

CHAPTER 7

Temperate Grasslands Vulnerable to Plant Invasions: Characteristics and Consequences

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7.1 INTRODUCTION

From at least the time of de Candolle's publication of *Géographie Botanique Raisonnée* in 1855 the great disparities in the extent of plant invasions worldwide have been the subject of continuing observation, conjecture, and analysis (Hooker, 1860; Darwin, 1872; Wallace, 1892; Salisbury, 1933; Crawley, 1986). Even though much of this inquiry is still based on anecdotes (Thellung, 1912; Ridley, 1930; Elton, 1958), several inextricably linked central questions have emerged. How has evolution seemingly predisposed the native floras in some regions such that members of these floras have repeatedly become naturalized elsewhere? Do these successful invaders come largely from communities less likely to be invaded themselves?

Clear answers are obviously elusive because any taxon reflects the often orthogonal forces in its phylogeny (Gould and Lewontin, 1979; Harper, 1981), a problem only exacerbated for comparisons among communities. But if we are to answer these questions satisfactorily, especially if the answers are to predict the course of future invasions (Forcella, 1985a; Forcella and Wood, 1984; Regal, 1986), sound experimentation and manipulation will stem in part from assembling observations of invasions with as few conflicting (and untestable) explanations as possible. One synthetic approach for organizing these observations relies on using a single biome that displays a wide range of responses to plant invasions (Naveh, 1967; Moore, 1983; Kruger *et al.*, this volume). Despite all the environmental variation within such a large biogeographic unit, the constituent communities still share similar climate, life forms, and resultant physiognomy, thereby eliminating at least some explanations for communities' varying vulnerabilities to invasion.

Temperate grasslands* provide examples to simultaneously explore these

*I define temperate grasslands (steppes) as naturally occurring treeless communities in middle latitudes (between 30° and about 50°); perennial grasses usually dominate these communities because soil moisture or effective precipitation is unfavorable to support the natural establishment of trees on level ground. With further aridity or saline soils shrubs may predominate. Fire and the role of animals do not in themselves explain the distribution of these grasslands.

central questions and their specific components. The temperate grasslands in Australia, South America and western North America (the Intermountain West and California's Central Valley) are among the extreme examples of what Elton (1958) has called, 'the great historical convulsions' of the earth's biota: massive changes in the species composition of once vast communities through the transoceanic transport of alien organisms and their subsequent incursion into new ranges.

In less than 300 years (and in most cases, little more than 100 years) much of the temperate grassland outside Eurasia (a collective area of 2.0×10^6 km² or more than the combined areas of Spain, France, Portugal, Belgium, the Netherlands, and West Germany) has been irreparably transformed by human settlement and the concomitant introduction of alien plants. Few other changes in the distribution of the earth's biota since the end of the Pleistocene have been as radical (cf. the spread and proliferation of humans) or as swift (cf. plant and animal invasions on remote islands).

Not all temperate grasslands have proven so vulnerable to plant invasions. The grasslands in Eurasia and especially in southern Africa and central North America have also received many alien plants, but these communities have changed comparatively little, except where plowed (Costello, 1944; Henderson and Wells, 1986). Consequently, within one major biogeographic unit, with representatives on six continents we can compare communities extensively transformed with those little altered by plant invasions.

This chapter is divided into three sections. The first section discusses those readily identifiable traits that made four temperate grasslands vulnerable to massive plant invasions and naturalizations. The second, longer section illustrates consequences of these characteristics in the transformation of the vegetation, while the third section deals with some potential hazards for these vulnerable grasslands.

7.2 TEMPERATE GRASSLANDS VULNERABLE TO PLANT INVASION: THE CHARACTERISTICS

The two quintessential characteristics of temperate grasslands vulnerable to plant invasion are the lack of large, hooved, congregating mammals in the Holocene or longer and dominance by caespitose grasses. These characteristics are so intrinsically related that a clear chronology of cause and effect cannot always be separated. For example, in each of these grasslands caespitose grasses persisted because large mammalian grazers were either rare or missing altogether. Yet in western North America, the phenology of these tussock grasses ensured that bovids remained so sparse that they had been almost extirpated before Europeans arrived.

7.2.1 The lack of large, hooved, congregating mammals

Each vulnerable grassland lacked sufficient large mammalian grazers to affect selection in perennial grasses. The lack of placental mammals in Australia (other than rodents, bats, and the dingo) before the introduction of many mammals with European colonization needs no elaboration (Archer, 1981). The largest native grazers were the red and the Eastern gray kangaroos; both species' adults weigh < 100 kg (Frith and Calaby, 1969). South America's native fauna includes placental mammals, but lacks bovids and sheep (Simpson, 1980), major phylogenetic lines for large, congregating grazers. The Holocene distribution of large grazers in North America represents a curious alternative situation: enormous herds of bison were supported on the Great Plains, yet these large (500 kg), congregating animals occurred only in small, isolated herds in the Intermountain West (Mack and Thompson, 1982) and probably none occurred in California's Central Valley by historic time (Roe, 1951). Elk, deer, and antelope are still prevalent but were apparently never abundant.

The low numbers of these animals in the Intermountain West is reflected in the Holocene fossil record (Schroedl, 1973), in the independent accounts of 19th century explorers (Mack and Thompson, 1982 and references therein), and even in the insect fauna. No members of *Onthophagus*, a widespread genus of dung beetles, are native to western North America, even though 34 species of this genus occur east of the Rockies (Howden, 1966). The phenology of the dominant C₃ caespitose grasses may account for this paucity of bison; in both vulnerable grasslands in western North America the native grasses on zonal soils are all vegetatively dormant by early summer when lactating bison need maximum green forage. The only green forage then available would have been limited to river valleys, thereby placing a severe constraint on the size and distribution of herds (Mack and Thompson, 1982).

7.2.2 The dominance of caespitose grasses

Why are communities dominated by caespitose grasses often so vulnerable to plant invasion? Much of the explanation stems from the morphology and phenology of caespitose or tussock grasses (Mack and Thompson, 1982). Tussock grasses develop by intervaginal tillering in which the emerging tillers remain erect inside the leaf sheath. A tightly-packed cluster of such erect tillers is much more exposed to grazing by ungulates than the low, sprawling form of rhizomatous grasses. In western North America the apical meristem in caespitose grasses becomes elevated as it resumes growth in late winter. Thus, the meristem is placed in jeopardy throughout its growing season to removal by grazers (Branson, 1953; Heady, 1975). Without the ability to readily produce axillary buds, the population of a caespitose grass persists on a site exclusively through sexual reproduction. But in a grazing environment the flowering tillers are often

removed. The seedlings of these grasses are also sensitive to grazing. In trials comparing the survival of the seedlings of *Agropyron spicatum*, a dominant caespitose grass in the Intermountain West, with seedlings of the aggressive alien *Bromus tectorum*, *Agropyron spicatum* seedlings routinely died if grazed once by voles. Seedlings of *Bromus tectorum* persisted even if similarly grazed every 2 weeks (Pyke, 1983).

Rhizomatous or turf grasses display alternative development: extravaginal tillering in which the emerging stem splits the leaf sheath. Consequently, the grass develops a sprawling habit because tillers remain prostrate. This crucial difference among grasses in their morphology has probably been under strong selection by grazers; grazed or clipped populations repeatedly display a prostrate habit under genetic control (Warwick and Briggs, 1978; Gray and Scott, 1980). The extent to which large mammalian grazing may have influenced natural selection in grasses is illustrated by the morphology of *Poa pratensis*, a rhizomatous grass now widely distributed as forage in temperate grasslands. *Poa pratensis* displays (1) bud height at ground level throughout the growing season, (2) underground rhizomes, (3) high shoot density, (4) short leaves and usually short stature, (5) a conduplicate stem and leaf, (6) tolerance of puddling (i.e., being covered by mud), and (7) a low flowering to vegetative culm ratio (Mack and Thompson, 1982 and references therein).

The hazards created for a caespitose grass by some grazers are not limited to herbivory; ungulates the size of modern cattle can cause much damage to herbaceous plants with their hooves. The damaged turf of rhizomatous grasses is readily replaced by vegetative propagation, an ability caespitose grasses usually lack (Jewiss, 1972). Such damage is intensified locally by large, gregarious animals such as bison through their wallowing and milling about. The native Holocene grazers in the vulnerable grasslands were either too light (e.g. the guanaco in South America, kangaroos in Australia, deer and antelope in North America) or too sparse (such as elk and bison in western North America) to affect selection in grasses through trampling.

In caespitose grasslands trampling can also alter community composition by destroying the matrix of small plants between the tussocks. For example, in undisturbed communities in the Intermountain West this matrix is occupied by herbaceous perennials, annuals, shrubs, and a cryptogamic crust composed of mosses, lichens, and liverworts. If intact, the crust restricts seedling establishment by preventing the radicle's contact with the mineral soil. But once the crust is broken by hooves, the mineral soil is exposed and seedlings may readily establish (Daubenmire, 1970). Once European settlers arrived, alien plants began to colonize these new and renewable sites of disturbance. Whether through grazing or trampling, or both, the common consequences of the introduction of livestock in the four vulnerable grasslands were destruction of the native caespitose grasses, dispersal of alien plants in fur or feces, and continual preparation of a

seed bed for aliens that evolved with large mammals in Eurasia and Africa (Roseveare, 1948; Burcham, 1957; Mack, 1981).

The caespitose habit does not always spell vulnerability to grazing and trampling, although that outcome commonly occurs. The few successful forage grasses naturalized on arid range lands in the Intermountain West are caespitose, most notably the *Agropyron cristatum*–*Agropyron desertorum* complex. They are native to arid central Asia where strong selection by native grazers has long operated. Among other features, these grasses have flexible resource allocation in which tillers are replaced while new root growth is curtailed (Caldwell *et al.*, 1981; Richards, 1984). These species present intriguing cases in which features have arisen that largely compensate for the possession of the caespitose habit in a grazing, trampling environment.

The comparative invulnerability of the other two temperate grasslands settled by Europeans, the Great Plains of North America and the South African veld, seems tied to their dominance by both rhizomatous and caespitose grasses tolerant of grazing. For the Great Plains this resistance to grazing correlates with the conspicuous replacement of stipoid grasses by genera from both Asia and southern North America (e.g. the rhizomatous genera *Buchloe* and *Bouteloua*), a replacement not duplicated in other temperate grasslands in the western hemisphere. Descendants of these Tertiary immigrants along with genera already present (e.g. *Andropogon*, *Sorghastrum*, *Panicum*) (Stebbins, 1975) likely underwent the strong selection by bison beginning in middle Pleistocene that led to their later resistance to livestock (Guthrie, 1970; Mack and Thompson, 1982). The other grasslands in the western hemisphere received different genera, such as *Agropyron* and *Festuca* in western North America and *Piptochaetium* in South America. Why did these other grasslands either not receive or not retain the same late Tertiary immigration as the Great Plains? The answer for western North America may lie in the apparent inability of the descendants of this Tertiary immigration, particularly the C₄ species, to tolerate summer drought (Teeri and Stowe, 1976; Ehleringer, 1978), perhaps the overriding climatic feature of both the Intermountain West and California's Central Valley.

7.3 TEMPERATE GRASSLANDS VULNERABLE TO INVASION: THE CONSEQUENCES

Despite the wide geographic separation of most of the vulnerable grasslands from each other, the chronologies of their transformations by alien plants are remarkably consistent. Each was colonized by western Europeans (mainly Britons and Spaniards) and later intensively settled by their descendants (Australians, Argentineans, and Americans). And each region was eventually developed to raise the cereals, legumes, and forage crops of western Europe. This similarity in agriculture coupled with these regions' similarity in evolutionary

history (and the resultant habit of the dominant grasses), overrode many regional differences in climate, soils, topography, and native flora. As a result, each now share much the same alien flora.

7.3.1 The temperate grasslands of South America

Temperate grasslands in South America are restricted to the southern end of the continent but include some of the highest latitude (about 54°) grasslands altered by alien plants. These treeless communities are readily divided into a humid grassland in Uruguay and northern Argentina (centering on the pampas south of Buenos Aires) and an arid steppe in Patagonia to the south. Together these two areas occupy over 1 million km² (Soriano, 1979).

The climate of the pampas is characterized by warm often humid summers and mild winters; temperatures usually remain well above freezing throughout the year (Trewartha and Horn, 1980). Annual precipitation can be as much as 1000 mm in the humid pampas near Buenos Aires, but declines markedly in the interior (Trenque Lauquen, 650 mm) and southward (Bahia Blanca, 635 mm). Although there is usually no droughty season, summer receives more precipitation than winter (Rumney, 1968).

The conspicuous dominants in the original pampean vegetation are all caespitose grasses (Cabrera, 1971). Prominent xeric grasses in the pampas south of Buenos Aires form the tallest layer in a multi-layered community and include *Agropyron laguroides*, *Aristida murina*, *Briza subaristata*, *Panicum bergii*, *Piptochaetium bicolor*, *Stipa hyalina*, and *Stipa papposa* (Parodi, 1930). Herbs, such as *Asclepias mellodora*, *Baccharis cordifolia*, *Heimia salicifolia*, *Melica macra*, *Sphaeralcea miniata*, and *Verbena chamaedryfolia*, occupy the shorter layers (Parodi, 1930; Soriano, 1979). With increasing aridity to the west, *Poa ligularis*, *Stipa ichu*, *Stipa tenuissima*, and *Stipa trichotoma* persist (Soriano, 1979).

Patagonia lies south of the pampas and is characterized by lower rainfall (< 500 mm per year) and lower plant coverage than in the pampas, but caespitose grasses are still conspicuous. *Stipa chrysophylla*, *Stipa humilis*, and *Stipa speciosa* along with *Bromus macranthus*, *Hordeum comosum*, and *Poa ligularis* and a shrub, *Mulinum spinosum*, tolerate these xeric conditions (Soriano, 1979). Further south a steppe dominated by *Festuca pallescens* borders the subantarctic forest.

7.3.1.1 The invasion of 'European cardoon and a tall thistle'

The pampas was the site of the earliest documented transformation of a landscape by alien plants. In 1833 HMS Beagle reached Bahia Blanca on the coast of central Argentina, and Darwin elected to explore the country north to Buenos Aires on horseback (Darwin, 1898). In the *Origin of Species* he remarked that the European cardoon (*Cynara cardunculus*) and a tall thistle (*Silybum marianum*) '... are now the commonest [plants] over the whole plains of La Plata, clothing square leagues of surface almost to the exclusion of every other plant...' (Darwin, 1872).

Darwin reckoned the new range of cardoon was already vast because even in southern Uruguay he found, 'very many (probably several hundred) square miles are covered by one mass of these prickly plants, and are impenetrable by man or beast. Over the undulating plains, where these great beds occur, nothing else can now live.' In the Banda Oriental, for example, the few estancias were restricted to valleys because these aliens dominated the zonal soil (Darwin, 1898).

The scenes Darwin reported had probably arisen in less than 75 years von Tschudi (1868) claims the cardoon was not in Argentina before about 1769. Hudson, who lived south of Buenos Aires in the 1840s, gives a graphic description of the environmental transformation caused by these alien plants. 'In places the land as far as one could see was covered with a dense growth of cardoon thistles, or wild artichoke, of a bluish or grey-green colour, while in other places the giant thistle [*S. marianum*] flourished... standing when in flower six to ten feet high' (Hudson, 1923). Prominence of *S. marianum* varied from year to year, but in a 'thistle year' the plants became so prominent they confined travel on horseback to narrow cattle tracks. Darwin (1898) learned that during such years robbers hid among the thistles. When he asked whether robbers were numerous in the area, the oblique answer was, 'The thistles are not up yet.'

By December the thistles' vegetative growth was dead, but the combustibility of the stalks greatly enhanced the danger of fire. The dried stalks of the cardoon and the giant thistle were nevertheless the main, if not the only, source of fuel in the treeless pampas, and large piles of the highly flammable stalks were stacked outside each hut (Hudson, 1923). In addition to altering the frequency and intensity of fire, their thick roots also influenced the structure of the stoneless soil (Haumann, 1927) and may have eliminated native plants locally by shading.

Referring to the cardoon, Darwin (1898) doubted, '... whether any case is on record, of an invasion on so grand a scale of one plant over the aborigines.' Even after myriad invasions over the last century and a half, the impact of these two composites in Argentina rivals the role of any other alien plants anywhere, including *Eichhornia crassipes* and *Salsola kali*. They were eventually controlled only with the extensive plowing of the pampas at the end of the 19th century, although both are still regarded as serious problems in Argentina (Marzocca, 1984).

7.3.1.2 Farming brings new invasions

von Tschudi (1868) claimed *C. cardunculus* arrived in Argentina in the hide of a donkey. Even if apocryphal, this example illustrates that many early plant immigrants probably arrived with livestock, and for 250 years these flat plains were grazed but not extensively plowed. But beginning in the mid-19th century immigrant farmers were encouraged to raise alfalfa as a means of raising even more livestock. Transforming the pampas from pasturage to farm land greatly expanded the opportunity for alien plant entry and establishment. Berg (1877) lists over a 100 vascular plants as adventive near Buenos Aires and in Patagonia; many species in his list are common contaminants of seed lots (e.g. *Capsella*

bursa-pastoris, *Chenopodium album*, *Marrubium vulgare*, *Stellaria media*) and were likely spread with farming.

Argentina has always had strong commercial ties to western Europe, and it is not surprising that most alien plants in Argentinean grasslands originated in Eurasia. Parodi (1930) considered 60 species as naturalized (as opposed to merely adventive) in the Pergamino District near Buenos Aires. His extensive list includes such well-known plant invaders as:

<i>Avena fatua</i>	<i>Avena ludoviciana</i>	<i>Brassica nigra</i>
<i>Bromus hordaceus</i>	<i>Centaurea melitensis</i>	<i>Poa annua</i>
<i>Cynodon dactylon</i>	<i>Erodium malacoides</i>	<i>Festuca myuros</i>
<i>Lactuca serriola</i>	<i>Lolium multiflorum</i>	<i>Marrubium vulgare</i>
<i>Medicago lupulina</i>	<i>Nasturtium officinale</i>	<i>Rumex crispus</i>
<i>Portulaca oleracea</i>	<i>Convolvulus arvensis</i>	<i>Silybum marianum</i>
<i>Sisymbrium officinale</i>	<i>Stellaria media</i>	<i>Urtica urens</i>

Parodi considered 16 species, including *Avena fatua*, *Avena ludoviciana*, *Briza minor*, *Bromus hordaceus*, *Festuca myuros*, *Genraium dissectum*, and *Lolium multiflorum* so common in fields as to be indistinguishable in their roles from natives. *Lolium multiflorum* replaces alien dicots such as *Conyza bonariensis* and *Carduus acanthoides* in succession in abandoned agricultural fields, although it may be replaced later by native perennial grasses (D'angela *et al.*, 1986).

The introduction, spread and persistence of many aliens can certainly be attributed to their close association with crops. The seeds of *Avena fatua* are common contaminants of wheat and barley, and seeds of *Lactuca serriola* and *Stellaria media* often occur in seed lots of alfalfa (Mack, 1986). Many annual bromes undoubtedly arrived in the pampas in contaminated wheat and are now naturalized (e.g. *Bromus japonicus*, *Bromus mollis*, *Bromus racemosus*) (Parodi, 1947).

Alien annual bromes are also prominent in the semi-arid steppe of Patagonia. Perhaps the most widespread alien in this group is *Bromus tectorum*, which has occupied many disturbed sites and occurs along roadways (Soriano, 1956a). Other alien bromes now naturalized in this most southerly temperate grassland include *Bromus rigidus*, *Bromus rubens*, *Bromus secalinus* and *Bromus sterilis* (Parodi, 1947). Although alien grasses are prominent, other Eurasian aliens such as *Capsella bursa-pastoris*, *Erodium cicutarium*, *Erysimum repandum*, *Microsteris gracilis*, *Sisymbrium altissimum*, and *Taxaracum officinale* are also common (Soriano, 1956a, 1956b).

More recent immigrants pose further threats in the pampas and Patagonia. Marzocca (1984) lists several dozen aliens deemed so serious as to be officially considered 'plagues of agriculture' in Argentina. His list includes *Carduus nutans*, *Centaurea calcitrapa*, *Cyperus rotundus*, *Kochia scoparia*, *Salsola kali*, and *Sorghum halepense*. He also lists *Diplotaxis tenuifolia* which was deliberately imported as a source of nectar for honeybees but is now spreading along

roadsides in Patagonia (G. de Fosse, personal communication). *Senecio madagascariensis* typifies many new plant immigrants that may become serious invaders. Although found in the 1940s around Bahia Blanca, the alien has since spread to the southern pampas where it inhabits both agricultural fields and disturbed sites (Verona *et al.*, 1982). The massive transformations of Argentinean vegetation that began with the introduction of the 'European cardoon and a tall thistle' clearly continue.

7.3.2 Grasslands in the Intermountain West of North America

I have recently reviewed the consequences of alien plant invasions in the intermountain grasslands of western North America (Mack, 1981, 1984, 1986). Consequently, the purpose of my brief comments here is to provide a basis for comparison with these other vulnerable grasslands.

The grasslands of the Intermountain West occur in a geomorphologically diverse region bounded by the Rocky Mountains to the east and the Cascade-Sierra Nevada Ranges to the west. To the north these grasslands border coniferous forest at the convergence of the Cascade and Rocky Mountains in central British Columbia; to the south they form a regional ecotone with desert in southern Nevada. The region's geomorphological diversity includes both broad plateaus drained by large rivers (principally the Columbia and the Snake) and many small forested mountain ranges in Oregon, Utah, and especially Nevada. Consequently, the area originally supporting temperate grassland appears in map view as a matrix surrounding these isolated uplands (Daubenmire, 1969).

The regional climate is influenced principally by the annual movement of the prevailing Westerlies and the reduction of the moisture in these air masses as they traverse the Cascade Range and the Sierra Nevada. As a result precipitation, including snow, is received primarily in autumn and winter. Summers are hot and dry (Daubenmire, 1970).

Where undisturbed, the temperate grasslands are either dominated solely by caespitose grasses (*Agropyron spicatum*, *Festuca idahoensis*, *Stipa comata*, and *Poa secunda*) or these grasses share dominance with drought-tolerant shrubs (principally *Artemisia tridentata* but also *Sarcobatus vermiculatus*, *Chrysothamnus nauseosus* and *Atriplex confertifolia*). Prominence of shrubs is usually in inverse relation to effective precipitation. The matrix between caespitose grasses and shrubs in these communities is occupied by annuals and perennial herbs, particularly composites (e.g. *Balsamorhiza sagittata*, *Helianthella uniflora*) and legumes (*Astragalus* spp. and *Lupinus* spp.). In addition the soil surface is covered by a thin cryptogamic crust (Daubenmire, 1969, 1970).

There were few permanent European settlements in this vast region until 1870. But the repeated discovery of gold soon after the American Civil War, followed by recognition of the potential of the Columbia and Snake River drainages for growing wheat, sparked rapid and intensive settlement from 1870 to 1890

(Meinig, 1968). Tracts unsuitable for crops were rapidly converted to pasturage. Even in areas never plowed, livestock soon destroyed the native communities. Here as in other vulnerable grasslands, this continual disturbance greatly facilitated the establishment of aliens (Mack, 1981).

Alien plants appeared with the first European settlements and became more diverse and conspicuous as settlement increased. *Agropyron repens*, *Hordeum pusillum*, and *Erodium cicutarium* appear in the few lists of plants collected before 1850 (Mack, 1986). Some, such as *Erodium cicutarium*, may have arrived as seeds attached to livestock. But the entry for most was through contaminated lots of crop seeds. Repeatedly agriculturists of the era complained about the accidental (or even deliberate) contamination of seed lots. By 1900 Seed Purity Laws had been enacted, but many noxious aliens had already entered the region; many more arrived later. For example, by 1929 the alien flora within five counties in eastern Washington and adjacent Idaho had grown to 200 species (Mack, 1986).

The speed and extent of these regional invasions was facilitated by a railroad system established simultaneously with the wave of human immigrants in the late 19th century. Many aliens were first recorded along railroad tracks (e.g. *Bromus tectorum* and *Salsola kali*) (Mack, 1981, 1986). As a result of this effective means of dispersal, some aliens filled their new ranges in as little as 40 years, such as *Bromus tectorum* which covered $> 200\,000\text{ km}^2$ between ca. 1890 and 1930 (Mack, 1981).

Although many aliens arrived and became naturalized, probably less than a dozen have become community dominants (e.g. *Avena fatua*, *Bromus tectorum*, *Cirsium vulgare*, *Elymus caput-medusae*, *Hologeton glomeratus*, *Poa pratensis*, *Salsola kali*, and *Sisymbrium altissimum*) (Young *et al.*, 1972; Yensen, 1981). Yet these species along with the natives, *Chrysothamnus nauseosus*, *Matricaria matricaroides*, *Plantago patagonica*, and *Achillea lanulosum*, have irreparably altered much of the regional vegetation in less than 50 years (Daubenmire, 1970). Neither the areal extent of this grassland, nor its floristic diversity, nor its interruption by mountains has had any measurable effect in retarding the spread of aliens. The outlook is only for more change in the vegetation as new immigrants (e.g. *Aegilops cylindrica*, *Euphorbia esula*, *Centaurea* spp., *Isatis tinctoria*, *Ventanata dubia*) displace the old through the same agencies that fostered earlier invasions: disturbance and transport.

7.3.3 Grasslands in the Central Valley of California

Between the Coast Ranges of California and the Sierra Nevada lies the Central Valley. This immense elongate trough is the drainage for two major rivers, the Sacramento and the San Joaquin, and their tributaries. Although part of the Valley originally contained marshes along these rivers, the zonal soils supported temperate grasslands. The Valley's climate is influenced by much the same forces that determine climate in the Intermountain West: the annual movements of the prevailing Westerlies and the orographic effect caused by the mountain ranges to the west. In summer the Westerlies move inland far north of California, and little

precipitation is received; summers are hot and mostly dry. Most precipitation falls in winter when the Valley lies within the storm track of the Westerlies. In any season however precipitation is reduced as it passes over the Coast Ranges (Major, 1977).

Other than remote islands, the vegetation in few other areas has been altered so completely by plant invasions. Consequently conjecture surrounds most of our knowledge of these grasslands, although the few fragments of putative pristine vegetation suggest *Stipa pulchra* was the chief dominant. It was associated with other perennial grasses including, *Aristida divaricata*, *Elymus glaucus*, *Festuca idahoensis*, *Koeleria cristata*, *Muhlenbergia rigens*, *Stipa cernua*, and *Stipa coronata*; all are caespitose (Heady, 1977; Daubenmire, 1978; Bartolome *et al.*, 1986). Among the native perennial grasses only *Elymus triticoides* is a sod-former (Burcham, 1957). Shrubs were not conspicuous except on alkali or saline soils, such as in the southern San Joaquin Valley (Heady, 1977).

The invasions of alien plants began with Spanish settlement in 1769, and by 1823 Spanish missions dotted the California coast as far north as Sonoma (Parish, 1920). Hendry's (1931) dissections of the adobe bricks used to build these missions reveal aliens, such as *Avena fatua*, *Brassica nigra*, *Centaurea melitensis*, *Chenopodium album*, *Hemizonia congesta*, *Hordeum pusillum*, and *Poa annua*, had entered California by 1824; *Erodium cicutarium*, *Rumex crispus*, and *Sonchus asper* had entered even earlier. The extent to which feral herds were responsible for spreading alien plants through the Central Valley cannot be accurately established. By at least 1772 the Spanish were entering the Valley, and it is likely they left livestock behind in their travels (Burcham, 1957). These animals and their descendants could have contributed to the introduction and dissemination of aliens. For example, *E. cicutarium* could have been easily spread by animals because its corkscrew awn tenaciously adheres to fur.

By whatever mechanisms, *Avena fatua* gained prominence early. Leonard traversed the Central Valley in 1833 and saw, 'a large prairie covered with wild oats—which at this season of the year when nothing but the stock remains, has much the appearance of common oats' (Leonard, 1934). The prominence of wild oats was independently cited by Bryant (1848) who travelled along the Mokelumne River, a tributary of the San Joaquin River, in 1846 and 1847.

The role Spanish settlements played in spreading alien plants was dwarfed by the human immigration sparked by the discovery of gold in the Central Valley in 1848. Not only did this event enormously increase the opportunity for alien plant entry in contaminated seed lots, imported forage, and packing materials, but American settlers also created a huge new market for the Central Valley's livestock. The huge numbers of cattle and sheep recorded for the Central Valley from the mid-19th century onward testify to the tremendous grazing and trampling these animals must have exerted on the communities dominated by caespitose grasses (Burcham, 1957). In a pattern repeated 25 years later in the Intermountain West, the rapid destruction of native grasslands by livestock sparked appeals for the importation of forage species (Bolander, 1866; Cronise,

1868). Such appeals were soon answered with the deliberate introduction of *Cynodon dactylon*, *Lolium perenne*, *Medicago lupulina*, and *Sorghum halepense* (Robbins, 1940).

Concomitant with the massive increase of livestock the native grasses entered a devastating cycle of human-induced changes and natural calamities. Both seedlings and adult plants of these native grasses were destroyed by heavy trampling and grazing; losses not readily replaced because the native grasses lack a large seed bank. Episodes of both severe drought and flooding between 1828 and the 1860s and the continual activity of livestock further combined to disrupt the age structure within these slow-growing plants. In contrast the alien annuals, such as *Avena fatua*, *Bromus rubens*, and *Festuca myuros* were much more tolerant of grazing. Even if devastated by the vagaries of weather, recruits of the alien species could emerge from a persistent seed bank (Baker, 1978).

Replacement of the native plants with aliens was not caused totally by livestock. By 1865 much of the Central Valley was devoted to the production of wheat, barley, and alfalfa (Brewer, 1883a), and this agriculture allowed many new aliens to be accidentally introduced. Many species in Robbins' (1940) list of early plant immigrants are common contaminants in the seed lots of legumes (e.g. *Anthemis cotula*, *Capsella bursa-pastoris*, *Plantago lanceolata*, *Plantago major*, *Portulaca oleracea*, *Rumex acetosella*, *Rumex crispus*, *Stellaria media*) or cereals (e.g. *Bromus secalinus*, *Convolvulus arvensis*, *Festuca myuros*, *Poa annua*), or both (e.g. *Sonchus asper*).

By 1880 transformation of the vegetation in the Central Valley to an annual grassland was virtually complete. Robbins (1940) lists 91 alien species established in California by 1860. His list includes composites such as *Cirsium arvense*, grasses such as *Avena fatua*, *Bromus rubens*, *Bromus rigidus*, and *Cynodon dactylon*, and other commonly dispersed species (*Marrubium vulgare*, *Verbascum thapsus*, and *Portulaca oleracea*).

The early plant immigrants have not always retained their role as dominants as newer immigrants reached the Central Valley. According to Burcham (1957), the dominance of alien plants in California, including the Central Valley, has gone through four phases.

Phase I dominants: (pre-1860)	<i>Avena fatua</i> and <i>Brassica</i> sp. (<i>nigra</i> ?).
Phase II dominants and associates: (ca. 1860–1880)	<i>Erodium cicutarium</i> , <i>Hordeum leporinum</i> , <i>Bromus</i> spp., <i>Gastrium ventricosum</i>
Phase III dominants: (early 1880s)	<i>Hordeum leporinum</i> , <i>Hordeum hystrix</i> , <i>Bromus rubens</i> , <i>Madia sativa</i> , <i>Centaurea melitensis</i>
Phase IV dominants: (modern)	<i>Elymus caput-medusae</i> , <i>Aegilops</i> <i>triucialis</i> , <i>Brachypodium distachyon</i>

Heady (1977) concurs with this basic scheme or replacement, while Baker (1978) views a three-phase transformation.

The evidence for some of Burcham's phases is equivocal. Contemporary accounts agree *Avena fatua* was the most conspicuous and probably the most prominent alien from 1840 to 1860 (Bolander, 1866; Brewer, 1883b). But by 1868, Cronise reported wild oats were, 'fast disappearing' in California due to overgrazing. In documenting the slow rise to prominence of *Erodium cicutarium* (filaree) Brewer (1883b) mentions Nuttall collected this species far in the interior of the state by 1836. Although Brewer claims filaree increased until perhaps 1865 to 1870 (simultaneous with the decline in *Avena fatua*), he clearly states that in comparison to wild oats, filaree, 'never had such possession of the soil anywhere.' *Hordeum leporinum* had arrived by the 1860s, but Brewer describes it only as occurring where overgrazing is too severe for either filaree or wild oats.

The case for Burcham's Phase III occurring in the Central Valley is not substantiated by his references: neither Brewer (1883b) nor Hilgard *et al.* (1882) mentions these aliens as dominant at that time. Instead Hilgard's (1891) discussion of important aliens in California is a more reliable account from which the relative status of aliens in the Central Valley can be gleaned. Apparently *Erodium cicutarium* was still prominent along with *Brassica nigra*, *Bromus mollis*, *Centaurea melitensis*, *Centaurea solstitialis*, *Eremocarpus setigerus*, *Erigeron canadense*, *Lolium temulentum*, and *Silene gallica*.

As Robbins (1940) points out, the absence of some aliens in Hilgard's list that became important in the 20th century, such as *Salsola kali*, suggests these aliens arrived or gained prominence more recently, or both. Late entry is perhaps best documented for *Elymus caput-medusae*, a dominant in Burcham's Phase IV. It was first recorded on the west coast in 1887 (McKell *et al.*, 1962) but is now an important alien in the Valley (Heady, 1977; Baker, 1978). Whatever the chronology of dominance, the vegetation in the Central Valley has long borne virtually no resemblance to the pre-settlement plant communities. The region illustrates the current extreme to which a temperate grassland can be altered by disturbance and plant introductions.

7.3.4 Australian temperate grasslands

The temperate grasslands of Australia defy clear delineation because so much of the continent, although arid is not temperate, and much temperate forest has been converted to grassland. Perhaps for these reasons Moore (1970a) and his collaborators view the extent of temperate grasslands as confined to a few small areas in eastern South Australia, and the tablelands in Victoria and New South Wales. Groves and Williams (1981) largely share this view. Much larger areas in southern Australia are, however, routinely considered shrub steppe and are environmentally similar to the arid shrub steppe; i.e. temperate, grassland, in the Intermountain West and Patagonia. From the standpoint of the consequences of

alien plant invasions for these treeless areas (as well as much grassland created from sclerophyllous woodland and eucalypt forest), they will be considered collectively in my discussion.

The interaction between precipitation and temperature dictates the extent of grasslands in Australia. Precipitation for most of these grasslands results from systematic cyclonic storms derived from maritime polar air; the bulk of this precipitation falls as rain in winter. Annual rainfall ranges from > 600 mm in New South Wales to about 250 mm along the diffuse border between shrub-steppe and desert in the center of the continent. Although frost may be frequent, it is rarely persistent; monthly average temperatures in summer can exceed 25 °C (Rumney, 1968; Beadle, 1981).

Here as in the other three invaded temperate grasslands I have considered, the dominant native grasses are all caespitose (Beadle, 1981), and especially in southeastern Australia they are now largely confined to railroad right of ways, cemeteries, and other sites long protected from grazing (Groves, 1965). Perhaps the most wide ranging caespitose grass, even if not dominant throughout its range within the mesic to humid grasslands, is *Themeda australis*. *Dichelachne crinita*, *Eryngium rostratum*, *Poa caespitosa* sensu lato, *Stipa aristiglumis*, and *Stipa bigeniculata* were common associates or dominant locally (Patton, 1936; Groves, 1965; Connor, 1963, Moore, 1970b). Large areas in southern Australia are dominated by chenopodiaceous shrubs with a matrix of perennial grasses and smaller forbs. The most common shrubs are *Atriplex vesicaria*, *Kochia sedifolia*, *Kochia pyramidata*, and *Kochia astrotricha* (Perry, 1970; Beadle, 1981).

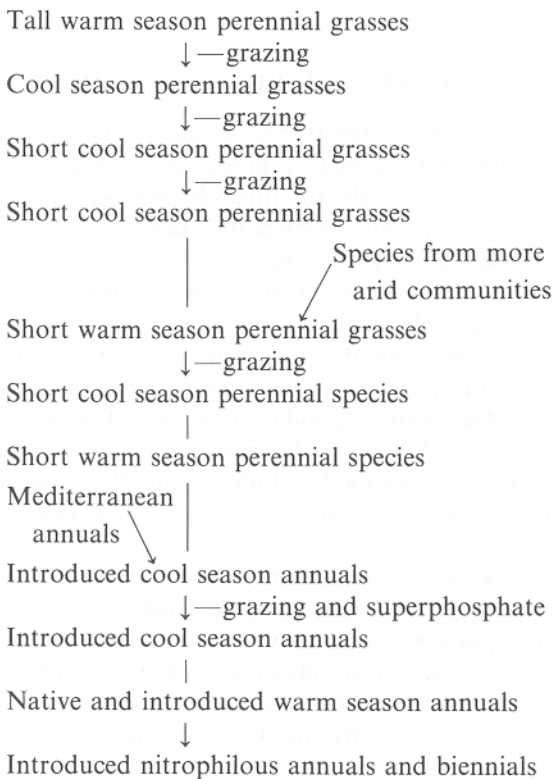
European settlement of temperate grasslands in southeastern Australia began by at least 1830 (Willis, 1964) and was largely completed in New South Wales by 1880 (Moore and Biddiscombe, 1964). The accompanying introduction of livestock led to a pronounced and usually rapid shift in these grasslands from dominance by perennial caespitose grasses, which produce most vegetative growth in summer, to communities dominated by alien annual grasses active in winter. The phenology of the wide ranging dominant, *Themeda australis*, has been often cited as one reason for this rapid species replacement (Moore, 1970b). In southeastern Australia maximum vegetative growth in *Themeda australis* occurs in summer when soil moisture is lowest (Groves, 1965). Consequently, this perennial may have been at a competitive disadvantage with aliens for which vegetative growth coincided with more abundant soil moisture in the winter.

As with the reconstruction of any 19th century events in sparsely settled grasslands, the epidemiologies of the early plant invasions in southern Australia are sketchy. Some of the earliest alien plant populations were established at Sydney, and many of the species Brown found at this settlement in 1802–1804 were candidates for introduction in the temperate grasslands to the west: *Cotula coronopifolia*, *Poa annua*, *Plantago major*, *Silene gallica*, and *Urtica urens* (Britten, 1906). Kloot (1983) estimates there were about 100 species naturalized in South Australia by 1855. Although not all reached the interior upon arrival, his list includes many weeds now common in temperate grasslands worldwide (e.g.

Avena fatua, *Centaurea melitensis*, *Cynodon dactylon*, *Cynara cardunculus*, *Galium aparine*, *Rumex acetosella*). *Silybum marianum* must have arrived some time earlier because its spread along with the contemporaneous invasion of *Cirsium vulgare* prompted the Thistle Act of 1851. These species were but a small fraction of the alien flora that was to descend upon southern Australia once human immigration soared in the remainder of the 19th century.

From the outset of settlement in southern Australia much of these temperate grasslands have been intensively managed as pastures rather than range land for cattle and sheep. This intense management has involved not only the deliberate introduction of numerous pasture grasses from Europe (e.g. *Poa pratensis*, *Lolium perenne*) but also the widespread application of superphosphate and the accumulation of soil N through the introduction of *Trifolium* spp. These practices in conjunction with alteration of the fire frequency and the continual disturbance caused by livestock have caused permanent species replacements. For a native caespitose grass the combination of fire followed by continued grazing may eliminate so many vegetative shoots that regeneration is thwarted (Groves and Williams, 1981).

Moore (1970a) has outlined the conversion as following a predictable scheme:



One of the early and most widely introduced aliens in both natural and derived grasslands in Australia has been *Trifolium subterraneum* and allied species. By raising the N or P level in the soil, clovers permit the entry of noxious aliens such as *Carduus pycnocephalus*, *Cirsium vulgare*, and *Silybum marianum* (Moore, 1959; Michael, 1970).

Even with differences in agricultural practice, the temperate grasslands in Australia share many of the same invaders naturalized elsewhere. In addition to those already mentioned in this section, species naturalized in Australia and shared among vulnerable temperate grasslands include *Avena ludoviciana*, *Erodium cicutarium*, *Hordeum glaucum*, *Hordeum leporinum*, *Stellaria media*, and *Xanthium* spp. (Michael, 1970; Beadle, 1981; Michael, 1981). Other aliens have become more prominent in Australia than elsewhere, such as *Echium plantagineum*, *Nasella trichotoma*, and *Oxalis pes-caprae*. Whatever the circumstances, the range of these aliens and newer immigrants is likely to expand (e.g. *Carduus nutans*, Medd and Smith, 1978). Kloot (1983) estimates five to six species per year become naturalized in South Australia alone, the same rate since ca. 1836. As a result of this continuing onslaught of aliens, Williams (1985) views the temperate grasslands along with other Australian vegetation as not yet in a 'steady state,' but certain to experience further consequences from plant invasions.

7.4 NEW POTENTIAL HAZARDS

At least as early as Columbus' second voyage to the western hemisphere, Europeans and their colonial descendants have made transoceanic introductions of plants (Crosby, 1952). Temperate grasslands are superbly well suited for growing most cereals, animal forage, and many other crops. As a result, these regions have probably been subjected more to the consequences of this transoceanic traffic than any other biome, with the possible exception of tropical islands. The extent and source of these plant introductions reflect in part the dietary preference of Europeans, but also the origin of many food and forage species in Eurasia. Temperate North America, for example, has contributed surprisingly few important cultivated crops (Hodge and Erlanson, 1956) or forage species (Hartley and Williams, 1956). Whenever the native flora in North America or elsewhere was found lacking in a food or forage crop, plants have been imported and established by governments or private ventures (Wickson, 1887; Ryerson, 1976; Williams, 1985).

These deliberate introductions have sometimes turned disastrous. Vulnerable temperate grasslands have repeatedly been the site of plant immigrants that escaped the bounds of crop field or pasture and are now obvious hazards to the native vegetation. *Sorghum halepense* was deliberately introduced in Argentina and the United States as a forage crop (Wickson, 1891) and is now a serious pest (Holm *et al.*, 1977). *Bromus tectorum* was introduced at least once in the

Intermountain West for the same purpose (Mack, 1981), and *Salsola kali* may have been deliberately introduced for the same purpose in the Dakotas (Dewey, 1894). Other aliens with medicinal or even ornamental value have readily established outside cultivation in a new range (e.g. *Datura stramonium*, *Marrubium vulgare*, *Nepeta cataria*, *Silybum marianum*).

The potential for further detrimental introductions, in a sense for history to repeat itself, arises in several areas of current agricultural research and commerce. Even today insufficient regard is often given to the potential hazard created by deliberate releases, as illustrated by *Kochia prostrata*. Introduced in the United States in the early 1960s because of its reputed value as forage in the Soviet Union (Keller and Bleak, 1974), this small shrub is now being released for commercial use in the western United States (Stevens *et al.*, 1985). Evaluation of this alien for release has apparently centered on its ability to tolerate its new range and its palatability for livestock (Keller and Bleak, 1974). The only detrimental feature investigated (and resolved) dealt with the possibility the plant might produce toxic amounts of oxalate (Davis, 1979). Its potential to invade sites for which it was not intended has apparently never been critically evaluated, although the shrub can spread rapidly by seed which it produces in huge quantities (about 1700 kg/ha/year) (Stevens *et al.*, 1985).

What effect could *Kochia prostrata* have on native grasslands? Stevens *et al.* (1985) claim the shrub does not reduce the density of established perennials but will reduce the dominance of *Bromus tectorum* and *Halogeton glomeratus*. Reports of competition with such aggressive aliens are nonetheless disturbing because the competitive ability of the seedlings of perennial grasses such as *Agropyron spicatum* is much lower than is the ability of *Bromus tectorum* (Daubenmire, 1970). Rather than an advantage, the ability of *Kochia prostrata* to colonize the space between caespitose grasses (Stevens *et al.*, 1985) may hasten the demise of native communities. Without acquired pests or parasites (Moore *et al.*, 1982) little may check its spread in western North America. The lack of assessment of the potential detrimental features of *Kochia prostrata* is surprising; another alien congener, *Kochia scoparia*, once also thought to be a desirable forage species, has instead become an invasive weed (Forcella, 1985b).

Ridley's (1930) tome on plant dispersal is testimony to the myriad means by which plants have been transported to new ranges; yet bizarre means still arise. Seed mixtures of both aliens and natives are now commercially available in the United States under such names as 'native wildflower mixtures' and 'Wildflower Meadow.' One seed purveyor even offers his wares (e.g. *Digitalis purpurea* and *Papaver rhoeas*) in packets prepared as attractive postcards. Consequently, the buyer may unwittingly disseminate aliens including, *Centaurea cyanus*, *Cosmos sulphureus*, *Cichorium intybus*, *Festuca ovina*, and unknown seed contaminants on abandoned ground in the misguided notion that such assemblages recreate an aesthetic, yet natural, community. The spread of plants without regard to their invasive ability occasionally verges on negligence. For example, *Hedychium*

gardnerianum (Kahili ginger) presents a serious eradication problem in Hawaii (Smith, 1985), yet seeds and cuttings of this aggressive alien are still sold locally for outdoor ornamental plantings. Although few serious naturalizations will probably arise in temperate grasslands from the dissemination of such commercial seeds (and their seed contaminants), this practice is nonetheless ludicrous and should be stopped.

Great care should even be exerted in selecting the parentage of hybrids planned for introduction. Further hybridization with natives may occur after release with the offspring displaying detrimental features of the parents (Baker, 1972). For example, fertile hybrids between the native *Agropyron spicatum* and the alien *Agropyron repens* (quackgrass) are being released in the Intermountain West. The two hybrid strains so far produced incorporate the nutritional value and climatic tolerance of *Agropyron spicatum* with the ability of *Agropyron repens* to tolerate livestock and to spread via rhizomes (Asay and Hansen, 1984). But *Agropyron repens* seems a poor choice for a parent; it is a competitively aggressive weed in many agricultural situations (Holm *et al.*, 1977) and is one of the few plants for which claims of allelopathic potential may be warranted (Buchholtz, 1971). Despite assurances that the vegetative spread inherited from *Agropyron repens* is '...under genetic control and can be successfully altered through selection' (Asay, 1983), the ominous potential exists of vegetatively-spreading weedy hybrids forming in nature.

The potential for uncontrolled hybridization also exists as new genotypes of forage species are created through techniques in recombinant DNA genetics. Alfalfa is one of the few forage species from which a hardy vascular plant can be grown from callus (Bingham *et al.*, 1975): a critical step in producing a new recombinant product. Consequently, it may provide the first genetically-altered material released in grasslands (e.g. a genotype with enhanced disease or herbicide resistance). Alfalfa is however an obligate outcrosser, and there is the unevaluated possibility that such an alfalfa recombinant could hybridize with weedy relatives, thereby significantly extending the range of any wild hybrids (M. Kahn, personal communication). The benefits of creating new genotypes by these techniques are obvious, and this approach should be fostered. But any releases should be tempered with knowledge that new genotypes are functionally similar to alien plants; potential consequences of their release need not be unforeseen given the history of agricultural invaders (Regal, 1986).

Any evaluation is long overdue on the merits of deliberately introducing plants into these four vulnerable grasslands; deliberate plant releases have occurred for at least 100 years in each region, the releases occur under governmental aegis (adding to the inertia against change), their effects (both beneficial and detrimental) are largely irreversible, and more releases are imminent. Rather than attempt a ban on future plant introductions, attempts should be made to develop guidelines to identify an invasive plant before release. In addition to an evaluation of the ecological traits of any proposed plant introduction (e.g.

dispersal mode, habitat specificity, reproductive potential, response to disturbance, competitive ability with natives), such guidelines will need to reflect a move beyond the largely *post hoc* explanations of naturalizations that now dominate the biology of invasions (Harper, 1965; Harper as cited in Holdgate, 1986). Our current understanding is uncomfortably reminiscent of the epigram often told about economics: any economist can explain in detail the causes of the last business recession, but no economist can predict the timing and cause of the next one. By this standard both economics and the biology of invasions appear as disciplines, but not yet sciences. One informative approach in the biology of invasions would involve comparative studies of the population biology of closely related, congeneric pairs living together: one naturalized, the other a less prevalent native or alien. The necessity of such investigations in vulnerable temperate grasslands is apparent because these regions will continue to attract much of the effort for plant introduction.

7.5 SUMMARY AND CONCLUSIONS

Each temperate grassland has had one of two evolutionary histories: long-term inhabitation by large, hooved, congregating mammalian grazers that imparted a resistance to plant invasions or no recent association with these grazers and correspondingly low resistance to plant invasion and community alteration. Resistance is expressed chiefly in the prominence and proliferation of rhizomatous grasses, the products of strong selection by continual grazing and trampling. In contrast those grasslands destined to be destroyed by plant invasions (grasslands in Argentina and Uruguay, the Intermountain West of western North America, the Central Valley of California, and southern Australia) were all dominated by caespitose grasses before European settlement. Both as adults and juveniles, these grasses display little tolerance of either grazing or trampling and are quickly eliminated from a community when disturbance is suddenly increased.

The level of disturbance increased in all temperate grasslands outside Eurasia with colonization by Europeans. The four vulnerable grasslands were rapidly colonized from *ca.* 1780 to *ca.* 1880. Each was first settled as pasturage for livestock but was soon converted in varying degrees to cereal agriculture. The inherent vulnerability of these regions to continual disturbance coupled with the massive entry and spread of aliens in contaminated seed lots, ensured the replacement of native species by aliens was intense, pervasive, and swift.

With so many similarities in the history and character of settlement, these vulnerable grasslands share many alien species, including *Silybum marianum*, *Cynara cardunculus*, *Salsola kali*, *Cirsium vulgare*, *Avena fatua*, and annual bromes. Although differing in ecological amplitude, all prominent aliens share the tolerance or requirement of continual disturbance as found in agroecosystems, a feature missing among the natives. Many of these invaders

originated in the grasslands of Eurasia; the same selection forces that predisposed the Eurasian grasslands to resist invasion also produced many aggressive invaders.

Perhaps a third of the naturalized flora in these vulnerable grasslands were introduced as forage, or for medicinal or ornamental purposes. There are clearly enormous risks associated with deliberately releasing alien plants in new ranges. Although plant introductions have long been encouraged by the governments in Argentina, Australia, and the United States, the overall wisdom of this practice for pasturage has never been formally discussed, much less critically evaluated. Any discussion on future conservation in these grasslands, however, may well be made moot by the continuing release of invasive cultivars.

It is the irony of temperate grasslands that some have produced many of the most aggressive plant invaders, while others are among the most susceptible communities to invasions. This extreme dichotomy illustrates that floras need not evolve on remote islands to reflect the lack of those selective forces, such as continual disturbance, suddenly imposed by humans. If the invasions of remote islands (Elton, 1958; Moore, 1983; Smith, 1985) and these invaded temperate grasslands are any guide, predicting vulnerable communities and future invaders will improve by being alert to those changes in an environment that coincide with the evolutionary history of potential invaders but are clearly unique to the natives.

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REFERENCES

- Archer, M. (1981). A review of the origins and radiations of Australian mammals. In: Keast, A. (Ed.), *Ecological Biogeography of Australia*, Vol. 3, Part 6, pp. 1435–88. W. Junk, The Hague.
- Asay, K. H. (1983). Promising new grasses for range seedings. In: Monsen, S. B., and Shaw, N. (Eds.), *Managing Intermountain Rangelands—Improvement of Range and Wildlife Habitats*, pp. 110–14. USDA—For. Ser. Gen. Tech. Rep. INT-157.
- Asay, K.H., and Hansen, W. T. (1984). Prospects for genetic improvement in the Quackgrass x Bluebunch Wheatgrass hybrid. *Crop Sci.*, **24**, 743–5.
- Baker, H. G. (1972). Migrations of weeds. In: Valentine, D. H. (Ed.), *Taxonomy, Phytogeography, and Evolution*, pp. 327–47. Academic Press, New York.
- Baker, H. G. (1978). Invasion and replacement in Californian and neotropical grasslands. In: Wilson, J. R. (Ed.), *Plant Relations in Pastures*, pp. 368–84. CSIRO East Melbourne, Australia.

- Bartolome, J. W., Klukkert, S. E., and Barry, W. J. (1986). Opal phytoliths as evidence for displacement of native Californian grassland. *Madrono*, **33**, 217–22.
- Beadle, N. C. W. (1981). *The Vegetation of Australia*, Cambridge University Press, Cambridge, 690 pp.
- Berg, C. (1877). Enumeracion de las plantas Europeas. *An. Soc. Cien. Argent.*, **3**, 183–206.
- Bingham, E. T., Hurley, L. V., Kaatz, D. M., and Saunders, J. W. (1975). Breeding alfalfa which regenerates from callus tissue in culture. *Crop Sci.*, **15**, 719–21.
- Bolander, H. N. (1866). The grasses of the state. In: *Appendix to Journals of Senate and Assembly of the 16th session of the Legislature of the State of California (1865–66)*, Vol. III, pp. 131–45.
- Branson, F. A. (1953). Two new factors affecting resistance of grasses to grazing. *J. Range Manage.*, **6**, 165–71.
- Brewer, W. H. (1883a). Report on the cereal production of the United States. In: *Report on the Productions of Agriculture as returned at the Tenth Census*. US Dept. Inter. Census Office. 47th Congress. 2nd session. Misc. Doc. 42. Part 3. 173 pp.
- Brewer, W. H. (1883b). Pasture and forage plants. In: *Report on Cattle, Sheep, and Swine. Report on the Productions of Agriculture as returned at the Tenth Census*, pp. 5–10. US Dept. Inter. Census Office. 47th Congress. 2nd session. Misc. Doc. 42. Part 3.
- Britten, J. (1906). Introduced plants at Sydney, 1802–4. *J. Bot.*, **44**, 234–5.
- Bryant, E. (1848). *What I Saw in California*, 2nd Edn. D. Appleton, New York, 455 pp.
- Buchholtz, K. P. (1971). The influence of allelopathy on mineral nutrition. In: US National Commission for I. B. P. (Eds.), *Biochemical Interactions Among Plants*, pp. 86–9. National Academy of Sciences, Washington, DC.
- Burcham, L. T. (1957). *California Range Land*. Dept. Nat. Resour. (California), Div. For., Sacramento, 261 pp.
- Cabrera, A. L. (1971). Fitogeografía de la Republica Argentina. *Boln. Soc. Argent. Bot.*, **14**, 1–42.
- Caldwell, M. M., Richards, J. H., Johnson, D. A., Nowak, R. S., and Dzurec, R. S. (1981). Coping with herbivory: Photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia (Berlin)*, **50**, 14–24.
- Connor, D. J. (1966). Vegetation studies in north-west Victoria II. The Horsham area. *Proc. R. Soc. Victoria*, **79**, 637–47.
- Costello, D. F. (1944). Natural revegetation of abandoned plowed land in the mixed prairie association of northeastern Colorado. *Ecology*, **25**, 312–26.
- Crawley, M. J. (1986). What makes a community invisable? In: Gray, A. J., Crawley, M. J., and Edwards, P. J. (Eds.), *Colonization, Succession and Stability*. Blackwell Scientific Publications, Oxford.
- Cronise, T. F. (1868). *The Natural Wealth of California*, H. H. Bancroft, San Francisco, 696 pp.
- Crosby, A. W. (1952). *The Columbian Exchange: Biological and Cultural Consequences of 1492*. Greenwood Press, Westport, Connecticut, 268 pp.
- D'angela, E., Leon, R. J. C., and Facelli, J. M. (1986). Pioneer stages in a secondary succession of a pampean subhumid grassland. *Flora*, **178**, 261–70.
- Darwin, C. (1872). *The Origin of Species*, Vol. 1, 6th Edn, John Murray, London, 365 pp.
- Darwin, C. (1898). *Journal of Researches into the Natural History and Geology of the Countries visited during the Voyage of H. M. S. Beagle Round the World, under the Command of Capt. Fitz Roy, R. N. D.* Appleton, New York, 519 pp.
- Daubenmire, R. (1969). Ecologic plant geography of the Pacific Northwest. *Madrono*, **20**, 111–28.
- Daubenmire, R. (1970). *Steppe Vegetation of Washington*. Wash. Agric. Exp. St. Tech. Bull. 62. 131 pp.

- Daubenmire, R. (1978). *Plant Geography*. Academic Press, New York, 338 pp.
- Davis, A. M. (1979). Forage quality of prostrate *Kochia* compared with three browse species. *Agron. J.*, **71**, 822–4.
- de Candolle, A. (1855). *Géographie Botanique Raisonnée*, Vol. 2. Librairie de Victor Mason, Paris, 1365 pp.
- Dewey, L. H. (1894). *The Russian Thistle*. US. Dept. Agric., Div. Botany Bull. 15. 26 pp.
- Ehleringer, J. R. (1978). Implications of quantum yield differences on the distribution of C3 and C4 grasses. *Oecologia (Berlin)*, **31**, 255–67.
- Elton, C. S. (1958). *The Ecology of Invasions by Animals and Plants*. Methuen, London, 181 pp.
- Forcella, F. (1985a). Final distribution is related to rate of spread in alien weeds. *Weed Res.*, **25**, 181–91.
- Forcella, F. (1985b). Spread of *kochia* in the Northwestern United States. *Weeds Today*, **16**(4), 4–6.
- Forcella, F., and Wood, J. T. (1984). Colonization potentials of alien weeds are related to their 'native' distributions: Implications for plant quarantine. *J. Aust. Inst. Agric. Sci.*, **50**/1, 35–41.
- Frith, H. J., and Calaby, J. H. (1969). *Kangaroos*. Humanities Press, New York, 209 pp.
- Gould, S. J., and Lewontin, R. C. (1979). Spandrels of San-Marco and the Panglossian paradigm—a critique of the adaptationist program. *Proc. R. Soc. London, B.*, **205**, 581–98.
- Gray, A. J., and Scott, R. (1980). A genecological study of *Puccinellia maritima* Huds. (Pal.) I. Variation estimated from single-plant samples from British populations. *New Phytol.*, **85**, 89–107.
- Groves, R. H. (1965). Growth of *Themeda australis* tussock grassland at St. Albans, Victoria. *Aust. J. Bot.*, **13**, 291–302.
- Groves, R. H., and Williams, O. B. (1981). Natural grasslands. In: Groves, R. H. (Ed.), *Australian Vegetation*, pp. 293–316. Cambridge University Press, Cambridge, UK.
- Guthrie, R. D. (1970). Bison evolution and zoogeography in North America during the Pleistocene. *Q. Rev. Biol.*, **45**, 1–15.
- Harper, J. L. (1965). Establishment, aggression, and cohabitation in weedy species. In: Baker, H. G., and Stebbins, G. L. (Eds.), *The Genetics of Colonizing Species*, pp. 245–65. Academic Press, New York.
- Harper, J. L. (1981). After description. In Newman, E. I. (Ed.), *The Plant Community as a Working Mechanism*. Special Publication of the British Ecological Society, No. 1, pp. 11–25. Blackwell Scientific Publications, Oxford.
- Hartley, W., and Williams, R. J. (1956). Centres of distribution of cultivated pasture grasses and their significance for plant introduction. *Proc. Int. Grassl. Congr.*, 7th, pp. 190–9.
- Hauman, L. (1927). Les modifications de la flore Argentine sous l'action de la civilisation. *Mem. Acad. R. Belg. 2nd series*, **9**, 1–100.
- Heady, H. F. (1975). *Rangeland Management*. McGraw-Hill, New York, 460 pp.
- Heady, H. F. (1977). Valley grassland. In: Barbour, M. G., and Major, J. (Eds.), *Terrestrial Vegetation of California*, pp. 491–514. Wiley-Interscience, John Wiley, New York.
- Henderson, L., and Wells, M. J. (1986). Alien plant invasions in the grassland and savanna biomes. In: Macdonald, I. A. W., Kruger, F. J., and Ferrar, A. A. (Eds.), *The Ecology and Management of Biological Invasions in Southern Africa*, Oxford University Press, Cape Town.
- Hendry, G. W. (1931). The adobe brick as a historical source. *Agric. Hist.*, **5**, 110–27.
- Hilgard, E. W. (1891). The weeds of California. In: *Report of the Work*, pp. 238–52. Univ. Calif., Berkeley, Agric. Exp. St.

- Hilgard, E. W., Jones, T. C., and Furnas, R. W. (1882). Report on the climatic and agricultural features and the agricultural practice and needs of the arid regions of the Pacific Slope, with notes on Arizona and New Mexico. US Dept Agric. [Department Reports No. 20]. 182 pp.
- Hodge, W. H., and Erlanson, C. O. (1956). Federal plant introduction—a review. *Econ. Bot.*, **10**, 299–334.
- Holdgate, M. W. (1986). Summary and conclusions: Characteristics and consequences of biological invasions. *Phil. Trans. R. Soc. Lond. B.*, **314**, 733–42.
- Holm, L. G., Plucknett, D. L., Pancho, J. V., and Herberger, J. P. (1977). *The World's Worst Weeds*. University Press of Hawaii, Honolulu, 609 pp.
- Hooker, J. D. (1860). *The Botany of the Antarctic Voyage*, Part III, *Flora Tasmaniae*, Vol. I Dicotyledones. L. Reeve, London, 799 pp.
- Howden, H. F. (1966). Some possible effects of the Pleistocene on the distributions of North American Scarabaeidae (Coleoptera). *Can. Entomol.*, **98**, 1177–90.
- Hudson, W. H. (1923). *Far Away and Long Ago*. J. M. Dent, London. AMS Press reprint, New York (1968), 332 pp.
- Jewiss, O. R. (1972). Tillering in grasses—its significance and control. *J. Br. Grassl. Soc.*, **27**, 65–82.
- Keller, W., and Bleak, A. T. (1974). *Kochia prostrata*: a shrub for western ranges? *Utah Sci.*, **35**, 24–5.
- Kloot, P. M. (1983). Early records of alien plants naturalised in South Australia. *J. Adelaide Bot. Gard.*, **6**, 93–131.
- Leonard, Z. (1934). *Narrative of the Adventures of Zenas Leonard, Written by Himself*. (Quaife, M. M., Ed.). Lakeside Press, Chicago, 278 pp.
- Mack, R. N. (1981). Invasion of *Bromus tectorum* L. into western North America: An ecological chronicle. *Agro-Ecosystems*, **7**, 145–65.
- Mack, R. N. (1984). Invaders at home on the range. *Nat. Hist.* **93**, 40–7.
- Mack, R. N. (1986). Alien plant invasion into the Intermountain West: A case history. In: Mooney, H. A., and Drake, J. A. (Eds.), *Ecology of Biological Invasions of North America and Hawaii*, pp. 191–213. Springer, New York.
- Mack, R. N., and Thompson, J. N. (1982). Evolution in steppe with few, large, hooved mammals. *Amer. Nat.*, **119**, 757–73.
- Major, J. (1977). California climate in relation to vegetation. In: Barbour, M.G., and Major, J. (Eds.), *Terrestrial Vegetation of California*, pp. 11–74. Wiley-Interscience, John Wiley, New York.
- Marzocca, A. (1984). *Manual de Malezas.*, 3rd Edn. Editorial Hemisferio Sur, Buenos Aires, 580 pp.
- McKell, C. M., Robison, J. P. and Major, J. (1962). Ecotypic variation in Medusahead, an introduced annual grass. *Ecology*, **43**, 686–98.
- Medd, R. W., and Smith, R. C. G. (1978). Prediction of the potential distribution of *Carduus nutans* (Nodding Thistle) in Australia. *J. Appl. Ecol.*, **15**, 603–12.
- Meinig, D. (1968). *The Great Columbia Plain*. University of Washington Press, Seattle, 576 pp.
- Michael, P. W. (1970). Weeds of grasslands. In: Moore, R. M. (Ed.) *Australian Grasslands*, pp. 349–60. Australian National University Press, Canberra.
- Michael, P. W. (1981). Alien plants. In: Groves, R. H. (Ed.) *Australian Vegetation*, pp. 44–64. Cambridge University Press, Cambridge.
- Moore, D. M. (1983). Human impact on island vegetation. In: Holzner, W., Wërger, M. J. A., and Ikusima, I. (Eds.), *Man's Impact on Vegetation*, pp. 237–46. Junk, The Hague.
- Moore, R. M. (1959). Ecological observations on plant communities grazed by sheep in

- Australia. In: Keast, A., Crocker, R. L., and Christian, C. S. (Eds.), *Biogeography and Ecology in Australia*, pp. 500–16. Junk, The Hague.
- Moore, R. M. (1970a). Australian grasslands. In: Moore, R. M. (Ed.), *Australian Grasslands*, pp. 87–100. Australian National University Press, Canberra.
- Moore, R. M. (1970b). *Australian Grasslands*. Australian National University Press, Canberra, 455 pp.
- Moore, R. M., and Biddiscombe, E. F. (1964). The effects of grazing on grasslands. In: Barnard, C. (Ed.), *Grasses and Grasslands*, pp. 221–35. Macmillan, London.
- Moore, T. B., Stevens, R., and McArthur, E. D. (1982). Preliminary study of some insects associated with rangeland shrubs with emphasis on *Kochia prostrata*. *J. Range Manage.*, **35**, 128–30.
- Naveh, Z. (1967). Mediterranean ecosystems and vegetation types in California and Israel. *Ecology*, **48**, 445–59.
- Parish, S. B. (1920). The immigrant plants of southern California. *South. Calif. Acad. Sci. Bull.*, **19**, 3–30.
- Parodi, L. R. (1930). Ensayo fitogeográfico sobre el partido de Pergamino. *Rev. Fac. Agron. Vet. Univ. Buenos Aires*, **7**, 65–271.
- Parodi, L. R. (1947). Las gramíneas del género *Bromus* adventicias en La Argentina. *Rev. Argent. Agron.*, **14**, 1–19.
- Patton, R. T. (1936). Ecological studies in Victoria. IV. Basalt plains association. *Proc. R. Soc. Victoria*, **48**, 172–90.
- Perry, R. A. (1970). Arid shrublands and grasslands. In: Moore, R. M. (Ed.) *Australian Grasslands*, pp. 246–59. Australian National University, Canberra.
- Pyke, D. A. (1983). Demographic responses of *Bromus tectorum* and seedlings of *Agropyron spicatum* to grazing by cricetids. Ph.D. thesis, Washington State University, Pullman.
- Regal, P. J. (1986). Models of genetically engineered organisms and their ecological impact. In: Mooney, H. A., and Drake, J. A. (Eds.), *Ecology of Biological Invasions of North America and Hawaii*, pp. 111–29. Springer, New York.
- Richards, J. H. (1984). Root growth response to defoliation in two *Agropyron* bunchgrasses: Field observations with an improved root periscope. *Oecologia (Berlin)*, **64**, 21–5.
- Ridley, H. N. (1930). *The Dispersal of Plants Throughout the World*. L. Reeve, Kent., 744 pp.
- Robbins, W. W. (1940). *Alien Plants Growing without Cultivation in California*. Univ. Calif., Berkeley, Agric. Exp. St. Bull. 637. 128 pp.
- Roe, F. G. (1951). *The North American Buffalo: A Critical Study of the Species in its Wild State*. University of Toronto Press, Toronto, 957 pp.
- Roseveare, G. M. (1948). *The Grasslands of Latin America*. Imp. Bur. Pastures Field Crops, Aberystwyth, Bull. 36. 271 pp.
- Rumney, G. R. (1968). *Climatology and the World's Climates*. Macmillan, New York, 656 pp.
- Ryerson, K. A. (1976). Plant introductions. *Agric. Hist.*, **50**, 248–57.
- Salisbury, E. J. (1933). The East Anglian flora: A study in comparative plant geography. *Trans. Norfolk & Norwich Naturalist's Soc.*, **13**, 191–263.
- Schroedl, G. F. (1973). The archaeological occurrence of bison in the southern plateau. Ph.D. thesis, Washington State University, Pullman.
- Simpson, G. G. (1980). *Splendid Isolation: The Curious History of South American Mammals*. Yale University Press, New Haven, pp. 266.
- Smith, C. W. (1985). Impact of alien plants on Hawaii's native biota. In: Stone, C. P., and Scott, J. M. (Eds.), *Hawaii's Terrestrial Ecosystems: Preservation and Management*, pp. 180–250. Cooperative National Park Resources Studies Unit, University of Hawaii, Honolulu.

- Soriano, A. (1956a). Los distritos florísticos de la Provincia Patagónica. *Rev. Invest. Agric.*, **10**, 323–47.
- Soriano, A. (1956b). Aspectos ecológicos y pastorales de la vegetación patagónica relacionados con su estado y capacidad de recuperación. *Rev. Invest. Agric.*, **10**, 349–72.
- Soriano, A. (1979). Distribution of grasses and grasslands of South America. In: Numata, M. (Ed.), *Ecology of Grasslands and Bamboolands in the World*, pp. 84–91. Junk, The Hague.
- Stebbins, G. L. (1975). The role of polyploid complexes in the evolution of North American Grasslands. *Taxon*, **24**, 91–106.
- Stevens, R., Jorgensen, K. R., McArthur, E. D., and Davis, J. N. (1985). 'Immigrant' forage Kochia. *Rangelands*, **7**(1), 22–3.
- Teeri, J. A., and Stowe, L. G. (1976). Climatic patterns and the distributions of C4 grasses in North America. *Oecologia (Berlin)*, **23**, 1–12.
- Thellung, A. (1912). La flore adventice de Montpellier. *Mém. Soc. Natn. Sci. Nat. Math. Cherbourg*, **38**, 57–728.
- Trewartha, G. T., and Horn, L. H. (1980). *An Introduction to Climate*, 5th Edn. McGraw-Hill, New York, 416 pp.
- Tschudi, J. J., von. (1868). *Reisen durch Sudamerika*, Vol. 4. Leipzig: Verlag F. A. Brockhaus. Stuttgart: Omnitypic—Gesellschaft Nachf. Leopold Zechall reprint; 1971. 320pp.
- Verona, C. A., Fernandez, O. N., Montes, L., and Alonso, S. I. (1982). Problemática agroecológica y biología de *Senecio madagascariensis* Poiré (Compositae). I. Problemática agroecológica y biología de la maleza. *Ecología (Argentina)*, **7**, 17–30.
- Wallace, A. R. (1892). *Island Life*, 2nd Edn. Macmillan, London, 563 pp.
- Warwick, S. I., and Briggs, D. (1978). The genecology of lawn weeds. I. Population differentiation in *Poa annua* L. in a mosaic environment of bowling green lawns and flower beds. *New Phytol.*, **81**, 711–23.
- Wickson, E. J. (1887). Report on grasses, forage plants, and cereals. Appendix II. In *Supplement to the Biennial Report of the Board of Regents*, pp. 81–107. Univ. Calif., Berkeley, Agric. Exp. St.
- Wickson, E. J. (1891). Grasses and forage plants. In: *Report of Work*, pp. 201–20. Univ. Calif., Berkeley, Agric. Exp. St.
- Williams, O. B. (1985). Population dynamics of Australian plant communities, with special reference to the invasion of neophytes. In: White, J. (Ed.), *The Population Structure of Vegetation*, pp. 623–35. Junk, The Hague.
- Willis, J. H. (1964). Vegetation of the basalt plains in western Victoria. *Proc. R. Soc. Victoria*, **77**, 397–418.
- Yensen, D. (1981). The 1900 invasion of alien plants into southern Idaho. *Great Basin Nat.*, **41**, 176–83.
- Young, J. A., Evans, R. A., and Major, J. (1972). Alien plants in the Great Basin. *J. Range Manage.*, **25**, 194–201.