

istic species are — among the grasses — *Schizachyrium tenerum*, *Agenium villosum* and *Trachypogon montufari* — and among the broad-leaved herbs — *Gomphrena celosioides*, *Mitracarpus megapotamicus*, *Euphorbia papillosa* and *E. selloi*.

Very frequent graminoids in the communities considered by Rosengurtt (1944) on the deep soils of Palleros, in addition to the four grasses mentioned above, are (Gallinal et al., 1938):

<i>Andropogon ternatus</i>	<i>Paspalum plicatulum</i>
<i>Sporobolus indicus</i>	<i>Briza subaristata</i>
<i>Panicum sabulorum</i>	<i>Bothriochloa saccharoides</i>
<i>Panicum decipiens</i>	<i>Setaria geniculata</i>
<i>Rottboellia selloana</i>	<i>Juncus imbricatus</i>
<i>Melica brasiliana</i>	<i>Eryngium paniculatum</i>

Gnaphalium spicatum (a broad-leaved herb belonging to the Asteraceae) and the introduced grasses *Aira caryophyllea*, *Briza minor* and *Vulpia bromoides* are also common. Legumes are well represented in these grasslands by species of the genera:

<i>Adesmia</i>	<i>Medicago</i>	<i>Stylosanthes</i>
<i>Arachis</i>	<i>Mimosa</i>	<i>Trifolium</i>
<i>Desmodium</i>	<i>Phaseolus</i>	<i>Vicia</i>
<i>Lupinus</i>		

North of the Vacacai and Ibicuí rivers, the grasslands have been much modified, both structurally and floristically. Overgrazing has changed them into a low and discontinuous sward, with foliage cover not exceeding 60%, floristically poor, and dominated by *Paspalum notatum* ("grama forquilha"), with scattered tussocks of *Aristida pallens* ("barba de node") (Martinez-Crovetto, 1965; DPP, 1973). In this region, the vegetation on the knolls in areas of lateritic soils is dominated by the four important grasses listed above. Associated grasses include *Aristida jubata*, *Elyonurus muticus*, *Hypogynium virgatum*, *Axonopus suffultus* and *Eragrostis airoides* (Fernandez et al., 1983).

In some habitats, tall-grass formations of *Erianthus trinitii* grow over a turf of *Axonopus compressus*, *Paspalum notatum* and *P. plicatulum*. *Piptochaetium stipoides* and *Sporobolus aeneus* are also present.

In the humid soils of valleys, tall-grass communities of *Paspalum quadrifarium* prevail. Associated species include the grasses *Rottboellia selloana*, *Eriochloa punctata*, *Eragrostis bahiensis*, *Stipa phil-*

ippii and *Phalaris platensis*. The important broad-leaved herbs include *Eryngium echinatum*, *Sisyrinchium* sp. and *Verbena litoralis*.

Areas subject to extended flooding on the west side of Río Uruguay support a grassland known as "malezal", with pedestalled bunches (Stoddart et al., 1975), where *Andropogon lateralis* prevails together with several other grasses (*Panicum milioides*, *Paspalum* spp., *Luziola* spp., *Leersia hexandra* and *Sorghastrum agrostoides*) and some broad-leaved herbs (*Cuphea glutinosa*, *Hydrocotyle* sp. and *Polygala molluginifolia*) (Van der Sluijs, 1971). Other tall-grass communities are dominated by characteristic species of the northern campos — *Paspalum exaltatum* (Gallinal et al., 1938), *Paspalum haumani* or *P. rufum*. However, *Panicum prionitis*, a tall grass present in permanently wet sites, is much more abundant to the west, in the Chaco region.

Open woodlands composed of *Acacia* spp., *Scutia buxifolia*, *Schinus* spp. and *Eugenia* spp., occur in some hilly areas of the northern campos. *Syagrus yatay*, a palm, grows in more or less open woodland in the campos of eastern Uruguay in the eastern part of Entre Ríos Province, and in the southern part of Misiones Province.

STRUCTURE AND FUNCTION¹

This description of vegetation from the functional viewpoint will focus exclusively on the grasslands of the flooding pampa, also known as the Salado river basin. In this region frequent flooding and drought have determined that most of this area remains as rangelands, a condition unlike much of the rest of the pampas.

Grasslands of the flooding pampa were lightly grazed for millennia until the arrival of Europeans in the 16th century. They modified these grasslands with the introduction of domestic herbivores and probably the frequent use of fire. No relict grasslands are known in the flooding pampa. Experiments aimed at assessing the effects of grazing upon the structure and function of grasslands were based on the comparison between grazed areas and exclosures 4 to 6 years old.

¹By O.E. Sala.

Phenology

The grasslands of the flooding pampa are composed of a large number of species which do not share a common phenological pattern. Only during June and July are no reproductive phenophases recorded in the whole community (León and Bertiller, 1982). During the rest of the year, species in vegetative stages occur together with others that are in bloom or fruit. Expanding leaves and new tillers are present throughout the year. Within a population of a perennial species, and even within the same individual, different phenophases occur at the same time.

Consequently, phenological patterns in these grasslands contrast with those of grasslands with a fairly well-defined growing season (French and Sauer, 1974). Availability of water or temperature level are frequently determining factors. In most natural grasslands, the occurrence of a very dry or very cold period determines a definite beginning and end of the growing season. Therefore, phenological phases proceed regularly and rapidly during a short period of the year, and with small differences in time among species.

Primary production

Above-ground primary production. Studies of biomass dynamics and aerial net primary productivity have shown that the growing season is not well defined in these grasslands. Sala et al. (1981a) found that green biomass did not vary significantly during 1975 in ungrazed areas (Fig. 19.16). The maximum green standing crop was 222 g m^{-2} , in early summer, and the minimum value was 155 g m^{-2} . Other authors have reported similar values for the same site in previous years. Fonseca et al. (1976) estimated maximum green standing crop to be 210 g m^{-2} and 117 g m^{-2} , for ungrazed and grazed areas respectively, during 1972. Ares and Trabucco (1976), using a double sampling technique (Wilm et al., 1944), reported a lower value (155 g m^{-2}) for this ungrazed area during the same year.

Above-ground net primary productivity (NPP) was estimated by summation of positive increments in green biomass by species plus two correction factors for senescence and decay (Sala et al., 1981a). The annual above-ground production for

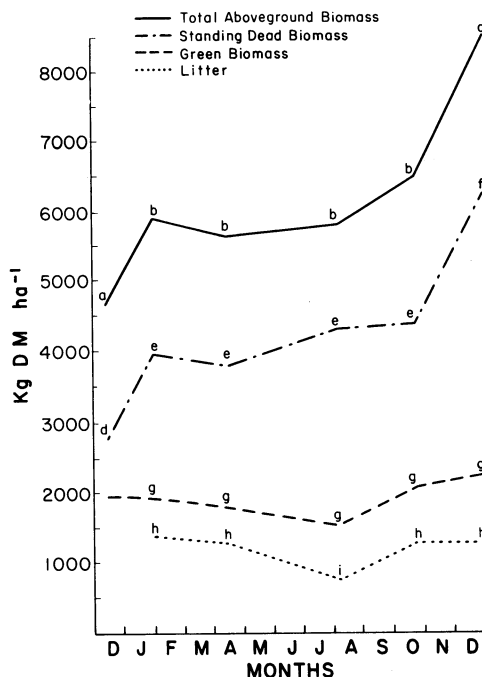


Fig. 19.16. Total above-ground, standing-dead, green and litter biomass for each of six harvests during 1975 in Pila (Province of Buenos Aires). Data were collected in a 4-year old enclosure. Within any curve, the same letter above two or more points indicates that the values are not significantly different at the 5% level of probability. [From Sala et al. (1981a).]

1975 was 532 g m^{-2} of dry matter, which corresponded to $1.46 \text{ g m}^{-2} \text{ d}^{-1}$ (Fig. 19.16).

Grasslands of the flooding pampa fit into Group 6 of Lauenroth's (1979) classification, which had an average annual above-ground production of 525 g m^{-2} , a value very similar to that reported for the flooding pampa. Lauenroth's Group 6 is characterized by the lack of a significant drought period at any time during the year. Lauenroth used climate diagrams (Walter, 1968) in his analysis of patterns of primary production in grassland on a world-wide basis, combining them into groups by means of a hierarchical clustering algorithm. Climate diagrams for most sites in the flooding pampa suggest that the grasslands of the entire area fit into this same group (see Azul in Fig. 2.10). These diagrams are based on long-term averages which mask the frequent occurrence of droughts. Sala et al. (1981b) reported low values for soil water potential ($-4 \text{ MPa} = \text{pF } 4.6$) in the uppermost soil horizon during prolonged periods in summer.

The grasslands of the flooding pampa are similar to those of the North American tall-grass prairie (Chapter 12) which is one of the best known grassland regions of Lauenroth's Group 6. Walter (1967) made a similar comparison, noting the marked similarities between the climate diagrams of Buenos Aires and Oklahoma City. A thorough review by Risser et al. (1981) of above-ground NPP in tall-grass prairie showed large variability in the data among years and an annual mean above-ground NPP of 567 g m^{-2} , which also is quite close to the estimate for the flooding pampa in 1975.

Productivity had a clear seasonal pattern, in contrast to the small temporal changes in green standing crop. The estimates of Sala et al. (1981a) indicated that maximum productivity occurred during spring and early summer, when it reached a rate of $3.1 \text{ g m}^{-2} \text{ d}^{-1}$ (Fig. 19.16). During this season soil water is still readily available (Sala et al., 1981b) and temperatures apparently do not limit carbon assimilation. A minimum productivity rate of $0.33 \text{ g m}^{-2} \text{ d}^{-1}$ was recorded during fall and early winter (Fig. 19.16).

The species of this grassland fall into two groups in respect to the time of year during which productivity is concentrated. Cool-season species have a productivity peak in late winter and early spring, whereas warm-season species concentrate their productivity in summer and fall. Spring above-ground NPP was accounted for by a few cool-season species, such as *Briza subaristata*, *Carex phalaroides* and *Danthonia montevidensis*. In contrast, during summer and fall total above-ground NPP was distributed among a larger number of species, each of them accounting for a small fraction of the total (Sala et al., 1981a).

In an attempt to assess the production capabilities of each species independently of its initial biomass, an efficiency index similar to that developed by Briggs et al. (1920), the relative productivity rate (RPR), was devised. The specific RPR is equal to the productivity of a given species per unit of average biomass for the period under consideration (Fig. 19.17). Species within the cool-season or warm-season groups shared a common pattern of phenology and productivity, and they had similar values of maximum RPR. It is likely that they also share a common photosynthetic pathway. Warm-season species, such as *Bothriochloa*

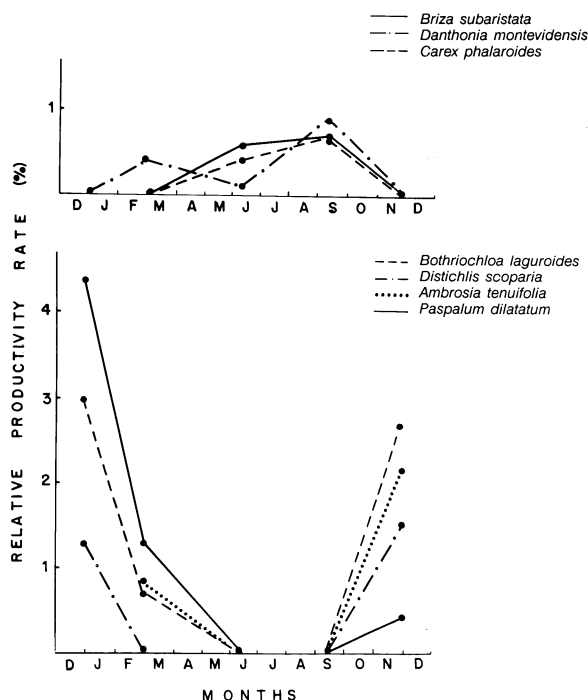


Fig. 19.17. Relative productivity rates of cool-season species (upper) and warm-season species (lower) for the upland community of the flooding pampa during 1975. [From Sala et al. (1981a).]

la laguroides and *Paspalum dilatatum*, had higher values of RPR than cool-season species. These are considered as C_4 species. Information on the photosynthetic pathway is not available for other warm-season species, but several species of the same genera in other grasslands do possess the C_4 pathway (Smith and Brown, 1973; Waller and Lewis, 1979).

Under-ground primary production. Although the study of under-ground processes has been neglected frequently in grasslands, they must be considered in functional analysis, for several reasons. Firstly, a larger fraction of the energy captured in photosynthesis is routed to under-ground than to above-ground compartments (Coleman et al., 1976; Sims et al., 1978); secondly, most of the nutrient circulation processes occur under ground (Clark, 1977; Woodmansee et al., 1981); and, finally, the largest proportion of nutrients and energy flows through under-ground decomposers and consumers (Woodmansee et al., 1978).

Study of under-ground biomass in this grassland was undertaken by extracting soil cores, and separating roots from soil by washing on a sieve (Soriano et al., 1977). Mean total under-ground biomass during 1975 in an ungrazed grassland was 1956 g m^{-2} , with a seasonal range between 2183 and 1660 g m^{-2} (Fig. 19.18). These values are higher than those reported for the North American tall-grass prairie (which range from 680 to 1900 g m^{-2}) (Sims et al., 1978; Risser et al., 1981).

The root/shoot ratio in the ungrazed area of grassland is 2.6, based on a comparison of the maximum biomass (green plus dead shoots) in the canopy (Fig. 19.16) with the above values for under-ground parts. This is a value characteristic of warmer and more humid grasslands, which generally range between 2 and 6. Cooler and drier sites have higher ratios, between 6 and 13 (Sims et al., 1978).

The following description of the vertical distribution of plant biomass in the soil is based on data for ungrazed grassland in the autumn of 1975 (Soriano et al., 1977). Under-ground biomass rapidly decreased with depth (Fig. 19.19), a power function being adequate to describe the relationship between depth and root biomass. More than 65% is concentrated in the uppermost 10 cm of soil and approximately 85% above a depth of 30 cm. The remaining 15% is located between 30 and 70 cm. This distribution pattern is similar to

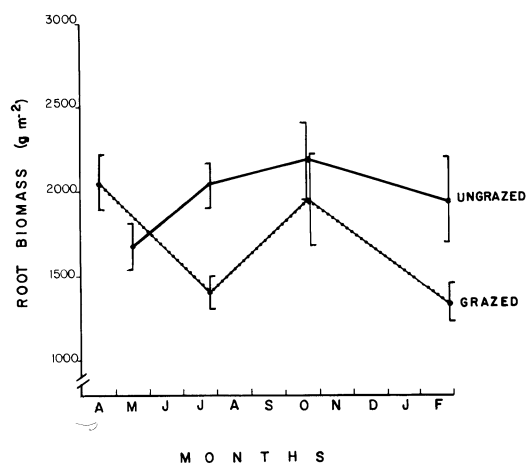


Fig. 19.18. A comparison of biomass of under-ground plant parts in grazed and ungrazed grassland at different times during 1975. Each point represents the mean of nine replications and vertical bars represent ± 1 S.E. [From Soriano et al. (1977).]

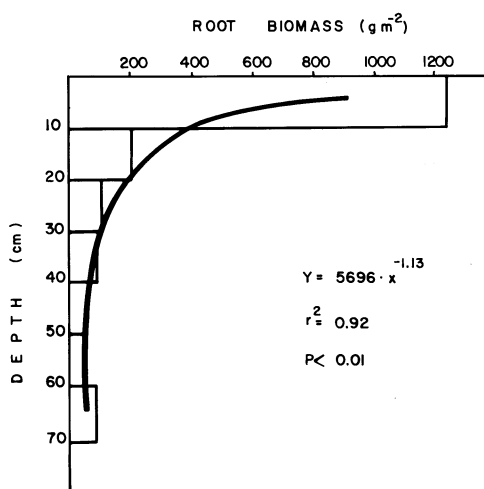


Fig. 19.19. Vertical distribution of under-ground plant biomass during the autumn of 1975 and a power function which fitted the data. Each data-point represents the mean of nine replications. [From Soriano et al. (1977).]

that of most temperate subhumid grasslands (Sims and Singh, 1978a). A very few roots occur below a depth of 70 cm, perhaps because of the presence of an impervious B horizon.

Biomass data were used to estimate under-ground NPP in the grassland of the flooding pampa by summing positive increases in total under-ground biomass between successive dates. Under-ground NPP in ungrazed grassland was estimated to be $496 \text{ g m}^{-2} \text{ yr}^{-1}$, only 17% lower than above-ground productivity. The under-ground/above-ground productivity ratio was 0.9 — considerably lower than the root/shoot ratio of 2.6 — suggesting that the turnover rate in the under-ground system is slower than above the soil surface.

Turnover rates for this grassland were calculated by dividing production by peak biomass, following the method suggested by Dahlman and Kucera (1965). By this approach, the annual turnover rate for the under-ground system was 0.23, which appears to be similar to that reported (25% per annum) for the tall-grass prairie in the U.S.A. by Risser et al. (1981). Above-ground turnover rate was 24% per annum if calculated using peak total above-ground biomass in the denominator or 62% per annum if using peak green biomass. The first approach makes the rate comparable with the under-ground rate, whereas the second one makes

it comparable with above-ground turnover rates calculated for other systems. Regardless of the method chosen, shoot material turns over faster than root material. Above-ground turnover rates faster than 100% per annum have been reported also for the tall-grass prairie (Risser et al., 1981).

The seasonal pattern of under-ground plant biomass in grazed grassland was somewhat different from that in the ungrazed site (Fig. 19.18). In the ungrazed site, no significant differences were shown in total root biomass during the year, although the highest values were obtained in spring. In the grazed treatment, differences in root biomass among seasons were larger than in the ungrazed site, but only the spring peak was significantly different from the others. Exclusion of ungulates from the grassland increased the annual mean total root biomass from 1688 to 1964 g m⁻². Although the biomass was higher in the ungrazed treatment, net root production was lower — 496 g as compared to 623 g m⁻² yr⁻¹. Consequently, under-ground turnover rates were higher in the grazed site (31 vs. 23% per annum).

Sims et al. (1978) concluded, from an analysis of the effect of grazing in ten different grasslands of North America, that under-ground plant biomass increased in cooler sites, but was either unaffected or slightly reduced by grazing in warmer sites. The flooding pampa had a response similar to warmer sites, since total under-ground biomass decreased as a result of grazing.

Plant community structure

The structure of vegetation is the result of adaptation to the environment by the component species and their influence on abiotic conditions. The environment has an important role in shaping plant community structure, and structure is an important determinant of ecosystem functioning. Structure provides constraints to ecosystem processes, which in turn affect structure. Among the effects of grazing by domesticated herbivores, particularly of heavy grazing, is the resultant change in floristic composition and in growth-form composition. Such range improvement practices as burning or use of selective herbicides are directed towards modifying plant community structure.

Comparison of the leaf-area profile, in grazed and ungrazed grassland, has been used in the

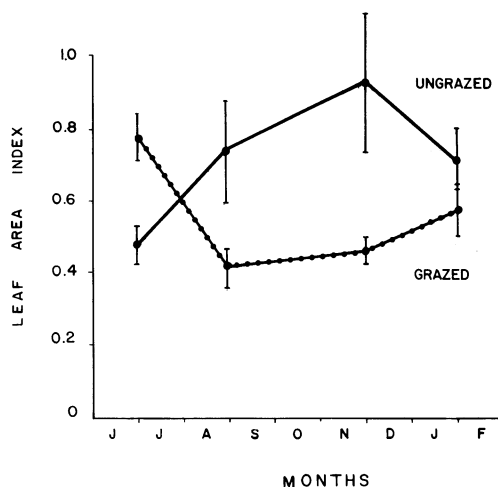


Fig. 19.20. Green-leaf-area index at four times of the year, in grazed and ungrazed areas. Each data-point is the mean of five replications. [From Sala et al. (1986).]

flooding pampa as a means of evaluating the effect of grazing on canopy structure (Sala et al., 1986). Measurements were made for each of seven horizontal layers at four different times during the year, using an electronic leaf-area meter. Total green-leaf-area index (LAI) in the ungrazed treatment ranged between 0.9 and 0.5, while in the grazed area it ranged between 0.8 and 0.4 (Fig. 19.20). Annual average LAI increased only 30% after 4 years of protection. The seasonal pattern of total LAI in the ungrazed area was similar to the patterns for aerial net productivity rate and total green biomass (Fig. 19.16). Values reached a maximum in spring and a minimum during autumn. There was a marked effect on the distribution of leaves in the profile. Most of the green material, in the grazed treatment, was concentrated in the 5-cm layer above the soil surface. However, in the ungrazed site, leaf area was relatively evenly distributed to a height of 40 cm (Fig. 19.21).

Knight (1973) also found a minimal effect of grazing pressure by livestock upon total LAI for the short-grass steppe in the U.S.A. His measurements attained a maximum of 0.5, which is lower than the value for the flooding pampa, and was made in an area with a much shorter growing season and in a drier climate.

Maximum LAI values recorded here are much lower than those reported for field crops. For

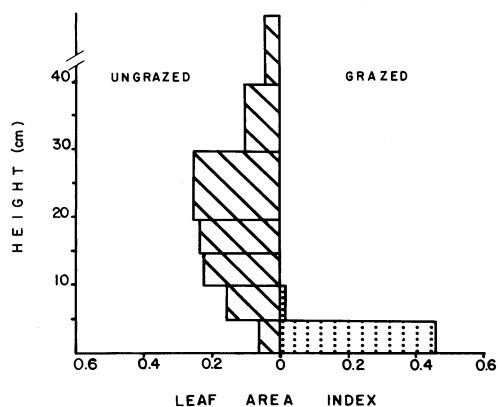


Fig. 19.21. Green-leaf-area index for various layers within the canopy of ungrazed and grazed grassland during spring. Each data-point is the mean of five replications. [From Sala et al. (1986).]

example, wheat growing in a site climatically similar to the flooding pampa, but receiving energy subsidies standard for an agroecosystem, attained a maximum LAI of 4 (Puckridge, 1971). However, annual mean LAI was similar in both systems, because the wheat cycle was shorter, lasting only 100 days.

Grazed and ungrazed versions of this grassland were compared also in terms of basal cover and horizontal distribution of plants (Sala et al., 1986). Basal cover, estimated by means of the line-intercept method (Phillips, 1959), ranged between 20 and 30% at different times of the year, and no significant differences were observed between the grazed and ungrazed treatments. However, grazing did affect horizontal distribution of plants. Mean distance between individuals was 2.9 cm ($SE \pm 0.4$ cm) in the grazed area and 4.4 cm ($SE \pm 0.9$ cm) in the ungrazed treatment. This increased density under grazing was the result of the large tussocks (of ungrazed grassland) dividing into a larger number of smaller plants. This resulted in a more even distribution of leaves on the horizontal plane in the grazed area.

Large tussocks characteristic of the ungrazed treatment changed the quality of light transmitted through the canopy. Deregibus et al. (1985) found that the red/far-red (R/FR) ratio of the light reaching the soil surface was drastically reduced. Above the canopy the R/FR ratio was 1.2, whereas below the canopy R/FR was 0.6 on average during the day. This degree of change in light quality was

found to be sufficient to reduce the tillering rate of *Lolium multiflorum* plants in the laboratory (Deregibus et al., 1983).

The reduction in size of bunches and the changes in light quality occurred as changes took place in floristic composition. During the first 4 years after exclusion of large ungulates, relative basal cover of the major grass species (*Briza subaristata*, *Danthonia montevidensis*, *Sporobolus indicus* and *Stipa neesiana*) increased from 43% ($SE \pm 15\%$) to 97% ($SE \pm 2\%$). In contrast, broad-leaved herbs and annuals, which accounted, respectively, for 30% ($SE \pm 12\%$) and 22% ($SE \pm 0.7\%$) of basal cover in the grazed area, had disappeared in the enclosure. Most of the broad-leaved herbs (*Eclipta bellidioides*, *Gamochaeta* sp., *Leontodon taraxacoides*, *Mentha pulegium*, *Phyla canescens* and *Plantago* sp.) have a prostrate habit. The annuals included grasses (*Briza minor*, *Lolium multiflorum* and *Vulpia dertonensis*) and broad-leaved herbs (*Linum usitatissimum* and *Lythrum hyssopifolia*).

Species diversity was greater in the grazed area. The Shannon and Wiener index (Legendre and Legendre, 1983, p. 83) was 3.0 in the ungrazed and 3.7 in the grazed areas (Sala et al., 1986). Total number of species was greater in the grazed area, since it possessed all the species of the ungrazed area plus several exotic species. Most of these adventives are cool-season species originating in the Mediterranean region. Higher diversity in grazed areas than in enclosures located in similar sites was also reported for the grasslands of the Serengeti (McNaughton, 1979). The changes in floristic composition and size of tussocks that took place in the enclosure give some indication of the nature of pristine grassland in this region. Apparently, grazing opened new microhabitats which were rapidly occupied by invaders.

Energy flow

A simplified energy-flow diagram for ungrazed grassland in the flooding pampa was constructed by utilizing information on the dynamics of above-ground and under-ground biomass (Fig. 19.22). Biomass data were converted into energy units using mean values (16.7 and 19.7 kJ g^{-1} for shoots and under-ground parts, respectively) suggested by Sims and Singh (1978b). This diagram was constructed using the symbolism proposed by H.T.

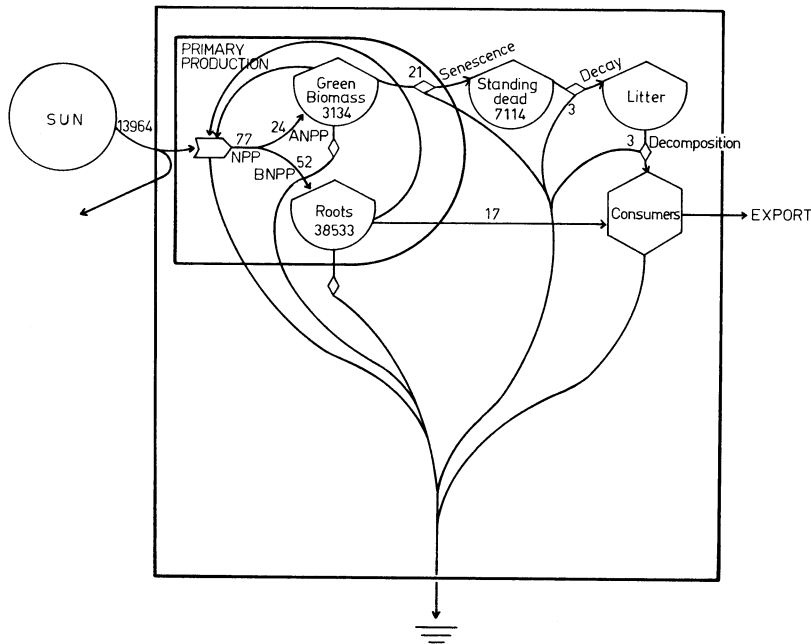


Fig. 19.22. Diagram of energy flow for the ungrazed treatment in the grassland of the flooding pampa. The circle indicates a source of energy from outside the system. The bullet indicates processes involved in producing high-quality energy from a dilute source. The pointed block is used to show the interaction of two or more types of energy required for processes. The water tank symbol indicates storage of energy within the system. The hexagonal symbol indicates that inputs are consumed and transformed into high-quality outputs. The arrows pointing downward symbolize loss of degraded energy. Flow rates are annual averages in $\text{kJ m}^{-2} \text{d}^{-1}$, and numbers in storage tanks are annual means of standing-crop energy in kJ m^{-2} .

Odum (1972). Values in the diagram are annual means for rates of processes such as productivity, or annual means of state variables, such as green biomass. The diagram is not intended as an exhaustive representation of the average status of all the compartments and of the multiple relationships among them, but presents in a synthetic manner some of the data already reported. The diagram includes a single source of energy, the sun, which supplies energy for primary production. Energy is stored, as biomass, in various compartments. Energy is lost by respiration flow to "heat sinks". Energy from four biomass storage boxes flows to consumers and decomposers collectively (E.P. Odum, 1971). Comparison of input and output flows of the biomass storages indicated that, after 4 years of protection from grazing, green biomass and litter compartments were close to a steady state, and surplus energy accumulated rapidly in the above-ground standing-dead material and in total under-ground plant biomass.

The information obtained in these studies of

responses of grassland to exclusion of grazing by livestock can be used to develop a hypothesis concerning the nature of the grassland prior to exploitation by European colonists. The hypothesis states that, originally, the major attributes of these grasslands were subject to cyclical changes. A constructive phase would exhibit trends similar to those observed throughout the 4 years of enclosure described above: an increase in size and reduction in density of tussocks; an accumulation of standing-dead material; a decrease in abundance of species with horizontally oriented leaves, and an increase in those with erect leaves; and changes in the quality of light passing through the canopy. This constructive phase would end with a disturbance, a pulse, which might be due to fire, grazing, drought or flooding. Afterwards a new constructive phase would begin.

Fire would be an endogenous pulse, since accumulation of standing-dead material during the constructive phase would increase the probability of occurrence of fire. Grazing and flood pulses

would be exogenous, since the probability of their occurrence is independent of the developmental stage.

Fences and water holes were developed by graziers of European origin, who introduced sheep and cattle and, apparently, increased grazing pressure. At present, cattle graze year-around and stocking rate changes little throughout the year. The system is maintained in a state of low variability and low standing crop, and fire has been suppressed. Pulses have been eliminated and cyclical succession has been halted. Conditions have become more stable, since most attributes change less through time than in the pulsed system. In contrast, the original pulsed system would be more resilient (Walker et al., 1981).

Holling (1973) contrasted resilience with local stability near an equilibrium. Stability is related to resistance to small disturbances. Resilience emphasizes the existence of more than one domain of attraction and the maintenance of global structure, despite variability. The modified system would seem to be much more sensitive to errors in management and to exogenous events. It is conceivable that the present system could change to a completely different mode of behaviour after a major disturbance from drought, flooding or overgrazing. Furthermore, some of the less productive units which make up the mosaic of communities in the flooding pampa (León, 1975) could have resulted from a particular event, or a combination of several events, acting upon a system which had slowly lost resilience as a result of managerial actions.

Response to water stress

The grasslands of the flooding pampa are subjected periodically to flooding and drought. Floods occur almost every year, although their duration varies widely (Ameghino, 1886; Langmann, 1959). Small floods occur very frequently, mainly during early spring (Paruelo and Sala, 1990). They usually last only a fortnight and cover the grasslands with only 5 to 10 cm of water. In contrast, large floods, which last several months, are rare. Analysis of 40 years of records did not show any season in which they are most likely to occur. Paruelo and Sala (1990) hypothesized that both types of floods are the result of different mechanisms. Conditions

during summer are usually very dry, with the soil water potential in the uppermost 15 cm of soil being as low as -4 MPa ($= pF$ 4.6) (Fig. 19.23).

Two main groups of grasses can be distinguished on the basis of their response to flooding and drought (Sala et al., 1981b). The response of each species coincides with its behaviour in respect to phenology and productivity. The cool-season species generally have lower values of leaf water potential than the warm-season species. This difference was observed from dawn to dusk, but was most evident at noon (Fig. 19.24). Differences between these two groups of species occurred throughout the year, but were exaggerated in spring during flooding. Following flooding, cool-season species showed symptoms of severe water deficit, whereas warm-season species had the highest leaf water potential of the year (Fig. 19.24). The mechanisms for this differential response are unknown. One does not even know if it is due to physiological differences between species or is only

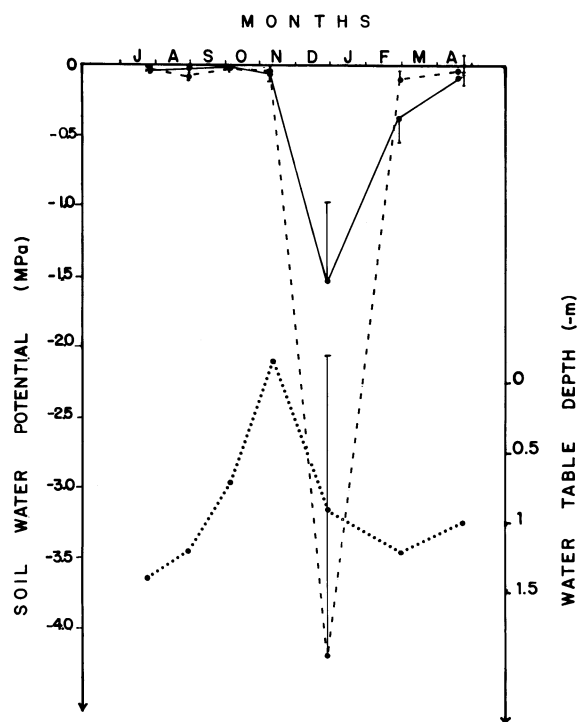


Fig. 19.23. Dynamics of soil water potential during 1977-78, at depths of 5 cm and 15 cm. Each data-point is the mean of nine replications and vertical bars represent ± 1 S.E. Changes in depth of the water table during the year are also illustrated.

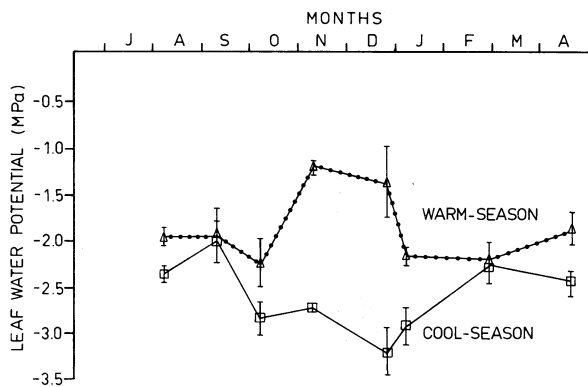


Fig. 19.24. Noon leaf water potential for cool-season and warm-season species. Each data-point is the mean of nine replications, and vertical bars represent ± 1 S.E.

a matter of coincidence of flooding with a particular phenological stage. Reproductive phases for the warm-season species always occur during the flood-free period of the year. Regardless of the causes of the observed differences, warm-season species, which had higher relative productivity (Fig. 19.17), and presumably use the C_4 fixation pathway, are definitely better adapted to the changing conditions of water availability which characterize the flooding pampa.

FAUNA¹

Even though the meagre scientific knowledge of the fauna of the Río de la Plata grasslands does not enable one to make biogeographical generalizations (Reig, 1964), it seems reasonable to accept, as a first approximation, the zoogeographic limits proposed by Ringelet (1955) and Ringelet and Aramburu (1957). According to these authors, the Pampean region is a transitional zone between the Guayanian-Brazilian subregion of the Subtropical Dominion and the Austral subregion (Ringelet, 1955; Dalby, 1975).

Other workers have also tried to set zoogeographical limits related to the distribution of mammals or other faunistic elements (Cabrera and Yepes, 1940; Fittkau, 1969), or by using physiographic, edaphic and climatic approaches (Cabrera, 1953, 1968). Zoogeographical territories are usually associated with phytosociological territories, so it is necessary, as far as possible, to

examine ecological limits to find clearer boundaries for vegetation and fauna.

Ringelet and Aramburu (1957) cited more than 600 species of vertebrates in the region. This number might be even higher if more information was available for the fauna of the southern part of Brazil. The fauna of Buenos Aires Province is dramatically impoverished in number of species in each class of vertebrates, as compared to the mesopotamic pampa and the southern and northern campos (Ringelet, 1955; Gallardo, 1974, 1976).

The South American fauna is one of the richest of the world. Here only the most important vertebrate species will be considered.

Mammals

The principal large herbivore of the pampas was *Ozotoceros bezoarticus celer* (pampas deer). A small population, of no more than 300 animals, survives now only in wildlife reserves in the eastern part of the Buenos Aires and San Luis Provinces.

Lagostomus maximus maximus ("vizcacha"), *Didelphis azarae* and *Lutreolina crassicaudata* (oposums) are abundant (Cabrera and Willink, 1973). Several small rodents are abundant, including: species of *Akodon*, *Bolomys*, *Calomys*, *Oryzomys*, *Oxymycterus* and *Scapteromys* (rat and mice); species of *Cavia*, *Galea* and *Microcavia* ("cuises"); *Ctenomys* spp. ("tucu-tucu"); *Phyllotis darwini xanthopygus* ("pericote amarillento"); and *Reithrodontomys auritus* (coney rat). *Monodelphis dimidiata* (a small opossum) and *Marmosa pusilla* ("marmosa") are less abundant.

Predators are no longer abundant. *Leo onca palustris* ("ameghino" — jaguar) and *Felis concolor hudsoni* (puma) formerly lived in this region but are now extinct. *Dusicyon gymnocercus* (a grey fox) is now rare. Among the surviving predators are two species of *Conepatus* (skunk), *Galictis cuja huronax* ("huron") and *Felis colocolo pajeros* and *Felis geoffroyi geoffroyi* ("gato pajero" and "gato montés" — small cats) (Cabrera and Willink, 1973; Freiberg, 1982).

Several armadillos are common, including *ChaetophRACTUS villosus* (Fig. 19.25), *Chlamyphorus truncatus* and *Dasypus hybridus*. *ChaetophRACTUS*

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