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The Grasslands and Steppes of Patagonia and the Río de la Plata Plains

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The Patagonian steppes and the Río de la Plata grasslands occupy a vast proportion of the plains, plateaus, and hills of southern South America, and are characterized by the almost absolute absence of trees. Prairies and steppes (grass and low shrubs) are the dominant physiognomic types, and forests are restricted to some riparian corridors. Savannas become important only in the ecotones of these regions, whereas meadows may be locally important under particular topographic or edaphic conditions. The Río de la Plata grasslands (RPG), one of the most important grassland regions in the world, extend between 28°S and 38°S latitude, covering about 700,000 km² of eastern Argentina, Uruguay, and southern Brazil (fig. 14.1). The boundaries of these grasslands include the Atlantic coastline to the east, dry temperate forests to the south and west, and subtropical humid forests to the north. Woody vegetation within the region is restricted to small areas near water bodies, such as the gallery forests along the large Paraná and Uruguay rivers and their tributary

streams. The Patagonian steppes occupy the southern tip of the continent from approximately 40°S, and are framed by the Andes to the west and the Atlantic coast to the east and south and cover more than 800,000 km² of Chile and Argentina. Toward the west, the region displays a sharp ecotone with the subantarctic forests, whereas to the north it grades into a broad zone of Monte scrublands in central Argentina. The RPG and the Patagonian steppes are separated by a wide strip of woody vegetation, the Monte and Espinal phytogeographic units (see chapter 10; Cabrera and Willkins, 1973).

In this chapter, we describe the heterogeneity and main characteristics of the dominant ecosystems of the Patagonian steppes and the RPG, focusing on environmental controls and human-induced changes. Although numerous criteria have been applied to describe the internal heterogeneity of both regions, we emphasize here the structural and functional attributes of vegetation as integrators of climate, physiography, and land use.

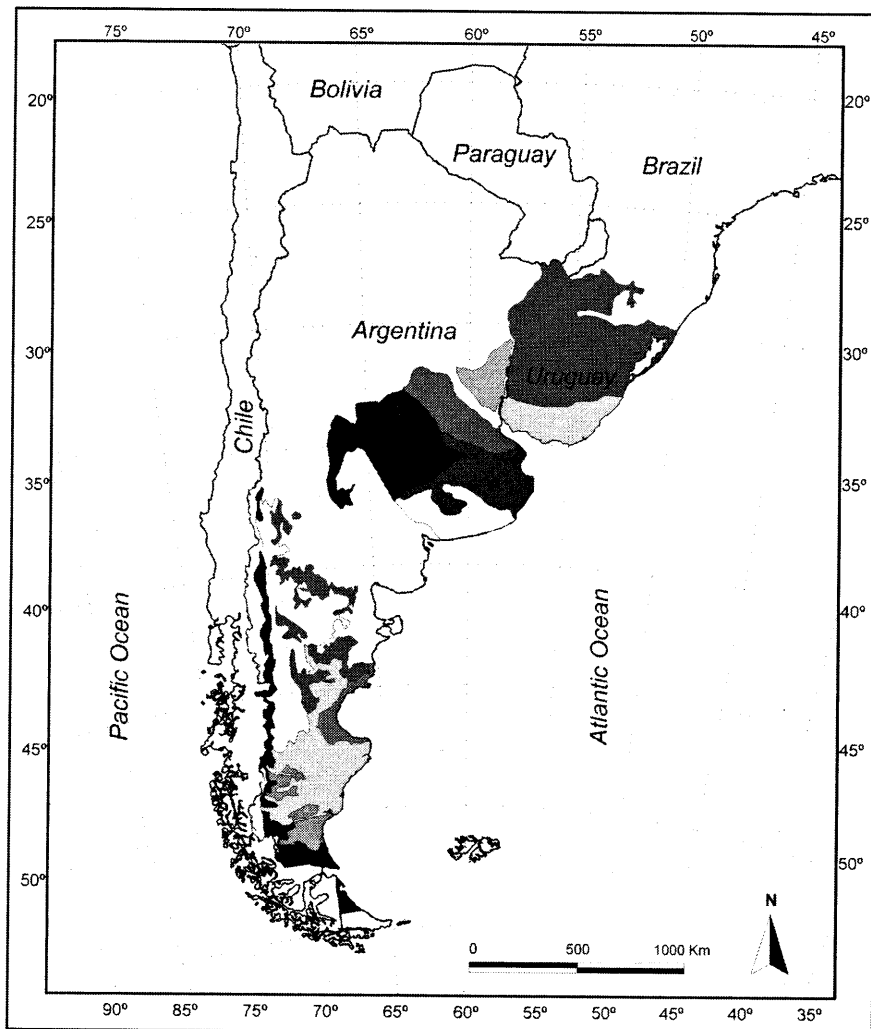


Figure 14.1 Río de la Plata grasslands and Patagonian steppes, based on the boundaries defined by Soriano (1991) and León et al. (1998)

14.1 Climate, Physiography, and Soils

14.1.1 General Climate

A key climatic feature of southern South America and other temperate regions of the Southern Hemisphere that distinguishes them from their Northern Hemisphere counterparts is the relatively low thermal amplitude caused by the low ratio of land mass to ocean in this portion of the world. This contrast may control the differences between the Southern and Northern Hemispheres in the structure and functioning of their respective prairies and steppes (Paruelo et al., 1995, 1998a). Both Patagonia and the RPG lie between the semi-permanent anticyclones of the South Pacific and South Atlantic Oceans (centered around 30°S) and the subpolar low-pressure belts around 60°S (see chapter 3; Prohaska, 1976, Paruelo et al., 1998b). During the southern summer, the RPG are also influenced by a low-pressure center developed over northern Argentina (25°S),

probably associated with the Intertropical Convergence Zone (Frere et al., 1978). Although both areas can be classified as temperate, the RPG experience subtropical influences toward their northern boundary.

The western sector of the South Atlantic anticyclone conveys most of the humidity received by the RPG. Warm humid air masses generated within this anticyclone interact on their way toward the region with dry polar air masses coming from the southwest that travel over the dry areas of Patagonia. Such interaction generates most of the frontal precipitation over the area. The lack of major orographic features that could alter the course of these air masses results in a gentle NE-SW precipitation gradient that ranges from 1,500 mm/yr in southern Brazil to 600 mm/yr in central Argentina (fig. 14.2). Conditions change from humid to semiarid across this gradient, leading to important changes in vegetation and land uses (Soriano 1991). While the more continental areas toward the north and west of the RPG have rainfall maxima in spring and fall and a minimum in win-

ter (fig. 14.2), heavy winter rainstorms associated with cyclogenesis over the central part of the area and strong southeasterly winds (*sudestada*) balance rainfall seasonality toward the south and east of the region (Prohaska, 1976). In the northeastern portion of the region (southern Brazil and eastern Uruguay), the Atlantic anticyclone determines an increase in winter precipitation. Mean annual temperatures increase northward, from 14°C to 19°C. Although winters are relatively mild and snowfall is infrequent or nonexistent, frosts are common and may extend well into spring and fall in the southern part of this region.

Pacific air masses have an overriding influence on the Patagonian climate. Strong, constant westerly winds dominate the region. The seasonal displacement of the low- and high-pressure systems and the equatorward ocean current determine the seasonal pattern of precipitation in Patagonia. During winter, the higher intensity of the subpolar low, the northward displacement of the Pacific high, and higher ocean temperatures relative to the continent determine an increase in precipitation over the region. The result is a clear winter-distribution pattern of precipitation over most of the area (fig. 14.2). In Patagonia, 46% of precipitation falls in winter (Jobbágy et al., 1995). Where the influence of Atlantic air masses has some importance (toward Patagonia's northern and southern extremes), precipitation is more evenly distributed over the year. The north-south orientation of the Andes on the western border of Patagonia plays a crucial role in determining the latter's climate. The Patagonian steppes are located in the rain shadow of mountains that impose an important barrier to humid air masses coming from the Pacific Ocean. Humidity is released on the western slopes of the Andes and air masses entering the Patagonian steppe become warmer and drier through adiabatic processes as they descend the eastern slopes.

The characteristics outlined above result in a strong west-east gradient of precipitation across the region (Barros and Mattio, 1979), with total annual precipitation decreasing exponentially east of the Andes. For the areas that are not directly influenced by the Atlantic, more than 90% of the mean annual precipitation variation over the region is accounted for by the distance from the Andes (Jobbágy et al., 1995). Within a precipitation gradient that may reach more than 4,000 mm/yr in the western subantarctic forests, the Patagonian steppes occur where precipitation levels are less than 600 mm/yr in the north and less than 350 mm in the south, with most of the intervening region receiving less than 200 mm (Paruelo et al., 1998b). Winter distribution of precipitation results in a strong water deficit in summer (Paruelo and Sala, 1995; Paruelo et al., 2000). According to the bioclimatic classification of Le Houreou (1996) (based on the ratio of potential evapotranspiration to mean annual precipitation), more than 55% of Patagonia is arid or hyperarid and only 9% subhumid (Paruelo et al., 1998b). As precipitation increases westward, the summer deficit

decreases and has a later onset in the season, an aspect that is mirrored by vegetation phenology (Jobbágy et al., 2002).

Thermal belts in Patagonia succeed one another from northeast to southwest, following the effects of increasing latitude and altitude. Mean annual temperature ranges from 12°C along the northern margins of the region to 3°C in Tierra del Fuego. The strong westerly winds that blow over Patagonia reduce the perceived temperature (wind chill), on average 4.2°C. The wind-chill effect is more pronounced in summer, generating the cool (or even cold) summers that characterize the Patagonian climate (Coronato, 1993).

The Patagonia and RPG regions have their closest climatic analogues in North America in the intermountain zone in the western United States and in the humid portion of the tallgrass prairie, respectively (Paruelo et al., 1995). Patagonia and the Intermountain West both experience relatively low mean annual precipitation (150–500 mm MAP) and temperature (0 to 12°C MAT) (Adler et al., 2006). Most of the Río de la Plata grasslands occur in areas characterized by much higher precipitation (>1,000 mm MAP) and temperatures (15–20°C MAT), and a lack of clear seasonality in precipitation. Areas displaying such climates in North America correspond to the transition between grasslands and forests. The lack of such a transition in South America, and the presence of grasslands under climatic conditions that would appear to support forest vegetation based on relationships observed in the Northern Hemisphere, have puzzled plant geographers and ecologists for at least a century (Parodi, 1942; Ellenberg, 1962; Walter, 1968).

14.1.2 Landforms, Geologic History, and Soil Gradients

Perhaps the most significant event shaping the landscapes that host the Río de la Plata grasslands and the Patagonian steppes has been the uplift of the Andes, the most recent phase of which began in middle Miocene time, around 14 million years ago (see chapter 1). In a region of strong westerly winds, this massive barrier has modified the climate leeward of the mountains, creating conditions favorable to desiccating winds and desertification. Meanwhile, rivers and winds have transported large quantities of sediment from the eroding mountains toward the plains and plateaus farther east. There, aided by local alluvial activity and soil-forming processes, these sediments have come to shape the distinctive landscapes of the Patagonian steppes, the Pampas, and parts of the Campos regions in the Río de la Plata plains (Teruggi, 1957; Zarate, 2003).

Most of the Río de la Plata grasslands occur over a vast plain, the Pampas, formed by thick Quaternary loess deposits that have experienced varying degrees of local reworking. Exceptions to this general pattern are a few isolated uplands in Argentina, where Precambrian-Paleozoic crystalline rocks have not been fully buried by sediment, and

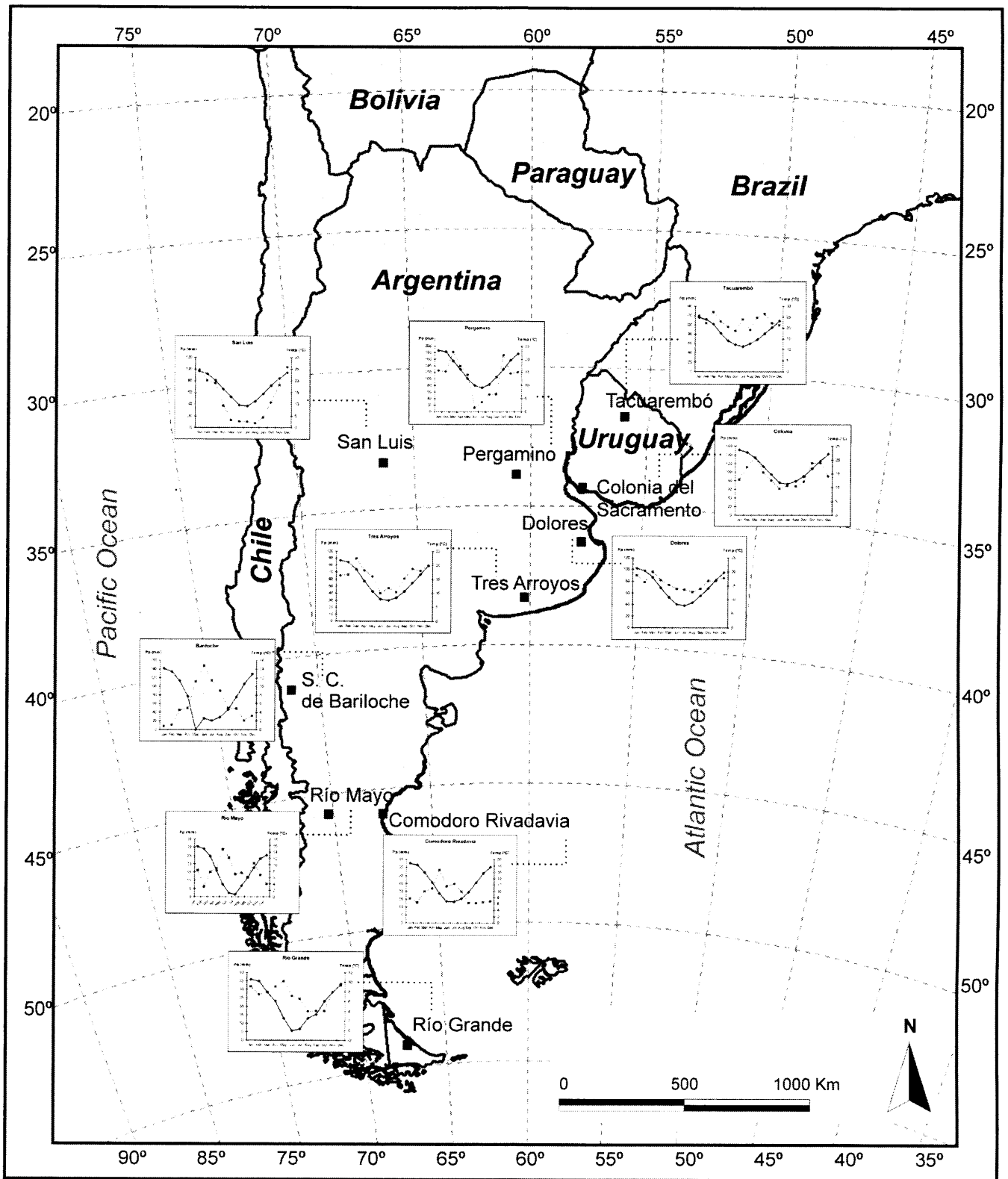


Figure 14.2 Climatograms for selected locations across the main climatic gradients of the Río de la Plata grasslands and the Patagonian steppes

most of the Uruguayan and Brazilian portions of the region, where a diverse array of rocks such as Precambrian granite, Carboniferous sandstone, and Jurassic basalt is exposed to surface and soil-forming processes.

The dominant loessic sediments of the Pampas are characterized by their unconsolidated nature, silt to fine-sand texture typical of wind-transported material, and large contributions of volcanic material. Most primary loess has been subsequently reworked by winds and streams, and by pedogenesis (Zarate, 2003). In general, these sediments are younger and coarser towards the west, where past and present climates have been more xeric and dust sources less remote. Towards the east, these loess mantles are thinner and older, becoming restricted to hill tops and fluvial terraces to the east of the Uruguay River (Panario and Gutierrez, 1999). The relatively young and flat aeolian landscape of the Pampas constrains surface-water transport, generating shallow groundwater tables under present humid conditions. This translates into a dense network of shallow and stagnant water bodies that expand over a significant proportion of the territory during wet years (Tricart, 1973). This hydrological context has made flooding and salt accumulation key driving forces for soil and ecosystem development.

Along a west-east gradient across the Pampas, soils developed on Quaternary sediment shift from mollic Entisols with incipient horizon differentiation to well-developed Mollisols with high clay accumulation in subsurface horizons (INTA, 1989). In general, these soils have high organic matter content and base saturation, posing few or no constraints for agriculture (see chapter 7). Low topographic sites host sodic and/or hydromorphic soils (natric and aquic Mollisols to Alfisols), which dominate the landscape matrix in the flattest portions of the region. Similar soil-landscape situations have been described for the plains in Hungary (Toth and Jozefaciuk, 2002) and eastern Siberia (Bazilievich, 1970). In the Uruguayan and Brazilian Campos, a more complex array of parent materials and topographic forms has resulted in higher soil heterogeneity. While well developed Mollisols similar to those of the eastern Pampas are frequent here, widespread shallow soils over rock outcrops (Entisols) and profiles with poor base-saturation are a distinctive feature (Alfisols, Inceptisols, and Oxisols in the northern edge of the region) (Duran, 1991).

Plateaus or *mesetas* are among the most characteristic features of the Patagonian steppe, decreasing in elevation from the eastern foothills of the Andes towards the Atlantic coast. Volcanic forms and sierras occur within these plateaus in northern Patagonia and central Patagonia, respectively. An earlier Cenozoic warm moist period in Patagonia, suggested by fossil evidence and large coal deposits, ended when uplift of the Andes in the Miocene imposed a barrier to the transport of moisture from the Pacific Ocean by the prevailing westerly winds (Volkheimer, 1983). Major glaciations of the Andes probably began in the Pliocene and were broadly contemporary with

volcanic activity, resulting in interbedded tills and basalts (Mercer, 1976; Strelin et al., 1999). A complex interaction among Andean glaciation, volcanism, crustal adjustments, and downstream glaciofluvial and fluvial activity has produced Patagonia's present landscape of plateaus and terraces, one of whose most striking features, as noted by early naturalists like Darwin, is the widespread occurrence of pebbles or *rodados patagónicos* (Darwin, 1842; Strelin et al., 1999). Glacier expansion during Pleistocene cold stages reached its maximum around 170,000 years ago but was confined to the Andes and their foothills (Clapperton, 1994). However, its indirect influence farther east is seen in the legacy of glaciofluvial processes on the Patagonian steppe and of loess on the Pampas.

With few exceptions, the drainage network of Patagonia consists of several west-east running rivers that drain the humid slopes of the Andes and cross the steppes on their way to the Atlantic, maintaining riparian systems across the whole region. In addition to riparian environments, the Patagonian landscape hosts a profuse network of flood meadows or *mallines* associated with groundwater discharge and low-order water courses (Iriondo et al., 1974). In the western steppes, these units can occupy as much as 5% of the landscape, providing a crucial resource to wildlife and domestic herbivores (Paruelo et al., 2004). *Mallines* are supported on water drained from the steppes, resulting mainly from winter precipitation (Paruelo et al., 2000).

Glacial detritus and volcanic materials represent the major soil parent materials of the Patagonian steppe. Mollic soils are common in the more humid and cold plateaus of the western steppes, dominated by grasses in their pristine condition. Toward the east, under drier and warmer climates, Aridisols and Entisols dominate the landscape and thick cemented calcic horizons are widespread (del Valle, 1998). Rounded pebbles and gravels associated with glaciofluvial processes are characteristic of the Patagonian steppe soils and responsible for the formation of extensive desert pavements where wind erosion has been able to remove finer materials. Buried soil horizons are common throughout the area, reflecting the influence of past climatic conditions on pedogenesis. In flooded meadows, soils tend to be rich in organic matter, fitting the definition of Mollisols with hydromorphic and/or sodic characteristics, depending on their hydrological balance.

14.2 Vegetation

14.2.1 Main Vegetation Units of the Río de la Plata Grasslands

The major internal subdivisions of the RPG were defined and described by Rolando León (in Soriano 1991), based on geomorphic, hydrologic, and edaphic features and their linkages with natural vegetation and land use (fig. 14.3).

Such characterization of the heterogeneity of the area summarizes and integrates information of the flora at both regional (Vervoorst, 1967; Cabrera and Willkins, 1973) and local scales (León et al., 1979; Collantes et al., 1981; Lewis et al., 1985; Faggi, 1986; Burkart et al., 1998, 1990; Batista et al., 1988; Cantero and León, 1999; Perelman et al., 2001). We describe here the natural vegetation of these regions based mainly on that seminal description.

The four northern subdivisions share several features in common, particularly hilly relief and the existence of a well-defined drainage system (fig. 14.3). The Rolling Pampa is now covered largely by annual crops, with a predominance of soybean. Although its original vegetation can only be inferred from a few isolated remnants of unploughed vegetation and from early, but postcolonial, botanical descriptions, it is clear that these prairies were formerly dominated by tussock grasses that covered most of the ground. Dominants comprise several warm-season (C_4) and cool-season (C_3) grasses in approximately similar proportion. The most common genera among the grasses are *Stipa*, *Piptochaetium*, *Paspalum*, and *Bothriochloa*. Shrubs are little represented, but in some places, probably as a result of disturbance, one of several species of Compositae (*Baccharis* and *Eupatorium*) may become locally dominant. Small dicots grow in between grasses and

are favored by grazing. The Southern Campos are floristically very similar to the Rolling Pampa, but the influence of agriculture has been lower, probably due to relatively shallow soils (fig. 14.4). The Mesopotamic Pampa, located between the Paraná and Uruguay Rivers, is similar in relief to the two previous units, but its soils have a finer texture. Vegetation is also similar, but is enriched in subtropical elements (warm-season grasses such as *Axonopus* and *Schizachyrium*). Cool-season grasses are still present, but rarely become dominant. Finally, the Northern Campos are structurally similar to the other northern subregions, but here species composition becomes even more enriched in subtropical species (*Andropogon*). Soriano et al. (1991) distinguished several features within this subregion, such as the strong impact of grazing on species composition, the response of vegetation heterogeneity to topography, and the flat areas or *malezal* subject to extended flooding west of the Uruguay River. Phytogeographical analysis of that portion of the Northern Campos associated with basaltic substrate has revealed a mosaic of three communities (hydrophytic and mesophytic prairies, and grass steppes), the spatial distribution of which is mainly related to soil depth (Lezama et al., 2004).

The three southern subdivisions of the RPG, all in Argentina, comprise the Flooding Pampa, the Inner Pampa,



Figure 14.3 Main subdivisions of the Rio de la Plata grasslands, as defined by R.J.C. León in Soriano (1991)

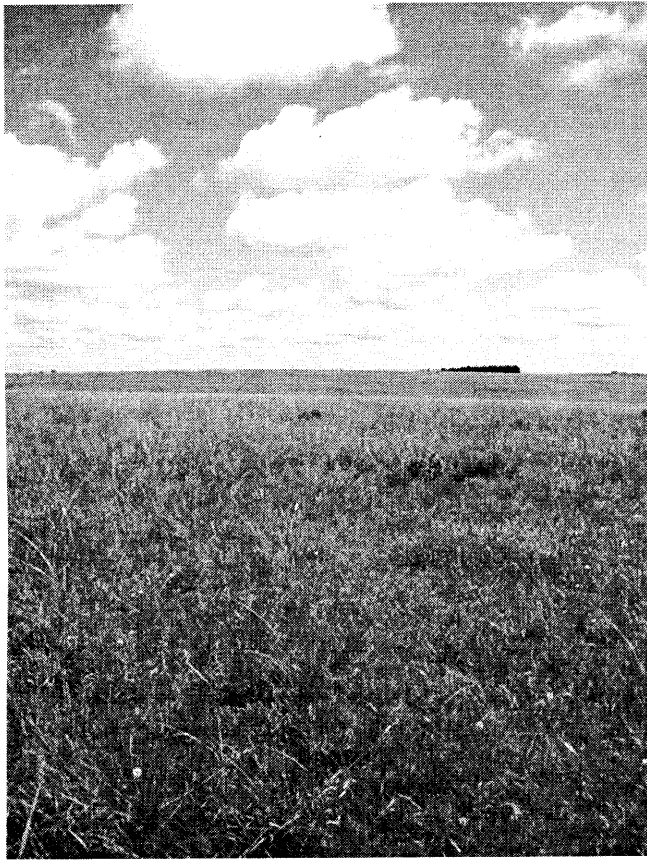


Figure 14.4 Grazed prairie of the Southern Campos of the Río de la Plata grasslands (photo: J.M. Paruelo)

and the Austral Pampa (fig. 14.3). The Flooding Pampa is composed of depressions associated with the Salado and Laprida river basins in Buenos Aires Province. Extensive areas with virtually no slope give the impression of homogeneity, but a closer look reveals an intrinsic mosaic of plant communities. A large proportion of the variation of plant species composition is included in small 0.1–10 km² areas. Minimal topographic variations and patches with high soil salinity are responsible for this pattern. Five vegetation units are associated with these environmental variations (Perelman et al., 2001). Three of them correspond to a topographic gradient, from small, slightly elevated hills that are never flooded (mesophytic meadows, with *Stipa trichotoma*, *S. charruana*, *Diodia dasycephala*, *Sida rhombifolia*), to flat areas occasionally flooded (humid mesophytic meadows, with *Mentha pulegium*, *Leontodon taraxacoides*), to extended lowlands regularly flooded for several months (humid prairies, with *Leersia hexandra*, *Paspalidium paludivagum*). The other two vegetation units correspond to halophytic steppes and humid halophytic steppes (with *Distichlis spicata*, *D. scoparia*, *Sporobolus pyramidatus*, *Sida leprosa*, *Salicornia*), which occupy soils with sodic salinity frequently influenced by flooding. As a result of the

strong constraints generated by the flooding regime and the high salinity of some soils, agriculture is restricted to areas where mesophytic meadows should be found.

The Inner Pampa to the west also lacks an obvious drainage system, but soils have a coarser texture and, as a result, are not extensively flooded. They have been widely converted to agriculture. With less precipitation than the other two subregions, vegetation is less dense and hardly reaches a 100% cover. According to the history of grazing by livestock, these grasslands may be dominated by different native grass (*Sorghastrum pellitum*, *Elionurus muticus*) and perennial dicot species, or even by exotic weeds (Soriano, 1991).

The Austral Pampa in the south is associated with the ancient rocks and later sedimentary covers of the Sierra Tandilia and Sierra de la Ventana, and their slopes towards the Atlantic Ocean (Soriano, 1991). These hills rarely exceed 1,000 m and, except for rocky outcrops, the high fertility of their soils has facilitated the conversion of most of this subregion to extensive agriculture, with a predominance of wheat. The vegetation replaced by these crops was dominated by several tussock, cool-season grasses (*Stipa*, *Piptochaetium*), some common to other subregions. In contrast, the rocky areas have a distinct composition of grasses and dense areas dominated by shrubs.

14.2.2 Main Vegetation Units of Patagonia

The grasslands and steppes of Patagonia are very heterogeneous, both physiognomically and floristically. This high heterogeneity contradicts the common perception of Patagonia as a vast desert at the southern end of the world. Vegetation types range from semi-deserts to humid prairies with a large variety of shrub and grass steppes in between. This vegetation heterogeneity reflects the constraints imposed by the climatic, topographic, and edaphic features of the region. In the following paragraphs we describe the internal heterogeneity of the typical vegetation units (i.e., phytogeographical districts) of the Patagonian Phytogeographical Province (Soriano, 1956, see details in León et al., 1998) (fig. 14.5).

Grass steppes characterize the most humid districts of the region, the Subandean and Magellanic Districts, which are dominated by grasses of the genus *Festuca* (*F. pallidissima* and *F. gracillima*, respectively), accompanied by several other grasses, highly preferred by native and exotic herbivores, and sometimes by shrubs (fig. 14.6). In the Subandean District (fig. 14.4), shrubs (*Mulinum spinosum*, *Senecio filaginoides*, and *Acaena splendens*) seem to be indicative of degradation by grazing (León and Aguiar, 1985; Bertiller et al., 1995). In the Magellanic District, shrubs are common constituents of the grass steppe, differing between the most xeric soils (*Nardophyllum bryoides*) and the most humid and acidic soils (*Chilliotrichum diffusum* and *Empetrum rubrum*) (Collantes et al., 1999).

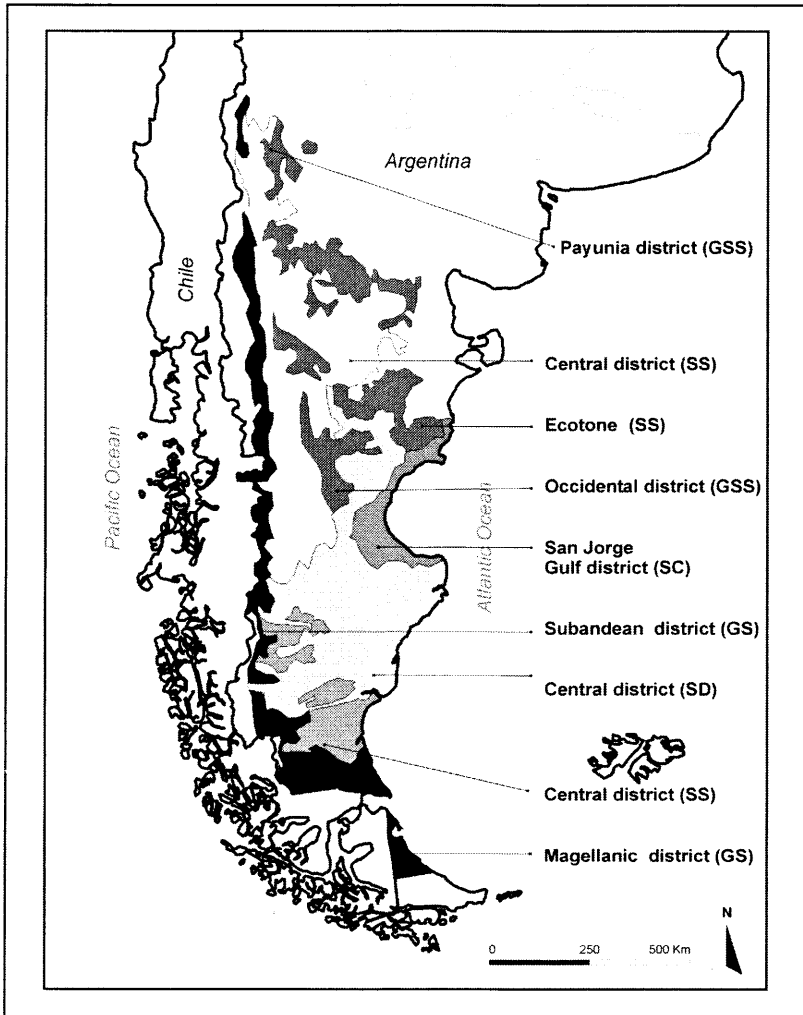


Figure 14.5 Main subdivisions (phytogeographical districts) of Patagonian steppes, as defined by Soriano (1956) and León et al. (1998). GS: grass steppes, SS: shrub steppes, GSS: grass-shrub steppes, SD: semi-deserts, SC: scrublands.



Figure 14.6 Grass steppe of *Festuca pallescens* in western Patagonia (Subandean District) (photo: J.M. Paruelo)

East of the Subandean District, shrub-grass steppes occupy the semiarid environments of the Occidental District and Payunia District. The vegetation of the Occidental District (fig. 14.5) is a shrub-grass steppe dominated by the shrubs *Mulinum spinosum*, *Senecio filaginoides*, and *Adesmia volkmanni*, and the grasses *Stipa speciosa*, *S. humilis*, and *Poa ligularis* (fig. 14.7; Golluscio et al., 1982). As in the Subandean District, the north-south extent of the Occidental District only modifies the accompanying species. In contrast, the Payunia District is an intricate mosaic of shrub steppes whose dominant species vary according to edaphic substrate, elevation, and topography. Patagonian shrub species, as commonly found in the Occidental District, alternate with shrub species typical of the neighboring Monte Phytogeographical Province (see chapter 10).

Shrub-grass steppes also dominate most of the San Jorge Gulf District, where the local climate is strongly influenced by sea breezes coming off the Atlantic Ocean and by the humidity delivered by westerly winds passing over the large Musters and Colhue Huapi lakes (Coronato, 1996). This district includes two different vegetation units that are not distinguishable at the spatial resolution of figure 14.5. The slopes of the Montemayor, Pampa del Castillo, and Pampa de Salamanca plateaus are occupied by scrublands dominated by *Colliguaya integerrima* and *Trevoa patagonica*, two phanerophytes up to 2 m tall. In contrast, the plateau surfaces are occupied by shrub-grass steppes physiognomically similar to those of the Occidental District (Soriano, 1956; Bertiller et al., 1981).

The most arid environments of the Patagonian Province are included within the Central District (fig. 14.5). As precipitation is uniformly scarce, vegetation varies according to topography, soils, and temperature. The most extensive vegetation unit is a semi-desert dominated by the dwarf shrubs *Nassauvia glomerulosa*, *N. ulicina*, and *Chuquiraga aurea*. Plant height (<30 cm) and cover (<30%) are very low in these communities, which are often located on soils with heavy clay pans close to the surface and a highly unfavorable water balance. The rest of the district is occupied by shrub steppes, all of them growing on deeper and/or coarser soils, but each dominated by a different suite of shrub species. The most important of these shrub steppes are dominated by *Chuquiraga avellanadae* (<50 cm height; <50% cover), on the plateaus located at the northeast end of the district; by *Colliguaya integerrima* (150 cm height, 65% cover) on the basaltic hills located at the northwest end; by *Nardophyllum obtusifolium* (60 cm height; 50% cover) on the hills located in the west-center; and by *Junellia tridens* (70 cm height, 60% cover) in the plateaus located at the south end of the district (León et al., 1998).

The vegetation of the Patagonian districts displays heterogeneity of a finer grain in association with altitude, slope, and exposure (Jobbágy et al., 1996, Paruelo et al., 2004). Prairies and meadows (*mallines*) are distributed throughout the region and are generally associated with rivers, creeks, valley bottoms, or local springs, where the high water availability generates a completely different physiognomic type (fig. 14.8). The plant cover in these systems is often 100%, and mesophytic grasses (*Poa*



Figure 14.7 Shrub-grass steppe of the Occidental District of Patagonia (photo: N. Fernández)



Figure 14.8 Meadow (mallín) surrounded by shrub steppes in Patagonia (photo: N. Fernández)

pratensis, *Deschampsia flexuosa*, etc.), rushes (*Juncus balticus*), and sedges (*Carex* spp.) dominate. Most of the species currently present in the *mallines* are cosmopolitan or exotic, mainly from Europe.

14.2.3 Ecosystems Functioning Gradients

The environmental heterogeneity and the gradients in vegetation structure described for both the RPG and Patagonia lead to profound changes in ecosystems functioning, which is the exchange of matter and energy between biota and the abiotic environment. Net primary production (NPP) and its seasonal dynamics have been identified as a key ecosystem attribute able to integrate different aspects of ecosystem functioning. Satellite data provide a simple and powerful alternative for describing regional patterns of NPP from the normalized difference vegetation index (NDVI), a spectral index derived from reflectance in the red and infrared bands of the electromagnetic spectrum (Running et al., 2000). Paruelo and Lauenroth (1995, 1998) showed that three attributes of the annual curve of the NDVI capture the main characteristics of the seasonal dynamics of carbon gains: the NDVI integral (NDVI-I), the relative range of NDVI (RREL), and the date of maximum NDVI (DMAX). Moreover, these three attributes of the NDVI curve have been used to define ecosystem functional types (EFT) for the temperate areas of South America (Paruelo et al., 2001). EFT are areas presenting a similar functioning as defined by the NDVI-I, the RREL, and the DMAX.

In the RPG, net primary production levels, as suggested by remote sensing proxies, decrease from NE to SW follow-

ing the dominant precipitation gradient (fig. 14.9, top left). Such changes in NDVI-I translate into twofold differences in above-ground net primary production (ANPP) between the extremes (Oesterheld et al., 1998). In Patagonia, net primary production patterns deduced from NDVI-I follow a W-E gradient axis that is also associated with the dominant precipitation gradient. Both areas clearly reflect the strong control exerted by precipitation on the carbon uptake of grassland and shrubland worldwide (Lauenroth, 1979; Sala et al., 1988). In Patagonia, the climate gradient not only affects total carbon uptake but also its interannual variability, which increases with aridity (Jobbágy et al., 2002). At a finer spatial scale, topography, landscape configuration, and land use also play an important role in controlling net primary production patterns. In Patagonia, Paruelo et al. (2004) found that the diversity of vegetation units explained a significant portion of the spatial variability of ANPP not accounted for by climate: the more diverse a landscape, the higher the ANPP.

For the RPG, 80% of the variance of the NDVI-I of uncropped areas is explained by rainfall and 9% by potential evapotranspiration. Land-use/land-cover changes (mainly agriculture expansion) have a relatively small impact on NDVI-I (less than 15%) (Guerschman et al., 2003).

In Patagonia, the seasonality of carbon uptake, as described by the NDVI relative range (RREL), shows a similar spatial pattern as NDVI-I (fig. 14.9, top right): the relative difference between maximum and minimum production through the year increases as MAP increases. Such behavior results mainly from changes in maximum productivity, which are associated with precipitation. NPP minima are

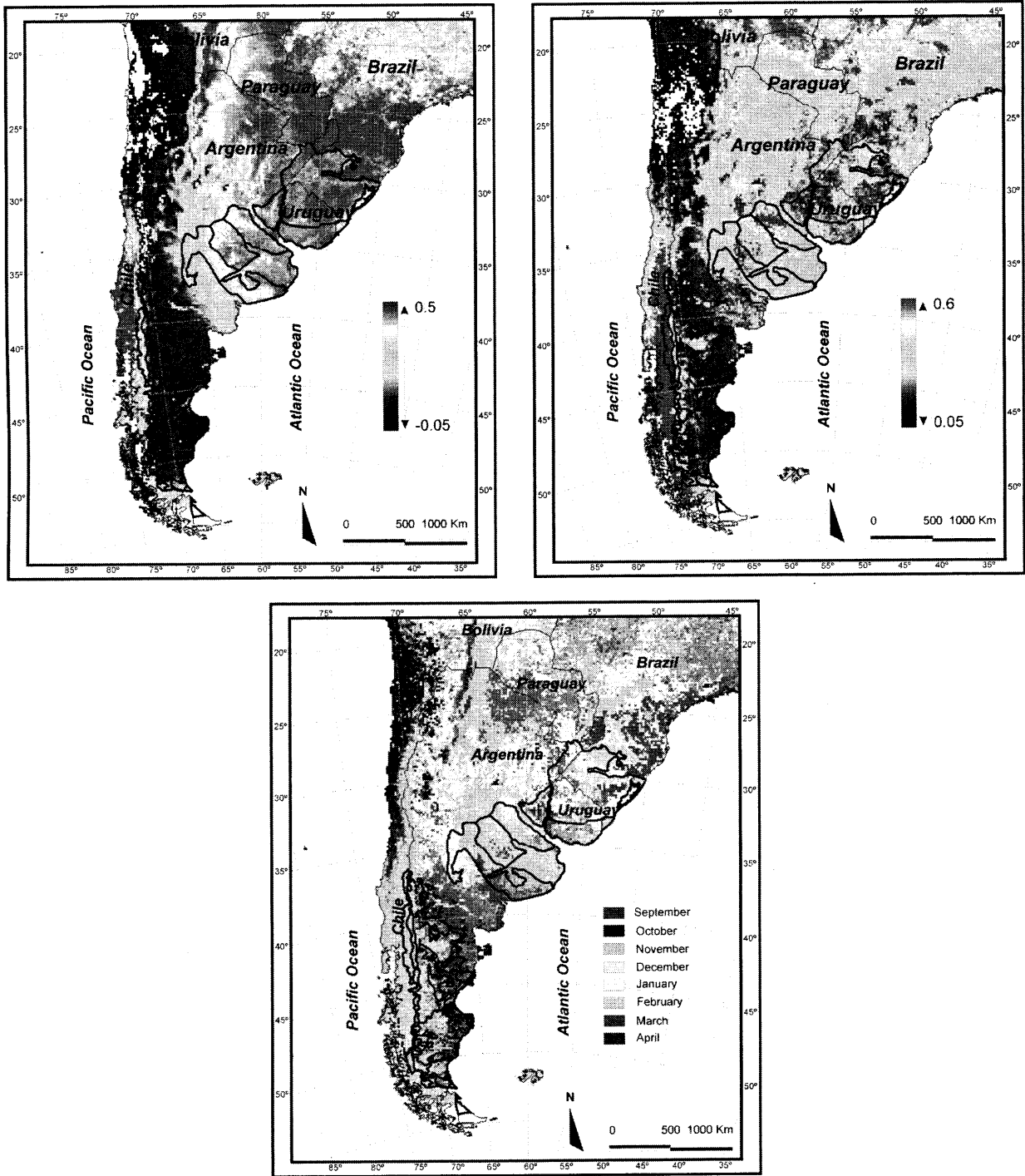


Figure 14.9 Top left: Annual integration of the normalized difference vegetation index (NDVI-I), a spectral index used as a surrogate of net primary production (NPP). Top right: Relative annual range of NDVI (maximum minus minimum NDVI relative to NDVI-I), a descriptor of NPP seasonality. Bottom: Date of maximum NDVI. Data were derived from the Pathfinder AVHRR Land database (NASA) and are averages over the 1981–2000 period. Figures based on Paruelo et al. (2001). See color insert.

independent of precipitation and are associated with thermal restrictions on plant growth during winter. In the RPG, the patterns of NDVI-I and RREL differ. Two factors contribute to such differences. First, the environmental controls of spatial variation in uncropped areas differ between attributes. Instead of MAP, as in the case of the NDVI-I, RREL is associated mainly with changes in potential evapotranspiration and in rainfall seasonality. Second, land use has a strong impact on seasonality: annual crops increase RREL up to 80% (Guerschman et al., 2003).

An additional description of the seasonality of C uptake is provided by the date of maximum NDVI (D_{MAX}) (fig. 14.9, bottom). In Patagonia, the production peak (as described by the NDVI) is concentrated in the period November–January, with a few exceptions along the coast. In the western portion of Patagonia, the date of maximum NDVI is delayed as MAP increases (Jobbágy et al., 2002). In the RPG, the pattern is more complicated and heterogeneity is quite high: peak NDVI may occur between October and April. Though a substantial portion of the heterogeneity (73%) of the date of maximum NDVI in areas with low human impact on vegetation is explained by environmental variables, land-use/land-cover change has an overriding effect. Cropping modifies the date of peak NPP by up to 150 days (Guerschman et al., 2003).

These regional patterns of primary productivity are matched by strong patterns of livestock biomass and, as a result, the proportion of ANPP consumed by herbivores. Livestock biomass across rangelands of Argentina and Uruguay (largely from Patagonia and the RPG) increases more than proportionally as ANPP increases (Oesterheld et al., 1992). This livestock pressure is 10 times greater than that observed in natural ecosystems with similar primary productivity (McNaughton et al., 1989). The logarithmic increase of livestock biomass with ANPP or its surrogate, NDVI-I, may result from a higher forage quality in areas with high ANPP (Oesterheld et al., 1998). In addition, it may be influenced by the negative correlation between NDVI-I and both its seasonal and its interannual variability: more productive areas are also those with more reliable levels of ANPP, which allows ranchers to set livestock densities closer to the average carrying capacity (Oesterheld et al., 1998).

In a study based on correlative models that describe the climatic controls of grassland structure and functioning at regional scales, Paruelo et al. (1998b) analyzed the similarity of structural and functional characteristics of temperate grassland and shrubland ecosystems of North and South America. The evaluation included models that describe the regional distribution of plant functional types (C₃ and C₄ grasses and shrubs), soil organic carbon, and the annual amount and seasonality of above-ground net primary production. North and South America offer a unique opportunity to test the generality of regional models. As outlined above, temperate zones of North and South

America show important climatic similarities (Paruelo et al., 1995). However, the flora and fauna of both continents are partially unrelated from an evolutionary viewpoint; North America belongs to the Holarctic realm and South America to the Neotropical realm (Udvardy, 1975). The estimates derived from the models were compared against observed data collected in South America, independent from those used to generate the models in North America. The results support the notion that, in climatically similar regions, structural and functional attributes, such as plant functional-type composition, soil organic carbon, and above-ground net primary productivity, have similar environmental controls, independent of the evolutionary history of the regions. Adler et al. (2005) went a step further by performing comparative experiments on the response of plant traits to grazing across analogous climatic gradients in sagebrush steppe of the United States and in the Patagonian steppe of Argentina. They found that poor-quality graminoids make the Patagonian steppe particularly resistant to overgrazing. Dominance by such species would be a consequence of the relatively long evolutionary history of grazing in Patagonia, where generalist herbivores would have exerted stronger selective pressures (Lauenroth, 1998), a hypothesis contrary to previous assumptions (Milchunas et al., 1988).

14.3 Changes in Land Use and Land Cover: Agriculture, Afforestation, and Grazing

Human transformation of this portion of South America started recently compared to temperate areas of the Old World or even of North America. The replacement of natural vegetation by crops in the RPG had its onset at the beginning of the twentieth century, with increasing European immigration. Irrigation and fertilization did not expand as widely as in the Great Plains, with the former being very rare and the latter only becoming more important over the past two decades (Hall et al., 1991).

Land-cover changes provide one of the clearest examples of the contrasts between the developed north and the developing south. Whereas the northern temperate regions are seeing a spontaneous expansion of forests over land that had been devoted to crop production (Dong et al., 2003), in the southern regions annual crops are taking over native ecosystems and new land-cover shifts are emerging—such as grassland afforestation. Superimposed on these land-cover changes are differing patterns of nitrogen deposition, acid rain, and other biogeochemical alterations that widen the divergence between southern and northern ecosystems.

Three main land-use changes can be identified in the RPG: replacement of grasslands by annual and forage crops, replacement of grasslands by tree-plantations, and

intensification of grazing in native prairies. Areas receiving less than 500 mm/yr of precipitation had almost no agriculture. In areas with higher than 500 mm/yr, the proportion of the area under irrigation is lower than 0.045 and represents less than 7% of the total cropped area (Guerschman et al., 2003). The spatial variability in cropped area is associated with soil restrictions. For example, salinity and soil drainage constrain agriculture in the Flooding Pampa, whereas soil depth becomes limiting in parts of the Uruguayan Campos. Agriculture has strongly impacted the Rolling, Inner, and Austral Pampas in such a way that the natural vegetation is unknown and probably poorly represented in what might be considered relict areas. In meadows and the humid western grass steppes of Patagonia, sporadic agriculture may also play an important role as a disturbance agent.

As shown above, land-use change (particularly crop expansion) has had a significant effect on the seasonality of carbon gains and almost no effect on the total amount of carbon fixed (Guerschman et al., 2003). Agriculture basically modifies the shape of the seasonal curve of primary production but not the area beneath the curve. An increase in croplands also reduces the interannual variability of the seasonal patterns of carbon gains (Guerschman et al., 2003).

Shifts in vegetation cover can have strong and often devastating effects on ecosystems and societies, as illustrated by cases across the globe of massive replacement of native forests with pastures. Southern South America is experiencing an opposite—and less well understood—type of land-use shift: that of the conversion of native grasslands to tree plantations. Afforestation of some of the most productive native grasslands of the continent is already rapid and will probably be reinforced by the prospective carbon sequestration market. During the 1970s and 1980s, federal laws promoting afforestation with fast-growing tree species spurred the expansion of tree plantations over vast areas of Uruguay and Argentina. In coming decades, forestry probably will be the only subsidized land use in these countries. In the early years, afforestation projects were funded by national investment and were often integrated with local industrial processing (Jobbágy et al., 2005). But in the 1990s, more and more multinational companies became the major tree-planters and channeled most of the production to overseas industries. Highly productive grasslands in which crop production was usually not feasible (rocky or sandy soils, steep slopes, etc.) supported most of these plantations, shifting vast territories and their towns from a ranching to a forestry-based economy (Jobbágy et al., 2005). Afforestation has had a large and varied ecological impact. Soils under eucalypt plantations have been acidified to levels similar to those associated with acid rain in industrialized areas of the Northern Hemisphere (Jobbágy and Jackson, 2003). This acidification is probably due to high rates of calcium cycling following tree establishment because trees use and cycle more calcium than

grasses. In addition, the establishment of tree plantations has had striking effects on evapotranspiration, increasing it up to 80% (Nosetto et al., 2005). Depending on the hydraulic properties of the soils and aquifers, tree plantation can also affect groundwater hydrology and salt dynamics, resulting in groundwater consumption of up to 300 mm/yr and large accumulations of salts in soils and aquifers (Jobbágy and Jackson, 2004; Nosetto et al., 2005).

Grazing is the main cause of vegetation changes in Patagonia and non-agricultural areas of the Pampas. Grazing effects depend on three broad categories of factors: grazing history, physical environment, and plant functional types available in the potential biota. Many large herbivores grazed in the region until the late Pleistocene extinctions around 10,000 years ago, which coincided with a large-scale reduction in grass species (see chapter 8; Markgraf, 1985). Afterward, the guanaco (*Lama guanicoe*) and the Pampas deer (Venado de las Pampas) (*Ozotoceros bezoarticus*) remained the main large herbivores, accompanied by one of the two ostrich species (Lesser Rhea, *Pterocnemia pennata* in Patagonia, and Greater Rhea, *Rhea americana*, in the RPG) (Bucher, 1987). Domestic herbivores were introduced in the sixteenth and early twentieth centuries in the Pampas and Patagonia, respectively. A key difference between natural and domestic herbivory is selectivity. Natural herbivores are allowed to select their diet at different spatial scales, from landscapes to individual plants. In contrast, domestic grazers are confined by fences and other husbandry practices. As we move from southern Patagonia to the Pampas there is change from sheep to cattle husbandry. The relative importance of sheep and cattle determines the grazing regime (i.e., intensity and selectivity) (Oesterheld et al., 1992).

As discussed above, the region encompasses a gradient of temperature and precipitation, although precipitation seems to be the main determinant of primary production and potential plant functional types, which in turn determine the response of vegetation to grazing. How do the grasslands and steppes of the RPP and Patagonia respond to grazing? We focus here on the effects of grazing on ecosystem types that exhibit the greatest vegetation heterogeneity and for which data are available.

Grazing has been perceived to be the main agent of desertification in Patagonia (Soriano and Movia, 1986; Ares et al., 1990). However the impact of grazing varies widely among vegetation units, as illustrated from the shrub steppes of the Occidental District of Patagonia and the grass steppes of the Subandean District of Patagonia. The grass-shrub steppes of the Occidental District (fig. 14.5) (45°S, 70°W) show in general no major changes in vegetation physiognomy due to grazing. The steppes have kept a structure defined by two strata: shrubs and tussock grasses. The relative abundance of perennial and annual species does not change. The main changes induced by grazing are floristic (Perelman et al., 1997). Tussocks and shrubs are rep-

resented in the group of decreaseers as well as in the increaseers. In contrast, the grass steppes of Subandean District (45°S, 71°W) have experienced dramatic physiognomic changes due to grazing. As grazing impact increases, the dominant tussock grass species (*Festuca pallescens*) decreases and total plant cover decreases from 85% to less than 40%. Shrub encroachment is the final stage of grazing degradation of the grass steppes formerly dominated by *Festuca* (León and Aguiar, 1985; Bertiller et al., 1995). *Mulinum spinosum* or *Acaena splendens* become the dominant shrub species. Such changes reduce primary production (Páruelo et al., 2004) and modify water dynamics and herbivore biomass (Aguiar et al., 1996). In both vegetation units plant diversity is higher in ungrazed areas.

Many studies identify domestic herbivore grazing as a key factor in shaping the structure and functioning of the RPG (e.g., Sala et al., 1986; Rusch and Oesterheld, 1997; Lavado and Taboada, 1985; Chaneton et al., 1996). In the Uruguayan Campos, for example, grazing increases the relative abundance of summer (C₄) grasses, which in turn determine changes in the seasonal dynamics of primary production, moving the peak of production from spring to summer (Altesor et al., 2005). However, the response of vegetation to herbivory varies among subregions. Even though grazing increased species richness both in the Flooding Pampa (36°S, 58°W) and in the Uruguayan Campos (34°S, 50°W), in the first case the increase was accounted for by exotic cool season forbs, whereas in the second case the plant functional types that increased were prostrate grasses (Chaneton et al., 2002; Rush and Oesterheld, 1997; Sala et al., 1986; Altesor et al., 1998; Rodríguez et al., 2003).

Grazing may either increase or decrease above-ground net primary production (ANPP). Rusch and Oesterheld (1997) found in the Flooding Pampa that ungrazed areas showed higher ANPP than grazed plots, even if the initial biomass was the same. Altesor et al. (2005) found that grazed areas produced 51% more than the ungrazed paired situation. However, when the initial biomass was the same, ungrazed areas were 29% more productive. Such differences may be associated with the effects of the structural changes promoted by grazing (species and plant functional type composition, biomass vertical distribution) on the resource level (water, nutrients and light). By removing or avoiding the accumulation of senescent material, grazing may increase radiation interception. As far as light is the limiting factor, grazing would increase ANPP. Long-term grazing significantly reduced ANPP in the grass-shrub steppes of Patagonia (Adler et al., 2005).

Although most of the rangelands in Patagonia and the RPG include woody plants, grazing did not necessarily promote their increase. The only clear case of shrub encroachment is found in the *Festuca pallescens* steppes in western Patagonia (see above). Aguiar and Sala (1998) proposed that woody species will be promoted only in those

communities lacking grasses able to avoid grazing either because they are prostrate or unpalatable.

Some other disturbances may affect the grasslands and steppes of southern South America: fire and oil industry activities. In the RPG, fire is now restricted to the Campos subdivisions and small patches in the Mesopotamic Pampa and the Flooding Pampa. Fires are usually set by ranchers to eliminate low-quality forage and favor the regrowth of a more palatable and nutritious biomass. Agricultural use has significantly reduced fire frequency in the RPG (Di Bella et al., 2006). Summer fire can be an important disturbance agent in Patagonia, where accumulation of dry dead biomass is common. However, as electric storms are rare in Patagonia, fires are usually anthropogenic, associated with railway lines or human settlements. Fire frequency increases toward the boundary with the Monte scrublands. Oil extraction activities are the most intensive disturbance in Patagonia, though restricted in extent. Grazing affects almost all the region, but nowhere has it completely eliminated plant cover. Oil exploration and extraction cause extremely severe and irreversible damage in focal areas because they remove all vegetation cover, and often entire soil layers. Agriculture and fire have intermediate effects between oil extraction and grazing, both in terms of the extent and intensity of disturbance.

14.4 Conclusion

The plains, plateaus, and hills of Patagonia and the Río de la Plata host some of the largest extensions of semi-natural rangelands on Earth. The initial appearance of human populations in these areas was relatively late compared to most other continents, and population densities remained low until the late nineteenth-century period of European settlement. Patagonia is the last region of the Americas to be reached by humans entering via the Bering Strait, and also one of the last regions to be colonized by Europeans. Domestic livestock were introduced, depending on the area, between 100 and 400 years ago. Agriculture occupied a relatively small fraction of the area, even in the most humid zones.

At the onset of the twenty-first century, however, rapid changes are taking place, both in Patagonia and the Río de la Plata region. Natural resources in Patagonia have come under intense pressure due to extractive activities (mainly oil exploitation), and sheep grazing has generated desertification in many foci across this ecologically fragile region. Impacts of sheep on this landscape have become more extensive during the past decade due to a reduction in wool prices, the lack of productive alternative land uses, and the absence of an environmental policy from federal and state agencies and governments. Poor understanding of the heterogeneity of Patagonian ecosystems and how they respond to environmental stresses and disturbances has also

contributed to the degradation processes. In the Río de la Plata grasslands several factors, including the prices of commodities (mainly soybean) and the expansion of low-tillage techniques, are promoting a fast expansion of agriculture over natural and semi-natural grasslands. While producing significant economic benefits from the exports generated, land use in Patagonia and the Río de la Plata plains is modifying the structure and functioning of ecosystems in a way that compromises their ability to provide basic ecosystem services. The extremely small area under governmental protection aggravates the threat to these unique ecosystems.

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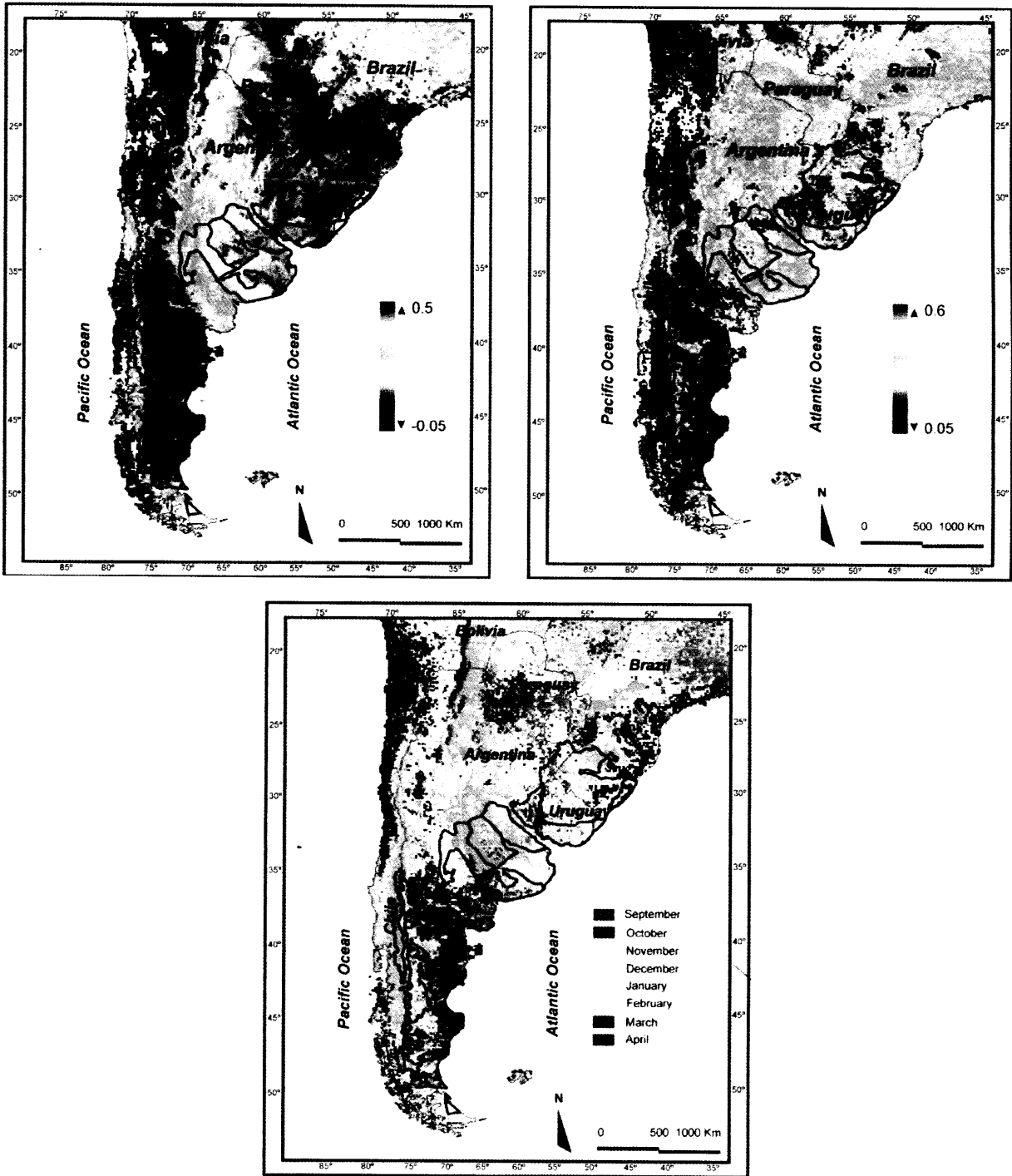


Figure 14.9 Top left: Annual integration of the normalized difference vegetation index (NDVI-I), a spectral index used as a surrogate of net primary production (NPP). Top right: Relative annual range of NDVI (maximum minus minimum NDVI relative to NDVI-I), a descriptor of NPP seasonality. Bottom: Date of maximum NDVI. Data were derived from the Pathfinder AVHRR Land database (NASA) and are averages over the 1981–2000 period. Figures based on Paruelo et al. (2001).