Revista Chilena de Historia Natural
60: 265-273, 1987

Herbivory in arid and semi-arid regions of Argentina

Herbivoría en regiones áridas y semiáridas de Argentina

ENRIQUE H. BUCHER

Centro de Zoología Aplicada, Casilla 122, Córdoba 5000, Argentina

ABSTRACT

Terrestrial herbivory in the Chaco, Monte and Patagonia natural regions of Argentina shows similar patterns to equivalent regions of North America, as well as distinctive features. Peculiarities include the near absence of native large herbivores, the high diversity and abundance of leaf-cuting ants, and a considerable number of plants showing adaptations against predation and for dispersion by large herbivores. All these features might be linked to evolutionary interactions with the diverse fauna of large herbivores which became extinct during the Pleistocene. Overgrazing from domestic ungulates in the Chaco has transformed the original parkland landscape provoking widespread encroachment of woody vegetation, the near extinction of grasslands and some of their largest herbivores, and an increment of medium-sized rodents, which, in turn, can keep the system in a new "disclimaxic" equilibrium. In the Monte and Patagonia the results of overgrazing on the natural vegetation have also been dramatic, although less spectacular in terms of landscape alteration. These characteristics suggest lines along which future research efforts could be focused.

Key words: Neotropical semi-arid regions, Chaco, Monte, Patagonia, savannas, herbivory, grazing effects, leaf-cutting ants.

RESUMEN

La herbivoría terrestre en las regiones naturales del Chaco, Monte y Patagonia de la Argentina muestra patrones similares con regiones equivalentes de Norte America, así como características peculiares. Estas últimas incluyen una marcada pobreza de grandes herbívoros, la gran abundancia y diversidad de hormigas cortadoras de hojas, y un considerable número de plantas que muestran adaptaciones contra la depredación y para la dispersión por grandes herbívoros. Todas estas características pueden ser vinculadas con la diversa fauna de grandes herbívoros que se extinguió durante el Pleistoceno. El sobrepastoreo por ungulados domésticos ha transformado el paisaje de parque original del Chaco, a través de una invasión generalizada de la vegetación leñosa, la casi extinción de los pastizales y de algunos de sus grandes herbívoros, y un incremento de roedores de tamaño mediano, los cuales pueden mantener el sistema en un nuevo equilibrio "disclimáxico". En el Monte y Patagonia los efectos del sobrepastoreo han sido también intensos, aunque menos espectaculares en términos de alteración del paisaje. Estas características sugieren líneas a lo largo de las cuales pueden orientarse futuros esfuerzos de investigación.

Palabras clave: Regiones semiáridas neotropicales, Chaco, Monte, Patagonia, sabanas, herbivoría, efectos del pastoreo, hormigas cortadoras de hojas.

INTRODUCTION

There is evidence that the dynamics, stability and resilience of semi-arid ecosystems (particularly savannas) can be significantly affected by herbivores. The wild herbivores of natural savannas, both vertebrates and invertebrates, may often play an important role in shaping plant survival strategies and plant community composition, structure, and function. Moreover, these ecosystems are usually very sensitive to grazing by domestic ungulates which may be associated with other forms of human intervention (fires, cutting of trees and shrubs) (Walker & Noy-Meir 1982).

As I will show later, there are indications that all these factors play a relevant role in the vast semi-arid ecosystems of Argentina. Unfortunately, and because of the limited information available, only very general aspects of the subject can be analyzed. Consequently, I have decided to focus this paper on two aspects which may provide useful starting points: a) the species composition of the herbivore and primary producer guilds, and b) the impact produced by introduced domestic livestock. By analyzing the similarities and pecularities of these aspects when compared with equivalent biomes of North America and other regions

(Received 12 January 1987. Accepted 30 October 1987.)

of the world, important questions may develop that help to provide new perspectives for future research.

The philosophy behind this review is management, as well as theory. I believe in the need of filling the gap between ecological theory and management, particularly in South America. It may benefit both sides, since we can expect that much of the development of Ecology as a science in the post-descriptive phase will arise from the study of man-managed ecosystems.

ECOLOGICAL OUTLINE

My comments will refer to the following semi-arid lowland natural regions of Argentina: western Chaco, Monte, and Patagonia (Cabrera & Willink 1973) (Fig. 1). I am not including the high-altitude Puna desert, because of the scarcity of available information. Ecologically similar arid regions of North America are Sinaloa, Sonora, and the Great Basin, respectively (Mares *et al.* 1985).

The western Chaco extends in northern Argentina from the 700 mm rainfall contact line with the central Chaco up to the foot of the western Sierras; and from the Pilcomayo river in the north to central Argentina in the south. Annual rainfall decreases to 450 mm in the west, and is concentrated in the summer months. The dry season lasts from six to seven months. The predominant vegetation is a medium to tall xerophyllous subtropical forest (Bucher 1982).

The Monte is a phytogeographical province oriented as a relatively narrow north-south belt along the eastern side of the Andes. To the south it broadens and extends to the Atlantic coast in the provinces of Rio Negro and Chubut. Rains average less than 200 mm a year in most localities and never exceed 600 mm; evaporation exceeds rainfall throughout the region. The rain falls in spring and summer. The predominant vegetation is a xerophytic scrubland, dominated by species of creosote bush or jarilla (*Larrea* spp.), associated with a number of other xerophytic or aphyllous shrubs (Mares *et al.* 1985).

The Patagonian steppe is limited to the east and south by the Atlantic Ocean. On the west it changes quite abruptly to *Nothofagus* forest. To the north it borders with the Monte. Its climate is the result of the rain-shadow effect of the southern Andes in elevating and drying the moist westerly winds from the Pacific. Consequently the region not only is devoid of rains but is also subjected to a steady westerly wind of fair intensity that has a tremendous drying effect. The scarce rainfall is fairly well distributed throughout the year with a slight increase during winter months. Summers are cold and winters relatively mild (Soriano 1983).

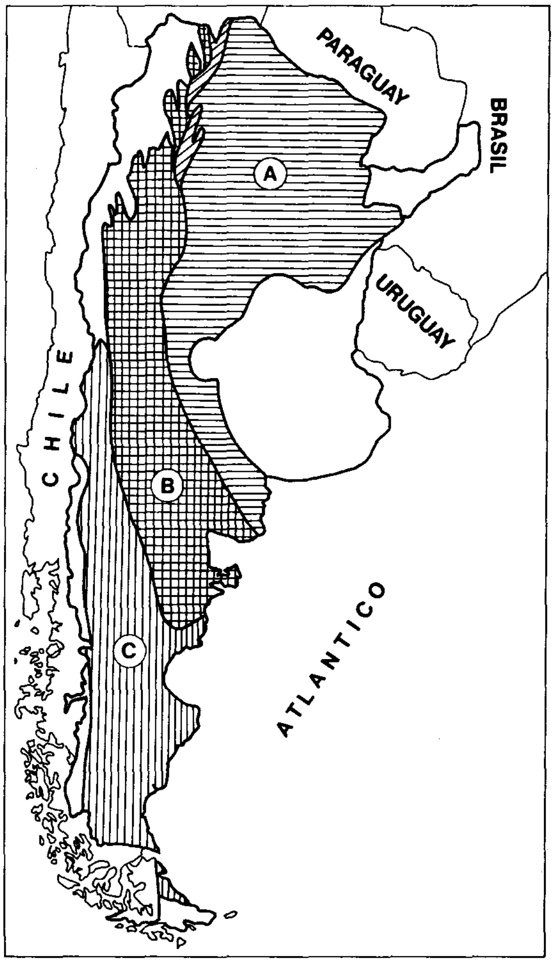

Fig. 1: The arid and semi-arid regions of Argentina here described. A, Chaco; B, Monte; C, Patagonia (after Cabrera & Willink 1973).

Las regiones áridas y semiáridas de Argentina aquí descritas (según Cabrera & Willink 1973).

THE PLANT-HERBIVORE COMPONENT

Here I want to focus on those elements that seem to give a distinctiveness to the

Argentine semi-deserts, particularly when compared with equivalent areas of North America. Details of species composition and adaptations can be found in Orians & Solbrig (1977a), Bucher (1980, 1982), Soriano (1983), and Mares *et al.* (1985).

The herbivores

A tentative list of distinctive features that characterize the herbivore fauna can be summarized as follows:

a) Scarcity of large herbivores:

In the Chaco, the large-sized herbivore assemblage before European colonization was very limited in species diversity, comprising only the guanaco (*Lama guanicoe*), two species of deer (*Blastocerus dichotomus* and *Ozotocerus bezoarticus*), and the tapir (*Tapirus terrestris*) (Bucher 1980) (Fig. 2). In the Monte and Patagonia it was even more reduced, with the guanaco as the only representative.

This impoverished fauna contrasts with the diversity of groups composing the large herbivore category during the Pleistocene. At that time present-day herbivores may have co-existed with several other species of Glyptodontidae, Megatheriidae, Mylodontidae, Machrauchenidae, Toxodontidae, Gomphoteridae, and Equiidae, including grazers, browsers, and folivores (Patterson & Pascual 1972) (Fig. 2). They certainly exerted important selective pressures on the vegetation, and some of its anti-herbivore traits might have been molded at that time through evolutionary interaction with this megafauna, as has been proposed by Janzen & Martin (1981) in the case of fruit dispersal in the tropics (see below).

b) The abundance and diversity of leaf cutting ants:

In contrast to their limited representation in North America, leaf-cutting ants are extremely abundant and diverse in the Chaco, and to a lesser extent in the Monte (Kusnezov 1963, Bucher 1980). In the Chaco, the dominant species belong to the genera *Atta* and *Acromyrmex*. *Atta vollenweideri* and *Atta saltensis* are abundant and occur mainly in open habitats, their large nests being very conspicuous. *Acromyrmex* spp. have smaller nests and are found predominantly under forest cover. Leaf-cutting ants are considered among the main herbivores in the Chaco, and in some areas are regarded as the main competitor of domestic cattle (Bucher 1980, Robinson & Fowler 1982), although generally their foraging niches only overlap to a limited degree (E.H. Bucher & C. Saravia Toledo, unpublished data).

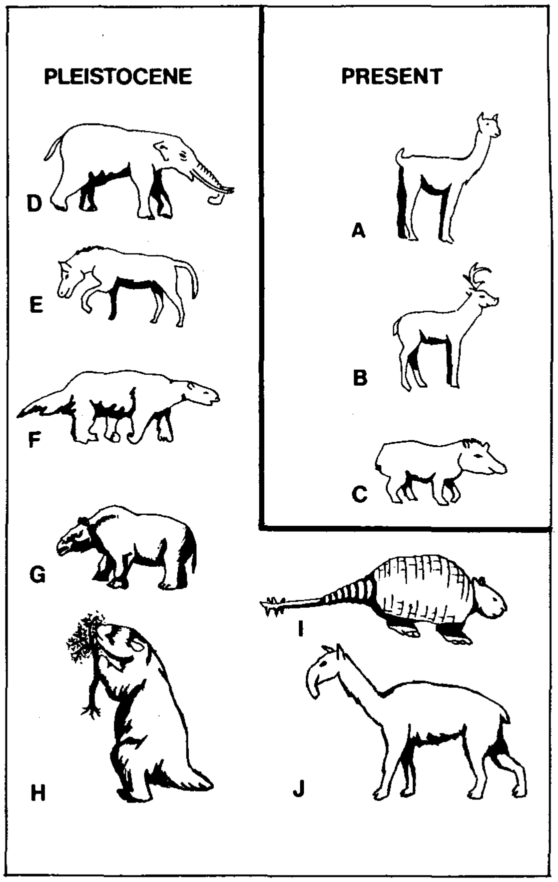

Fig. 2: The components of the large herbivore category in the Chaco, including the extinct Pleistocene groups that possibly occurred in the región. A, Camelidae; B, Cervidae; C, Tapiridae; D, Gomphotheriidae; E, Equidae; F, Mylodontidae; G, Toxodontidae; H, Megatheriidae; I, Glyptodontidae; and J, Macraucheniidae.

Los componentes de la categoría de grandes herbívoros del Chaco, incluyendo los grupos pleistocénicos extintos que probablemente ocurrieron en la región.

The consumer potential of grass-cutting ants has been estimated from year-long measurements of grass intake by foragers, and by grass productivity in enclosures. *Atta vollenweideri* forages, on a dry weight basis, 201 to 217 kg/colony/year, equalling 87 to 911 kg/ha/yr, depending upon colony density. Productivity studies suggest that *A. vollenweideri* may forage up to 972 kg/ha/yr (= 231 kg/colony/year) (Robinson & Fowler 1982).

Leaf-cutting ants differentially select vegetation for fungal substrate. Both chemical and physical parameters of the vegetation influence plant acceptability by the ants. New or tender growth of many plant species is preferentially harvested, and significant preferences are present for different species of plants (Fowler & Stiles 1980). The ants attack specific trees for generally very short periods of time with the distribution of the attacks being highly skewed toward few foraging episodes; plants flushing new leaves, or flowering being those at higher risk (Cherret 1972, Lewis 1975, Rockwood 1976). This may indicate an increasing degree of relative unpalatability of the individual plant attacked. Also, colony densities and success rate of colony establishment are higher in agricultural situations, in which crop-plant species are assumed to have a lower level of secondary chemical defenses (Fowler & Stiles 1980). Different species of leaf-cutting ants occurring in the same area tend to be clearly isolated from one another either by food or micro-habitat preferences (Bucher & Montenegro 1974).

We can speculate that leaf-cutting ants might have diversified by occupying the "empty niches" left after the extinction of the rich herbivore vertebrate fauna of the Pleistocene. There is evidence indicating that the Attini may have evolved precisely in the South American subtropics (Fowler 1983).

Besides their activity as plant predators, leaf-cutting ants also affect vegetation through soil alteration. It has been estimated that about 1.1 tons/ha/year of soil are turned up annually by *Atta vollenweideri* in the Chaco, altering microtopography and soil physical and chemical properties which in turn affect nutrient availability, plant growth, and succession (Bucher 1980).

c) The existence of irregular episodes of severe defoliation by insects:

The migratory locust *Schistocerca americana* had been an extremely abundant herbivore in Chaco and Monte until recently, when it was brought under control by spraying the oviposition areas. Its periodical but irregular invasions reached the whole Chaco and the northern Monte (Bucher 1980). No equivalent herbivore occurs in semi-arid North America.

Irregular occurrence of massive defoliation due to population outbreaks of leaf-eating lepidopterans are frequent in the Chaco. Although it is not a specifically Chaco-related phenomenon, its importance in some years may be outstanding (Bucher 1980).

The plants

Floras of North and South America show little similarity at the specific level, but a great deal of similarity at the supraspecific one. This is particularly true for the Monte, where the disjunct *Larrea tridentata* and *Larrea divaricata* are the most common, abundant and characteristic species in the Sonoran Desert and over large areas of the Monte, respectively. Other common genera include *Prosopis, Acacia, Celtis, Opuntia,* and *Jathropa* (Mares *et al.* 1985).

Whether the tacit assumption of coevolutionary relationships between herbivores and vegetation does apply to the South American semi-arid regions has scarcely been addressed. It could be expected that herbivores affect vegetation structure and composition by their effects on particular plants and plant populations which may in turn adopt a variety of defensive strategies. These defences may include protective plant structures, chemicals, and a variety of life history and phenological adaptations which may serve to increase fitness and reduce predation (Wagner this volume).

Structural repellents such as thorns, spines or a "twiggy" growth form are widespread, especially in the Chaco. They seem to characterize those woody plants with highly nutritious foliage, such as cacti and legumes. Thorny cacti (particulary *Opuntia quimilo*) usually increase in heavily grazed areas, and tend to develop a pure stand belt around houses where goat and cattle grazing is more intense. Its fruits are also eaten and dispersed by cattle (Morello & Saravia Toledo 1959). Legumes such as *Acacia,* and *Prosopis* are usually spiniscent, and also tend to increase under strong grazing pressure, their fruits are also dispersed by cattle (Morello & Saravia Toledo 1959). As a general pattern, *Prosopis* trees with a basically Chacoan distribution (such as *P. kuntzei, P. vinal, P. vinalillo, P. rajasiana, P. sericantha,* and *P. elata*) show larger thorns than those species whose distribution is rather peripheral to the Chaco, and basically associated with the Monte, such as *P. alba* and *P. nigra* (Burkart 1952). Outstanding examples of thorniness are *P. vinal* and particularly *P. kuntzei,* a stem-photosynthesizing tree with reduced foliage (Fig. 3). In both species thorns are formidable (they may reach more than 30 cm) and cover the whole adult tree, particularly in *P. kuntzei.* This contrasts with many of the heavily thorny African acacias which lose their thorns when they reach canopy heights of five meters –the upper level of browsing by giraffes (Cummings 1982). Such defences seem excessive when related to the modest set of contemporary Chacoan herbivores.

Another case of marked spiniscency are the bottle trees *Chorisia speciosa* and *C. insignis* (Bombacaceae), whose expanded, water-storing trunks are covered with strong conical spines of about 4 cm long. Their pith is avidly eaten by cattle when the spiny bark is removed (pers. obs.).

Again, one may speculate about the possibility that the wide occurrence and intensity of thorniness in the Chaco –certainly at the same level as that which occurs in the African savannas– could indicate a remaining "anachronistic" adaptation against the extinct pleistocene megafauna. This megafauna must have exerted strong selective pressures, particularly in the Chaco, since according to what is seen in Africa today large herbivores should have been more abundant there than in the drier Monte (McNaughton & Georgiadis 1986). Large spines covering the whole tree (as in the case of *Prosopis kuntzei*) may have proven necessary against a huge *Megatherium,* "a browser pulling branches to their mouth while standing semi-erect, supported by its massive tail" (Martin & Klein 1984). It is pertinent to note that while the Neotropical and African acacias have abundant and large thorns, these are absent from Australian acacias which have not been subjected to depredations by large browsing herbivores. In the case of cacti,

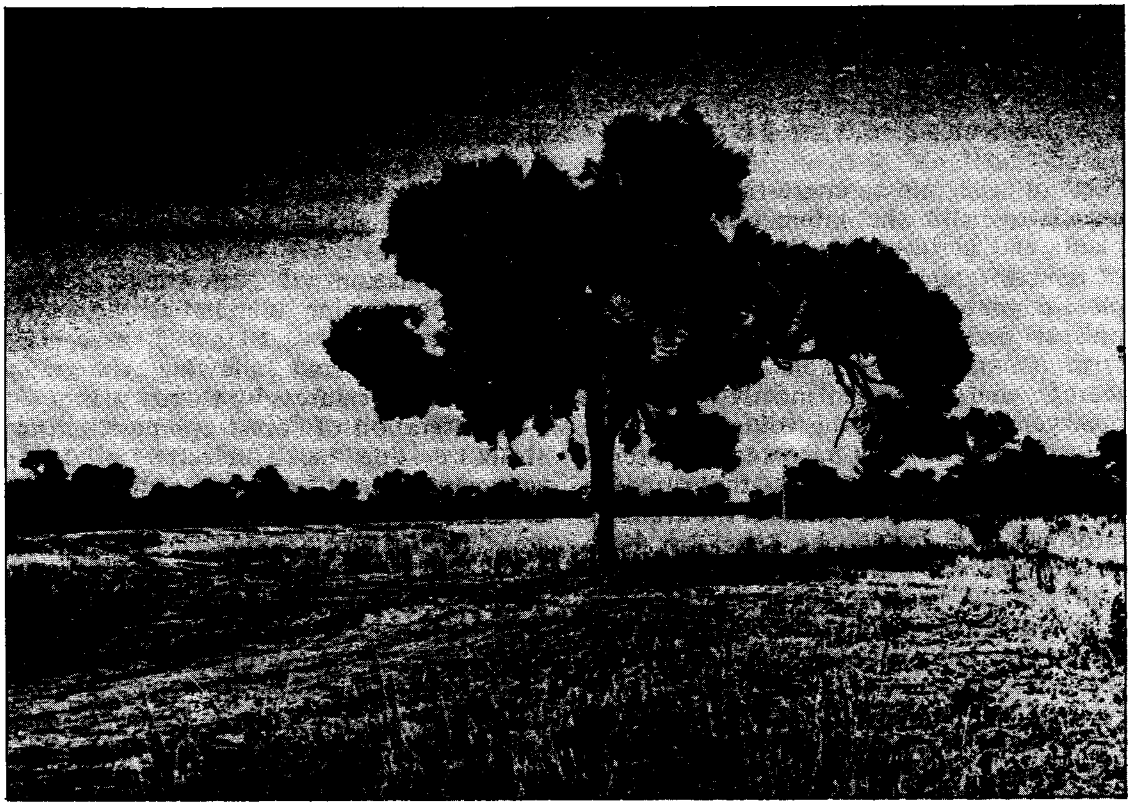

Fig. 3: Prosopis kuntzei, a typical Chaco tree with reduced foliage and completely covered with large thorns. Perhaps an "anachronistic" adaptation against large herbivores such as the extinct *Megatherium*?

Prosopis kuntzei, un típico árbol chaqueño con follaje reducido y cubierto con grandes espinas. ¿Tal vez una adaptación "anacrónica" contra grandes herbívoros como el extinto *Megatherium*?

Opuntia spininess has also been linked to evolutionary interaction with the extinct megafauna by Janzen (1986) in semi-arid Mexico.

Secondary plant compounds provide an important defence against herbivory (see Wagner this volume). Unfortunately, the influence of secondary compounds on the diet of herbivores does not appear to have been adequately explored in this part of the World. Although the available information is scarce, it appears that chemical defences in plants are widespread in the arid regions of Argentina (Orians & Solbrig 1977 b). These authors did not find evidence that basic chemical defences of various plant life forms differ in the Monte and Sonoran deserts. The same is likely to apply to the Chaco since the Monte has its primary floristic connection with the Chaco (Mares *et al.* 1985).

Ant-plant associations have been found in the Chaco, where several species of ants are known to live in cavities within the large thorns of *Prosopis vinal.* However, it is not clear whether there is any kind of mutualistic anti-herbivore defence behavior from the ants (Kusnezov 1963).

PLANT-HERBIVORE INTERACTIONS

One of the most interesting problems associated with the interactions between plants and herbivores is the understanding of how different grazing patterns influence plant-community composition. Most of our present understanding comes from long-term studies undertaken for empirical reasons, and connected mostly with range management (Wagner this volume).

In the case of the Chaco and other semi-arid regions of Argentina, the situation is even more critical in terms of the available information, because the topic has been little explored within a systematic and experimental framework. Nevertheless, the relatively recent colonization by Europeans has provided us with important information about the response of these particular ecosystems to alterations induced by man, and particularly to the massive introduction of domestic herbivores, which can be considered as a megascale experiment. The following analysis of its results may provide us with a useful overview that can reveal general patterns and provide important management tools.

The western Chaco before the European immigration

In the Chaco, the primitive landscape, just before the European immigrants arrived, was a parkland with patches of hardwood intermingled with fire-maintained grasslands. This mosaic of vegetation was kept stable by periodic fires produced by lightning or by the Indians, who were skilled in managing fire. Fires were fuelled by a considerable biomass of grass accumulated during the preceeding wet season. Few woody plants are adapted to resist repeated exposure to fire, and even fewer are favored by it. In contrast, grasslands respond positively to burning, through rapid germination, vegetative growth and reproduction. Thus the succession of fires prevented woodlands from encroaching on the grassland (Bucher 1982). Such "fire-climax" is common to many other semi-arid savannas throughout the World (Walker & Noy-Meyr 1982).

The impact of domestic herbivores

The European colonization of western Chaco and the Monte resulted in a dramatic alteration of the ecosystem, mainly as a consequence of the introduction of domestic herbivores (particularly cattle and goats), through the following processes (Bucher 1982):

1. Elimination of "fire-climax" grasslands. Overgrazing eliminated the necessary fuel (dry grass biomass), preventing periodic fires and allowing the rapid invasion of open areas by woody plants.

2. Alteration of forest composition and structure, due to: a) selective predation on many forest species seedlings. This effect was dramatic on some dominant trees, particularly *Schinopsis* spp., resulting in the near elimination of this valuable species even in areas where no timber activity had been carried out. b) Dramatic expansion of some unpalatable woody species, in many cases through endozooic dispersion by cattle (particularly *Prosopis* and *Acacia* spp.). The "large herbivore syndrome" (presence of thorns, unpalatability, endozooic dispersion) was widespread in many plant species of the Chaco forest, suggesting once again some degree of evolution under large-herbivore grazing pressure. c) Selective felling of

valuable timber species, which prevented seed production and further altered the habitat structure.

All of these factors contributed to the change of forests and woodlands into dense thorny thickets which at present extend monotonously over large areas. The processes described above have been repeated with minor variations and on different time-scales throughout the world (Schofield & Bucher 1986). The only major difference in the Chaco has been the relatively recent time-scale (less than sixty years in many cases) and relatively good historical documentation (see Morello & Saravia Toledo 1959, Bucher 1982).

The drastic and generalized elimination of suitable habitats, coupled with competition with domestic herbivores, and an increasing hunting pressure greatly affected the native fauna. The main grassland herbivore species declined rapidly (deer, guanaco, and the greater Rhea *Rhea americana*), and concurrently, a marked increase of two medium-sized rodents, the salt-desert cavy (*Pediolagus salinicola*) and the vizcacha (*Lagostomus maximus*), has followed in many areas (Bucher 1980). This increase parallels the well known relationship between rodent and rabbit abundance and rangeland deterioration in the western United States and elsewhere (Wagner, this volume).

There is evidence indicating that once a critical density of the above mentioned rodents is reached, they are capable of keeping the vegetation in a depleted condition, even after the removal of cattle and goats. Either of the two species can prevent the survival of the dominant tree seedlings and consequently, drastically affect the vegetation structure. The recovery of grassland and forest condition from this new stable equilibrium usually requires the removal of these rodents provided that the soil seed stock is not depleted (C. Saravia Toledo, pers. com.).

The resulting dense thornscrub which today covers millions of hectares in the western Chaco bears little resemblance to the original landscape, even in areas considered as "virgin forest" in terms of timber exploitation. The Chaco is a good example of how more subtle factors –such as differential grazing– may result in dramatic alterations in the plant community composition (see Wagner, this volume). For many unaware ecologists, the large areas of apparently little-disturbed forests found today in the western Chaco may appear attractive as "near climax" site studies, although in reality they are the result of profound alterations induced by man's activities.

On the other hand, shifts in vegetative composition induced by grazing may prove an important management tool when applied to wildlife management. Wildlife is usually very sensitive to habitat alteration, and by moving forward or backward along the successional framework through quite simple manipulations, considerable changes in populations of wild animals can be expected (Wagner, this volume).

In the Monte and Patagonian desert, the results of overgrazing on the natural vegetation have also been dramatic, although less spectacular in terms of physiognomy alteration. Grasses are very susceptible in the Monte, and have been reduced to near extinction in large portions of the region (Bragadin 1959).

In Patagonia, as in the Monte, the guanaco (*Lama guanicoe*) was the largest native herbivore before the introduction of sheep. Overgrazing by sheep resulted in the following changes (Soriano 1983): a) reduction in plant diversity; b) reduction in shrub density; c) reduction in the relationship of live to dead tissue in the dominant grasses; d) increment of ephemeroids; and e) reduction in frequency of occurrence of large denuded patches.

Compared with the system before sheep introduction, present productivity is lower in periods of average or above-average precipitation, and equal or perhaps higher during extreme drought periods. This is so because both ephemeroids and shrubs are strictly periodic in their annual cycle. They may contribute very little or no biomass if their growth period coincides with very dry conditions. On the other hand, the opportunistic bunch grasses do not become completely dormant during the annual cycle, even when the driest conditions occur (Soriano 1983).

COMMENTS AND CONCLUSIONS

This review, although limited in scope because of the scant information available, suggests that herbivory in the semi-arid regions of Argentina shows similarities with equivalent ecosystems of North

America, as well as some distinctive features. Peculiarities include the near absence of native large herbivores, the high diversity and abundance of leaf-cutting ants, and a number of plant species apparently showing anachronistic adaptations against predation and for dispersion by large herbivores. All of these features might be linked to evolutionary interactions with the extinct Tertiary fauna.

Herbivory (overgrazing) by domestic herbivores in the Chaco has provoked encroachment of woody vegetation, the near disappearance of grasslands, extinction of some large herbivores, and an increment of medium-sized rodents. These rodents, in turn, are able to keep the system in a new, more or less stable "disclimaxic" equilibrium. In the Monte and Patagonia the results of overgrazing on the natural vegetation have also been dramatic, although less spectacular in terms of landscape alteration.

These features that characterize herbivory in arid and semi-arid regions of South America indicate lines along which future research efforts could be focussed. Specifically, the following aspects seem worth exploring.

A detailed comparative analysis of the plant-herbivore interactions and species composition among equivalent semi-arid regions of North and South America, as well as other equivalent areas of the World, may provide new insights into the influence of history and environment in shaping trophic links at the plant-herbivore level. Of particular interest would be a comparison between the Chaco and other dry savannas of Africa and Australia, which show very different plant and herbivore assemblages under similar climatic conditions. Within this context, it should be particularly worthwhile to start studies directed toward determining the role of the extinct megafauna in the evolutionary history of the New World subtropical arid land vegetation. The past 10,000 years are a kind of continental-scale experiment which deserves special attention, especially if we consider that the interaction of the large herbivores with the herbaceous plants is much stronger in semi-arid ecosystems than in lowland Neotropical forests (Janzen 1986).

Anatomical (particularly spines), chemical, and life-story strategies developed by plants, as well as the corresponding herbivores' counter-adaptations, should be studied in detail. Of particular interest is the role played by leaf cutting ants, especially in the semi-arid Chaco ecosystem. Do the ants compete among them and with other vertebrate and invertebrate herbivores? How comparable are plant chemical defences against vertebrates with those aimed at the ants', garden fungi?

The possible existence of secondary stable equilibrium points, such as those that result from the increase of medium sized rodents in overgrazed areas, deserves further research. Whether they are stable in the long term, and to what extent, are important questions which may contribute to our understanding of the stability and resilience of semi-arid ecosystems.

Finally, it should be stressed that interactions between trophic levels cannot be studied in isolation. Second order interactions are nearly always present, sometimes acting in opposite directions, as is the case of those herbivores that feed on leaves of a given plant and at the same time disperse its fruits and seeds. When seeking for "ultimate" explanations of ecological interactions, we badly need information at the species level, where all of the ecological interactions affect simultaneously the evolution of adaptive traits. Without that, generalizations may result rather vague and partial, lacking predictive value. The fundamental question of whether communities possess emergent properties needs a lot of detailed, time consuming, autecological research.

ACKNOWLEDGMENTS

I am indebted to Carlos Saravia Toledo for his invitation to work at Campos del Norte ranch in J.V. González, Salta, Argentina, giving me the opportunity to learn from his enormous experience and knowledge of the Chaco; and for his comments on the manuscript. The study was supported by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), most recently through PID 3908102; and by the Natural Resources Program, Secretaría de Ciencia y Tecnología (SECYT) of Argentina.

LITERATURE CITED

BRAGADIN E (1959) Las pasturas en la región de los Llanos (provincia de La Rioja). Revista Agronómica del Noroeste Argentino 3: 289-340.

BUCHER EH (1980) Ecología de la fauna chaqueña. Una revisión. Ecosur (Argentina) 7: 111-159.

BUCHER EH (1982) Chaco and Caatinga-South American arid savannas, woodlands and thickets. In Huntley B & B Walker (Eds.) Ecology of Tropical Savannas: 47-49. Springer Verlag, Berlin.

BUCHER EH & RA MONTENEGRO (1974) Hábitos forrajeros de cuatro hormigas simpátridas del género *Acromyrmex* (Hymenoptera, Formicidae). Ecologia (Argentina) 2: 47-53.

BURKART A (1952) Las Leguminosas Argentinas. Acme Agency, Buenos Aires.

CABRERA A & A WILLINK (1973) Biogeografía de America Latina. OEA, Serie Biología N^{o}. 13, Washington, D.C.

CHERRET JM (1972) Chemical aspects of plant attack by leaf-cutting ants. In Harbourne J (Ed.) Phytochemical Ecology: 235-257. Academic Press, New York, New York.

CUMMINGS DHM (1982) The influence of large herbivores on savanna structure in Africa. In Huntley B & B Walker (Eds.) Ecology of Tropical Savannas: 217-245, Springer Verlag, Berlin.

FOWLER H (1983) Latitudinal gradients and diversity of the leaf-cutting ants (*Atta* and *Acromyrmex*) (Hymenoptera-Formicidae). Revista de Biología Tropical 31: 213-116.

FOWLER H & EW STILES (1980) Conservative resource management by leaf-cutting ants? The role of foraging, territories and trails, and environmental patchiness. Sociobiology 5: 25-41.

JANZEN DH 1986. Chihuahuan desert nopaleras: defaunated big mammal vegetation. Annual Review of Ecology and Systematics 17: 595-636.

JANZEN DH & PS MARTIN (1981) Neotropical anachronisms: the fruits the Gomphoteres ate. Science 215: 19-27.

KUSNEZOV N (1963) Zoogeografía de las hormigas en Sudamerica. Acta Zoologica Lilloana (Argentina) 19: 25-186.

LEWIS T (1975) Colony size, density and distribution of the leaf-cutting ant *Acromyrmex octospinosus* (Formicidae, Attini) in fields. Transactions of the Royal Entomological Society of London 127: 51-64.

MARES MA, J MORELLO & G GOLDSTEIN (1985) The Monte desert and other subtropical semiarid biomes of Argentina, with comments on their relation to North American arid areas. In Evenari M, I Noy-Meir & DW Goodall (Eds.) Hot deserts and arid shrublands: 203-237. Elsevier, Amsterdam.

MARTIN P & R KLEIN (Eds.) (1984) Quaternary extinctions. University of Arizona Press, Phoenix, Arizona.

MCNAUGHTON SJ & NJ GEORGIADIS (1986) Ecology of african grazing and browsing mammals. Annual Review of Ecology and Sistematics 17: 39-65.

MORELLO J & C SARAVIA TOLEDO (1959) El bosque chaqueño I. Paisaje primitivo, paisaje natural y paisaje cultural en el oriente de Salta. Revista Agronomica del Noroeste Argentino 3: 5-81.

ORIANS G & O SOLBRIG (Eds.) (1977 a) Convergent evolution in warm deserts. Dowden, Hutchinson & Ross, Inc. Stroudsburg, Pennsylvania.

ORIANS G & O SOLBRIG (1977 b) Degree of convergence of ecosystem characteristics. In Orians G & O Solbrig (Eds.) Convergent evolution in warm deserts: 225-255. Dowden, Hutchinson & Ross, Ine. Stroudsburg, Pennsylvania.

PATTERSON B & R PASCUAL (1972) The fossil mammal fauna of South America. In Keast A, F Erk & B Glass (Eds.) Evolution, mammals, and the southern continents: 247-309. State University of New York Press, Albany, New York.

ROBINSON SW & HG FOWLER (1982) Foraging and pest potential of paraguayan grass-cutting ants (*Atta* and *Acromyrmex*) to the cattle industry. Zeitschrift fur angewandte Entomologie 93: 42-54.

ROCKWOOD LL (1976) Plant selection and foraging patterns in two species of leaf-cutting ants (*Atta*). Ecology 57: 48-61.

SCHOFIELD CJ & EH BUCHER (1986) Industrial contributions to desertification in South America. Trends in Ecology and Evolution 1: 78-80.

SORIANO A (1983) Deserts and semi-deserts of Patagonia. In West NE (Ed.) Temperate Deserts and Semi-deserts: 423-459. Elsevier, Amsterdam.

WALKER B & I NOY-MEIR (1982) Aspects of the stability and resilience of savanna ecosystems. In Huntley B & B Walker (Eds.) Ecology of Tropical Savannas: 556-590. Springer Verlag, Berlin.