ONE

Introduction

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Grassland ecosystems are one of the most recognizable components of California's wildlands, and one the state's most important natural resources both from the perspective of biodiversity and economic values. Over 10% of California's land area is currently grassland, and this habitat type is home to a many of the threatened and endangered animals and plants in the state (Jantz et al., Chapter 23). Yet these ecosystems have been subject to greater manipulation or destruction than any other vegetation type in the state. Ongoing conversion of grasslands to other uses and the incursion of human population centers into formerly intact habitats have placed enormous pressure on these ecosystems at the local and statewide level. In coming decades, further projected population growth, changes in land use, and alteration of climate will bring even greater pressures and make the need to understand the ecological factors that influence the state's grasslands even more pressing.

Partly because of the wide range of uses and challenges that California's grasslands face, they have been the subject of much research. The last attempt to summarize the state of knowledge of California grasslands came in 1989, with a focus mostly on the annual grassland ecosystem (Huenneke and Mooney 1989b). Since that time, there has been an explosion of research on the ecology, management, and conservation of grasslands of California. Over 1,000 papers were published between 1990 and 2006 that included the terms *California, grassland,* and *ecology* in their titles or abstracts. Among the greatest advances in the past 16 years has been a greater understanding of the interactions between annual species and perennial ones, including the native perennial grasses that likely once dominated much of the region. We also know much more about plant-soil relations, the soil microbial community, restoration of native biodiversity, the importance and recruitment of oaks, and the ecophysiology of California grassland plants.

California's Mediterranean grasslands differ from other important North American grasslands in ways that make their separate consideration worthwhile. Most obviously, the climate experienced by California's grasslands, with its Mediterranean pattern of cool, wet winters and warm, dry summers (Reever Morghan et al., Chapter 7) contrasts with the Continental climate found in other grasslands. Because of the strong within-season and season-to-season variability in rainfall, the timing and amount of water available to plants may play a more important role in determining the dynamics of species composition, productivity, and nutrient cycling in California than in most other regions of North America. A second difference is that the flora of California grasslands is dominated primarily by species, especially annual grasses and forbs, whose active growth is during the "cool season" in contrast to the warm-season species found in grasslands elsewhere. Furthermore, annual species are more important in California's Mediterranean grasslands than in most other North American grasslands—indeed, in most grasslands of the world—although the successful invasion of *Bromus tectorum* (cheatgrass) in Great Basin shrublands is leading to the conversion of millions of hectares of habitat in the Intermountain West into annual-dominated grasslands. A final way in which California grasslands differ from most other grasslands is in their domination by non-native species. The conversion from a native- to a largely non-native-dominated flora occurred over the nineteenth and twentieth centuries and is discussed in several chapters herein.

In spite of these differences, information learned by studying California grasslands has informed ecological questions that are relevant to ecosystems around the world. Examples include studies of impacts, ecology and control of invasive non-native species (D'Antonio et al., Chapter 6; Stromberg et al., Chapter 21; and DiTomaso et al., Chapter 22), population genetics (Rice and Espeland, Chapter 11), interactions

SIDEBAR 1.1 HISTORICAL FACTORS THAT INFLUENCE INTERPRETATION OF GRASSLAND ECOLOGY

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Changes in Climate As recently as 4,000–6,000 years ago, rainfall amounts in California were considerably greater and supported a more mesic-type flora than the one present today (Wigand et al., Chapter 4; Edwards 1992). As precipitation decreased, the climate shifted to a more xeric, Mediterranean type and altered the temporal distribution of rainfall, thereby creating drier conditions in the summer, shorter growing seasons, and changes in plant demography. The relict populations of Giant Redwood (*Sequoia gigantea*), Monterey Pine (*Pinus radiata*), and other species are indicative of a more mesic past, both inland and on the coast.

Loss of Large Herbivores Edwards and colleagues (Wigand et al., Chapter 4; Edwards 1992) used Rancho La Brea tar pit data to conclude that as many as 18–19 large browsing and grazing taxa were present in recent prehistory (~6,000 years before present). The ecological impact of the loss of these herbivores cannot be adequately estimated or fully appreciated. However, despite the evidence of a long history of herbivory on the West Coast, it is very possible that the composition of the California grasslands was not the result of a close association with frequent or heavy grazing (Painter 1995; Hamilton 1997b; Mensing 1998). Edwards' (1992) data suggested a predominantly browsing herbivore fauna. The ecological significance of a nongrazing evolutionary history lies in the abrupt shift toward grazing management with European settlement. Burcham (1956, 1957) chronicled the use, and likely overuse, of the land and the possible interactions that may have occurred with other factors such as extended drought and the invasion of non-native species at the time of European contact. A likely consequence of the unprecedented severity of grazing that coincided with other biotic and abiotic changes would have been the greatly reduced abundance and distribution of grazing-intolerant species, including some bunchgrasses.

Fire Suppression It is difficult to describe with great accuracy the fire regime in California grasslands prior to European settlement, but it was certainly very different from the regime today (Reiner, Chapter 18). Minnich (1983) documented the tremendous reduction in fire frequency in southern California, as compared to Baja California, due to anthropogenic fire suppression. Arguments in favor of the importance of fire to the health of native bunchgrasses have been made (Menke 1992; Dyer and Rice 1997b; Seabloom et al. 2005), although the net effects at the community level of the reduced fire frequency are poorly understood (but see D. Dyer 2003). Fire was and is a controlling factor in grassland structure and function, capable of influencing standing biomass, nutrient cycling, competitive interactions, and a number of other basic grassland processes (Reiner, Chapter 18).

Influence of Indigenous Cultures The transition from a mesic climate to the one now characterized as Mediterranean was coincident with the development and growth of Native American cultures in California (Anderson, Chapter 5). How rapidly native cultures grew and affected natural disturbance regimes is unknown. However, it is well established that hunting, fire, horticulture, and seasonal movements were part of these societies.

Hydrological Changes Over the twentieth century, every major river draining the Sierra Nevada mountains, except the Sacramento River, has been dammed for flood control or hydroelectric purposes. The tremendous impact of flood control on the hydrology of the San Joaquin Valley cannot be overstated. Historical records of the eastern Valley floor indicate an unbroken alluvial floodplain covered with oak

riparian habitat stretching from well north of Sacramento to at least Porterville in the south, a distance of some 300 miles (Heady 1988). All water flow is now regulated, riparian areas are fragmented, and, with very few exceptions, all native habitat has been replaced (due largely to agricultural conversion) and few native plant species remain. Furthermore, changes in hydrology following flood control have altered silt deposition, with important ecosystem consequences. Silt deposition renews nutrient availability, restores soil cation exchange capacity, and washes out accumulated salts. Without overland flooding, soils can become impoverished followed by slow degradation of the communities they support. This may have contributed to the long-term reduction in Valley grassland biomass (suggested in Burcham 1957).

Invasion of Non-native Species California's habitats, and its grasslands in particular, have been strongly impacted by the introduction of non-native plant and animal species (D'Antonio et al., Chapter 6). Some 1,050 non-native plant species are listed in the *Jepson Manual* (Hickman 1993), with the expectation that more will arrive (Rejmánek and Randall 1994). Nearly half of these exotic species are annuals, and their introduction has biased the California flora as a whole towards annual lifeforms (Heady 1988). The "annualization" of the California flora is reflected in California's grassland communities, many of which have been converted from perennial to annual dominance. The lack of detailed presettlement botanical information greatly compounds the challenge presented by non-native species for interpreting ecological relationships between native species and their environment (Wigand et al., Chapter 4). As a result, an understanding of the processes that have driven changes in community composition and species richness in the state (or variation in impacts of exotic species by region) remains impossible to address.

between plants and soil nutrient dynamics (Eviner and Firestone, Chapter 8; Jackson et al., Chapter 9; and Harpole et al., Chapter 10), and responses to climate change (Dukes and Shaw, Chapter 19). In addition, the uneasy relationship between wildlands and urbanization may be more acute in California grasslands than in any other ecosystem in the world. Huge areas of California grassland and oak savanna are being converted from agricultural lands to low-density suburban and ranchette development or to vineyards. The consequences of these land use changes for open space and biodiversity, as well as the legal and regulatory responses (Jantz et al., Chapter 23), can inform conservationists and policy-makers elsewhere.

The broad goal of this book is to present a state-of-the-art synthesis by scientists studying California grasslands on the status of our knowledge of the history, ecology, and management of this important ecosystem. We also hope that it will serve to identify holes in our knowledge and to provide a basis for research for the next generation. The book begins with an overview (Chapters 2 and 3) that presents the nomenclature, systematics, and classifications of the important plant species and communities. The next three chapters (Chapters 4–6) present the historical context, including the past vegetation composition, the role of native peoples, and the invasion of California grasslands by nonindigenous grasses and forbs with European settlement and into the present. The third section, "Resources" (Chapters 7–10), presents a detailed analysis of climatic and soil conditions that play an important role in determining the phenology, distribution, and species composition of grasslands and that are in turn influenced by these same factors. The fourth section, "Ecological Interactions" (Chapters 11–19), discusses population and community ecology, including population genetics, interactions between plant species, herbivory, the role of fire, and global climate change. The final section, "Policy and Management" (Chapters 20–23) reviews the management of grazing in public and private lands, the use of restoration science and other integrative management tools to combat exotic species and restore native biodiversity, and the conservation of biodiversity and open space.

We have chosen to focus primarily on the grassland ecosystems, which we define as herbaceous-dominated nonagricultural communities, found within the California floristic province. Though important grasslands are found in the Great Basin and Desert provinces and in Sierran montane meadows in California, we do not specifically consider them here. Instead, we focus on the coastal prairie, Coast Range grasslands, and grasslands of the Great Valley region. These grasslands grade into one another and, in some areas, grade into oak savanna and eventually oak woodland habitats. They all share the strong presence of European annual species, a history of use by both native peoples and European settlers, and an evolutionary history that includes isolation from the Great Basin flora by the Sierra Nevada. Grass-dominated communities outside the California floristic province are occasionally mentioned, but this volume should not be considered a complete review of those important systems.

Any consideration of the ecology of California's grasslands today must be tempered by recognition of historical factors that influence the patterns on today's landscapes (e.g., Sidebar 1-1). Our ability to fully understand these grassland ecosystems is, therefore, constrained by events in the past that have altered biotic and abiotic processes in ways that are often difficult to decipher. Like many other ecosystems, contemporary research is taking place in a setting where community composition is still adjusting to potentially profound short- and long-term shifts in biotic and abiotic stresses and ecological relationships. Specific historical factors are dealt with in detail in such chapters as Chapters 4 (Wigand et al.), 6 (D'Antonio et al.), and 18 (Reiner), but the influence of the forces described in these chapters is a backdrop that affects the topics in most of these chapters. We believe that embracing the variability of process, pattern, and history is critical to managing and restoring these structurally simple but ecologically dynamic and complex ecosystems.