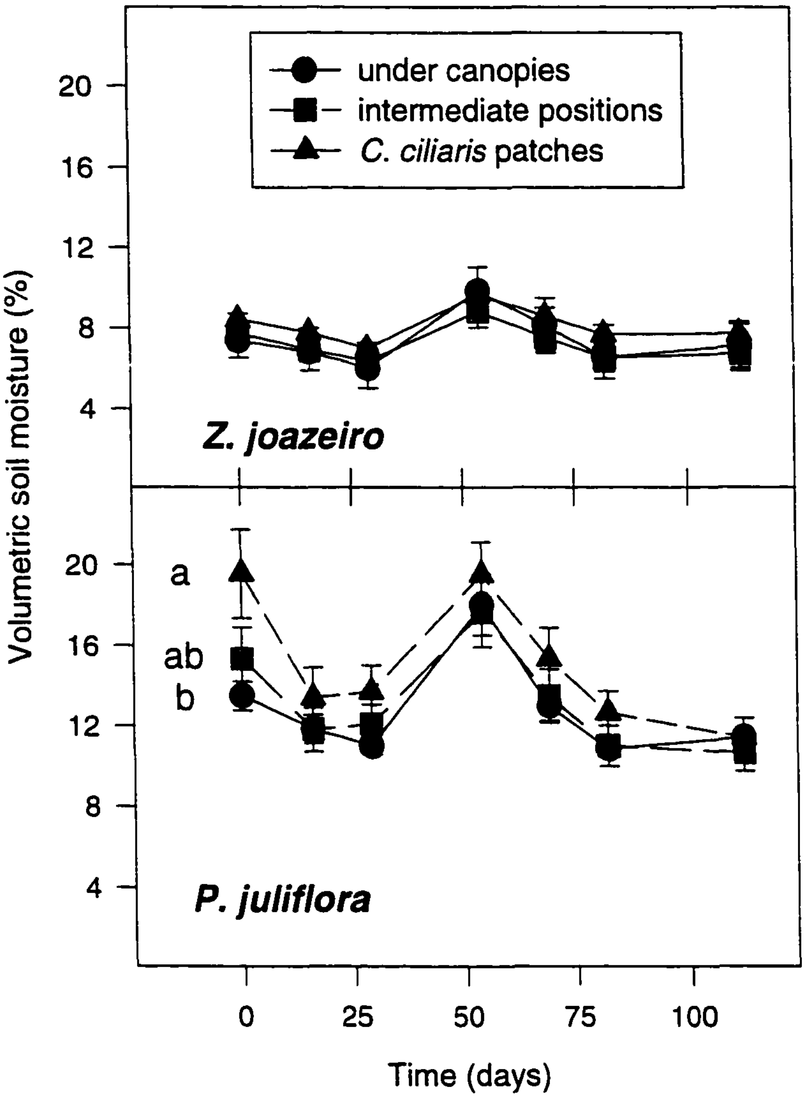

Fig. 1. Soil moisture (0 to 28 cm) under the canopies of *P. juliflora* and *Z. joazeiro* trees, in intermediate positions, and in patches of *C. ciliaris* from late January to mid-May of 1998. Error bars represent standard error for the means (n=5). Means within a sampling date followed by different letters are significantly different at $P < 0.05$.

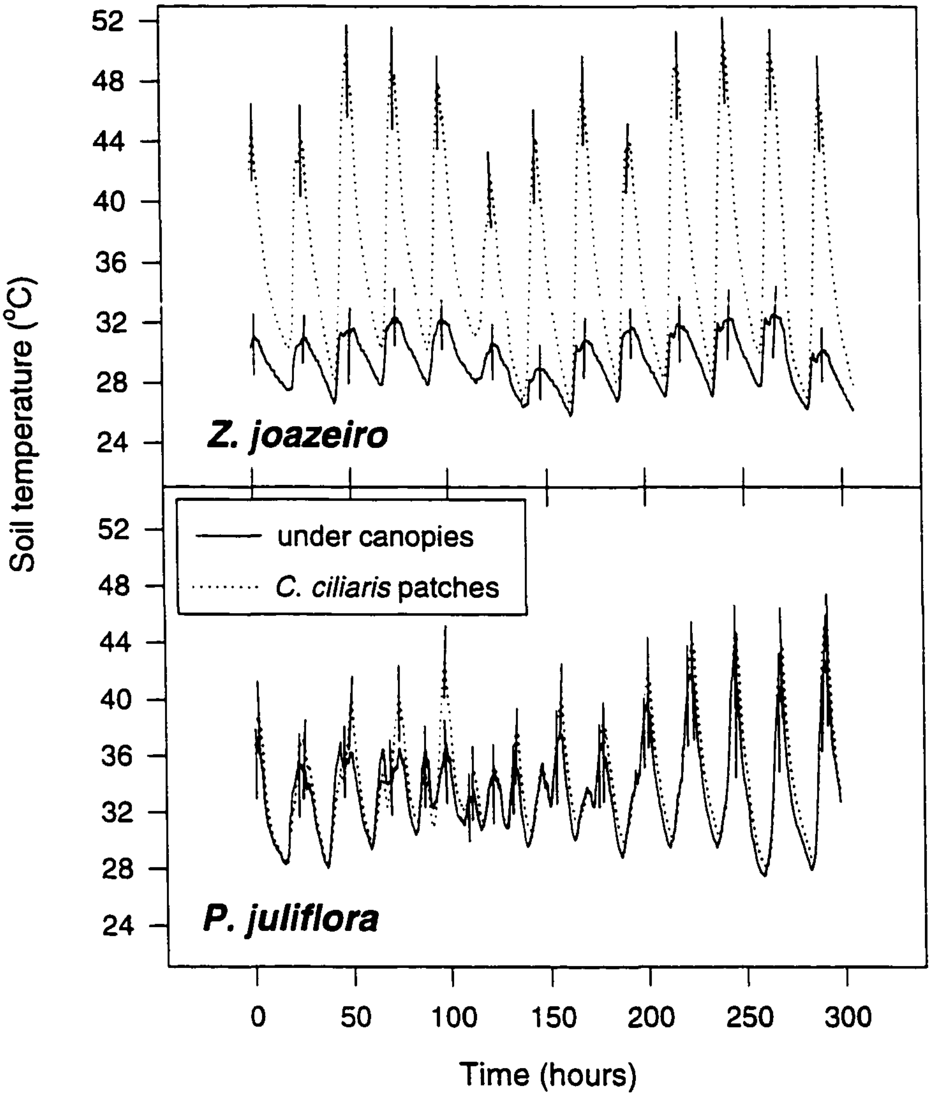

Fig. 2. Mean (n=4) soil temperature (1 to 6 cm) in patches of *C. ciliaris* and under the canopies of *P. juliflora* and *Z. joazeiro* trees during February 1998. Vertical lines correspond to the 95% confidence interval for the means (n=4) of maximum temperatures in each position.

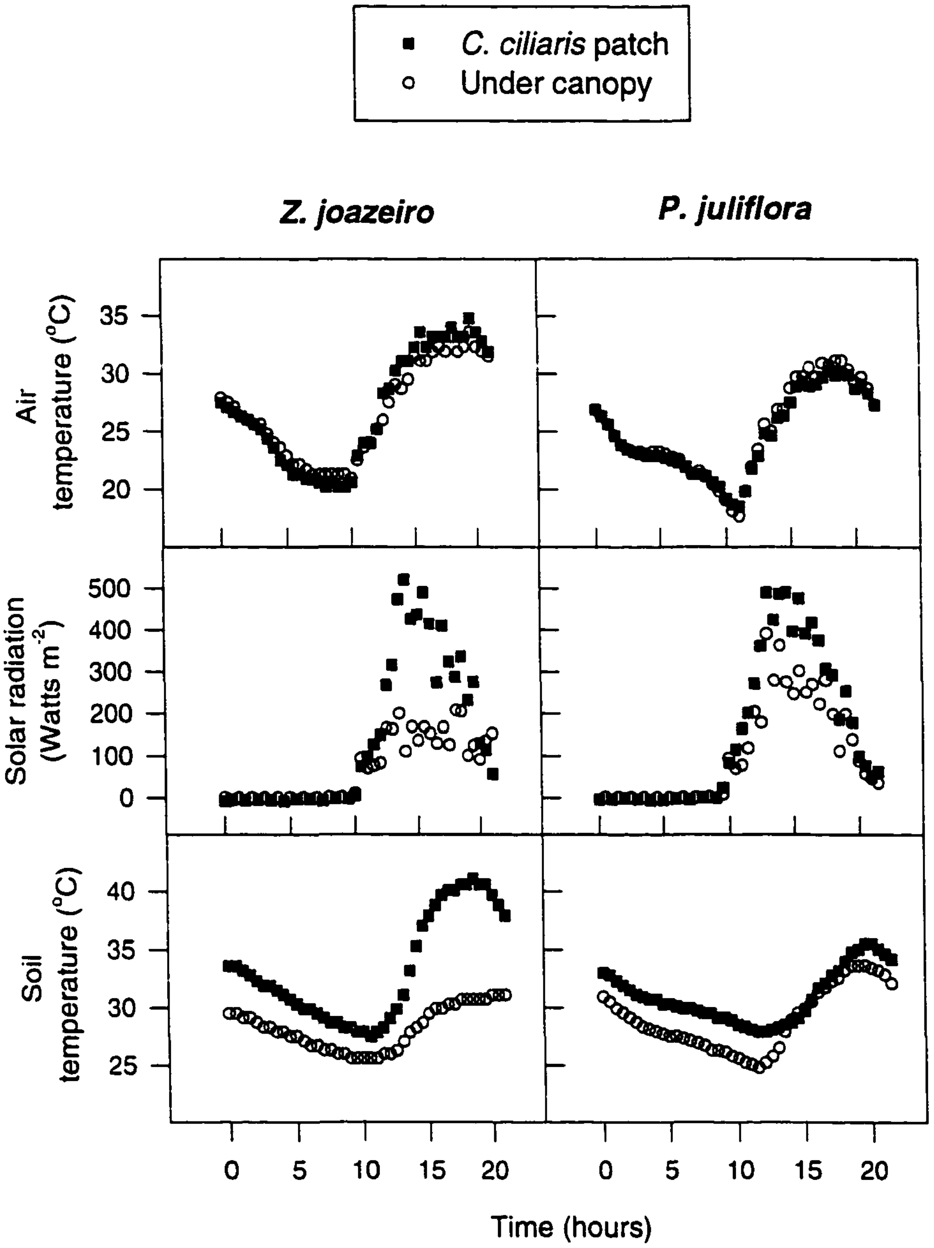

Figure 3. Air temperature, soil temperature (0 to 6 cm), and total solar radiation under the canopies of *Z. joazeiro* and *P. juliflora* trees and in an open patch of *C. ciliaris* during a 22 hour period from 7 pm to 5 pm.

CHAPTER IV

Effects of herbivory and proximity to surface water on C and N dynamics on the elk winter range in Rocky Mountain National Park [1]

Rômulo S.C. Menezes [2,3], Edward T. Elliott [3], David W. Valentine [4], and Stephen A. Williams [3]

---

[1] Manuscript submitted to Journal of Range Management

[2] Corresponding author. Research Fellow of Brazilian CNPq. Soil and Crop Sciences Department, Colorado State University, Fort Collins, CO, 80523. E-mail: romulo@nrel.ecolostate.edu

[3] Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, 80523

[4] Department of Forest Sciences, University of Alaska, Fairbanks, AK, 99775-7200

Abstract

It has been suggested that recent increases in elk herbivory and changes in hydrology towards drier conditions have contributed to declines in willow (*Salix* spp.) communities in the winter ranges for elk in Rocky Mountain National Park (RMNP). During the fall of 1994, we constructed twelve large elk exclosures in two watersheds of the winter range for elk in RMNP, and we conducted field experiments during the growing seasons of 1995 to 1999 to investigate the effects of herbivory and proximity to surface water on the dynamics of C and N. We found that elk herbivory led to increases ($P < 0.05$) in N concentration of willow litter and decreases in litterfall biomass, but herbivory did not affect losses of C and N from litter in any of the growing seasons. Soil moisture levels were higher in lower landscape positions, which probably lead to higher ($P = 0.001$) C losses from litter, in comparison to upper landscape positions. In plots where N fertilizer was added, we observed an increase ($P < 0.05$) in willow shoot length, shoot biomass, and the average amount of N in the shoots, indicating that availability of N is limiting plant growth in our study sites. Elk herbivory had no effect on soil inorganic N availability and in situ net N mineralization rates, maybe because of the short time since treatment establishment (4 years). However, we estimated that the return of N to the soil in grazed plots could be as much as 265% of the N return in exclosed plots, perhaps due to N transfers from the summer range to the winter range. Our results demonstrate that elk herbivory and proximity to surface water had significant influences on the biogeochemical cycles of the winter ranges for elk in RMNP. Greater return of N to the soil combined with increased litter quality in the grazed plots indicate that elk could

contribute to increases in N cycling rates and availability in the long-term, which could lead to changes in ecosystem structure and function in the winter range for elk in RMNP.

Index words: Willow, *Salix*, *Carex*, litter, nitrogen availability, grazing, browsing.

Introduction

Since 1968, elk (*Cervus elaphus*) numbers in Rocky Mountain National Park (RMNP), Colorado have been managed under a policy of natural regulation, which rests on the assumption that density-dependent mechanisms would result in an equilibrium between large ungulate herbivores and plant resources. During this period, elk numbers have increased from approximately 1,000 to about 3,300 animals, and park managers are concerned about the effects of these increases on the soils and vegetation of the elk winter range within the park (Singer et al. 1998b).

Willow (*Salix* spp.) communities have reportedly been declining in elk winter ranges of RMNP during the last few decades (Hess 1993; Singer et al. 1998b), and similar declines have also been reported for Yellowstone National Park (Chadde and Kay 1991, Kay and Wagner 1994, Singer et al. 1998a). In addition to increased elk herbivory, two other factors have been proposed to explain these declines in willow communities: (1) climates are warmer and drier this century, possibly resulting in lowered stream flows and less water availability to plants (Singer et al. 1998b); and (2) beaver populations have declined on the eastern slope of RMNP (Stevens and Christianson 1980), which may further contribute towards the drying of these ecosystems.

Large herbivores can significantly influence plant community structure and biogeochemical cycles within the soil-plant system (Frank et al. 1994, Frank and

Groffman 1998, Hamilton et al. 1998, Schuman et al. 1999, Wijnen 1999). Herbivores can influence nutrient cycling by removing plant biomass and returning more readily available nutrients to the soil (McNaughton et al. 1988, Frank et al. 1994, Hamilton et al. 1998), increasing soil N mineralization rates and plant N uptake (Frank and Groffman 1998, Wijnen et al.1999), and spatially redistributing nutrients within the landscape (McNaughton 1985, Afzal and Adams 1992, Russelle 1992). In some N-limited systems, herbivory may lead to slower rates of nutrient cycling due to increases in the dominance of non-browsed plant species, which may produce litter with low nutrient concentrations or with high concentrations of secondary compounds (Pastor et al. 1993, Ritchie et al. 1998). In addition, herbivory can influence plant growth and physiology (Toft et al. 1987, Welker and Briske 1992, Fahnestock and Detling 1999, Singer et al. 1998a, b) and alter carbon and nitrogen allocation within plants (Welker et al. 1987, 1985, Holland and Detling 1990, Singer et al. 1998a, Alstad et al. 1999). Changes in the root to shoot ratio following browsing may lead to improvements in the water balance of plants (Welker and Menke 1990), while the removal of meristems (Briske 1986) or overgrazing (Pengelly 1963, Singer et al. 1998a) may reduce their future growth potential. Whether herbivory has a positive or negative influence on plants may depend in part on the specific characteristics of each system (Georgiadis et al. 1989, Hamilton et al. 1998, Mazancourt et al. 1998, Alstad et al. 1999).

Beaver (*Castor canadensis*) can also influence plant communities and biogeochemical cycles of ecosystems. By building dams, beavers contribute to the entrapment of sediment and organic matter and modify nutrient cycling and decomposition dynamics (Naiman et al. 1986). Active beaver ponds may increase the inputs of N and P to the flooded systems (Naiman and Melillo 1984) and increase water availability to plants, which enhance the conditions for willow growth and reestablishment of shoots, sprouts, and seedlings (Singer et al. 1998b, Naiman et al. 1986). It has been suggested that the observed declines in beaver populations in the eastern slope of RMNP have contributed to a decrease in the surface area of water (ponds and streams) within the winter range of elk since the beginning of this century (Singer et al. 1998b). These reductions in surface water may alter the biogeochemical cycles of those ecosystems, and could further reduce the ability of willow to respond to elk herbivory.

Plant-available N is usually a limiting element for plant growth in terrestrial ecosystems (Power 1977, Kiehl et al. 1997, Wijnen 1999) and the cycling of N in these systems is linked to the C cycle by internal organic matter transfers and positive and negative feedback loops between decomposers, plants, and herbivores (Aber and Melillo 1991, Pastor and Naiman 1992). Therefore, the dynamics of C and N are of critical importance to primary productivity and overall ecosystem function (Power 1994, Schuman et al. 1999). There is no available information about the effects of elk herbivory or the reduction in surface water on the dynamics of C and N in the winter ranges of elk in RMNP. This information is necessary for helping park managers formulate policies that will maintain elk and beaver populations at levels that are adequate for preserving the natural functioning of these ecosystems. Therefore, the objective of this study was to perform experimental field manipulations to investigate the effects of elk herbivory and proximity to surface water on the C and N cycles in the winter ranges of elk in RMNP.

Methods

Study Sites

The low elevation winter range for elk in Rocky Mountain National Park (RMNP) encompasses about 10,000 ha, which includes land within the eastern side of the park and private and national forest lands outside the park in the town of Estes Park and Estes Valley, Colorado (Singer et al. 1998b). Our study sites were located in two riparian ecosystems on the northeastern side of RMNP: Moraine Park (Big Thompson River watershed, elevation 2,481 m) and Horseshoe Park (Fall River watershed, elevation 2,598 m). The two watersheds are within 5 km of each other and have perennial alpine snowfields at their headwaters. Mean annual precipitation for the sites is 41 cm (Singer et al. 1998b) and peak stream flow usually occurs in early to mid-June (USDA 1995, 1996, and 1997). The 30-year average temperature for the adjacent Estes Valley ranges from 9 to 17°C during the five-month growing season of May through September (Alstad et al. 1999). The study area consists of wet meadows dominated by willow (*S. monticola*, *S. geyeriana*, and *S. planifolia*), other shrubs such as birch (*Betula* spp.), sedges (*Carex* spp.), rushes (*Juncus balticus*), and grasses (*Phleum* spp., *Calamagrostis* spp., *Bromus* spp., *Poa* spp.). The elk population of Estes Valley numbers about 3,300 animals, of which about one third generally spends the winter within the park (Larkins 1997, Singer et al. 1998b).

Experimental Treatments

In the wet meadows of both parks, twelve 30 m x 46 m exclosures were erected within willow communities along the rivers between August and November of 1994. Next to each exclosure, 30 m x 46 m plots were chosen and marked off as paired plots open to grazing (grazed plots). Each site consisted of an exclosure and a grazed plot. Eight sites (four in Moraine Park and four in Horseshoe Park) were placed in areas with little or no beaver activity, and contained heavily browsed willow (short willow). The other four sites (two in each park) were located in wetter areas, generally containing taller willow plants subjected to less severe browsing by elk (tall willow). In half of the short willow sites (two in each park), hydro-manipulation treatments were imposed by placing sheet metal check dams on ephemeral stream channels both inside the exclosures and in the grazed plots. We expected these check dams to catch snowmelt and rain runoff through the spring and raise the water table at the sites. Twenty-five dams were installed in April and May 1995 and were relatively successful in holding additional water at these sites. The dams were intended to add water, but in no way was the treatment able to simulate water additions in the amounts accomplished by beaver dams on larger, permanent streams (Singer et al. 1997). In each exclosure and associated grazed plot, an average of five shallow (0.5 m to 2 m) wells were installed in the spring of 1995 for the purpose of monitoring groundwater levels. During early 1996 and 1997, three dams were constructed by beaver near two sites within the wetter area of Moraine Park, but these dams were washed out during the spring flood of 1996 and 1997.

The area within each exclosure was sub-divided in 15 x 23 m sub-plots and two treatments were imposed throughout the period of the study: (1) 75% current annual growth (CAG) removal (clipped plots), and (2) no clipping at all (ungrazed plots). The

75% CAG removal treatment was applied between January and April of 1995, 1996, 1997, and 1998, and consisted of clipping all forage shrubs and herbaceous plants in each sub-plot. All clipped plant biomass was removed from the exclosures.

Litterfall

Litter was collected in each experimental plot during the fall of 1995, 1996, and 1997, through the use of fifteen greenhouse trays (totaling ~ 2.3 m^2) arranged in a 5 x 3 regularly spaced grid (9.1 x 15.9 m). The grids were established randomly within each sub-plot before willow senescence began, and each tray was anchored to the ground using two or more large spikes. Litter was collected weekly from early September to late October until litterfall was complete. The litter was then composited within each experimental replication, sorted by genus and litter type, air dried, and weighed. Oven-dry corrections were applied within each category by drying a subsample at 60 °C. Litterfall biomass was calculated as oven dry mass per unit area. Total N and C content of litter was determined using a LECO CHN-1000 analyzer.

Litter Decomposition

During September and October of 1994, we collected litter material to generate a standard litter that was used in the decomposition experiments. Willow leaf litter was collected by locating greenhouse trays directly under willow canopies. *Carex* litter was collected by clipping and collecting dead biomass throughout the study area. We dried all litter in a 35 °C forced air oven, and subsamples (2 g) from the two standard litter types (willow leaves and *Carex* tissue) were enclosed in 1 mm nylon mesh bags. The bags were used in litter decomposition experiments to investigate the effects of herbivory, landscape position, and plant cover on the decomposition rates of willow and *Carex* litter during the 1995, 1996, and 1997 growing seasons. In all experiments, the litterbags were left in the field during the entire length of the growing season (from late May until mid-September), and then collected, air-dried, weighed, ground to a fine powder, and stored until analysis. Carbon and N in the decomposed litter were analyzed using a LECO CHN-1000 analyzer, and C and N losses were calculated in an ash-free dry weight basis by subtracting the amounts in the pre-decomposition from the post-decomposition litter.

During the growing season of 1995, four bags of each litter type (willow leaves and *Carex* tissue) were randomly placed within the exclosures in the ungrazed plots and outside the exclosures in the grazed plots for all of the twelve sites. In 1996 and 1997, in each of the ungrazed and grazed plots, we selected two willow shrubs located at two different landscape positions: (1) lower landscape positions, next to a stream or a pond, and (2) upper landscape positions, at least 10 m away from a stream or a pond and 0.5 m higher in the landscape than lower landscape positions. Bags of both willow and *Carex* litter were placed under the canopies of the selected willow and in open grass areas next (within 2 m) to the shrubs. Two bags of each litter type were placed within each treatment replication in order to reduce microsite variability.

Elk Dung Quantification

We estimated the amount of C and N returned to the soil in elk dung by counting the number of scat piles along 30 m transects within our experimental grazed plots, and measuring the concentrations of C and N in the dung. The survey was conducted after the elk herds left the winter range for the summer range during late spring 1997. We selected eight grazed plots (four in each park) and established four randomly placed transects per plot. In each transect, we measured the distance from the scat piles to the transect, and calculated the density of piles per area. Only scat piles that were visually identified as from the previous fall and winter were counted. In order to estimate dry matter and C and N content in each dung pile we obtained fifty-one samples (twenty-six from Horseshoe Park and twenty-five from Moraine Park) by collecting all dung from fresh piles during late Fall of 1997. After collection, the samples were air-dried, weighed, ground to a fine powder, and sub-sampled for determination of moisture and ash content. The concentrations of C and N in the dung were determined using a LECO CHN-1000 analyzer and expressed on an ash-free dry weight basis.

Soil Characteristics and N Availability

Soil samples (0-15 cm) were collected in July 1997 from the grazed, ungrazed, and clipped plots. Within each treatment replication, a total of twenty-five to thirty cores were randomly collected with a soil core sampler 2 cm in diameter and combined in a paper bag. After collection, the samples were taken to the laboratory, air-dried, and passed through a 2 mm sieve. Soil particle distribution was measured in each sample using the hydrometer method (Gee and Bauder 1986). Sub-samples (10 g) of each sample were ground to a fine powder with a ball mill. The sand fraction (>53 μm) of each sample was ground to a fine powder with a ball mill, for determination of particulate organic matter (POM) C and N (Cambardella and Elliott 1992). Total C and N in the total soil and sand fraction were determined with a LECO CHN-1000 analyzer.

In addition, during the summer of 1996 we collected soil samples (0-20 cm) under willow trees and in associated open grass areas next (within 2 m) to the trees. A total of thirty-three pairs of samples (shrub canopy plus open grass) were taken from the twelve ungrazed plots within the exclosures of Moraine Park and Horseshoe Park. The samples were air-dried and sieved through a 2 mm screen. Sub-samples (10 g) of each sample were ground to a fine powder with a ball mill, and total soil C and N were determined using a LECO CHN -1000 analyzer.

Soil moisture (0 to 14 cm) measurements were performed weekly in eight sites in Moraine Park and Horseshoe Park (four in each watershed) by Time Domain Reflectometry (TDR) (Ledieu et al. 1986) with a Trase System model 6050x1 during the growing season of 1997. Within each site and grazing treatment, soil moisture was measured under willow canopies and in associated *Carex* plots next to the willow shrubs in both upper and lower landscape positions.

Within three ungrazed plots in each park, soil temperature was measured in using HOBO® temperature data loggers during the growing season of 1997. The loggers were wrapped with a thin plastic film to avoid damage by soil moisture, and were buried in a vertical position from 1 to 6 cm of depth. In each of the sites, we performed comparisons of soil temperature between (1) willow canopies and *Carex* plots and (2) streamside and upper landscape positions. The temperature measurements were performed every 15 minutes for periods of 7 to 14 days.

In 1995, 1996, and 1998 soil *in situ* N availability in the experimental plots was assessed using ion-exchange resin bags. Paired cation and anion resin bags made from nylon stockings and containing about 15 cm^3 of exchange resins were placed 5 cm beneath the soil surface (Binkley 1984). In 1995 and 1996, fifteen pairs of resin bags were placed in a regularly spaced grid (9.1 x 15.9 m) within each treatment (grazed, ungrazed, clipped) in the twelve sites. In order to analyze the temporal variability of N availability, two sets of bags were placed in each treatment during each of the growing seasons of 1995 and 1996. The first set was left in place from mid-June to mid-July, and the second set from mid-July to mid-August. A different experimental procedure was utilized in 1998, in which six pairs of resin bags were randomly placed within each of the twelve ungrazed and grazed plots, and left in the field from May to October. For all three years, after removal of the bags, the N adsorbed in the resins was extracted with 50 ml of 2 M KCl, and the extracts were frozen until analysis on an Alpkem automated spectrometer.

In 1997 and 1998, *in situ* measurements of net N mineralization were performed by conducting field soil incubations as described in Kolberg et al. (1997) using aluminum cores 15 cm long and 5 cm in diameter. During the 1997 growing season, cores were placed in upper and lower landscape positions within the twelve ungrazed and grazed plots of the two watersheds. Within each landscape position and grazing treatment, cores were placed under willow shrubs and in associated *Carex* patches within 2 m of the willow plants. Four cores were placed inside each treatment replicate in order to reduce micro-site variability. Cation and anion resin bags were placed in the bottom of each core to capture the inorganic N leached from the core. During the 1998 growing season, six open-top field soil incubation cores were placed within the ungrazed and grazed plots in three different six-week incubation periods (June to July, July to August, and August to October). Net soil N mineralized during the incubation periods was calculated by subtracting the initial amount of inorganic N in the soil from the final amount of inorganic N after the incubations, and the results were expressed in g N m^{-2}.

Nitrogen Fertilization

In each ungrazed and grazed plot in the twelve sites, we placed two paired circular subplots (each with 2 m radius) around willow plants at the end of the growing season of 1998. Within each pair of circular subplots, we applied two fertilization treatments: (1) no fertilization, and (2) 10 g N m^{-2} as ammonium nitrate. During late July 1999, willow shoots (current year growth) were collected from the plants inside the subplots, dried at 60 °C, weighed, and ground to a fine powder. Concentrations of C and N in shoots were determined using a LECO CHN -1000 analyzer.

Statistical Analyses

Statistical analyses were performed using the SAS Statistical Package (SAS, Version 6.12, SAS Institute Inc., Cary, NC, 1995). There were no significant interactions at any level including watershed, willow height, and hydro-manipulations. Therefore, the data from the experiments on litterfall, litter nutrient content, soil characteristics, and elk dung deposition were analyzed for the effect of elk herbivory using a randomized complete block design. The data from the experiments on litter decomposition and soil N availability were analyzed using a split-plot design with herbivory manipulations as the main treatments and landscape position or canopy position as sub-plots.

Results and Discussion

Litterfall

Litterfall biomass in the ungrazed and clipped plots was greater ($P < 0.05$) than in the grazed plots for the three growing seasons (Table 1). Across all growing seasons, litterfall biomass averaged 65.6 and 33.0 g m^{-2} inside and outside the exclosures, respectively. On average, willow leaves accounted for 58 % of the litterfall biomass followed by herbs (20 %), other shrub leaves (16 %), wood (5 %), and unidentified material (1%). However, the use of trays for collecting litterfall may underestimate the amount of grass litterfall, since a significant portion of the senescent tillers still remain attached to the plant and were not collected and counted as litter. Willow leaf litterfall in the ungrazed and clipped plots was greater ($P < 0.05$) than in the grazed plots during the 1995 and 1997 seasons, but in 1996 there were no significant differences between clipped and grazed plots (Table 1). Leaf litter from other shrubs, mostly birch (*Betula* spp.), was significantly lower in the grazed plots when compared to the clipping treatment inside the exclosures, but there were no differences between grazed and ungrazed plots. No grazing treatment differences were observed for the amounts of herb or wood litter during the three growing seasons.

Litterfall biomass was lower in the grazed plots, in comparison to the clipped and ungrazed plots, due to elk browsing during early fall before leaf senescence. However, inside the exclosures, even the removal of 75% of current annual growth in the clipped plots did not result in significant differences between the ungrazed and clipped plots during the three growing seasons. We suggest this lack of difference between clipped and ungrazed plots occurred in part because the artificial clipping of willow did not satisfactorily simulate elk browsing. Other studies have demonstrated the limitations of clipping experiments to reflect accurately the natural patterns of herbivory (Paige 1999). Visual observations in our field plots suggested that clipped plants inside the exclosures were morphologically similar to the plants in the ungrazed treatment, regarding height and canopy structure, while the grazed plants were apparently more suppressed and shorter than the plants in the two treatments inside the exclosures. These patterns probably result from the additional damage to willow leaders caused by elk when striping off leaves from the plants, as compared to artificial clipping. On average, elk may browse on more than 70% of the leaders in each plant in our study sites, and may remove nearly 40% of the length of each leader (Singer et al. 1998b). Additional field observations from our experiments demonstrate that an average of 20% of the length of browsed willow leaders may die after elk browsing due to bark damage, while only 2% of the length of the leader may die in the case of artificially clipped plants (R. Peinetti, pers. comm., 1999). We suggest that the differences in growth and litterfall observed between grazed and clipped treatments in our study may result from: (1) greater leader damage during elk browsing, in comparison to artificial clipping, and/or (2) greater increases in plant height in clipped plants, in comparison to grazed plants, due to differences in the patterns of tissue removal during elk browsing or artificial clipping, which may influence canopy architecture. Overall, we suggest that the clipped plants in our study were able to overcompensate for the biomass removal and achieve greater fitness, in comparison to browsed plants, but additional studies are needed to test this hypothesis.

Willow leaf litter in the ungrazed and clipped plots had lower ($P < 0.05$) N content and higher ($P < 0.05$) C to N ratio than willow leaf litter in the grazed plots, but no significant treatment differences were found in litter from other shrubs, *Carex*, or forbs

(Table 2). Similar to our findings, Alstad et al. (1999) reported that early season willow tissue N concentration in plants under elk herbivory in our sites was significantly higher than in plants protected from herbivory. Often, grazing leads to increases in plant tissue N (McNaughton 1985, Holland and Dettling 1990, Coughenour 1991, Hamilton et al. 1998) due to faster nutrient cycling and uptake by plants or a reduction in tissue biomass for allocation of N. Higher N concentration and lower C to N ratios in litter may lead to faster litter decomposition and greater nutrient availability (Ritchie et al. 1998, Irons et al. 1991). In our study site, the effects of elk herbivory on willow litter N concentration could lead to increases in the rate of litter decomposition and nutrient cycling, which could lead to changes in species composition and ecosystem functioning (Aber and Melillo 1991, Holland et al. 1992, Ritchie et al. 1998, Stohlgren et al. 1999).

Litter Decomposition

Grazing had no effect on the decomposition of willow and *Carex* litter in any of our experiments, but C and N losses between willow and *Carex* litter bags were significantly different. In the three growing seasons, C losses from willow litter bags were higher ($P < 0.05$) than from *Carex* litter bags (Table 3). Interestingly, N losses from willow litter were lower than from *Carex* litter (Table 3), maybe because willow litter has a higher content of secondary compounds or promotes greater N immobilization during decomposition, when compared to *Carex* litter. Browsed willow plants may increase the concentration of defense compounds, such as tannins, as a response to prevent further herbivory (Singer et al. 1994). The standard litter utilized in our decomposition studies had a relatively high concentration of tannins, averaging 70.7 mg g^{-1} dry $matter^{-1}$ (Cates,

R. 1998). Our findings indicate that, even though willow litter has a lower C to N ratio when compared to Carex litter, the presence of secondary compounds in willow litter may have caused a significant reduction in the losses of litter N when compared to *Carex* litter.

In 1996, C losses from litter bags were higher ($P = 0.001$) in streamside positions than in upper landscape positions, but no significant differences were observed for N losses during 1996 or C and N losses during 1997 (Table 4). Soil moisture is usually an important factor contributing to decomposition and, in general, litter decomposition increases with increasing soil moisture in semi-arid ecosystems (Schlesinger 1997). Higher C losses observed in streamside positions in our study are likely due to higher soil water availability (Figure 1). However, no significant differences in willow or *Carex* litter decomposition were observed between streamside and upper landscape positions around the two beaver ponds in 1996. Average C and N losses from litter bags of the two litter types placed around the ponds were 36.4 and 2.9%, respectively. The lack of consistent differences in litter decomposition between different landscape positions in our experiments may have occurred because 1996 and 1997 had higher rainfall levels than the long term average for those sites (Alstad et al. 1999). For these reasons, the differences in soil moisture may not have been as pronounced between landscape positions as they would have been in drier years, especially towards the end of the growing season, as indicated by the increases in soil moisture in July 1997 (Figure 1).

Litter bags placed under willow canopies lost significantly more C and N than bags placed in *Carex* plots (Table 5), even though soil moisture levels were slightly lower under willow canopies, compared to *Carex* plots, especially in Horseshoe park (Figure 1).

Average maximum soil temperatures from 1 to 6 cm in depth during the 1997 growing season were significantly lower under willow canopies than in *Carex* plots in both Moraine and Horseshoe parks (Figure 2). These results indicate that the presence of willow shrubs has a significant influence on microclimatic conditions in our sites, contributing to reductions in soil temperature and soil moisture. We suggest that the rate of nutrient loss from litter bags was higher under willow canopies because: (1) shading by willow canopies may decrease soil temperature and help preserve moisture at the top few centimeters of the litter layer and soil, and this may enhance litter decomposition and/or (2) *Carex* plants may have held litter bags off of soil, which may have let them dry out more and decompose less than bags placed under willow canopies.

Return of N to the Soil

Based on the biomass and N content of aboveground litter in our sites (Tables 2 and 3), we calculated that the N return to the soil in litterfall during the 1997 growing season was greater ($P < 0.05$) in the ungrazed and clipped plots (0.83 and 0.82 g N m^{-2}, respectively) than in the grazed plots (0.42 g N m^{-2}), excluding the contribution of N in wood litter in all treatments. Similar to our findings, Pastor et al. (1993) found that moose browsing led to decreases in the amount of litterfall and nutrient return to the soil in litter. In our site, litter from willow, other shrubs, and herbs contributed to 62, 17, and 21% of the N returned to the soil inside the exclosures, and 51, 16, and 33 % of the N returned to the soil in grazed plots, respectively. Elk dung biomass deposited on the soil during the 1997-98 season averaged 42.2 ± 6.2 g m^{-2} across all sites. This value is similar to those reported by Frank and McNaughton (1992), who found that average herbivore dung deposition during the 5 month season in the winter range of Yellowstone National Park was 76.9 ± 30.1 g N m^{-2}. In our sites, average elk dung N concentration in the samples collected in late fall of 1997 was 2.0 %. Based on our results, we estimated that approximately 0.87 ± 0.12 g N m^{-2} returned to the soil in elk dung during the 1997-98 winter season in our study site. Therefore, the amount of N returned to the soil as elk dung plus plant litter averaged 1.3 g m^{-2} in the grazed plots. The estimated amount of N returned to the soil in elk urine in our sites, based on the diet and specific characteristics of the herd, could be approximately 98% of the N returned to the soil in dung (K. Schoenecker, pers. comm., 1999). Based on these estimates, after including the potential N inputs from urine, the total amount of N returned to the soil in the grazed plots could be as high as 2.2 g N m^{-2}, which corresponds to 265% of the N returned as aboveground litter in the exclosed plots. Our results are consistent with the findings of Frank and McNaughton (1992), who found that elk and bison populations in Yellowstone National Park excreted 0.81 to 4.60 g N m^{-2} yr^{-1}, an amount that corresponded to roughly 4 times the amount of N returned in litterfall. In addition, those authors concluded that the intensity of herbivory was positively associated with both aboveground net primary production and the return of nutrients to the soil. Ungulates usually accelerate nutrient cycling by modifying the amount and quality of residues returned to the soil (Hobbs 1996). Similar to the findings of Frank et al. (1994) in Yellowstone, a portion of the excess N returned to the soil by elk in our study sites, may correspond to transfers from the summer range. During winter, elk migrate from the summer range to the winter range at lower elevations to avoid snow and usually lose weight and N (F. Singer, pers. comm., 1999). Our results indicate that elk may be promoting a net transfer of N from the summer range to the winter range, and the extent of these transfers are likely related to the number of elk in this system. In the long-term, these N transfers could increase N availability, which in its turn may affect ecosystem structure and functioning (Aber and Melillo 1991, Holland et al. 1992, Ritchie et al. 1998, Stohlgren et al. 1999).

Soil Characteristics and N Availability

There were no significant differences ($P < 0.05$) in total soil C and N, POM C and N, soil texture, and soil pH between grazing treatments in our sites within the 4 years after the establishment of the exclosures (Table 6). Similar to our findings, Frank and Groffman (1998) found no differences in soil total C and N between grazed plots and exclosed plots that had been protected from herbivory for 33 to 37 years in Yellowstone National Park. However, those authors found that herbivores improved the quality of soil organic matter, increasing the labile fractions and decreasing the recalcitrant fractions. In our study, the relatively short time (4 years) since the establishment of the exclosures may not have allowed for the development of significant differences in the organic matter fractions between herbivory treatments. In addition, we found no differences in total soil C and N (0 to 30 cm) between soil samples taken in *Carex* plots or under willow canopies. Total soil C and N averaged 6.2 and 0.44 g kg^{-1} in *Carex* plots and 5.8 and 0.40 g kg^{-1} under willow canopies, respectively.

In all experiments with both ion-exchange resin bags and field soil core incubations, there were no significant differences in soil N availability between grazing treatments during the four years of the study. Several studies have reported increases in the rates of soil N mineralization with herbivory (McNaughton 1985, McNaughton et al.

1988, Holland and Detling 1990, Frank and Evans 1997). Frank and Groffman (1998), reported that N availability in plots grazed by elk was 100% higher than exclosed plots. Again, we suggest that the time since the establishment of the exclosures in our study did not allow for the development of detectable differences in soil N mineralization and availability between grazing treatments.

The assessment of N availability with ion-exchange resin bags during 1995 and 1996 indicated that, in general, both NH_4^+-N and NO_3^--N availability were higher ($P < 0.05$) during early to mid-season and declined afterwards (Table 7). In 1998, there was only one resin bag incubation period, and the total amount of N adsorbed to the bags was slightly higher than the sum of both periods of either 1995 or 1996, probably because the incubation period in 1998 was a few weeks longer. On average, the amount of NH_4^+-N adsorbed to the resin bags was 137 to 412% higher than NO_3^--N during the three growing seasons. The higher proportions of soil NH_4^+-N could benefit plant productivity in our sites, since plants with an evolutionary history of grazing show elevated growth responses to ammonium relative to other inorganic forms of N, particularly when subject to defoliation (Ruess 1984, Ruess and McNaughton 1987, Hobbs 1996). Similarly to the results from the experiments with ion-exchange resin bags, the amounts of net NH_4^+-N mineralized in the soil cores were usually higher than NO_3^--N (Table 8). In addition, total inorganic N in the soil was higher during early to mid-season during the 1998 growing season (Table 8). If plant uptake is higher during early to mid-season when plant growth and nutrient requirements are probably greater, the higher availability of nutrients during that period may contribute to the synchronization of nutrient supply and demand and enhance primary production and nutrient retention within the system (Myers et al. 1994).

Interestingly, the presence of willow had a significant effect on N availability in our experiments with ion-exchange resin bags. During both incubation periods of 1996, the amounts of inorganic N adsorbed to resin bags located under willow canopies was higher ($P < 0.05$) than in bags placed in *Carex* plots (Table 9), but no significant differences were observed during 1995. The higher N availability may be a consequence of higher amounts of litter N inputs and higher rates of N loss from litter under willow canopies, as indicated by our findings in 1996.

The data from the N fertilization experiment demonstrated that willow growth in the winter ranges for elk is limited by N availability, independently of grazing treatment. Both inside and outside the exclosures, N fertilizer additions increased ($P < 0.05$) willow shoot length, shoot biomass, and the amount of N in the shoots (Table 10). We suggest that elk herbivory could lead to long-term increases in N availability in our sites, because of induced increases in both litter quality and return of N to the soil. Increases in N availability could lead to changes in plant species composition and significantly alter ecosystem functioning, because of shifts in the competitive interactions between plant species (Tilman 1982, 1988, Holland et al. 1992, Sterner 1994, Ritchie et al. 1998). Stohlgren et al. (1999) reported that exotic species were more likely to invade landscape patches higher soil N and moisture, which could lead to a decline in native plant species and ecosystem diversity (Billings 1990, D'Antonio and Vitousek 1992).

Conclusions

Herbivory by elk significantly influenced the biogeochemical cycles of the winter ranges for elk in RMNP. Losses of C from litter and soil moisture were greater in streamside positions, when compared to upper landscape patches, indicating that reductions in surface water may lead to lower decomposition rates in our site. Elk browsing reduced the amount of litterfall biomass and the amount of N returned to the soil in litter. However, we estimated that the return of N to the soil through elk excretions plus aboveground litter in the grazed plots could be as much as 265% greater than inside the exclosures, maybe due to transfers of N from the summer range to the winter range. Willow litter contributed to 51 to 62 % of the N returned to the soil in litterfall, and browsing by elk significantly increased the N concentration and reduced the C to N ratio of willow litter. We found no differences in soil total C and N, POM C and N, and N availability between grazed and ungrazed plots during the period of our study, maybe because there was not enough time (4 years) to develop significant differences between herbivory treatments. Nitrogen fertilization significantly increased willow shoot length, shoot biomass, and the average amount of N in the shoots, indicating that availability of N is a limiting factor for willow growth in our study sites. Greater return of N to the soil combined with increased litter quality in the grazed plots indicate that elk could contribute to increases in N cycling rates and availability in the long-term in our sites. Increased N availability could lead to changes in plant species composition and ecosystem functioning.

Acnowledgements

We thank J. Gensen, L. Hoogenstein, M. Kaye, R. Rochelle, M. Schrijvers, L. Schroeder, L. Zeigenfuss, J. Williams, and T. Wotan for assistance with field and laboratory work. We also thank F. Singer and D. Binkley for helping with the design and data analysis of some of the experiments. This study was primarily funded by the Biological Resources Division of the U.S. Geological Survey and also by the National Park Service.

References

Aber, J.D. and J.M. Melillo. 1991. Terrestrial ecosystems. Saunders Coll. Publ. Philadelphia, PA.

Afzal, M. and W.A. Adams. 1992. Heterogeneity of soil mineral nitrogen in pasture grazed by cattle. Soil Sci. 56: 1160-1166.

Alstad, K.P., J.M. Welker, S. Williams, and M.J. Trlica. 1999. Carbon and water relations of *Salix monticola* in response to winter browsing and changes in surface water hydrology: an isotopic study using $\delta^{13}C$ and $\delta^{18}0$. Oecologia, *In Press*.

Billings, W.D. 1990. *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. pp. 301-322. In: G.M. Woodwell (ed.) The earth in transition: patterns and processes of biotic impoverishment. Cambridge University Press, Cambridge, UK.

Binkley, D. 1984. Ion exchange bags: factors affecting estimates of nitrogen availability. Soil Sci. Soc. Am. J. 48:1181-1184.

Briske, D.D. 1986. Plant responses to defoliation: morphological considerations and allocation priorities. pp. 425-427. In: P.J. Joss, P.W. Lynch, and O.B. William (eds.) Rangelands: a resource under siege. Proceedings of the Second International Rangeland Congress, Australian Academy of Sciences, Canberra, Australia.

Cambardella, C.A. and E.T. Elliott. 1992. Particulate soil organic-matter changes across a grassland cultivation sequence. Soil Sci. Soc. Am. J. 56:777-783.

Cates, R. 1998. Response of willow secondary metabolites to mechanical clipping, ungulate grazing, and litter decomposition. In: Large mammalian herbivores, plant interactions and ecosystem processes in five national parks. Third annual report to Biological Resources Division, USGS.

Chadde, S.W. and C.E. Kay. 1991. Tall willow communities in Yellowstone's northern range: a test of the "natural regulation" paradigm. pp. 231-261. In R.B. Keiter and M.S. Boyce (eds.) The greater Yellowstone ecosystem: redefining America's Wilderness Heritage. Yale University Press, New York, New York.

Coughenour, M.B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone northern winter range. J. Appl. Ecol. 28: 71-82.

D'Antonio, C.M. and P.M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23: 63-87.

Fahnestock, J.T. and J.K. Detling. 1999. Plant responses to defoliation and resource supplementation in the Pryor Mountains. Oikos (submitted).

Frank, D.A. and P.M. Groffman. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. Ecology 79: 2229-2241.

Frank, D.A. and R.D. Evans. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. Ecology 78: 2238-2248.

Frank, D.A., R.S. Inouye, N. Huntly, G.W. Minshall, and J.E. Anderson. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. Biogeochemistry 26: 163-188.

Frank, D.A. and S.J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73: 2043-2058.

Frank, D.A. and S.J. McNaughton. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Ecology 73: 2043-2058.

Gee, G.W. and J.W. Bauder. 1986. Particle-size analysis. pp. 383-411. In: A. Klute (ed.) Methods of soil analysis. Part 1. 2nd ed. Agron. Monogr. 9. ASA and SSSA, Madison, WI.

Georgiadis, N.J., R.W. Reuss, S.J. McNaughton, and D. Western. 1989. Ecological conditions that determine when grazing stimulates grass production. Oecologia 81: 316-322.

Hamilton III, E.W., M.S. Giovannini, S.A. Moses, J.S. Coleman, and S.J. McNaughton. 1998. Biomass and mineral element responses of a Serengeti short-grass species to nitrogen supply and defoliation: compensation requires a critical [N]. Oecologia 116: 407-418.

Hess, K. 1993. Rocky times in Rocky Mountain National Park. University Press of Colorado, Niwot.

Hobbs, N.T. 1996. Modification of ecosystems by ungulates. J. Wildl. Manage. 60:695-713.

Holland E.A. and J.K. Detling. 1990. Plant response to herbivory and belowground nitrogen cycling. Ecology 71:1040-1049.

Holland, E.A., W.J. Parton, J.K. Detling, and L. Coppock. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. Am. Nat. 140: 685-706.

Irons, J.G., M.W. Oswood, R.J. Stout, and C.M. Pringle. 1991. Latitudinal patterns in leaf-litter breakdown – is temperature really impostant? Freshwater Biology 32: 401-411.

Kay, C.E. and F.H. Wagner. 1994. Historical condition of woody vegetation on Yellowstone's northern range. pp. 151-169. In D.G. Despain (ed.) Plants and their environments. National Park Service, Technical Report 93.

Kiehl, K, P. Esselink, and J.P. Baker. 1997. Nutrient limitation and plant-species composition in temperate salt marshes. Oecologia 111: 325-330.

Kolberg, R.L., B. Rouppet, D.G. Westfall, and G.A. Peterson. 1997. Evaluation of an in situ net soil nitrogen mineralization method in dryland agroecosystems. Soil Sci. Soc. Am. J. 61:504-508.

Larkins, K.F. 1997. Patterns of elk movement and distribution in and adjacent to the eastern boundary of Rocky Mountain National Park. Thesis, University of Nothern Colorado, Greeley.

Ledieu, J., P. de Ridder, P. de Clerk, and S. Dautrebande. 1986. A method of measuring soil moisture by time-domain reflectometry. Journal of Hydrology 88: 319-328.

Mazancourt, C., M. Loreau, and L. Abbadie. 1998. Grazing optimization and nutrient cycling: when do herbivores enhance plant production. Ecology 79:2242-2252.

McNaughton, S.J. 1985. The ecology of a grazing system: The Serengeti. Ecol. Monogr. 55: 259-294.

McNaughton, S.J., R.W. Reuss, and S.W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. Bioscience 38:794-800.

Myers, R.J.K., C.A. Palm, E. Cuevas, I.U.N. Gunatilleke, and M. Brossard. 1994. The synchronization of nutrient mineralization and plant nutrient demand. pp. 81-116 In: P.L. Woomer and M.J. Swift (eds.) The biological management of tropical soil fertility. TSBF and Sayce Publishing, UK.

Naiman, R.J. and J.M. Melillo. 1984. Nitrogen budget of a sub-arctic stream altered by beaver (*Castor canadensis*). Oecologia 62:150-155.

Naiman, R.J., J.M. Melillo, and J.E. Hobbie. 1986. Ecosystem alteration of boreal forest stream by beaver (*Castor canadensis*). Ecology 67: 1254-1269.

Paige, K.N. 1999. Regrowth following ungulate herbivory in *Ipomopsis aggregata*: geographic evidence for overcompensation. Oecologia 118: 316-323.

Pastor, J., B. Dewey, R.J. Naiman, P.F. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Pak. Ecology 74: 467-480.

Pastor, J. and R.J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. Am. Nat. 139: 690-705.

Pengelly, W.L. 1963. Thunder on the Yellowstone. Naturalist 14:18-25.

Power, J.F. 1977. Nitrogen transformations in the grassland ecosystem. pp. 195-204. In: J.K. Marshall (ed.) The belowground ecosystem: a synthesis of plant-associated processes. Range Science Department, Science Series No. 26, Colorado State University, Fort Collins, CO, USA.

Power, J.F. 1994. Understanding the nutrient cycling process. Journal of Soil and Water Conservation 49 (2/suplemental): 16-23.

Ritchie, M.E., D. Tilman, and J.M.H. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology 79: 165-177.

Russele, M.P. 1992. Nitrogen cycle in pasture and range. J. Prod. Agric. 5:13-23.

Ruess, R.W. 1984. Nutrient movement and grazing - experimental effects of clipping and nitrogen source on nutrient uptake in *Kyllinga nervosa*. Oikos 43: 183-188.

Ruess, R.W. and S.J. McNaughton. 1987. Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. Oikos 49: 101-110.

SAS Institute. 1995. SAS User's Guide. Release 6.12. SAS Institute Inc., Cary, NC.

Schlesinger, W.H. 1997. Biogeochemistry: An analysis of global change. Academic Press, San Diego, USA.

Schuman, G.E., J.D. Reeder, J.T. Manley, R.H. Hart, and W.A. Manley. 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecol. Appl. 9: 65-71.

Singer, F.J., D.M. Swift, M.B. Coughenour, and J.D. Varley. 1998a. Thunder on the Yellowstone revisited: an assessment of management of native ungulates by natural regulation, 1968-1993. Wildlife Society Bulletin 26:375-390.

Singer, F.J., E.T. Elliott, M.B. Coughenour, J.M. Welker, D.W. Valentine, S.A. Williams, L.C. Zeigenfuss, K.P. Alstad, and R.S.C. Menezes. 1997. Large mammalian herbivores, plant interactions and ecosystem processes in five national parks. Second Annual Report to Biological Resources Division, USGS.

Singer, F.J., L.C. Zeigenfuss, R.G. Cates, and D.T. Barnett. 1998b. Elk, multiple factors, and persistence of *S. monticola* in national parks. Wildlife Society Bulletin, 26:419-428.

Singer, F.J., L. Mack, and R.G. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. J. Range Manag. 47: 435-443.

Sterner, R.W. 1994. Elemental stoichiometry of species in ecosystems. pp. 240-252. In: C.G. Jones and J.H. Lawton (eds.) Linking species and ecosystems. Chapman and Hall, New York, New York.

Stevens, D.R. and S. Christianson. 1980. Beaver populations on the East slope of Rocky Mountain National Park. Special Report to Rocky Mountain National Park, Estes Park, CO.

Stohlgren, T.J., D. Binkley, G.W. Chong, M.A. Kalkhan, L.D. Schell, K.A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69: 25-46.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey.

Tilman, D. 1988. Plant strategies and the dynamic and structure of plant communities. Princeton University Press, Princeton, New Jersey.

Toft, N.L., S.J. McNaughton, and N.J. Geogiadis. 1987. Effects of water stress and simulated grazing on leaf elongation and water relations of an East African grass, *Eustachys paspaloides*. Aust. J. Plant Physiol. 14:211-226.

U.S.D.A. Snow Survey Office (1995, 1996, and 1997). Snowpack data for Rocky Mountain National Park. National Resources Conservation Service. Lakewood, CO.

Welker, J.M. and D.D. Briske. 1992. Clonal biology of the temperate caespitose graminoid *Schizachyrium scoparium*: A synthesis with reference to climate change. Oikos 56:357-363.

Welker, J.M. and J.W. Menke. 1990. The influence of simulated browsing on tissue water relations, growth and survival of *Quercus douglasii* (Hook and Arn.) seedlings under slow and rapid rates of soil drought. Funct. Ecol. 4:807-817.

Welker, J.M., D.D. Briske, and R.W. Weaver. 1987. Nitrogen-15 partitioning within a three generation tiller sequence of the bunchgrass *Schizachyrium scoparium*: Response to selective defoliation. Oecologia 24:330-334.

Welker, J.M., E.J. Rykiel, D.D. Briske, and J.D. Goeschl. 1985. Carbon import among vegetative tillers within two bunchgrasses: Assessment with carbon-11 labeling. Oecologia 67:209-212.

Wijnen, H.J., R. van der Wal, and J.P. Bakker. 1999. The impact of herbivores on nitrogen mineralization rate: consequences for salt-marsh succession. Oecologia: 118: 225-231.

Table 1. Litterfall biomass in ungrazed, clipped, and grazed plots of Moraine Park and Horseshoe Park during 1995, 1996, and 1997. Values represent means (n = 12) with standard errors in parentheses. Means within the same group followed by different letters are significantly different at $P < 0.05$.

	Litterfall (g m^{-2})					
Treatment	Willow (*Salix* spp.) leaves	Other shrub Leaves[1]	Herbs[2]	Wood	Unidentified material	All litter
1995						
Ungrazed	32.9 (9.8) a	5.9 (2.7) ab	10.1 (2.4)	3.0 (1.0)	0.6 (0.2)	52.5 (10.2) a
Clipped	34.1 (8.5) a	13.2 (6.3) a	8.0 (1.0)	4.4 (1.4)	0.3 (0.1)	60.0 (8.9) a
Grazed	19.1 (7.1) b	1.7 (0.6) b	6.4 (0.9)	3.1 (1.4)	0.5 (0.2)	30.9 (8.5) b
1996						
Ungrazed	55.0 (13.6) a	9.1 (3.9) ab	3.1 (0.6)	3.1 (1.1)	1.4 (0.4)	71.6 (12.6) a
Clipped	47.1 (10.6) ab	18.3 (8.6) a	2.6 90.5)	1.6 (0.4)	0.8 (0.2)	70.2 (9.7) a
Grazed	26.6 (8.1) b	3.7 (0.8) b	3.4 (0.5)	5.1 (2.2)	0.7 (0.3)	39.4 (9.1) b
1997						
Ungrazed	45.3 (12.3) a	8.7 (4.0) ab	14.3 (3.3)	3.1 (1.0)	-	71.5 (11.1) a
Clipped	41.6 (10.4) a	15.5 (6.3) a	7.2 (0.7)	2.2 (0.7)	-	66.4 (10.1) a
Grazed	15.9 (6.0) b	3.0 (0.9) b	7.5 (1.0)	2.4 (1.1)	-	28.8 (7.1) b

---

[1] Mostly birch (*Betula* spp.) leaves.

[2] Litter material from forbs and *Carex* spp. combined.

Table 2. Nitrogen content and carbon to nitrogen ratio of different litter types in ungrazed, clipped, and grazed plots of Moraine Park and Horseshoe Park in 1997. Values represent means (n = 12) with standard errors in parentheses. Means within the same group followed by different letters are significantly different at $P < 0.05$.

Treatment	Willow (*Salix* spp.) leaves	Other shrub leaves [1]	*Carex*	Forbs
Nitrogen (%)				
Ungrazed	1.25 (0.10) b	1.23 (0.15)	1.40 (0.11)	1.79 (0.13)
Clipped	1.27 (0.09) b	1.11 (0.13)	1.22 (0.08)	1.71 (0.15)
Grazed	1.49 (0.08) a	1.09 (0.11)	1.23 (0.09)	1.82 (0.12)
Carbon to nitrogen ratio				
Ungrazed	45.8 (3.2) a	48.5 (12.0)	37.2 (2.9)	31.0 (3.0)
Clipped	43.0 (4.2) a	53.4 (11.6)	42.1 (2.8)	32.6 (2.9)
Grazed	37.7 (3.1) b	49.9 (14.3)	43.5 (3.1)	31.4 (2.6)

[1] Mostly birch (*Betula* spp.) leaves.

Table 3. Carbon and nitrogen losses from willow (*Salix* spp.) and *Carex* leaf litter bags in Moraine Park and Horseshoe Park during the growing seasons of 1995, 1996, and 1997. Values represent means (n = 12) with standard errors in parentheses.

Litter type	% C loss	% N loss
1995		
Willow	30.2 (2.7)	6.3 (2.0)
Carex	22.9 (2.6)	10.3 (2.1)
P-value	N.S.[1]	0.026
1996		
Willow	29.0 (1.9)	3.4 (5.1)
Carex	22.9 (2.4)	15.2 (4.7)
P-value	0.046	0.005
1997		
Willow	22.1 (1.4)	2.7 (2.4)
Carex	16.4 (1.8)	16.7 (4.3)
P-value	0.013	0.005

[1] Not significantly different at $P < 0.05$.

Table 4. Carbon and nitrogen losses from litter bags placed in upper and lower landscape positions of Moraine Park and Horseshoe Park during the growing seasons of 1996 and 1997. Values represent means (n = 12) with standard errors in parentheses.

Landscape position	% C loss	% N loss
1996		
Streamside	31.7 (2.3)	5.7 (6.1)
Upper landscape	20.3 (1.9)	12.8 (6.0)
P-value	0.001	N.S.[1]
1997		
Streamside	18.1 (1.9)	6.5 (4.2)
Upper landscape	20.4 (1.3)	12.9 (2.7)
P-value	N.S	N.S.

[1] Not significantly different at $P < 0.05$.

Table 5. Carbon and nitrogen losses from litter bags placed under willow (*Salix* spp.) canopies and in *Carex* spp. plots in Moraine Park and Horseshoe Park during the growing seasons of 1996 and 1997. Values represent means (n = 8) with standard errors in parentheses.

Position	% C loss	% N loss
1996		
Willow canopies	35.7 (1.7)	24.2 (1.8)
Carex plots	7.7 (2.9)	-1.6 (2.4)
P-value	0.001	0.022
1997		
Willow canopies	23.1 (1.5)	15.5 (1.7)
Carex plots	16.0 (3.5)	3.4 (3.5)
P-value	0.001	0.012

Table 6. Soil characteristics (0-15 cm) of ungrazed, clipped, and grazed plots of Moraine Park and Horseshoe Park in July 1997. Values represent means (n = 12) with standard errors within parentheses.

Treatment	Total C	Total N	POM C	POM N	Sand	Silt	Clay	pH[1]
	g kg soil^{-1}							
Ungrazed	50.3 (9.0)	3.38 (0.63)	15.9 (3.5)	0.81 (0.19)	523 (59)	209 (40)	152 (19)	4.64 (0.10)
Clipped	47.7 (7.1)	3.27 (0.54)	13.3 (2.0)	0.63 (0.09)	494 (55)	235 (47)	161 (25)	4.67 (0.12)
Grazed	42.7 (6.2)	2.82 (0.44)	11.3 (2.0)	0.53 (0.12)	549 (37)	234 (29)	118 (19)	4.60 (0.11)

[1] Measured in water (2:1, water:soil)

Table 7. Inorganic nitrogen adsorbed to ion exchange resin bags during different incubation periods during 1995 and 1996, and from one incubation period during 1998. Values represent means (n = 12) with standard errors within parentheses.

	NO_3^--N	NH_4^+-N	NO_3^--N + NH_4^+-N
Incubation period	mg bag $^{-1}$		
1995			
June to July	1.08 (0.23)	4.45 (0.63)	5.53 (1.45)
July to August	0.64 (0.32)	2.12 (0.44)	2.78 (1.29)
P-value	0.015[1]	0.001	0.001
1996			
June to July	0.95 (0.52)	3.39 (0.81)	4.34 (1.14)
July to August	1.05 (0.55)	1.44 (0.53)	2.49 (0.87)
P-value	N.S.[2]	0.001	0.001
1998			
July to October	3.01 (0.55)	7.29 (1.98)	10.30 (2.43)

---

[1] *P*-value of comparisons between means of incubation periods.

[2] Not significantly different at $P < 0.05$.

Table 8. Inorganic nitrogen mineralized during field soil incubations (0 to 15 cm) using aluminum cores during 1997 and 1998. Values represent means for all treatments (n = 12) with standard errors within parentheses.

	Mineralized nitrogen (g m^{-2})		
Incubation period [1]	NO_3^-	NH_4^+	$NO_3^- + NH_4^+$
1997			
June to July	0.11 (0.04)	0.55 (0.15)	0.66 (0.16)
1998			
June to July	0.71 (0.44)	0.81 (0.80)	1.51 (0.77)
July to August	1.13 (0.38)	1.33 (0.95)	2.46 (1.17)
August to October	0.51 (0.23)	0.34 (0.52)	0.85 (0.59)

[1] Length of incubation period: 1997 = 4 weeks; 1998 = 6 weeks each period.

Table 9. Inorganic nitrogen adsorbed to ion exchange resin bags under willow (*Salix* spp.) canopies and in *Carex* spp. plots during different incubation periods of the 1995 and 1996 growing seasons. Values represent means (n = 12) with standard errors within parentheses.

	Inorganic N (mg bag $^{-1}$)	
Position	June to July	July to August
1995		
Willow canopies	5.69 (2.13)	2.87 (1.20)
Carex plots	5.80 (1.92)	2.87 (1.11)
P-value	N.S. [1]	N.S.
1996		
Willow canopies	4.98 (0.77)	3.07 (0.55)
Carex plots	4.01 (0.68)	2.42 (0.37)
P-value	0.018	N.S.

[1] Not significantly different at $P < 0.05$.

Table 10. Effects of nitrogen fertilization on willow (*Salix* spp.) growth and N assimilation during the growing season of 1999. Values represent means (n = 12) followed by standard errors between parentheses.

Treatment	Shoot length cm	Shoot biomass g	Shoot concentration %	Amount of N per shoot g
N fertilizer (10 g N m^{-2})	28.6 (1.4) a[1]	27.3 (2.5) a	2.25 (0.05)	0.62 (0.06) a
No fertilization	22.5 (1.1) b	20.2 (2.4) b	2.14 (0.06)	0.43 (0.05) b

---

[1] Means followed by different letters are significantly different at $P < 0.05$.

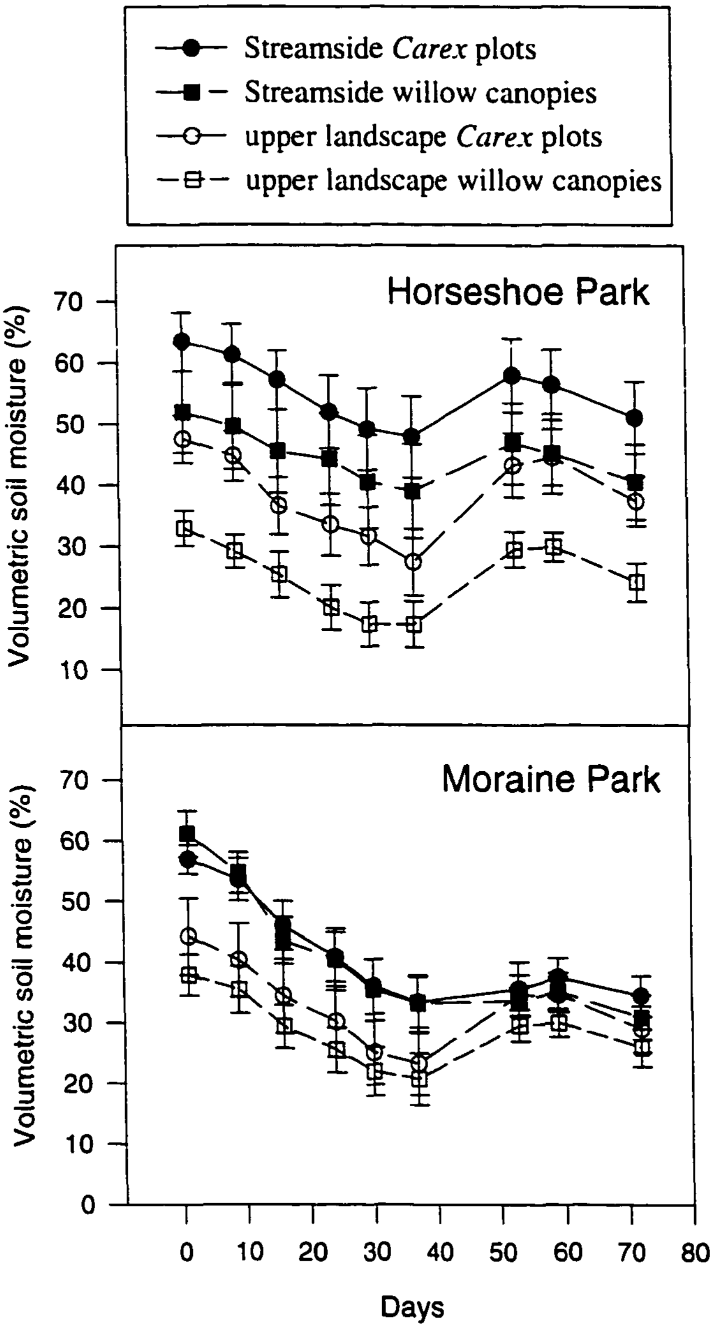

Figure 1. Soil moisture (0 to 14 cm) under *Salix* canopies and in *Carex* plots in upper and lower landscape positions of Horseshoe Park and Moraine Park from early June to late August of 1997. Error bars represent standard error of the means (n = 8).

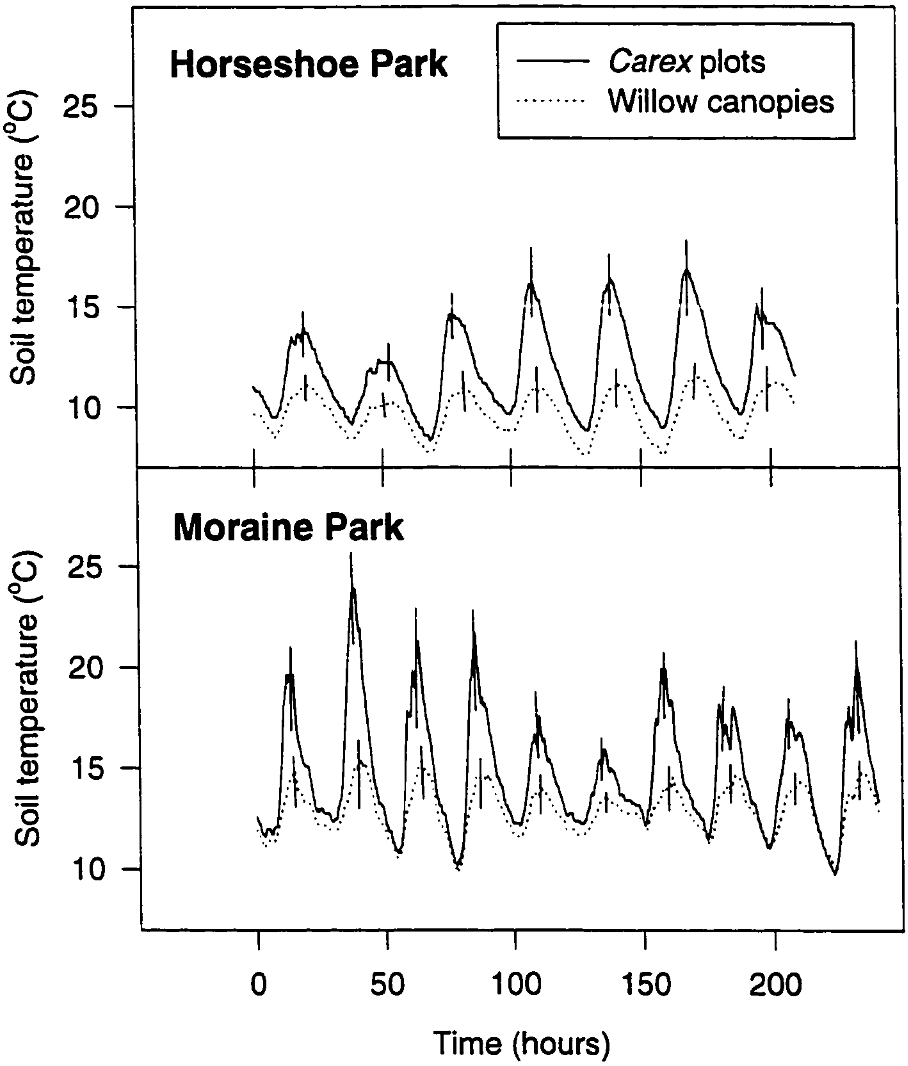

Figure 2. Soil temperature (1 to 6 cm) under willow canopies and in *Carex* plots in Horseshoe Park and Moraine park during July 1997. Vertical lines represent the range of the 95% confidence interval for the means of maximum temperatures (n = 3).

CHAPTER V

Isotopic evidence of the effects of herbivory and landscape position on plant nitrogen sources in a riparian ecosystem [1]

Rômulo S.C. Menezes [2,3], Edward T. Elliott [3], and Jeffrey M. Welker [4]

---

[1] Manuscript submitted to Oecologia

[2] Corresponding author. Research Fellow of Brazilian CNPq, Soil and Crop Sciences Department, Colorado State University, Fort Collins, CO, 80523. Fax: 970-491-1965, E-mail: romulo@nrel.colostate.edu

[3] Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, 80521

[4] Department of Renewable Resources, University of Wyoming, Laramie, WY, 82071

Abstract

During the last few decades, changes in ungulate browsing and surface water hydrology have occurred in elk winter ranges in Rocky Mountain National Park (RMNP). These changes may be influencing the biogeochemistry and vegetation structure of these habitats, as evidenced by the decline in willow (*Salix* spp.) communities. Previous studies in riparian areas of RMNP demonstrated that *Carex* spp. and *S. monticola* utilize different proportions of groundwater vs. rainwater across different landscape positions in those habitats. However, whether these two plant growth forms differ in their sources of N has remained unknown. We conducted field studies in elk winter ranges in RMNP during the growing seasons of 1997 and 1998 . In these studies, we utilized ^{15}N natural abundance and non-isotopic techniques to identify the N sources of *S. monticola* and *Carex* under different herbivory treatments and landscape positions. Based on the isotopic evidence, we found that *Carex* plants seemed to acquire smaller proportions of groundwater N in upper landscape positions in comparison to the woody *Salix* species, suggesting that the deeper rooting characteristics of *Salix* may allow these plants to access more groundwater N. However, grazed *S. monticola* plants in upper landscape positions seemed to acquire less groundwater N as compared to *S. monticola* plants protected from herbivory. Therefore, it appears that herbivory by elk and the shifts in landscape hydrology, caused by reductions in beaver activity and a warming and drying trend, could have an interacting effect on *S. monticola* by increasing the frequency of drought stress and possibly reducing the availability of nitrogen. The combination of these factors could

explain in part the decline of *S. monticola* communities across riparian habitats in Rocky Mountain National Park.

Index words: ^{15}N natural abundance, willow, *Salix*, *Carex*, elk, beaver, Rocky Mountain National Park

Introduction

Changes in ungulate browsing and hydrology have occurred in the winter ranges for elk in Rocky Mountain National Park (RMNP) during the last few decades, and these changes may be influencing the biogeochemistry and vegetation structure of these systems as evidenced by reductions in willow (*Salix* spp.) growth (Singer et al. 1998). Elk numbers have increased by approximately three-fold (Singer et al. 1998) over the last 30 years, and nowadays a high density of elk (*Cervus elaphus*) browses these systems in winter. Changes in the hydrology of these systems are evident from aerial photographs between 1937 and 1996, which indicate that rivers are now less braided and that there is less surface water than in the beginning of this century (R. Peinetti, pers. comm., 1999). These changes in hydrology are probably a result of the observed declines in beaver (*Castor canadensis*) activity (Stevens and Christianson 1980), which may alter the biogeochemical cycles by altering the availability of stream and groundwater (Terwillinger and Pastor 1999, Naiman et al. 1994).

Alstad et al. (1999), based on $\delta\ ^{18}$O measurements, found that *Carex* and *Salix* in the elk winter ranges RMNP utilize water from different sources. *Salix* appears to rely on groundwater (80% of total water uptake) which is recharged by streamwater throughout the floodplains. In addition, water sources of *Salix* seemed to be independent of landscape position and consistent throughout the growing season. In contrast, *Carex* utilized mostly groundwater early in the season but seemed to take up increasing amounts of rainwater (up to 50%) towards the end of the season, especially when located in upper landscape positions. These differences in water source between the two plant functional groups may result from differences in rooting characteristics, but whether these two plant growth forms differ in their sources of N is unknown. Based on the $\delta\,^{18}O$ measurements of Alstad et al. (1999), we anticipated that *Salix* may be relying more strongly on groundwater N in comparison to *Carex*, especially in the case of plants located in upper landscape positions.

The mineral nutrition of plants in native habitats influences a suite of physiological and ecological processes such as carbon exchange, stress resistance, and competitive interactions (Nadelhoffer et al. 1999, Welker et al. 1991, Welker et al. 1987, Chapin 1980). Of the nutrients that may influence and limit plant growth, nitrogen is usually the most limiting element in terrestrial ecosystems (Nadelhoffer et al. 1999, Aber et al. 1989). Identifying the sources of plant nitrogen in terrestrial ecosystems can not be easily done, but stable isotope techniques can be employed (Michelsen et al. 1998, Nadelhoffer et al. 1996, Garten 1993) specially under controlled experimentation and in combination with non-isotopic techniques (Handley and Scrimgeour 1997). Plants may acquire two forms of nitrogen mineralized from soil organic matter (NH_4^+ and NO_3^-) that may have different $\delta^{15}N$ values due to kinetic effects on isotope discrimination during organic matter decomposition (Shearer and Kohl 1986, Evans et al. 1996). In addition, a few studies have reported the uptake of organic forms of N from soil by some plants in artic ecosystems (Chapin et al. 1993, Kielland 1994, Nasholm et al. 1998), but the relevance of the uptake of soil organic N forms by plants in other systems, including our study sites, is unknown, and still needs further investigation. In riparian habitats, soil inorganic N is not the only N source, as ground and stream water may contain inorganic N. Therefore, in riparian ecosystems, if the $\delta^{15}N$ signature of soil and water N sources differ, stable isotope techniques could be useful in combination with other approaches to characterize the patterns of plant N uptake (Handley and Raven 1992).

The primary questions asked by this study were : (1) Are there differences in the N uptake patterns of *S. monticola* and *Carex* in different landscape positions? (2) How does winter elk herbivory affect the patterns of N uptake by *S. monticola* and *Carex* in different landscape positions? Based on these questions, we hypothesized that: (1) *Carex* relies mostly on soil inorganic N in upper landscape positions, and on both soil inorganic N and groundwater N in lower landscape positions, following the patterns of water uptake; (2) regardless of landscape position, *S. monticola* plants protected from herbivory utilize a mixture of both groundwater and soil inorganic N because these plants, independently of landscape position, have access to the groundwater table; and (3) *S. monticola* plants under elk herbivory in upper landscape positions take up less groundwater N because herbivory by elk may lead to a reduction in belowground C allocation and limit the ability of these plants to reach the groundwater.

In order to test our hypotheses, we conducted field studies on the elk winter ranges in RMNP during the growing seasons of 1997 and 1998. In these studies, we utilized both ^{15}N natural abundance and non-isotopic biogeochemical techniques to identify the nitrogen sources of *S. monticola* and *Carex* plants under herbivory treatments and different landscape positions.

Methods

Study Sites

Our study sites were located in two riparian ecosystems on the northeastern side of Rocky Mountain National Park: Moraine Park (Big Thompson River watershed, elevation 2,481 m) and Horseshoe Park (Fall River watershed, elevation 2,598 m). The two watersheds are within 5 km of each other and have perennial alpine snowfields at their headwaters (Baron 1992). Mean annual precipitation for the sites is 41 cm (Singer et al. 1998) and peak stream flow usually occurs in early to mid-June (USDA 1995 and 1996). The 30-year average temperature for the adjacent Estes Valley ranges from 9 to 17°C during the five-month growing season of May through September (Alstad et al. 1999). The study area consists of open grasslands and wet meadows dominated by sedges (*Carex* spp.) and *Salix* (*Salix monticola, S. geyeriana, and S. planifolia*), with some birch (*Betula* spp.) (Singer et al. 1998). Among the *Salix* species, *S. monticola* is dominant in most areas and for this reason it was selected as the target species for this study.

Grazing Treatments

Twelve 30 m x 46 m exclosures were erected to eliminate elk browsing (ungrazed plots) at randomly chosen sites within both riparian zones (six sites each in Horseshoe Park and Moraine Park) between August and November of 1994. Near each exclosure, a 30 m x 46 m plot area was marked off as a paired plot that was grazed by elk in winter (grazed plots). In each exclosure and associated grazed plot, an average of five shallow (0.5 m to 2 m) wells were installed using PVC pipes in the fall of 1994 to monitor groundwater levels and groundwater chemistry.

Design of Preliminary Experiment in 1997

Eight of the twelve sites in Moraine and Horseshoe Parks were selected (four sites in each park), and two *S. monticola* plants were selected within each grazing treatment (grazed and ungrazed) for physiological and biogeochemical measurements. One representative plant was chosen in close proximity to streams ("streamside") and another in areas distant from streams ("upper landscape", which were at least 10 m in a horizontal direction from streams and approximately 0.4 to 0.6 m higher in elevation than streamside plants), resulting in a total of 32 selected plants and four experimental replications in each park. *Carex* plots (1 m x 1 m) were marked next to each selected *S. monticola* plant (within 2 m of distance). During August 1997, samples from non-photosynthetic tissue were collected from current year growth of *S. monticola* and *Carex* plants, dried at 60°C for 72 hours, ground in a ball mill to pass a 0.5 mm sieve, and stored until analysis. Concentrations of carbon and nitrogen in plant tissue were determined using a LECO CHN Analyzer.

Surface water samples were collected with plastic vials from the Big Thompson and Fall Rivers in June, July, and August. Samples collected at different dates from each river, combined in a single sample, and kept frozen until isotopic and chemical analyses.

In July 1997, four-week in situ field soil incubations using aluminum cores (5 cm in diameter, 15 cm in length) were conducted according to the methodology described by Kolberg et al. (1997). Incubation cores (n = 5) were placed next to plants located at both streamside and upper landscape positions. At the end of the incubation period, the soil cores were collected, placed in plastic bags, kept refrigerated in coolers, taken to the laboratory, and kept refrigerated. Within two days of collection, the total soil weight of each sample was recorded, sub-samples (25 g) were extracted with 50 ml of 2 M KCl for one hour, filtered, and the extracts were kept frozen until analysis. The total inorganic N (NH_4^+ plus NO_3^-) in river water samples and soil KCl extracts were diffused into 5 mm acidified filter paper disks according to the methodology described by Khan et al. (1998).

Experimental Design and Sampling in 1998

After observing a sharp contrast in the isotopic signatures of N sources and plants during the growing season of 1997, we established a different experimental design and conducted a more detailed study during the growing season of 1998. In this study, a total of 50 *S. monticola* plants (23 and 27 in browsed and unbrowsed plots, respectively) were selected within the 12 research sites of Moraine Park and Horseshoe Park. All the selected plants were located within 3 m from a well, in order to allow groundwater sampling and the determination of the exact water table depth next to each selected plant. Plants selected within the same site and browsing treatment were located at positions with different water table depths. Next to each *S. monticola* plant (within 1 m), an associated *Carex* plot (0.5 m x 0.5 m) was marked for the purpose of collecting *Carex* tissue samples. *S. monticola* and *Carex* tissue samples (current year growth) were collected in both early July and early September, dried at 60°C for 72 hours, and then ground in a ball mill to pass a 0.5 mm sieve. Concentrations of carbon and nitrogen in plant tissue was determined using a LECO CHN Analyzer.

River water samples were collected from both the Big Thompson and Fall Rivers in mid-July, mid-August, and mid-September by immersing a 3.8 L container at different points along the river surface in the area of the experimental plots. The water samples were kept refrigerated in coolers until the inorganic N was diffused into 5 mm acidified filter paper disks as described by Khan et al. (1998).

Groundwater depth was monitored throughout the season by measuring the water levels in the wells associated with the plants. Groundwater samples (3.8 L) were collected in early August in each well using a small manual pump. A sub-sample (20 ml) from each groundwater and river water sample was placed into scintillation vials and frozen for the determination of groundwater N concentration using an Alpkem automated spectrophotometer. The remaining volume of each groundwater and river water sample was passed through a plastic column (20 cm long, 2 cm in diameter) filled with equal amounts of cation and anion exchange resins (US Filter, Pittsburgh, PA). After all the water had gone through the column, the resin within each column was placed in a 250 ml Erlenmeyer flask and sequentially shaken for 15 minutes with five 30-ml aliquots of 2 M KCl as recommended by Kolberg et al. (1997). After each extraction, the extract was drained from the flask by placing a patch of nylon cloth at the mouth of the flask, and the five 30 ml aliquots from each sample were poured into a 200 ml plastic container and kept frozen until analysis. Before isotopic analysis, the N in river water and groundwater samples was diffused into 5 mm acidified filter paper disks, according to the methodology described by Khan et al. (1998).

In early August, next to each *S. monticola* plant and *Carex* plot, three soil cores were collected (2.5 cm in diameter) to the depth of the groundwater. Each core was subdivided in 15 cm intervals up to a depth of 60 cm and 30 cm intervals up to a depth of 120 cm, depending on the depth of the water table. The soil from all three cores was combined by depth, placed in plastic bags, transported to the laboratory, air-dried, passed through a 2 mm sieve, and ground in a ball mill to pass a 0.25 mm sieve. Concentrations of total soil C and N were determined using a LECO CHN Analyzer.

Within and adjacent to the 12 exclosures, field soil incubations using aluminum cores (5 cm in diameter, 15 cm of depth) were installed next to 19 *S. monticola* plants and within the *Carex* plots, following the same procedure as described above for the 1997 growing season (Kolberg et al. 1997). For isotopic analysis, the inorganic N in the KCl extracts was diffused into 5 mm acidified filter paper disks as described by Khan et al. (1998).

Isotopic Analyses

The isotopic signatures of plant tissue, total soil N, and diffusion disks from water samples and extracts were determined using a Carlo-Erba NA 1500 Series 2 Carbon and Nitrogen Analyzer attached to a VG-Optima mass spectrometer at the Natural Resource Ecology Laboratory, Colorado State University. Natural ^{15}N abundance is expressed as delta units (δ), which denotes parts per thousand deviations (‰), from the ratio ^{15}N:^{14}N in atmospheric N_2,

$$\delta^{15}N = [(^{15/14}R_{sample} - {}^{15/14}R_{standard}) / {}^{15/14}R_{standard}] \times 10^3,$$

where R is the isotopic ratio and the standard is N_2 of air, which has a δ value of 0‰ (Handley and Scrimgeour 1997, Hogberg 1997).

Statistical Analyses

Statistical analyses were performed using the SAS Statistical Package (SAS 1995, Version 6.12, SAS Institute Inc., Cary, NC). During the 1997 growing season, plant tissue $\delta^{15}N$ was analyzed using a split-plot design with grazing treatments as the main factor and landscape positions as sub-plots. During the 1998 growing season, correlation and regression analyses were used to test our a-priori hypotheses regarding the relationships between the $\delta^{15}N$ values of plant, soil or water, and landscape position.

Results

Preliminary Experiment – 1997 Growing Season

The $\delta^{15}N$ values of soil inorganic N in the experimental plots of Moraine and Horseshoe parks averaged -6.14 ‰ (± 0.51) and were significantly ($P = 0.003$) more depleted than river water $\delta^{15}N$ values from Big Thompson and Fall rivers, which averaged -1.00 ‰ (± 0.52). The sharp contrast between $\delta^{15}N$ values of potential plant N sources in our sites is very relevant, as it corresponds to the differences in plant tissue $\delta^{15}N$ values in different landscape positions.

Tissue $\delta^{15}N$ values of *Carex* plants ranged from −10.6 to +3.2 ‰, while for *S. monticola* plants these values ranged from -4.3 to +2.2 ‰. There were no significant effects of elk herbivory on plant tissue $\delta^{15}N$ values, but landscape position had a significant effect on *Carex* tissue $\delta^{15}N$ (Table 1). *Carex* plants located in upper landscape positions had $\delta^{15}N$ values similar to the $\delta^{15}N$ values of soil inorganic N, while the $\delta^{15}N$ values of *Carex* plants located adjacent to streams were significantly ($P < 0.05$) more enriched. To the contrary, *S. monticola* tissue $\delta^{15}N$ was not affected by landscape position and was consistently near the value of stream water $\delta^{15}N$.

1998 Growing Season

The patterns of $\delta^{15}N$ values of *S. monticola* and *Carex* leaf tissue in 1998 were similar to 1997. *Carex* tissue $\delta^{15}N$ was significantly influenced by landscape position (shallow water table depth is associated with streamside locations and deeper water table depth is associated with upland locations), during both July and September (Fig. 1). In contrast, *S. monticola* $\delta^{15}N$ was not significantly affected by landscape position (water table depth), with the exception of grazed plants in July (Fig. 1). For both *Carex* and *S. monticola*, there were no significant differences between the regression lines of the two grazing treatments in both sampling dates.

The data from our non-isotopic measurements yielded no significant differences between treatments. Throughout the growing season, there were no significant correlations between plant tissue total nitrogen content and water table depth or total soil N. *S. monticola* tissue nitrogen concentration (% dry weight) was significantly higher ($P < 0.05$) in grazed than in ungrazed plots in both sampling dates, averaging 2.72 % and 2.27 % in July, and decreasing to 2.23 % and 2.06 % in September, in grazed and ungrazed plots, respectively. *Carex* tissue total nitrogen content was not significantly affected by elk grazing in the two sampling dates, and averaged 1.91 % and 1.87 % in July and 1.61 % and 1.48 % in September for grazed and ungrazed plants, respectively.

Total soil $\delta^{15}N$ (0 to 15 cm) ranged from –2.8 ‰ to + 8.0 ‰, and was significantly more depleted in upper landscape positions (Fig. 2a). Soil inorganic nitrogen $\delta^{15}N$ (0 to 15 cm) ranged from –10.4 ‰ to +5.4 ‰, and also presented a significant positive correlation with water table depth, being significantly more depleted in upper landscape positions (Fig. 2b). A significant correlation ($P < 0.001$, $r = 0.73$) was observed between $\delta^{15}N$ values of inorganic N and that of total soil N in the upper soil horizon and, on average, $\delta^{15}N$ of inorganic soil N was 2.7 ‰ more depleted in relation to total soil $\delta^{15}N$. Because field soil incubations were performed only in ungrazed plots, values of $\delta^{15}N$ of inorganic soil N in grazed plots were estimated with a linear equation, *Y*

$= -3.71 + 1.77\,X$ ($r^2 = 0.53$), where Y is estimated $\delta^{15}N$ of inorganic soil N and X is $\delta^{15}N$ of total soil N. Groundwater $\delta^{15}N$ correlated negatively to water table depth in ungrazed plots (Fig. 2c), but no significant correlation ($P = 0.164$) was observed in the grazed plots. River water $\delta^{15}N$ ranged from + 0.58 ‰ to + 2.93 ‰, and averaged + 1.68 ‰ (± 0.94).

Carex tissue $\delta^{15}N$ was significantly correlated to total soil $\delta^{15}N$ only in the case of grazed plants collected in September, but *S. monticola* tissue $\delta^{15}N$ values of grazed and ungrazed plants were correlated to total soil $\delta^{15}N$ in both sampling dates (Fig. 3). The regression lines of the relationships between total soil $\delta^{15}N$ and tissue $\delta^{15}N$ from grazed and ungrazed *Carex* plants were significantly different ($P < 0.05$) in September, which suggests that grazed *Carex* plants may rely relatively more on soil N than groundwater N in comparison to ungrazed *Carex* plants and that the reliance on soil N may increase over the course of the summer (Fig. 3).

No significant correlations were observed between *Carex* tissue $\delta^{15}N$ and groundwater $\delta^{15}N$, regardless of grazing regime or sampling date (Fig. 4). In contrast, there were significant correlations between groundwater $\delta^{15}N$ and tissue $\delta^{15}N$ ungrazed *S. monticola* plants in both July and September (Fig. 4). Interestingly, no significant correlations were observed in the case of grazed *S. monticola* plants (Fig. 4), which suggests grazed *S. monticola* plants may use less groundwater N. Tissue $\delta^{15}N$ values of *Carex* plants ranged from – 2.6 to + 4.53 ‰, while for *S. monticola* plants these values ranged from - 4.0 to + 2.6 ‰. On average, $\delta^{15}N$ values of *S. monticola* tissue were 2.4

and 6.9 ‰ more depleted than soil $\delta^{15}N$ and groundwater $\delta^{15}N$, respectively. Similarly, $\delta^{15}N$ values of *Carex* tissue were 1.8 and 6.7 ‰ more depleted than soil $\delta^{15}N$ and groundwater $\delta^{15}N$, respectively.

Discussion

The two potential inorganic N sources for riparian plants, being either from soil or from groundwater, differed in their $\delta^{15}N$ values by an average of 5 ‰ during the growing season of 1997. This difference is an important part of our study as it corresponds to the differences in the $\delta^{15}N$ values of plant tissue under divergent experimental treatments. The range of plant tissue $\delta^{15}N$ values observed in our study is consistent with values reported for plant tissue in terrestrial ecosystems, which usually vary between –5 to +2 ‰, but in some cases could range between -10 and +10‰ (Virginia and Delwiche 1982, Vitousek et al. 1989, Nadelhoffer and Fry 1994, Frank and Evans 1997). In general, the differences between plant tissue $\delta^{15}N$ and groundwater $\delta^{15}N$ in our study were consistently much higher (c. 7 ‰) than the differences between plant tissue $\delta^{15}N$ and total soil $\delta^{15}N$ (c. 2 ‰), which suggests that both *S. monticola* and *Carex* plants in our sites may rely mostly on uptake of soil N as opposed to groundwater N.

Effect of Landscape Position on N Sources

During 1997 we found that *Carex* tissue in lower landscape positions consistently exhibited enriched $\delta^{15}N$ values when compared to *Carex* plants growing in upland positions in the landscape (Table 1). In contrast, $\delta^{15}N$ values of *S. monticola* tissue were not significantly different between landscape positions (Table 1). This evidence suggests that the shallow-rooted graminoid may be relying more on soil N and acquiring smaller proportions of river-ground water N in upper landscape positions in comparison to the woody *S. monticola* species. This general interpretation is supported by our additional finding during 1998, in which a significant correlation was observed for *Carex* tissue $\delta^{15}N$ and water table depth (Fig. 1), indicating that the lower the water table (i.e., less access to groundwater N), the more depleted the $\delta^{15}N$ values of *Carex* tissue. To the contrary, *S. monticola* leaf $\delta^{15}N$ values were not associated with water table depth (Fig. 1) with the exception of grazed plants in July. These findings suggest that the deeper rooting characteristics of *S. monticola* may allow these plants to tap groundwater N independent of landscape position, but grazing may limit the access to groundwater in upper landscape sites. Similar to our results, previous studies have reported higher tissue $\delta^{15}N$ values in plants growing in lower landscape positions in comparison to plants in upper landscape positions (Garten 1993, Sutherland et al. 1993).

The observations presented here that landscape position influences facets of mineral nutrition of riparian vegetation are corroborated by a previous study conducted by Alstad et al. (1999) addressing water sources of these same species in the same experiment. Measurements of $\delta^{18}O$ showed that *Carex* plants in upper landscape positions relied strongly on rain water acquired from upper soil layers, while *Carex* plants located adjacent to streams and *S. monticola* plants in both landscapes positions, primarily use streamwater. The agreement between the patterns of $\delta^{18}O$ and $\delta^{15}N$ values in plant tissue strongly support our hypotheses regarding the patterns of N uptake by *S. monticola* and *Carex* in our study sites. These findings further demonstrate the usefulness of stable isotopes in ecological studies, since we were not able to detect any influence of landscape position or herbivory on plant N sources based solely on the non-isotopic data we collected.

Effect of herbivory on N sources

Our findings also suggest that elk herbivory may have a significant effect on the patterns of N uptake by *S. monticola* plants. As indicated by the correlations between groundwater $\delta^{15}N$ and *S. monticola* tissue $\delta^{15}N$ (Fig. 4), grazed *S. monticola* plants may have a more limited access to groundwater N than *S. monticola* plants protected from herbivory. These findings were corroborated by a parallel investigation, based on non-isotopic techniques, of the N balance of *Salix* plants conducted in our study site, which indicate that grazed *S. monticola* plants may not have as much access to groundwater N when compared to ungrazed *S. monticola* plants. The findings from this parallel study demonstrated that ungrazed *S. monticola* plants could take up at least 7% of the annual requirements of N from the groundwater, which was higher ($P < 0.001$) than that of grazed plants, which averaged only 4% (R. Peinetti, pers. comm., 1999).

We suggest that grazed *S. monticola* plants may have less access to groundwater N due to a less developed rooting system. A carbon-balance study conducted in our site indicated that grazed *S. monticola* plants might allocate less carbon to the rooting system, in comparison to *S. monticola* plants protected from herbivory (R. Peinetti, pers. comm., 1999). In addition, several previous studies have reported that heavily grazed plants often allocate a smaller proportion of their photosynthetically fixed carbon to belowground structures than do ungrazed or lightly grazed plants (Detling 1987, Briske and Richards 1995, Detling 1998).

In nitrogen limited systems, competition for soil N by coexisting plants may cause plants to resort to different sources of N in order to meet their physiological requirements (Michelsen et al. 1996, Schulze et al. 1994, Welker et al. 1991). Menezes et al. (1999) conducted fertilization experiments in our study sites and found that N availability significantly limits growth and uptake of N by *S. monticola* plants. Therefore, the ability of plants to use more than one source may be of significant importance for plant growth, development, and survival. A reduced ability by grazed *S. monticola* plants to access different sources of N could significantly reduce the ability of *Salix* plants to respond to herbivory.

Summary and Conclusions

We summarize our findings in Figure 5, which illustrates the suggested patterns of N uptake by grazed and ungrazed *S. monticola* and *Carex* plants in different landscape positions, and shows the average $\delta^{15}N$ values of N sources and plant tissue under those treatments during the growing season of 1998. In conclusion, we suggest that shifts in landscape hydrology, due to reductions in beaver activity and a warming and drying trend, combined with intense elk herbivory, may have a compounding effect on *Salix* by increasing the frequency of drought stress and possibly reducing the availability of nitrogen. Since *Salix* growth and uptake of N is limited by N availability in our sites, reductions in stream water N sources could increase the limitation of N to these plants and lead to lower rates of photosynthesis and growth. We suggest that these effects explain in part the sensitivity of *Salix* communities to elk browsing and their decline across elk winter ranges in Rocky Mountain National Park.

Acknowledgements

We thank Steve Williams, Margot Kaye, Rick Rochelle, Jennifer Williams, and Tricia Wotan for assistance with field and laboratory work. Helpful comments to the manuscript were provided by Dan Binkley, Jason Kaye, Therese Johnson, Ryan Monello, and Michael Coughenour. This study was primarily funded by the Biological Resources Division of the U.S. Geological Survey and also by the National Park Service.

References

Aber JD, Nadelhoffer KJ, Studler P, Melillo JM (1989) Nitrogen saturation in northern forest ecosystems. Bioscience 39: 378-385

Alstad KP, Welker JM, Williams SA, Trlica MJ (1999) Carbon and water relations of *Salix monticola* in response to winter browsing and changes in surface water hydrology: an isotopic study using $\delta^{13}C$ and $\delta^{18}0$. Oecologia, *In Press*.

Baron J (1992) Surface waters. In: Baron J (ed) Biogeochemistry of a subalpine ecosystem: Loch Vale Watershed. Vol. 70. Springer-Verlag, New York, pp 142-183

Briske DD, Richards JH (1995) Plant responses to defoliation: a physiologic, morphologic, and demographic evaluation. pp. 635-710. In: Bedunah J and Sosebee RE (eds) Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, Colorado

Chapin, FS (1980) Mineral nutrition of wild plants. Annu Rev Ecol Syst 11: 233-260

Chapin FS, Moilanen L, and Kielland K (1993) Preferential use of organic nitrogen for growth by a non-mycorrhizal artic sedge. Nature 361: 150-153

Detling JK (1987) Grass response to herbivory. pp. 56-68 In: JL Capinera (ed) Integrated pest management on rangeland: a short grass prairie perspective. Westview Press, Boulder, Colorado

Detling JK (1998) Mammalian hervivores: ecosystem-level effects in two grassland national parks. Wildlife Society Bulletin 26: 438-448

Evans RD, Bloom AJ, Sukrapanna SS, Ehleringer JR (1996) Nitrogen isotope composition of tomato (*Lycopersicom esculentum* Mill. Cv. T-5) growth under ammonium or nitrate nutrition. Plant, Cell, and Environment 19: 1317-1323

Frank DA, Evans RD (1997) Effects of native grazers on grassland N cycling in Yellowstone National Park. Ecology 78: 2238-2248

Garten CT Jr (1993) Variation in foliar ^{15}N abundance and the availability of soil nitrogen on Walker Branch Watershed. Ecology 74: 2098-2113

Handley LL, Raven JA (1992) The use of natural abundance of nitrogen isotope in plant physiology and ecology. Plant, Cell, and Environment 15: 965-985

Handley LL, Scrimgeour CM (1997) Terrestrial plant ecology and ^{15}N natural abundance: the present limits to interpretation for uncultivated systems with original data from a Scottish old field. Advances in Ecol Res 27:133-212

Hogberg P (1997) ^{15}N natural abundance in soil-plant systems. New Phytol. 137:179-203

Khan SA, Mulvaney RL, Brooks PD (1998) Diffusion methods for automated nitrogen-15 analysis using acidified disks. Soil Sci Soc Am J 62:406-412

Koelland K (1994) Amino acid absorption by artic plants: implications for plant nutrition and nitrogen cycling. Ecology 75: 2373-2383

Kolberg RL, Rouppet B, Westfall DG, Peterson GA (1997) Evaluation of an In Situ net soil nitrogen mineralization method in dryland agroecosystems. Soil Sci Soc Am J 61:504-508

Menezes RSC, Elliott ET, Valentine DW, Williams SA (1999) Effects of herbivory and proximity to surface water on C and N biogeochemical cycles of elk winter ranges in Rocky Mountain National Park. J Range Manage, Submitted

Michelsen A., Schmidt IK, Jonasson S, Quarmby C, Sleep D (1996) Leaf ^{15}N abundance of subartic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. Oecologia 105: 53-63

Nadelhoffer KJ, Emmett BA, Gundersen P, Kjonaas OJ, Koopmans CJ, Scheleppi P, Tietema A, Wright RF (1999) Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. Nature 398: 145-148

Nadelhoffer KJ, Fry B (1994) Nitrogen isotope studies in forest ecosystems. In: Lajtha K, Michener RH (eds) Stable isotopes in ecology and environmental science. Blackwell Scientific Publications, London, pp 22-44

Nadelhoffer KJ, Shaver G, Fry B, Giblin A, Johnson L, McKane R (1996) ^{15}N natural abundance and N use by tundra plants. Oecologia 107: 386-394

Naiman RJ, Pinay G, Johnston C, and Pastor J (1994) Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. Ecology 75:905-921

Nasholm T, Ekblad A, Nordin A, Giesler R, Hogberg M, and Hogberg P (1998) Boreal forest plants take up organic nitrogen. Nature 392: 914-916

SAS Institute. 1995. SAS User's Guide. Release 6.12. SAS Institute Inc., Cary, NC.

Shearer G, Kohl DH (1986) N_2-fixation in field settings: Estimations based on natural ^{15}N abundance. Australian J. of Plant Physiol. 13: 699-756

Schulze ED, Chapin FS III, Gebauer G (1994). Nitrogen nutrition and isotope differences among life forms at the nothern treeline of Alaska. Oecologia 100: 406-412

Singer FJ, Zeigenfuss LC, Cates RG, Barnett DT (1998) Elk, multiple factors, and persistence of *S. monticola* in national parks. Wildlife Society Bulletin 26:419-428

Stevens DR, Christianson S (1980) Beaver populations on the East slope of Rocky Mountain National Park. Special Report to Rocky Mountain National Park, Estes Park, CO

Sutherland RA, Kessel C van, Farrel RE, Pennock DJ (1993) Landscape-scale variations in plant and soil nitrogen-15 natural abundance. Soil Sci. Soc. Am. J. 57: 169-178

Terwilliger J, Pastor J (1999) Small mammals, ectomycorrhizae, and conifer succession in beaver meadows. Oikos 85:83-94

U.S.D.A. Snow Survey Office (1995 and 1996). Snowpack data for Rocky Mountain National Park. National Resources Conservation Service, Lakewood, CO

Virginia RA, Delwiche CC (1982) Natural N-15 abundance of presumed N-fixing and non-N-fixing plants from selected ecosystems. Oecologia 54: 317-325

Vitousek PM, Shearer G, Kohl DH (1989) Foliar ^{15}N abundance in Hawaiian rainforest: patterns and possible mechanisms. Oecologia 78: 383-388

Welker JM, Briske DD, Weaver RW (1987) Nitrogen-15 partitioning within a three generation tiller sequence of the bunchgrass Schizachyrium scoparium: Response to selective defoliation. Oecologia 24: 330-334

Welker JM, Gordon DR, Rice KJ (1991) Capture and allocation of nitrogen by *Quercus douglasii* seedlings in competition with annual and perennial grasses. Oecologia 87: 459-466

Table 1. $\delta^{15}N$ values of *S. monticola* and *Carex* tissue in upper landscape and streamside positions of Horseshoe Park and Moraine Park during August 1997. Values represent means (n=8) followed by the standard error between parentheses. Means followed by different letters are significantly different at $P < 0.05$.

	Plant tissue $\delta^{15}N$ (‰)	
Landscape position	*Carex*	*S. monticola*
	Horseshoe Park	
Upper landscape	-6.10 (2.34) a	-1.87 (0.44) a
Streamside	-0.74 (0.68) b	-1.82 (0.27) a
	Moraine Park	
Upper landscape	-10.84 (1.45) a	0.03 (0.41) a
Streamside	-2.28 (3.10) b	-0.41 (0.65) a

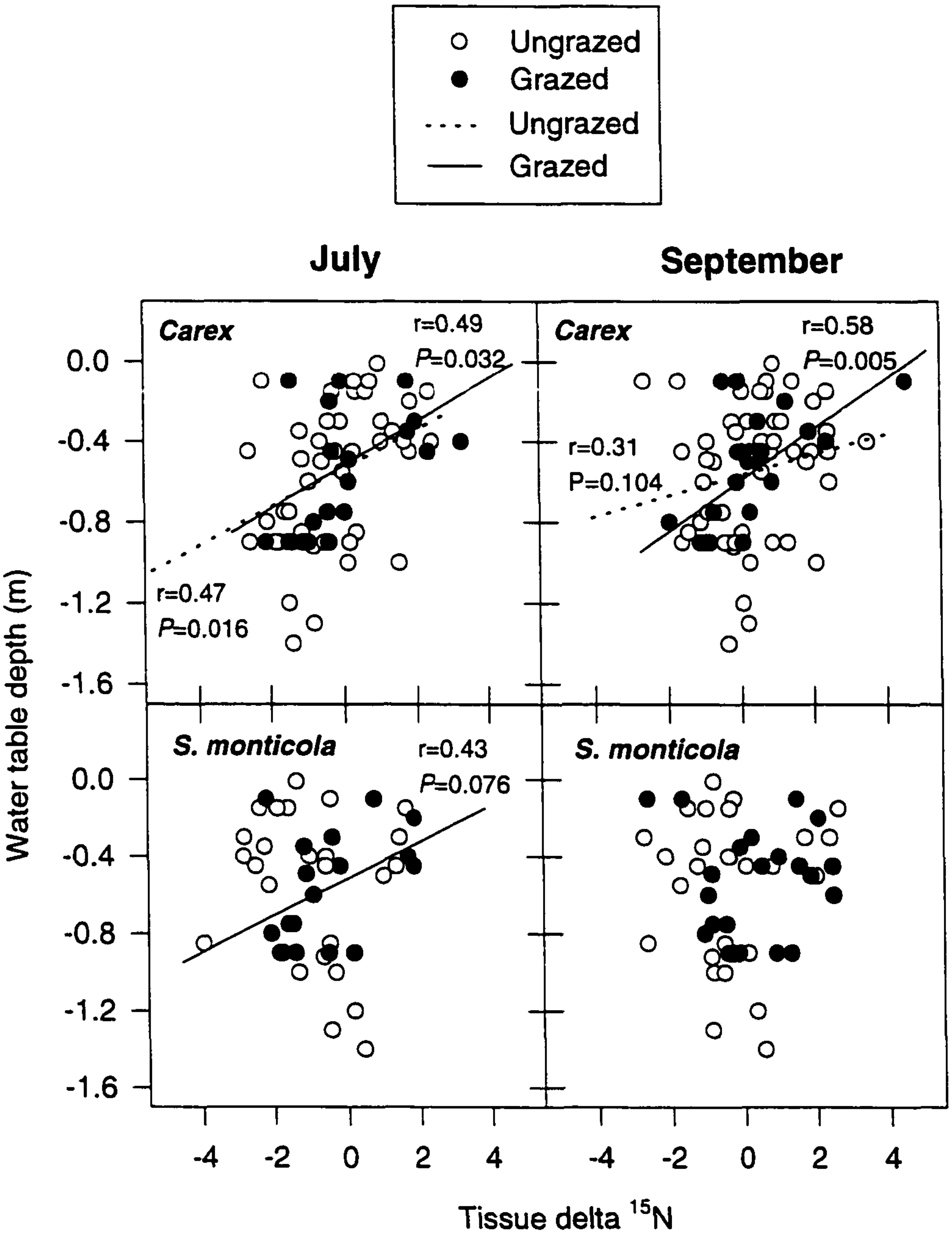

Figure 1. Correlations between tissue delta ^{15}N values of grazed and ungrazed *Carex* and *S. monticola* and water table depth in Moraine and Horseshoe parks in July and September of 1998. Correlations without lines are not significant at $P < 0.10$.

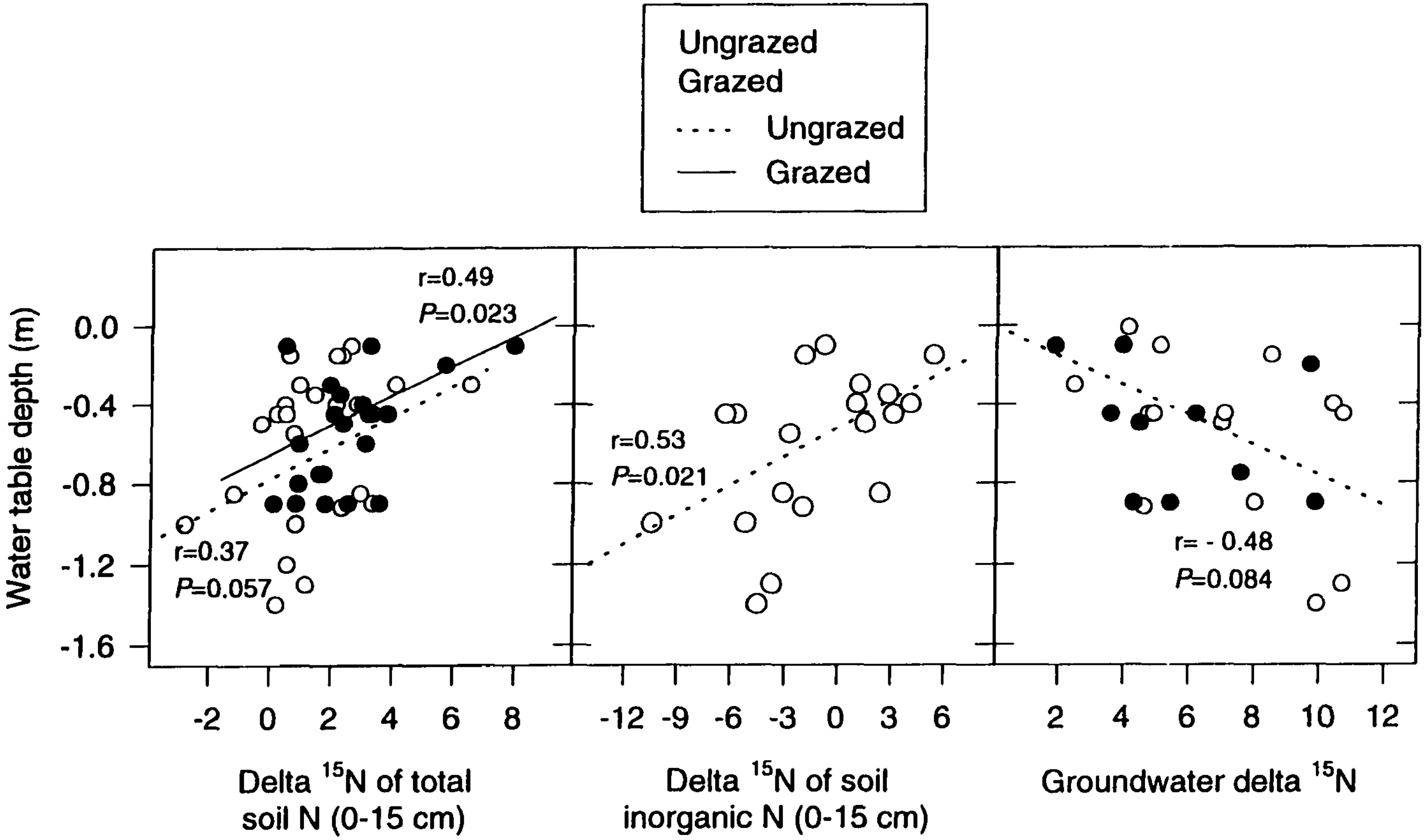

Figure 2. Correlations between water table depth and delta ^{15}N values of (a) soil total N, (b) inorganic soil N, and (c) groundwater N in grazed and ungrazed plots of Moraine and Horseshoe Parks during the growing season of 1998. Correlations without lines are not significant at $P < 0.10$.

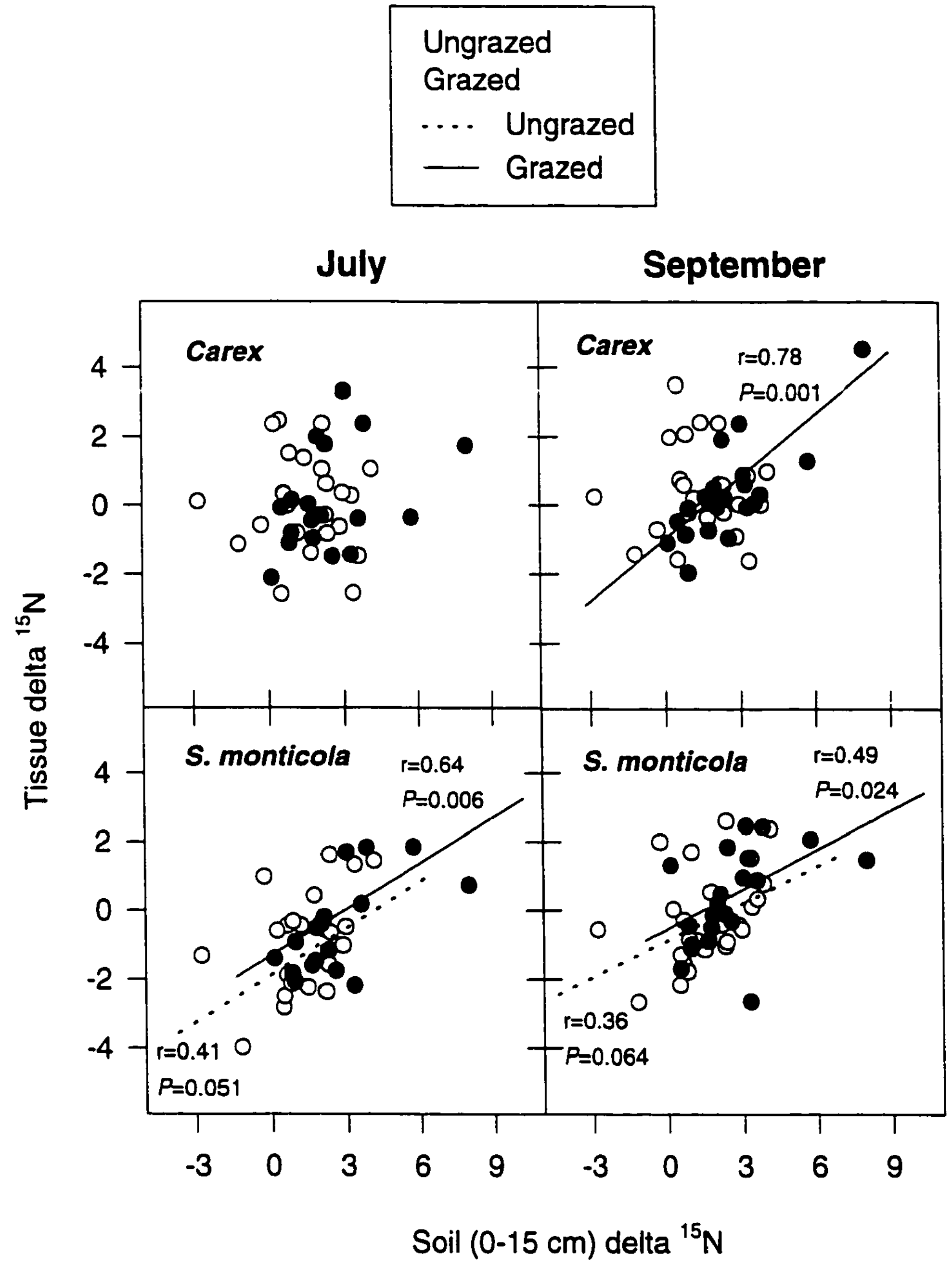

Figure 3. Correlations between delta ^{15}N values of total soil N and tissue of *Carex* and *S. monticola* in July and September of 1998 in grazed and ungrazed plots of Moraine and Horseshoe parks. Correlations without lines are not significant at $P < 0.10$.

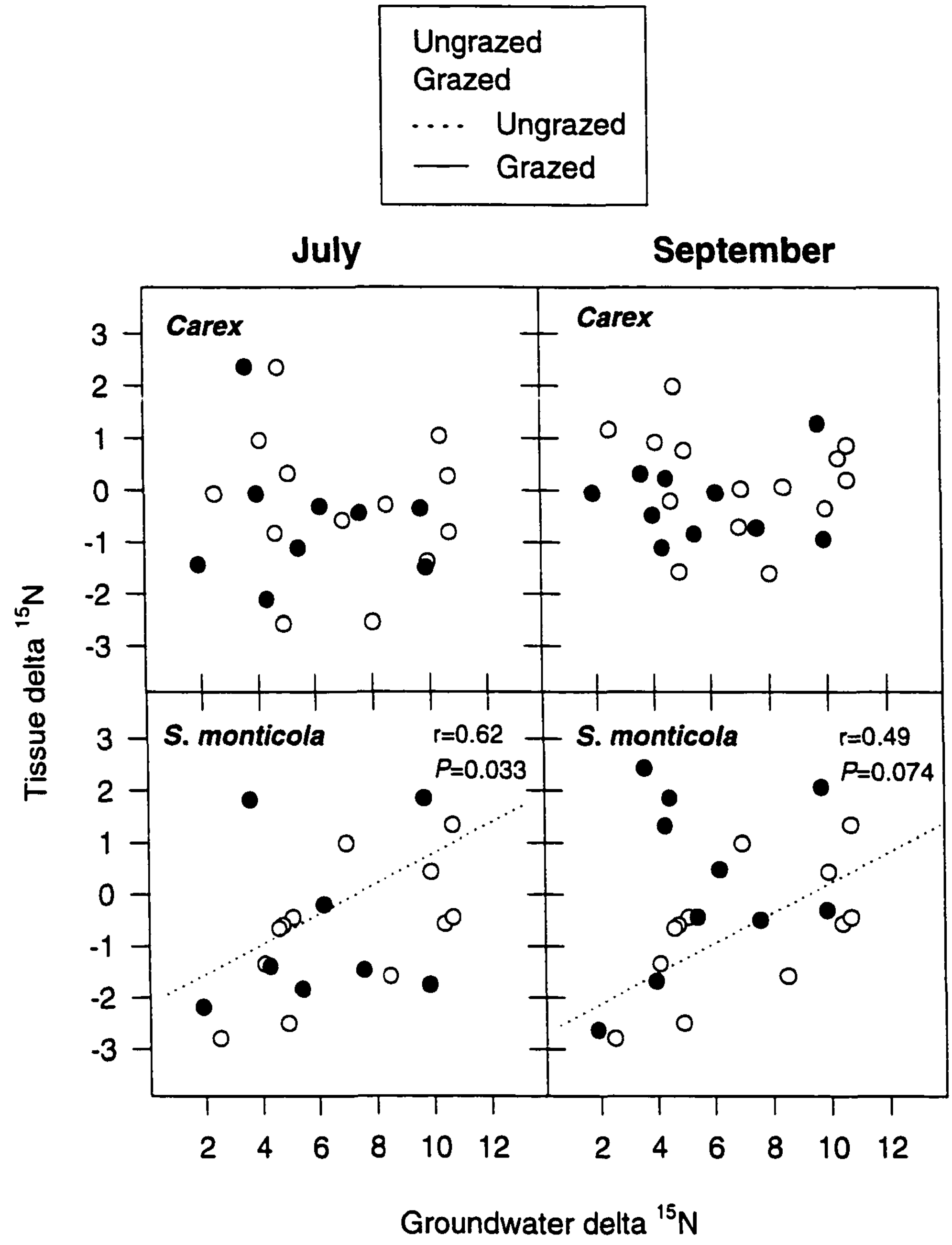

Figure 4. Correlations between delta ^{15}N values of groundwater and tissue of grazed and ungrazed *Carex* and *S. monticola* plants in Moraine and Horseshoe Parks during July and September of 1998. Correlations without lines are not significant at $P<0.10$.

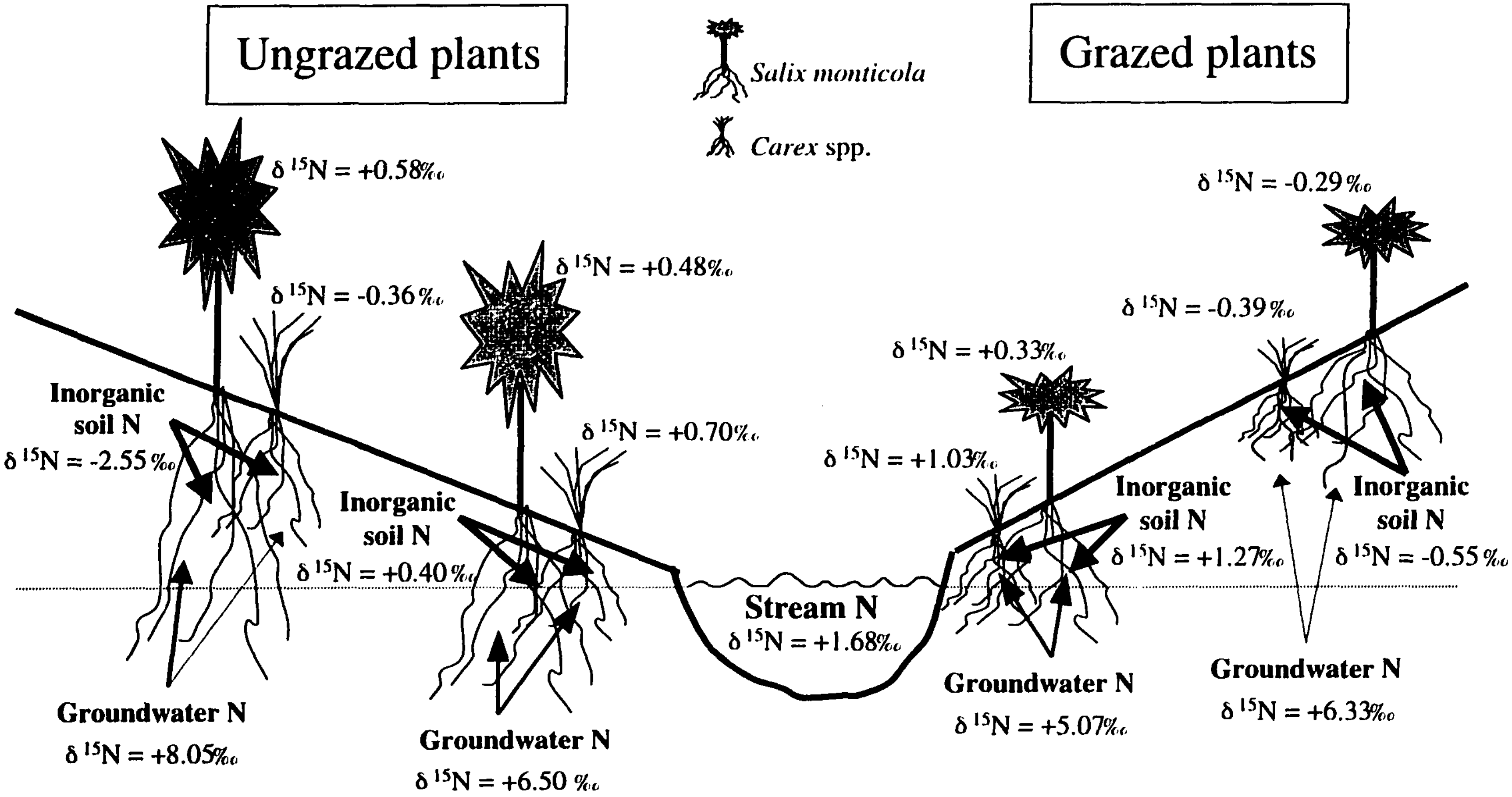

Figure 5. Hypothetical patterns of plant N uptake and average delta ^{15}N values of N sources and tissue of grazed and ungrazed *S. monticola* and *Carex* plants in upper and lower landscape positions of Moraine and Horseshoe parks during the growing season of 1998. Arrows with thicker lines indicate greater importance of N sources to plant N uptake.

CONCLUSIONS

In northeastern Brazil, the preservation of native tree species or the introduction of *P. juliflora* in pastures of *C. ciliaris* had a significant influence on soil and herbaceous understory characteristics, microclimate, and nutrient dynamics within our study sites. Herbaceous understory biomass was lower under the canopies of *P. juliflora* and *S. tuberosa*, when compared to patches of *C. ciliaris*, but presence of *Z. joazeiro* trees had no significant effect on herbaceous understory biomass. In general, the amount and availability of soil nutrients was greater beneath tree canopies, when compared to areas where the trees were removed, but these effects varied between different tree species and soil types. These findings indicate the need for a better understanding of the interactions between trees, soil, and herbaceous plants in semi-arid northeastern Brazil, which could give support to the development of sustainable agrosilvopastoral systems in the region.

In Rocky Mountain National Park (RMNP), Colorado, USA, we found that *Salix* shrubs had a significant influence on ecosystem processes in the elk winter range. *Salix* shrubs contributed to the majority of both the litterfall biomass and to the amount of N returned to the soil in litter, and also led to increases in N availability and litter decomposition rates. Herbivory by elk significantly reduced the amount of *Salix* litterfall and the amount of N returned to the soil in litter, but the estimated total amount of N returned to the soil in elk excrements was 265 % of the N returned in plots without herbivores, probably due to transfers of N from the summer range to the winter range. In addition, herbivores seemed to reduce the ability of *Salix* shrubs to take up N from the groundwater, which may negatively affect the ability of this plant species to respond to the increases in herbivory and changes in hydrology toward dryer conditions observed in those sites in the last few decades. In the long term, continued increases in elk herbivory could lead to increases in N inputs and availability in this ecosystem, which could lead to alterations in ecosystem structure and functioning.

Overall, we found that the presence and preservation of trees or shrubs in the semi-arid grazing systems in northeastern Brazil and RMNP contributed to increases in the capture, retention, and availability of nutrients and plant productivity in comparison to disturbed systems where the density of trees or shrubs was reduced.

REFERENCES

Aber, J.D., and J.M. Melillo. 1991. Terrestrial ecosystems. Saunders Coll. Publ. Philadelphia, PA.

Aber, J.D., K.J. Nadelhoffer, P. Studler, J.M. Melillo. 1989. Nitrogen saturation in northern forest ecosystems. Bioscience 39: 378-385.

Afzal, M., and W.A. Adams. 1992. Heterogeneity of soil mineral nitrogen in pasture grazed by cattle. Soil Sci. 56: 1160-1166.

Alstad, K.P., J.M. Welker, S. Williams, and M.J. Trlica. 1999. Carbon and water relations of *Salix monticola* in response to winter browsing and changes in surface water hydrology: an isotopic study using $\delta^{13}C$ and $\delta^{18}O$. Oecologia, *In Press*.

Amundson, R.G., R.A. Ali, and A.J. Belsky. 1995. Stomatal responsiveness to changing light intensity increases rain-use efficiency of below-crown vegetation in tropical savannas. J. Arid. Environments 29: 139-153.

Araujo Filho, J.A. 1990. Manipulação da vegetação lenhosa da caatinga para fins pastoris. Sobral, EMBRAPA-CNPC (EMBRAPA-CNPC. Circular Técnica, 11), 18 pp.

Araújo Filho, J.A. and F.C. Carvalho. 1996. Desenvolvimento sustentado da caatinga. In: Alvarez V.H., L.E.F. Fontes, and M.P.F. Fontes. O solo nos grandes domínios morfoclimáticos do Brasil e o desenvolvimento sustentado. Viçosa, SBCS - UFV. p.125-133.

Babos, K., and L.J.C. Cumana. 1992. Xylotomical study of some Venezuelan tree species (Mimosaceae I-IV). Acta Botanica Hungarica 37: 183-238.

Baron, J. 1992. Surface waters. In: Baron, J. (ed.) Biogeochemistry of a subalpine ecosystem: Loch Vale Watershed. Vol. 70. Springer-Verlag, New York, pp 142-183.

Belsky, A.J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. Ecology 75: 922-932.

Belsky, A.J., S.M. Mwonga, and J.M. Duxbury. 1993. Effects of widely spaced trees and livestock grazing on understory environments in tropical savannas. Agrofor. Syst. 24:1-20.

Billings, W.D. 1990. *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. p. 301-322. In: G.M. Woodwell (ed.) The earth in transition: patterns and processes of biotic impoverishment. Cambridge University Press, Cambridge, UK.

Binkley, D. 1984. Ion exchange bags: factors affecting estimates of nitrogen availability. Soil Sci. Soc. Am. J. 48:1181-1184.

Boecklen, W.J. and P.W. Price. 1990. Nonequilibrial community structure of sawflies on Arroyo Willow. Oecologia 85:483-491.

Boyer, J.S. 1996. Advances in drought tolerance in plants. Adv. Agron. 56:187-218.

Bremner, J.M., and C.S. Mulvaney. 1982. Nitrogen-Total. In: Page, A.L., R.H. Miller, and D.R. Keeney (eds.), Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties, Agronomy Monograph no. 9, (2nd Edition), pp 595-624. ASA-SSSA, Madison, USA.

Briske, D.D. 1986. Plant responses to defoliation: morphological considerations and allocation priorities. p. 425-427. In: P.J. Joss, P.W. Lynch, and O.B. William (eds.) Rangelands: a resource under siege. Proceedings of the second international rangeland congress, Australian Academy of Sciences, Canberra, Australia.

Briske, D.D. and J.H. Richards. 1995. Plant responses to defoliation: a physiologic, morphologic, and demographic evaluation. pp. 635-710. In: J. Bedunah and R.E. Sosebee (eds.) Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, Colorado.

Buchanan, M. and L.D. King. 1993. Carbon and phosphorus losses from decomposing crop residues in no-till and conventional till agroecosystems. Agron. J. 85: 631-638.

Burgess, S.S.O., M.A. Adams, N.C. Turner, and C.K. Ong. 1998. The redistribution of water by tree root systems. Oecologia 115: 306-311.

Caldwell, M.M., T.E. Dawson, and J.H. Richards. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113: 151-161.

Cambardella, C.A., and E.T. Elliott. 1992. Particulate soil organic-matter changes across a grassland cultivation sequence. Soil Sci. Soc. Am. J. 56:777-783.

Campbell, B.M., P. Frost, J.A. King, M. Mawanza, and L. Mhlanga. The influence of trees on soil fertility on two contrasting semi-arid soil types at Matopos, Zimbabwe. Agrofor. Syst., 28: 159-172, 1994.

Campo, J., V.J. Jaramillo, and J.M. Maass. 1998. Pulses of soil phosphorus availability in a Mexican tropical dry forest: effects of seasonality and level of wetting. Oecologia, 115:167-172.

Cates, R. 1998. Response of willow secondary metabolites to mechanical clipping, ungulate grazing, and litter decomposition. In: Large mammalian herbivores, plant interactions and ecosystem processes in five national parks. Third annual report to Biological Resources Division, USGS.

Caughley, G., N. Shepherd, and J. Short. 1987. Kangaroos: their ecology and management in sheep rangelands of Australia. Cambridge University Press, New York.

Chadde, S.W., and C.E. Kay. 1991. Tall willow communities in Yellowstone's northern range: a test of the "natural regulation" paradigm. pp. 231-261. In R.B. Keiter and M.S. Boyce (eds.) The greater Yellowstone ecosystem: redefining America's Wilderness Heritage. Yale University Press, New York.

Chapin, F.S., L. Moilanen, and K. Kielland. 1993. Preferential use of organic nitrogen for growth by a non-mycorrhizal artic sedge. Nature 361: 150-153.

Chapin, F.S., B.H. Walker, R.J. Hobbs, D.U. Hooper, J.H. Lawton, O.E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science 277:500-504.

Chapin, F.S. 1980. Mineral nutrition of wild plants. Annu. Rev. Ecol. Syst. 11: 233-260.

Coughenor, M.B., J.E. Ellis, D.M. Swift, D.L. Coppock, K.A. Galvin, J.T. McCabe, and T.C. Hart. 1985. Energy extraction and use in a nomadic pastoral ecosystem. Science 230:619-625.

Coughenour, M.B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone northern winter range. J. Appl. Ecol. 28: 71-82.

D'Antonio, C.M., and P.M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23: 63-87.

Dawson, T.E. 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant interactions. Oecologia 95: 565-574.

Detling, J.K. 1987. Grass response to herbivory. pp. 56-68. In: JL Capinera (ed.) Integrated pest management on rangeland: a short grass prairie perspective. Westview Press, Boulder, Colorado.

Detling, J.K. 1998. Mammalian hervivores: ecosystem-level effects in two grassland national parks. Wildlife Society Bulletin 26: 438-448.

Elliott, E.T., H.H. Janzen, C.A. Campbell, C.V. Cole, and R.J.K. Myers. 1993. Principles of ecosystem analysis and their application to integrated nutrient management and assessment of sustainability. pp. 35-57. In: R.C. Wood and J. Dumansky (eds.) Proceedings of the International Workshop on Sustainable Land Management for the 21st Century, University of Lethbridge, Lethbridge, Canada.

Ellis, J. 1994. Climate variability and complex ecosystem dynamics: implications for pastoral development. In: Scoones, I. (ed). Living with uncertainty: new directions in the pastoral development in Africa. Northern Yorkshire, Intermediate Technology Publications.

Ellis, J. and K.A. Galvin. 1994. Climate patterns and land-use practices in the dry zones of Africa. Bioscience 44:340-349.

Ellis, J.E. and D.M. Swift. 1988. Stability of African pastoral ecosystems: alternate paradigms and implications for development. J. Range Manag. 41:450-459.

Esechie, H. A. 1992. Distribution of chemical constituents in the plant parts of six tropical origin forage grasses at early anthesis. J. Sci. Food Agric. 58:435-438.

Evans, R.D., A.J. Bloom, S.S. Sukrapanna, and J.R. Ehleringer. 1996. Nitrogen isotope composition of tomato (*Lycopersicom esculentum* Mill. Cv. T-5) growth under ammonium or nitrate nutrition. Plant, Cell, and Environment 19: 1317-1323.

Fahnestock, J.T. and J.K. Detling. 1999. Plant responses to defoliation and resource supplementation in the Pryor Mountains. Oikos (submitted).

Farrel, J. 1990. The influence of trees in selected agroecosystems in Mexico. pp. 167-183. In Gliessman, S.R. (ed.) Agroecology: Researching the Ecological Basis for Sustainable Agriculture. Springer-Verlag, New York.

Farrel, J. 1990. The influence of trees in selected agroecosystems in Mexico. pp. 167-183. In: Gliessman, S.R. (ed.) Agroecology: Researching the ecological basis for sustainable agriculture.

FIBGE. 1977. Geografia do Brasil. Região Nordeste. Fundação Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

FIBGE. 1985. Atlas Nacional do Brasil. Região Nordeste. Fundação Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

Frank, D.A., and P.M. Groffman. 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. Ecology 79: 2229-2241.

Frank, D.A., and R.D. Evans. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. Ecology 78: 2238-2248.

Frank, D.A., and S.J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73: 2043-2058.

Frank, D.A., and S.J. McNaughton. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Ecology 73: 2043-2058.

Frank, D.A., R.S. Inouye, N. Huntly, G.W. Minshall, and J.E. Anderson. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. Biogeochemistry 26: 163-188.

Freitas, M.B., E.N. Choudhury, and C.M.B. Faria. 1981. Manejo e conservação de solo no agreste pernambucano. Boletim de pesquisa 6. CPATSA-EMBRAPA, Petrolina. 44 p.

Frossard, E., M. Brossard, M.J. Hedley, and A. Metherell. 1995. Reactions controlling the cycling of P in soils. pp. 107-137. In: Tiessen H (ed) Phosphorus in the global environment: transfers, cycle, and management. John Willey and Sons, England.

Garcia-Montiel, D.C. and D. Binkley. 1998. Effect of Eucalyptus saligna and Albizia falcataria on soil processes and nitrogen supply in Hawaii. Oecologia 113: 547-556.

Garten, C.T. 1993. Variation in foliar ^{15}N abundance and the availability of soil nitrogen on Walker Branch Watershed. Ecology 74: 2098-2113.

Gee, G.W. and J.W. Bauder. 1986. Particle-size analysis. pp. 383-411. In: A. Klute (ed.) Methods of soil analysis. Part 1. 2nd ed. Agron. Monogr. 9. ASA and SSSA, Madison, WI.

Georgiadis, N.J., R.W. Reuss, S.J. McNaughton, and D. Western. 1989. Ecological conditions that determine when grazing stimulates grass production. Oecologia 81: 316-322.

Gomes, G.M. and J.R. Vergolino. 1995. A macroeconomia do desenvolvimento nordestino: 1960/1994. Recife, Instituto Economistas de Pernambuco. p.6-160.

Gondim Filho, J.G.C. 1994. Sustentabilidade do desenvolvimento do semi-árido sob o ponto de vista dos recursos hídricos. Brasília, Projeto Áridas. 126 p.

Halvorson, J.J., J.L. Smith, H. Bolton Jr., and R.E. Rossi. 1995. Evaluating shrub-associated patterns of soil properties in a shrub-steppe ecosystem using multiple-variable geostatistics. Soil Sci. Soc. Am. J. 59:1476-1487.

Halvorson, J.J., J.L. Smith, H. Bolton Jr., and R.E. Rossi. 1995. Evaluating shrub-associated patterns of soil properties in a shrub-steppe ecosystem using multiple-variable geostatistics. Soil Sci. Soc. Am. J., 59:1476-1487.

Hamilton III, E.W., M.S. Giovannini, S.A. Moses, J.S. Coleman, and S.J. McNaughton. 1998. Biomass and mineral element responses of a Serengeti short-grass species to nitrogen supply and defoliation: compensation requires a critical [N]. Oecologia 116: 407-418.

Handley, L.L. and J.A. Raven. 1992. The use of natural abundance of nitrogen isotope in plant physiology and ecology. Plant, Cell, and Environment 15: 965-985.

Handley, L.L. and C.M. Scrimgeour. 1997. Terrestrial plant ecology and ^{15}N natural abundance: the present limits to interpretation for uncultivated systems with original data from a Scottish old field. Advances in Ecol. Res. 27:133-212.

Havard-Duclos, B. 1967. Les plantes fourragères tropicales. Paris, G.-P. Maisonneuve and Larose. 397 p.

Hess, K. 1993. Rocky times in Rocky Mountain National Park. University Press of Colorado, Niwot.

Hillel, D. 1998. Environmental soil physics. Academic Press, London, pp. 771.

Hobbs, N.T. 1996. Modification of ecosystems by ungulates. J. Wildl. Manage. 60:695-713.

Hogberg, P. 1997. ^{15}N natural abundance in soil-plant systems. New Phytol. 137:179-203.

Holbrook, N.M., J.L. Whitebeck, and H.A. Mooney. 1995. Drought responses of neotropical dry forests. pp. 243-276. In: Bullock, S.H., H.A. Mooney, and E. Medina, (eds.) Seasonally dry tropical forests. Cambridge University Press, Cambridge.

Holland, E.A. and J.K. Detling. 1990. Plant response to herbivory and belowground nitrogen cycling. Ecology 71:1040-1049.

Holland, E.A. and Colleman, D.C. 1987. Litter placement effects on microbial and organic matter dynamics in an agroecosystem. Ecology 68: 425-433.

Holland, E.A., W.J. Parton, J.K. Detling, and L. Coppock. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. Am. Nat. 140: 685-706.

Hunt, H.W., J.W.B. Stewart, and C.V. Cole. 1983. A conceptual model for interactions among carbon, nitrogen, sulphur, and phosphorus in grasslands. pp. 303-325. In: B. Bolin and R.B. Cook (eds.) The major biogeochemical cycles and their interactions. John Wiley, New York.

Irons, J.G., M.W. Oswood, R.J. Stout, and C.M. Pringle. 1991. Latitudinal patterns in leaf-litter breakdown – is temperature really impostant? Freshwater Biology 32: 401-411.

Jaramillo, V.J. and R.L. Sanford. 1995. Nutrient cycling in tropical deciduous forests. pp 346-361. In: Bullock, S.H., H.A. Mooney, and E. Medina (eds.) Seasonally dry tropical forests. Cambridge University Press, Cambridge.

Kauffman J. B., R.L. Sanford, D.L. Cummings, I.H. Salcedo, and E.V.S.B. Sampaio. 1993. Biomass and nutrient dynamics associated with slash fires in neotropical dry forests. Ecology 74: 140-151.

Kay, C.E., and F.H. Wagner. 1994. Historical condition of woody vegetation on Yellowstone's northern range. pp. 151-169. In: D.G. Despain (ed.) Plants and their environments. National Park Service, Technical Report 93.

Kessler, J.J. 1992. The influence of karite (*Vitellaria paradoxa*) and nere (*Parkia biglobosa*) trees on sorghum production in Burkina Faso. Agrofor. Syst. 17: 97-118.

Khan, S.A., R.L Mulvaney, and P.D. Brooks. 1998. Diffusion methods for automated nitrogen-15 analysis using acidified disks. Soil Sci. Soc. Am. J. 62: 406-412.

Kiehl, K., P. Esselink, and J.P. Baker. 1997. Nutrient limitation and plant-species composition in temperate salt marshes. Oecologia 111: 325-330.

Koelland, K. 1994. Amino acid absorption by artic plants: implications for plant nutrition and nitrogen cycling. Ecology 75: 2373-2383.

Kolberg, R.L., B. Rouppet, D.G. Westfall, and G.A. Peterson. 1997. Evaluation of an in situ net soil nitrogen mineralization method in dryland agroecosystems. Soil Sci. Soc. Am. J. 61:504-508.

Larkins, K.F. 1997. Patterns of elk movement and distribution in and adjacent to the eastern boundary of Rocky Mountain National Park. Thesis, University of Nothern Colorado, Greeley.

Ledieu, J., P. de Ridder, P. de Clerk, and S. Dautrebande. 1986. A method of measuring soil moisture by time-domain reflectometry. Journal of Hydrology 88: 319-328.

Leprun, J.C. 1983. Relatório de fim de convênio de manejo e conservação do solo no nordeste brasileiro (1982-1983). SUDENE, Recife. 290 p.

Leprun, J.C. and F.B.R. Silva. 1995. Les degradations des sols en régions semi-arides au Brésil et en Afrique de l'Ouest. Compaison et conséquences. Suggestions sur leurs réhabilitations respectives. pp. 267-291. In: Pontanier, R., A. M'Hiri, N. Akrimi, J. Aronson, and E. Le Floc'h. L'homme peut-il refaire ce qu'il a defait? Paris, John Libbey Eurotext.

Lugo, A.E. and P.G. Murphy. 1986. Nutrient dynamics of a Puerto Rican subtropical dry forest. J. Trop. Ecol. 2: 55-72.

Lugo, A.E., J.S. Baron, T.P. Frost, T.W. Cundy, and P. Dittberner. 1999. Ecosystem processes and functioning. pp. 219-254 In: N.C. Johnson, A.J. Malk, W.T. Sexton, and R.C. Szaro (eds.) Ecological Stewardship: A common reference for ecosystem management, Vol. 1. Elsevier Science, New York.

Machado, I.C., L.M. Barros, and E.V.S.B. Sampaio. 1997. Phenology of caatinga species at Serra Talhada, PE, Northeastern Brazil. Biotropica 29:57-68.

Malavolta, E., T.H. Liem, and A.C.P.A. Primavesi. 1986. Exigências nutricionais das plantas forrageiras. pp. 31-76. In: Matto, H.B., J.C. Werner, T. Yamada, and E. Malavolta (eds.) Calagem e adubação de pastagens. Assoc. Bras. Para Pesquisa da Potassa e do Fosfato, Piracicaba, Sao Paulo.

Mazancourt, C. de, M. Loreau, and L. Abbadie. 1998. Grazing optimization and nutrient cycling: when do herbivores enhance plant production. Ecology 79:2242-2252.

McLaughlin, M.J., A.M. Alston, and J.K. Martin. (1988a) Phosphorus cycling in wheat-pasture rotations. I. The source of phosphorus taken up by wheat. Aust. J. Soil Res. 26: 323-331.

McLaughlin, M.J., A.M. Alston, and J.K. Martin. 1988c. Phosphorus cycling in wheat-pasture rotations. III. Organic phosphorus turnover and phosphorus cycling. Aust. J. Soil Res. 26: 343-355.

McLaughlin, M.J., A.M. Alston, and J.K. Martin. 1988b. Phosphorus cycling in wheat-pasture rotations. II. The role of the microbial biomass in phosphorus cycling. Aust. J. Soil Res. 26: 333-341.

McNaughton, S.J. 1985. The ecology of a grazing system: The Serengeti. Ecol. Monogr. 55: 259-294.

McNaughton, S.J. 1977. Diversity and Stability of ecological communities – comment on the role of empiricism in ecology. Am. Nat. 111:515-525.

McNaughton, S.J., R.W. Reuss, and S.W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. Bioscience 38:794-800.

Medina, E. 1995. Diversity of life forms of higher plants in neotropical dry forests. pp. 221-242. In: Bullock, S.H., H.A. Mooney, and E. Medina (eds.) Seasonally dry tropical forests. Cambridge University Press, Cambridge.

Menezes, R.S.C. and I.H. Salcedo. 1999. Influence of tree species on the herbaceous understory and soil chemical characteristics in a silvopastoral system in semi-arid Northeastern Brazil. Revista Brasileira de Ciência do Solo. In Press.

Menezes, R.S.C., E.TA. Elliott, D.W. Valentine, and S.A. Williams. 1999. Effects of herbivory and proximity to surface water on C and N biogeochemical cycles of elk winter ranges in Rocky Mountain National Park. J Range Manage, Submitted.

Michelsen, A., I.K. Schmidt, S. Jonasson, C. Quarmby, and D. Sleep. 1996. Leaf ^{15}N abundance of subartic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. Oecologia 105: 53-63.

Mizrahi, Y., A. Nerd, and P.S. Nobel. 1997. Cacti as crops. Horticultural Reviews 18: 291-320.

Murphy, J. and J.P. Riley. 1962. A modified simple solution method for the determination of phosphate in natural waters. Anal. Chim. Acta. 27: 31-36.

Myers, R.J.K., C.A. Palm, E. Cuevas, I.U.N. Gunatilleke, and M. Brossard. 1994. The synchronization of nutrient mineralization and plant nutrient demand. pp. 81-116. In: P.L. Woomer and M.J. Swift (eds.) The biological management of tropical soil fertility. TSBF and Sayce Publishing, UK.

Nadelhoffer, K.J., B.A. Emmett, P. Gundersen, O.J. Kjonaas, C.J. Koopmans, P. Scheleppi, A. Tietema, and R.F. Wright. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. Nature 398: 145-148.

Nadelhoffer, K.J. and B. Fry. 1994. Nitrogen isotope studies in forest ecosystems. pp. 22-44. In: Lajtha K, Michener RH (eds.) Stable isotopes in ecology and environmental science. Blackwell Scientific Publications, London.

Nadelhoffer, K.J., G. Shaver, B. Fry, A. Giblin, L. Johnson, and R. McKane. 1996. ^{15}N natural abundance and N use by tundra plants. Oecologia 107: 386-394.

Naiman, R.J., G. Pinay, C. Johnston, and J. Pastor. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. Ecology 75:905-921.

Naiman, R.J. and J.M. Melillo. 1984. Nitrogen budget of a sub-arctic stream altered by beaver (*Castor canadensis*). Oecologia 62:150-155.

Naiman, R.J., J.M. Melillo, and J.E. Hobbie. 1986. Ecosystem alteration of boreal forest stream by beaver (*Castor canadensis*). Ecology 67: 1254-1269.

Nandwa, S.M. and M.A. Bekunda. 1998. Research on nutrient flows and balances in West Africa: state-of-the-art. Agriculture, Ecosystems and Environment 71: 1-4.

Nasholm, T., A. Ekblad, A. Nordin, R. Giesler, M. Hogberg, and P. Hogberg. 1998. Boreal forest plants take up organic nitrogen. Nature 392: 914-916.

Norman, M.J.T., C.J. Pearson, and P.G.E. Searle. 1984. The ecology of tropical food crops. Cambridge University Press, Cambridge. 369 p.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25-51.

Oliveira, J.B.de, P.K.T. Jacomine, and M.N. Camargo. 1992. Classes gerais de solos do Brasil. FUNEP, Jaboticabal. 201 p.

Olsen, S.R. and L.E. Sommers. 1982. Phosphorus. pp. 403-430. In: Page, A.Ll, R.H. Miller, and D.R. Keeney (eds.) Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties, Agronomy Monograph no. 9, (2nd Edition). ASA-SSSA, Madison.

Padilha, J.A. 1994. Programa "Base zero" do estado da Paraíba. pp.470-493. Anais da Conferência Nacional de Desertificação, Fortaleza, 1994. Fundação Grupo Esquel Brasil, Brasília.

Paige, K.N. 1999. Regrowth following ungulate herbivory in *Ipomopsis aggregata*: geographic evidence for overcompensation. Oecologia 118: 316-323.

Pandeya, S.C. and H. Lieth. 1993. Ecology of Cenchrus grass complex. Kluwer Academic Publishers, Dordrecht. 234 p.

Parker, K.W. and S.C. Martin. 1952. The mesquite problem on southern Arizona ranges. U.S. Dep. Agr. Circ. No 908. 70 pp.

Pastor, J., and R.J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. Am. Nat. 139: 690-705.

Pastor, J., B. Dewey, R.J. Naiman, P.F. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Pak. Ecology 74: 467-480.

Pengelly, W.L. 1963. Thunder on the Yellowstone. Naturalist 14:18-25.

PNUD-FAO-IBAMA-SUDENE. 1993. Documentos e relatório final. I Reunião sobre o Desenvolvimento do Setor Florestal do Nordeste. PNUD-FAO-IBAMA-SUDENE, Recife.

Power, J.F. 1977. Nitrogen transformations in the grassland ecosystem. pp. 195-204. In: J.K. Marshall (ed.) The belowground ecosystem: a synthesis of plant-associated processes. Range Science Department, Science Series No. 26, Colorado State University, Fort Collins, CO, USA.

Power, J.F. 1994. Understanding the nutrient cycling process. Journal of Soil and Water Conservation 49 (2/suplemental): 16-23.

Reddy, S.J. 1983. Climatic classification: the semi-arid tropics and its environment - a review. Pesq. Agropec. Bras. 18:823-847.

Reij, C., P. Mulder, and L. Begemann. 1988. Water harvesting for plant production. (Technical Paper 91). The World Bank, Washington. 123 p.

Reijntjes, C., B. Haverkort, and A. Walters-Bayer. 1994. Agricultura para o futuro: uma introdução à agricultura sustentável e de baixos insumos externos. ES-PTA, Rio de Janeiro. 324p.

Reynolds, J.F., R.A. Virginia, and J.M. Cornelius. 1990. Resource island formation associated with desert shrubs, creosote bush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*) and its role in the stability of desert ecosystems: a simulation analysis. Suppl. Bull. Ecol. Soc. Am. 70(2):299-300.

Rhoades, C.C. 1995. Seasonal pattern of nitrogen mineralization and soil *moisture Faidherbia albida* (syn *Acacia albida*) in central Malawi. Agrof. Syst. 29:133-145.

Rhoades, C.C. 1997. Single tree influences on soil properties in agroforestry: lessons from natural forest and savanna ecosystems. Agrofor. Syst. 35: 71-94.

Rhoades, C.C., R.L. Sanford, and D.B. Clark. Gender dependent influences on soil phosphorus by the deciduous lowland tropical tree *Simarouba amara*. Biotropica, 26: 362-368, 1994.

Richards, J.H. and M.M. Caldwell. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia 73: 486-489.

Ritchie, M.E., D. Tilman, and J.M.H. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology 79: 165-177.

Roy, S. and J.S. Singh. 1995. Seasonal and spatial dynamics of plant-available N and P pools and N-mineralization in relation to fine roots in a dry tropical forest habitat. Soil Biol. Biochem. 27: 33-40.

Ruess, R.W. 1984. Nutrient movement and grazing - experimental effects of clipping and nitrogen source on nutrient uptake in *Kyllinga nervosa*. Oikos 43: 183-188.

Ruess, R.W., and S.J. McNaughton. 1987. Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. Oikos 49: 101-110.

Russele, M.P. 1992. Nitrogen cycle in pasture and range. J. Prod. Agric. 5:13-23.

Salcedo, I.H. and R.S.C. Menezes. 1999. Mineralização comparativa de nitrogênio do solo, *in situ*, sob pastagem artificial e sob estrato arbóreo, no semi-árido de Pernambuco. Congresso Bras. Ci. Solo, 27. Brasília, Resumos.

Salcedo, I.H., H. Tiessen, and E.V.S.B. Sampaio. 1997. Nutrient availability in soil samples from shifiting cultivation sites in the semi-arid Caatinga of NE Brazil. Agric. Ecosys. Environ. 65:177-186.

Sampaio, E.V.S.B. 1995. Overview of the Brazilian caatinga. pp 35-63. In: Bullock, S.H., H.A. Mooney, and E. Medina (eds.) Seasonally dry tropical forests. Cambridge University Press, Cambridge.

Sampaio, E.V.S.B. and I.H. Salcedo. 1997. Diretrizes para o manejo sustentável dos solos brasileiros: região semi-árida. In: Anais do Congresso Brasileiro de Ciencia do Solo, 26. Rio de Janeiro, RJ.

Sampaio, E.V.S.B., I.H. Salcedo, and F.B.R. Silva. 1995. Fertilidade dos solos do semi-árido. In: J.R. Pereira and C.M.B. de Faria (eds.) Fertilizantes: Insumo básico para a agricultura e combate à fome. EMBRAPA-CPATSA/SBCS. Petrolina, PE. 273 p.

Sampaio, E.V.S.B., A.C.D. Antonino, H. Tiessen, and I.H. Salcedo. 1997. Utilização de fertilizante nitrogenado (^{15}N) em cultura de subsistência no semiárido nordestino. pp.803-808. In: IV Encontro Nacional de Aplicações Nucleares, Poços de Caldas, Anais, vol. 2.

Sampaio, E.V.S.B., E.L. Araújo, I.H. Salcedo, and H. Tiessen. 1998. Regeneração da vegetação de caatinga após corte e queima, em Serra Talhada, PE. Pesq. Agropec. Brasil. 33: 621-632.

Sampaio, Y., E.V.S.B. Sampaio, and E. Bastos. 1987. Parâmetros para a determinação de prioridades de pesquisas agropecuárias no Nordeste semi-árido. Departamento de Economia -PIMES/UFPE, Recife. 224 p.

Sanchez, P.A. 1995. Science in agroforestry. Agrofor. Syst. 30:5-55.

SAS Institute. 1995. SAS User's Guide. Release 6.12. SAS Institute Inc., Cary, NC.

Schlesinger, W.H. 1997. Biogeochemistry: An analysis of global change. Academic Press, San Diego, USA.

Schomberg, H.H. and J.L. Steiner. 1999. Nutrient dynamics of crop residues decomposing on a fallow no-till soil surface. Soil Sci. Soc. Am. J. 63: 607-613.

Schulze, E.D., F.S. Chapin, G. Gebauer. 1994. Nitrogen nutrition and isotope differences among life forms at the nothern treeline of Alaska. Oecologia 100: 406-412.

Schuman, G.E., J.D. Reeder, J.T. Manley, R.H. Hart, and W.A. Manley. 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecol. Appl. 9: 65-71.

Sharpley, A.N. and S.J. Smith. 1989. Mineralization of phosphorus from soil incubated with surface-applied and incorporated crop residue. J. Environ. Qual. 18: 101-105.

Shearer, G. and D.H. Kohl. 1986. N_2-fixation in field settings: Estimations based on natural ^{15}N abundance. Australian J. of Plant Physiol. 13: 699-756.

Sibbesen, E. 1977. A simple ion-exchange procedure for extracting plant available elements from soil. Plant Soil 46: 665-669.

Silva Filho, J.C. de. 1988. Tecnologia agrícola para o semi-árido brasileiro. FUNDAJ, Editora Massangana, Recife. 102 p.

Silva, V.M., J.A. Araujo Filho, E.R. Leite, V.L.A. Pereira, and S.A. Ugiette. 1995. Manipulação da caatinga e seu efeito sobre parâmetros fitossociógicos e de produção, em Serra Talhada, Pernambuco. pp 17-21. In: Reuniao da Sociedade Brasileira de Zootecnia, Brasília, Anais. SBZ, Brasília, Brasil.

Silva, A.S. and E.R. Porto. 1982. Utilização e conservação dos recursos hídricos em áreas rurais do trópico semi-árido do Brasil. Tecnologias de baixo custo. EMBRAPA-CPATSA, Petrolina. Documentos 14. 128 p.

Silva, F.B.R., G.R. Riché, J.P. Tonneau, N.C. Souza Neto, L.T.L. Brito, R.C. Correia, A.C. Cavalcanti, F.H.B.B. Silva, A.B. Silva, J.C. Araújo Filho, and A.P. Leite. 1993. Zoneamento agroecológico do nordeste: diagnóstico do quadro natural e agrossocioeconômico. EMBRAPA - CPATSA/CNPS, Petrolina.

Singer, F.J., D.M. Swift, M.B. Coughenour, and J.D. Varley. 1998a. Thunder on the Yellowstone revisited: an assessment of management of native ungulates by natural regulation, 1968-1993. Wildlife Society Bulletin 26:375-390.

Singer, F.J., E.T. Elliott, M.B. Coughenour, J.M. Welker, D.W. Valentine, S.A. Williams, L.C. Zeigenfuss, K.P. Alstad, and R.S.C. Menezes. 1997. Large mammalian herbivores, plant interactions and ecosystem processes in five national parks. Second annual report to Biological Resources Division, USGS.

Singer, F.J., L. Mack, and R.G. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. J. Range Manag. 47: 435-443.

Singer, F.J., L.C. Zeigenfuss, R.G. Cates, and D.T. Barnett. 1998b. Elk, multiple factors, and persistence of *S. monticola* in national parks. Wildlife Society Bulletin, 26:419-428.

Singh, R.P. 1975. Biomass, nutrient, and productivity structure of a stand of dry deciduous forest of Varanasi. Trop. Ecol. 37: 104-109.

Singh, M., M.L. Arrawatia, and V.P. Tewari. 1998. Agroforestry for sustainable development in arid zones of Rajasthan. International Tree Crops Journal 9:203-212.

Snyder, J.D. and J.A. Trofymow. 1984. A rapid accurate wet oxidation diffusion procedure for determining organic and inorganic carbon in plant and soil analysis. Commun. in Soil Sci. and Plant Anal. 15:587-597.

Sterner, R.W. 1994. Elemental stoichiometry of species in ecosystems. pp. 240-252. In: C.G. Jones and J.H. Lawton (eds.) Linking species and ecosystems. Chapman and Hall, New York.

Stevens, D.R. and S. Christianson. 1980. Beaver populations on the East slope of Rocky Mountain National Park. Special Report to Rocky Mountain National Park, Estes Park, CO.

Stewart, J.W.B., C.V. Cole, and D.G. Maynard. 1983. Interactions of biogeochemical cycles in grassland ecosystems. pp. 247-268 In: B. Bolin and R.B. Cook (eds.) The major biogeochemical cycles and their interactions. John Wiley, New York.

Stohlgren, T.J., D. Binkley, G.W. Chong, M.A. Kalkhan, L.D. Schell, K.A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69: 25-46.

Strange, E.M., P.B. Moyle, and T.C. Foin. 1992. Interactions between stochastic and deterministic processes in stream fish community assembly. Environm. Biol. Fishes 36:1-15.

SUDENE. 1997. Região Nordeste em números. SUDENE, Recife. 62 p.

Sutherland, R.A., C. van Kessel, R.E. Farrel, and D.J. Pennock. 1993. Landscape-scale variations in plant and soil nitrogen-15 natural abundance. Soil Sci. Soc. Am. J. 57: 169-178.

Terwilliger, J. and J. Pastor. 1999. Small mammals, ectomycorrhizae, and conifer succession in beaver meadows. Oikos 85:83-94.

Thomas, R.L., R.W. Sheard, and J.R. Moyer. 1967. Comparisson of conventional and automated procedures for N, P and K analysis of plant material using a single digestion. Agron. J. 59:240-243.

Tiedemann, A.R. and J.O. Klemmedson. 1973. Effect of mesquite on physical and chemical properties of the soil. J. Range Manag. 26:27-29.

Tiessen, H., E. Cuevas, and P. Chacon. 1994. The role of soil organic matter in sustaining soil fertility. Nature 371:783-785.

Tiessen, H., I.H. Salcedo, and E.V.S.B. Sampaio. 1992. Nutrient and soil organic matter dynamics under shifting cultivation in semi-arid northeatern Brazil. Agriculture, Ecosystems and Environment, 38:139-151.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey.

Tilman, D. 1988. Plant strategies and the dynamic and structure of plant communities. Princeton University Press, Princeton, New Jersey.

Toft, N.L., S.J. McNaughton, and N.J. Geogiadis. 1987. Effects of water stress and simulated grazing on leaf elongation and water relations of an East African grass, *Eustachys paspaloides*. Aust. J. Plant Physiol. 14:211-226.

U.S.D.A. Snow Survey Office. 1995, 1996, and 1997. Snowpack data for Rocky Mountain National Park. National Resources Conservation Service. Lakewood, CO.

Virginia, R.A. and C.C. Delwiche. 1982. Natural N-15 abundance of presumed N-fixing and non-N-fixing plants from selected ecosystems. Oecologia 54: 317-325.

Vitousek, P.M., G. Shearer, and D.H. Kohl. 1989. Foliar ^{15}N abundance in Hawaiian rainforest: patterns and possible mechanisms. Oecologia 78: 383-388.

Vitousek, P.M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65: 285-298.

Welker, J.M., D.D. Briske,and R.W. Weaver. 1987. Nitrogen-15 partitioning within a three generation tiller sequence of the bunchgrass Schizachyrium scoparium: Response to selective defoliation. Oecologia 24: 330-334.

Welker, J.M., D.R. Gordon, K.J. Rice. 1991. Capture and allocation of nitrogen by *Quercus douglasii* seedlings in competition with annual and perennial grasses. Oecologia 87: 459-466.

Welker, J.M. and D.D. Briske. 1992. Clonal biology of the temperate caespitose graminoid *Schizachyrium scoparium*: A synthesis with reference to climate change. Oikos 56:357-363.

Welker, J.M. and J.W. Menke. 1990. The influence of simulated browsing on tissue water relations, growth and survival of *Quercus douglasii* (Hook and Arn.) seedlings under slow and rapid rates of soil drought. Funct. Ecol. 4:807-817.

Welker, J.M., E.J. Rykiel, D.D. Briske, and J.D. Goeschl. 1985. Carbon import among vegetative tillers within two bunchgrasses: Assessment with carbon-11 labeling. Oecologia 67:209-212.

Weltzin, J.F. and M.B. Coughenour. 1990. Savanna tree influence on understory vegetation and soil nutrients in northwetern Kenya. J. Veg. Sci. 1: 325-334.

West, N.E. 1981. Nutrient cycling in desert ecossystems. pp 301-324. In: Goodall, D.W. and R.A. Perry (eds.) Arid land ecossystems: Structure, function, and management. Cambridge Univ. Press, Cambridge, UK.

Wick, B., H. Tiessen, and R.S.C. Menezes. 1999. Land quality changes following the conversion of the natural vegetation into silvo-pastoral systems in semi-arid NE Brazil. Plant and Soil (submitted).

Wiens, J.A. 1977. On competition and variable environments. Am. Sci. 65:590-597.

Wijnen, H.J., R. van der Wal, and J.P. Bakker. 1999. The impact of herbivores on nitrogen mineralization rate: consequences for salt-marsh succession. Oecologia: 118: 225-231.

Wortmann, C.S. and C.K. Kaizzi. 1998. Nutrient balances and expected effects of alternative practices in farming systems of Uganda. Agriculture, Ecosystems and Environment 71: 115-129.

Young, A. 1989. Agroforestry for soil conservation. CAB International, Wallingford, UK. 276 p.