

Historical Range of Variation Assessment for Wetland and Riparian Ecosystems, U.S. Forest Service Rocky Mountain Region

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Abstract

This document provides an overview of historical range of variation concepts and explores their application to wetland and riparian ecosystems in the US Forest Service Rocky Mountain Region (Region 2), which includes National Forests and National Grasslands occurring in the states of Colorado, Wyoming, Nebraska, Kansas, and South Dakota. For each of five ecosystem types—riparian areas, fens, wet meadows, salt flats, and marshes—we review key structural and functional characteristics including geomorphic setting, principal ecological drivers, classification, and dominant vegetation. In addition, we discuss anthropogenic factors known to influence the abundance or condition of each main wetland type.

Keywords: wetlands, wet meadows, fens, salt flats, riparian, marshes, Colorado, Wyoming, South Dakota, Kansas, Nebraska

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1. Introduction

Objectives of the Project

Although they comprise only a small percentage of the region's land area, wetland and riparian ecosystems are critical components of Rocky Mountain and Great Plains landscapes. These ecologically diverse ecosystems are found at all elevations and latitudes and provide a number of important economic and ecological functions (Gregory and others 1991; Mitsch and Gosselink 2007; Patten 1998). Critical as wildlife habitat (Brown and others 1996; Davidson and Knight 2001; Haukos 1992; Nelson and others 1984) and as local and regional centers of biodiversity (Naiman and others 1993; Nilsson and Svedmark 2002; Pollack 1998), these ecosystems support many biogeochemical, physical, and ecological processes not found elsewhere on western landscapes.

As wetland and riparian functions and values have become better understood, a variety of laws and regulations have been promulgated that are aimed at promoting wetland and riparian conservation. However, wetland and riparian areas have historically been heavily impacted by anthropogenic activities throughout North America (Brinson and Malvarez 2002; Graf 1999; Office of Technology Assessment 1984; Shafroth and others 1998; Tiner 1984). Demand for water, fertile land, and forage for livestock in the arid and semi-arid West has already affected many aquatic, riparian, and wetland areas; and pressures will likely increase with time, threatening the integrity and long-term viability of these vital ecosystems and the biota they support (Baron and others 2002; Pringle 2000).

As a principal land manager in the region, the U.S. Department of Agriculture, Forest Service (USFS) sits at the center of this conflict. Charged with simultaneously providing natural resources goods and services and conserving biodiversity and ecosystem integrity, the USFS must balance these often conflicting goals—a task that is made more difficult by the complexity of the social, economic, and ecological systems involved (Kaufmann and others 1994; Landres and others 1999). Recognizing this complexity, managers have increasingly looked to the scientific community to help inform and guide management and planning activities (Dale and others 2000; Thomas 1996).

Over the last several decades, a paradigm shift has occurred in the field of ecology, from a focus on stability and equilibrium, to an emphasis on concepts of variability, change, and dynamism (Holling 1996; Holling and Meffe 1996). Scientists have increasingly stressed the importance of disturbances to ecological systems (Turner and others 1996, 1998), and in response, managers have begun to apply such concepts to both individual species conservation efforts and broad-scale land management (Dale and others 2000). New conceptual and quantitative tools have been developed to relate ecological pattern to process at

different spatial and temporal scales (Turner 1989), often with an explicit focus on system variability. One concept that is increasingly relied upon to guide land management activities is the historical range of variability (HRV). Our primary objective in this assessment is to apply this concept, defined and described below, to riparian and wetland ecosystems of the USFS Rocky Mountain Region (Region 2).

Specifically, our goals are to: (1) outline the types of wetland and riparian ecosystems that occur on Region 2 National Forests and Grasslands; (2) identify and characterize the key variables driving vegetation patterns and functional attributes of wetlands and riparian systems at a range of spatial and temporal scales; and (3) use available data and information to make inferences regarding the HRV of key variables influencing wetlands and riparian areas prior to the mid-nineteenth Century when extensive Euro-American settlement in the region began. Unlike most previous HRV assessments prepared for Region 2 (e.g., Dillon and others 2005; Meyer and others 2003; Veblen and Donnegan 2005), the broad geographic scope of this assessment which encompasses 17 National Forests and 7 National Grasslands in 5 states (Figure 1) and high ecological and functional diversity of ecosystems in the assessment area preclude a fine-grained, spatially explicit analysis for each Forest and Grassland. Rather, our intent is (1) to provide a broad conceptual framework based on the best available scientific information

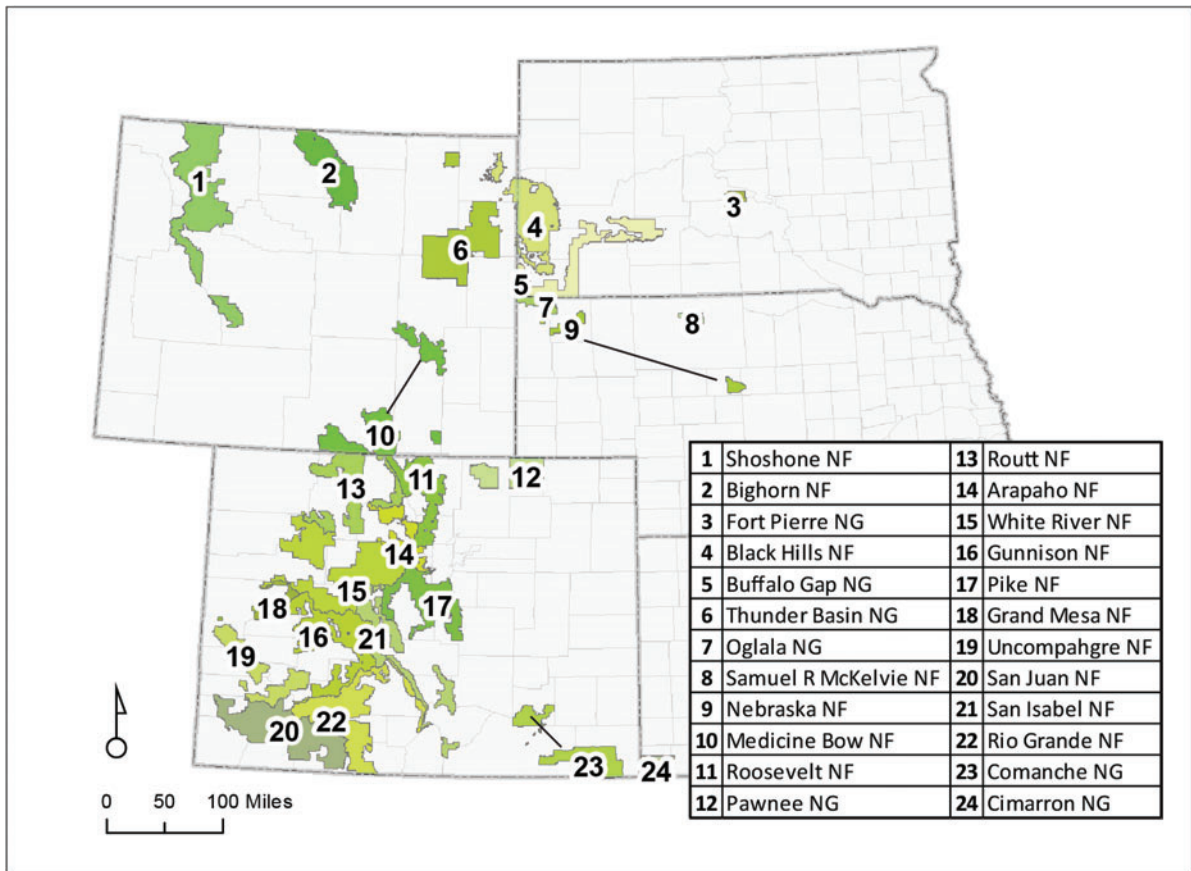


Figure 1. National Forests and Grasslands in the U.S. Forest Service Rocky Mountain Region.

from which managers or researchers can develop reasonable assessments of the HRV of wetlands or riparian systems in particular planning areas and (2) to provide a starting point for further site-specific research. There are many potential variables we could focus on, each operating at different spatial and temporal scales (Table 1), but our general emphasis is on variables operating at the scale of individual wetlands to watersheds.

Previous HRV Assessments in Region 2

Most previous HRV assessments in Region 2 have been prepared for individual National Forests and have been limited to upland forested ecosystem types (Dillon and others 2005; Kulakowski and Veblen 2006; Meyer and others 2003; Veblen and Donnegan 2005). Our overall objectives are similar to these assessments, but our focus is on a much broader geographic area and on multiple ecosystem types that differ widely in composition, structure, and function. These fundamental differences in scope among assessment efforts require the use of different conceptual and analytical approaches.

Even when applied in a qualitative rather than a quantitative statistical context, reference to a specific variable of interest is required for the HRV concept to have meaning. A variety of ecological attributes were examined in previous HRV analyses, spanning multiple spatial and temporal scales (Table 2). While our approach is similar, most of the specific ecological drivers and response variables

Table 1—Nested hierarchy of key spatial and temporal scales, ecological drivers, and ecological response variables relevant to the structure and function of a hypothetical wetland. Our assessment is primarily focused on drivers and response variables.

Level	Scale		Key ecological drivers	Potential response variables
	Time (yr)	Space (m ²)		
Leaf	0.001 to 1	0.01 to 0.1	Photosynthetically active radiation; osmotic pressure; tissue nutrient concentrations	Respiration photosynthesis decomposition
Plant	0.1 to 100	0.1 to 10	Soil water availability; nutrient concentrations; competition; herbivory	Plant productivity; root, shoot, and propagule production
Wetland	1 to 1000	1 to 1000	Water table depth; local hydrology; herbivory	Species diversity and productivity; decomposition; N mineralization; peat accumulation rate
Watershed	100 to 10,000	1000 to 10,000	Mass wasting; bedrock porosity; glacial history; fire history; beaver; stream discharge; sediment production	Distribution and abundance of different wetland types
Ecoregion	> 10,000	> 100,000	Lithology; tectonics; Milankovitch cycles	Adaptation; extinction; species radiation

Table 2—Examples of ecological variables examined in previous HRV assessments (left column) and those variables discussed in this assessment (right column). Variables of particular importance to specific ecosystem type(s) are indicated in parentheses (M = marsh, WM = wet meadow; F = fen; R = riparian; SF = salt flat). Definitions and descriptions of ecosystem types are presented later in the document.

Examples of ecosystem variables examined for upland HRV	Potential ecosystem variables of interest in wetland/riparian HRV
Snag density (Dillon et al. 2005)	Species composition (M, WM, SF, F, R)
Stand structure (Dillon et al. 2005)	Age-class distribution (R, WM)
Tree species and genetic diversity (Dillon et al. 2005)	Proportion woody cover (WM, F, R)
Tree density (Dillon et al. 2005)	Woody plant size/age distribution (WM, R)
Density and size of canopy gaps (Dillon et al. 2005)	Wetland abundance (M, WM, SF, F, R)
Density and cover of understory plants (Dillon et al. 2005)	Landscape diversity of wetland types (M, WM, SF, F, R)
Age-class structure of stands (Dillon et al. 2005)	Flood frequency, magnitude, & timing (M, WM, SF, F, R)
Size-class structure of stands (Dillon et al. 2005)	Course woody debris (R)
Course woody debris (Dillon et al. 2005)	Beaver abundance and use (R)
Seedling and sapling density (Dillon et al. 2005)	Sediment budget (M, WM, SF, F, R)
Fire (Dillon et al. 2005; Veblen and Donnegen 2003)	Carbon accumulation/loss dynamics (F)
Disease (Dillon et al. 2005; Veblen and Donnegen 2003)	Hydrologic variability (M, WM, SF, F, R)
Insects (Dillon et al. 2005; Veblen and Donnegen 2003)	Spatial and temporal patterns of woody plant establishment (WM, R)
Wind (Dillon et al. 2005; Veblen and Donnegen 2003)	Ground and surface water chemistry, nutrient fluxes (M, WM, SF, F, R) Wetland functions (groundwater recharge, discharge, biodiversity, storm water detention, etc.) (M, WM, SF, F, R)

for wetland and riparian ecosystems differ from those of upland forests. Even among wetland types, the most important variables may differ. For instance, shallow groundwater inflow is a key variable driving vegetation dynamics in fens, wet meadows, and some marshes (Galatowitsch and van der Valk 1998; Winter 1999; Winter and Rosenberry 1995), however it is not a critical driver of Great Plains riparian communities along ephemeral streams, which are influenced more by infrequent floods (Friedman and Lee 2002). Species composition can differ almost completely between two nearby fens within the same small watershed, but can be identical between cattail (*Typha* spp.) marshes hundreds of miles distant from one another. Variables examined in this and previous assessments are contrasted in Table 2 and are discussed in greater detail in chapters specific to each wetland type.

Organization of This Report _____

A major challenge in preparing an assessment of this scope is to provide a concise yet thorough framework in which to explore the ecological and historical factors shaping the HRV of different ecosystem types. In this chapter, we provide an overview of our objectives and an introduction to some of the basic HRV concepts and definitions used in earlier assessments and those we have applied to wetlands and riparian ecosystems in this document. In Chapter 2, we outline the primary resources and analytical approaches we used in assessing the HRV for wetland and riparian ecosystems. Many topics, such as broad-scale climatic trends and the human history of different parts of the study region are presented in Chapter 3, along with a review of wetland and riparian classifications. Subsequent chapters present an HRV assessment for each of the five major wetland and riparian ecosystem types that occur in USFS Region 2: riparian ecosystems, marshes, fens, salt flats, and wet meadows. In Chapter 8, we provide a synthesis of our findings and present suggestions for future research.

Historical Range of Variation Concepts _____

The underlying premise of the HRV approach is that by managing ecosystems for the range of processes that have characterized ecosystems in the past, land managers can maximize the likelihood of preserving into the future the widest compliment of species and important ecological functions (Landres and others 1999; Veblen 2003). Several closely related terms have been applied by previous authors, including “range of natural variability,” “reference variability” (Manley and others 1995), “natural variability” (Landres and others 1999), and “historic range of variability” (Dillon and others 2005; Meyer and others 2003; Morgan and others 1994; Veblen 2003). Common to all of these definitions is an explicit recognition of the dynamic nature of ecological systems and the necessity of analyzing ecosystems at multiple scales. Our HRV definition closely follows earlier ones: the spatial and temporal variation in key ecosystem processes and characteristics prior to major alteration by Euro-Americans—approximately the mid- to late-1800s for most of the region. Spatial and temporal scales must be explicitly discussed because there are differences in the timing and nature of initial Euro-American alteration of different parts of the region and among wetland and riparian ecosystem types. The most appropriate scales of analysis differ for each wetland type and are discussed within individual chapters.

Wetland Definitions and Applicable Laws _____

While few people have difficulty defining what constitutes a forest, there is no universal definition of a riparian area or wetland. Because of their high ecological diversity; special legal status under certain federal, state, and local laws; and unique place at the intersection of several scientific disciplines, a number of regulatory and scientific definitions have been developed. Regulatory definitions of wetlands, most notably the one used by U.S. Army Corps of Engineers

in regulating wetlands under Section 404 of the Clean Water Act (Tiner 1999), are geared towards developing consistent and uniform criteria for field delineation. Precise wetland boundaries are difficult to identify for a number of reasons (Choesin and Boerner 2002; Kirkman and others 1998). Interannual and decadal-scale variance in water availability can shrink or enlarge the area of saturated or flooded soils within the same site through time. The timing and duration of soil saturation may vary among years. Rare floods or plant colonization patterns may change landforms and their vegetation patterns. Plant species may have individualistic responses to environmental conditions producing complex distribution patterns (Tiner 1991).

More science-oriented definitions have been developed for wetlands and riparian areas, such as the one developed by the National Research Council (National Research Council 1995), that are broader in scope, emphasizing the unique suite of hydrological, chemical, and biological characteristics that differentiate wetlands from uplands. The definition developed by the U.S. Fish and Wildlife Service for use in its National Wetlands Inventory (NWI) program is commonly used and contains elements found in both the Corps of Engineers and National Research Council definitions (Cowardin and others 1979). All definitions recognize, to one degree or another, the key role of hydrologic processes in wetland formation and the resulting suite of soil and vegetation characteristics (Table 3).

Table 3—Principal wetland definitions used by Federal agencies.

U.S. Fish and Wildlife Service, National Wetlands Inventory program (Cowardin et al. 1979)

“Wetlands are lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water...wetlands must have one or more of the following three attributes: (1) at least periodically, the land supports predominately hydrophytes; (2) the substrate is predominately undrained hydric soil; and (3) the substrate is nonsoil and is saturated with water or covered with shallow water at some time during the growing season of each year”

U.S. Army Corps of Engineers, section 404 manual (1987)

“...those areas that are inundated or saturated by surface or groundwater at a frequency and duration sufficient to support, and that under normal circumstances do support, a prevalence of vegetation typically adapted for life in saturated soil conditions. Wetlands generally include swamps, marshes, bogs, and similar areas.” [33 CFR323.2(c); 1984]

National Research Council (1995)

“A wetland is an ecosystem that depends on constant or recurrent, shallow inundation or saturation at or near the surface of the substrate. The minimum essential characteristics of a wetland are recurrent, sustained inundation or saturation at or near the surface and the presence of physical, chemical, and biological features reflective of recurrent, sustained inundation or saturation. Common diagnostic features of wetlands are hydric soils and Hydrophytic vegetation. These features will be present except where specific physiochemical, biotic, or anthropogenic factors have removed them or prevented their development.”

USFS regulations: National Forest Management Act of 1976 – Section: 6(g)(3)(E)(iii)

Sec (E) insure that timber will be harvested from National Forest System lands only where:(i) soil, slope, or other watershed conditions will not be irreversibly damaged; (iii) *protection is provided for streams, stream-banks, shorelines, lakes, wetlands, and other bodies of water from detrimental changes in water temperatures, blockages of water courses, and deposits of sediment*, where harvests are likely to seriously and adversely affect water conditions or fish habitat.

A variety of regulatory and scientific definitions of riparian ecosystems have also been created. The term riparian is derived from the Latin *riparius* meaning stream bank (DeBano and Schmidt 2004). Some definitions retain this geographic perspective, including one used by the USFS that defines riparian areas as “geographically delineated areas with distinctive resource values and characteristics, that are comprised of aquatic and riparian ecosystems, floodplains, and wetlands. They include all areas within 100 feet from the edge of perennial streams or other water bodies...A riparian area is a transition between the aquatic ecosystem and the adjacent terrestrial ecosystem and is identified by soil characteristics and distinctive vegetation communities that require free and unbound water.” (USDA FS 2000). A significant point regarding this definition is that, while referencing certain soil and vegetation characteristics, all areas within a 100-foot buffer around a perennial surface water feature are considered riparian, regardless of ecological characteristics. Under this definition, all of the five ecosystem types covered in this report would be considered riparian if they occurred within this buffer. While the NWI definition classifies riparian areas as one type of wetland, the USFS definition considers wetlands such as marshes or fens to be a subset of the term riparian. An additional definition, formulated by the National Research Council, defines riparian areas as: “transitional between terrestrial and aquatic ecosystems and ... distinguished by gradient(s) in biophysical conditions, ecological processes, and biota. They are areas through which surface and subsurface hydrology connect water bodies with their adjacent uplands” (National Research Council 2002). Each of these definitions has value in a specific context.

2. Data and Information Sources

We utilized a wide range of information sources to make inferences on the HRV of key ecosystem parameters. Broadly, these can be classified into several categories: (1) contemporary studies examining the distribution, structure, or function of wetlands and riparian areas; (2) instrumental records (e.g., staff gauge and weather station data) and proxy evidence for past climates, hydrologic regimes, or vegetation; (3) studies documenting the effects of natural or anthropogenic disturbances on wetland and riparian ecosystems; (4) historical photographs or explorer accounts; and (5) discussions with scientists or USFS staff. Our report is largely a review of existing literature; however, we also analyzed primary vegetation and geospatial datasets to develop a better understanding of wetlands and riparian areas in the region.

We gave the greatest emphasis to peer-reviewed research. Unpublished theses and dissertations, USFS technical reports, and Forest Planning documents were also used, and they sometimes provided the only information on specific topics or ecosystem types. When available, we relied upon research conducted within Region 2 National Forests and Grasslands or from similar sites in the region. However, studies of certain processes and wetland and riparian types, such as ephemeral streams and salt flat ecosystems, are relatively rare, so where necessary, we relied upon information gleaned from studies outside of the region. Each National Forest and Grassland is unique in its ecological and human history; HRV assessments made using data from studies conducted offsite should therefore be viewed as hypotheses to be tested using data collected on site (Veblen 2003).

Instrumental Records ---

Stream gauges

An extensive network of stream gauges is located in the region, providing important data on the surface water resources (Table 4). The earliest stream gauges were established along major rivers in Region 2 beginning in the late 1800s, with many additional gauges added during the Twentieth Century, principally by the U.S. Geological Survey. Real-time and historical stream flow records are available for hundreds of stream gauges in Colorado, Wyoming, South Dakota, Nebraska, and Kansas, although their utility for evaluating historical stream flow patterns is often limited by short periods of record that fail to capture the full range of hydrologic variability that is important to geomorphic and vegetation dynamics. Moreover, very few small watersheds have been gauged, and as a consequence, there are relatively few studies of long-term stream flow variability in ephemeral and intermittent ecosystems.

Table 4—USGS stream gauges in Region 2 with the longest periods of record.

USGS site number	USGS site name	Years of availability	Length of record (yr)	State
13011000	Snake River near Moran	1904-present	99	WY
6693000	North Platte River at North Platte	1895-1997	102	NE
8251500	Rio Grande near Lobatos	1900-present	102	CO
6714000	South Platte River at Denver	1895-present	107	CO
6729500	South Boulder Creek near Eldorado Springs	1888-1995	107	CO
6724000	St. Vrain Creek at Lyons	1888-1998	110	CO
8220000	Rio Grande near Del Norte	1890-present	112	CO
7096000	Arkansas River at Canon City	1889-present	113	CO
6752000	Cache La Poudre River near Fort Collins	1882-present	120	CO
7144300	Arkansas River at Wichita	1877-present	125	KS
6889000	Kansas River at Topeka	1869-present	133	KS

Stream gauge data are essential to understanding riparian vegetation dynamics, as flooding regimes are one of the principal disturbance types controlling river geomorphology (Kochel 1988; Wolman and Miller 1960), plant establishment (Cooper and others 2003a; Johnson 2000), community composition, and vegetation structure (Baker 1989, 1990; Friedman and Auble 1999). Gauge data provide some of the best information to evaluate hydrological alterations of rivers including flow diversions, augmentations, or impoundments and the resulting changes in ecological systems (Andersson and others 2000; Cooper and others 1999; Johnson 1998; Richter and others 1996; Richter and others 1998). Records can also help evaluate indirect effects to riparian and wetland ecosystems resulting from logging, fire, or land use change in a watershed (Cleaveland 2000; Dwire and Kauffman 2003; Kondolf and others 2002; Legleiter and others 2003).

The two most basic types of information about rivers that can be gained from gauge records are stage—water depth above an arbitrary datum—and discharge—the volume of water flowing past a point for some period of time (Dunne and Leopold 1978). The two are related as a function of stream channel morphology and are directly correlated to the probability of flooding, a key factor governing riparian vegetation patterns. Instantaneous peak discharges are often more strongly correlated with vegetation establishment patterns than mean flows, although in many alluvial rivers, it is the more frequent bankfull discharges that accomplish the most geomorphic work (Leopold and others 1964; Wolman and Miller 1960). Both types of data were obtained from the USGS for a number of gauges, particularly those with long records.

Groundwater measurements

Despite the importance of groundwater to many wetlands, long-term datasets from groundwater monitoring wells and piezometers are relatively rare for most wetland and riparian ecosystems (Winter and Rosenberry 1998; Winter and others 2001). Where available, these data are typically of short duration, although even these provide important insights into wetland functions (Cooper and others

2003c; Scott and others 1999; Stromberg and others 1996; Winter and LaBaugh 2003). Because groundwater systems are often complex and poorly understood, our ability to confidently predict groundwater dynamics for wetlands, let alone assess historical groundwater dynamics, is limited. Available data are helpful for understanding the natural hydrologic functions of different wetland types and their susceptibility to anthropogenic change.

Weather stations

Weather stations, particularly those with long periods of record, provide data for understanding climatic variability at short and intermediate time scales; provide information needed to validate proxy models of past climatic conditions (Woodhouse and Overpeck 1998); and can provide information useful for interpreting the structure and function of contemporary wetlands and riparian ecosystems. To help characterize important differences across the region, we selected stations across a latitudinal and elevation gradient, focusing on stations with the longest records and those closest to USFS units. Like stream gauges, all weather stations postdate the arrival of Euro-Americans in the region, limiting the stations' direct utility for studies of historical climates.

Paleoclimatic, Paleohydrologic, and Paleoeological Studies

The longest instrumental records for the western United States are relatively brief compared with the time scales necessary to understand key geological, geomorphic, climatic, and ecological processes shaping wetland and riparian ecosystems. For instance, direct geomorphic drivers of riparian plant establishment, such as large floods or landslide events, or disturbances like fire or insect outbreaks, which can indirectly affect wetland or riparian systems by altering water or sediment fluxes, may occur at time scales of centuries or longer, while the glacial advances and retreats that created landforms suitable to the development of many montane and subalpine fens and wet meadows occur over tens of thousands of years. In addition, climatic variability at shorter annual and decadal scales is an important driver of the hydrologic function and species composition of wetlands such as marshes (Bolen and others 1989; Winter and others 2001) and salt flats (Ungar 1998) and would have been key to vegetation dynamics prior to Euro-American settlement.

Researchers working in a range of disciplines have developed methods for reconstructing past climates, hydrologic regimes, and plant communities. Sources of proxy evidence are tree rings, pack rat middens, plant macrofossils, ¹⁴C-dating of peat, microfossils such as pollen or phytoliths, lake sediments, lake levels, paleoflood indicators, and fossil dunes (Table 5). Collectively, these methods provide evidence for large climate shifts at a range of spatial and temporal

Table 5—Representative paleoecological and paleoclimatic studies relevant to this assessment.

Study type	Reference
Pollen	Fall 1992, Fall 1994, Denniston et al. 1999, Dean et al. 1996, Baker 1969, Whitlock and Millspaugh 2001, Whitlock 1993
Eolian activity	Forman et al. 2001, Dean et al. 1996, Clarke and Rendell 2003
Macrofossil	Baker 1969, Baker 2000
Packrat middens	Pearson and Betancourt 2002, Cole et al. 1997
Dendrological reconstructions	Yansa 1998, Woodhouse and Brown 2001, Grissino-Mayer and Swetnam 2000, Veblen et al. 2000, Sherriff et al. 2001, Mast et al. 1998, Woodhouse 2001, Graumlich et al. 2003
Speleotherms	Denniston et al. 1999
Lake sediments	Fritz 1996, Laird et al. 2003, Laird et al. 1996, Baker 1969

scales and, when interpreted in light of studies of modern ecosystems, provide a means of inferring past ecological function. As an example, pollen evidence has been commonly used to document vegetation responses to changing climates (Fall 1992, 1994; Meyer and others 2003; van Ahlefeldt 2000).

Classification of Region 2 Wetlands and Riparian Communities

Vegetation classifications are critical for identifying the types of plant communities occurring in any region and prioritizing conservation strategies. They also provide an effective way to understand the range of community types that occur with different hydrologic regimes and past disturbance regimes. Extensive work on vegetation classification has been done in Region 2, although most studies have been conducted for individual forests rather than for the entire region. An exception is the statewide wetlands classification produced by Colorado (Carsey and others 2003). To analyze the similarities and differences of wetland and riparian plant communities across Region 2, we gathered primary vegetation composition and cover data sets from the region and combined them into a relational database (MS Access, Microsoft, Inc.) (Table 6). These data were used as inputs into PC Ord (McCune and Mefford 1999), a multivariate statistics package for analysis.

Table 6—Sources of plot data used in vegetation classification

Classification and ordinations	Location and extent
Girard et al. 1997	Wyoming; Bighorn National Forest
Marriott and Faber-Langendoen 2000	South Dakota; Black Hills Ecoregion
CNHP & Cooper	Colorado; entire state
Cooper and Andrus 1994	Wyoming; Wind River Range
Heidel and Laursen 2003a	Wyoming; Medicine Bow National Forest
Jones 1992	Wyoming; Medicine Bow National Forest (riparian)
Walford et al. 1997	Wyoming; Shoshone National Forest
Jones and Walford 1995	Wyoming; Eastern Plains
NPS, VEG Bank	Nebraska; Agate Fossils National Monument

Historical Photographs and Accounts

The written accounts and photographs of early explorers and settlers can provide useful, if somewhat biased, insights into changes in wetlands and riparian ecosystems. Fur trappers were pursuing beaver throughout the Central and Southern Rockies by the 1820s (Wohl 2001), yet they left few accounts of their travels. Important written accounts of landscapes from members of early exploring parties to the Great Plains and Rocky Mountains are Edwin James' account of the Stephen Long expedition to Colorado in 1820 (Evans 1997) or George Custer's 1874 expedition through the Black Hills (Horsted and Grafe 2002). Photographers accompanying some of the early expeditions, including W. Illinsworth and W. H. Jackson, took many excellent photographs that provide visual evidence of some riparian and wetland areas in the early period of Euro-American settlement. Photographs and accounts were obtained from several sources, primarily the USGS photographic library in Lakewood, Colorado, the Denver Public Library's Western History collection, and a number of publications (e.g., Bradford 1998; Horsted and Grafe 2002).

3. Wetland and Riparian Ecosystems of Region 2: Structural and Functional Characteristics and Ecological and Historical Setting

Introduction

The relative abundance of water on a seasonal, annual, and long-term basis differentiates wetland and riparian ecosystems from uplands. The source of water (precipitation, surface flow, or groundwater) and its spatial and temporal distribution comprise an ecosystem's hydrologic regime, which influences a wide range of ecological attributes, from rates of nutrient cycling and productivity (Mitsch and Gosselink 2007; Pinay and Naiman 1991; Weltzin and others 2000) to floristic composition (Cooper and Andrus 1994; Seabloom and others 1998). At fine scales, the hydrologic regime operates as a driver of ecological structure and function, while at broader scales, it shapes patterns of wetland and riparian ecosystem abundance and distribution. Additional climatic and geological factors operating across a range of spatial and temporal scales affect biogeochemical processes and vegetation, either acting independently or through their control of hydrologic processes. Collectively, climate, geology, and hydrology form the template upon which wetlands and riparian ecosystems develop; it is largely by examining how they influence contemporary systems that we form a basis for inferring the HRV of key ecological attributes.

Also important to developing an HRV assessment is a critical examination of the human history of the region, prior to and following the arrival of Euro-Americans. Though there is continued debate regarding the extent and magnitude of their influence on natural systems (Denevan 1992; Flores 2001; Vale 1998), Native Americans likely had some impact on Region 2 ecosystems, at least locally, although there is insufficient information from which to draw general conclusions. There is less uncertainty regarding the impact of Euro-Americans on wetland and riparian ecosystems—since the Eighteenth Century, wetlands and riparian ecosystems have been among the most intensely and systematically altered in North America (Dahl 1990). The wide variety of impacts, detailed later in this and subsequent chapters, include hydrologic alterations associated with dams and water diversions (Graf 1999; Nilsson and Berggren 2000; Pringle 2000), agricultural drainage (Dahl 1990), grazing (Belsky and others 1999; Fleischner 1994; Patten 1998), and the widespread introduction of non-native species (Crooks 2002; Mack and others 2000; Stein and Flack 1996).

The extent and magnitude of Euro-American impacts across Region 2 are variable. Many systems, such as those found in remote wilderness areas, may have seen little direct impacts, while others, such as lower montane or Great Plains ecosystems, may have been more significantly altered. Our assessment of where and to what degree departures from the HRV may have occurred will, therefore, involve an examination of both the region's human and ecological history.

The ecosystem types we evaluate in this assessment vary considerably from one another in their relative abundance, landscape distribution, vegetation composition and dynamics, and functional characteristics. Because of these differences, separate assessments are presented for each major ecosystem type—fens, wet meadows, marshes, salt flats, and riparian areas. The main goal in this chapter is to characterize the key process variables and attributes that distinguish these major ecosystem types and control their structure and function. We also provide a broad overview of topics common to each, including: (1) the contemporary and historical climatic, geologic, and hydrologic patterns in the region, (2) a description of principal plant communities associated with different wetland types, (3) the major anthropogenic impacts to wetland and riparian ecosystems, and (4) a review of the human and ecological history of Region 2 as it pertains to the assessment.

Overview of the Principal Wetland and Riparian Types in the Region

Though frequently managed and regulated as a single resource, the wetland and riparian ecosystem types described in this document differ widely in their functional and structural characteristics. A common problem is the often ambiguous terminology used to describe wetlands and riparian ecosystems (Mitsch and Gosselink 2007). Many terms are regional in application and have had the effect of unnecessarily separating out systems which may, in fact, be quite similar in function. For example, playas—precipitation-driven depressional wetlands occurring in the Great Plains—are often thought to be restricted to the “Playa Lakes region” of Texas, New Mexico, Kansas, New Mexico, and Southeast Colorado (Nelson and others 1984). However, similar ecosystems can be found in eastern Wyoming, the rainwater basin of Nebraska, and unglaciated portions of the South Dakota mixed grass prairie (Smith 2003).

Likewise, some commonly used terms lump very different ecosystems together based on criteria with little ecological significance. For instance, riparian areas are often defined based on arbitrary geographic criteria, like absolute distance from a stream channel, resulting in the combination of communities with primarily surface water hydrologic regimes with those supported principally by groundwater. Though there may be some common species between these two ecosystems, it is likely that each would respond differently to a major change in the watershed such as dam construction, water diversion, or timber harvest. Given the goals of this assessment, it is critical to correctly identify ecosystems that function similarly. Since there are few data available that pertain directly to the historical variability of vegetation in wetland and riparian ecosystems, our HRV assessments are based largely on our understanding of how key drivers affect the structure and function of contemporary ecosystems, and how anthropogenic factors may have altered these drivers.

The five main ecosystem types that form the basis of this assessment possess certain hydrologic characteristics, which in turn drive additional differences in floristic composition, vegetation structure, and biogeochemical functioning. The following section outlines some of these differences, distinctions that will be addressed in greater detail in subsequent chapters.

Riparian areas

Riparian ecosystems are diverse in landform, hydrologic regime, vegetation, and ecological functioning and they occur in all portions of Region 2. Included are ecosystems found along steep, small-order headwater streams in the mountains, intermittent and ephemeral streams in the foothills and plains, and areas along broad, low-gradient alluvial rivers on the plains (National Research Council 2002). The principal characteristic unifying riparian ecosystems is the presence of unidirectional moving water, which has the potential to erode and transport sediment. The frequency, magnitude, and energy of floods, which vary widely due to differences in basin size, topography, and climatic regime, affect all ecological processes from nutrient cycling to plant establishment (Adair and others 2004; Cooper and others 2003b; Karrenberg and others 2002). Hydrologic regimes of riparian areas vary widely across the region, from relatively stable, groundwater-driven flows in the Sandhills of Nebraska (Bio/West 1986; Winter 1999) to infrequent and unpredictable flash floods associated with intermittent and ephemeral streams on the Great Plains (Friedman and Lee 2002) and lower-elevation mountain regions. Despite this complexity, there are definite patterns in vegetation structure and ecosystem function across elevation gradients, which provide a basis for characterizing riparian HRV.

Fens

Fens form in a variety of landscape settings and show great floristic diversity (Bedford and Godwin 2003; Cooper 1996). However, all fens share one basic characteristic: they have stable groundwater-driven hydrologic regimes with high water tables that retard organic matter decomposition and promote peat accumulation. Depending upon the geological characteristics of the watershed supplying their water, they can vary considerably in water chemistry. Fens are among the most floristically unique ecosystems in the region, often supporting rare or endemic species (Chadde and others 1998; Cooper and Andrus 1994; Cooper and Sanderson 1997; Heidel and Laursen 2003a,b; Weber 2003). In contrast to riparian areas, there is little sediment moving into or out of fens. Fens may occur adjacent to riparian areas in mountain valley bottoms; however, they have independent water sources and function quite differently from riparian areas. Fens may support floating mats of vegetation, which is unique among wetlands within the region.

Marshes

Marshes typically form in depressions and include such diverse systems as prairie potholes, playas, lacustrine fringe wetlands, and abandoned oxbow lakes on river flood plains. Marsh hydrology can be extremely variable and frequently includes both prolonged periods of inundation as well as extended dry periods, particularly during dry years (Winter and Rosenberry 1998; Winter and others 2001). A second key variable is water depth. Marshes periodically have deep standing water, which limits the species that occur to aquatic and wetland species tolerant of submersion. A third key variable is water and soil chemistry. Some marshes have significant flow-through of fresh water. In contrast, terminal basins, where water is lost primarily through evapotranspiration, may be highly saline, which affects species composition, litter decomposition, and productivity (Thormann and others 1999). Hydrologic variability, water depth, and salinity are key factors determining the species composition of marshes, both spatially within and among marsh complexes and temporally from wet to dry years (Seabloom and others 1998; Smith and Haukos 2002; van der Valk and others 1994). Seed banks play a particularly important role in marsh vegetation dynamics (Smith and Kadlec 1983; van der Valk and Davis 1976; Wilson and others 1993) with large fluctuations in species composition commonly occurring over relatively short time scales. The strong water depth gradients also generate distinct vegetation zonation patterns in many marshes (Johnson and others 1987; Lenssen and others 1999).

Wet meadows

Wet meadows are widespread and likely cover more area than all other wetland types combined in the region. They occur from the alpine zone to the plains; yet despite their relative abundance, there are relatively few studies examining their hydrologic and edaphic characteristics or vegetation dynamics. Although wet meadows typically exhibit seasonally saturated soils, they lack the perennial high water tables of fens or the large seasonal and inter-annual water table fluctuations that are characteristic of marshes (Mitsch and Gosselink 2007). Many wet meadows are managed for livestock forage and hay production, and in agricultural areas, meadows frequently develop down slope of unlined irrigation canals. Over long periods of time, wet meadows may form as marshes or beaver ponds become filled with sediment (Naiman and others 1994).

Salt flats

Salt flats are a widespread wetland type found at low elevations and intermountain basins through the West, but are poorly understood. They generally form in closed basins in areas with heavy-textured soils or where evaporation from a high water table promotes the accumulation of salts. High salt concentrations create a difficult environment for most plants; consequently, plant cover and productivity

is generally low and species composition is limited to salt-tolerant species (i.e., halophytes) (Dodd and Coupland 1966; Ungar 1966; Ungar 1974b). Ironically, because salt flats are so marginal in terms of forage production or suitability for crops, they may have been spared many of the anthropogenic impacts that affect the other primary wetland types.

Vegetation of Region 2 Wetlands and Riparian Areas

Wetlands and riparian areas support a variety of plant species and community types found nowhere else in Region 2 landscapes. For example, 183 of the nearly 600 ecological system types (groups of plant community types that tend to co-occur in similar ecological settings) defined by Commer and others (2003) in their analysis of Region 2 vegetation are found in wetlands. Wetlands and riparian systems function as both local and regional centers of biodiversity (Naiman and others 1993; Stohlgren and others 1997) and support many rare or endemic species (Cooper and others 2002; Cooper and Sanderson 1997; Heidel and Laursen 2003 a,b; Mellmann-Brown 2004).

Variation in a site's hydrologic and disturbance regimes strongly influence vegetation composition among wetland types. Environmental characteristics, such as periodic deep inundation in marshes or sustained high water tables in fens, limit the species that can occur at any site. Only species with the appropriate physiological and life history adaptations are able to persist and compete in the distinct environmental conditions typical of each wetland type. Examples of adaptations commonly found in wetland species are aerenchyma, adventitious roots, pressured gas flow, and salt tolerance (Mitsch and Gosselink 2007; Rood and others 2003a). As a consequence, many species found in wetlands occur only in wetlands. Some species show a range of fidelity for wetland habitats and are referred to as facultative wetland species (Reed 1988). Even within a particular species, there may be regional differences in the frequency at which plants are found in wetlands (Tiner 1999).

Overall variation in Region 2 wetland and riparian vegetation

An indirect ordination, shown in Figure 2, was created using detrended correspondence analysis (DCA) with the computer program PcOrd (McCune and Mefford 2006) and vegetation data from 5266 plots from wetland and riparian studies done in the region. Variation along axis 1 is due primarily to elevation and water table permanence. High-elevation sites with perennially high water tables occur on the left and low-elevation sites with varying water tables are on the right. Variation in Axis 2 is largely due to water chemistry, with saline sites near the top and freshwater sites at the bottom. Each plot is represented by one point and the centroids of key indicator species are shown in the ordination space.

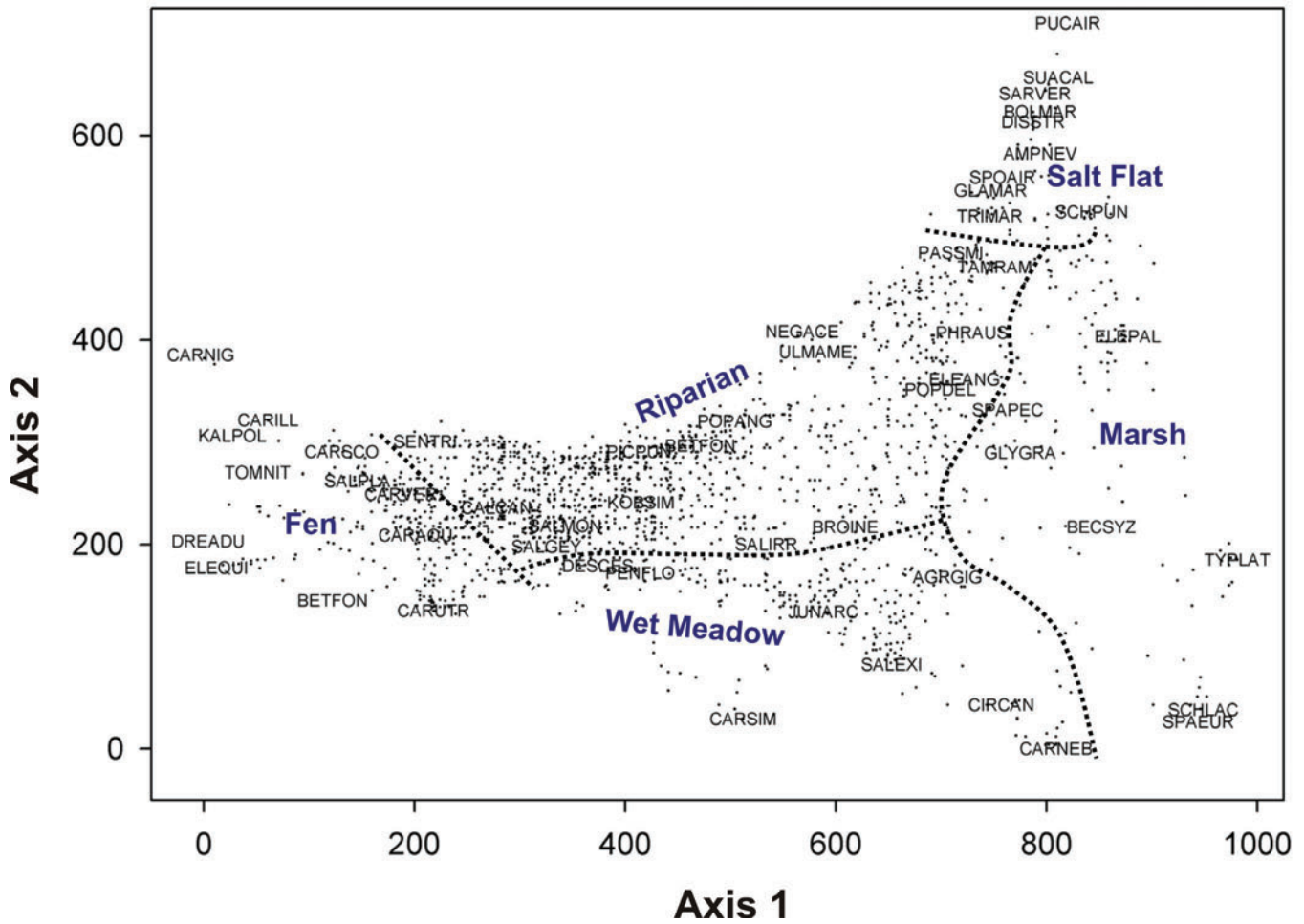


Figure 2—Ordination of Region 2 vegetation data. Common plant species are shown using the following abbreviations: CARNIG = *Carex nigricans*, DREADU = *Drepanocladus aduncus*, ELEQUI = *Eleocharis quinqueflora*, KALPOL = *Kalmia polifolia*, CARILL = *Carex illota*, TOMNIT = *To menthy pnum nitens*, BETFON = *Betula fontinalis*, CARSCO = *Carex scopulorum*, SALPLA = *Salix planifolia*, CARVES = *Carex vesicaria*, SENTRI = *Senecio triangularis*, CARAQU = *Carex aquatilis*, CARUTR = *Carex utriculata*, CALCAN = *Calamagrostis canadensis*, SALMON = *Salix monticola*, SALGEY = *Salix monticola*, DESCES = *Deschampsia cespitosa*, PENFLO = *Pentaphylloides floribunda*, PICPUN = *Picea pungens*, BETGLA = *Betula glandulosa*, POPANG = *Populus angustifolia*, SALIRR = *Salix irrorata*, CARSIM = *Carex simulata*, JUNARC = *Juncus arcticus*, SALEXI = *Salix exigua*, CARNEB = *Carex nebraskensis*, CIRCAN = *Cirsium canadensis*, AGRGIG = *Agrostis gigantea*, BROINE = *Bromopsis inermis*, NEGACE = *Negundo aceroides*, ULMAME = *Ulmus americanus*, POPDEL = *Populus deltoides*, ELEANG = *Eleagnus angustifolia*, PHRAUS = *Phragmites australis*, SPAEUR = TAMRAM = *Tamarix* spp., PASSMI = *Pascopyrum smithii*, PUCAIR = *Puccinellia airoides*, SUACAL = *Sueda calcioliformia*, SARVER = *Sarcobatus vermiculatus*, BOLMAR = *Bolboschoenus maritimus*, DISSTR = *Distichlis stricta*, AMPNEV = *Amphiscirpus nevadensis*, SPOAIR = *Sporobolus airoides*, GLAMAR = *Glaux maritimus*, TRIMAR = *Triglochin maritimum*, SCHPUN = *Schoenoplectus pungens*, ELEPAL = *Eleocharis palustris*, SPAPEC = *Spartina pectinatus*, GLYGRA = *Glyceria grandis*, BECSYZ = *Beckmannia syzygachne*, TYPLAT = *Typha latifolia*, SCHLAC = *Schoenoplectus lacustris*, SPAEUR = *Sparganium eurycarpum*.

The five major wetland types can be identified in the ordination space. Fens are on the far left, salt flats are on the top right, marshes are on the bottom right, wet meadows are on the bottom center, and riparian areas are elongated from the top right to the left. The riparian continuum includes springs and small head-water mountain streams with herbaceous communities dominated by *Senecio triangularis*, *Salix geyeriana* and other willow-dominated thickets along small to medium sized mountain rivers; *Populus angustifolia* and *Picea pungens*-dominated forests along mid-elevation mountain rivers; *Acer negundo* forests in canyons and foothills; and on the plains, *Salix irrorata* and *Populus deltoides* forests with *Tamarix* and *Elaeagnus angustifolia*.

A range of fen types occur, including basin types dominated by *Carex utriculata* and *Carex vesicaria*; slope fens dominated by *Eleocharis quinqueflora*, *Carex aquatilis*, and *Carex illota*; and wooded fens with *Kalmia polifolia* and *Salix planifolia*. Wet meadows include communities dominated by *Deschampsia cespitosa* at high elevations; *Juncus arcticus* at mid- to low-elevations; and *Carex nebraskensis* at lower elevations. A wide range of marshes occur and due to deep, prolonged inundation, many are monocultures or have very low floristic diversity. The deepest water sites have *Schoenoplectus lacustris* and *Typha latifolia*, while sites with more shallow water are dominated by *Eleocharis palustris* and *Schoenoplectus pungens*. The later species can also occupy marshes that are highly saline and that are found adjacent to salt flats. The salt flat communities are also species poor—often dominated by monocultures of halophytic species such as *Distichlis spicata*.

Climate

Issues of scale

As with the ecological parameters examined in this HRV assessment, climate variables require explicit spatial and temporal bounds for proper interpretation (Bradley 1999). Measures of central tendency and variability are dependent upon the scale of analysis. For instance, climatic variables such as global mean temperature are relatively stable at time scales of decades to centuries. However, the paleoclimatic record demonstrates significant variation over time scales of tens of thousands to millions of years. Similarly, notions of change are frequently scale dependent. Climatic patterns can be heterogeneous over relatively small spatial scales due to factors such as local topography.

Spatial and temporal climate patterns and historical variability

Directly measured climate records provide important although temporally limited data for evaluating climatic variability. Assessments of historical climates from paleoclimatic and instrumental records are, for some wetland types, the primary information source for making inferences on the HRV for hydrologic and ecological variables since no reliable instrumental data are available. Unlike forests, where tree rings or stand structure can provide evidence of past disturbance regimes and vegetation dynamics, herbaceous-dominated ecosystems such as marshes or wet meadows generally leave little evidence of long-term dynamics. Additionally, relative to forests, few studies have successfully reconstructed historical conditions or dynamics in wetlands or riparian ecosystems.

Climate integrates the mean and variability of atmospheric conditions, including temperature, precipitation, humidity, and solar radiation, and exerts a key influence on the Earth's biota. Over broad spatial and temporal scales, it is a major driver of geomorphic as well as ecological processes, influencing patterns of glaciations (Bradley 1999), erosion and sediment dynamics, and drainage network formation (Knighton 1998; Leopold and others 1964; Rosgen 1996). It is also a principal determinant of the distribution and functional characteristics of the wetland and riparian ecosystem types found in Region 2. The climatic variables of greatest significance to wetland and riparian ecosystems are temperature and precipitation, which vary along both latitude and elevation gradients. However, considerable variability can occur at a given latitude or elevation due to factors such as land form and land use (Kittel and others 2002).

As a fundamental thermodynamic control on rates of chemical, physical, and biological processes, temperature—its range, minimum, and maximum values—is an important factor that shapes such diverse phenomena as species ranges, biogeochemical cycling, erosion and mass wasting rates, and hydrologic cycling. Temperature regimes throughout Region 2 are continental in character, exhibiting greater summer and wintertime temperature fluctuations relative to maritime regions (Kittel and others 2002).

Mean annual temperature at a given elevation increases from north to south, although this is due more to differences in winter than in summer temperatures (Kittel and others 2002). The relationship between elevation and temperature, both minimum and maximum values, varies in an approximately linear fashion, with cooler temperatures observed at higher elevations (Figures 3, 5). In mountainous areas of Wyoming and Colorado, steep elevation gradients and complex topography create environmental heterogeneity that is not present in the Great Plains.

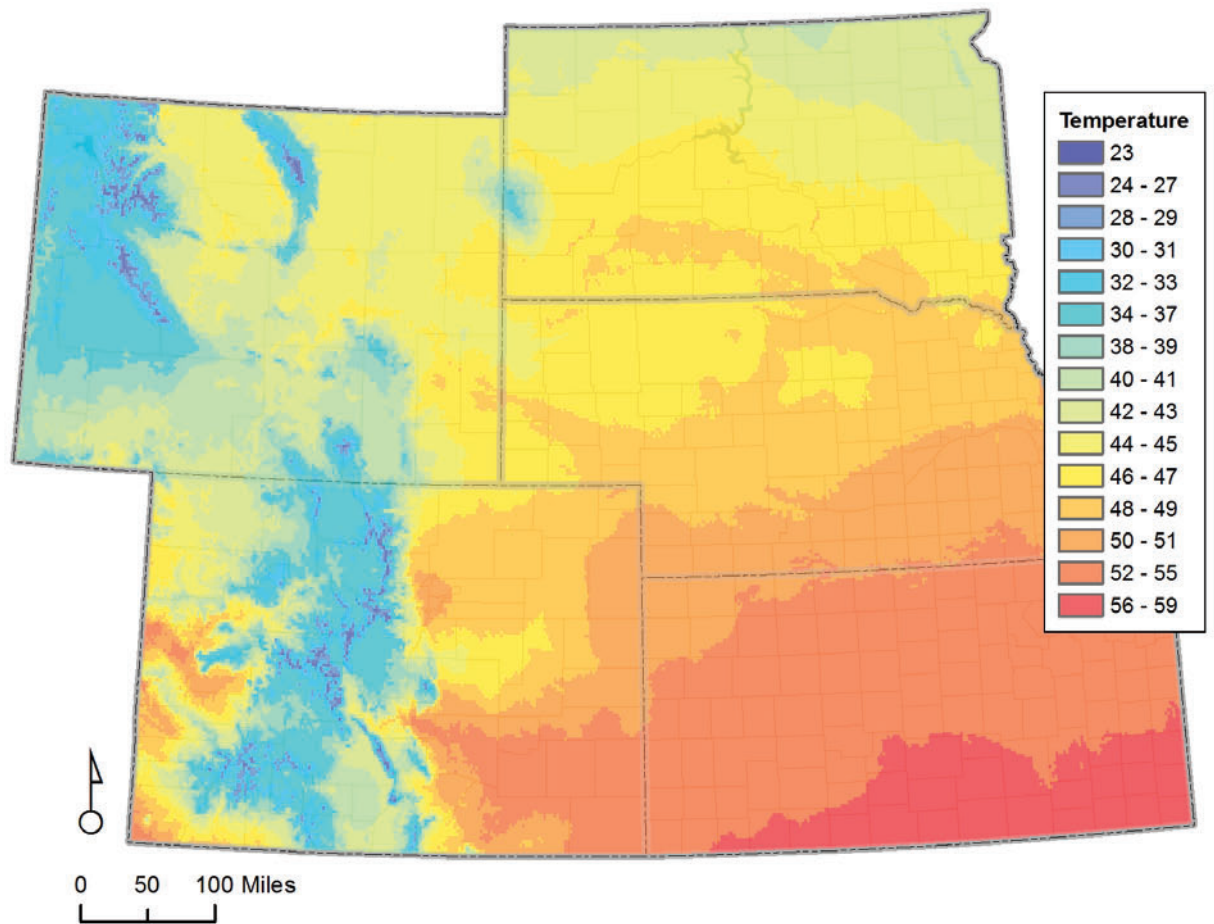


Figure 3—PRISM mean annual temperature (°F) for Region 2 from the National Climatic Data Center’s U.S. National 1971-2000 Climate normals (data online: <http://datagateway.nrcs.usda.gov/>).

Precipitation patterns may influence groundwater-driven wetlands by controlling aquifer recharge. Unlike temperature, only weak trends between precipitation and latitude occur. Elevation and topography are much stronger controls on precipitation due to orographic effects, which occur when moist air is lifted and cools as it moves over a mountain range (Bradley 1999). A higher amount of precipitation falls on the windward side of a mountain ridge, and precipitation is generally significantly lower on the lee side of mountains, resulting in the formation of a rain shadow. The effect of mountain ranges on spatial patterns of precipitation is evident in maps of precipitation in the region—significantly greater heterogeneity occurs in the mountainous portions of Wyoming and Colorado relative to the Great Plains (Figures 4, 5).

The seasonality of precipitation varies across the region due to regional synoptic weather patterns—an important factor influencing Region 2 wetlands and riparian areas. Monsoonal precipitation, typified by intense late summer thunderstorms, is important in the southern tier of National Forests (Kittel and others 2002) but is uncommon farther north. Monsoonal precipitation may produce the largest floods on some low-elevation streams (Fleener 1997) and recharge aquifers that sustain fens at higher elevations (Cooper 1990a).

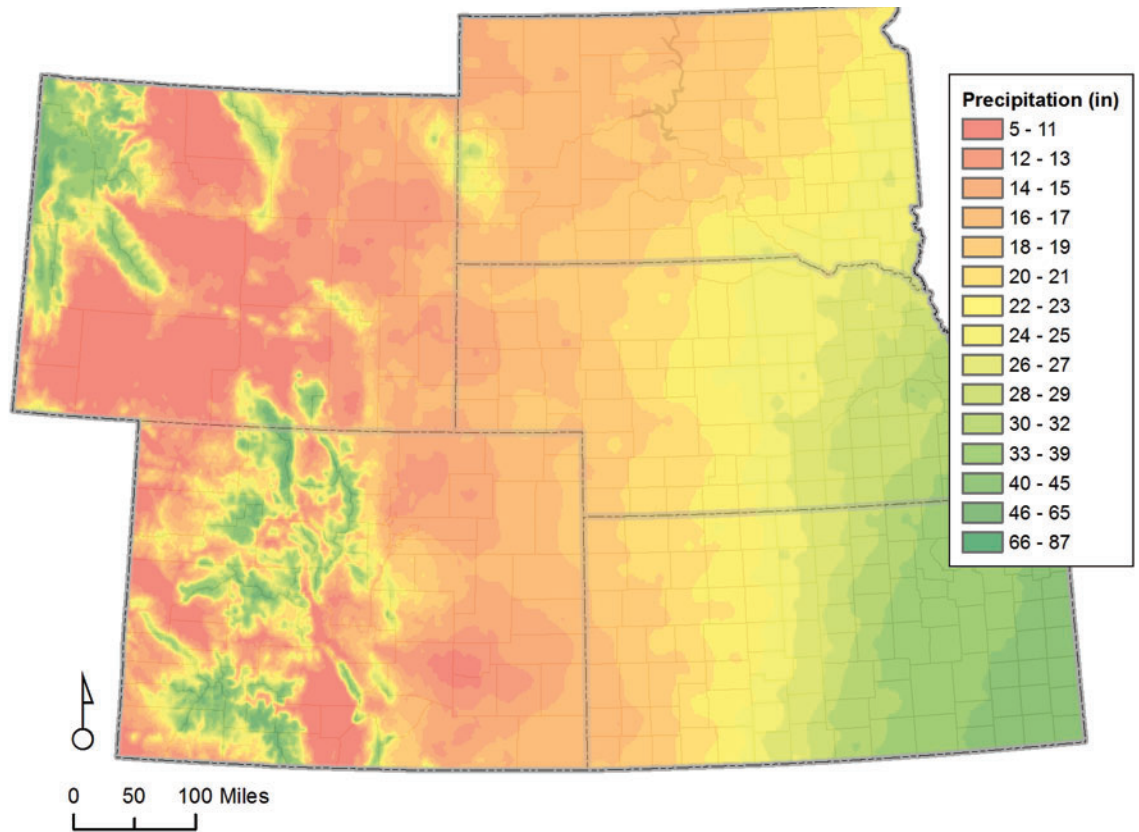


Figure 4—PRISM mean annual precipitation (inches) from the National Climatic Data Center’s U.S. National 1971-2000 Climate normals (Data online: <http://datagateway.nrcs.usda.gov/>).

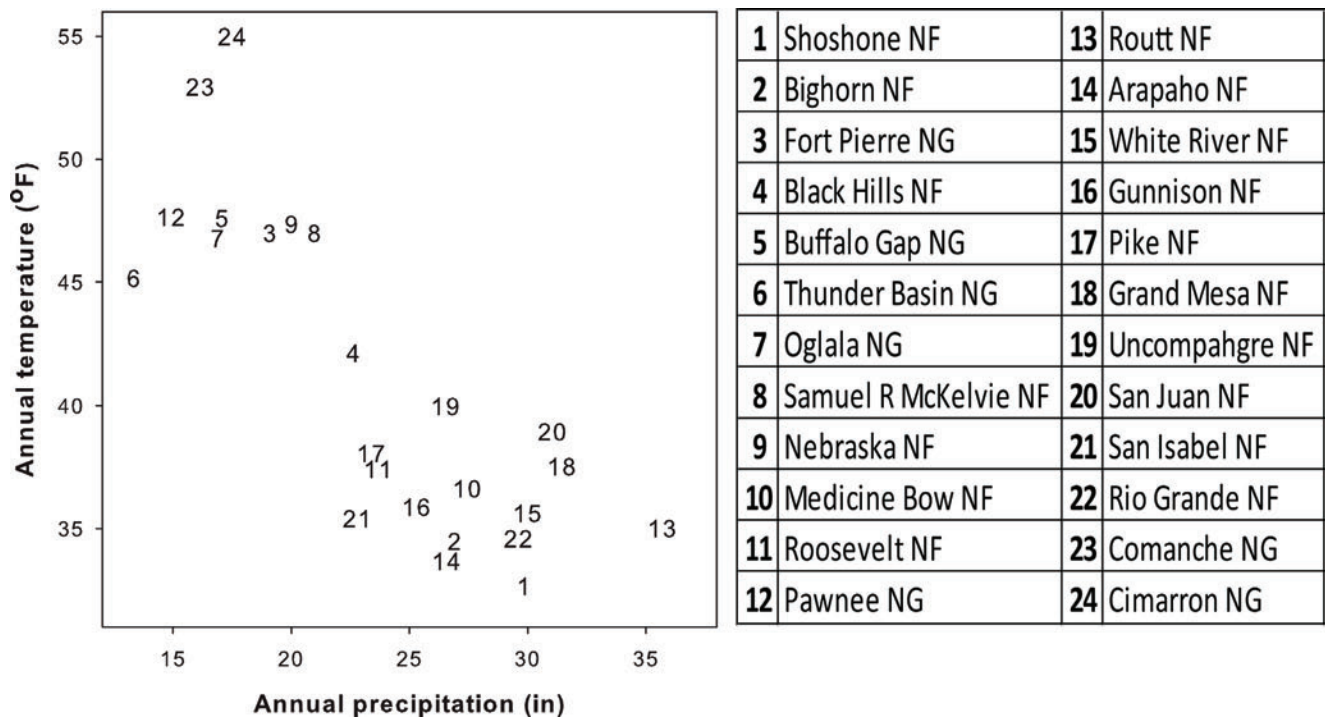


Figure 5—Mean annual temperature and annual precipitation plotted for each USFS unit. Values from PRISM GIS layers (1971 to 2000 normals) were extracted for each USFS unit using zonal statistics in ArcGIS (Data online: <http://datagateway.nrcs.usda.gov/>).

Potential evapotranspiration (PET) refers to the potential rate of evaporation and transpiration under optimal soil moisture and plant cover conditions (Dunne and Leopold 1978). The PET/precipitation ratio provides a measure of a region's aridity. Regions with a PET/precipitation ratio greater than 1.0 have a moisture deficit, while regions with a ratio less than 1.0 have a moisture excess. This ratio may influence seasonal soil water content, runoff, and hydrologic conditions needed to support wetlands. Evaporation is driven in large part by temperature and it shows a similar pattern at broad spatial scales. Because PET greatly exceeds precipitation for most of the region, wetlands are generally less abundant than in more humid areas such as the southeast United States (Kroes and Brinson 2004).

Drought, defined here as the prolonged and abnormal absence of precipitation, influences wetlands and riparian areas in many ways, including its influence on fire regimes in adjacent ecosystems (Donnegan and others 2001; Hessl and others 2004; Swetnam and Betancourt 1998) and its control on hydrologic regimes and, therefore, vegetation dynamics, in marshes and riparian areas (Hardy 1995; Rejmankova and others 1999; Winter and Rosenberry 1998).

Palmer Drought Severity Index (PDSI) integrates temperature and rainfall data to determine relative dryness (Barry and Chorley 2003) at a time scale of months. A PDSI value of 0 indicates average precipitation, negative values indicate increasing drought conditions, and positive values indicate wetter conditions. A PDSI value of -2 indicates moderate drought, while -4 indicates extreme drought. Since the PDSI is standardized to local climate, it can be applied to any region. Though drought is unpredictable, instrumental records and paleoclimatic reconstructions have documented numerous drought episodes and indicate that moderate to extreme drought recurs at decadal to millennial scales (Cook and others 1999).

PDSI records document three major decadal-scale moisture regimes on the Great Plains. The early part of the Twentieth Century, from approximately 1905 to 1917 when a large influx of homesteaders immigrated to the region, was one of the wettest periods since the Sixteenth Century (Figure 6). Paleoclimatic reconstructions of PDSI values indicate that similar wet periods (pluvials) occurred in the Sixteenth, Seventeenth, and Nineteenth centuries (Fye and others 2003) (Figure 7). There is only a weak correspondence between precipitation records and climatic reconstructions from Colorado and Wyoming and those from the Plains, suggesting different large-scale climatic drivers. The "dust bowl" drought of the 1930s has no analog for size or severity in the historical record. However, a "megadrought" in the late Sixteenth Century that was concentrated over the Southwest appears to have surpassed the 1930s drought in severity and duration (Acuna-Soto and others 2002; Fye and others 2003).

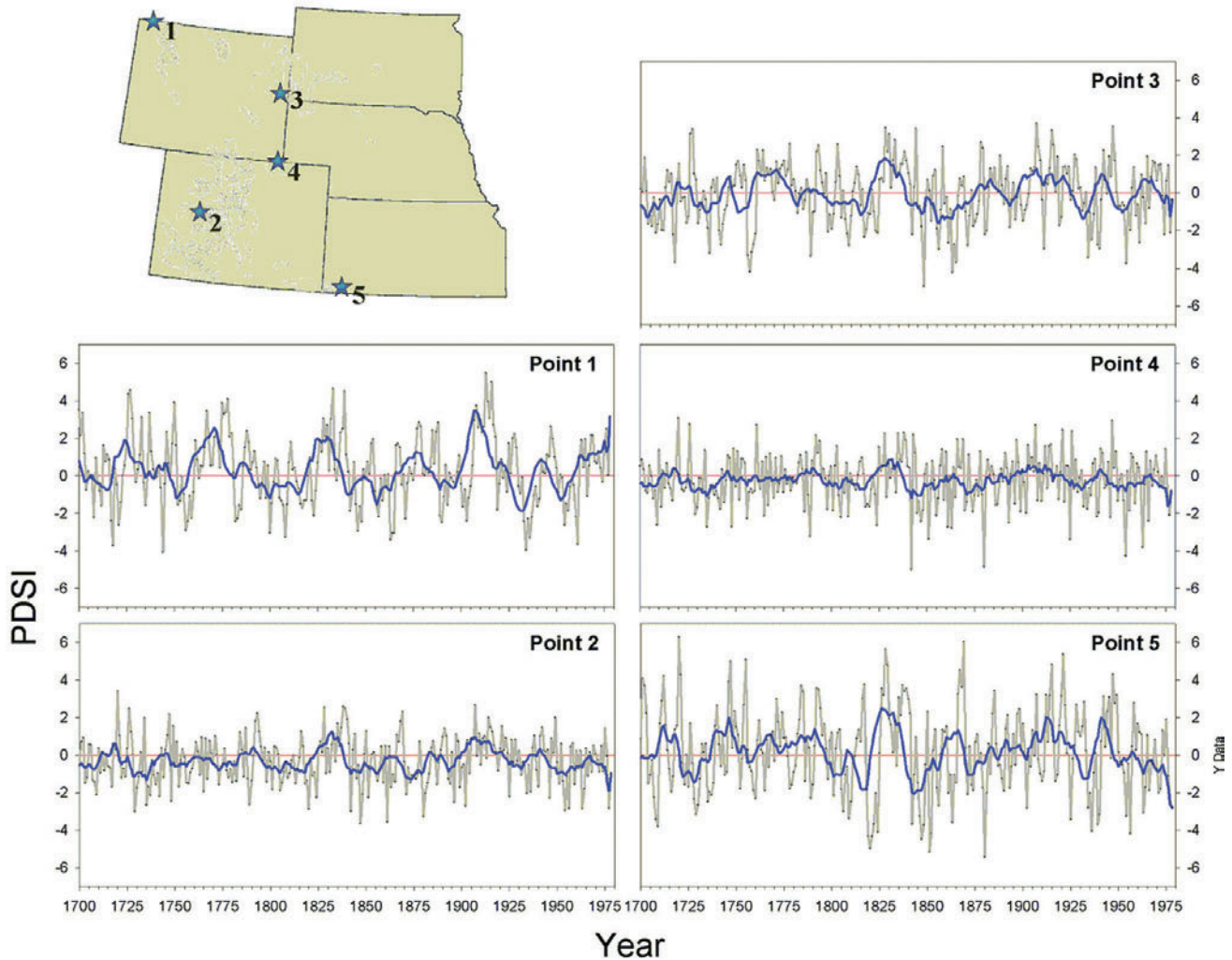


Figure 6—Palmer drought severity index (PDSI) estimates (gray lines), 5 year running averages (blue line), and overall averages (red lines) reconstructed from regional networks of tree rings for five locations in Region 2. (Data obtained online from the NOAA Paleoclimatology Program, http://www.ngdc.noaa.gov/paleo/drought/drght_data.html).

Paleoclimatic studies have utilized a variety of climate proxies, including tree rings (Gray and others 2003; Woodhouse 2003), dune accretion (Clarke and Rendell 2003; Dean and others 1996), pollen records (Fall 1992; Fredlund 1995; Laird and others 1996), lake levels and sediments (Arnou and Stephens 1990; Fritz and others 2000), and ice cores (Soon and Baliunas 2003) to document climatic variability for times scales that range from millennia to centuries and decades. Climate variability may have broad impacts on species ranges, extinction, endemism (Weber 2003), community composition (Whitlock and Millspaugh 2001), disturbance regimes such as fire and insect outbreaks in upland ecosystem (Grissino-Mayer and Swetnam 2000; Sherriff and others 2001; Swetnam and Betancourt 1998), and flooding in riparian ecosystems (Graumlich and others 2003; Knox 2000; Woodhouse 2001).

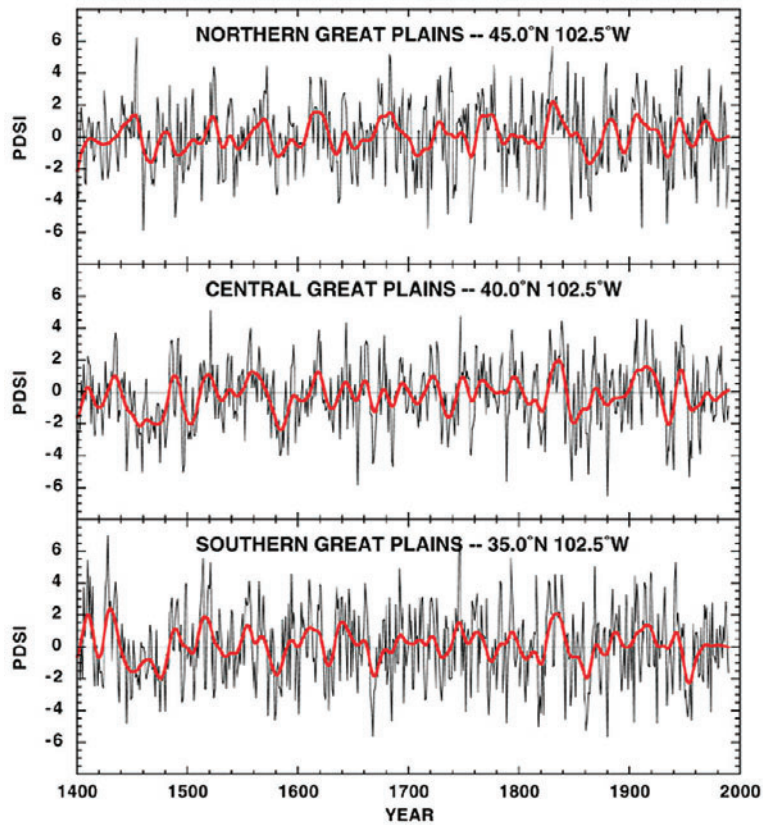


Figure 7—Summer Palmer Drought Severity Indices (PDSI) from 1400 to 2000 from three locations in the southern, central, and northern Great Plains along longitude 102.5°W at latitudes 35°N, 40°N and 45°N. Values to 1978 are tree-ring reconstructed data while those from 1979 to 1990 are instrumental PDSI data for the same grid points. (Source: <http://wf.ncdc.noaa.gov/oa/climate/research/2002/sep/st105dv00pcp200209.html#wgppaleo>).

The El Niño Southern Oscillation (ENSO) is characterized by an increase in the sea surface temperature in the eastern equatorial Pacific Ocean and occurs on average every three to seven years (Barry and Chorley 2003). ENSO patterns have been correlated with anomalous climatic conditions across the world, including areas in USFS Region 2 (Cayan and others 1999; Hidalgo and Dracup 2003), and are correlated with a wide range of regional climatic, hydrologic, and ecological factors, including streamflow variability (Andrews and others 2004), changes in fire frequency and magnitude (Hessl and others 2004), and the occurrence of extreme weather events (Cayan and others 1999). Drought characteristics, at least in the central United States, appear to be weakly correlated with ENSO events and more strongly correlated with the interdecadal climate mode called the Pacific Decadal Oscillation (PDO) (Englehart and Douglas 2003). Considering the overall importance of climate to patterns of wetland distribution and function, understanding large-scale climate drivers like ENSO and PDO can provide insight into the natural variability of wetlands.

Geomorphology and Geology

Wetland and riparian ecosystems are influenced by a variety of geologic and geomorphic factors operating over multiple spatial and temporal scales. Over broad geological time scales, processes of uplift and erosion, influenced by lithology and climate, are largely responsible for the physiographic characteristics of contemporary landscapes. Differences between the tectonically active landscapes of the Rocky Mountains and those of the Great Plains broadly determine the landscape distribution of different wetland types. The mineralogy and grain structure of geological strata influences processes such as infiltration, sediment yield (Knighton 1998), and groundwater chemistry (Winter 2001) and varies at a range of scales.

Although some geological processes, such as mountain uplift, are practically invariable over the time scales that are relevant to management (decades to centuries), others, such as fluvial geomorphic processes or slope failures, are more highly dynamic over shorter temporal scales and can influence the formation and function of wetland and riparian ecosystems. Many geologic and geomorphic processes such as glaciation, although not presently active, are critical for understanding where and in what form wetlands and riparian ecosystems are found.

Glacial processes have significantly influenced wetland distribution and function in portions of Region 2. In North America, some of the highest wetland densities occur in areas affected by past continental glacial advances, most notably the prairie pothole region of eastern South and North Dakota, Minnesota, and southern Canada (van der Valk 1989). Although no Forest or Grassland in Region 2 was covered by continental glaciers, localized ice caps and valley glaciers were widespread in the mountains in the past, and many small glaciers still occur at high elevations in Wyoming and Colorado (Figure 8). Although presently small and shrinking, glaciers were larger and more active during the Pleistocene and had lasting effects on the physiographic characteristics of many montane and subalpine valleys. Many wetlands occur in landforms formed by glacial retreat such as kettle basins—small depressions caused by the melting of buried ice masses (Winter and Woo 1990). In addition, in many mountain valleys, glaciers have indirectly influenced valley form by depositing end moraines and flattening valley gradients, thereby retarding the runoff of water. Glaciers also influenced areas downstream, shaping the form of many river floodplains and terrace systems by paleo-flood events associated with glacial melting (Knighton 1998).

Extensive sand dune complexes are located in several parts of the region, including in the Nebraska National Forest, which includes a portion of the Nebraska Sandhills. Smaller dune systems occur in Wyoming, Kansas, and Colorado. Because of the high permeability and hydraulic conductivity of sand substrates, little to no surface runoff occurs during precipitation events. Consequently, water storage is high and sites may support extensive groundwater flow systems. These sites can support wetlands where local or regional groundwater systems intersect the ground surface, typically in interdunal areas (Drda 1998; Novacek 1989).

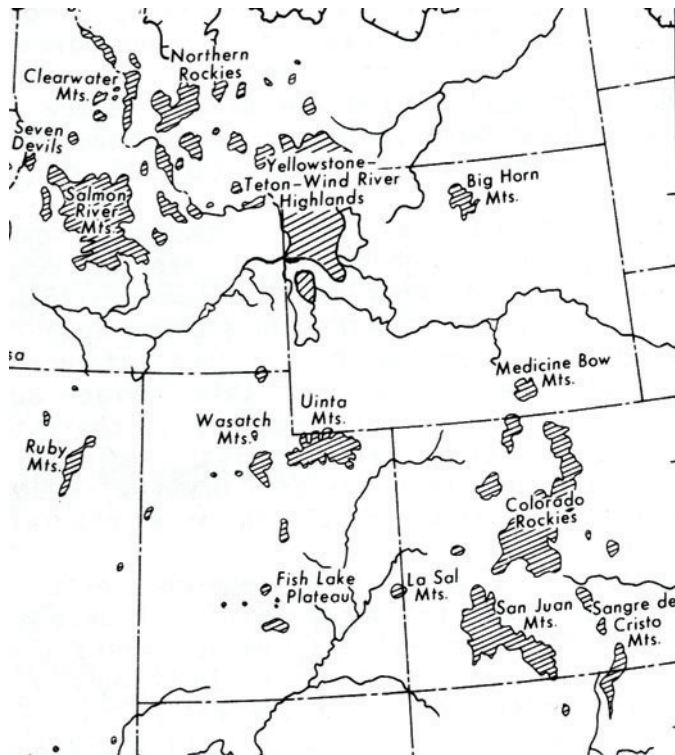


Figure 8—Approximate extent of mountain glaciation during the Pleistocene (source: Windell et al. 1986).

The hydrologic characteristics of streams formed in these settings are strongly driven by groundwater inflows and are unusual for Region 2 in their flow stability. The Nebraska Sandhills and similar eolian features are also important barometers of historical climate change. Stratigraphic and radiocarbon studies conducted in Kansas, Colorado, and Nebraska have demonstrated multiple episodes of increased dune activity resulting from prolonged drought conditions over the last millennium (Clarke and Rendell 2003; Forman and Maat 1990; Muhs and Holliday 1995).

Bedrock geology can influence wetlands and riparian areas by influencing sediment yield and composition. Igneous rock types, such as granite, yield relatively low amounts of coarse sediment relative to sedimentary rock types such as sandstones or limestone (Knighton 1998). Differences in permeability among different rock strata or the presence of faults or rock fractures can create preferential flow pathways resulting in the formation of seeps and springs. These lithologic differences influence patterns of groundwater recharge and discharge and may affect water table dynamics in wetlands and riparian ecosystems. An example is the variable surface water flows in streams flowing through limestone in the Black Hills region of South Dakota (Driscoll and others 2000).

Lithology can also influence the concentrations of elements and compounds that control wetland water alkalinity and that affect plant growth (e.g., calcium, magnesium, and potassium). This variation is driven by different rates and modes of weathering between rock types. Calcareous rocks, such as limestone, contain calcium carbonate, which reacts with the weak acids typically present in rainfall, groundwater, and snowmelt. This chemical weathering can release minerals into solution, concentrations of which can subsequently be modified by hydrologic mixing with groundwater, precipitation, or surface water. Water chemistry variability forms an important environmental gradient that influences vegetation patterns in fens (Cooper 1996; Demars and others 1997; Johnson and Steingraeber 2003).

The specific geological factors important to ecosystem formation and function vary among different wetland and riparian types. Mass wasting events such as landslides can influence riparian ecosystems by damming streams and increasing sediment flux but may have little effect on plains marsh or salt flat ecosystems.

Hydrologic Drivers of Wetland and Riparian Ecosystem Structure and Function

Hydrologic processes control most wetland and riparian functions. Riparian plant establishment is linked to the frequency and magnitude of flooding (Auble and others 1994; Baker 1990; Cooper and others 2003a; Friedman and Lee 2002; Johnson 2000; Scott and others 1997). Water depth and duration controls species composition in marshes (Haukos and Smith 2001; Kantrud and others 1989b; Neill 1990; van der Valk and others 1994), while water table dynamics influence carbon accumulation rates in fens (Chimner and Cooper 2003; Chimner and others 2002). Because of its fundamental importance, many classification systems, such as that developed by the National Wetlands Inventory (Cowardin and others 1979), use hydrologic regime in differentiating wetland types. The primary ecosystem types examined in this assessment can be defined solely in terms of their characteristic hydrologic regimes.

Several hydrologic variables are key drivers of wetland and riparian ecosystem dynamics. They include whether soils are saturated, deeply inundated, or subject to erosive, high energy floods; and the timing of water availability, referring to both the seasonality and length of saturation or inundation. These factors act as a sieve on the pool of potential species capable of occupying the system, allowing only those species with the required physiological, morphological, or life history adaptations to establish and be recruited (Keddy 2000). Lastly, the source of water supporting a wetland or riparian area (i.e., whether it is principally precipitation, surface, or groundwater) and the flow paths taken before and after entering the system can affect a variety of important ecological functions. For instance, the

availability of mineral ions such as Ca^{2+} , and pH influences species composition in many fens (Bedford 1996; Boeye and others 1994; Jeglum 1971; Tahvanainen and others 2003). Likewise, marsh water chemistry varies depending on the influence of local and regional groundwater flow patterns (LaBaugh 1987; Nicholson 1995; Stewart and Kantrud 1971).

The amplitude and frequency of water table variation is an important difference between wetland and riparian ecosystem types. Inundation can result in plant mortality (Amlin and Rood 2001; Friedman and Auble 1999), as can dry conditions resulting from low water tables (Shafroth and others 2000). In flooded areas, periodic drawdowns can expose substrates and allow new plant establishment either from the soil seed bank, as occurs in many marshes (Haukos and Smith 1994; Smith and Kadlec 1983; Wilson and others 1993), or through seed rain, as occurs in many riparian areas (Auble and Scott 1998; Karrenberg and others 2002). Water table depth variation differs among wetland types. For example, fens have relatively low inter-annual water table depth variation compared to marshes. Likewise, fen water tables are more stable over annual and decadal scales—a necessary condition for peat accumulation. Precipitation events that allow playas on the southern plains to fill with water are highly unpredictable from year to year, and species composition is strongly controlled by seed bank dynamics (Haukos and Smith 1993). In contrast, less hydrodynamically variable fens are typically dominated by long-lived clonal perennial species such as *Carex aquatilis* (Chadde and others 1998; Cooper 1996; Cooper and Andrus 1994).

Hydrologic processes supporting wetlands and riparian areas can be complex. Some wetland complexes have multiple, nested groundwater flow systems (Winter and others 2001). Wetlands occur where local variation in subsurface hydraulic conductivity and permeability form a perched water table, or where a change in slope causes groundwater to discharge to the surface (Winter and Woo 1990). Wetlands dominated by groundwater versus surface water and precipitation may respond differently to climatic variability (Winter 2000). Wetlands that are dependent primarily on precipitation for their water supply, such as playas, are highly vulnerable; while those that are dependent primarily on discharge from regional groundwater flow systems, such as fens, are the least vulnerable (Winter 2000).

The affinity or tolerance of individual species for particular hydrologic conditions is highly variable both within and among wetland types. The wide variety of physiological and life history adaptations exhibited by wetland plants, coupled with the hydrologic variability characteristic of most wetlands and riparian areas, drives the “individualistic” (*sensu* Gleason 1926) response of wetland communities to natural and anthropogenic changes (van der Valk 1981).

Disturbance Regimes

Disturbance regime also influences wetland and riparian area distribution and ecological structure and function. Various definitions of disturbance have been developed, some more easily applied to wetland and riparian ecosystems than others. In this assessment, we follow Keddy (2000), who defined disturbance as “a short-lived event that causes a measurable change in the properties of an ecological community.” Two key parts of the definition are the duration of the event—short relative to the lifespan of the dominant species in the systems—and the presence of a measurable change in some ecological characteristic. Among the most commonly examined response variables are plant mortality or reductions in biomass. There are several attributes that together comprise an ecosystem’s disturbance regime, including the extent, magnitude, frequency, predictability, and return rate of disturbance (Table 7). Each component influences ecological structure and function and varies in character among disturbance agents and ecosystem types. For example, the frequency and predictability of large-magnitude floods along intermittent and ephemeral Great Plains streams is quite different than for headwater streams in mountain areas. This is important because floods of equal duration or frequency, but of different intensity, may have different ecological effects. Disturbance types particularly important to wetlands and riparian areas include water level variation, bank erosion, sediment deposition, fire, herbivory, ice flows, and wave action (Auble and Scott 1998; Bendix and Hupp 2000; Katz 2001; Keddy 2000; Kellogg and Bridgman 2004; Pettit and Froend 2001; Scott and others 1997).

Table 7—Commonly measured components of disturbance regimes (source: Sousa 1985)

Disturbance regime characteristic	Definition and example applications
Aerial extent	The size of the disturbed area. It is generally the easiest component to measure and can be expressed in either absolute (m ² or acres) or relative terms (% of wetland).
Magnitude	Two central components: <i>Intensity</i> : an objective measure of the strength of the disturbance agent (depth or duration of flooding, shear stress, temperature of fire). <i>Severity</i> : A measure of the ecological or physical response to the disturbance agent (% mortality and % biomass).
Frequency	The number of disturbance per unit time. Can be expressed differently based on the spatial scale used. Two commonly used approaches are: <i>Random point frequency</i> : the mean number of disturbance events per unit time at any random point. Often reported as the recurrence or return interval. <i>Regional frequency</i> : the total number of disturbances that occur in a geographical area per unit time.
Predictability	Typically measured as the variance on the mean time between disturbances.
Rotation rate	The mean time required to disturb the entire area in question.

Ecoregions of Region 2

Because of the large geographic scope of this HRV assessment, the ecoregional classification originally developed by Bailey (1980) provides an effective structure to examine historical and current patterns of wetland and riparian distribution, form, and function. The classification is hierarchical in nature and recognizes that, since climate ultimately governs energy and moisture gradients, differences in continental and regional climatic regimes and gross physiography act as the primary controls over more localized ecosystems (Bailey 1980).

At the broadest scale, Bailey's classification identifies three ecoregional levels: Domains, Division, and Provinces. Domains are subcontinental areas of broad climatic similarity, while Divisions are subdivisions of domains delineated on the basis of water deficit, which differentiates, for example, the "Dry Domain" into semi-arid, steppe, or arid desert, which are important controls of many biological and physical processes. Provinces identify climatic sub-zones controlled primarily by continental weather patterns such as length of dry season and duration of cold temperatures as well as similar soil orders and overlap considerably with areas of similar potential natural vegetation such as those mapped by Kuchler (Kuchler 1964). At finer scales, geomorphic processes, topography, and stratigraphy, which influence hydrologic function, soil-forming processes, and the potential natural community, are used to delineate Sections. These represent broad areas of similar sub-regional climate, geomorphic process, stratigraphy, geologic origin, and topography. Fifteen Sections have been identified in Region 2. Although finer hierarchical scales have been identified, because of the large geographic scope of this assessment, Sections will be the smallest level discussed. Characteristic wetland and riparian types present in each Section are discussed in subsequent chapters.

Human History of the Region

Native American history as it pertains to HRV—Although the magnitude of anthropogenic changes to ecological systems during the Twentieth Century has no historical precedent, humans have long been effective at altering their environment. Compared to much of Africa, Asia, and Europe, humans are relatively recent components of North American ecosystems, with conventional wisdom suggesting the arrival of humans via a Bering Sea land bridge approximately 13,500 years before present (BP) (Fiedel 1999). Paleo-Indian hunters may have contributed to the large-scale extinction of large mammal species at the end of the Pleistocene (Alroy 2001; Haynes 2002). How humans impacted ecological systems remains a point of controversy among anthropologists, historians, and ecologists. The influence of Native Americans on ecosystems is a critical component of all HRV assessments since these assessments typically assume that the variability of processes and conditions being described occurred under little or no human influence prior to the arrival of Euro-Americans (Landres and others 1999).

There are two competing views about Native American influence on ecosystems. One emphasizes the importance of Native Americans in altering their environments (Kay 1994), for example, through effects on fire regimes (Delcourt and Delcourt 1997; Denevan 1992; Mann 2005; Pyne 1982). Native American burning has been demonstrated to be at least locally important in most temperate North American regions, from the pine barrens of the Northeast (Lorimer and White 2003) to the American Southwest (Fulé and others 1997), and from the forests of Great Lakes region (Clark and Royall 1995) to the Black Hills (Brown and Sieg 1996).

A competing viewpoint argues that Native American alteration of ecosystems is overstated, and that with certain exceptions, Native Americans had minor impacts on pre-settlement landscapes. The so-called “myth of the humanized landscape” (Vale 1998) has been argued most effectively for remote western landscapes where aboriginal population densities and technologies are presumed to have been too low to have resulted in widespread or persistent ecological impacts (Baker and Ehle 2001; Vale 1998). An additional question, important to this assessment, is whether the most common forms of Native American influence, such as altered fire regimes, were important drivers of wetland and riparian area structure and function.

There is little evidence of direct aboriginal impacts on wetland and riparian ecosystems in the present Region 2 area. Unlike Native cultures in Central America, Mexico or the Eastern United States, Native Americans on the Great Plains and Rocky Mountains were largely nomadic, with cultures based largely on big game hunting. Unlike woodland cultures or the ancestral Puebloan people in the Southwest, Native Americans in the western Great Plains and Rocky Mountains practiced no significant agriculture. Instead, they tracked large animals and moved from favorable over-wintering locations from the base of the Rockies to the high country and back again seasonally (West 1998). This migration pattern was practiced for thousands of years, as supported by archeological evidence of large game drives throughout the region (Benedict and Olsen 1978). Though these original inhabitants would undoubtedly have utilized streams as water sources and travel ways, the difficulties of a hunting and gathering lifestyle probably demanded that groups remain relatively small, thereby minimizing the overall impacts to wetlands and riparian systems.

The arrival of Europeans on the continent had immediate impacts on Native peoples, even those located far from newly established colonies (Mann 2011). Cholera, small pox, measles, and venereal diseases decimated native populations. Denevan (1992) estimated that from 1492 to 1800, the North American native population dropped from 3.8 million to approximately 1 million—a decline of nearly 75%. A second destabilizing factor that influenced Native societies was the introduction of new technologies, most notably guns, iron-works, and horses (West 1998). These greatly altered traditional ways of life and catalyzed significant changes in the ways Native tribes interacted among themselves, with Euro-Americans, and with their environment (Carlson 1998; Flores 2001).

Though accompanying the earliest Spanish expeditions during the Sixteenth Century, it wasn't until after the Pueblo revolt of 1680 that large numbers of horses began to appear among Native Americans (Beck and Haas 1989). It is difficult to overstate the effect of horses on Native American economic and social systems. As the number of horses available through trade or raiding increased during the Eighteenth Century, several Indian tribes embraced the new technology. An example is the western or plains Sioux, comprising two broad divisions, the Nakota and Lakota. From their original territory in the Great Lakes region, they emigrated to the Minnesota prairies, then on to the Missouri River Valley. By the late Eighteenth Century, they had expanded west and south into the major bison ranges, and by 1830, they had become the preeminent power in the northern plains (West 1998).

In 1680, the Cheyenne abandoned their homes on the upper Mississippi and began a long westward migration toward the Minnesota River, then to the James River in present day North Dakota. Nearly a century later, in response to attacks from other Native American groups and the ravages of old world diseases, they began moving westward again, drawn toward the plains by horses and bison. They moved quickly through the Dakotas, rapidly acquiring horses as they went, thus, completing their transformation to a nomadic culture centered on the accumulation and trade of horses and bison (West 1998).

The Ute Indians historically ranged across present day western Colorado and much of the northern Colorado Plateau. Separate bands occupied the mountains and the more arid regions to the south and west, with each group migrating seasonally to follow food resources particular to their environment. In the late Seventeenth and early Eighteenth centuries, Utes obtained horses and livestock from the Pueblo peoples of northern New Mexico (Beck and Haas 1989), initiating a significant cultural transformation. In the years and decades that followed, the Utes became increasingly involved in raiding and trading horses, becoming a critical conduit for the dispersion of the horse northward.

Though of obvious historical significance, it is unclear how the changes resulting from Native American adaptation to horses would have affected wetlands or riparian ecosystem. West (1998) estimated that six horses *per person* were minimally needed to sustain the nomadic plains tribes with nearly a dozen required for a more secure existence. It follows that even relatively small groups would have had sizable herds in need of forage, which would have been most abundant along river bottoms, in riparian zones. Large groups would have had even greater potential to degrade sites, particularly when stays were long, such as when groups over-wintered. One trader noted in his accounts a gathering of approximately 6000 Lakota and Cheyenne Indians along the Arkansas River, which could have included over 25,000 horses (West 1998). The demand for firewood and forage year after year would likely have affected the structure of cottonwood stands, inhibiting seedling establishment and recruitment.

The greater hunting efficiency allowed by the horse led to increased participation by Native Americans in the commercial trade of buffalo robes (Flores 2001). However, this period of relative abundance was short lived. Several factors led to the nearly complete depopulation of bison on the Great Plains. Although estimates of the original Great Plains bison population widely vary from approximately 30 million animals (Flores 2001) to nearly 70 million (Beck and Haas 1989), by 1890, only a few hundred remained. With the disappearance of bison, the complex social, economic, and ecological systems that had characterized the plains came to an end, with an uncertain but probably measurable impact on wetland and riparian ecosystems.

The fur trade—Until the middle part of the Nineteenth Century, when gold was discovered in California and later the Colorado Rockies, the most significant European and American presence in the Rocky Mountains and Great Plains was associated with the fur trade. Even at its peak, the number of trappers was relatively low; however, trappers were catalysts for enormous social, economic, and ecological change, with a legacy lasting to the present day (Beck and Haas 1989; Sandoz 1978).

Although hides from a variety of animals, including bison, deer, river otter, muskrat, raccoon, and fox were traded, it was the trapping and trade of beaver pelts that drove much of the early Euro-American exploration and exploitation of the region (Sandoz 1978). Demand for beaver pelts was driven primarily by the western European hat-making industry, although beaver were also valued for castoreum, an alkaloid produced by their perineal scent glands used in the manufacture of perfumes and medicines (Wishart 1992). Native Americans were a major source of beaver pelts for the Canadian and Great Lakes fur trade, which flourished beginning in the late Seventeenth Century (Sandoz 1978). However, it was not until favorable reports from Lewis and Clark's 1804 to 1806 expedition that significant numbers of trappers moved to the Rocky Mountains (Wishart 1992).

In 1807, Manuel Lisa organized the first American trading and trapping expedition to the northern Rockies, ascending the Missouri River and establishing a trading post at the junction of the Bighorn and Yellowstone Rivers (Sandoz 1978). Two years later, Lisa took on new partners, forming the St. Louis Missouri Fur Company, and later, the Missouri Fur Company. Their activities, along with those of the American Fur Company (founded in 1808 by John Jacob Astor), were generally confined to the Missouri River watershed, but likely would have affected streams on what are now the Shoshone and Bighorn National Forests.

Extensive exploration and trapping in the Central and Southern Rockies, including many future National Forests, developed later. In the 1830s, trappers such as the legendary Kit Carson worked their way up the Arkansas and Rio Grande valleys of Colorado from settlements in Taos and Santa Fe, undoubtedly reaching into several present day National Forests. By the late 1830s, two factors drastically reduced the trade in beaver pelts: (1) fashion trends in men's hats had shifted from beaver to silk, causing a plunge in the market value of beaver pelts; and (2) more importantly ecologically, the relentless competition of the late 1820s and early 1830s decimated beaver populations, first in more accessible areas of the central Rocky Mountains, then in other parts of the range (Wishart 1992).

In many portions of the West, large numbers of beaver were trapped. William Ashley wrote of Jed Smith's visit to a trading post on the upper Columbia River that, "...it appeared from the account, that they had taken in the last four years within that district eighty thousand beaver, equal to one hundred and sixty thousand pounds of furs." Later, Ashley noted, "You can form some idea of the quantity of beaver that country once possessed, when I tell you that some of our hunters had taken upwards of one hundred in the last spring hunt out of streams which had been trapped, as I am informed, every season for the last four years" (Dale 1941). Although difficult to identify precisely, the ecological impacts of such intense levels of trapping would likely have been great considering the large role beaver play in regulating the geomorphic and ecological attributes of riparian systems (Brown and others 1996; Butler and Malanson 1995; Naiman and others 1988). Beaver populations have recovered in many areas, but total population estimates across the species' range are estimated to be significantly less than prior to the arrival of Euro-Americans on the continent.

Military, scientific, and commercial surveys—The earliest formal exploration by Europeans of the region was undertaken by the Spanish. The purposes of their travels varied but included practical objectives like identifying mineral resources and finding ways to link their California and New Mexican settlements, as well as political ones, such as subjugating rebellious natives and defending their claims against the incursions of British and French interests (White 1994). Although explorers such as Vargas (1694), Ulibarri (1706), Villasur (1720), Rivera (1765), and Dominguez (1776) entered into present day Colorado (Noel and others 1994), they recorded minimal information on the natural ecosystems they passed through.

Formal American government exploration was similarly driven by a mix of political and economic interests. Both Lewis and Clark's and Zebulon Pike's expeditions were commissioned to explore and assert United States control of the new territories acquired under the Louisiana Purchase (Noel and others 1994).

In addition to increasing knowledge of the region's geography and its suitability for settlement, these expeditions and others that followed, such as Stephen Long's 1820 expedition up the Platte River drainage to the Colorado Front Range, made some of the first detailed observations and collections of natural history information (Evans 1997). The 1840s and 1850s brought a number of Government commissioned expeditions that greatly expanded American consciousness of and enthusiasm for the West (Gilbert 1966; Goetzmann 1960). Among the most famous were John C. Fremont's expeditions, the accounts of which helped spark the flow of emigrants to the west coast (Beck and Haas 1989).

Although of historical interest, the value of these explorer's narratives for our assessment is limited. The amount of territory actually traversed by these early exploring parties was small relative to the total land area of the region. Since exploring parties generally followed rivers, numerous accounts reference riparian communities. However, the language in these descriptions is frequently vague or focused on more practical issues such as the quantity and quality of forage. Perhaps the most significant limitation of these narratives is there is no means to extrapolate to wider areas. For instance, differing accounts of the amount of tree and shrub cover along plains streams can be found, making more general assessments regarding vegetation difficult.

Euro-American settlers—The timing of Euro-American settlement varied across the region, but generally was late relative to areas on the west coast. Beginning in the 1840s, the number of Euro-American emigrants moving through the Great Plains and over the Rockies increased dramatically, particularly following the discovery of gold in California. However, most only passed through the region and probably had a relatively minor impact on the area.

The first wagon train of pioneers en route to the west coast crossed the continental divide at South Pass in 1841, one year prior to the departure of John C. Fremont's expedition along the same route (Beck and Haas 1989). This route, the Oregon-California trail, became the most important passage for emigrants traveling west, and it was also utilized by Mormons making their way toward Utah (Beck and Haas 1989). During the next 18 years, over 300,000 persons traveling with at least 1.5 million oxen, cattle, sheep, and horses traveled up the Platte Valley (West 1995). Though this route had been employed by Native Americans, trappers, and traders for decades, the greatly increased number of travelers severely taxed resources along the river valleys—a problem exacerbated by the arrival of drought conditions in the late 1840s (West 1998). The cumulative impacts to riparian communities from harvesting fire wood and grazing were likely significant but fairly localized. Since most travelers did not range far from the main trail, their impacts to current Region 2 National Forests were likely negligible.

More significant changes followed the discovery of gold in the South Platte River along Colorado's Front Range in 1858. An estimated 100,000 people traveled to Colorado the following year, beginning a period of rapid transformation for the region (Noel and others 1994). Within 20 years, mining camps were common throughout the region. Reports of gold in the Black Hills of South Dakota in 1874 by General George Custer's expedition caused a similarly large influx of prospectors (Froiland 1990; Horsted and Grafe 2002), with the populations of both states dramatically increasing over the next several decades. Two types of mining operations occurred: placer mines, which recovered minerals in surface deposits such as stream alluvium, and lode or hard rock mines (Wohl 2001). Both kinds of operations evolved over time and resulted in different kinds of impacts to wetlands and riparian ecosystems.

To supply the burgeoning population of miners, numerous towns and cities developed on the plains. Boulder and Denver prospered as agricultural and trade centers and rapidly expanded as the number of miners entering the region increased (Noel and others 1994). To meet the new demand for water by cities and agriculture, the first of many irrigation and water control projects in the region was developed. The appropriation of water for municipal and agricultural uses proceeded rapidly, with ditches established as early as 1859 in several Front Range locations (Jones and Cech 2009; Wohl 2001). The first significant reservoir was completed in 1869 to supply water to the expanding network of ditches in the region, and by 1882, irrigators had established the first major diversion over the continental divide (Wohl 2001). These trends would continue throughout the Nineteenth and early Twentieth Centuries, as demand for water and storage increased. Collectively, these developments would become a major factor influencing wetland and riparian ecosystems.

Ranching also developed rapidly during the Nineteenth Century. Driven by local demand for meat from local populations as well as the possibility of high profits in the eastern markets, ranchers introduced thousands of head of cattle to present day National Forests (White 1994). Large herds of longhorn cattle were brought from Texas and released to graze in meadows and, each fall, were rounded up and driven to more favorable winter range in the lower valleys. Large herds of sheep were common in the Forests bordering New Mexico, and were introduced more widely through the region in the 1890s leading to significant conflict with cattle ranchers (Sypolt 1974).

The development of the railroads in the western United States precipitated additional changes to the region. Between 1855 and 1900, over 26,000 miles of track were constructed—nearly a 3,000 percent increase in total rail length from 1855 (Robertson 1991). This expansion mirrored the rapid population growth occurring in the region and hastened the end of Native American presence outside of reservations. In addition to the social and economic impacts, railroad construction also impacted riparian areas. Rail lines were frequently built parallel to the major rivers, requiring that armoring such as rip-rap be applied to protect the new lines, thereby altering the natural channel dimensions (Wohl 2001).

Early concerns about the sustainability of resource use in the West led Congress to pass the General Revision Act in 1891, which allowed the President to proclaim forest reserves (Bradford 1998). Several forest reserves were subsequently created making them precursors to modern National Forests. It wasn't until 1905 that Congress officially established the United States Forest Service (USFS), transferring the forest reserves from the General Land Office to the Department of Agriculture. During the dustbowl drought of the 1930s, Congress passed the Bankhead-Jones Farm Tenant Act, authorizing the Soil Conservation Service to purchase sub-marginal farm land. Responsibility for these lands shifted among several different Federal agencies until 1954, when it was transferred to the USFS, resulting in the formation of the new National Grasslands.

Overview of Anthropogenic Impacts to Wetlands and Riparian Ecosystems

Wetlands and riparian areas are among the most heavily disturbed ecosystems in North America. It has been estimated that since the Late Eighteenth Century, 35 to 40 percent of the wetlands have been lost in South Dakota, Nebraska, and Wyoming, with wetland losses in Colorado and Kansas approaching 50 percent (Dahl 1990). Since much of the wetland losses have resulted from agricultural activities such as draining and tilling, a minor historical land use for most Forest Service units, it is likely that these estimated rates of wetland loss are higher than has occurred on USFS managed lands.

A variety of anthropogenic factors have altered the structure and function of wetlands and riparian ecosystems, including many found in Region 2. Several general concepts that have been developed are useful for describing how anthropogenic changes may have impacted ecological systems. Ecological integrity has been defined as the ability of a system to support and maintain a "...balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to the natural habitat of the region" (Karr and Dudley 1981). Alternatively, ecological condition has been used to describe the extent to which a given site departs from full ecological integrity and can be defined as the relative ability of a wetland to support and maintain its complexity and capacity for self-organization with respect to species composition, physio-chemical characteristics, and functional processes (Fennessy and others 2004). These concepts provide a means of assessing differences between wetlands of a similar class with and without the effects of human alterations—a key objective in this HRV assessment.

The value attributed to wetland and riparian ecosystems is largely based on the various ecological, biogeochemical, and hydrologic functions they provide. These functions are numerous and varied, ranging from maintenance of species

diversity to biogeochemical cycling, and differ depending on the type of wetland and its landscape context. Although management and regulation generally strive, implicitly or explicitly, to preserve or restore ecological function, there is still considerable uncertainty on how to best identify and measure function. Numerous systems have been developed, such as the Hydrogeomorphic Method (HGM) (Brinson 1993a; Hauer and Smith 1998), that are applied by wetland managers.

Central to the idea of managing ecosystems within their historical range of variation is that, by maintaining or restoring the ecological integrity of ecosystems, managers are most likely to preserve or enhance important functions. Also, most stressors affecting ecosystems do not occur in isolation. Departures from the historical range of variation for many systems may be caused by the cumulative effects of several different factors, such as overgrazing, roads, and invasive species, and may occur abruptly at some threshold rather than gradually.

Some of the most significant anthropogenic changes to wetland and riparian ecosystems include hydrologic changes associated with flow regulation and the removal of beaver (Graf 1999; Nilsson and Berggren 2000; Wohl 2001), the introduction and spread of non-native species (Stein and Flack 1996; Stohlgren and others 1999), livestock grazing (Belsky and others 1999; Fleischner 1994), and cumulative effects on water and sediment dynamics associated with broad-scale changes to watersheds, such as altered fire regimes resulting from land use change and fire suppression (Dwire and Kauffman 2003). Winters and others (2004) identified a total of 24 anthropogenic activities affecting aquatic, riparian, and wetland resources, organized into seven basic groups (Table 8).

Table 8—Anthropogenic activities arranged by primary use categories identified by Winters et al. (2004).

Water use	Transportation	Recreation	Biological	Mineral extraction	Vegetation management	Urbanization
Stream Diversions	Roads	Developed Recreation	Invasive Species	Hardrock Mining	Domestic Grazing	Transmission Corridors
Reservoirs	Trails	Dispersed Recreation	Beaver Removal	Placer Mining	Large Wild Ungulates	Urbanization
Ditches	Railroads	Ski Area Development	Pesticide	Energy Development	Commercial	
Transbasin Diversions	Off Road Vehicle Use				Timber Harvest	
Spring Development					Natural Fire	
					Prescribed Fire	
					Tie Drives	

The relative importance of these activities varies by wetland type and by National Forest or Grassland. For instance, placer and hard rock mining activities are relevant only in USFS units containing highly mineralized bedrock outcrops and are more likely to impact riparian systems than fens. A discussion of anthropogenic impacts to wetland and riparian areas is central to our HRV assessment and will, therefore, be presented in greater detail in subsequent chapters. The following is a broad overview of the major anthropogenic activities, following the structure laid out by Winters and others (2004).

Water developments

The development of water storage and diversion structures closely followed Euro-American settlement of the region. Although most initial developments were for agriculture and mining activities (Wohl 2001), there has been in recent years a trend toward increased municipal use (Wilkinson 1992). Most of the major rivers flowing through Region 2 are dammed, and numerous transbasin diversions have been constructed to augment natural stream flows to areas with large agricultural or municipal demand such as the South Platte basin. In addition to developments affecting large perennial rivers, many intermittent and ephemeral wetlands on the plains were altered by the construction of livestock watering impoundments (Smith and others 2002).

Groundwater extraction for irrigation purposes affects some wetland and riparian ecosystems (Cooper and others 2003c; Elmore and others 2003; Stromberg and others 1996). For example, there has been increasing concern about the effect of center-pivot irrigation in the Nebraska Sandhills, which uses groundwater extracted from the regional groundwater system (Bio/West 1986; Novacek 1989). However, since irrigated agriculture is an uncommon land use in most Region 2 National Forests and Grasslands, the impacts of groundwater extraction on USFS lands is likely small and limited to localized areas in the immediate vicinity of pumping wells.

Water developments can have a wide variety of geomorphic, hydrologic, and ecological effects on wetland and riparian ecosystems. Physical changes include alteration of stream channel morphology (e.g., width/depth ratio and sinuosity), rates of sediment production or mobilization, and changes in the timing and magnitude of floods (Brandt 2000; Hirsch and others 1990; Kondolf 1997). Since flooding is one of the principal disturbances affecting vegetation in riparian areas and a primary control on the water table dynamics controlling vegetation in some other wetland types, such as marshes found in oxbows along river floodplains, these hydrologic changes can have profound effects on the patterns of plant establishment and mortality (Nilsson and Berggren 2000; Patten 1998). A variety of studies have demonstrated that altered flood regimes can reduce opportunities for the establishment of native species in the Genera *Populus* and *Salix*, and favor the spread of non-native species such as *Tamarix* spp. (Cooper and others 1999; Shafroth and others 1998) and *Elaeagnus angustifolia* (Russian-olive) (Katz 2001; Lesica and Miles 1999).

Water developments can alter the amount and distribution of wetland and riparian ecosystems. For example, reservoirs formed behind large dams may destroy riparian communities, resulting in an overall decrease in riparian area. However, marsh communities may form along reservoir margins, resulting in a net increase in the areas occupied by marsh vegetation. Another example is the large number of livestock water impoundments constructed along intermittent streams in many National Grasslands. These can create marsh type habitats that would otherwise be rare or absent.

Herbivory

Wild ungulates—Prior to the arrival of Euro-Americans, most areas of Region 2 supported native ungulate species including elk, deer, moose, bison, bighorn sheep, and pronghorn antelope. However, the importance of native grazers to the region's ecology, particularly wetland and riparian areas, is unclear. Because of their great abundance, pre-Euro-American bison populations (Flores 1991) almost certainly had significant impacts on wetlands. For instance, bison were observed to use playas as wallows (Smith 2003) and, like domestic livestock, seasonally utilized river bottoms for forage and shelter during inclement weather. Though impossible to quantify the relative effects, these activities would likely have affected both the composition and structure of wetland and riparian communities.

Although there are no reliable estimates of pre-Euro-American period elk and deer populations, these species would have been expected to utilize, at least seasonally, riparian and wetland areas. Behavioral and dietary studies of contemporary elk herds, for example, have demonstrated that wetland and riparian species such as willows (*Salix* spp.) and sedges (*Carex* spp.) are important components of native ungulate diets (Hobbs and others 1981; Hunt 1979). Several studies have shown that elk herds are capable of significantly altering riparian communities, affecting the structure and regeneration of willows and cottonwood (*Populus* spp.) (Beschta 2003; Brookshire and others 2002; Peinetti and others 2002b; Zeigenfuss and others 2002). However, these examples are not likely representative of pre-Euro-American settlement conditions, as contemporary elk population densities and foraging behaviors developed in the absence of significant predators. Other ungulates, notably moose, heavily utilize riparian areas (Oedekoven and Lindzey 1987) and can have large impacts on vegetation, at least locally.

Though large wild ungulates can impact resources in similar ways as domestic livestock, wild ungulates tend to be more dispersed across the landscape, and therefore less likely to drive vegetation dynamics in wetland and riparian ecosystems. However, since populations of native ungulates are often intensely managed and most systems lack significant predator densities (excluding humans), the effects of contemporary native ungulate populations may not be representative of pre Euro-American settlement impacts, and their impacts on wetland and riparian systems outside the HRV.

Livestock—Livestock grazing represents one of the most widespread historical and current land uses in Region 2. Domestic animals, including horses, sheep, and cattle, accompanied early European explorers and settlers. The horse, in particular, was rapidly and widely adopted by Native Americans, greatly altering their social systems and relationship with their environment (Flores 2001; West 1998). With the exception of horses and the raising of sheep by the Navajo in the Southwest, Native Americans did not widely adopt domestic livestock. However, with increased Euro-American settlement during the Nineteenth Century, there was a large increase in the number of livestock moving through the region (White 1994). The increased demand for commodities in the east and the expanding settlements in the west, coupled with increased efficiencies in transporting and marketing those commodities that was achieved with the spread of railroads, led to an explosion in livestock numbers, and within only a few years, many rangelands were seriously overstocked (Pieper 1994). The creation of public land management agencies like the USFS, increasingly led to greater management livestock populations, and for most USFS units, current livestock numbers are significantly lower than historical levels (Elmore and Kauffman 1994).

Livestock can impact wetlands and riparian areas in a variety of ways. Overgrazing can lead to significant changes in vegetation structure, negatively impacting wildlife and fish habitat (Fleischner 1994; Knapp and Mathews 1996; Schulz and Leininger 1991). Livestock grazing can reduce seed production and establishment by native vegetation (Brookshire and others 2002), affecting the successional dynamics of riparian ecosystems. Changes in species composition, increases in the incidence of exotic species, and changes in channel morphology have also been documented (Belsky and others 1999; Chaney and others 1990; Fleischner 1994). Moderate grazing can also have positive effects, particularly in ecosystems that have an evolutionary history of grazing. Grazing effects and potential departures from the HRV of wetlands and riparian areas are discussed in greater detail in subsequent chapters.

Invasive species

The introduction and spread of invasive and non-native species is one of the most significant changes to ecosystems across North America. Several different terms have been developed to describe non-native species. Weeds are defined as any plant that poses a major threat to agriculture and/or natural ecosystems; alien species are species introduced and occurring in locations beyond their known historical range; and invasive species are species that demonstrate rapid growth and spread and are capable of invading habitats and displacing native species. It is important to note that some species such as cattails (*Typha* spp.), though native to a particular area, may become invasive if environmental conditions change, for example, following disturbance. Likewise, some alien species, though well established in an area, may have few deleterious effects on native ecosystems.

Alien and invasive species can have a variety of effects on native ecosystems. These include hydrologic and geomorphic changes, as has been documented with salt cedar (*Tamarix ramosissima*) (Busch and Smith 1995; Tickner and others 2001), reductions in native species cover and diversity due to competitive exclusion (Hager 2004), and reduced forage for wildlife and livestock. Invasion by exotic shrubs can alter vegetation structure, by decreasing, or, in the case of *Tamarix* spp. and willow flycatchers in the Southwest, increasing the suitability of habitat for birds (Graf and others 2002; Stevens and others 2001; Stoleson and Finch 2001). The introduction of non-native species can significantly alter natural disturbance regimes, with large implications not only for biodiversity but for a range of additional ecological characteristics like biogeochemical cycling rates (Mack and D'Antonio 1998; Mack and others 2001). Changes in nutrient availability associated with invasions of nitrogen-fixing plants like *Elaeagnus angustifolia* can promote the spread of additional exotics (Simons and Seastedt 1999), causing positive feedback that leads to increased degradation of ecosystem integrity.

The distribution and abundance of exotic species varies considerably based on the life history and physiological tolerance of specific invasive species as well as on a variety of ecological characteristics that influence ecosystem vulnerability to invasion such as fertility and disturbance frequency. In general, many non-native species respond positively to disturbance, which is one of several reasons for the higher incidence of exotics associated with roads and other disturbed environments (Gelbard and Belnap 2003; Parendes and Jones 2000). Exotic species are often more common in areas with high diversity. For example, Stohlgren and others (1999) found higher numbers of exotic species in communities with higher numbers of native species such as wet meadows. Similar patterns of exotic species cover have been observed in riparian areas as well (Stohlgren and others 1997; Stohlgren and others 1998).

Mineral extraction

Mineral extraction activities have been an important factor in the human and ecological history of Region 2. Initial Euro-American settlement patterns in the region were driven by the discovery of gold, which determined where many contemporary cities and towns were initiated and the patterns of public land ownership on many National Forests. Mining activities have had a variety of impacts on wetland and riparian ecosystems, and though the extent of mining activities has generally decreased relative to historical levels, mining is still relatively common in the region.

Placer and hard rock mining have occurred in the region. The mining of placer deposits, which can be conducted via several techniques, including hydraulic mining and dredging, represents a direct disturbance to riparian areas and adjacent wetlands. Impacts included direct removal of vegetation and the alteration of the stream channel shape and hydraulics through placement of tailings deposits. When evaluating the effects of past placer mining, it is important to know the amount and distribution of mined areas and the specific methods used to recover mineral deposits (Winters and others 2004). An additional form of surface mining of importance to wetlands and riparian areas is aggregate mining for construction use. Alluvial gravel and sand deposits are mined directly and can cause a variety of hydrologic, geomorphic, and ecological effects. For instance, the mining of alluvium within active stream channels can cause channel incision, which may then propagate up- and downstream of the mine, reducing overall channel instability and lowering alluvial water tables (Kondolf 1997; Scott and others 1999). Gravel mining can result in either an increase or decrease in total wetland area resulting from the conversion of riparian forests to large open water gravel pits, which can support a narrow fringe of marsh communities along their boundaries.

Hard rock mining can occur in both subterranean and in open pits and was widespread in mineralized areas of Region 2. Though a celebrated part of the region's history, in many instances, mining has left a toxic environmental legacy, and abandoned mines represent one of the greatest environmental problems plaguing the region. One of the most common problems is the degradation of water quality due to heavy metal contamination. The magnitude and nature of the problems and their effect on wetland and riparian resources can vary depending on the specific ores mined and the processing methods used. Additional mining impacts can include transport and deposition of tailings downstream of mine sites and the release of acidic and metal-laden runoff from tailing piles, shafts, and adits (Clements and Kiffney 1994; Howe and Noble 1985).

Development of energy resources, specifically oil, natural gas, coal, and, most recently, coal-bed methane, can also alter wetlands and riparian ecosystems. Although direct impacts can occur, most impacts are indirectly caused by the construction and maintenance of the extensive infrastructure required to access, store, and distribute the commodity. Impacts include chemical contamination, increased erosion and sedimentation, and hydrologic modification. The relative importance of each of these impacts likely varies depending on the specific commodity being extracted; the density of wells, pipelines, and access roads; and the specific climatic, physiographic, and geological setting.

Although the technology driving it is of recent origin, coal-bed methane development may have a greater effect on wetlands and riparian systems than traditional oil and gas extraction methods. A large amount of water is produced during coal-bed methane production, potentially altering the hydrologic regime of associated wetlands and streams. Changes in the magnitude and timing of streamflow can alter vegetation patterns by decreasing opportunities for native plant establishment or by facilitating the spread of exotic species and can result

in greater channel instability. Additionally, groundwater pumping may lower local water tables, negatively affecting dependent wetlands. Also, high levels of salts in pumped groundwater have the potential to alter the productivity of soils in affected areas.

Transportation

Roads influence many ecosystems in Region 2, including wetlands and riparian areas. Historically, roads and other linear transportation features, such as trails were constructed along valley bottoms, directly impacting riparian systems and associated wetlands. Streams were often channelized and wetlands were filled to remove obstacles that blocked road construction. The relatively high road densities found on many National Forests and Grasslands can have a variety of direct and indirect impacts on native vegetation. These can work independent of or synergistically with other agents of change, such as exotic species in affecting riparian and wetland ecosystems.

Transportation networks can have significant effects on local and watershed-scale hydrologic processes. Roads and trails and their associated engineering structures such as culverts, dips, and ditches, can significantly alter natural drainage patterns (Forman and Sperling 2002). Interception and infiltration rates generally decrease due to the removal of vegetation and soil compaction or paving, altering the hydrologic response of basins to both annual snowmelt runoff episodes and isolated convective storm events (Jones 2000; Jones and others 2000). The increased prominence of overland flow processes can cause more rapid and intense hydrograph response to precipitation events, resulting in greater stream energy and erosion potential.

Transportation networks can have a variety of additional effects on wetlands, including the introduction of pollutants from vehicle exhaust or fluid leaks (Havlick 2002) and the alteration of water chemistry (e.g., conductivity, cation concentrations, and pH) due to road dust, increased sediment deposition, and chemicals used in road maintenance, such as de-icing agents (Trombulak and Frissell 2000; Wilcox 1986a; Wilcox 1986b). A number of variables that can influence the effects of roads, including road density, road slope, and surface type and the number, size, and design of engineering structures. Since these can vary so greatly within and among National Forests, formulating general statements regarding their effect on wetlands and riparian systems is difficult.

Railroads are an additional component of the transportation infrastructure with the potential to affect wetlands or riparian areas (Winters and others 2004). Effects can include some of the same kinds previously described for roads, such as alteration of surface and subsurface water flow. In addition, water contamination can occur from leaking train cars, maintenance equipment, or creosote-impregnated railroad ties (Winters and others 2004). However, railroad densities are generally much lower than those of roads, so their direct effect on the HRV of wetlands and riparian areas at landscape and regional scales is likely small.

Recreation

A variety of recreation activities impact riparian areas and wetlands. The magnitude and nature of impacts differ as a function of the kind of activity and the particular system in question. Although non-motorized, dispersed recreational activities such as fishing can have direct effects on vegetation through trampling, these effects tend to be localized in nature. In general, developed recreation has a greater potential for impacts. For example, the cutting of trees as part of ski area development can alter the amount and quality of surface and subsurface runoff, indirectly affecting dependent wetlands and riparian areas. In addition, surface water diversions for snowmaking at ski areas can reduce available water for riparian areas. The relative importance of such activities varies among USFS units, being of greatest importance in areas with large concentrations of developed ski areas (e.g., the White River National Forest) and of no consequence in others.

Additional impacts to wetlands from winter recreation can occur from activities such as cross-county skiing, snowshoeing, or snowmobiling. Compaction of accumulated snow alters the thermal properties of snow, potentially delaying spring melt and altering soil temperature profiles. These effects are again going to be localized in nature and of greatest importance to specific wetland types such as fens.

Fire

Fire is a natural component of nearly all Region 2 ecosystems, including wetlands and riparian areas. However, the specific effects of fire, both natural and anthropogenic in origin, differ greatly depending on a wide range of factors. These include variables related to the fire, such as fire intensity and duration, which directly impact vegetation through plant mortality (DeBano and others 1998). At landscape scales, the relationship of wetland and riparian communities to fire is driven largely by the disturbance regimes of surrounding cover types. However, the significant differences in vegetation composition, hydrogeomorphology, microclimate, and fuels characteristics between wetlands and riparian areas and surrounding uplands may contribute to different fire regimes and behavior. The frequency of fire may be lower and fire severity may be more moderate than in adjacent uplands, but there are documented instances where fires appear to burn wetland and riparian areas with comparable frequency (Dwire and Kauffman 2003).

Because of their small area and the presence, at least seasonally, of saturated or inundated soils, fires rarely start in wetlands. Consequently, the fire regimes characterizing the surrounding landscape, including those that deviate from their HRV due to anthropogenic influences such as fire suppression, strongly influence fire regimes in wetlands. Land use and management may affect fire regimes and

properties through additional mechanisms such as livestock grazing, logging, hydrologic alterations such as damming or flow regulation, or the introduction of invasive species that change the composition, structure, and distribution of fuel loads (Dwire and Kauffman 2003). An example of the latter is the introduction and spread of Tamarisk along many riparian areas in the region, which has resulted in significant shifts in fire behavior and fire regimes (Busch 1995; Busch and Smith 1995). The cumulative impacts from anthropogenic alterations are most likely to influence fire attributes during periods of drought or extreme fire weather (Dwire and Kauffman 2003).

Functional differences in attributes such as mean water table depth among wetland types also influences the response of wetlands to fire. For instance, direct fire effects are relatively minor in subalpine fens, due in part to their high, stable water tables. In contrast, marshes on the Great Plains, which in some years may become completely dry, may experience more frequent and severe fires. Many wetland and riparian species, including members of the Salicaceae family such as *Salix* spp. *Populus* spp., are capable of re-sprouting or vegetatively spreading, allowing recovery following both flood and fire disturbances (Mitsch and Gosselink 2007). The adaptations to fluvial disturbances may facilitate survival and reestablishment following fires, contributing to the rapid recovery of many wetland or riparian ecosystems (Dwire and Kauffman 2003).

Vegetation management

Direct vegetation management such as timber harvest occurring in landscapes surrounding wetlands and riparian areas may influence their structure and function. For example, timber harvest may alter the quantity and quality of surface and subsurface water reaching riparian areas (Stottlemyer and Troendle 1999; Stottlemyer and Troendle 2001; Troendle and King 1985). Tree harvest may reduce the amount of rain or snow intercepted and subsequently lost by evaporation or sublimation and may affect runoff by influencing evapotranspiration (ET) rates and promoting increased snowpack accumulation in openings, with affects on water yields lasting, at declining levels, for up to 80 years (Troendle and King 1985). In addition to the effects of commercial logging, many ecosystems have been affected by historical utilization of forests associated with Euro-American settlement and development. For example, large volumes of timber were harvested for use as railroad ties, charcoal, and mining supports in many parts of the Rocky Mountains (Wohl 2001). In some areas, severe impacts to riparian areas resulted from the use of tie drives to transport lumber (Wohl 2001; Young and others 1994).

Beaver

Few mammals, with the obvious exception of humans, have as large of an ecological impact as the beaver (*Castor canadensis*). Through their feeding and dam building activities, beaver strongly modify local hydrologic regimes and influence a wide range of biotic and biogeochemical processes (Burns and McDonnell 1998; Johnston and Naiman 1990a,b; Naiman and others 1994). In many areas of Region 2, the arrival of beaver trappers marked the first significant interaction of native peoples and landscapes with Europeans (Sandoz 1978). However, because they primarily affect riparian ecosystems, a more detailed discussion of their influence is presented in a subsequent chapter.

Cumulative watershed impacts

Individual anthropogenic impacts may act synergistically on watershed processes (Reid 1993; Winter 1988). For instance, the cumulative effects of tree harvest, road construction, and fire in a given watershed may result in greater changes to water and sediment yields than expected by simply summing the contributions of each individual stressor. Consequently, discussion of cumulative effects, presented in subsequent chapters, is warranted for this assessment

4. Historical Range of Variation for Region 2 Riparian Ecosystems

Definitions and Concepts of Riparian ---

The term riparian has been variously defined and applied. The term originates from the Latin word *riparius*, which means “belonging to a bank or shore” and indicates a place on the landscape adjacent to a stream, but is also used to refer to areas that are periodically flooded. Some definitions of riparian, such as the one used by the U.S. Fish and Wildlife Service, emphasize geographic proximity to water bodies, while others are based on either biological or hydrologic criteria. An overview of riparian definitions is presented in Chapter 1. The definition we apply in this assessment closely follows that used by Naiman and Decamps (1997): the portion of the stream channel occurring between the low and high water marks and adjacent terrestrial areas extending from the high water mark toward the uplands where vegetation may be influenced by elevated water tables or flooding. A key element of this definition is the existence of a physical connection, at least intermittently, between the stream and riparian area. In the case of ephemeral streams, this connection may be limited to the physical effects of infrequent flood events. In contrast, along perennial systems, streams may exert a more constant and dominant control on ecological function through flooding as well as by influencing water table dynamics.

Structural and functional characteristics vary widely among different riparian ecosystem types, making generalizations difficult, but there are several characteristics common to all ecosystems. Most important is the presence, at least periodically, of flowing water. Flood events are key drivers of geomorphic, biogeochemical, and biological characteristics of riparian areas (Bowden 1987; Knighton 1998; Pinay and others 2002; Wohl 2000), and they act to differentiate riparian from other ecosystem types supporting mesic or hydric plant species. Riparian areas also commonly have elevated water tables relative to adjacent uplands and support distinct vegetation associations (Carsey and others 2003), although this is not always true in ephemeral or intermittent systems (Shaw 2006). In many arid and semi-arid areas, riparian areas provide the only arboreal habitats in the landscape, thus providing essential habitat for birds and other dependent wildlife species (Finch and Ruggiero 1993).

Geomorphic Setting and Principal Ecological Drivers ---

In contrast to fens, where geomorphic changes are extremely slow, streams and their associated riparian zones are highly dynamic. Region 2 riparian areas occur in a variety of geomorphic settings, along high-gradient, bedrock-dominated

streams to low-gradient, alluvial rivers on the plains. Principal drivers of geomorphic processes at broad temporal and spatial scales include geology, climate, and tectonics. At the time scales most relevant to this assessment, these variables are effectively independent, driving such dependent processes like vegetation composition and structure, channel, morphology, and hydrologic regime (Figure 9, Table 9). While at local or reach scales, riparian vegetation is often determined by factors such as cross-sectional morphology, flood frequency, moisture gradients, and biotic factors such as beaver, these processes reflect the influence of macro-scale processes (Baker 1989).

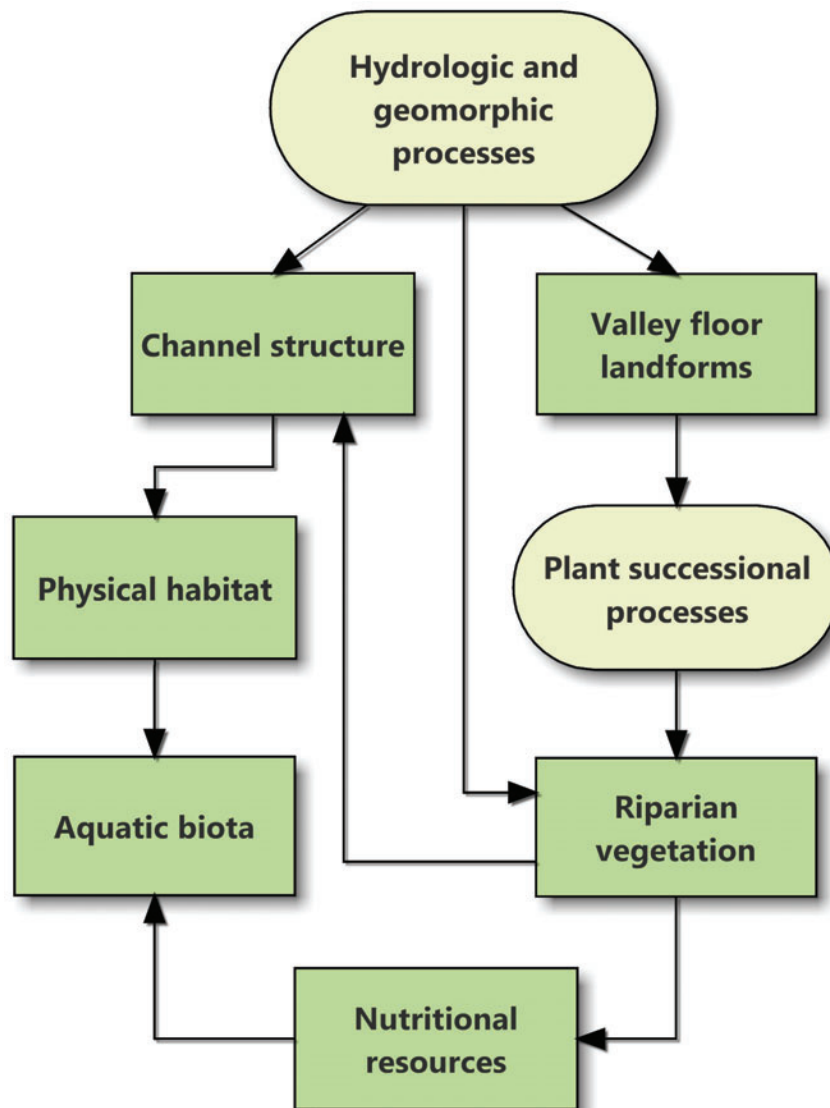


Figure 9—Schematic model illustrating the relationships among geomorphic processes, terrestrial plant succession, and aquatic ecosystems in riparian zones. Directions of arrows indicate predominant influences of geomorphic and biological components (rectangles) (Modified from Gregory and others 1991).

Table 9—Scale dependency of variables affecting geomorphic and hydrologic characteristics of riverine systems (Knighton 1998).

Variable	Medium time scale 10³-10⁴ years	Short time scale 10¹-10² years	Instantaneous time scale <10⁻¹ years
Geology	Independent	Independent	Independent
Climate	Independent	Independent	Independent
Regional relief	Independent	Independent	Independent
Vegetation properties	Dependent	Dependent	Independent
Mean water and sediment discharge	Dependent	Dependent	Independent
Channel morphology	Dependent	Dependent	Independent
Instantaneous flow characteristics	Indeterminate/ Irrelevant	Indeterminate/ Irrelevant	Dependent

Regional climate characteristics of particular importance for riparian ecosystems include the amount, form, and seasonality of precipitation, temperature and wind, as well as the timing of snowmelt. These factors influence stream flow regimes, including flow variability, base, mean, and peak flow volumes, and fluvial geomorphic processes such as sediment erosion and deposition (Wohl 2000). Climate also directly affects ecosystems through its influence on energy and water exchanges between riparian areas and adjacent aquatic and upland areas (Naiman and Decamps 1997), influencing basic ecological attributes such as primary productivity, plant establishment and mortality, and competition (Mitsch and Gosselink 2007).

Basin physiography, including watershed size, relief, and elevation, are also of broad importance to riparian areas. For example, orographic effects in mountainous terrain strongly influence precipitation patterns (Kittel and others 2002), directly affecting stream flow regimes. Watershed size influences a variety of processes that are important to riparian areas such as flow volume, flood frequency and magnitude, and measures of flood variability. Stream gradient influences the relationship between mean and peak flood levels and stream energy, variables of particular importance to reach-scale fluvial geomorphic processes and riparian vegetation dynamics (Knighton 1998; Wohl 2000).

Other broad-scale factors influencing riparian ecosystems include lithology and glacial history (Wohl 2000). Erosion and sediment transport characteristics for rivers in the same climate regime may differ depending on whether the dominant rock types are igneous or sedimentary. The spatial patterns of flow volume along rivers flowing through limestone, for example, can be highly variable due to the effect of dissolution features on surface and groundwater flow (Driscoll and others 2000). While no USFS unit in Region 2 was directly affected by continental glaciation, periodic expansion of glaciers originating in high mountain cirques have shaped many alpine and subalpine landscapes in Colorado and Wyoming, creating broad, U-shaped valleys instead of the V-shaped valleys characteristic of unglaciated areas (Windell and others 1986).

Complex interactions over a range of spatial and temporal scales occur among hydrologic and geomorphic processes, terrestrial plant succession, and aquatic ecosystems (Gregory and others 1991), making the task of isolating the influence of individual processes difficult. Many studies of riparian ecology emphasize geomorphic processes as key drivers of ecological processes. These create a mosaic of landforms such as channels, floodplains, point bars, and in-channel islands, which function differently regarding hydrologic regime and disturbance, such as flooding (Gregory and others 1991). These functional processes in turn drive the spatial pattern and successional development of riparian vegetation (Hughes 1997).

Hydrologic, ecological, and disturbance processes

The relative importance of different water sources varies for riparian areas. Surface water can originate as overland flow, shallow subsurface storm flow, direct precipitation, and recharge from local alluvial aquifers. Water can leave riparian systems through direct evaporation, transpiration, overbank flooding, and percolation into alluvial or bedrock aquifers (Dunne and Leopold 1978; USDA NRCS 1998) (Figure 10). The importance of each water budget component varies among riparian areas. Whether precipitation falls mainly as rain or snow influences stream flow regimes and dependent biota. High flows following rainstorms may occur hours or even minutes after precipitation events, depending on soil permeability and other watershed characteristics. In contrast, where snow is the dominant form of precipitation, melting may occur over a period of days or weeks and slowly build the peak flood discharge (Poff and others 1997).

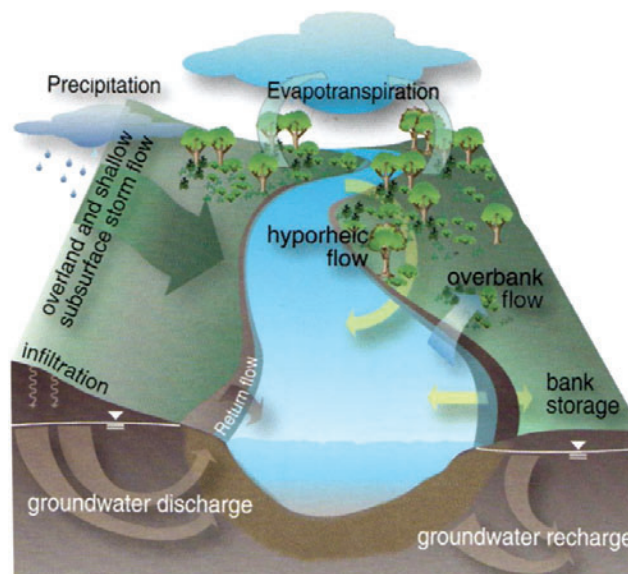


Figure 10—Principal hydrologic pathways in riparian areas (FISRWG 1998).

Vegetation in Region 2 riparian ecosystems is distinct from uplands because of the greater availability of water in an otherwise water-limited landscape (Goodwin and others 1997). Typically, species composition changes with increasing distance from and elevation above the stream channel due to differences in water table depth and flood frequency, although the specific pattern varies widely among rivers and between individual stream reaches. Key variables driving vegetation dynamics in riparian sites are base and mean flow levels; the magnitude, seasonality, and frequency of peak flows; and the relative influence of groundwater on water tables.

Hydrologic attributes vary widely among rivers in Region 2 (Figure 11). The flow regime of rivers can be examined in terms of magnitude, frequency, duration, timing, and rate of change (Poff and others 1997) (Table 10). Streams in mountainous areas with snowmelt-dominated precipitation regimes typically have pronounced peak flows during the spring and early summer, corresponding with the melt-off of snow from higher basins (for an example, see the hydrograph of the Big Thompson River in Figure 11). Although these peak flows can vary widely in magnitude depending on factors such as snow-pack depth, temperature, and precipitation (e.g., rain on snow) events, they are relatively predictable as far as timing is concerned. In contrast, intermittent and ephemeral streams with small basins and precipitation regimes dominated by convective rain fall events can be highly variable in magnitude, timing, rate of change, duration, and frequency (Friedman and Lee 2002; Shaw 2006).

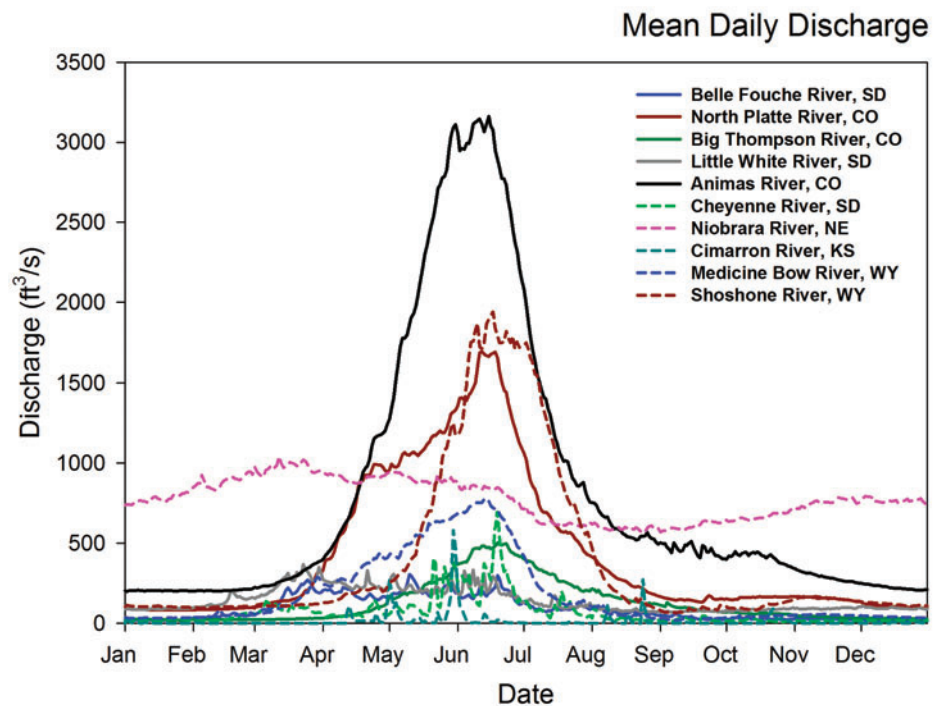


Figure 11—Typical discharge hydrographs for a range of Region 2 rivers. Rivers originating in the high mountains such as the Animas and Shoshone have large, snowmelt-dominated peak discharges. In contrast, flood flows along Great Plains rivers such as the Cimarron and Cheyenne are driven principally by rain events and are frequently less predictable and more flashy in nature. The Niobrara River and other rivers in the Sandhills region of Nebraska have continuous groundwater inputs and relatively steady stream discharge year round.

Table 10—General characteristics of flow regimes in rivers (Poff et al. 1997).

Flow characteristic	Description
<i>Magnitude</i>	The amount of water moving past a fixed location per unit time; can refer either to absolute or to relative discharge (e.g., the amount of water that inundates a floodplain).
<i>Frequency</i>	How often a flow above a given magnitude recurs over some specified time interval. Frequency of occurrence is inversely related to flow magnitude.
<i>Duration</i>	The period of time associated with a specific flow condition; can be defined relative to a particular flow event (e.g., a floodplain may be inundated for a specific number of days by a ten-year flood), or it can be defined as a composite expressed over a specified time period (e.g., the number of days in a year when flow exceeds some value).
<i>Timing</i>	The regularity with which flows of a defined magnitude occur. For example, annual peak flows may occur with low seasonal predictability or with high seasonal predictability.
<i>Rate of change</i>	How quickly flow changes from one magnitude to another; flashy streams have rapid rates of change, whereas stable streams have slow rates of change.

Streams associated with eolian features (e.g., the Nebraska Sandhills) represent one end of flooding and stage variability gradients. Because of the high permeability and hydraulic conductivity of the sands composing landforms, almost no surface runoff is formed during precipitation events. Surface water in streams, lakes, and wetlands originates as groundwater discharge, and stage and discharge levels remain relatively stable seasonally and annually. An example is the Niobrara River in the Nebraska Sandhills (Figure 11); water tables are stable and flood frequency is low enough to allow for the development of fens adjacent to streams.

Peak flow characteristics are also an important factor influencing riparian vegetation. High magnitude floods are important agents of geomorphic change and represent a major disturbance agent in riparian ecosystems. As with other hydrologic measures, patterns of peak flow vary among Region 2 rivers (Figure 12). Landscape changes affecting stream power or material flows inevitably affect riparian area characteristics (Naiman and Decamps 1997; Naiman and others 1993).

Riparian ecosystems are generally maintained by an active natural disturbance regime operating over multiple spatial and temporal scales. Natural physical disturbance agents include floods, fire, landslides, avalanches, and channel migration. These perturbations and the ecological responses to the changed conditions are important because many anthropogenic impacts are manifested through changes to disturbance regimes (Brinson 1981; Patten 1998; Shafroth and others 2002).

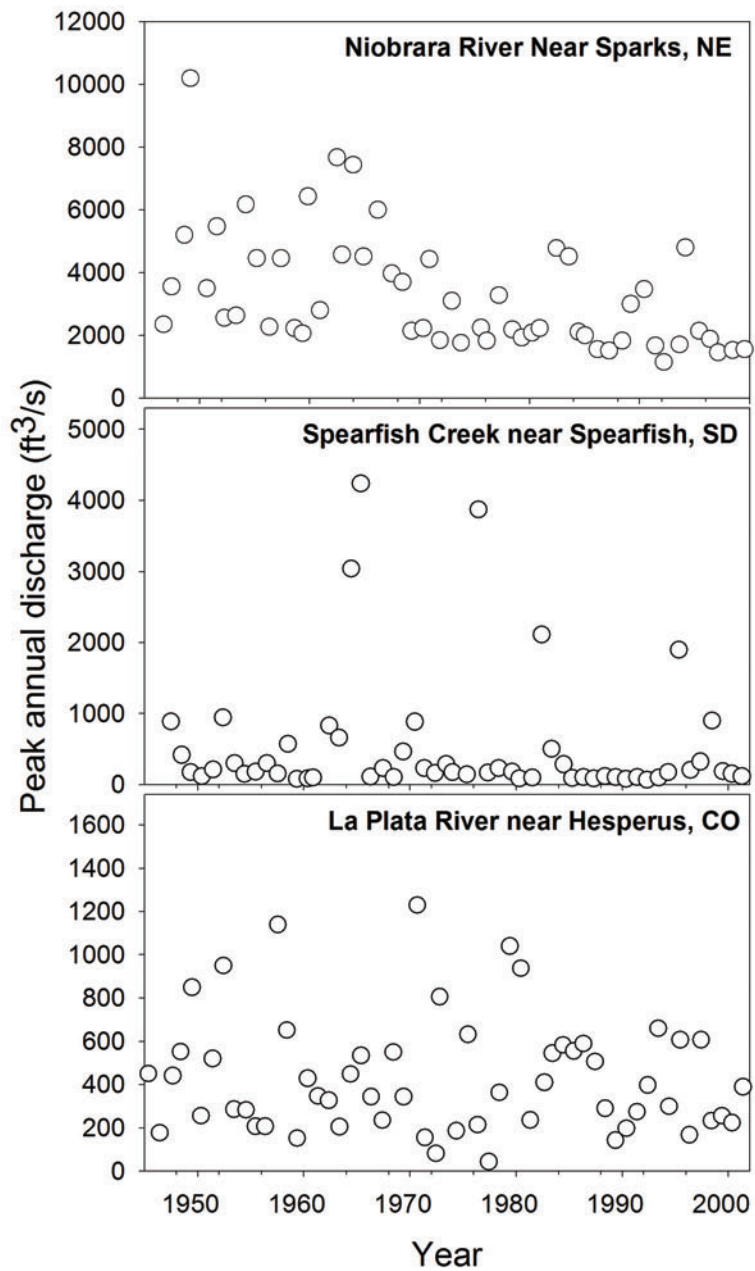


Figure 12—Plots demonstrating different inter-annual patterns of peak annual discharge for three streams in the region. Although there is considerable variability in the magnitude of peak flows, peak annual discharge on the Niobrara River (upper panel) is greater than $\sim 51 \text{ m}^3/\text{s}$ for all years of record, illustrating the influence of groundwater inputs from the adjacent Sandhills in maintaining minimum flows. In contrast, Spearfish Creek (middle panel), which lacks similar groundwater inputs and instead loses water as it flows through limestone-dominated Spearfish Canyon, exhibits a wider range of variability in peak annual flows. The La Plata River exhibits characteristics intermediate between the two, exhibiting greater inter-annual variability than Spearfish Creek, but fewer extreme events.

Turner and others (1993) considered four major factors in characterizing the landscape dynamics of disturbances: (1) disturbance frequency (or its inverse, the interval between successive disturbances), (2) rate of recovery from disturbance, (3) the size or spatial extent of the disturbance events, and (4) the size or spatial extent of the landscape (Turner and others 1993). Characteristics for each of these factors vary with disturbance type and geographically throughout Region 2, making generalizations difficult.

Floods are the most important disturbance type in many riparian ecosystems. Because floods have such a broad range in magnitude, it is useful to reserve the term “flood disturbance” for those flows that directly or indirectly cause plant mortality. The effect of floods on riparian vegetation includes direct plant mortality, as well as indirect effects on vegetation through altered environmental conditions and resource availability. Ice flows can also be a factor influencing patterns of mortality among riparian species (Auble and Scott 1998).

Through their foraging, beaver can profoundly change the age and size structure of woody riparian communities (Baker and others 2005a; Breck and others 2003; Johnston and Naiman 1990b). Their dam building activities strongly modify local hydrology, thereby influencing a wide range of biotic and abiotic processes. Beaver dams can radically change hydrologic regimes, expanding wetland area and altering sediment regimes (Butler and Malanson 1995; Meentemeyer and Butler 1999; Wohl 2000). Widely recognized as a keystone species, beaver are an important factor influencing local and regional biodiversity patterns and geomorphic change (Dickens 2003; Johnston and Naiman 1987; Naiman and others 1994; Wright and others 2003; Wright 2002).

Specific ecological effects from beaver dams can vary depending on the size and ecological context of the river and the age and function of dams. The life-span of dams and associated ponds can vary widely, from less than one year to decades or longer depending on characteristics such as stream mean and peak discharge, gradient, and power (Collen and Gibson 2001; Gurnell 1998). Beaver dam failure can also modify stream channels and open up large areas for new willow establishment, and dams can cause channel evulsions, allowing for plant establishment in the abandoned channel (Cooper and others 2006).

The effects of beaver on riparian ecosystems vary depending on the spatial scale considered. The landscape pattern of beaver-altered habitat changes along stream channels in response to pond age, successional status, and the local environment (Naiman 1988; Ray and others 2001; Wright and others 2003). There is also an important temporal component to landscape-level patterns of beaver occupation influenced by factors such as beaver population abundance and dam persistence.

Although widely studied in upland forests, relatively few studies have investigated the role of fire in western riparian ecosystems. Research suggests that in montane and subalpine settings, fire frequency in riparian areas is often lower than in adjacent upland cover types, although differences may be minor in drier habitats like ponderosa pine forests and grasslands (Dwire and Kauffman 2003). Because fire regimes vary so widely among upland cover types, generalizations are difficult to make for riparian areas. However, the broad gradients in fire frequency that are documented for uplands—high-elevation ecosystems rarely experiencing fire and low-elevation shrublands and grasslands experiencing relatively frequent fires—likely apply to riparian systems (Pyne and others 1996).

Effects of fire on individual riparian species can include injury or mortality (Brown and others 2000). Some species are more resistant than others to the effects of fire because of morphological or physiological characteristics such as thick bark. For example, mature *Populus deltoides* have thick bark with relatively low specific gravity and thermal conductivity. As a result, it takes a fairly long exposure to high temperatures to transmit enough heat to cambial layers to cause mortality (Brown and others 2000). In contrast, non-woody species, thin-barked woody plants, and seedlings and saplings of woody species are more vulnerable to damage from fires (Whelan 1995).

Fires may promote the establishment of certain species by clearing vegetation and litter, providing sites for seedling germination (Whelan 1995). Openings in closed forest canopies also allow for shade-intolerant species such as aspen, willows, and cottonwoods to thrive. Fire may also favor species capable of resprouting such as *Populus angustifolia* (Gom and Rood 1999). Many other species, including several common riparian shrubs such as *Alnus* spp. (alder), *Betula* spp., *Ribes* spp., *Rosa* spp., *Salix* spp., and *Symphoricarpos* spp. can sprout from stumps, root crowns, and belowground stems following fire (Dwire and Kauffman 2003).

Riparian Classification and Gradients ---

The spatial connectivity of riparian areas with streams influences the flow of energy, propagation of disturbance (e.g., flooding), and a variety of ecological processes such as plant and animal dispersal. Along streams, material and energy flow longitudinally along channels, laterally between the channel and floodplains, and vertically with the soil and groundwater environment (Naiman and Decamps 1997; Stanford and Ward 1988; Vannote and others 1980). These, together with the temporal dimension, have been described as the four dimensions of rivers (Ward 1989) and form a basis for understanding different functional processes in riparian ecosystems.

Riparian areas are highly connected upstream and downstream, and diverse physical and ecological processes prevent the formulation of a single, all-purpose classification. Numerous classification schemes have been developed for rivers. Some emphasize hydrologic or geomorphic characteristics (Montgomery 1999; Newson and others 1998; Rosgen 1994), while others emphasize biotic elements such as vegetation (Carsey and others 2003; Girard and others 1997b; Jones and Walford 1995; Walford and others 1997). Others, are more integrative, combining biological and physical elements (Brinson and others 1995; Euliss and others 2004; Zogg and Barnes 1995).

One basic distinction among rivers is the duration of flow. Perennial systems have flow throughout the year. Flow in intermittent and ephemeral systems is limited temporally to specific periods when groundwater or precipitation inputs are available. Divisions between intermittent and ephemeral streams are somewhat arbitrary and are generally made in reference to the length of time surface flows are present and the frequency of flow events. Another distinction is whether the flow of groundwater is toward the river—gaining—or whether the direction of groundwater flow is from the river to the riparian zone and uplands—losing. Notably, individual rivers can have both gaining and losing reaches, affecting plant growth (Harner and Stanford 2003).

Another distinction commonly made among streams is that of stream order. Stream order designations (e.g., first, second, and so on) refer to the relative position of a stream segment in a drainage basin network. First order streams are the smallest, unbranched, perennial tributaries; the junction of two first-order streams produces a second-order stream; the junction of two second-order streams produces a third-order stream, etc. (Knighton 1998). A variety of changes in structure and function occur along gradients from low-order headwater systems to larger, high-order systems (Brinson 1993b; Naiman and others 1987). For example, sources of floodwater delivery change dominance from groundwater discharge and overland runoff in low-order streams to dominance by overbank flooding in high-order streams (Brinson 1993b). Geomorphic characteristics such as sediment delivery and dominant sediment size also vary systematically along streams (Church 2002).

The size of riparian areas differs along broad geographic and elevation gradients. For example, although more numerous, small headwater streams are often almost completely embedded in the surrounding forest. The riparian zone is larger in mid-sized streams and generally contains distinct patches of vegetation determined by long-term (>50 years) channel dynamics and the annual discharge regime (Naiman and Decamps 1997). The riparian areas and floodplains adjacent to large streams can be physically complex and characterized by long periods of seasonal flooding, lateral channel migration, the presence oxbow lakes in old river channels, and a diverse mosaic of wetland communities.

Using the classification scheme developed by Cowardin and others (1979) and used by the National Wetlands Inventory (NWI) mapping program, riparian areas may be placed in either the palustrine or riverine system. Within each system except palustrine, subsystems are identified, with four for riverine wetlands: tidal, lower perennial, upper perennial, and intermittent (Tiner 1999). Only the last three are relevant to Region 2. Within each subsystem, a variety of classes can be designated based on substrate conditions or vegetation (Cowardin and others 1979).

The Hydrogeomorphic (HGM) approach, developed for wetland functional assessments, emphasizes hydrologic and geomorphic processes as they influence wetland and riparian ecosystem structure and function (Brinson 1993a). Riparian ecosystems are in the Riverine HGM class (Brinson and others 1995; Hauer and others 2002a). Riverine wetlands can be further divided into subclasses that more precisely reflect stream flow and fluvial processes (Tiner 1999) (Figure 13).

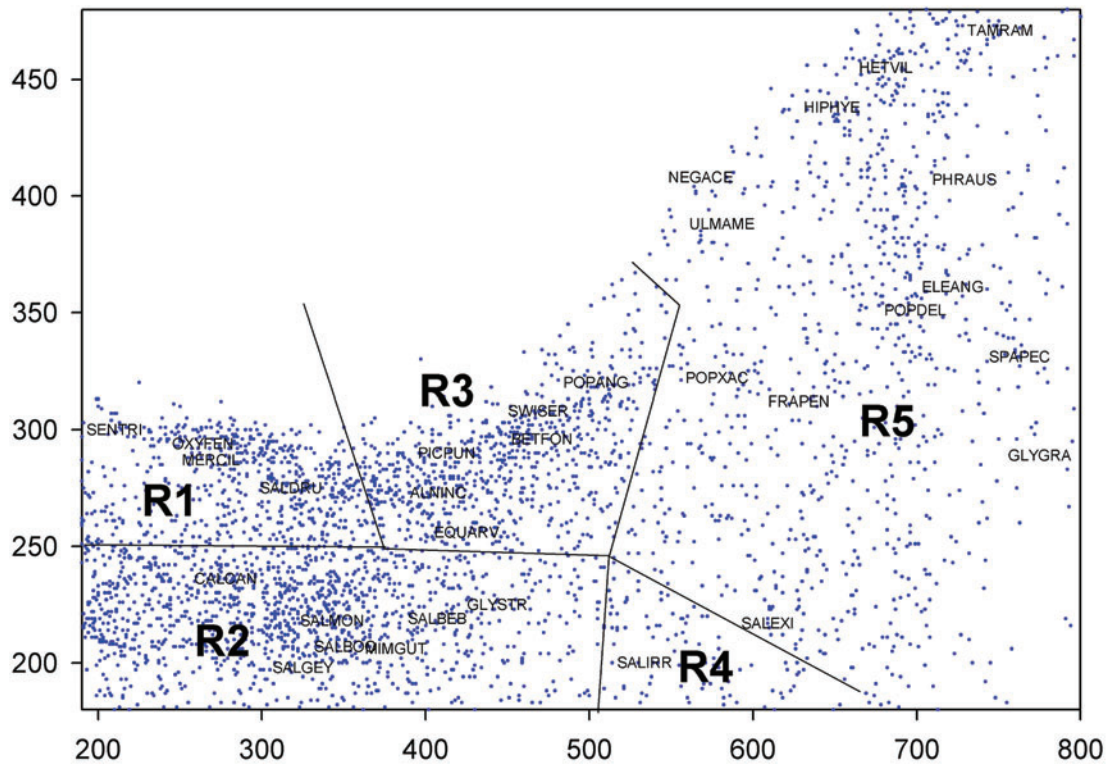


Figure 13—DCA ordination of Region 2 riparian vegetation data illustrating main HGM subclasses as identified by Cooper (1998). See Chapter 2 for description of methods used in ordination and data set description.

In a classification of Colorado wetlands using HGM as a base, Cooper (1998) described a total of five Riverine subclasses. Wetlands in the Riverine subclass 1 (R1) typically occur along steep-gradient, low-order streams and springs on coarse-textured substrates (Cooper 1998a). Thirteen R1 plant associations were defined by Carsey and others (2003) for this subclass mostly occurring in the subalpine zone. Riverine subclass 2 (R2) communities occur on coarse and fine-textured substrates along moderate-gradient streams at intermediate elevations and often support beaver pond complexes. In their analysis, Carsey and others (2003) identified 46 plant associations including coniferous and deciduous forests, shrublands, and herbaceous types. Riverine Subclass 3 includes shrub and tree-dominated riparian areas along middle-elevation reaches of low-order and mid-order streams. Subclass R4 occupies lower-elevation canyons in the foothills and plateaus along larger rivers or small intermittent streams (Carsey and others 2003). Seventy-six plant associations were identified in these two combined subclasses. Subclass 5 (R5) wetlands are found on low-elevation floodplains of mid- to high-order streams. Substrates are typically fine-textured and streamflow is usually perennial but occasionally intermittent. Associations in this subclass are most common below 7000 ft (2130 m) but may occur up to 9,800 ft (2,990 m). Thirty-four plant associations were identified in the R5 subclass, including shrublands, grasslands, or deciduous woodlands (Carsey and others 2003).

Riparian vegetation in the region

Zonation within riparian areas—Because of the linear nature of riparian environments, gradients in key environmental variables and resulting vegetation patterns vary both laterally and longitudinally, although the scale differs depending on the direction examined. Variation across mountain stream valleys is typically seen on a scale of meters, while longitudinal variation may be more appropriately measured in kilometers (Bendix 1994). Key gradients driving vegetation patterns laterally across streams are water table depth, elevation, soil characteristics, and flood disturbance. These often create distinct vegetation zones across riparian areas. Along meandering rivers with broad floodplains, episodic flood events and channel migration cause pulses of establishment of woody species such as willow and cottonwood, creating patches of different age.

Water source affects both the width of the riparian zone and its vegetation composition. For example, water tables along intermittent and ephemeral streams often drop well below stream channels, limiting plant species to deep rooted phreatophytes or upland species that are tolerant of low soil moisture (Goodwin and others 1997). In contrast, many headwater streams receive perennial groundwater inputs from side slopes, helping to maintain high water tables long after seasonal peak flows have diminished. Whether a stream is gaining or losing also affects the sensitivity of riparian communities to changes in surface water regimes associated with river regulation.

Longitudinal changes in riparian communities—Longitudinal changes in riparian vegetation can differ among streams depending on stream length and elevation gradient. A typical progression along a Region 2 river might proceed as follows. In high-elevation headwater areas, vegetation is often dominated by herbaceous plants, such as *Senecio triangularis*, *Mertensia ciliata*, and *Cardamine cordifolia*. Low stature shrubs, such as *Salix planifolia*, may also be common, particularly where shallow groundwater and snowmelt are the principal water sources. Moving downstream, the stature, composition, and diversity of shrub dominants typically increases. *Salix* spp. are dominant in broad, open basins and low-gradient streams, and along higher-gradient streams, *Alnus incana* ssp. *tenuifolia* and *Betula fontinalis* are abundant. Along larger, mid-elevation montane streams, and lower in the foothill valleys, riparian forests dominated by *Populus angustifolia* and *Picea pungens* are common along with the various shrub and herbaceous species. Streams in the lowlands are often dominated by large cottonwoods such as *Populus deltoides* in the Great Plains and *P. fremontii* west of the Continental Divide. Certain species tend to be diagnostic of particular riparian types (Figure 13, Table 11).

Region 2 supports a wide range of specific riparian vegetation types. Using GAP data, the Nature Conservancy developed a vegetation classification for all of Region 2 based on the primary classification unit ecological systems, defined as assemblages of biological communities found in sites with similar physical environments, disturbance regimes, underlying environmental features, or environmental gradients (Comer and others 2003b). In their analysis, Comer and others (2003b) describe three riparian ecological systems, comprising approximately 2.48 percent of the Region 2 area (Table 12).

Western Great Plains riparian/western Great Plains floodplain—The western Great Plains riparian/floodplain system includes riparian areas associated with medium and small rivers and streams throughout the western Great Plains. It extends through the central shortgrass prairie and northern Great Plains steppe into Wyoming, and it occurs on alluvial soils in highly variable landscape settings, from deep cut ravines to wide, braided streambeds (Comer and others 2003b). Relative to larger rivers, these systems have relatively flashy hydrologic regimes. Common species include *Populus deltoides*, *Salix exigua*, *Artemisia cana* ssp. *cana*, *Pascopyrum smithii*, *Sporobolus cryptandrus*, and *Schizachyrium scoparium*. Non-native species including *Tamarix* spp. and *Elaeagnus angustifolia* may dominate in heavily degraded areas, (Comer and others 2003b).

Rocky Mountain subalpine-montane riparian shrubland—The Rocky Mountain subalpine-montane riparian shrubland system occurs throughout the Rocky Mountain cordillera from New Mexico to Montana and includes montane to subalpine riparian shrublands in narrow to wide, low-gradient valley bottoms and floodplains with sinuous stream channels (Comer and others 2003b).

Table 11—HGM indicator species identified by Cooper (1998).

Scientific name	Common name	HGM subclass
<i>Mertensia ciliata</i>	tall fringed bluebells	R1
<i>Mimulus guttatus</i>	seep monkeyflower	R1
<i>Oxypolis fendleri</i>	Fendler's cowbane	R1
<i>Calamagrostis canadensis</i>	bluejoint reedgrass	R1
<i>Cardamine cordifolia</i>	heartleaf bittercress	R1
<i>Glyceria striata</i>	fowl mannagrass	R1
<i>Salix boothii</i>	Booth willow	R2
<i>Salix geyeriana</i>	Geyer willow	R2
<i>Salix monticola</i>	Rocky Mountain willow	R2
<i>Geum macrophyllum</i> var. <i>perincisum</i>	largeleaf avens	R2
<i>Heracleum maximum</i>	common cowparsnip	R2
<i>Cornus sericea</i> ssp. <i>sericea</i>	red-osier dogwood	R3
<i>Picea pungens</i>	blue spruce	R3
<i>Poa pratensis</i>	Kentucky bluegrass	R3
<i>Populus angustifolia</i>	narrowleaf cottonwood	R3
<i>Rosa woodsii</i>	Woods' rose	R3
<i>Rudbeckia laciniata</i> var. <i>ampla</i>	cutleaf coneflower	R3
<i>Salix ligulifolia</i>	strapleaf willow	R3
<i>Alnus incana</i> ssp. <i>tenuifolia</i>	thinleaf alder	R3
<i>Equisetum arvense</i>	field horsetail	R3
<i>Acer negundo</i> var. <i>interius</i>	boxelder	R4
<i>Salix irrorata</i>	dewystem willow	R4
<i>Agrostis gigantea</i>	redtop	R4
<i>Bromus inermis</i>	smooth brome	R4
<i>Carex pellita</i>	woolly sedge	R4
<i>Corylus cornuta</i>	beaked hazelnut	R4
<i>Hordeum jubatum</i> ssp. <i>jubatum</i>	foxtail barley	R4
<i>Juncus torreyi</i>	Torrey's rush	R4
<i>Phragmites australis</i>	common reed	R5
<i>Populus deltoides</i>	eastern cottonwood	R5
<i>Rhus trilobata</i> var. <i>trilobata</i>	skunkbush sumac	R5
<i>Salix amygdaloides</i>	peachleaf willow	R5
<i>Salix exigua</i>	narrowleaf willow	R5
<i>Salix fragilis</i>	crack willow	R5
<i>Spartina gracilis</i>	alkali cordgrass	R5
<i>Spartina pectinata</i>	prairie cordgrass	R5
<i>Tamarix ramosissima</i>	saltcedar	R5
<i>Vitis riparia</i>	riverbank grape	R5
<i>Carex emoryi</i>	Emory's sedge	R5
<i>Chrysothamnus linifolius</i>	spearleaf rabbitbrush	R5
<i>Elaeagnus angustifolia</i>	Russian olive	R5
<i>Lycopus americanus</i>	American water horehound	R5

Table 12—Approximate area of different Region 2 ecological systems as determined by Comer et al. (2003). Riparian systems are indicated in bold.

Ecological Systems	Hectares	Percent area
Inter-Mountain Basins Playa	12,749	0.0
North American Arid West Emergent Marsh	128,301	0.1
North Central Interior Floodplain/Wooded Draw	771,987	0.7
Rocky Mountain Subalpine Mesic Meadow	884,960	0.8
Western Great Plains Closed Depression	817,203	0.7
Western Great Plains Riparian/ Western Great Plains Floodplain	1,488,930	1.3
Western Great Plains Saline Depression	2,828	0.0
Rocky Mountain Subalpine Mesic-Spruce-Fir Forest and Woodland	48,164	0.0
Rocky Mountain Lower Montane Foothill Riparian Woodland and Shrubland	848,753	0.7
Rocky Mountain Subalpine-Montane Riparian Shrubland	475,655	0.4
Region 2 Total	113,543,893	

These communities are typically found at higher elevations, from 5577 to 11,400 ft (1700 to 3475 m). Communities often form a mosaic of shrub- and herb-dominated vegetation types with species such as *Alnus incana*, *Betula nana*, *B. occidentalis*, *Cornus sericea*, and a number of different willows, including *Salix* spp. (Comer and others 2003b).

Rocky Mountain lower montane foothills riparian woodland—The Rocky Mountain lower montane foothills riparian woodland includes seasonally flooded conifer and aspen woodlands found at montane to subalpine elevations of the Rocky Mountain cordillera. These are found on floodplains or terraces between 4900 and 10,825 ft (1500 and 3300 m) above sea level (Comer and others 2003b). Dominant species include *Abies lasiocarpa*, *Picea engelmannii*, *Pseudotsuga menziesii*, *Picea pungens*, *Populus tremuloides*, and *Juniperus scopulorum*. Also commonly present are *Alnus incana*, *Pinus contorta*, *Populus angustifolia*, *Acer negundo*, and *Juniperus osteosperma*.

HRV of Riparian Ecosystems in Region 2 _____

Overview of anthropogenic impacts

Streams and rivers are among the most systematically altered ecosystems in North America. Anthropogenic impacts are diverse and include both direct alterations occurring within ecosystem boundaries and indirect alterations. The latter include alterations to contributing watersheds that affect the quantity, quality, or timing of sediment, water, or other critical inputs such as plant propagules. Because of the large geographic scope of this assessment and the high ecological diversity of riparian types in Region 2, it is not possible to provide a single estimate of the HRV and possible deviations since the arrival of Euro-Americans that would be applicable to all wetland and riparian ecosystems. Our approach is to provide a review of the main anthropogenic impacts that have affected riparian areas in the region with the understanding that the relative importance of any particular impact on the HRV of a given area will differ (Table 13).

Flow regulation and diversion—Since the mid-Nineteenth Century, water in Region 2 has been used to support municipalities, agriculture, power production, mining, and recreation. The infrastructure and consumptive uses of water increased dramatically during the mid-Twentieth Century with a large increase in the number of dams constructed on rivers in the region (Graf 1999; Wohl 2000) (Figure 14). Reservoir storage on the North Platte River, for example, experienced more than an eight-fold increase between 1900 and the present.

Dams have been constructed for a variety of purposes. In the NID dataset, the use ascribed to 34.5 percent of dams in Region 2 is fire/farm pond. These are generally small dams and are most concentrated in the plains. The next most common use listed is flood control (20.4 percent) followed by water supply (16 percent) and irrigation (15.6 percent). Hydroelectric is listed as the primary purpose for only 0.7 percent of dams; however, this portion includes some of the largest dams in the region.

Dams are distributed throughout the region, from small earthen dams on headwater streams to large dams on big rivers managed for electricity production and water storage. In terms of overall numbers, dams are most densely concentrated in areas of agricultural production such as eastern and central South Dakota, Kansas, and Nebraska. Dams are also concentrated along population centers, for example, the Colorado Front Range. Because the majority of rivers in the region originate as snowmelt in the mountains, many large dams occur in mountainous areas.

Table 13—Summary of main impacts to rivers in the Front Range of Colorado and their approximate primary period of impact (Wohl 2005).

Land use	Period	Influence on rivers
Beaver trapping	1815–1840	Removal of beaver dams increased flow velocity, stream bed and bank erosion. Decreased sediment storage, channel stability, and diversity.
Placer mining	1859–1940s	Direct effects: Disruption of stream bed and bank structure, increased sediment and channel mobility, altered flow regime (if diversion occurs), and introduced toxic contaminants such as mercury. Indirect effects: increased regional population, the amount of timber harvested, the number of transportation corridors, and the amount of sediment and contaminants entering channels.
Railroad tie drives	1860s–1890s	Effects included modification of the channels prior to tie drives (e.g., the removal of obstructions and naturally occurring wood and the blocking-off of overbank areas); scouring effects from pulses of water and wood.
Diversions and dams	1859 to present	Altered magnitude, duration, and frequency of flows, as well as sediment transport, disturbance regimes, water chemistry, and water temperatures.
Timber harvest	1859–1940s	Effects included destabilizing hill slopes and increasing water and sediment yields to rivers.
Transportation corridors, such as roads and railroads	1860 to present	Effects include increasing sediment to rivers from destabilized hill slopes, erosion of unpaved roads, and application of traction sand and gravel during the winter. Transportation corridors also reduce the width of the floodplain and riparian corridors.
Lode mining	1859–1980s	Effects include increased sediment yield from hill slopes and introduction of toxic contaminants to rivers.
Urbanization	1859 to present	Effects include an initial increase of water and sediment yield to rivers, followed by an increase primarily in water yield that introduces contaminants into rivers and constrains channel and floodplain space and mobility.
River recreation	1909 to present	Fishing creates pressure on native species and promotes the introduction of other species. Whitewater rafting locally creates trampled streambanks with compaction, decreased infiltration, increased runoff and erosion, and damage to riparian vegetation.
Grazing	1860 to present	Effects include removing riparian vegetation and compacting streambanks, bank erosion, wider and shallower channel cross-sections, finer stream bed substrates, increased nutrient input to rivers, warmer water temperatures, and reduced aquatic and riparian habitat.

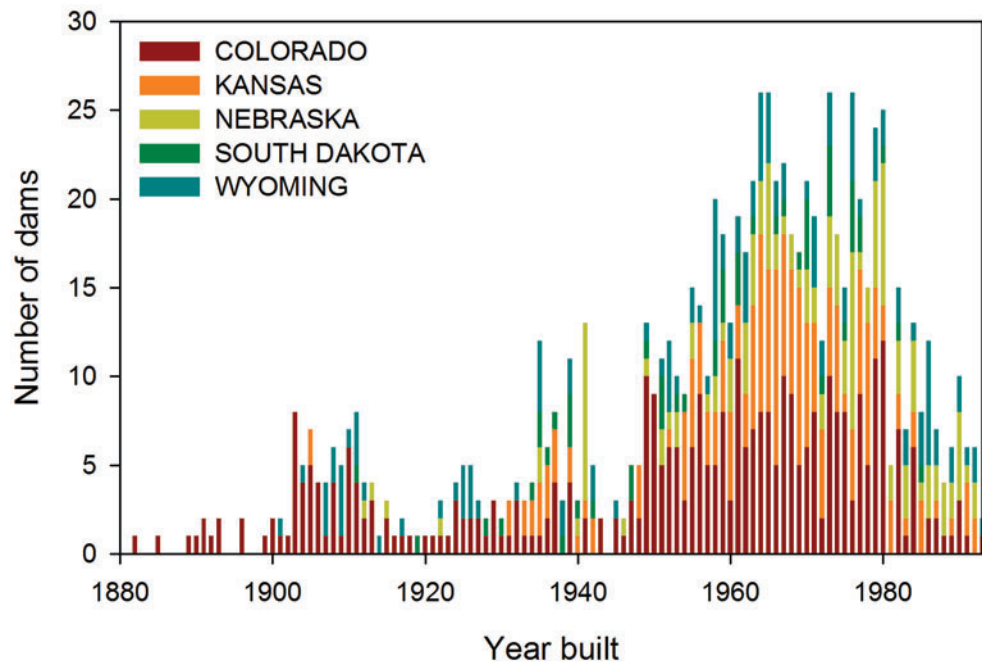


Figure 14—Dam construction in the states that are part of Region 2; data from National Inventory of Dams (U.S. Army Corps of Engineers 1996).

In addition to large dams, numerous trans-basin diversions occur throughout the region, affecting both receiving and donor rivers (Henszey 1993; Johnson and others 1999; Pringle 2000; Woods and Cooper 2005). These convey water over drainage divides using tunnels or ditches intercepting tributaries (Chimner and Cooper 2003; Woods and Cooper 2005). General effects can include altered hydrologic regimes, disturbance processes, chemical cycling, and community composition (Adair and others 2004; Nilsson and Berggren 2000; Wohl 2000). Trans-basin diversions are most numerous in Colorado, with nearly 40 structures found in the South Platte basin (Wohl 2001). Hydrologic and ecological effects vary among streams. For example, high-gradient, step-pool streams are less likely to see major changes in response to increased discharge than lower-gradient streams (Wohl 2000).

Hydrologic effects of dams and diversions vary but typically include alteration of the magnitude of monthly water conditions, reduction in the magnitude and duration of annual extreme discharge events, the changes in the timing of annual extreme discharge events, and the frequency and duration of high/low flow pulses and hydrograph changes (Richter and others 1997). Changes in magnitude can cause increased scour of vegetation, promote the invasion of exotic species, and reduce water and nutrients to floodplain vegetation (Nilsson and Svedmark 2002; Poff and Hart 2002). Water releases from reservoirs may cause channel incision, isolating adjacent floodplains or tributary outlets (Kondolf 1997; Petts 1984).

On large rivers throughout the West, the decline of native cottonwood riparian forests has been a large concern (Cooper and others 2003b; Patten 1998). Because cottonwoods depend on shallow floodplain groundwater, they are particularly vulnerable to modifications of river flow. Hydrologic modifications from river regulation can reduce cottonwood growth rates and cause canopy dieback and tree death, as well as inhibit new seedling establishment and recruitment (Mahoney and Rood 1998; Williams and Cooper 2005). Changes in the timing of peak flows can also affect *Populus* spp. and *Salix* spp., which disperse seed in the early summer and produce non-persistent seeds with narrow windows of viability (Karrenberg and others 2002). Management of dams for hydropower typically involves dramatic daily flow variation (Poff and Hart 2002; Poff and others 1997).

Large changes in disturbance frequency or level of landscape connectivity can disrupt plant dispersal, resulting in reduced plant diversity and compromised ecological integrity (Andersson and others 2000; Merritt and Wohl 2002; Merritt and Wohl 2006). For example, Merritt and Wohl (2006) found significant differences in community composition upstream and downstream from reservoirs in Colorado, suggesting that 50 to 100 years of fragmentation has caused community-wide effects along Rocky Mountain streams, which the authors partially attributed to dispersal limitation due to dams and reservoirs. Landscape-level impacts are particularly important if one considers the extent of river regulation. For example, less than 50 high-quality, undammed rivers longer than 200 km remain in the continental United States (Benke 1990).

Beaver trapping—The first and one of the largest impacts to riparian areas by Euro-Americans in Region 2 was the trapping and near removal of beaver from regional streams. Beaver were widespread throughout most of North America, numbering between 60 and 400 million before European settlement. Although natural predators such as wolves, coyotes, and bear opportunistically fed on beaver, until Europeans arrived in North America, beaver populations were controlled principally by disease and food availability (Sandoz 1978). Beaver played a keystone role in riparian ecosystem functioning, profoundly altering the vegetation and hydrologic regimes of their environment through their feeding and dam building activities. Beaver dams and their associated ponds elevate water tables, trap sediment, and alter biogeochemistry (Naiman and others 1988).

Most beaver populations were decimated by fur trappers during the 1700s and 1800s (Sandoz 1978; Wishart 1974). By 1840, beaver populations were depleted in many areas of the Rocky Mountains (Travis and others 2002). Although beaver reintroduction and a decline in demand for pelts has helped populations to recover throughout much of their former range, beaver have failed to recover in some riparian environments that have become heavily browsed by livestock or ungulates since European settlement (Baker and others 2005a).

In some areas, the removal of beaver increased stream channel down-cutting, reducing the complexity of wetland habitats (Wohl 2001). In Rocky Mountain National Park, beaver absence caused in part by habitat degradation from excessive elk populations has resulted in the conversion of willow riparian shrub communities to dry meadows (Baker and others 2005a; Peinetti and others 2002a). Considering their importance as geomorphic and ecological drivers, the decimation of beaver populations represents one of the most significant deviations from the HRV for riparian ecosystems.

Agricultural impacts—Agricultural impacts include all activities directly related to the production of food, feed, or fiber, excluding the raising of domesticated animals, which is discussed subsequently. Agricultural impacts can include direct effects on riparian vegetation and functions such as vegetation clearing or channel realignment, soil compaction by heavy machinery. Indirect effects can include fragmentation and reduction of wildlife habitat, reduced plant diversity and invasion of exotic species, and increased water temperature (USDA NRCS 1998).

The extent, nature, and magnitude of impacts to riparian ecosystems from historical and contemporary agricultural activities in Region 2 vary widely. Excluding ranching, most mountainous areas have never supported agriculture. In contrast, agriculture on the Great Plains and Intermountain valleys is common. Euro-American settlement and agriculture in the region began in the mid-Nineteenth Century, largely to support population growth in mining areas, and it increased with the completion of the railroads. Proximity to water was a priority, so riparian areas tended to be among the first that were cleared and settled. The dust bowl drought of the 1930s, in particular, saw the failure of many farms, especially in areas west of the 100th meridian. Many of these lands ultimately entered the public domain and are managed as National Grasslands. Although, the Great Plains experienced substantial declines in population between 1950 and 2000, the area in crops declined by less than 1 percent overall (Brown and others 2005).

Livestock grazing—Livestock grazing can have significant impacts on riparian ecosystems, as illustrated by a variety of studies (Belsky and others 1999; Chaney and others 1990; Fleischner 1994). Effects include removing riparian vegetation and compacting streambanks, bank erosion, wider and shallower channel cross-sections, finer stream bed substrates, increased nutrient input to rivers, warmer water temperatures, and impaired aquatic and riparian habitat. Fleischner (1994) identified three principal impacts of livestock grazing: (1) changes of species composition, including decreases in density and biomass of individual species, reduction of species richness, and changing community organization; (2) disruption of ecosystem function, including altered nutrient cycling and successional patterns; and (3) alteration of ecosystem structure, including changing vegetation stratification, soil erosion, and decreasing availability of water to biotic communities. Livestock can also impact riparian areas by transporting seeds and vegetative propagules of invasive species (Belsky and others 1999).

Historically, many areas in the region were overgrazed, although livestock numbers are now significantly lower than at their historical peak (Elmore and Kauffman 1994). The legacy of overgrazing varies over the region; some areas have recovered while others still bear scars, particularly in areas where significant geomorphic change such as channel downcutting has occurred. The level of impact can vary widely depending on the sensitivity of the system, and the intensity and seasonality of grazing (Chaney and others 1990).

In general, impacts to riparian areas depend on the species of livestock and the characteristics of the habitat present (Gillen and others 1985; Marlow and Pogacnik 1986). Cattle, in particular, are typically regarded as having the greatest potential impact on riparian systems. They tend to prefer low-gradient riparian systems because of available water and abundant palatable forage (Belsky and others 1999). Seasonality of use also affects cattle use and impacts. For example, late summer pastures tend to have more concentrated cattle use in riparian areas (Parsons and others 2003). In contrast, sheep typically prefer uplands, utilizing riparian areas more to acquire water than for forage (Glimp and Swanson 1994); however, in sufficient numbers, they too can cause significant physical site impacts.

Native ungulates can also have significant effects on wetlands and riparian areas. Impacts to the physical environment include soil compaction and bank instability, direct effects to vegetation like herbivory and trampling, and indirect effects like nutrient enrichment via urine or fecal deposits (Hobbs 1996; Opperman and Merenlender 2000). Moose use riparian systems almost exclusively in the summer and can have significant effects on *Salix* spp. (Oedekoven and Lindzey 1987; Singer and others 1994). Historically, elk would have been less common in open riparian areas due to predation avoidance behavior; however, the extirpation of predators such as wolves has resulted in large increases in elk populations in several areas of the Rocky Mountains (Coughenour and Singer 1996; Peinetti and others 2002b). In addition to their greater numbers, elk spend a large amount of time in riparian areas, causing significant impacts to riparian vegetation (Beschta 2003; Fortin and others 2005; Ripple and Beschta 2004; Wolff and Van Horn 2003).

Bison were widespread throughout the Great Plains and some intermountain basins prior to the arrival of Euro-American in the region (Knapp and others 1999). Their effects on riparian areas are generally poorly studied but are likely similar to those of cattle, including soil compaction and bank instability, herbivory, and nutrient enrichment via urine or fecal deposits (Hobbs 1996). However, bison feeding behavior differs from that of cattle, both in terms of preferred species and habitats. Like cattle, bison feed primarily on grasses and sedges, and avoid herbaceous dicotyledons and woody species, which usually constitute less than 10 percent of their diet (Knapp and others 1999), although they generally spend less time in riparian areas. Their impacts were likely more localized than those of cattle and centered around major stream crossings (Fritz and Dodds 1999).

The elimination of bison has been cited, along with other environmental changes such as the cessation of prairie fires and river regulation, as a possible factor influencing the expansion of woodlands along the Platte River system in Nebraska over the last century (Johnson 1994).

Timber harvest—The effects of timber harvest on riparian areas has a variety of direct and indirect effects on biophysical processes and habitat characteristics. Impacts can include changes in the timing or magnitude of runoff events, reduced stability of stream banks, increased sediment supply to channels, and changes in in-channel sediment storage and structure. Timber harvest can also directly impact riparian areas by causing plant mortality. Logging can affect stream flow by altering the watershed processes controlling water movement from hillsides to stream channels. Other activities associated with timber harvest, including skid trails, landings, and roads, can also impact riparian and wetland resources.

Changes in basin vegetation cover due to timber harvest can alter surface runoff from basins through effects on evapotranspiration rates and snowpack accumulation patterns. For example, canopy removal in a subalpine watershed in Colorado increased precipitation reaching the forest floor by approximately 40 percent and, increased peak snowpack water equivalent by more than 35 percent (Stottlemeyer and Troendle 1999; Stottlemeyer and Troendle 2001). Clearcutting and partial thinning both result in increased total annual and peak streamflow in logged watersheds (Troendle and King 1987).

Of particular historical importance to many riparian systems were tie-drives. Beginning in the 1860s, demand for timber increased dramatically, driven in part by the expansion of the railroads (Wohl 2005). Rivers were used to transport huge numbers of railroad ties downstream from harvest areas to collection points. Wohl (2005) reported that more than 200,000 ties went down Colorado's Poudre River in Colorado annually from 1868 to 1870. To facilitate conveyance of the ties, stream channels were often strongly modified, for example, by artificially straightening meanders with cutoffs. Additional impacts resulted from the scouring effect of moving large log masses downstream. Impacts to some streams are still discernible over a century after the drives occurred and can include reduced levels of mature riparian vegetation and wider, shallower channels with less pool volume (Neal and Zubick 2003; Wohl 2005; Young and others 1994).

Mining impacts—Mineral extraction was one of the primary historical drivers of Euro-American settlement in many portions of Region 2 (West 1998). Mining is still widespread in the region, although the number of active operations is a fraction of historical levels (Table 14). Impacts from mining's legacy are among the most pressing environmental concerns in the region today (Limerick and others 2005; Wohl 2001).

Table 14—Mining claim totals by type and status in Colorado (Hyndman and Campbell 1999).

Type of Claim	Lode	Placer	Mill	Tunnel	All claims
Number of open mining claims	7,491	2,058	222	17	9,788
Number of closed mining claims	216,206	18,638	3,502	121	238,467
Grand Totals	223,697	20,696	3,724	138	248,255

Placer mining was a significant historical disturbance to many aquatic and riparian habitats in the region, accomplished with hand operation of gold pans, shovels, and sluices and later by larger scale hydraulic mining and dredging (Wohl 2005). Dredging entails the excavation of the streambed and floodplain, which destroys vegetation and undermines channel stability. The spoils are typically spread or piled on the valley margin and are often difficult to revegetate. In hydraulic mining, jets of water are directed onto ore-bearing alluvial deposits. Because of environmental concerns, hydraulic mining is generally prohibited through legislation, but early gold miners widely employed the technique.

Gravel and sand mining has increased in some areas of Region 2 in response to demand from development. Extraction of aggregate materials from rivers and streams alters channel morphology, streambank stability, channel patterns, and riparian vegetation (Kondolf 1994; Kondolf and Swanson 1993). Effects can include increased sedimentation, introduction of contaminants, widening of channels, direct loss of vegetation, and modification of streams and wetlands due to tailings (Meador and Layher 1998; Scott and others 1999). Aggregate operations are generally confined to sites along larger alluvial rivers where significant deposits are available.

Hard rock mining influences many riparian areas through disruption of the stream bed and bank structure, increased sediment and channel mobility, altered flow regimes, and the introduction of contaminants such as lead and mercury (NRC 1999; Wohl 2001). Hard rock mining can significantly impair water quality and effect aquatic, riparian, and wetland biota. Specific impacts differ depending on the type of ore, and the extraction and processing methods used. Because mines typically extend below the regional water table, groundwater may flow into the mine pit, ultimately exiting contaminated with metals through drainage adits (Limerick and others 2005). Overburden, waste rock dumps, tailing impoundments, leach pads, process ponds, and mills can serve as sources of contaminants like heavy metals that negatively affect the quality of surface and groundwater.

Energy development—Energy development, including coal, oil, and gas development, is an additional anthropogenic factor that locally impacts riparian areas in the region. Direct effects from extraction activities are generally minor, although indirect effects from the associated infrastructure such as roads may be more common. A notable exception is coal-bed methane (CBM), which typically produces large volumes of water. CBM discharge waters often cause an increase of salinity and sodicity within exposed soils, altering soil physical and chemical properties and affecting the density and diversity of vegetation (Stearns and others 2005). CBM operations are concentrated in certain portions of the region such as the Powder River Basin (USDI 2000), and, thus, are not a factor for much of Region 2 riparian ecosystems.

Transportation—Transportation infrastructure, including roads, trails, and railroads, have affected riparian areas by altering local and watershed-scale hydrologic processes. Structures such as bridges and railroad prisms may confine river channels, in turn causing increased flow velocity, which scours and coarsens bed sediments (Wohl 2005). Engineering structures such as culverts and ditches can alter natural drainage patterns, reduce interception and infiltration rates due to the removal of vegetation and soil compaction, and alter the hydrologic response of basins to both annual snowmelt runoff episodes and isolated convective storm events (Forman and Sperling 2002; Jones 2000). In addition, increased overland flow typically results in a more rapid and extreme hydrologic response to precipitation events.

Additional effects can include the introduction of pollutants and the alteration of water chemistry from road dust, vehicle exhaust, and chemicals such as deicing agents used in road maintenance (Trombulak and Frissell 2000; Wilcox 1986a; Wilcox 1986b). Road density; slope and surface type; and the number, size, and design of engineering structures are all factors that influence the specific impact of roads. Transportation infrastructure can also affect riparian ecosystems by promoting weed invasions. Construction or maintenance activities create disturbances conducive to the establishment of many exotics and provide an effective conduit for the dispersal of weed propagules (Gelbard and Belnap 2003; Parendes and Jones 2000).

Urbanization—Impairment of riparian communities commonly accompanies urban and exurban development (Hansen and others 2005). For example, Auble and others (1997) observed declining *Populus deltoides* establishment on the floodplain and terrace of Boulder Creek in Boulder, Colorado from 1937 to 1992, attributing the decline in part to the effects of stream diversions and channel stabilization. These changes led to decreased channel movement, reductions in peak flow volume and flood frequency, reducing opportunities for cottonwood establishment and favoring exotic species like *Salix fragilis* and *Elaeagnus angustifolia* (Auble and others 1997).

Atmospheric deposition of airborne pollutants such as nitrogen may impact riparian ecosystems in the region (Fenn and others 2003a). Typically, hotspots of elevated nitrogen deposition occur downwind of large metropolitan centers, although elevated levels can also be observed in the proximity of large agricultural operations (Fenn and others 2003b), and most areas of Region 2 are exposed to some level of atmospheric nitrogen deposition.

Invasive species—The spread of non-native species is changing the biotic composition of many Region 2 riparian ecosystems. Woody species, including *Tamarix* spp. and *Elaeagnus angustifolia*, are particularly widespread along large rivers at low elevations in the region, as are herbaceous species such as *Phalaris arundinacea* (reed-canary grass) (Katz and Shafroth 2003; Pearce and Smith 2003). Stands of exotic plants can be dense, effectively shading out seedlings of native competitors like cottonwoods and preventing their establishment (Cooper and others 1999). *Tamarix* spp. can alter geomorphic processes, cause channel narrowing by promoting island formation and growth, affect water tables, and alter fire regimes (Di Tomaso 1998). As a nitrogen fixer, *Elaeagnus angustifolia* can influence biogeochemical process, possibly facilitating invasion by other invasive species (Simons and Seastedt 1999).

In sampling the woody riparian species present at 475 randomly selected stream gauging stations in 17 western states, Friedman and others (2005) found that *Tamarix ramosissima* and *Elaeagnus angustifolia* are widespread across the western United States. They found that the two species are now the third and fourth most frequently occurring woody riparian plants in the region; and based on mean normalized cover, are the second and fifth most dominant woody riparian species. The frequency of occurrence of *T. ramosissima* may be constrained by sensitivity to frost, while the frequency of *E. angustifolia* decreases with increasing minimum temperatures (Friedman and others 2005).

Cumulative and threshold effects—To understand possible deviations from the HRV of riparian ecosystems, evaluation of individual stressors alone is insufficient. Increasingly, cumulative impacts (defined as the incremental effect of an impact added to other past, present, and reasonably foreseeable future impacts) have become a concern for wetlands and watershed managers (Gosselink and Lee 1989; Johnston 1994; Preston and Bedford 1988). Cumulative effects can be direct or indirect, i.e., they can occur at a location distant from the impacts. For example, hydrologic modifications from dams can cause impacts to riparian systems hundreds of miles downstream from the location of a particular dam.

Effects can accumulate in a variety of ways. Perturbations that are tightly crowded spatially or temporally can overwhelm a system's ability to recover from disturbances (Johnston 1994). In addition, disturbances can interact synergistically to produce effects qualitatively and quantitatively different from the individual disturbances. For example, dams, diversions, flow regulation, stream channelization, wetlands drainage, and groundwater extraction can interact, creating conditions that facilitate the proliferation of exotic species in riparian habitats (Busch and Smith 1995; Cooper and others 1999; Pringle 2000; Shafroth and others 2002).

Changes in the landscape configuration of wetlands and riparian areas may also affect ecosystems at the site and reach level. For example, native cottonwood forests along the upper Colorado River systems are increasingly fragmented due, in part, to the increasing dominance of *Tamarix* spp. and the conversion of floodplains to land uses like agriculture (Northcott and others 2006). The resulting isolation of remaining stands may constrain future cottonwood establishment in otherwise suitable areas, as seed dispersal rain levels may be inadequate for regeneration.

Cumulative effects may occur gradually or appear once an ecological threshold is reached (i.e., a point at which there is an abrupt change in an ecosystem quality, property, or phenomenon, or where small changes in an environmental driver produce large responses in the ecosystem) (Groffman and others 2006). For example, many riparian areas in Rocky Mountain National Park have historically supported high beaver densities (Packard 1947). When beavers cut willows for dam construction, they closely crop plants to the ground surface. Following abandonment, heavily used sites are generally unsuitable for new beaver occupation until resprouting willows have had an opportunity to grow to sufficient size again to provide enough browse and building materials. However, intense elk browsing can maintain willows in a short stature, reducing the suitability of habitat for beaver (Baker and others 2005a; Mitchell and others 2000). Over time, this has contributed to a decline in beaver populations, altering the basic geomorphic and ecological processes of sites and constraining new willow establishment (Cooper and others 2006; Gage and Cooper 2005; Peinetti and others 2002b).

HRV assessment for high-elevation springs and creeks

Composition and stand structure—Riparian ecosystems associated with small, low-order headwater streams are typically dominated by low-stature, shrub-dominated or herbaceous communities. Vegetation associations vary across the region but are often dominated by herbaceous dicotyledonous species, including *Caltha leptosepala*, *Mimulus guttatus*, *Saxifraga odontoloma*, *Mertensia ciliata*, *Cardamine cordifolia* and *Senecio triangularis*, or monocots such as *Calamagrostis canadensis*, *Glyceria striata*, and *Carex utriculata* (Carsey and others 2003; Walford and others 1997). Woody species may be present in some areas and include the willows *Salix brachycarpa*, *S. wolfii*, and *S. planifolia*, and *Betula glandulosa*. When present, woody species rarely exceed 3.3 ft (1 m) in height.

High-elevation springs and creeks are little altered compared with riparian areas at lower elevations. As a consequence, the species composition and structure of these communities appears to be within the HRV. Other than the presence of exotic plants such as dandelion (*Taraxacum officinale*), high-elevation springs and brooks generally lack invasive plants. Because there is a simple vertical structure of vegetation in pristine communities, no significant changes from the HRV are likely.

Hydrologic regimes—As a class, brooks and streams at higher elevations may represent the most hydrologically intact and unmodified riparian ecosystem types in the region. Springs and brooks are fed largely by snowmelt or groundwater discharge from shallow aquifers—water sources that in many cases are too dispersed, small, and high-elevation to be efficiently exploited by humans in most cases. However, there are notable exceptions, such as Spring Creek on the Grand Mesa National Forest in Colorado, where surface water is diverted for irrigating high-elevation pastures. Other examples of high-elevation diversions of very small streams also occur, often for water supply storage in reservoirs. However, these impacts are localized and most hydrologic variables of interest, such as flood magnitude, duration, frequency, and timing, are likely within the HRV for the vast majority of brooks and small streams.

Woody plant establishment—There is scant information available about the population structure and establishment dynamics of riparian communities along brooks and springs. Many of the woody species that occur in these communities are capable of vegetative reproduction (Cottrell 1993, 1995). Because of the relatively low incidence of physical disturbance compared to lower elevations and lower energy fluvial settings, sexual reproduction is probably episodic. *Salix* spp., while low in stature, can be of significant age, reproducing vegetatively for centuries (Cooper and others 2006). Although there are few data from which to make an assessment, it appears that establishment dynamics are likely within the HRV, except where high native or domestic ungulate use has severely impacted the structure of willow stands.

Fire regimes—Fire regimes in many portions of the region are outside of the HRV, particularly at lower elevations (Dillon and others 2005; Grissino-Mayer and others 2004; Meyer and others 2003; Veblen and Donnegan 2005). However, under natural fire regimes, fire is a rare occurrence in alpine and subalpine areas (Sherriff and others 2001; Sibold and others 2006). As a consequence, the fire disturbance regime appears to be within the HRV for high-elevation brooks and springs.

Beaver abundance—Beavers typically inhabit streams large enough to support their dams and with a sufficient base of suitable plants available for food and dam construction. Total biomass of winter food cache plants, specifically woody species like aspen, willow, and cottonwood, may be limiting in many high-elevation sites (Allen 1983). Beavers do inhabit ponds in subalpine fens but typically at low densities. This suggests that anthropogenic impacts to beaver populations and associated ecological effects were likely smaller than those seen along larger streams and at lower elevations.

HRV assessment for high- to middle-elevation riparian shrublands

Composition and stand structure—Shrub-dominated riparian ecosystems are one of the most distinctive features of middle- to high-elevation valleys throughout the region (Comer and others 2003). Although a variety of plant associations have been described based upon floristics (Carsey and others 2003; Walford and others 1997), ecological processes are generally similar across these types. At the highest elevations, low stature willow stands are common due to the very heavy snow load and are typically dominated by *Salix wolfii* and *S. planifolia*, with herbaceous associates, including *Calamagrostis canadensis* and *Carex aquatilis* (Carsey and others 2003). At lower elevations, community stature typically increases and a different suite of woody species become dominant, including *Salix monticola*, *S. boothii*, *S. drummondiana*, *S. geyeriana*, and *S. bebbiana*. Common herbaceous associates are *Calamagrostis canadensis*, *Heracleum maximum* and *Geum macrophyllum*, and in former beaver ponds, *Carex aquatilis* and *C. utriculata* are common (Carsey and others 2003).

A variety of anthropogenic impacts have placed many middle-elevation riparian shrublands out of the HRV for vegetation composition. At lower elevations, exotic species may be common due to amenable environmental conditions for their spread and greater levels of anthropogenic disturbance. Notable exotics are *Breca arvensis* and a variety of introduced pasture grasses, such as *Agrostis gigantea*, *A. stolonifera*, *Dactylis glomerata*, and *Bromopsis inermis*. Although no invasive woody species occur, non-native species herbs are common in the understory of many riparian communities.

Significant departures from historical conditions have been caused primarily by livestock and high native ungulate population herbivory and trampling. Both can affect vegetation structure by direct browsing of mature plants, reduced recruitment of seedlings due to trampling effects, and complex interactions with beaver, which can result in the conversion of tall (>21 ft) morphotype willows to short (approximately 3.3 ft) morphotype plants that are insufficient for dam creation (Baker and others 2005a,b; Brookshire and others 2002; Peinetti 2000; Peinetti and others 2001; Schulz and Leininger 1990). In addition to ungulate impacts, cover of willows has decreased along many rivers due to direct clearing (Figure 15).

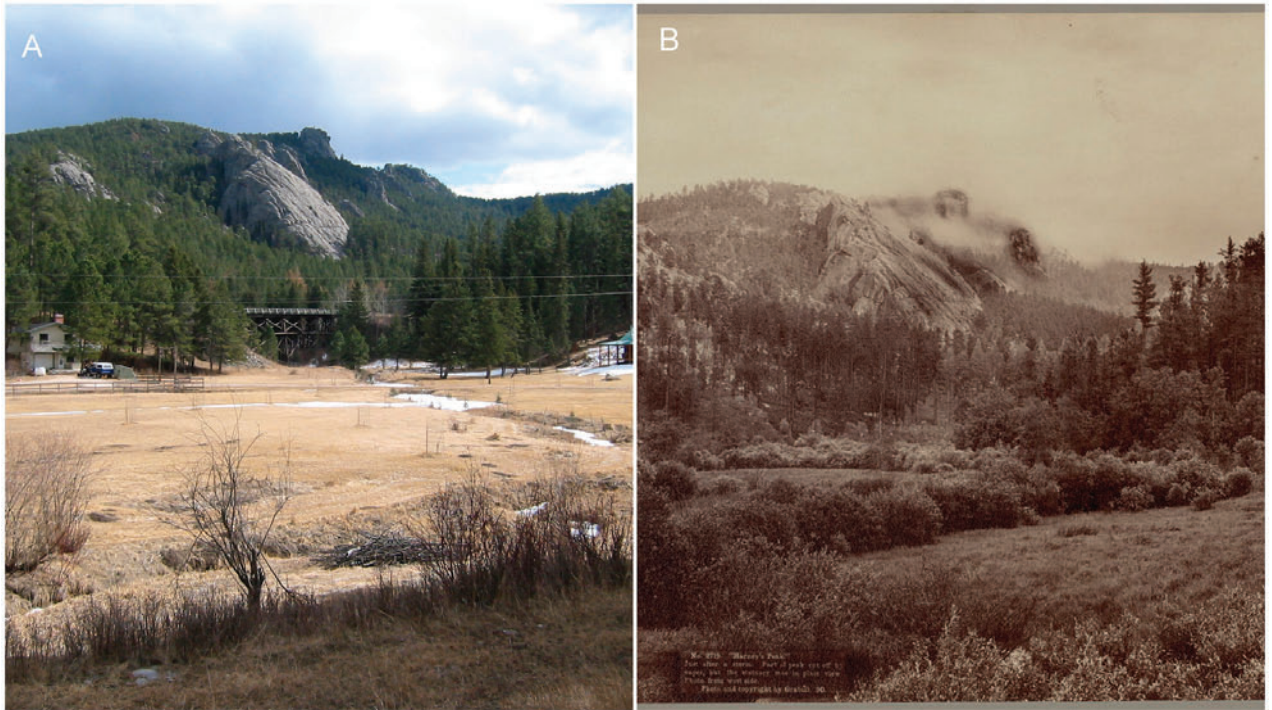


Figure 15— (A) 2005 illustrating changes in willow riparian communities from land use, (B) Tenderfoot Creek, Blackhills, SD, about 7 miles north of Custer, SD., in 1890.

Hydrologic regimes—Hydrologic processes in many high- and mid-elevation riparian areas have been altered by anthropogenic activities and now likely lie outside of the HRV. The primary cause is flow regulation from dams and diversions (Baxter 1977; Nilsson and Svedmark 2002; Pringle 2000; Wohl 2005). A large number of dams occur in mountainous parts of Region 2, although the effects of these hydrologic changes on riparian vegetation are poorly known when compared with riparian vegetation along large, low-elevation rivers. Specific hydrologic effects of these dams vary depending on size and management but can include reduced frequency and magnitude of peak flows increased base flows, and a reduction of flow variability. Reduced beaver populations relative to historical levels have also likely affected the hydrologic functioning of many mid- to high-elevation riparian areas.

Woody plant establishment—The spatial and temporal dynamics of willow and other riparian shrub dynamics are complex. Establishment events can occur regularly along some streams and some landforms, for example, along the margins of meander bends or episodically associated with low frequency event like high magnitude floods, oxbow formation, or beaver dam failure (Cooper and others 2006; Dickens 2003; Gage and Cooper 2005) (Table 15). Because establishment is intimately tied to basic hydrologic processes, changes in hydrologic regimes and beaver populations seen in many portions of the region have likely altered woody plant establishment dynamics, placing them outside of the HRV. More research, however, is needed to understand whether such departures are widespread.

Table 15—Main patterns of willow establishment along the Big Thompson River in Rocky Mountain National Park in relation geomorphic and hydrologic characteristics (Cooper et al. 2006).

Geomorphic process	Landform	Effective flood regime	Willow establishment patterns
Meandering	Point bar	Moderate to high flows (2–5-year return interval flow)	<ul style="list-style-type: none"> • Continuous establishment • Continuous establishment at intermediate elevations above channel
Beaver pond drainage	Abandoned beaver pond	Flood event (>5-year return interval flow)	<ul style="list-style-type: none"> • Periodic establishment prior to dam breach • Brief episodes of widespread establishment following abandonment • Establishment at high elevations relative to active channel
Channel avulsion	Abandoned channel	Moderate to high flows (2–5-year return interval flow)	<ul style="list-style-type: none"> • Continuous establishment over limited period of time (as oxbow fills) • Establishment at low to moderate elevations relative to active channel

Salix spp., and other members of the family Salicaceae such as *Populus* spp., disperse seeds for a brief period in early summer, usually timed to follow peak discharge along snowmelt dominated streams (Gage and Cooper 2005; Karrenberg and others 2002; Moss 1938). These seeds exhibit high initial germinability; however, their viability rapidly decreases over time and if seeds do not reach suitable bare, moist substrates for establishment soon after dispersal, the seed desiccates. Where the timing and magnitude of floods has been altered due to river regulation, willow establishment may be reduced or eliminated.

Excessively high populations of native ungulates have altered establishment dynamics in some areas of the Rocky Mountain region. For example, elk browsing has been identified as a primary cause of willow decline in montane willow carrs in Rocky Mountain National Park (Dickens 2003; Peinetti and others 2001; Peinetti and others 2002a). High densities of elk may reduce opportunities for establishment in several ways. Where elk numbers are high, they may trample or browse nearly all seedlings. In addition, willow aments form in the spring on last year’s stem tissue and browsing that removes young stems eliminates tissue that could bear aments, thereby reducing or completely eliminating seed production (Kay and Chadde 1992). Willow seed rain levels drop off steeply with increasing distance from seed-producing plants and heavily browsed areas have been shown to have seed rain levels two orders of magnitude lower than lightly browsed stands (Gage and Cooper 2005).

Fire regimes—Although fire regimes in riparian areas typically differ in basic characteristics from adjacent uplands, ignitions in riparian areas are rare, so fires must spread from the surrounding landscape (Dwire and Kauffman 2003). Changes in fire regimes in upland forests documented in some portions of the region may have indirectly affected the frequency of fires in riparian areas, pushing them outside of the HRV. However, what little evidence there is suggests that fire's role in mid- to high-elevation shrub carrs is minor, so such changes may not have much consequence for riparian vegetation communities. Wolf (2004) found that the 1988 fires in Yellowstone National Park triggered the largest willow recruitment event during 1989 in recent decades, likely due to upland erosion and sediment deposition in riparian areas.

Beaver abundance—Beaver are keystone species in middle- to high-elevation shrublands, strongly influencing shrubland structure and function (Naiman and others 1988). Beavers utilize willows for food and dam building and can significantly affect the structure of riparian communities, reducing *Salix* spp. stature and favoring non-preferred woody species like *Betula occidentalis*. However, their greatest effect on riparian communities is a result of their modification of hydrologic regimes. Beaver dams can inundate large areas of floodplains, significantly affecting biogeochemical processes, sediment dynamics, and groundwater flow patterns. For example, Westbrook and others (2006) found that a beaver dam complex on the Colorado River influenced the surface inundation, groundwater levels, and groundwater flow patterns over a greater area and for a longer duration than a flood with a 10-year recurrence-interval when the dam was absent.

Historically, beaver would likely have occurred in nearly all major drainages supporting riparian shrublands. Most of these watersheds were affected by beaver trapping in the Nineteenth Century, and while populations have recovered in some areas, overall numbers are still well below historical levels (Wohl 2001). Thus, it is likely that measures related to beaver, such as the density of beaver and beaver ponds, is likely outside of the HRV for many watersheds in the region.

HRV assessment for high-gradient riparian forests at medium elevations

Composition and stand structure—Forested riparian communities dominate streams in subalpine and montane areas of the region, particularly along higher-gradient reaches with narrow channels (Peet 1981). Although specific vegetation types vary with elevation and latitude, riparian areas throughout the region share similar structural and functional characteristics.

In subalpine areas, dominant overstory species include conifers that are typical of the surrounding upland forests, including *Abies lasiocarpa* and *Picea engelmannii*, and deciduous species such as *Populus tremuloides* (Peet 1981). Although overstory dominants may not significantly differ from surrounding forests, these riparian forests typically support hydrophytic or mesophytic shrubs not found outside of riparian zones, including species of *Salix* and *Alnus*, as well as herbaceous species such as *Mertensia ciliata* (Carsey and others 2003). In lower elevation montane areas, overstory dominants include *Populus angustifolia* and, in the southern part of the region, *Picea pungens*.

In general, mountains have fewer non-native plants than lowland areas, perhaps due to the greater prevalence of National Parks and Forests, which have had less intensive land uses compared with agricultural and urbanized landscapes (Parks and others 2005). However, exotic species can be locally abundant, particularly where sites have been disturbed. The most common exotics are introduced pasture grasses such as *Phleum pratense* (Carsey and others 2003) and widely distributed herbaceous dicots such as *Taraxacum officinale* and *Verbascum thapsus* (Carsey and others 2003; Parks and others 2005). These species may contribute minor cover and, unlike lower-elevation riparian ecosystems, no exotic tree or shrub species occur in montane or subalpine riparian forests. As a consequence, most riparian forests are likely within the HRV for most measures of species composition, although the lack of vegetation composition data for pre-Euro-American periods reduces our confidence in this assessment.

We found little evidence to suggest that the age and size structure of communities is outside of the HRV for most Region 2 riparian forests, although the lack of research conducted along montane and subalpine streams prevents us from making definitive conclusions. Certainly, structure in areas that are subject to more intensive anthropogenic impacts, such as logging or tie-drives, may have pushed conditions outside of the HRV for specific areas (Wohl 2005). Likewise, where streams have been highly modified by flow regulation, altered woody plant establishment and recruitment may have resulted in stand and age structures outside of the HRV. Areas subjected to intense grazing by livestock brought to the Rocky Mountains to support the burgeoning mining population (Veblen and Donnegan 2005) may also exhibit compositional or structural differences from historical conditions. In general, contemporary stocking rates are well below those seen at the peak of grazing in the early-Twentieth Century, so many areas that were degraded in the past may have recovered.

For forest communities in narrow valley settings, age and size structure may be driven in large part by disturbances that originate outside of the riparian zone such as fire and flooding. Thus, where altered landscape disturbance regimes have pushed upland forests outside of the HRV, the structure of riparian communities may also be affected. This is more likely to be the case in lower elevation areas that historically had more frequent fires than in the subalpine, where pre-Euro-American fire return intervals were low (Aplet and others 1988; Dillon and others 2005; Sherriff and others 2001; Sibold and others 2006; Veblen and Donnegan 2005).

Hydrologic regimes—Montane and subalpine forests experience seasonal floods driven by spring snowmelt, although peak flows may also occur following convective summer thunderstorms. Such storms are particularly prevalent in the southwest portion of Region 2 (Baker 1990; Fleener 1997). Many mountain streams, particularly at high elevations, are gaining with respect to groundwater. Consequently, vegetation may be only weakly dependent on surface water levels in streams. The importance of flood regimes on vegetation dynamics may be linked more to flood influences on processes of plant establishment. Here, high magnitude, low-frequency events are of primary importance, as only these have sufficient power to create disturbance patches important for seed germination of species like willows (Karrenberg and others 2002).

Although most research and discussion on river regulation has occurred on large rivers, many small to moderate sized streams have also been modified (Pringle 2000). The hydrologic regimes of many streams have been pushed outside of the HRV (Richter and others 1996). Effects include reductions in the magnitude of peak flows, reduced mean flows, altered flood timing, and changes in water thermal characteristics (Baxter 1977). Specific effects differ as a function of a variety of factors, such as the size and location of the dam or diversion, the hydrologic characteristics of the impacted stream, and management characteristics including the seasonality of water releases and diversions.

Woody plant establishment—The greatest impact of flow regulation on montane and subalpine riparian forests is likely through effects on woody plant establishment. Although little research has been conducted on woody plant dynamics in montane riparian communities, the existing studies suggest that establishment is episodic. In southwest Colorado, Baker (1990) found that stands of *Populus angustifolia* originated in ten to thirteen discrete periods between the mid-Nineteenth and late-Twentieth Centuries (Baker 1990).

Years with high seedling establishment may be associated with broad scale climate factors. For example, Baker (1990) identified winter conditions in the North Pacific and a persistent late summer Arizona monsoon as important variables in the establishment of *Populus angustifolia* in southwest Colorado. His models suggested that good seedling years occurred more frequently (approximately every 3.4 years) than stand-origin years (approximately 10-15 years) and that good seedling years and stand-origin years were more common from 1848 to 1985 than from 1556 to 1848 due to more frequent cool, wet years since 1848 (Baker 1990).

A variety of studies have examined the flow requirements for the establishment of cottonwood species, including *Populus angustifolia*. Along smaller montane streams and relatively large semi-arid rivers, only floods of sufficient magnitude can create nursery sites for seed germination and they must be timed before seedling release (Mahoney and Rood 1998; Samuelson and Rood 2004). In addition, it is critical for both *Salix* spp. and *Populus* spp. establishment that sufficient soil water is available through the summer to prevent drought-induced mortality (Gage and Cooper 2004a; Kranjcec and others 1998; Woods and Cooper 2005).

Fire regimes—Fire regimes in many portions of the region are outside of the HRV, particularly at lower elevations with relatively active historical fire regimes (Dillon and others 2005; Grissino-Mayer and others 2004; Meyer and others 2003; Veblen and Donnegan 2005). Fire regimes in riparian areas, particularly narrow, forested ones, are driven by the fire regimes in surrounding landscapes (Dwire and Kauffman 2003). Where significant departures from the HRV of upland fire regimes have occurred, they have likely also affected riparian areas.

Beaver abundance—As detailed elsewhere in this assessment, changes in beaver abundance are one of the primary anthropogenic impacts forcing riparian ecosystems outside of the HRV. However, beavers typically favor streams with gentle gradients and in wide valley settings (Allen 1983); thus, it is likely that historical levels of beaver were low to begin with in the high gradient riparian forests at middle and high elevations. As a result, current beaver densities may be within the HRV for most streams, although departures from the HRV have likely occurred in some individual streams.

HRV assessment for low-gradient riparian forests and shrublands and middle and low elevations

Composition and stand structure—Because of the varied hydrologic regimes and geomorphic settings characterizing low-elevation riparian ecosystems in the region, there is considerable diversity among riparian forest and shrub communities. Native overstory dominants vary, but typically include species such as cottonwoods (*Populus deltoides* in the Great Plains, *P. fremontii* west of the continental divide, and *P. balsamifera* ssp. *trichocarpa* in the northern portion of the region) and willows (*Salix exigua*, *S. goodingii*). A variety of other native tree and shrub species in a number of genera may be present including *Fraxinus*, *Quercus*, *Ulmus*, *Chrysothamnus*, *Symphoricarpos*, *Amelanchier*, *Rhus*, *Cornus*, *Prunus*, *Shepherdia*, *Rosa*, *Sarcobatus*, and *Purshia* spp. (Carsey and others 2003; Comer and others 2003b). Herbaceous components vary as well depending on particular vegetation association.

Compositionally, many of the riparian areas in this group are outside of the HRV due to the presence of non-native species. For example, *Tamarix* spp. and *Elaeagnus angustifolia* are widespread throughout the region, occurring along streams of all sizes and flow regimes (Di Tomaso 1998; Friedman and others 2005; Lesica and Miles 2001; Pearce and Smith 2003; Stein and Flack 1996). These two species represent the third and fourth most frequently occurring woody riparian plants along low-elevation streams in the West (Friedman and others 2005). Exotic herbaceous species are also common and range from non-native pasture grasses that were purposely introduced such as *Poa pratensis* and *Bromopsis inermis*, to noxious weed species such as *Bromus tectorum*, *Euphorbia* spp., and *Breca arvensis* (DiTomaso and Healy 2003; Whitson and Burrill 2000). As an example of the near ubiquity of exotic species along low-elevation rivers, exotic species comprised one-third or greater of all species observed in plots

along both a regulated and unregulated river in northwest Colorado (Uowolo and others 2005). The rapid spread of exotic shrubs along rivers, upwards of approximately 20 km/year (Graf 1978), has been attributed to several factors. For example, *Tamarix* produces abundant, viable, aerially dispersed seed, and vast numbers of seedlings may occur in suitable habitat; these occupy similar habitats as cottonwood and willow.

In general, exotic species richness is greater in more species-rich communities (Stohlgren and others 1999; Stohlgren and others 1998). For example, 63 percent of the variance in exotic species richness was explained by a positive relationship with native species richness along the Green and Yampa Rivers in Northwest Colorado (Uowolo and others 2005). However, results of that study did not indicate that river regulation increased the probability of invasion in contrast to studies conducted in other regions (Decamps and others 1995). Overall patterns of species richness differ among age classes within and between regulated and unregulated rivers. Along both kinds of rivers, species richness was greatest in the youngest age classes and declined as stand age increased (Uowolo and others 2005). Thus, major changes in age structure of riparian communities may indirectly affect diversity at landscape scales.

In addition to non-native species, changes in hydrologic regimes have allowed the invasion of flood-intolerant shrub species into riparian communities. For example, Merritt and Cooper (2000) described channel narrowing processes along the regulated Green River in northwest Colorado (Figure 16) and noted the increasing presence of flood-intolerant species such as rabbitbrush (*Chrysothamnus nauseosus*) and greasewood (*Sarcobatus vermiculatus*). These shrubs are highly sensitive to soil saturation (Groeneveld and Crowley 1988) and are only able to survive because of the elimination of high peak flows (Merritt and Cooper 2000; Williams and Cooper 2005).

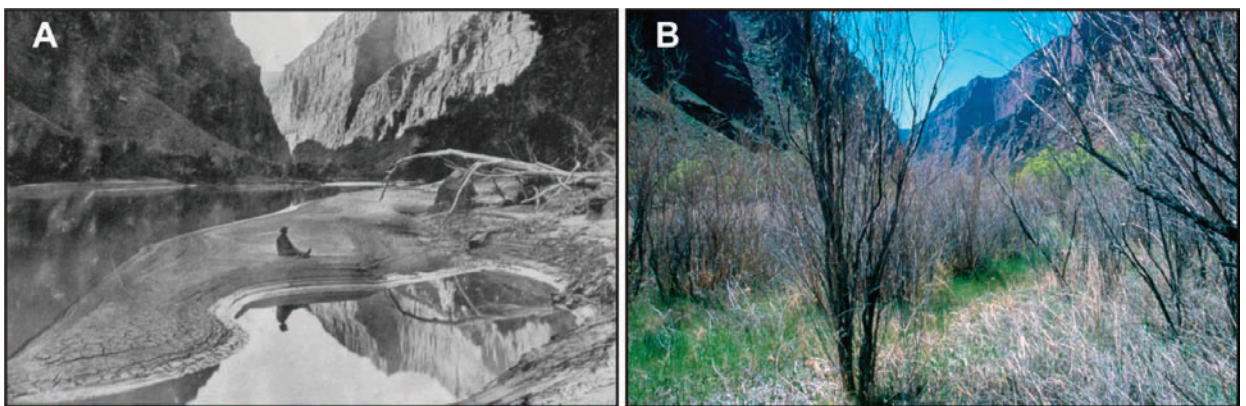


Figure 16—Images of Lodore Canyon in 1870 (A) and present (B) illustrating vegetation changes driven by *Tamarix* invasion.

The vertical structure of many low-elevation riparian communities in Region 2 is also outside of the HRV due to changes in canopy height, architecture and spatial arrangement. The invasion and increasing dominance of exotic shrubs like *Tamarix* spp. and *Elaeagnus angustifolia* have altered the structure of many riparian communities, resulting in closed canopy stands that are more dense than native stands thereby reducing light to the forest floor and suppressing seedlings of full-sun plants like *Populus* spp. (Cooper and others 1999). In addition, the widespread failure of native species to regenerate due to factors such as river regulation (Rood and others 1995) has altered the structure of riparian communities (Cooper and others 1999; Shafroth and others 2002; Williams and Cooper 2005).

Where extreme reductions in peak flow, river stage, floodplain water table levels, and soil water recharge occur, severe water stress may develop in riparian trees, causing the dieback of leaves, branches, and roots in the upper soil profile as well as plant mortality (Amlin and Rood 2003; Williams and Cooper 2005). The sacrifice of branches appears to be an adaptive response to drought, improving the water relations of remaining branches as leaf area adjusts to available water (Horton and others 2001; Rood and others 2000, 2003a). Xylem cavitation and increased stomatal closure followed by leaf senescence and branch death has been reported for *Populus deltoides* and *P. fremontii* in response to drought; however, *P. trichocarpa*, *P. angustifolia*, and *P. balsamifera* experience the patchy summer branch senescence typical of *P. deltoides* and *P. fremontii* less frequently (Rood and others 2000).

Changes in root distribution and abundance have also been documented along regulated rivers. For example, Williams and Cooper (2005) reported that *Populus fremontii* root density was highest at depths of 2.5 to 4.9 ft (0.75 to 1.50 m) along the unregulated Yampa River versus 5.7 to 7.4 ft (1.75 to 2.25 m) along the regulated Green River. They also found that the density of roots in the upper 7.4 ft of soil was more than double at the unregulated than the regulated site. In the unregulated site, the soil depths with the highest root density corresponded to the average peak water table elevation for the previous 10 years and where loam-textured soil layers with high water-holding capacity occurred, while the vertical distribution of roots at the regulated site was relatively uniform with depth (Williams and Cooper 2005).

In addition to reach-scale changes in structure due to factors such as grazing, *Tamarix* spp. invasion, and poor *Populus* spp. regeneration, the landscape structure, including the size and distribution of any low-elevation riparian systems has changed relative to historical conditions. Many riparian forests are highly fragmented due to the effects of land use changes (Table 16). In many areas, the average patch area of riparian forests has declined along larger rivers.

Table 16—Proportions of the floodplains in each of seven land cover categories—Cottonwood Forest (C), Agriculture (Ag), Industry (I), Roads (Rd), Urban (U), Open Water (W), and Other (O)—delineated by Northcott et al. (2006) for the Upper Colorado River Basin.

Mainstem river	River regulation regime	Proportion of total floodplain area in land cover category (%)							Proportion of floodplain area developed (%)
		C	Ag	I	Rd	U	W	O	
White	0	58	32	1	0	0	0	7	34
San Miguel	0	60	22	6	1	5	1	5	34
Yampa	0	19	52	0	0	0	0	29	52
Lower Dolores	1	38	4	0	0	0	0	48	28
Lower Colorado	1	61	30	3	0	0	0	7	33
Upper Colorado	1	47	31	14	2	3	0	3	50
North Fork of the Gunnison	1	39	51	8	1	1	0	2	60
Lower Green	1	38	27	0	0	0	31	3	60
Upper Dolores	2	40	5	0	0	0	0	55	5
Upper Green	2	70	4	0	0	0	19	7	23

Hydrologic regimes—The hydrologic regimes of low-elevation riparian ecosystems have been significantly altered by flow regulation, and many hydrologic variables are now outside of the HRV (Patten 1998; Rood and Heinze-Milne 1989; Williams and Cooper 2005). Nearly all major rivers in the region have been dammed, altering the natural flow regimes (Graf 1999; Patten 1998; Poff and others 1997). Intermittent and ephemeral drainages have also been impacted by dams, although not as systematically as perennial rivers. Many of these streams have had dugouts or livestock impoundments created in-channel to intercept flows (Smith and others 2002).

Multiple examples of hydrologic effects of flow regulation on riparian communities can be found across the region. For example, reduced magnitude and frequency of floods and an increase in base flow levels has been documented along the regulated Green River, reducing overall flow variance and leaving soils on former floodplains in a state of perpetual drought. These changes have facilitated the invasion of drought-tolerant exotics such as *Tamarix* spp. and flood intolerant species such as rabbitbrush, and they have hastened the decline of mature *Populus* spp. trees on floodplains and allowed for the development of marsh communities on bars (Merritt and Cooper 2000). Along the Platte River, reductions in peak flow (Figure 17) have initiated channel adjustments, including narrowing of the river, which is correlated with the expansion of riparian forests relative to historical conditions (Johnson 1994).

Groundwater pumping has impacted cottonwood forests in some areas. Groundwater pumping can reduce water table depths, resulting in severe drought stress, branch cavitation and dieback, and, in some instances, tree death. Along the South Platte River in Colorado, *Populus deltoides* trees responded to abrupt alluvial water table decline with decreased shoot water potential followed by leaf mortality (Cooper and others 2003c). Xylem pressure potentials in stems and rates of leaf loss were significantly related to the magnitude of water table declines, and impacted trees experienced crown dieback caused by xylem cavitation (Cooper and others 2003c).

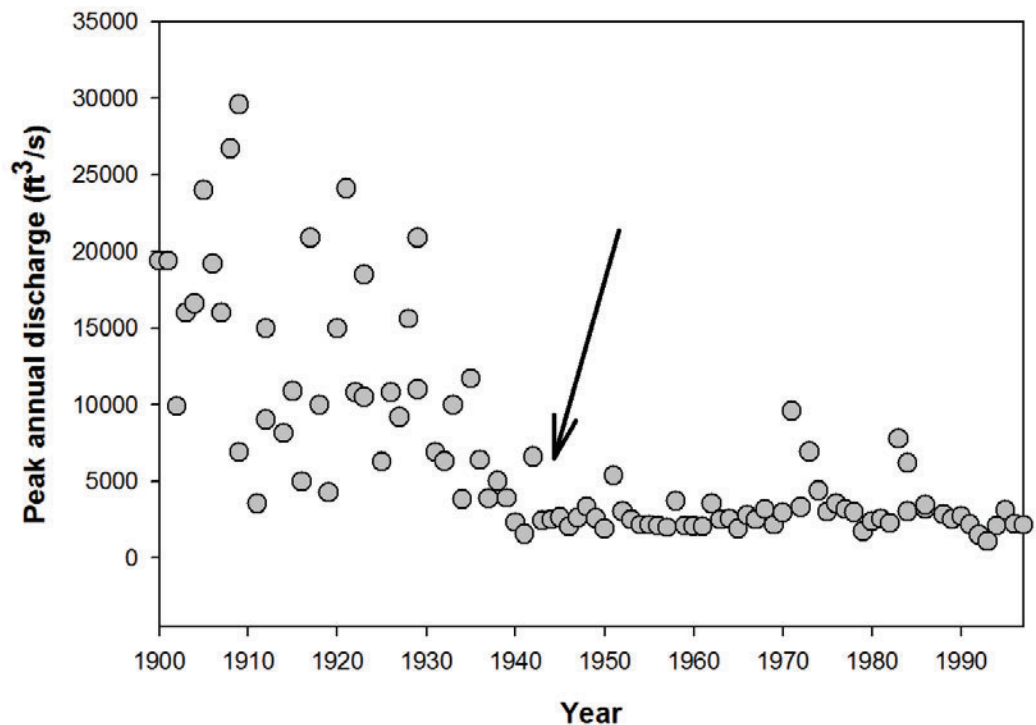


Figure 17—Instantaneous peak flow at North Platte River at North Platte, NE (USGS gauge #06693000). Note the sharp decrease in flow variability and peak flow magnitude following 1940.

Vegetation establishment and successional dynamics—Several conditions must be met for cottonwood and willow establishment, including: the presence of suitable substrates for seed germination, adequate levels of seed rain, and sufficient soil moisture during the late summer months when seedlings are vulnerable to water stress (Amlin and Rood 2002; Cooper and others 1999; Sacchi and Price 1992). Although cottonwood seedlings can appear over a wide elevational gradient following a flood event, seedlings may require three to four years to grow roots to the late summer water table, during which they are susceptible to mortality from desiccation (Cooper and others 1999). In addition, floods in the years following initial seedling establishment can influence patterns of seedling recruitment into successive age and size classes. For example, very high peak flows in the years immediately following seed germination may wash away seedlings in low topographic positions.

The timing of dispersal of cottonwood and willow seeds is also critical. Seed dispersal typically coincides with the timing of peak snowmelt-driven floods, which, for many rivers, occurs in late May to early June. Although the viability of seed is usually very high (Cooper and others 1999; Gage and Cooper 2004a), viability rapidly drops following dispersal; thus, these species form no soil seed bank. Where flow regulation has altered the timing of floods, establishment may be constrained due to a lack of synchrony between dispersal and the availability of suitable substrates for seed germination.

Some life history characteristics of exotics may influence their spread along many rivers. For example, *Tamarix* spp. produces seed for a longer proportion of the summer than cottonwoods and willows (Cooper and others 1999). These characteristics along with the species' greater drought and salt tolerance relative to native woody plants, have allowed *Tamarix* spp. to thrive, particularly along rivers where climate change and flow regulation have altered flood regimes.

Establishment dynamics of woody riparian species are complex and vary naturally among species and rivers. Establishment events can be either gradual or episodic, resulting in the varied age and size structures often seen in riparian communities. For example, cottonwood establishment can occur associated with the formation of point bars along meandering channels in an incremental process dominated by moderately high flows occurring every few years (Shafroth and others 1998) (Figure 18). Where establishment occurs in such a fashion, stands may develop with relatively varied age and size structure along a given stream reach (Johnson and others 1976; Merritt and Cooper 2000). Along meandering channels, the rate of meandering directly influences the relative abundance and spatial distribution of the bare sites required for *Populus* spp. and *Salix* spp. seed germination (Bradley and Smith 1986; Johnson 1994). In contrast, establishment along ephemeral streams may more closely match the history of extreme floods (Friedman and Lee 2002). Because of the dependency of many riparian species on floods for establishment, establishment dynamics on regulated rivers are typically outside of the HRV (Cooper and others 1999; Katz 2001; Nilsson and Svedmark 2002; Stromberg 1998).

Vegetation dynamics along low-gradient riparian ecosystems at low and intermediate elevations can be complex, with a variety of physical and biological factors influencing community development and successional patterns. Fluvial processes are central in creating the bare alluvium required for cottonwoods and willows to establish from seed (Karrenberg and others 2002); although once established, the specific successional trajectory of stand can vary.

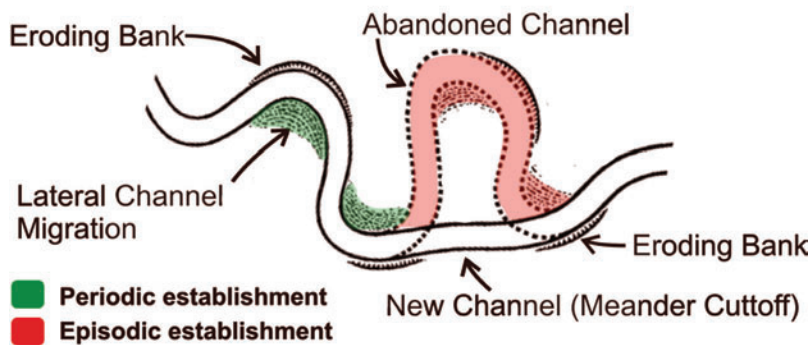


Figure 18—Schematic illustrating processes of lateral channel migration and meander cutoff (modified from Richter and Richter 2000). Establishment of cottonwoods and willows may occur more regularly as a consequence of channel migration and point bar formation (green areas), as new sites for establishment are created by the erosion of stream banks on the outsides of meander bends and the deposition of transported sediments on point bars. Rare events, such as channel abandonment or beaver pond failure, may open large areas of suitable substrate for establishment, allowing for the formation of large cohorts of seedlings (Cooper and others 2006; Westbrook and others 2006).

Richter and Richter (2000) developed a model to describe the development and successional dynamics of *Populus angustifolia* communities along the Yampa River in Colorado (Figure 19). In addition, their model includes a variety of shrub and herbaceous communities, which may co-occur as distinct patches on the landscape. Hydrologic regime, including both flooding and water table dynamics, is the key determinant of the particular patch types and their relative abundances on the landscape. Although this model was developed for the Yampa River, the model's overall structure is more widely applied. The specific patch types and transitions vary depending on factors such as river size, flood regime, regional floristic composition, and elevation. Along intermittent and ephemeral streams, fluvial marsh patches are not present in the model, while xeric communities may be important components.

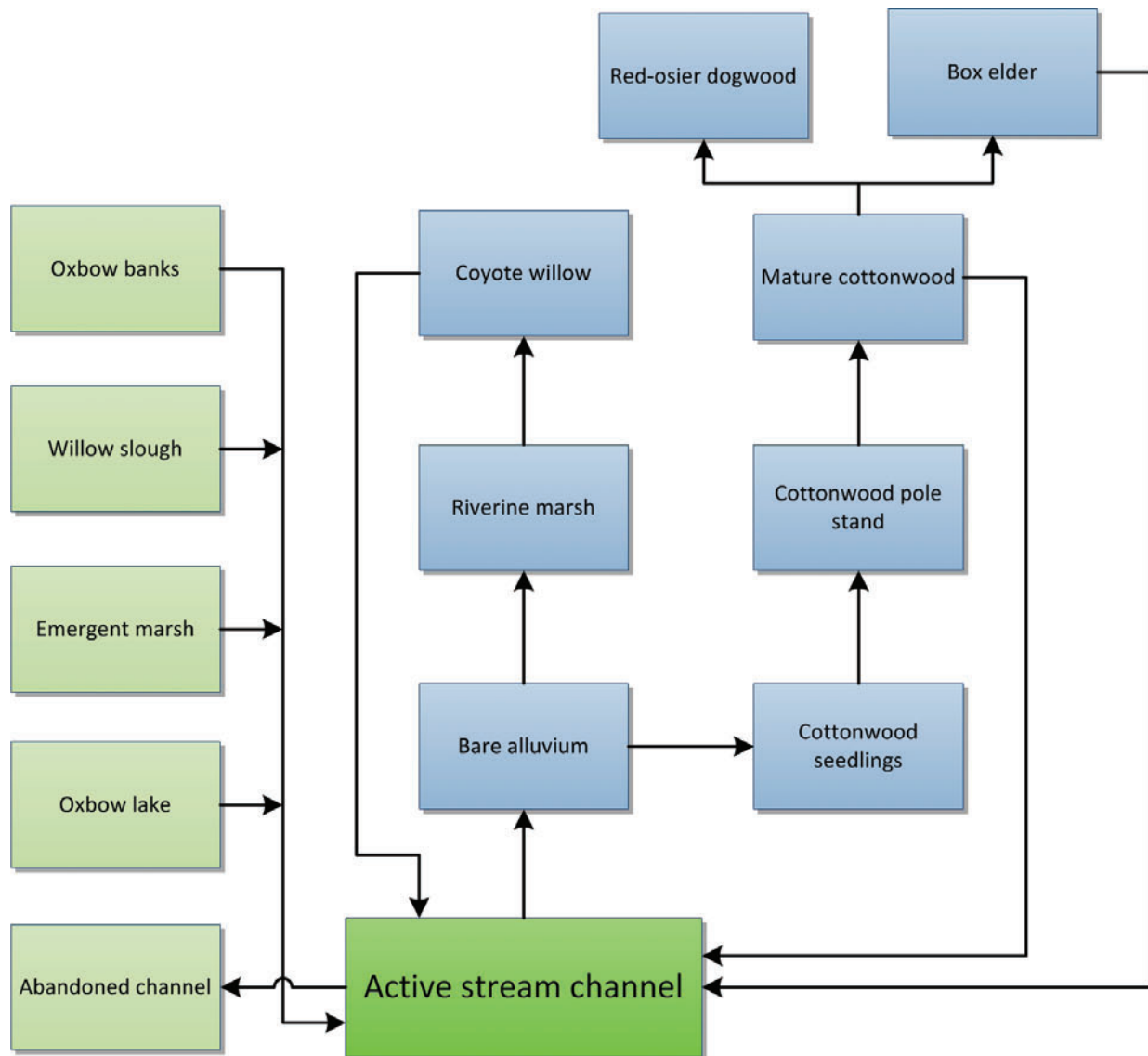


Figure 19—Flow chart illustrating a conceptual model of riparian patch succession and woody plant establishment along the Yampa River (re-drawn from Richter and Richter 2000).

Because floods are the main disturbance agent creating conditions for new *Populus* spp. establishment, the frequency and magnitude of floods are central to the successional dynamics of lowland riparian areas. Along unconfined alluvial rivers, geomorphic processes such as channel meandering are also important; as channels migrate across floodplains, cottonwood patches may become isolated from the physical effects of flooding and stands may persist throughout succession, ultimately forming late-successional cottonwood gallery forests (Johnson and others 1976; Stromberg 1997). As a result, stands with a range of ages may be present at any given time across a gradient from channel margin to high floodplain surfaces (Lyttle and Merritt 2004).

At broad scales, hydrologic and geomorphic processes are influenced by watershed characteristics such as watershed size, vegetation cover, and land use. These characteristics explain, in part, differences in vegetation dynamics among rivers. Three ephemeral stream types, based on basin and flow characteristics, were identified in Arizona (Shaw 2006). Type I streams drain small watersheds, are highly vulnerable to flood disturbance, and have xeric alluvial groundwater regimes. Streams of this type are typically occupied by upland plant associations. Type II streams have larger watersheds, more moderate shear stresses, more persistent alluvial groundwater, and support a mix of upland and mesophytic riparian species such as cottonwoods. Type III reaches drain large watersheds and have hydrologic regimes driven mainly by upstream hydro-climatic conditions. These streams have the lowest bankfull shear stresses and perennial water tables that span expansive floodplains and support riparian tree and shrub communities (Shaw 2006).

Channel narrowing has occurred along many regulated rivers, altering geomorphic and hydrologic characteristics and vegetation. As vegetation becomes established in the active channel, plants may facilitate sediment accretion by increasing hydraulic roughness and increasing sediment deposition rates. Such changes may accelerate the establishment of exotic species, as has been suggested for the lower Green River (Allred and Schmidt 1999; Graf 1978; Merritt and Cooper 2000). Although *Populus* spp. have been declining along many rivers that are experiencing channel narrowing, narrowing has been linked to the expansion of *Populus deltoides* forests along the Platte River (Johnson 1994).

In addition to flow regulation, cottonwood regeneration rates are typically reduced in areas subject to intense human activities such as land clearing associated with agriculture. For example, Northcott and others (2006) found that the widespread anthropogenic development of riverine floodplains in the upper Colorado River basin may be as significant of a factor in the low levels of *Populus* spp. regeneration observed throughout the region. The authors found that the likelihood of young *Populus fremontii* cohorts along floodplains was reduced by 65 percent by development (Northcott and others 2006), and they suggested that riparian forests may also be in jeopardy along unregulated rivers.

Fire regimes—Altered fire regimes in upland areas have likely pushed riparian fire regimes outside of the HRV for some streams, although little research has been directed to the question. Structural and composition changes in riparian vegetation (e.g., *Tamarix* spp. invasion) have also likely altered the dynamics of fire in many low-elevation riparian areas (Busch and Smith 1993; Di Tomaso 1998). However, any changes are likely highly coupled to changes in upland fire regimes and are expected to vary widely across the region.

Beaver abundance—The widespread trapping of beaver impacted low-elevation streams as well as higher mountain ecosystems. Slow recovery of populations in many portions of the region suggests that population densities may still be outside of the HRV in some areas. However, the effects of such changes on riparian area function is poorly understood along larger rivers where beavers do not build dams but rather den in river banks (Breck and others 2001, 2003).

Management Opportunities and Constraints _____

Management opportunities

As knowledge of the impacts and threats to riparian resources has increased, so too have opportunities for improved management. However, more area-specific research is needed to improve our understanding of the abundance, distribution, and condition of riparian areas at the scale of individual National Forests. By developing a more thorough accounting of the kinds of historical and contemporary impacts affecting a given stream, specific management prescriptions can be developed.

Because so many riparian areas are functionally impaired, many opportunities exist for restoring and enhancing riparian areas in the region. The scientific foundation of riparian restoration has improved over the years, and guidance can be found for many of the specific riparian types in Region 2 (Allen and others 1997; Hughes and others 2005; Hughes and Rood 2003; Rood and others 2003b; Wohl 2005). However, there are many constraints that limit management and restoration options. The prior appropriation doctrine governing water allocation in states like Colorado has not traditionally recognized in-stream flows for ecological purposes. Societal demands for water associated with regional population growth are likely to increase as are periods of increased scarcity resulting from climate change (Baron and others 2002; Patten 1998; Pringle 2000).

A broad goal should be to identify systems where ecological integrity is relatively intact and develop means to ensure the protection of these ecosystems as centers of natural biodiversity, management models, and benchmarks for future ecological research (Frissell and Bayles 1996). Broad-scale inventories of riparian area condition can identify sites where dams or diversions are present but are unneeded or inefficient. There are numerous small earthen dams in high basins

throughout the region (Pringle 2000), many of which occur on Federal lands. Built early in the period of Euro-American settlement, many of these have functionally been replaced by larger engineering structures downstream and may be ideal candidates for removal.

More quantitative analyses of flow regimes on regulated and unregulated rivers are needed. Richter and others (1996) provided a useful framework for such analyses, using specific indicators of hydrologic alteration based upon available hydrologic data from existing measurement points such as stream gauges or model-generated data in which 32 parameters, organized into 5 groups, are used to statistically characterize hydrologic variation within each year. These metrics can be used to evaluate the effects of hydrologic perturbations associated with activities such as dams and stream diversions (Richter and others 1996). Application of an objective, quantitative approach to characterizing anthropogenic impacts to riverine systems would provide an effective tool for identifying impaired systems and prioritizing restoration activities.

Restoration

Due to the high connectivity of streams and riparian ecosystems, impacts from dams can impact riparian areas distant from the source of the impact. Riparian restoration, even of small sites, requires a watershed approach (Wohl and others 2005). Restoration conducted in a watershed context demands critical examination of geomorphic and hydrologic processes and vegetation at multiple scales. Harris and Olson (1997) describe four key spatial scales relevant to riparian restoration: (1) the entire stream and its associated floodplain; (2) the stream reach; (3) the plant community; and (4) the specific site (physical setting). Different actions can be taken at each of these scales to improve riparian area condition and function. For example, at the broadest scales, management of flows along regulated rivers can be improved to better mimic historical flow characteristics. At intermediate and fine spatial scales, a variety of approaches can be taken to identify good sites for restoration. O'Neill and others (1997) used a GIS and color-infrared aerial photographs to evaluate sites for restoration potential on the Arkansas River in Colorado. The authors found that at the reach scale, specific stream power was a useful index for discriminating between high-energy reaches with low restoration potential and low-energy sites with high restoration potential (O'Neill and others 1997).

GIS analyses in conjunction with field data collection have been used elsewhere to evaluate the degree of impact to riparian ecosystems and to identify restoration candidates (Russell and others 1997). For example, Northcott and others (2006) used GIS and aerial photo analyses to evaluate the regeneration of *Populus fremontii* forests along the upper Colorado River basin in relation to land use and river regulation. Such approaches may be useful in other watersheds.

Because of the many physical and biological variables important to riparian area structure and function, data must be collected and incorporated into restoration plans. Particularly important elements are identification of the geomorphic and hydrologic characteristics of impacted streams and, where available, reference streams. Failure to properly characterize hydrologic regimes is perhaps the single greatest cause of failure in river restoration (Kondolf 1998; Kondolf and Micheli 1995; Wohl and others 2005).

Flow regulation represents the single greatest anthropogenic impact to riparian ecosystems; thus, where possible, decommissioning unnecessary dams and diversions should be pursued. However, because of the increasing demands on water resources forecasted for the region, wide-scale decommissioning of dams is unlikely. Improving management of flows for riparian communities may represent a more achievable approach to restoring desired ecological characteristics back into the HRV. The use of controlled releases from dams to mimic historical floods has been conducted on several large rivers, with the principal goal of improving the viability aquatic and riparian ecosystems, particularly endangered fish.

An example is the controlled release from Flaming Gorge reservoir in 1999. High snowmelt runoff down the Green River filled Flaming Gorge Reservoir and necessitated a controlled release, which had a maximum discharge (10,948 ft³/s) that closely approximated the pre-dam mean annual peak flow and was the second highest flow since dam completion. Controlled releases have also been conducted on the Colorado River below Glen Canyon dam with some success (Patten and others 2001; Schmidt and others 2001). For example, a seven-day experimental controlled flood was conducted at Glen Canyon Dam in 1996; peak discharge was limited to 44,991 ft³/s, lower than pre-dam spring floods. Rood and others (2003) describe a restoration program along the Truckee River—aimed at halting the collapse of the Federally endangered cui-ui sucker (*Chasmistes cujus*), an endemic fish species—in which flows were increased during the spring to permit fish spawning. The higher flows were successful at increasing fish reproduction and resulted in extensive *Populus fremontii* and *Salix exigua* seedling recruitment. These results suggest that instream flow regulation can promote ecosystem restoration along other dammed rivers worldwide (Rood and others 2003b). Where water table decline rates can be made to mimic natural recession, establishment of native woody plant seedlings may be achieved (Auble and others 1994; Mahoney and Rood 1998; Rood and others 1998; Shafroth and others 1998).

Other factors that need to be addressed in restoration design are herbivory from livestock and native ungulates. Either can represent a significant limitation to restoration success unless addressed, for example, through the construction of exclosures (Brookshire and others 2002; Elmore and Kauffman 1994; Gage and Cooper 2004b; Opperman and Merenlender 2000). Population control of unnaturally high ungulate populations or modification of behavior through the reintroduction of predators may be a successful element of riparian restoration in some areas (Beschta 2003; Ripple and Beschta 2003).

Future research—Although some topics in riparian ecology and associated disciplines like fluvial geomorphology and hydrology have been extensively studied, there are many topics for which little information has been collected. For example, while requirements for low-elevation *Populus* spp. establishment are well known, little research has been directed towards establishment dynamics of high-elevation willow carrs. Although studied for some species (Amlin and Rood 2001, 2002), more information regarding tolerable rates of water-table decline and flood depths is needed for many species. Where economic and political constraints allow, controlled releases from dams should be more extensively studied. Also unknown for many riparian community types is the minimum flow needed to promote establishment of native woody species. Such information would be useful for managers addressing riparian ecosystems in developing flow management.

We also need a better understanding of the effects of diversions on small order streams. Do plants respond differently to flow diversion along gaining versus losing streams? How do communities respond to small versus large impoundments? Although it has been the focus of some studies (Dominick and O'Neill 1998; Henszey 1993), relatively little work has been done on the effects of flow augmentation. Hyporheic flows have been shown to affect cottonwood growth (Harner and Stanford 2003), but little is known about their effects on other native or exotic woody species.

Many studies have examined the effects of native ungulates on willows (Brookshire and others 2002; Manoukian and Marlow 2002; Maschinski 2001; Singer and others 1994; Zeigenfuss and others 2002), although most have been conducted on low- and mid-elevation community types. Less is known about effects on willows at higher elevations. Also poorly understood are the effects of moose on woody shrubs. Much of the existing literature regarding native ungulate effects involve elk (Baker and others 2005a; Baker and others 2005b; Peinetti and others 2001; Ripple and Beschta 2004; Singer and others 1998).

Management constraints

The prevalence of hydrologic changes to streams is probably the single greatest factor impacting riparian areas in the region, and represents the greatest constraint on managing rivers for ecological function. Despite greater recognition of the ecological impacts of dams and diversions by scientists, forecasts of future population growth and water demands make wide-spread dam removal unlikely (Baron and others 2002; Naiman and Turner 2000; Tockner and Stanford 2002).

Climate change is an additional factor likely to impact riparian areas in the future, although the problem is largely beyond the scope of land managers. There is considerable uncertainty about its effects in the region. Increased regional temperatures and precipitation have been predicted under some scenarios, although the confidence in these predictions is low (U.S. EPA 1998a, 1998b, 1998c; Wagner 2003). This underlying uncertainty regarding possible changes makes developing of mitigation plans difficult. One thing managers can do is to institute baseline data collection and monitoring efforts.

5. Historical Range of Variation for Region 2 Marshes

Definitions and Concepts of Marshes ---

The term marsh has been variously used by different authors. Keddy (2000) defined marshes as “wetland communities dominated by herbaceous plants rooted in hydric soils, but not peat”. In contrast, Mitsch and Gosselink (2000) applied a more general definition: “frequently or continually inundated wetlands characterized by emergent herbaceous vegetation adapted to saturated soil conditions.” Weller (1994) described marshes as “any low area that will hold water over soil, even temporarily, forming a suitable basin for the invasion of water-tolerant, rooted, soft-stemmed plants (hydrophytes) such as grasses, sedges, cattails, and bulrushes.” Each of these definitions emphasizes vegetation, soil characteristics, and hydrology, although in different terms. Marshes can generally be recognized by (1) the dominance of emergent, non-woody vegetation such as grasses, sedges, and rushes; (2) the presence of a shallow-water hydrologic regime; and (3) minor or non-existent accumulations of peat (Mitsch and Gosselink 2007).

Marshes in Region 2 are diverse functionally and compositionally and range from cattail-dominated wetlands on the plains to sedge-dominated ecosystems along the margins of montane lake basins. Additional examples include playas (depressional wetlands hydrologically supported principally by precipitation and surface runoff) and emergent plant communities found in abandoned meander bends or oxbows of large alluvial rivers. Though occurring along a wide elevational and latitudinal gradient and supporting diverse plant communities, marshes share some fundamental hydrologic attributes; these drive key ecological processes and effectively differentiate these systems from other wetland types such as fens or wet meadows.

Geomorphic Setting and Principal Ecological Drivers ---

Marshes are broadly distributed throughout Region 2, occurring in all National Forest units. However, there are significant differences in the abundance, distribution, and functional characteristics of marshes within the region. Several ecological drivers are particularly important in creating these patterns. At broad regional and landscape scales, climate and basin physiography are most important, while at more localized scales, the morphology of individual basins supporting marshes is key, with each driver primarily influencing vegetation patterns and ecological function through their effects on hydrology (Kantrud and others 1989a) (Figure 20).

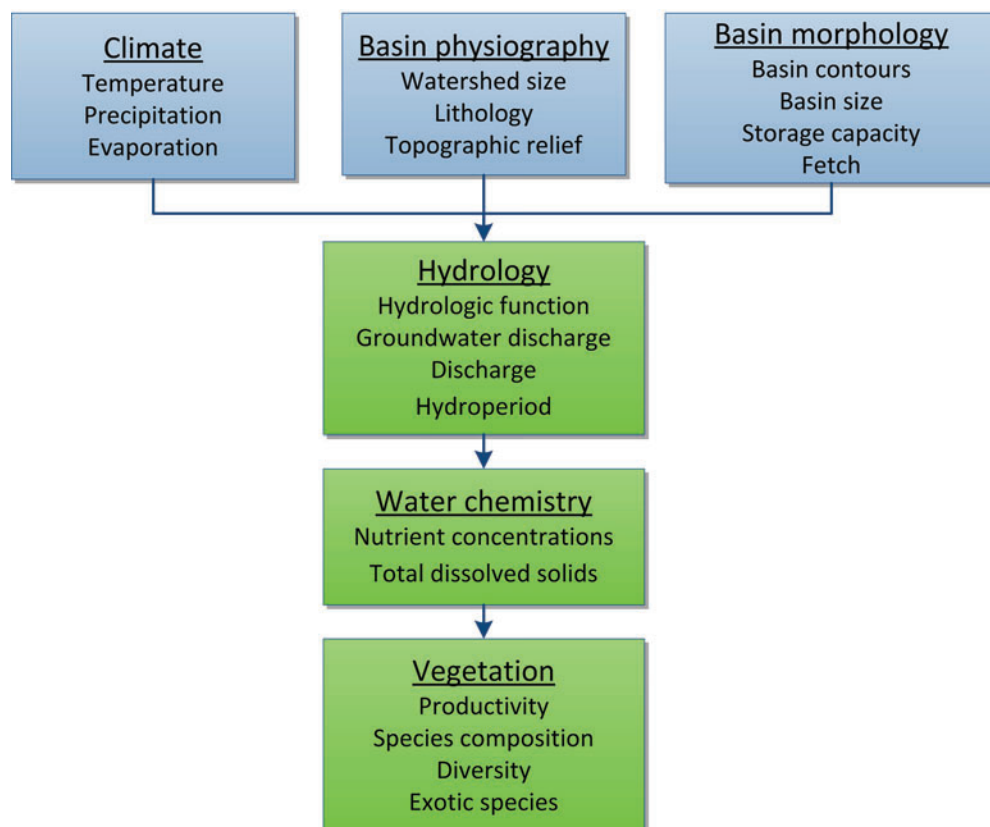


Figure 20—Schematic illustration of broad-scale drivers of marsh formation, ecological function, and vegetation patterns (modified from Kantrud 1989).

Differences in climate occurring along the region’s elevational and geographic gradients have a strong influence on the relative abundance of marsh ecosystems, their functional characteristics, and their characteristic plant communities. The specific climatic variables most important to marsh formation, persistence, and function are temperature and precipitation. These variables in turn determine whether conditions of moisture surplus or moisture deficit occur—a basic climatic control of marsh distribution and hydrologic function (Kantrud and others 1989a,b; Winter and Rosenberry 1998).

Many marshes are hydrologically supported primarily by precipitation and surface water runoff (Mitsch and Gosselink 2007; Weller 1994; Winter and others 2001) and are therefore particularly responsive to climatic fluctuations (Winter 2000) (Figure 21). Orographic effects in mountainous areas strongly influence precipitation patterns (Kittel and others 2002), thereby influencing landscape level patterns of marsh abundance, structure, and function in mountainous portions of Region 2. Orographic effects are not a factor in areas with small elevation gradients such as the Great Plains, which generally receive lower total precipitation relative to higher-elevation areas at the same latitude. In addition, temporal patterns of precipitation are often more variable. As a consequence, water levels in marsh types, such as playas, that rely nearly exclusively on direct precipitation and runoff from surrounding areas are particularly variable, a central factor shaping vegetation patterns in these systems (Smith 2003; Weathers 2000).

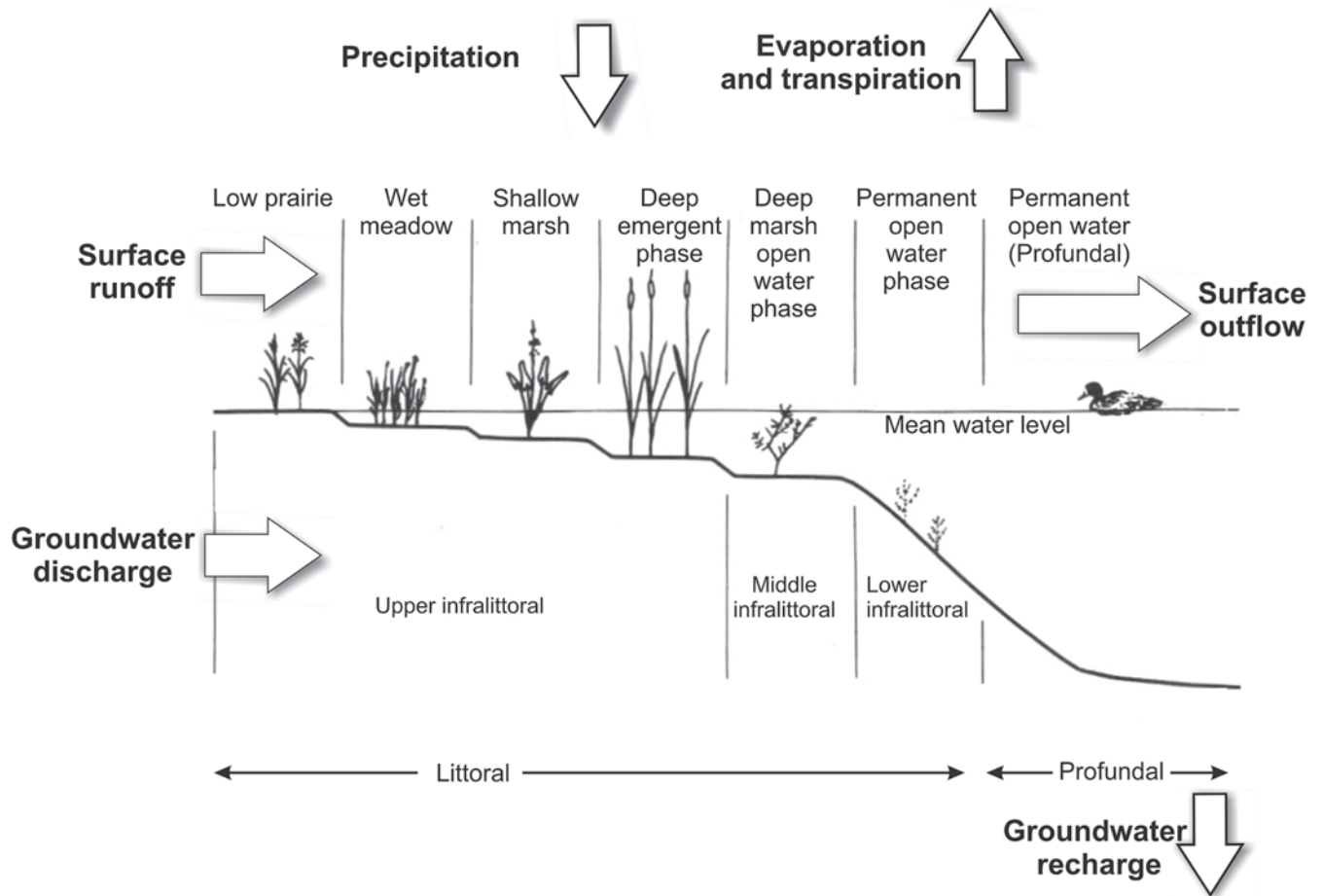


Figure 21—Dominant water sources supporting a prairie pothole marsh. Note that the importance of each hydrologic input or output varies from wetland to wetland (Kantrud et al. 1989a).

Basin physiography is an additional broad-scale driver of marsh abundance, structure, and function (Kantrud and others 1989a) (Figure 20). Variables of particular importance are the size of contributing watersheds, patterns of topographic relief, and lithology. Because of the region’s diverse climates and geological composition, the specific geomorphic settings in which marshes form vary. All marshes are found associated with topographic depressions, although the size, morphology, and origin of landforms differ widely. Marshes occur in small, barely noticeable depressions as well as in large lake basins. Since marsh communities commonly fringe open-water lacustrine systems, they are also found associated with the numerous man-made ponds and lakes in the region, ranging from large storage reservoirs to small livestock watering impoundments (Evans and Kerbs 1977; Rumble 1989).

Landforms supporting marshes are formed by a variety of mechanisms, including fluvial, eolian, and glacial erosion processes (Bolen and others 1989; Mitsch and Gosselink 2007; Weller 1994). Given the region's semi-arid climate, overall wetland area is generally greater at higher elevations due to the cooler and wetter microclimates. However, the relative abundance and distribution of marshes is also strongly shaped by the physiographic and geologic characteristics of particular landscapes. For example, marshes occur at very high densities in glaciated portions of the Great Plains. The so-called "prairie pothole" region has a very high density of marshes, as does the playa lakes region (Kantrud and others 1989a; Smith 2003). In contrast, marshes are generally rare in many mountainous areas, where steep topography provides few sites suitable for marsh formation.

Past glaciation is an important factor influencing broad-scale patterns of marsh occurrence in many northern regions, but with the exception of the eastern portion of South Dakota, none of the states encompassing Region 2 was directly affected by continental glaciation. However, periodic expansion of glaciers originating in high mountain cirques have helped shape many alpine and subalpine landscapes in Colorado and Wyoming, often creating a high density of depressional basins filled with lakes or kettle ponds. Depending on basin physiography, they often support emergent marsh vegetation (Winter and Woo 1990).

Other geological factors that influence marsh distribution and function include the mineralogy and grain structure of geological strata underlying the wetlands. Lithology can influence basic hydrologic processes such as infiltration, groundwater recharge, and discharge, in part shaping individual wetland hydrologic regimes. Lithology can also strongly affect water chemistry parameters, including nutrient concentrations and salinity levels (Winter 2001). Lithology, along with climate and tectonics, also affect the physiographic characteristics of landscapes, thereby influencing marsh distribution and functional characteristics.

Also worth noting are the extensive dune fields located throughout the region, especially the Nebraska Sandhills, as well as smaller features found in Wyoming, Kansas, and Colorado. Because of sand's high permeability and hydraulic conductivity, almost no surface runoff is formed during precipitation events. As a result, wetlands only occur where groundwater systems approach the surface, typically between dunes (Drda 1998; Novacek 1989). In some areas, these interdunal lakes and wetlands can be quite abundant, often supporting a high density of marshes. Studies have demonstrated that these eolian features alternate between periods of relative stability and increased dune activity resulting from prolonged drought conditions (Clarke and Rendell 2003; Forman and Maat 1990; Muhs and Holliday 1995).

Although generally discussed in the context of riparian areas, beaver are an additional factor that can affect marsh development. The construction of ponds can lead to the formation of marsh communities; depending on the stability of dams, these can persist on landscapes for decades (Naiman and others 1988). Although exhibiting different functional attributes than marshes formed in depressions,

the reduction in stream energy and impoundment of water can create conditions suitable for the development of emergent species. The lifespan of dams and associated ponds can vary widely, from less than one year to decades or longer depending on characteristics such as mean and peak discharge, stream gradient, and stream power (Collen and Gibson 2001; Gurnell 1998), which affects vegetation response and subsequent successional development.

Hydrologic, ecological, and disturbance processes

In both pristine and anthropogenically altered or created systems, the hydrologic regime is a primary factor that influences wetland structure and function, affecting everything from the physiological performance of individual plants (Wilson and Keddy 1985) to rates of productivity, nutrient cycling, and species composition (Neill 1993, 1995; van der Valk 1994; van der Valk and others 1994). A key attribute that distinguishes marshes is the presence of standing water, at least on an intermittent or seasonal basis, although fens may also support shallow surface water features (e.g., flarks or pools). Many marshes also naturally exhibit relatively high intra- and inter-annual variability in the depth of inundation and water table depths (Winter and others 2001). Characterizing the amplitude and temporal frequency of such fluctuations is, therefore, essential to understanding marsh function and response to anthropogenic activities.

The seasonality, depth, and duration of inundation or saturation (i.e., hydroperiod) all influence marsh function and vegetation dynamics (Weller 1994) and vary widely among different wetland types and within an individual class of wetlands such as marshes (Winter and Woo 1990). Variability in these key hydrologic attributes is important in structuring species composition, both spatially, within marsh complexes, and temporally, from wet to dry years (Seabloom and others 1998; Smith and Haukos 2002; van der Valk and others 1994). Consequently, most wetland classification schemes incorporate some degree of hydrological characterization (Brinson 1993a; Cowardin and others 1979; Zoltai and Vitt 1995). In contrast to fens, where mean water depth is a significant predictor of vegetation patterns, measures of hydrologic variability are often better predictors of vegetation patterns in marshes (Asada 2002).

As with wetlands in general, marsh formation is ultimately dependent upon the presence of sufficiently wet conditions to drive the development of hydric soils and vegetation. A wetland's water balance, i.e., the difference between water inflows and outflows and storage, drives the local hydrology, which helps shape vegetation (Mitsch and Gosselink 2007; Winter and Woo 1990). Hydrologic inputs include direct precipitation, surface water inflows, and groundwater discharge. Outflows can occur as surface water, direct evaporation, plant transpiration, or percolation into groundwater aquifers. The relative importance of each of these processes varies widely among marshes as functions of climate, lithology, and physiographic setting and is largely responsible for the different hydrological regimes occurring in Region 2 marshes.

The source of water to wetlands—precipitation, overland flow, and/or groundwater—varies among marshes in the region. Although direct precipitation inputs are certainly important components of marsh water budgets, unlike specific wetland types such as ombrotrophic bogs or vernal pools, many marshes also rely upon significant surface or groundwater inflows (Mitsch and Gosselink 2007; Weller 1994). Exceptions are playas and similar marsh types, which receive water almost exclusively as surface runoff or direct precipitation inputs (Bolen and others 1989; Smith 2003).

Research in a variety of settings has demonstrated that many wetlands, including marshes, are integral parts of groundwater flow systems (van der Valk 2005; Winter and others 2001). In regional groundwater flow systems, recharge typically occurs at high topographic areas, while discharge occurs at low areas. However, local flow systems associated with wetlands are often superimposed on these regional systems, resulting in complex interactions between groundwater and surface water, regardless of regional topographic position (Winter and Woo 1990). Consequently, generalizations are difficult to make regarding hydrologic function.

Considering the importance of hydrologic regime to patterns of vegetation composition and dynamics, assessments of the current or past conditions need to be made in light of hydrology. Unfortunately, hydrologic data are rare for marshes, although a handful of long-term studies are available (Labaugh and others 1996; Winter and Rosenberry 1995). For historical reconstructions, the paucity of hydrologic data necessitates the use of proxy information such as paleoclimatic reconstructions and knowledge gleaned from contemporary studies of human impacts to marshes.

Although hydrology is the single most important factor influencing marsh vegetation dynamics, other disturbance agents can also be important. Fire is a nearly ubiquitous disturbance type in North American terrestrial ecosystems; and over sufficiently long time scales, nearly all terrestrial ecosystem types in the region, except alpine tundra, experience it (Pyne and others 1996). Although fire is regarded as a key disturbance type influencing vegetation patterns in upland ecosystems in Region 2 Forests and Grasslands (Dillon and others 2005; Goldblum and Veblen 1992; Romme 1982; Sherriff and others 2001), the historical importance of fire in structuring wetlands, and marsh ecosystems in particular, is less evident.

The effect of fire on marshes has received some study, but mostly from outside of the region. For example, many marshes in the Gulf Coast region are intensively managed through a combination of fall/winter burning and construction of impoundments to improve wintering waterfowl habitat and create emergent wetlands (Gabrey and others 1999). The use of fire in marsh management is also practiced in the Great Plains. For example, fire has been used as a tool to control cattails with the objective of improving habitat for migratory birds (Higgins and others 1989; Kostecke and others 2004).

Studies document the use of fire in marshes to open up dense stands of vegetation, to control plant succession, and to promote production and palatability of the aquatic plants providing forage for waterfowl (Ford and Grace 1998).

Fire can affect marshes in variety of ways. One obvious effect is through direct plant mortality, although the susceptibility of different species varies. In general, fire reduces aboveground biomass in marshes; for example, in a study of Louisiana coastal marshes, mean total biomass was over 1.5 times greater in the plots that remained unburned than in those that were burned (Taylor and others 1994). Different marsh vegetation types may differ in their response to fire. For example, Smith and Kadlec (1985) found in a study of Utah marshes that vegetation regrowth was rapid following fire in communities dominated by *Typha* spp., *Scirpus lacustris*, and *S. maritimus*, but was very limited in more saline sites dominated by *Distichlis spicata* (Smith and Kadlec 1985). Fire effects may differ depending on the seasonality of burning. For example, Mallik and Wein (1986) found that fire reduced *Typha glauca* cover, stem density, and plant height regardless of the seasonality of burning, but reductions were significantly greater following summer burns (Mallik and Wein 1986).

In addition to direct effects such as plant mortality, fire can indirectly affect vegetation through a variety of mechanisms. For example, in marsh communities along Great Salt Lake in Utah, fire was observed to promote increased herbivore use of the habitat, presumably due to increases in protein content of the vegetation following fire (Smith and Kadlec 1985). However, such an effect has not always been reported; Taylor and others (1994) found no short-term change in herbivory impacts due to burning in a Louisiana coastal marsh. Additional effects are changes in water and soil chemistry such as short-term increases in nutrient availability (Boerner 1982).

Because marshes are geographically discreet features and comprise such a small portion of landscapes, the likelihood of natural ignition in marshes is extremely small. Therefore, characteristics of the fire regime, fire frequency in particular, are derived from the surrounding forest, shrub, or grassland cover. These can vary widely across the region, making generalizations difficult. In addition, complicating the assessment of historical conditions is the uncertain and variable role of Native Americans in shaping fire regimes (Vale 2002). They likely had relatively significant influence on grassland fire regimes. For example, Higgins (1986) concluded that fires set by Native Americans occurred primarily during two periods: March through May, with a peak in April, and July through early November, with a peak in October. Natural ignition from lightning also commonly occurred, generally during summer and early fall when thunderstorms are most common (Higgins and others 1989). Higgins also suggested that nearly all fires during the fall-winter period that have been reported in journals and letters from the region since about 1750 were probably not caused by lightning strikes, but rather were ignited by humans (Bragg 1995; Higgins 1984).

Native American influences on forest fire regimes across Region 2 are relatively poorly understood and probably varied across the region. While burning by native peoples was likely a factor of local importance, particularly at lower elevations, it is likely that their impact to larger landscapes was relatively modest (Baker and Ehle 2001). Fire return intervals in the region's forests vary widely among different cover types and specific regions and have varied temporally in response to both natural climatic variability and anthropogenic influences. In general, fire return intervals in lower-elevation cover types (e.g., ponderosa pine) would have been much shorter than in higher elevations cover types (e.g., subalpine spruce-fir forests). However, the abundance of marshes is generally very low in the lower forested zones of the region.

Considering the active fire regimes characterizing much of the region's forests and grasslands, it is reasonable to conclude that fire affects Region 2 marshes on at least an occasional basis. Although not likely to affect the overall occurrence of marshes on the landscape, fires likely had impacts on species composition. For example, cattail-dominated marshes in North Dakota were apparently less common in the early Twentieth Century; they were typically restricted to the margins of large freshwater lakes (Kantrud 1992). The more restricted distribution of cattail in the past may have been due to the influence of prairie fires and large ungulate grazing.

A variety of animals may use marshes directly or indirectly, thereby affecting vegetation patterns. Herbivory is one of the most obvious direct impacts, although its importance can vary widely depending on the nature of the wetland and of the fauna in question. Historically, large mammals such as bison would have at least occasionally utilized marshes for water and possibly forage. However, there is insufficient evidence to make broad generalizations about their ecological effects on marshes. It is likely that effects resembled, in part, those observed from livestock use of wetlands and could include plant mortality from direct herbivory and trampling, soil compaction, and reduction in overall plant cover.

An additional animal of importance to marshes is the muskrat, which is widely distributed throughout Region 2, found along the edges of alpine tarns to riparian wetlands on the plains and in semi-desert valleys (CDOW 2005). Muskrats are primarily herbivores, feeding on a range of aquatic and emergent species. Several studies, particularly in the prairie pothole region, indicate that muskrats can have significant effects on marsh vegetation structure. Muskrat "eat-outs," impacting nearly all emergent plants in a marsh, are common and along with climatically induced hydrologic change, can drive cyclical vegetation patterns observed in many pothole wetlands (van der Valk and Davis 1978).

A wide variety of birds utilize marshes, although how they affect vegetation patterns, as opposed to how vegetation influences habitat suitability, is largely unexamined. Some birds such as geese can influence marsh vegetation by direct herbivory (Belanger and Bedard 1994; Smith and Odum 1981; van den Wyngaert and others 2003). In addition, waterfowl may influence marsh ecosystems indirectly by serving as vectors for seeds (Charalambidou and Santamaria 2005) and by influencing nutrient dynamics (Post and others 1998).

Marsh Classification and Gradients

Typically, marshes are described in terms of both vegetation and hydrology, with an emphasis placed on the presence of emergent herbaceous plant species and at least occasional inundation. Several different wetland types meet this definition, going by various names regionally. Specific types of non-tidal marshes include prairie potholes, playas, lacustrine fringe wetlands, and kettle ponds.

True prairie potholes do not occur in USFS Region 2, but because of their great importance to migratory birds, they are among the most studied marsh types in North America and deserve discussion in this assessment. The term “prairie pothole” is generally reserved for glacially-formed shallow depressional wetlands distributed throughout the upper Midwest and Canadian plains. Prairie potholes can be inundated on a temporary, seasonal, semi-permanent, or permanent basis, with the specific hydrologic regime being dependent on factors such as basin size, hydrologic connectivity to adjacent wetlands and groundwater systems, and climate patterns (Arndt and Richardson 1988; Galatowitsch and van der Valk 1996; Kantrud and others 1989b).

Generally speaking, playas are a special type of marsh found in arid or semi-arid regions that have distinct wet and dry seasons. In North America, the term playa is typically reserved for small marshes formed in basins similar to prairie potholes but of different geologic origin and function. Playas are found in greatest abundance in the southern Great Plains, specifically the “Playa Lakes region” of Texas, New Mexico, Kansas, and southeast Colorado (Bolen and others 1989; Nelson and others 1984). There is still some controversy regarding their origin, with evaporative and dissolution processes, wind erosion, and bison wallowing all cited as possible causes of playa formation (Hovorka 1995; Rosen 1994). Most exhibit a distinct circular or oval shape when viewed from overhead, a factor driving the intense speculation among geologists regarding their origins (Smith 2003). Playas are supported hydrologically almost exclusively by precipitation, with flood waters retained due to the presence of impermeable clay layers in the bottom of basins (Smith 2003). Although they are often thought to be restricted to the playa lakes region centered in Texas, similar systems can be found in eastern Wyoming, the rainwater basin of Nebraska, and unglaciated portions of the South Dakota mixed grass prairie (Smith 2003).

Marshes also commonly occur along the margins of ponds, lakes and reservoirs. Such wetland communities have been characterized as “lacustrine fringe,” a generic term describing hydrogeomorphic setting (Brinson 1993a). Lacustrine fringe wetlands are broadly distributed along both natural and artificial water bodies throughout Region 2, occurring on the plains as well as in the mountains. Their presence or absence, as well as their relative width along shorelines can vary with basin size and shape, water management, or factors such as exposure to wave action. For example, communities are generally lacking along lakes or reservoirs with steep banks or with highly variable water levels as is often seen with managed reservoirs. Due to winds or currents, surface water movement is generally horizontal, but vertical fluctuations resulting from seasonal water level fluctuations can also occur, particularly in heavily managed systems. Lacustrine fringe wetlands always occur adjacent to open water aquatic systems, differentiating them from marshes formed in many smaller basins.

The term “kettle pond” refers to depressional ponds or wetlands found in glaciated landscapes. Generally, geologists reserve the term for features formed by the melting of large ice blocks lodged in deposits of glacial till or outwash, although the term is often generically applied to any small depression resulting from glacial action (Elias 1995; Zogg and Barnes 1995). Vegetation and hydrology in potholes can vary, with marsh communities often grading into either floating aquatic communities or peat-forming systems. Although relatively rare landscape features, wetlands that are formed in potholes often support marsh species and communities.

Marshes in Region 2 would be placed in either the palustrine or lacustrine systems according to the classification scheme employed by the U.S. Fish and Wildlife Service’s National Wetlands Inventory (NWI) program (Cowardin and others 1979). Most marshes would be placed in the emergent (EM) class. Specific subclass and modifiers (e.g., salinity and water regime) can vary from wetland to wetland.

An additional framework developed to classify wetlands is the Hydrogeomorphic approach (HGM) developed by Brinson (1993a). From this original framework, a variety of regional classifications have been developed (Cooper 1998a; Hauer and others 2002a, 2002b; Stutheit and others 2004). Cooper (1998) investigated the relationship among geomorphology, wetland vegetation, and wetland functions in Colorado and produced an HGM classification with four hydrogeomorphic classes: riverine, slope, depression, and mineral soil flats. Within these, he identified several subclasses that are comprised of wetlands sharing general characteristics and similar functions. Landscape position and water source supporting the wetland are the critical factors that distinguish the four classes. In the Cooper classification, all marshes fall into the Depressional class, with differences among marsh types driving placement of wetlands into one of five subclasses (Table 17).

Table 17—Hydrogeomorphic (HGM) classes identified by Cooper (1998) as part of the statewide wetlands classification of Colorado (Carsey and others 2003).

HGM Subclass	Description	Characteristic species
Depressional 1	Mid- to high-elevation basins with peat soils and lake fringes with or without peat soils.	<i>Carex utriculata</i>
Depressional 2	Permanently or semi-permanently flooded low-elevation basins, including reservoir and pond margin wetlands as well as marshes.	<i>Typha</i> spp., <i>Scirpus</i> spp.
Depressional 3	Seasonally flooded low-elevation basins that are dry for long periods.	<i>Eleocharis palustris</i>
Depressional 4	Temporarily flooded low-elevation basins flooded for short periods in the spring and early summer.	<i>Polygonum lapathifolium</i>
Depressional 5	Intermittently flooded low-elevation basins that are not flooded annually or are largely barren of vegetation.	<i>Xanthium strumarium</i>

Carsey and others (2003) combined several of Cooper’s original subclasses as part of their comprehensive, statewide classification in Colorado. Wetlands placed in the Depressional subclass 1 (D1) are found in mid to high-elevation basins with peat soils along with communities along the fringes of lakes. Most of the basin peatland types would be considered fens, not marshes, but some of the lacustrine fringe wetlands on mineral substrates would be considered marshes. Carsey and others (2003) identified two seasonally flooded herbaceous wetland types in this subclass: *Carex utriculata* and *Carex aquatilis-Carex utriculata*, the former being most common.

Depressional wetlands in subclasses 2 and 3 (D2/D3) occur at lower elevations and have permanently or semi-permanently flooded hydrologic regimes. Examples include reservoir and pond margins as well as smaller basin marshes. Vegetation is typically dominated by species such as cattails, bulrushes, sedges, grasses, and rushes. Carsey and others (2003) identified 14 plant associations in this subclass. Wetlands in Depressional Subclasses 4 and 5 (D4/5) are found in low-elevation basins that are temporarily or intermittently flooded. Marsh types in these subclasses include playa lakes. Vegetation cover is often poorly developed, and the depression bottom may be barren (Carsey and others 2003). Also included are abandoned beaver ponds and small irrigation ponds. Twelve plant associations were identified by Carsey and others (2003) in these subclasses, all dominated by forbs or graminoids.

Water chemistry can vary widely among marshes, with the concentration of salts being a particularly important variable influencing marsh vegetation. Depending on the concentration of ions, water in marshes can be classified as fresh, brackish, or saline. “Brackish” has generally been used to refer to waters of intermediate salinity (Stewart and Kantrud 1972) and the term “saline” can be used to indicate the presence of any one of a number of cations (calcium, magnesium, sodium, and potassium) or anions (carbonate, sulfate, and chloride) (Cowardin and others 1979). Salinities are usually expressed in units of specific conductance or as percent salt (Ungar 1974a), although various descriptive modifiers have been developed as part of different classifications.

Marsh Vegetation in the Region ---

When analyzed over a range of time periods, many marshes exhibit wide water level fluctuations around a long-term mean. Evidence suggests that such oscillatory water level fluctuations have occurred for thousands of years and are key drivers of changes in wetland vegetation (van der Valk 2005). Alternating wet and dry periods help create two kinds of vegetation change: fluctuations and successions. The former refers to changes in the relative abundance of species between the wet and dry phases of the cycles and occurs whenever the range of water levels during a cycle is small, as in seasonal wetlands. In contrast, successions are large shifts in species composition occurring where the range of water levels is large, as in semi-permanent wetlands (van der Valk 2005).

High water levels during the wet phase of successions often eliminate most emergent species, while low water levels during the dry phase allows for the re-establishment of species from seed (Galatowitsch and van der Valk 1996; Seabloom and Van Der Valk 2003). The role of seed banks is particularly important in reestablishment of plants in most marsh types and has received considerable attention in the literature (Baldwin and others 1996; Galatowitsch and van der Valk 1996; van der Valk and Davis 1976, 1978; Wilson and others 1993).

A commonly observed feature of many marshes is the presence of distinct patterns of zonation, with different communities arranged in concentric areas around open water or the deepest portion of the marsh. Such zonation patterns are a common feature in a variety of marsh types including playas, prairie potholes, and lacustrine fringe (Hoagland and Collins 1997; Kantrud and others 1989a; Spence 1982). Although there are certainly differences in composition among individual marshes, groups of species tend to occur in roughly the same relative position along flooding gradients. Zonation patterns are often quite distinct and can be caused by a variety of factors, but hydrology, specifically the depth and length of inundation, appears to be the most important factor (Seabloom and van der Valk 2003; van der Valk 1994). These variables can affect standing vegetation by impacting physiological performance of plants and are important factors shaping seed germination and seedling recruitment patterns (Seabloom and Van Der Valk 2003; Wilson and Keddy 1985; Wilson and others 1993). Although the concentric rings of vegetation in marshes appear simple, research suggests that the species composition of these zones is the outcome of complex interactions between abiotic conditions and differential rates of propagule dispersal, seed germination, and seedling recruitment, all of which can be affected by antecedent conditions.

For example, Seabloom and others (2001) found that the importance of historical recruitment events declines relative to nature of the current conditions after one to two years after a major hydrologic change is imposed (Seabloom and others 2001). Welling and others (1988) examined establishment of common emergent marsh species along a height gradient and found that differences in environmental conditions seem to have had less impact than the distribution of seeds

on the distribution of seedlings. The authors suggested that these differences in distributions along the height gradient between seedlings and adult plants were due in part to post-recruitment processes (Welling and others 1988).

Region 2 supports a wide range of marsh communities, not surprising considering the size and diversity of the region. Several different vegetation classification schemes have been undertaken, differing in methods and geographic scope. For example, the Nature Conservancy (TNC) developed a vegetation classification for all of Region 2, using “ecological systems” as the primary classification unit (Comer and others 2003b). Ecological systems data are coarser in scale than either alliance or plant associations, which represent the finest classification units defined by the National Vegetation Classification system (Comer and others 2003b). In their analysis of Ecological Systems in Region 2, Comer and others (2003b) described three marsh system types, collectively comprising less than 1 percent of the region’s land area (Table 18). The authors used TNC ecoregions to more explicitly tie their classification geographically to Region 2, but some systems, notably the North American Arid West Emergent Marsh, were very similar across multiple Ecological Divisions (Comer and others 2003b).

Carsey and others (2003) describe 21 different marsh vegetation associations (Table 19). These include monotypic communities dominated by hydrophytes such as cattails (*Typha* spp.) and bulrushes (*Schoenoplectus* spp.) as well as communities dominated by facultative species such as buffalo grass (*Buchloe dactyloides*) and western wheatgrass (*Pascopyrum smithii*). These latter communities are typical of playas, which are flooded with the lowest frequency of any marsh type in the region. Non-native species such as barnyard grass (*Echinochloa crus-galli*) and reed canary grass (*Phalaris arundinacea*) are dominants in two of the vegetation types. Indicator species for HGM subclasses were also reported (Carsey and others 2003).

Table 18—Approximate area of different Region 2 ecological systems relevant to marshes as reported by Comer and others (2003). Marsh systems are indicated in bold.

Ecological systems	Hectares	Percent area
Inter-Mountain Basins Playa	12,749	0.0
North American Arid West Emergent Marsh	128,301	0.1
North Central Interior Floodplain/Wooded Draw	771,987	0.7
Rocky Mountain Subalpine Mesic Meadow	884,960	0.8
Western Great Plains Closed Depression	817,203	0.7
Western Great Plains Riparian/Western Great Plains Floodplain	1,488,930	1.3
Western Great Plains Saline Depression	2828	0.0
Rocky Mountain Subalpine-Montane Riparian Woodland and Shrubland	71	0.0
Rocky Mountain Subalpine Mesic-Spruce-Fir Forest and Woodland	48,164	0.0
Rocky Mountain Lower Montane Foothill Riparian Woodland and Shrubland	848,753	0.7
Rocky Mountain Subalpine-Montane Riparian Shrubland	475,655	0.4
Region 2 total	113,543,893	

Table 19—Vegetation types identified by Carsey and others (2003) and organized by HGM subclass.

Scientific description	Depressional subclass 1 Common description
<i>Carex aquatilis</i> – <i>Carex utriculata</i> herbaceous vegetation	water sedge – beaked sedge herbaceous vegetation
<i>Carex utriculata</i> herbaceous vegetation	beaked sedge herbaceous vegetation
Depressional subclasses 2 and 3	
<i>Bidens cernua</i> herbaceous vegetation	nodding beggartick herbaceous vegetation
<i>Carex nebrascensis</i> herbaceous vegetation	Nebraska sedge herbaceous vegetation
<i>Carex pellita</i> (<i>lanuginosa</i>) herbaceous vegetation	woolly sedge herbaceous vegetation
<i>Eleocharis palustris</i> herbaceous vegetation	marsh spikerush herbaceous vegetation
<i>Glyceria grandis</i> herbaceous vegetation	American mannagrass herbaceous vegetation
<i>Hordeum</i> (<i>Critesion</i>) <i>jubatum</i> herbaceous vegetation	foxtail barley herbaceous vegetation
<i>Phalaris arundinacea</i> western herbaceous vegetation	reed canary grass western herbaceous vegetation
<i>Schoenoplectus acutus</i> - <i>Schoenoplectus tabernaemontani</i> herbaceous vegetation	hardstem bulrush -softstem bulrush herbaceous vegetation
<i>Schoenoplectus pungens</i> herbaceous vegetation	threesquare bulrush herbaceous vegetation
<i>Scirpus pallidus</i> herbaceous vegetation	cloaked bulrush herbaceous vegetation
<i>Typha angustifolia</i> – <i>Typha latifolia</i> herbaceous vegetation	cattail herbaceous vegetation
Depressional subclasses 3 and 4	
<i>Alopecurus aequalis</i> herbaceous vegetation	shortawn foxtail herbaceous vegetation
<i>Echinochloa crus-galli</i> herbaceous vegetation	barnyardgrass herbaceous vegetation
<i>Eleocharis acicularis</i> herbaceous vegetation	needle spikerush herbaceous vegetation
<i>Hordeum</i> (<i>Critesion</i>) <i>jubatum</i> herbaceous vegetation	foxtail barley herbaceous vegetation
<i>Pascopyrum smithii</i> –(<i>Buchloe dactyloides</i>) - <i>Ambrosia linearis</i> - <i>Ratibida tagetes</i> herbaceous vegetation	western wheatgrass -(buffalo grass) -plains ambrosia -coneflower herbaceous vegetation
<i>Polygonum arenastrum</i> herbaceous vegetation	ovalleaf knotweed herbaceous vegetation
<i>Polygonum lapathifolium</i> herbaceous vegetation	smartweed herbaceous vegetation
<i>Veronica catenata</i> – <i>Juncus bufonius</i> herbaceous vegetation	speedwell – toad rush herbaceous vegetation
<i>Xanthium strumarium</i> herbaceous vegetation	rough cockleburr herbaceous vegetation

HRV of Marshes in Region 2

As discussed in Chapter 3, there are relatively few historical or archeological resources available from which to make confident assessments about the abundance or condition of wetlands prior to large-scale Euro-American settlement. For most of Region 2, including the central and northern Great Plains and major mountain ranges of present-day Colorado and Wyoming, initial European exploration was by French and French-Canadian trappers seeking beaver and other pelts (Goetzmann and Williams 1992). Unfortunately, they generally left no records of their travels useful for our purposes.

Likewise, there are few resources from which to evaluate the influence of native peoples on marshes of the region. Although only a handful of wetland sites have yielded significant archeological evidence of Native American use (Reider 1990), it is likely that they utilized wetlands on occasion for water. It is also likely that some direct utilization of marsh plants for food may have occurred. For example, the young shoots, young and mature rhizomes, staminate flowers, and pollen of cattails are all edible and may have been utilized for food. However, it is unlikely that subsistence-based utilization of *Typha* spp. or other marsh species would have been intense or prolonged enough to result in lasting effects to marshes.

Overview of anthropogenic impacts

Since no data are available detailing historical wetland conditions or abundance, our assessment is, by necessity, derived largely from an analysis of contemporary studies of anthropogenic impacts to marshes. Although many were not conducted in Region 2 proper, they offer valuable insights into how humans can alter marshes, either indirectly or directly. However, because of the widely varying nature of marshes in the region and the differing historical and ecological context of each National Forest or Grassland, our generalizations need to be viewed with caution.

Direct hydrologic alteration, typically draining for agricultural purposes, is likely the most significant anthropogenic impact to marshes in the region. Agricultural impacts were, by far, the greatest contributor to wetland loss according from the late Eighteenth to the late Twentieth Century (Dahl 1990). Indirect hydrologic alterations are also common, whereby the quality, quantity, or timing of surface and groundwater flow into marshes is changed as a result of indirect effects in surrounding areas. Examples include reductions or increases in surface flow from road networks or lowered water tables resulting from groundwater pumping (Richter and others 1996). An additional example is the effect of storm water and irrigation outflows. Because marshes are formed in basins, they are often used as detention ponds. Such incidental inflows from adjacent irrigated areas were identified as a central factor changing species composition in playas (Hoagland and Collins 1997).

One significant difference between contemporary and historical landscapes is the presence of extensive road networks. These can significantly alter local and watershed-scale hydrologic processes, thereby affecting marsh function. By affecting natural drainage patterns, roads and their associated engineering structures such as culverts and ditches can alter natural drainage patterns and reduce interception and infiltration rates by removing vegetation and causing soil compaction (Forman and Sperling 2002; Jones and others 2000).

In addition to hydrologic impacts, roads can be a source of pollutants to marshes and can alter water chemistry parameters (e.g., cation concentrations, conductivity, and pH) through road dust, increased sediment deposition, and the direct application of chemicals (e.g., deicing agents used in road maintenance) (Trombulak and Frissell 2000; Wilcox 1986a, 1986b). Changes to marsh water chemistry can also occur in agricultural or suburban settings, where increased nutrient concentration in runoff can cause significant changes to vegetation (Aldous and others 2005; Drexler and Bedford 2002; van der Hoek and others 2004).

Domestic livestock can have significant effects on wetland flora through direct effects like herbivory and trampling and through indirect effects like nutrient enrichment via urine or fecal deposits (Gunnell and Smith 1972). Livestock can also alter soil physical properties due to hoof action and can serve as a vector for the spread of non-native propagules (Belsky and others 1999; Keeley and others 2003). It is important to note that many portions of the region historically supported bison, whose general effects on vegetation, in some ways, resemble those of cattle (Plumb and Dodd 1993). However, considering the differences in the numbers and distribution of livestock versus historical bison populations, such comparisons may not be valid. In general, marshes appear to be more resilient relative to arid uplands to livestock grazing (Fleischner 1994), although there is scarce evidence one way or another.

Changes in the fire regimes of many of the region's upland ecosystems relative to historical conditions are well documented (Brown and Sieg 1999; Donnegan and others 2001; Meyer and others 2003; Tinker and others 2003). As a consequence, changes in the frequency of fire in marshes have likely resulted. In addition to the direct effects of fire, fire in adjacent uplands may result in increased water and sediment yield and changes in water chemistry, although the magnitude of these changes relative to pre-fire conditions should decrease over time as the density and cover of upland vegetation increases (Troendle and King 1985). In some areas, native peoples may have influenced marsh vegetation through burning. For example, Davis and others (2002) concluded that prior to the historic period, burning was frequent enough to exclude woody plants (*Celtis*, *Cephalanthus*, *Populus*, *Fraxinus*, and *Salix* spp.) from and suppress the abundance of *Scirpus* spp. (Davis and others 2002).

Changes in the abundance and distribution of marshes

Marshes are found throughout North America, covering an estimated 10,000,000 ha (24,710,500 acres) in the coterminous United States (Mitsch and Gosselink 2007). Reliable statistics pertaining to marshes in Region 2 are lacking, but in their analysis of GAP vegetation data, Comer and others (2003) present a value of 960,000 ha (2,372,211 acres) for the three main Ecological System types they identify as characteristic of marshes. Although much of the region has been mapped as part of the NWI project, although maps for many areas have yet to be digitized and data are in many instance decades old, limiting the accuracy

and feasibility of potential analyses. In the contemporary Region 2 landscapes, wetland acreage is generally greater in montane areas relative to the areas of the Great Plains. This also applies to marshes, particularly in regard to USFS lands in Region 2, as most National Grasslands tend to have fewer water resources relative to surrounding lands that were better able to sustain homesteaders and thus remained in private hands.

The natural distribution of different marsh types varies widely. For example, playas occur exclusively on the Great Plains. They are most abundant in the Playa Lakes Region in the southern Great Plains, where nearly 20,000 playa basins have been estimated to occur (Wood 2002). The Playa Lakes Region is centered in Texas, but extends into southeastern Colorado and southwestern Kansas, areas that support moderately high numbers of playas (Table 20). Playas, or functionally similar systems, also occur elsewhere in Region 2. For example, nearly 14,000 ha of playas are thought to exist in the Rainwater Basin in Nebraska (Smith 2003), and approximately 450 playas have been documented in Wyoming’s Powder River Basin (Brough 1996). Playa numbers elsewhere in Wyoming or in northeastern Colorado are unknown (Smith 2003). Other marsh types are more widely distributed. For example, lacustrine fringe communities can occur along lake and reservoir margins from the plains to the alpine, although plant community composition changes over the elevation gradient.

Pre-settlement distribution of marshes would have been governed largely by the previously discussed drivers of climate, hydrology, and geology. The latter can be regarded as largely invariable over the time period covered by this assessment (approximately 1600 to 1850 for pre-settlement and 1850 to present for post-settlement), although climate has fluctuated widely in this time period, undoubtedly affecting marsh hydrology.

Table 20—Number and area of playa basins in Colorado and Kansas (Guthry and others 1981, as presented in Smith 2003).

State/county	Number of playas	Area (ha)
Colorado		
Baca	198	675
Kansas		
Grant	232	752
Haskell	701	2755
Meade	712	3645
Morton	58	430
Seward	294	1734
Stanton	676	1900
Stevens	133	746
Total	2806	11,962

Because of the importance of marshes in the Great Plains to migratory birds, they have generally received proportionally more study than marshes in mountainous regions. In addition, many marsh types like prairie potholes are easily photo-interpreted because of their distinctive morphology and the lack of forest cover (Tiner 1999). Several additional factors also contribute to our poorer understanding of the distribution of montane marshes. One issue is that the classification used in NWI mapping efforts doesn't directly facilitate separation of marshes from other wetland types such as wet meadows and fens, all of which are generally classified as palustrine wetlands. However some estimates are available for more limited geographic areas.

The abundance of marshes on the contemporary landscape is undoubtedly lower than prior to Euro-American settlement of the region, although precise estimates of wetland loss are not available. Studies conducted at broad scales suggest that impacts have been significant. The total wetland area in the conterminous United States in the 1780s has been estimated at 221 million acres (Dahl 1990); by the 1980s, only 103 million acres were thought to remain (Dahl and Johnson 1991). Over the past 200 years, 22 states have lost more than 50 percent of their wetland habitat; estimates of wetland losses in Region 2 states are generally lower but are still significant. However, it is unknown what proportion of lost wetlands were marshes.

Although the overall trend in wetland area nationally and in Region 2 is certainly negative, causes and patterns of wetland loss vary geographically and among wetland types. Wetlands in the more arable portions of the Great Plains are among the most heavily impacted, largely due to agricultural draining (Brinson and Malvarez 2002; Mccauley and Jenkins 2005). Water control associated with urbanization has also had significant impacts, though effects are concentrated where current or past population growth and economic development have been greatest.

Complicating our assessment of historical changes in marsh abundance and distribution is the widespread occurrence of man-made water bodies and wetlands across the contemporary landscapes. These wetlands have often been purposefully created for reasons such as regulatory compliance (e.g., mitigation activities required under Section 404 of the Clean Water Act) or wildlife habitat improvement, although many have been created incidentally as part of water storage projects for agricultural and municipal use, flood control, or power generation use. Examples range from the large reservoirs built on the region's big rivers to the numerous livestock watering impoundments scattered throughout the high plains. Many of these were constructed in the 1930s and 1940s with the aid and encouragement of Government cost-sharing programs. Although not built or managed for ecological functions, many of these features support emergent vegetation and provide habitat value for wildlife (Rumble 1989; Uresk and Severson 1988). Other sources of man-made water bodies on the contemporary landscape

include coal, bentonite, and gravel surface mine impoundments and water treatment ponds (Barrett 1999; Mckinstry and Anderson 2002; Rumble and others 1985). Some of these impoundments do support small marsh communities along their margins, although often their steep banks limit the occurrence of emergent vegetation communities (Rumble and others 1985).

As part of its responsibilities under the Dam Safety Acts of 1972 and 1986, the U.S. Army Corps of Engineers produced the National Inventory of Dams (NID), which lists all artificial barriers that impound or divert water and that are 25 ft or more in height or have a maximum water storage capacity of fifty acre-feet or more (National Atlas 2002). Graf (1999) analyzed the NID and concluded that there are approximately 75,000 artificial dams across the United States which impound an amount of water approximately equivalent to one year's runoff from the continent (Graf 1999). In our analyses of the NID data from Region 2, we found a total of 882 features, the majority of which occurred in Colorado. The primary purpose listed for most of these dams was either irrigation or flood control, with a more limited number of features classified for fish and wildlife, hydroelectric, or other uses (National Atlas 2002).

Unfortunately, neither the NID data nor other widely available digital data sets such as the hydrography layer available from the National Atlas or the Census Bureau's TIGER data, provides comprehensive information on small water bodies. While the NID data provide a fairly complete inventory of large features, they miss virtually all features smaller than 10^5 m², which includes most small water bodies such as livestock watering ponds, thus grossly underestimating the total area of created ponds and wetlands in the region (Smith and others 2002). Although their distribution is poorly understood, collectively these features have great importance, resulting in regionally elevated evaporation rates, decreased downstream flow, and altered groundwater recharge and sediment transport rates. In addition, they represent novel aquatic and wetland habitats that may at least partially compensate for—but spatially redistribute—wetlands lost to anthropogenic activities (Smith and others 2002).

Livestock watering ponds can be classified as retention reservoirs, pit reservoirs (i.e., dugouts), and pit retention reservoirs (Lokomoen 1973). Retention reservoirs involve the construction of small dams across intermittent streams or gullies to intercept spring runoff or rainwater from upland slopes, while pit reservoirs are steep-sided and are generally supported from groundwater as well as surface runoff (Olsen 1999). The design of pit retention reservoirs is similar to pit reservoirs except that spoil material is placed on the downstream side as a dam in order to flood the shallow area around the dugout (Payne 1992). The differences in design have implications for marsh development, as emergent species are unable to colonize if banks are too steep, as is often the case with dugouts.

Morphological characteristics such as pond shape and size also influence the suitability of ponds for waterfowl use (Evans and Kerbs 1977; Lokemoen 1973; Rumble 1985). For example Lokemoen (1973) suggested that the minimum pond size be 0.6 ha, while Uresk and Severson (1998) found that ponds with gently sloping shorelines and abundant emergent vegetation support greater densities of birds (Uresk and Severson 1988).

Although contributing a small fraction of the region's total marsh area, marsh communities have also been documented as occurring along regulated sections of the Colorado River. These systems are relatively novel features, rare in pre-settlement landscapes because of the effects of scouring floods (Stevens and others 1995). Following the completion of the Glen Canyon dam in 1963, reduction in flood frequency permitted widespread marsh development. These features have low stability in the face of large spring floods but are able to quickly redevelop after scouring by what are now rare high flows (Stevens and others 1995). Although not documented in the literature, similar processes may also allow for the marsh development along other larger regulated rivers in the region.

Marsh structure and function

Previously prepared HRV assessments in the region have included analyses of structural and compositional attributes of vegetation. The importance of these variables for forested cover types is clear, as large shifts in forest composition or stand structure can have important repercussions for processes such as fire regimes or wildlife habitat (Meyer and others 2003; Veblen and Donnegan 2005). In addition, there are many examples from the scientific literature of methodological approaches for characterizing such changes and understanding their implications (Morgan and others 1994; Nonaka and Spies 2005; Veblen 2003). Although vegetation composition and structure are key attributes for marsh ecosystems as well, several factors limit the analytical approaches available for characterizing their dynamics at the broad spatial and temporal scales of this HRV assessment.

Studies have documented increases in the amount and density of vegetation cover in many Great Plains marshes. For example, Root and Ryan (2004) examined the changes in habitat for piping plovers at two North Dakota alkaline wetland complexes from 1938 to 1997, observing declines in beach habitat and an increase in vegetation cover, suggesting that long-term changes in factors such as groundwater hydrology, livestock grazing intensity, or fire frequency may be negatively affecting beach availability, impairing long-term recovery of threatened piping plovers (Root and Ryan 2004). Changes in marsh structure resulting from the development of dense, closed stands of species like cattails are widely noted in the literature and are a principal concern of many wetland managers trying to improve waterfowl habitat (Kantrud 1990, 1992; Weller 1994). Changes in the amplitude of water level fluctuations can result in shifts in species diversity (Keddy 2000) (Figure 22).

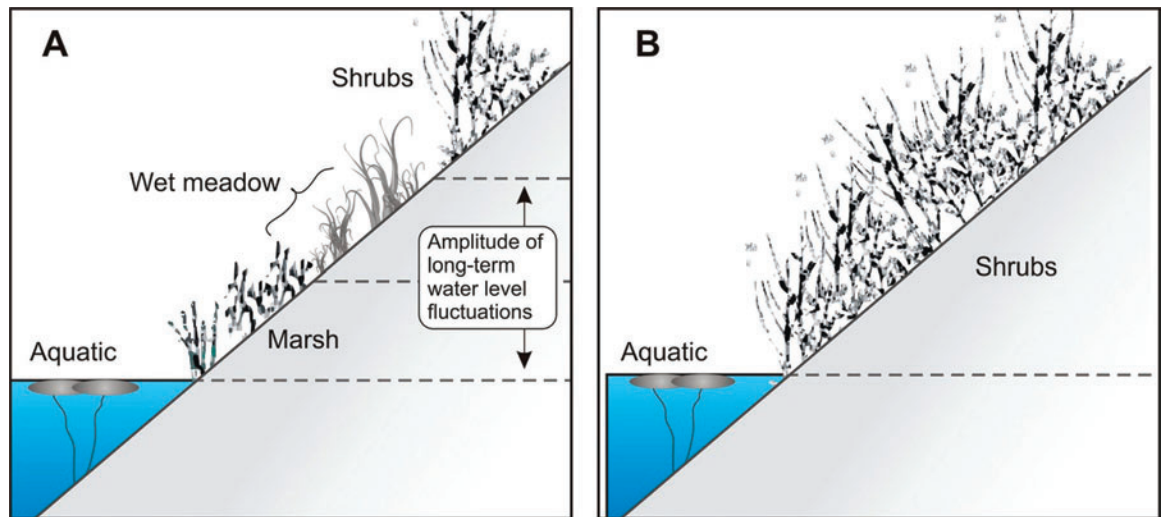


Figure 22—Reduction of community diversity associated with the stabilization of water levels. The four zones depicted in panel A have been reduced to only two in panel B (Figure modified from Keddy 2000).

Changes in vegetation relative to historical (i.e., pre-1850) conditions vary among marsh types and the mechanisms of anthropogenic influence. For example, Hoagland and Collins (1997) attributed differences between the species composition of playas examined in their study to that presented in earlier studies to differences in surrounding land use and the influence of irrigation inflows from surrounding areas on hydrologic regime. Elsewhere in the region, changes in the frequency of fire and grazing practices have been used to explain shifts in vegetation composition or structure (Higgins 1986; Kantrud 1990).

The introduction and spread of non-native species is widely regarded as one of the greatest anthropogenic impacts to native communities (Brinson and Malvarez 2002; Mack and D'Antonio 1998; Mack and others 2000). Although generalizations are difficult to make, there are several species that are regarded as problems in wetlands such as marshes. *Phalaris arundinacea* (reed canary grass) is widespread throughout Region 2, occurring in variety of habitats in addition to marshes. Although there is lack of consensus as to its status as native or introduced, exotic cultivars of the species were once widely planted, a factor likely related to its observed aggressiveness (Merigliano and Lesica 1998). It appears that reed canary grass responds positively to hydrologic alteration, likely an additional factor in its spread (Galatowitsch and others 1999). Its relatively great height per unit of biomass and its adaptable morphology have both been cited as possible reasons for its high competitive ability in wetlands (Miller and Zedler 2003). It often forms monotypic stands—crowding out other species, especially smaller graminoids and forbs (Barnes 1999)—and has been shown to reduce species diversity, particularly in disturbed wetlands (Kercher and others 2004).

Cattails (*Typha* spp.) are often species of additional concern, despite that they are one of the principal marsh dominants globally, occurring in both coastal and freshwater marshes. Often, they are widely viewed as aggressive invaders by wetland and wildlife managers because of their propensity to form uniform stands. The genus includes *Typha domingensis*, *T. angustifolia*, and *T. latifolia*, all of which have been documented in the region (Smith 2005). *Typha latifolia* and *T. domingensis* are regarded as native, the latter confined to the southern part of the region, but evidence suggests that *T. angustifolia* is introduced (Kantrud 1992). *Typha angustifolia* and *T. latifolia* readily hybridize, and their hybrid, *Typha x glauca*, is known to be an aggressive competitor in marshes. Cattails, particularly *T. angustifolia* and its hybrids, tend to be most aggressive and problematic in disturbed wetlands and those receiving elevated levels of nutrients such as marshes found in agricultural or urban watersheds (Woo and Zedler 2002).

The distinctive flowering spike in *Typha* spp. can produce hundreds of thousands seeds, which are efficiently wind-dispersed and germinate on bare wet soils or under very shallow water (Lombardi and others 1997). These characteristics, as well as ability of the plants to rapidly form clones by means of rhizomes, allows cattails to form large, persistent, and often monospecific stands (Smith 2005). These stands are a problem in many prairie wetlands because they alter habitat structure and function, resulting in a decrease in use by wildlife species (Kantrud 1992; Kostecke and others 2004).

Purple loosestrife (*Lythrum salicaria*) is another species credited with dramatically changing the vegetation of many North American wetlands (Galatowitsch and others 1999). The species appears dependent on disturbance for seed germination (Rachich and Reader 1999). Following invasion, purple loosestrife often forms dense nearly monospecific stands, often displacing native species and reducing community diversity (Thompson and others 1987). The success of purple loosestrife may result from its ability to tolerate a wide range of environmental factors, to spread vegetatively, and to tolerate increased disturbance (Gaudet and Keddy 1995; Thompson and others 1987), although which factors are most important is unknown (Fernberg 1997).

Disturbance regimes

While there has been no research specifically examining change in disturbance process such as fire in Region 2 marshes, changes in fire regimes have been extensively studied in the region's upland ecosystems. Since fires rarely originate in marshes, but rather spread from adjacent uplands, research documenting changes in the fire regime of the surrounding landscape are relevant. Studies have documented shifts in the frequency and magnitude of fires in a variety of cover types since Euro-American settlement of the region, in some instances pushing fire regimes out of the HRV. For example, studies in the Colorado Front Range have found that fire frequency increased following initial Euro-American settlement, but declined below historical levels beginning in the early to mid-Twentieth Century as fire suppression became standard policy and improved suppression techniques were developed (Veblen and Lorenz 199; Veblen and others 2000).

In the Great Plains, changes in fire regimes appear to be caused by several factors. Changes in the seasonality and number of ignitions are largely the result of human activities, although lightning fires are still common during the late summer months (Higgins 1984). Regardless of ignition source, there have been changes in the relative size and seasonality of fires compared to historical conditions, a function, in part, of cultural obstacles and practices such as roads, cultivated fields, and heavy grazing (Higgins 1984). Wright and Bailey (1982) estimated fire frequency of 5 to 10 years on level-to-rolling topography and 20 to 30 years in areas with more dissected topography. Fire reconstructions near Devils Tower suggest that prior to 1770, the mean interval between fires was 27 years, while from 1770 to 1900, the fire return interval declined to 14 years (Fisher and others 1987). In the Thunder Basin National Grasslands, the Weibull Median Probability Interval for the entire period of record was 7.4 years; 7.9 years for the non-suppression period (1565 to 1939); and 6.7 years for the suppression period (1940 to 1988) (Perryman and Laycock 2000). Based on the position of scars within annual growth rings, Perryman and Laycock (2000) also suggest that most fires (80 percent) occurred during the latter stages of the growing season or during the dormant period.

Management Opportunities and Constraints _____

Management opportunities

A variety of approaches can be taken to better manage marsh resources. One of the most basic is to improve understanding of existing resources, including marsh abundance, distribution, and condition—the latter being best interpreted in relation to known marsh functions. Such information, in conjunction with proactive planning, can be used to avoid impacts to marshes resulting from management actions and, if impossible, to mitigate impacts. In addition, there are innumerable opportunities for marsh restoration and enhancement throughout the region. Many existing wetlands exhibit poor function, which with relatively modest investments of time and money, can be markedly improved. Likewise, the art and science of wetland creation has improved in recent decades and a wide variety of resources are available to facilitate wetland creation (Campbell and Ogden 1999; Colorado Natural Areas Program 1998; Galatowitsch and van der Valk 1998; Kusler and Kentula 1990; Mancini and Schneller-McDonald 1989; Wheeler 1995).

Although extensive wetlands mapping efforts have been conducted within the region, typically involving some form of remote sensing imagery such as aerial photographs, their utility is often limited. For example, although widely available, NWI maps are often quite dated and can poorly reflect existing conditions, particularly in areas with rapid land use change. Also, digital versions of NWI data are unavailable for many parts of Region 2, reducing their utility to planners. Although existing paper maps can be digitized, this can be a time-consuming and expensive process.

Wetland resources on several National Forests, for example the Bighorn and Pike/San Isabel, have been mapped. These data can be invaluable for conducting broad-scale resource assessments and planning activities such as the Aquatic, Wetland, and Riparian Assessment efforts completed or underway in several Region 2 National Forests (Winters and others 2005). Data can also be used to identify areas for site-specific assessments of wetland condition and threats.

Restoration opportunities

Wetland mitigation, whereby wetland losses are compensated by wetland restoration, creation, or enhancement, is a central component to wetlands policy in the United States (Ambrose 1999; Mitsch and Gosselink 2007). Regulatory requirements for mitigation of impacts to existing wetland resources have been a major driving force behind much of the research into marsh creation and enhancement. However, recent studies evaluating the efficacy of mitigation policies on achieving the goal of “no net loss” of wetlands are less than encouraging. On the basis of area alone, it appears that mitigation requirements have not resulted in equal replacement of lost wetlands (Sifneos and others 1992). When functional attributes are evaluated, most mitigation wetlands fare even worse relative to their natural counterparts (Ambrose 1999). These studies highlight the difficulty in effectively creating wetlands with similar functional attributes as natural systems and the desirability of avoiding impacts whenever possible.

Management constraints

Changes in regulatory mechanisms protecting marshes—Wetland regulations have a long history of controversy and many specific points of practice have been decided by courts rather than by legislators or regulators. The main mechanism governing impacts to wetlands has been Section 404 of the Clean Water Act, which has historically placed regulatory oversight on a range of activities impacting wetlands with the U.S. Army Corps of Engineers. However, recent Supreme Court decisions have effectively removed the Corps of Engineers’ regulatory oversight for most wetlands lacking clear connections to surface water bodies such as streams. Many marshes lack surface water connections to navigable waters of the United States and may therefore be considered isolated under U.S. Corps of Engineers jurisdiction through the Clean Water Act (Tiner 2003; Tiner and others 2002). It is also important to note that silvicultural activities are specifically exempted from Clean Water Act Section 404 regulations.

Climate change—Unlike issues of local or regional scope, there is little that managers can do to prevent climate changes widely predicted to occur in coming decades and centuries. Although there are still considerable differences in opinion on the topic, the general consensus among climate researchers is that global temperatures have risen and are likely to continue to rise. Because of their strong dependence on watershed-scale hydrologic processes, wetlands may be especially sensitive to major shifts in temperature or precipitation.

Specific impacts are difficult to predict and are dependent on the magnitude and direction of change in key climate parameters. Parameters of particular importance to marsh ecosystems are precipitation, including both total amounts and seasonality, and temperature, which affects a range of processes from the scale of individual plants to entire ecosystems. Some regional climate change scenarios call for both increased regional temperatures and precipitation, although whether such changes will actually occur is unknown (U.S. EPA 1998a, 1998b, 1998c; Wagner 2003).

Because of the underlying uncertainty regarding possible changes, it is nearly impossible to develop rigid mitigation plans for marshes. Managers can focus on identifying key marsh resources and instituting baseline data collection and monitoring efforts. With a relatively modest expenditure of time and money, it is possible to collect enough hydrologic and vegetation data to evaluate changes over time. Availability of such baseline data can greatly facilitate the development of adaptive management plans.

6. Historical Range of Variation for Region 2 Fens

Definitions and Concepts of Fens

Fens are peat-accumulating wetlands (peatlands) that receive some of their water supply from surrounding mineral soils (Mitsch and Gosselink 2007). The accumulation of peat, i.e., incompletely decomposed organic matter, is the primary diagnostic characteristic differentiating fens from other wetland types in Region 2, although there are many additional hydrologic and floristic differences. The accumulation of peat is a direct consequence of stable, elevated water tables, which slow decomposition rates and allow for net accumulation of organic matter (Belyea and Malmer 2004; Crum 1988; Glaser 1987; Gorham 1957). In Europe, peatlands are generally referred to as mires with a variety of terminology used to subdivide ecosystems based on water chemistry, floristics, water source, or landform setting (Heathwaite and others 1993; Wheeler and Proctor 2000). Both peatland and mire are general terms, referring to the full range of peat-accumulating ecosystems; the term fen encompasses a subset of these wetlands.

Fens are at least partially supported hydrologically by influxes of groundwater enriched in mineral ions through contact with surrounding bedrock or mineral soils. This differentiates fens from bogs, which are peatland ecosystems that receive their water and nutrients exclusively from atmospheric deposition (Crum 1988; Gorham 1957). For ombrotrophic peatlands (bogs) to form, precipitation must exceed evapotranspiration and create a positive water balance (Bragazza and others 2005; Siegel 1988). Because evapotranspiration exceeds precipitation in much of Region 2, no ombrotrophic peatlands occur (Windell and others 1986).

Soils in peatlands, including fens, are predominantly organic in composition and are classified as Histosols if organic horizons exceed 40 cm in depth within the top 80 cm (U.S. Department of Agriculture 1999). Peat soils have distinctly different physical and chemical characteristics than mineral soils, including low bulk density and high water holding capacity, which influence ecosystem functioning (Moorhead and others 2000; Mulqueen 1986). The specific composition and characteristics of peat soils can vary widely as a function of the botanical composition of peat, degree of decomposition, and mineral content can vary within a stratigraphic sequence and among different peatlands (Glaser 1987). While soils in fens are predominantly organic, areas of mineral soil can occur. In addition, in calcareous fens, accumulated tufa or marl deposits can form (Johnson and Steingraeber 2003). Because peat accumulation rates in the region are slow, on the order of approximately 20 cm/1000 years in many areas (Chimner and others 2002), fens cannot persist in sites with high rates of mineral sediment influx from adjacent slopes.

Fens are common at high latitudes, where cool temperatures, low evapotranspiration rates, and high precipitation create conditions amenable to peat formation. In North America, fens are widely distributed throughout Canada, Alaska, and the Northern Great Lakes states, as well as areas along the Atlantic coast (Mitsch and Gosselink 2007). However, within Region 2, sites with the necessary surplus water balance needed to maintain high water tables throughout the growing season and allow for peat development are generally restricted to wet and cool microsites in the mountains (Chimner and Cooper 2003; Cooper 1998a). Exceptions do occur, for example, fens occur in the Nebraska Sandhills (Steinauer and others 1996), although these represent a small portion of all fens in the region.

Fen geomorphic setting and geochemical characteristics vary across the region (Figure 23). These variables are important drivers of fen vegetation and are central to many fen classification schemes. An understanding of how these variables influence the development, structure, and function of fens is essential for conceptualizing the historical range of variation and possible departures from the HRV due to anthropogenic impacts.

Geomorphic Setting and Principal Ecological Drivers

Geomorphic setting

Within Region 2, fens have formed in a limited range of geomorphic and landscape settings that possess the necessary hydrologic and microclimatic conditions for peat accumulation (Windell and others 1986). Fens form in two general physiographic settings: slopes and basins (Figure 24). Several landform configurations produce groundwater discharge systems capable of supporting fens in montane landscapes. These can include discrete hillslope springs, upwelling springs, closed basins, and open-basin hillslopes.

Fens may occur at discrete springs formed where preferential groundwater flow paths discharge to the surface, for example, at the contact between two rock strata or at slope discontinuities. If aquifers supporting springs are sufficiently large and can maintain high water tables, peat can accumulate. In many broad valleys, springs may occur at or near the toe of hillslopes. Here, multiple groundwater flow paths may coalesce and emerge at the ground surface. Spring mounds may be formed if vegetation completely overgrows and contains an upwelling spring, with the vertical hydraulic pressure of the spring driving vertical accumulation of peat (Figure 25).

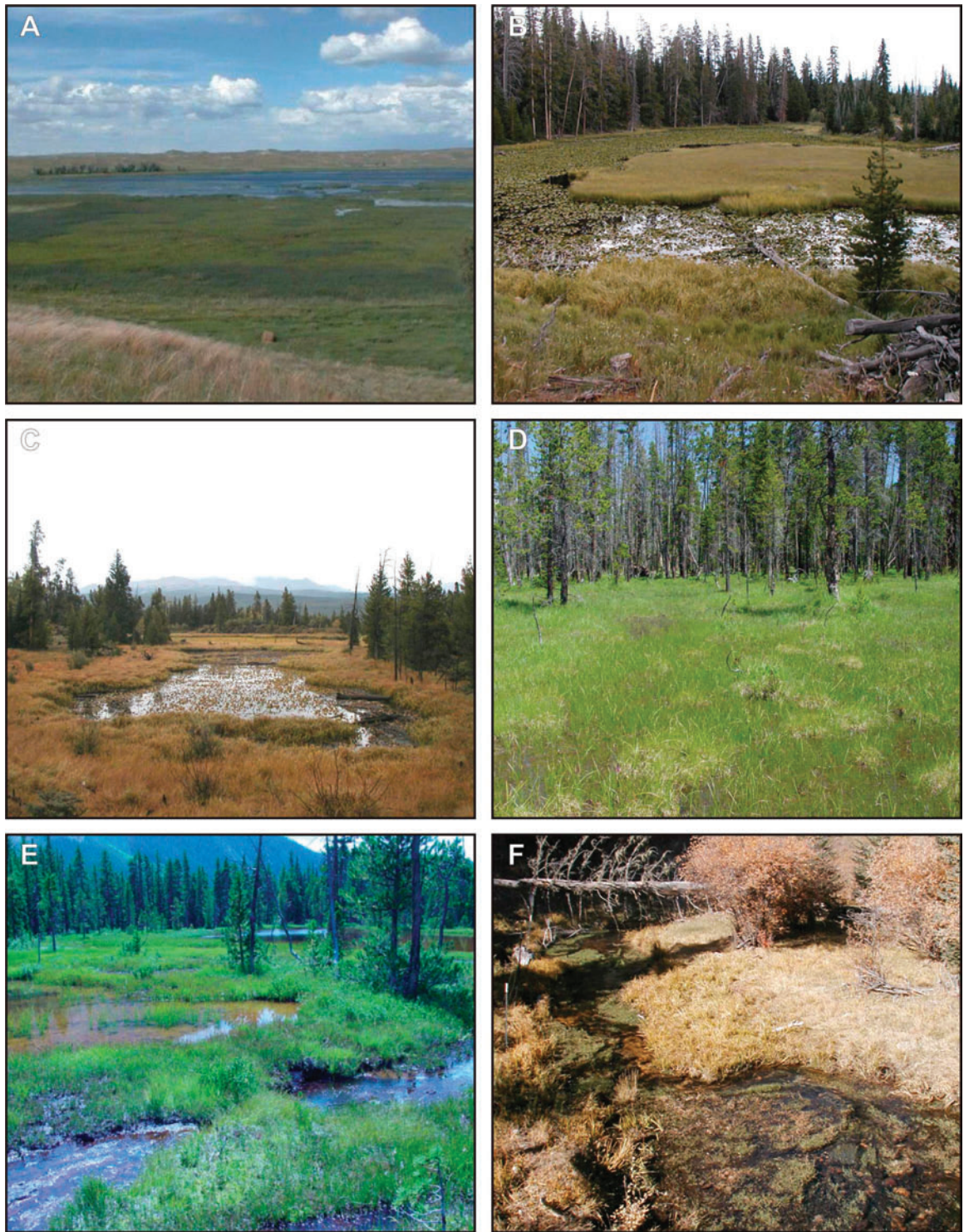


Figure 23—Examples of fens in the five-state area encompassing Region 2: (A) Jumbo Fen, Nebraska; (B) unnamed kettle pond fen, Routt National Forest, Colorado; (C) unnamed kettle pond, Bighorn National Forest, Wyoming; (D) unnamed rich fen, Yellowstone National Park; (E) Mount Emmons iron fen, Colorado; (F) Black Fox iron fen, Black Hills National Forest, South Dakota.

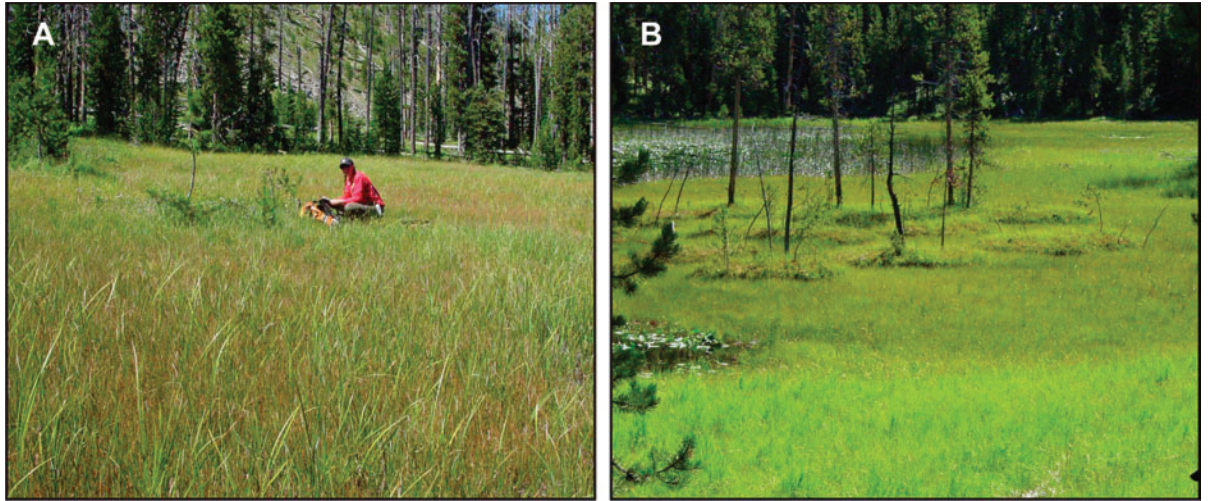


Figure 24—Wyoming fens formed in slope (A) and basin (B) geomorphic settings (photo: D. Cooper).

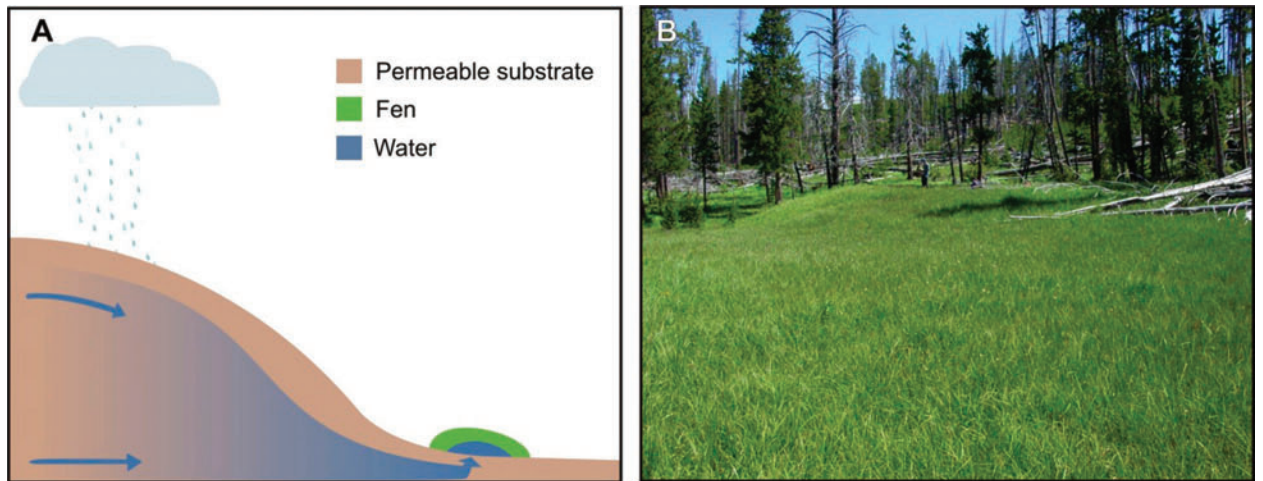


Figure 25—Schematic diagram (A) illustrating a spring mound fen and an example (B) found in Yellowstone National Park (B) (photo: D. Cooper).

Fens also occur in depressions or basins, commonly associated with ponds or lakes (Figure 24b). These features are most abundant in glaciated landscapes. Basin fens may support floating peat mats that are capable of rising and falling as water levels change, allowing the peat surface to maintain contact with the water surface. Basin size and depth are important variables affecting the development and functional characteristics of basin fens (Cooper and Arp 2002).

Fens formed in depressions may support larger, more developed peat bodies than those formed in slope settings. Frequently, they develop complex microtopography (e.g., strings and flarks) and water flow paths, such as flow-around channels as the basin fills and a gently sloping fen develops (Cooper and Arp 2002). In contrast, more steeply sloping fens have smaller, poorly developed peat bodies and may have a greater extent of mineral soil. The rate of water inflow and outflow (flux) is typically greater for fens formed on slopes than on depressions.

Key drivers and ecological processes

Several ecological drivers operating hierarchically affect fen formation and function across Region 2, with the relative importance of each varying depending on the spatial and temporal scale being considered. At the broadest scales, the regional flora, climate, and geology are most important (Bedford 1996; Major 1951); at intermediate and fine spatial scales, chemical and hydrological gradients become key (Cooper and Andrus 1994; Hajkova and others 2004; Tahvanainen and others 2002). Within individual fens, biotic interactions, microtopography, and disturbance processes shape patterns of vegetation and succession (Kennedy and others 2003; Kotowski and van Diggelen 2004; Mulligan and Gignac 2002).

Climate—Climatic variables such as annual precipitation and maximum temperature vary along latitudinal gradients in the region, affecting patterns of fen distribution and abundance. Other characteristics such as the seasonality of precipitation also vary, in part because of the differing influence of regional climate patterns like the El Niño-Southern Oscillation (ENSO) and Pacific Decadal Oscillation (Hauer and others 1997; Hidalgo and Dracup 2003; Schoennagel and others 2005; Sheppard and others 2002).

Because fen water tables are generally high in the spring and early summer due to snowmelt runoff, precipitation patterns in the late summer, following snowpack melt-out, are important for peat accumulation patterns. For example, in the San Juan Mountains of Colorado, the maintenance of high water tables in fens during the late summer depends on the southwestern monsoon providing rain (Cooper and Arp 2002). In Southern Rocky Mountain fens, much of the peat accumulated during the Holocene may have occurred during climate periods when mid- to late-summer precipitation totals were consistently high (Cooper 1998a).

At any latitude, fine-scale variation in key climatic variables is also important. Precipitation and temperature vary as a function of elevation (Barry and Chorley 2003; Hauer and others 1997), in part explaining the greater abundance of fens at high elevations. The physiography of contributing watersheds can indirectly influence hydrologic processes such as the depth of snow accumulation and the rate of melting, thereby affecting water tables in fens.

Geology—A variety of geologic factors affect fen abundance, distribution, biota, and functions. Because fens receive inputs of groundwater, the mineralogy of watersheds can influence water chemistry, which affects biotic composition (Cooper 1996; Cooper and Andrus 1994; Hajek and others 2002; Lemly and Cooper 2011), and ecological processes such as productivity (Chapin and others 2004; Szumigalski and Bayley 1996b; Szumigalski 1995; Thormann and Bayley 1997a) and decomposition (Szumigalski and Bayley 1996a; Thormann and others 2001; Turetsky and Ripley 2005; Verhoeven and Arts 1992). Watershed mineralogy affects groundwater chemistry by contributing minerals through leaching of chemicals in solution and the transport of minerals in suspension (Godwin and others 2002).

A particularly important factor to fens is the abundance of calcium rich rocks in the watershed. Areas with bedrock dominated by granitic and metamorphic rocks often support fens with low pH; while watersheds composed of limestone, dolomite, or shale produce circumneutral to high pH and higher concentrations of mineral ions (Tahvanainen 2004; Tahvanainen and others 2002; Windell and others 1986). For example, highly alkaline and mineralized water discharging into calcareous fens in South Park, Colorado, flows through calcareous glacial outwash, alluvial deposits, and deep bedrock formations (Cooper 1996; Cooper and Sanderson 1997; Johnson and Steingraeber 2003; Sanderson and March 1996).

Surficial geologic deposits, particularly from past glaciations, influence fen distribution and function (Windell and others 1986). During the Pleistocene, valley glaciers formed in many mountainous areas of Region 2, eroding and redistributing large quantities of rock and sediment from watersheds (Richmond 1960, 1986; Thornbury 1965; Wright and Porter 1983). Many areas have experienced multiple glacial epochs, extensively reworking landscapes. The resulting landforms strongly influence contemporary patterns of fen occurrence. For example, fens have formed in kettles, features formed by stagnant ice blocks that were buried in outwash or moraines as glaciers retreated (Menzies 2002). Fens can also be found in drainages partially impounded by lateral or terminal moraines (Figure 26).

Hydrologic regime—At fine and intermediate spatial scales, hydrologic regime is the primary factor governing the structure and function of wetlands, including fens (Mitsch and Gosselink 2007). Relative to other wetland types such as marshes or riparian areas, fens have stable water supplies with water tables at or close to the ground surface for most of the growing season (Windell and others 1986; Winter and others 2001). Unlike marshes, fens do not experience deep inundation, although some microsites such as pools and water tracks can have greater than 20 cm of standing water seasonally (Cooper 1990a).



Figure 26—Two photographs, illustrating at different scales, a lateral moraine dammed basin supporting a fen in Rocky Mountain National Park, Colorado (photos: D. Cooper). The glacier flowed from right to left in the valley shown in the foreground.

Although fens often occur in stream valleys as part of larger wetland complexes, unlike riparian ecosystems, fens do not experience high-velocity surface flows or sediment deposition from fluvial processes. Hydrologic inputs to fens include direct precipitation, surface water, and groundwater. The relative importance of each differs among fens and can vary among microsites within individual wetlands (Koerselman 1989).

All fens receive some water via direct precipitation, with the relative amount scaled to fen area. However, because no ombrotrophic peatlands occur in Region 2, precipitation is likely the least important contributor to fen hydrologic regimes. Much of water entering fens via rain may be lost through evapotranspiration (Gorham and Hofstetter 1971), although accumulated snow pack overlying some fens may be an important source of water to subalpine fens (Windell and others 1986). Microsites, such as the upper portions of hummocks, may be effectively isolated from groundwater and be more dependent on precipitation.

Surface water inputs to fens can occur as sheet flow or channelized flow. Where measurements have been made, flow rates are relatively low, although their importance to fen hydrologic budgets may be significant. Large, channelized streams do not generally occur in fens because high stream energy can lead to peat erosion. Sheet flow, particularly from seasonal snowmelt, may contribute a significant amount of water to fens, although such inputs may be small relative to water stored in the peat body. In larger fens, sheet flow may coalesce to form water tracks, often around the margins of peat bodies (Cooper and Arp 2002; Glaser and others 1981; Heinselman 1970).

Groundwater is the most important source of water to fens. Because of the region's relatively dry summers and the small size of many contributing fen watersheds, precipitation and surface water flows alone are insufficient to support fen hydrologic regimes. In addition to contributing to high water tables, groundwater discharging into fens is cold, further inhibiting decomposition and promoting peat accumulation.

Groundwater in the peat bodies of fens is hydraulically connected to underlying mineral soils (Siegel 1983, 1988). Because of its direct contact with minerals in bedrock or alluvium, groundwater generally has higher mineral ion concentrations than either surface water or precipitation. The highly variable conductivity in peat soils and complex mixing of water sources creates significant physiochemical heterogeneity, an important driver of fine-scale community diversity in fens.

Groundwater entering fens can originate in local, intermediate, and regional groundwater aquifers, with the relative importance of each varying among wetlands (Chapman and others 2003; Godwin and others 2002; Winter and others 2001). For example, calcareous fens in South Park, Colorado, receive groundwater from shallow outwash and alluvial aquifers as well as from deep bedrock aquifers (Johnson and Steingraeber 2003). The specific flow paths taken by groundwater are often complex and influenced by factors such as the geological makeup and physiographic characteristics of contributing watersheds. For example, coarse glacial deposits with high permeability can link recharge and discharge areas, transmitting groundwater to fens (Almendinger and Leete 1998).

Hydrologic regimes within individual fens can be variable, and differences in the amplitude and timing of water table fluctuations can occur among sites such as fen margins, spring discharge zones, or floating mats. Because floating mats rise and fall with changes in pond levels, plants rooted in these environments such as *Carex limosa*, *C. lasiocarpa*, and *Menyanthes trifoliata* may experience little seasonal variance in relative water tables even though water levels in surrounding portions of the fen may drop significantly (Figure 27) (Gage and Cooper 2006b).

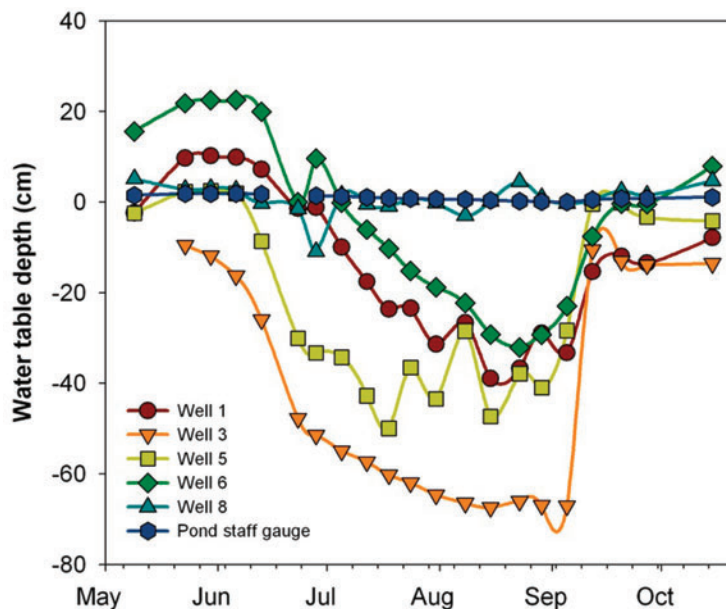


Figure 27—Hydrographs for Buckbean Fen, San Juan National Forest, Colorado, illustrating variability of water table depths in different portions of the fen (Cooper: unpublished data). Well 8 is located within a floating mat.

Hydrologic processes in eolian environments like the Nebraska Sandhills differ from those in montane areas. Because of the high infiltration rates characteristic of sandy soils, little surface runoff occurs following precipitation events (McCarragher 1977). Instead, water infiltrates the ground and contributes to local and regional aquifers. These aquifers discharge to the surface in interdunal areas and support lakes, ponds, and wetlands, including fens (Borgmann-Ingwersen 1998; Steinauer and others 1996). Fens may form when the hydraulic pressure of the groundwater exceeds surface resistance, for example, when groundwater is “mounded” under a dune adjacent to a valley (Bleed 1998; Borgmann-Ingwersen 1998). Hydrologic regimes in these settings are generally quite stable, and radiocarbon dating of peat deposits in Sandhills fens suggests that some may exceed 12,000 years in age (Ponte 1995).

While hydrologic processes vary widely among fens as a function of factors such as geologic and geomorphic setting, overall hydrologic *regimes* are relatively similar across floristic and geographic gradients. As a pre-condition for peat accumulation, all fens, whether in the Black Hills of South Dakota or the San Juan Mountains of Colorado, have water tables at or near the surface for a most or all of the growing season. Although it is common for water tables to drop in the mid- to late-summer in many fens, rarely do they drop to a meter below the ground surface (Figure 27). During extreme or prolonged droughts, water tables may decline more steeply, but if such conditions persist for extended periods of time allowing peat soils to dry out, oxidation of peat will occur, eventually leading to the loss of the peat body.

Likewise, hydrologic regimes in fens with differing floristic composition and water chemistry often share similar hydrologic regimes. For example, hydrologic data from studies of iron fens and extreme rich fens, which exist at near opposite ends of the pH gradient, both have elevated water tables at or near the surface for much of the growing season (Cooper 2003; Johnson 2003).

Water and peat chemistry—Water and peat chemistry vary widely among fens. Several factors influence fen biogeochemistry, including biotic and abiotic processes (Shotyk 1988). The chemical characteristics of peatlands most commonly analyzed by ecologists include alkalinity/acidity, cation concentrations (e.g., Ca^{2+} and Mg^{2+}), and the abundance and form of nutrients such as NH_4^+ and NO_3^- (Bragazza and others 1998). Variation in these chemical attributes among fen types include those associated with the poor to rich water chemical gradient, while those within individual fens include the mire expanse to mire margin gradient identified by ecologists as major controls on the vegetation of peatlands (Cooper 1996; Malmer 1985). Hydrochemical variability is an additional source of environmental heterogeneity, a factor contributing to the high species richness seen in many fens (Boeye and others 1994).

As discussed for geological drivers, the mineralogy of surrounding landscapes is an important factor influencing fen water chemistry. In watersheds where relatively soluble minerals are prevalent, groundwater inputs to fens can contain abundant dissolved solids. In contrast, in areas composed of relatively insoluble minerals such as quartz, the mineral content of groundwater is typically more dilute (Tahvanainen 2004). The presence of minerals in groundwater also influences the pH of fens through the ability of mineral bases to neutralize organic acids produced by decomposing organic matter (Shotyk 1988).

Much of the spatial and temporal variability in fen water and peat chemistry can be attributed to differences in the relative quality and quantity of groundwater entering fens (Chapman and others 2003). Organic acids found in surface water mixes with inorganic solutes contributed by groundwater discharge, often with a significantly different pH (Siegel and others 2006). Complicated flow paths and patterns of groundwater and surface water mixing in fens can lead to high variation in characteristics such as pH and Ca^{2+} concentration. For example, two distinct water sources support an iron fen found near Mount Emmons, Colorado. Water discharging from adjacent slopes passes through pyrite-rich bedrock has very low pH, while water discharging from an underlying moraine has significantly higher pH (Figure 28) (Cooper 2003).

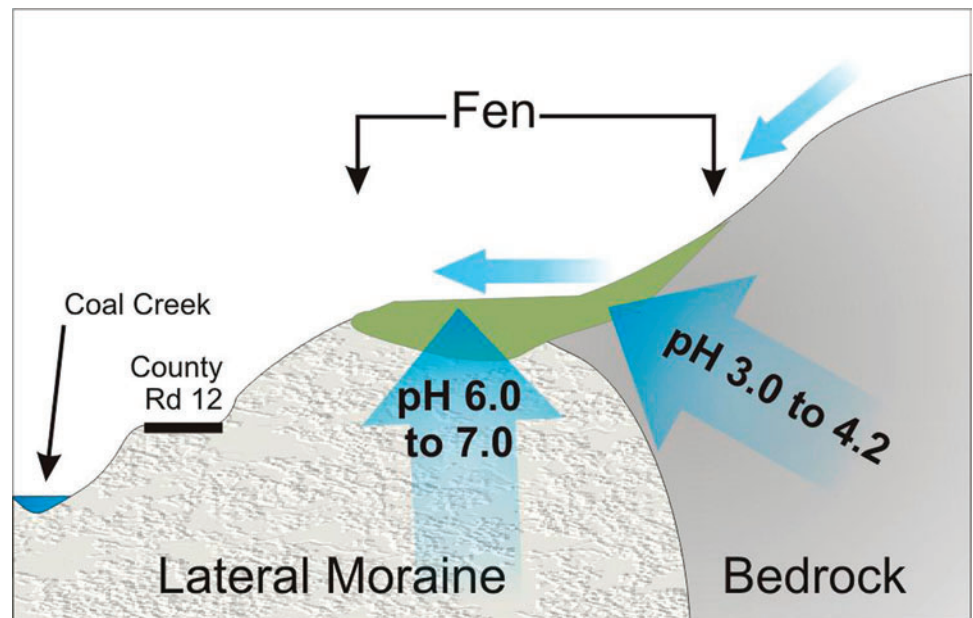


Figure 28—Schematic cross-section of the Mount Emmons iron fen in Gunnison County, Colorado. Groundwater discharging into the fen from bedrock of meta-sedimentary composition (right) is strongly acidic due to high concentrations of iron and sulfur. However, the fen has formed upon a lateral moraine composed of till containing calcareous material, from which it receives inputs of groundwater with higher pH.

In addition to the external factors such as the mineralogy of contributing watersheds, autochthonous factors (i.e., those originating within fens) can also be important influences on water and peat chemistry, particularly at fine spatial scales. For example, decomposition of plant material produces strong organic acids, which, if unbuffered, contribute to the low pH found in some fens (Shotyk 1988). Also important in communities or microsites dominated by *Sphagnum* species are processes of active cation exchange (Clymo 1963; Gies and Lotscher 1973; Spearing 1972). For example, the pH on the top of *Sphagnum*-dominated hummocks may be significantly lower than surrounding areas (Clymo and others 1984).

As with most terrestrial ecosystems, nitrogen is typically the limiting macro-nutrient in fens, although phosphorus may also be limiting in some wetlands (Beltman and others 1996; Mitsch and Gosselink 2007; Thormann and Bayley 1997b). Nitrogen inputs to fens include wet and dry atmospheric deposition and the mineralization of organic matter (Bayley and others 2005). Nitrate reduction, nitrogen (N_2) fixation, and denitrification are the main processes controlling the flux of nitrogen in fens, although the relative importance of each vary widely depending on site-specific hydrologic characteristics (Beltman and others 1996; Oien 2004). For instance, the concentration of nitrate (NO_3^-) in perennially saturated and anoxic sites such as floating peat mats is typically low because nitrifying bacteria are not present (Williams and Wheatley 1988). The importance of atmospheric inputs has likely increased relative to historical conditions as a result of increased anthropogenic inputs from industrial and agricultural activities (Baron and others 2000; Fenn and others 2003a; Fenn and others 2003b; Kittel and others 2002).

Although commonly used to infer nutrient status, pH gradients do not necessarily parallel nutrient gradients. Often, concentrations of nutrients such as NO_3^- , NH_4^+ , and PO_4^{3-} vary more in individual wetlands due to hydrologic factors than among fens of different types (Bedford and others 1999; Bragazza and Gerdol 2002; Bragazza and others 2005). For example, large differences in nutrients are often seen between the edge and center of peatlands (Bragazza and others 2005; Cooper 1990a), although not in all fens (Cooper and Andrus 1994). Variation also can occur vertically within a peat profile (Williams and others 1979).

Microsite development—Peatlands commonly develop microtopographical features, including hummocks, peat mounds, ridges (strings), and pools (hollows or flarks) (Figure 29) (Cooper and Andrus 1994; Foster and others 1988; Glaser 1987). The development of microtopographic features is pronounced in patterned fens (termed “aapamires” in the European literature), which are generally restricted to boreal and subarctic regions, although patterned fens occur throughout the Rocky Mountains (Chadde and others 1998; Windell and others 1986). Microtopographic features form in other fen types, especially peat hummocks.

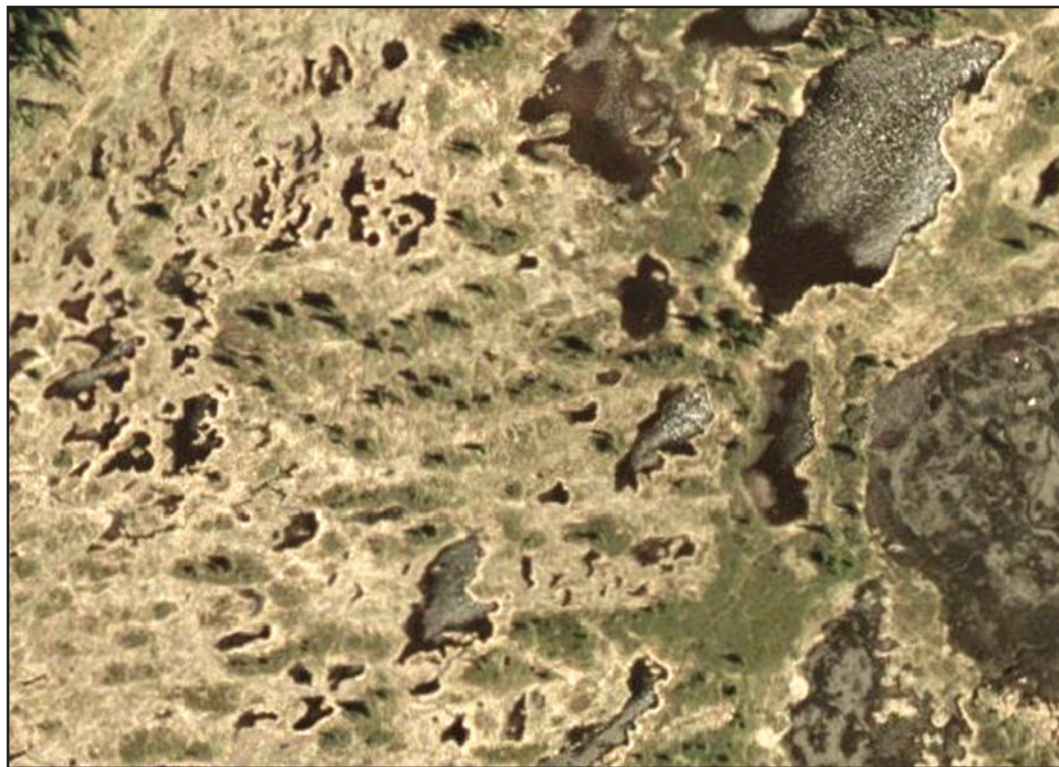


Figure 29—Fen on the Roosevelt National Forest, Colorado, near Left Hand Reservoir, exhibiting well-developed microtopography. Note the alternating pools (dark areas) and strings.

Microtopographic features develop as a function of variable water flow, vegetation development, and peat accumulation. Strings and flarks are typically arranged perpendicular to the predominant direction of water flow (Glaser 1987; Grittinger 1970). Spatial variability in hydrologic regimes drive differences in plant composition, productivity, and decomposition, which over time, lead to the development of microtopographic features (Malmer and Wallén 1999).

Hydrologic variables, pH, and cation concentrations can vary considerably among microsites, influencing vegetation patterns and providing a diversity of niches for individual species. The resulting fine-scale environmental heterogeneity is one factor contributing to the high species diversity found in many fens. Many species commonly have distinct affinities for particular microsites, particularly bryophytes (Bragazza 1997; Pykala 1994; Vitt and Slack 1984). Autogenic processes of peat accumulation and microsite development also influence the temporal dynamics of peatland vegetation. For example, an increase in the relative depth to the water table resulting from vertical accumulation of peat has been found to promote increased shrub cover and shifts in the distribution of monocot species (Bragazza 2006).

Concentrated groundwater discharge can lead to the development of peat mounds, convex accumulations of peat that rise above surrounding areas. In the Nebraska Sandhills, these occur where hydraulic pressure pushes up against a layer of peat and are functionally similar to the spring mounds found in some montane fens (Figures 25, 30). Peat mounds may range in size from a few square meters to over a hectare and can rise over 2 m above adjacent fen and meadow areas (Borgmann-Ingwersen 1998). Peat mounds may also become hydrologically disconnected from groundwater and dry out (Steinauer 1992).

Disturbance processes—Disturbance regimes in fens are a relatively minor driver of vegetation dynamics compared to other wetlands types such as riparian areas. Particular disturbances that may be locally important to fens are fire and grazing, although neither is well understood. Data from both historical and contemporary landscapes are lacking, so inferences must be made from anecdotal accounts and case studies examining effects, often from research conducted outside of the region.

While fire regimes have been extensively studied for forested ecosystems in Region 2, few studies have directly addressed the issue for fens. Unlike boreal regions, where peatlands comprise a large proportion of the landscape, fens in Region 2 occur as relatively small and discrete patches in a matrix of mostly forested landscapes. The likelihood of ignitions occurring in fens is therefore small, and fire must spread from adjacent ecosystems to directly affect fens.

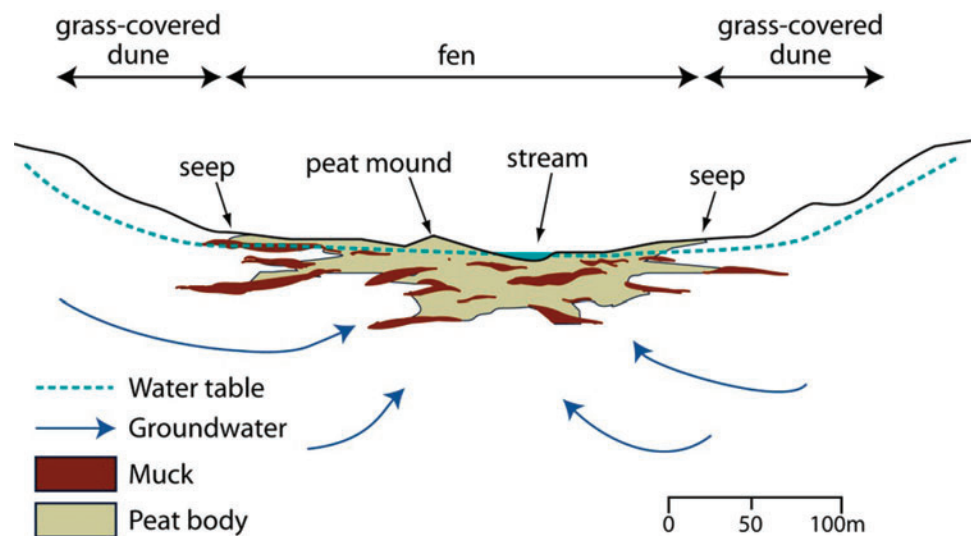


Figure 30—Cross section through a Nebraska Sandhills fen illustrating landscape setting and groundwater flow patterns (Re-drawn from Borgmann-Ingwersen 1998).

Fire regimes vary widely within the region's forests, influenced by cover type, physiography, and climate. The latter is a particularly important factor influencing landscape-scale patterns of fire occurrence, with regional climatic phenomena such as ENSO showing a strong correlation with the frequency of fires and the amount of area burned (Brown and Wu 2005; Kitzberger and others 2001; Veblen and others 2000). The link between regional climate patterns and fire frequency has been demonstrated for Canadian peatlands, where researchers found a positive relationship between the area of peatland burned and several climate variables calculated using a fire weather index (Turetsky and others 2004). Fire regimes of subalpine forests in Region 2 are often relatively long compared to boreal landscapes (Kasischke and Turetsky 2006; Sherriff and others 2001; Weir and others 2000), suggesting that fire may play a relatively small role in the dynamics of fens.

Since fens typically remain saturated for much of the fire season, their ability to sustain fire is low relative to drier upland areas. Although peat will readily burn if sufficiently dry, the presence of saturated areas will generally limit the extent of peat loss. As a result, the direct impact of fire to fens is likely patchy with relatively modest areas experiencing peat loss, except during prolonged droughts. The pattern of direct effects are correlated with microtopographic patterns of surface relief (Benscoter and others 2005a, 2005b; Benscoter and Wieder 2003).

Fire can have a variety of indirect and direct impacts on fens. Through direct plant mortality, fires can influence community composition, particularly as species vary in their resilience to the effects of fire (Bowles and others 1996). For example, fire can maintain open conditions in some fens by selectively killing woody species (Jacobson and others 1991). Fire in adjacent uplands may also indirectly affect fens by increasing water and sediment yield and affecting water chemistry. For example, fens may experience a flush of nutrients such as nitrogen following fire (Anderson and Menges 1997; Dikici and Yilmaz 2006). As the density and cover of upland vegetation increases over time, the magnitude of these effects relative to pre-fire conditions likely declines.

Another natural disturbance potentially affecting fens is native ungulate grazing. Effects can include plant mortality due to herbivory or trampling as well as effects on water chemistry and nutrient availability through urine and fecal deposits (Frank and Evans 1997; Pellerin and others 2006). While anecdotal evidence suggests that local impacts to vegetation can be significant, because of variable population density and migratory behavior, it is unlikely that native ungulates have been a major disturbance agent in fens at broad spatial or temporal scales.

Other disturbance events potentially affecting fens are mass wasting events such as landslides. These may episodically contribute pulses of sediment to fens, affecting ecological functions such as peat accumulation. However, because the physiographic and geological setting of fens is so variable, such events are unimportant for most fens.

The response of fen vegetation to disturbances likely varies in relation to several factors, including the spatial extent and severity of disturbance and the composition of the pre-disturbance vegetation. These influence processes of colonization and recruitment. For example, some fen species can form persistent seeds banks, allowing for rapid re-colonization following disturbance (Leck and Schutz 2005; Schütz and Rave 1999; Sundberg and Rydin 2000). The landscape context of fens may also be important. For example, the proximity of undisturbed fens will influence the availability of propagules for re-colonization (Tackenberg and others 2003).

Fen development and succession—The incomplete decomposition of organic matter in fens is due to reduced microbial activity in anoxic, waterlogged soils. The physical characteristics of all peat soils differ from mineral soils, although there is considerable variability among peat types in characteristics such as bulk density, cation exchange capacity, and hydraulic conductivity (Mulqueen 1986). Peat soils vary depending on the botanical composition of organic material and the depth and degree of decomposition (Glaser 1987). For example, peat derived primarily from mosses differs from that derived from vascular plants (Shotyk 1988).

Moss-derived peat is formed in *Sphagnum*-dominated fens as well as those dominated by “brown moss” genera such as *Scorpidium*, *Callierigon*, and *Drepanocladus* (Glaser 1987). However, within many Region 2 fens, peat soils are largely derived from sedge species, such as *Carex aquatilis*, *C. utriculata*, *C. limosa*, and *C. lasiocarpa* (Cooper 1990a). The dominant structural components of such soils are belowground in origin and are mainly comprised of interwoven roots and rhizomes of sedges. Typically, little above-ground material is incorporated into the peat body because above-ground decomposition rates exceed production; however, anaerobic conditions below-ground retard decomposition and allow for peat accumulation (Chimner and others 2002). Patterns of peat accumulation likely differ in fens dominated by bryophytes such as *Sphagnum* spp., where living biomass and net primary production is concentrated above-ground (Reader and Stewart 1972).

Although the predominant source of organic matter in most peatlands is from vegetation growing onsite, surrounding areas can contribute large amounts of organic matter. For example, needles, cones, and twigs from adjacent Engelmann spruce-dominated uplands contributed the majority of sediment influx to fens in the San Juan Mountains of Colorado (Cooper and Arp 2002). Large trees can fall into peatlands and are often abundant in peat profiles (Carrara and others 1991; Cooper and Arp 2002). The contribution of mineral sediment to fens may be episodic and tied to climate. For example, the stratigraphy of Sandhills fens suggests that during dry climatic periods, sand may drift onto fens from the surrounding uplands, creating distinct sand layers within the peat body (Ponte 1995).

Peat accumulation in fens is ultimately controlled by hydrologic and climatic variables. However, because peat development is largely an autogenic process—driven by the relationship between production and decomposition of organic matter within the fen—changes in vegetation composition and microtopography associated with peatland development and succession can lead to non-linear peat accumulation patterns. For example, modeling and reconstruction of carbon sequestration in a Swedish peatland showed distinct patterns over time, with abrupt changes associated with shifts in vegetation and the dominant bryophyte species, as well as gradual decreases associated with increasing humification of newly formed peat (Belyea and Malmer 2004). However, some studies have found that long-term rates of peat accumulation are relatively steady, despite significant variability in the short-term rates of peat formation (Belyea and Clymo 2001). Such differences may be the result of feedback mechanisms between the rate of peat formation and the thickness of the aerobic surface layer (i.e., acrotelm), whereby individual microtopographic features such as hummocks, lawns, and pools expand or contract vertically in response to fluctuations in the position of the water table, compensating for climate-mediated hydrologic variation (Belyea and Clymo 2001).

Peat accumulation rates measured within Region 2 fens vary, ranging from approximately 1 to 5 cm/century (Table 21). Mean annual carbon accumulation rates for Colorado fens are approximately 25 g C/m² year (Chimner 2000); however, rates can vary widely in relation to hydrologic and climatic factors, and are often negative during dry periods or in hydrologically modified fens (Chimner and others 2010). For example, estimated annual carbon budgets ranged from -142 to 180 g C/m²-year in a fen in Rocky Mountain National Park, Colorado (Chimner and Cooper 2003). Fen ages are also variable, as indicated by radiocarbon dating. Based on ¹⁴C dates, some fens appear to have originated soon after the retreat of glaciers nearly 12,000 years BP (Cooper 1990a), while others are younger (Madole 1976).

Maximum peat depths reported for fens in the Nebraska Sandhills are over 7 m in depth (Borgmann-Ingwersen 1998), and radiocarbon dates from basal peat cores indicate that many of the fens came into existence soon after the formation of the Sandhills, over 12,000 years BP (Ponte 1995). At that time, spruce forests dominated the region and as the glaciers retreated and the climate warmed, boreal species eventually died and semi-arid grasslands developed. However, several plant species with boreal affinities still occur in Nebraska fens (Gage and Cooper 2006b; Steinauer and others 1996).

Table 21—Peat depths, radiocarbon dates, and peat accumulation rates for selected Colorado fens.

Location	Elevation (m)	Basal date YBP	Peat depth (m)	Accumulation rate (mm/yr)
Placer Gulch Bog (Carrara and others 1991)	3,600	8,790±260	0.85	0.10
High Creek Windmill Fen (Cooper 1990b)	3,010	8,270±140	0.90	0.11
Green Mountain Pond (Cooper 1990a)	2,865	11,820±170	1.5	0.13
Big Meadows (Cooper 1990a)	2,865	11,230±170	1.5	0.13
Sacramento Creek (Cooper 1990b)	3,100	9,820±150	2.13	0.22
Buffalo Pass (Madole 1980)	3,146	7,730±250	1.93	0.25
East Lost Park Fen (Cooper 1990b)	3,100	10,080±150	2.64	0.26
Iron Bog (Fall 1997)	2,290	8,260±220	2.20	0.27
Silver Lake Bog (Pennak 1963)	2,979	6,190±300	1.75	0.28
Eureka Gulch Bog (Carrara and others 1991)	3,665	6,180±160	2.40	0.29
Cottongrass Fen (Cooper and Arp 2002)		10,460±240	3.4	0.33
Carpenter's Fen (Cooper 1990b)	3,150	9,280±180	3.20	0.34
McMaster's Fen	3,175	9,220±110	3.33	0.36
Dome Creek Meadow (Feiler and others 1997)		7,800±100	3.62	0.46

If the necessary conditions of water surplus are present to allow peat accumulation, fens may develop through three general processes. Terrestrialization refers to the process by which a water body fills with sediments and peat. In contrast, paludification describes the conversion of uplands to peatland through increased waterlogging of soils as developing peat impedes drainage. Paludification can be initiated by climate change, beaver dams, or geomorphic changes (Mitsch and Gosselink 2007). Flow-through succession, also termed topogenous development, is intermediate in characteristics between terrestrialization and paludification. This process occurs in lake basins that have continuous surface water inflows and outflows. Gradual accumulation of sediment and organic matter in the lake bottom coupled with the peat accumulation from emergent marsh plants along the lake margins eventually result in the lake bottom rising above the water level, diverting stream flows around the main peat body (Mitsch and Gosselink 2007) (Figure 31). Terrestrialization and flow-through succession appear to be of greatest importance within Region 2, while globally, paludification is likely responsible for most of the peatland area (Bauer and others 2003).

A variety of factors may influence fen development and succession. These include basin size, stability of the water level, slope processes, and landform morphology. The developmental trajectory of fens in larger basins can differ from those in smaller basins, even within the same small watershed (Figure 32) (Cooper and Arp 2002). Research suggests that the development of fens is individualistic across landscapes, with varying patterns of peat accumulations in different landform types (Heinselman 1970). The sensitivity of fens to environmental change likely varies, with individual responses depending on both peatland type and the relative stability of hydrological conditions supporting peat accumulation (Bauer and others 2003).

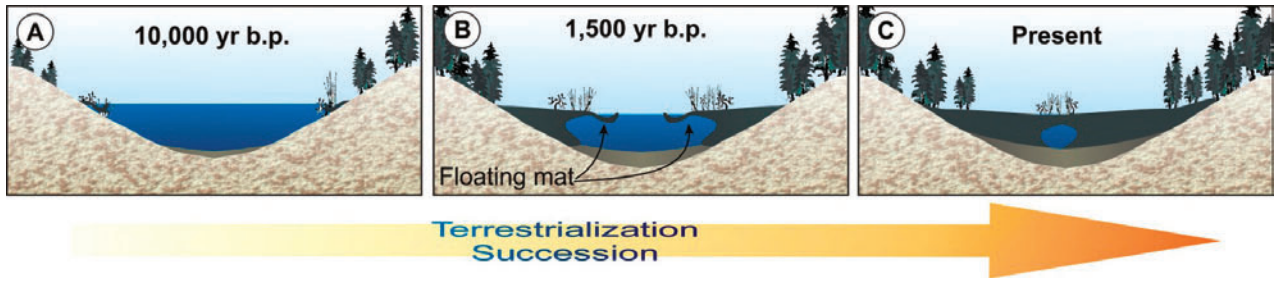


Figure 31—Schematic cross sections (A-C) illustrating the geomorphic and successional development of a hypothetical small kettle pond into a sedge-dominated fen. Early in the basin’s development (A), sedges colonize the margin of the recently formed kettle lake, developing over time into a floating mat dominated by densely interwoven rhizomatous species such as *Carex lasiocarpa*, *C. limosa*, and *Menyanthes trifoliata* (B). Ultimately, as the process of terrestrialization continues, the open water environment characteristic of earlier stages is lost (C).

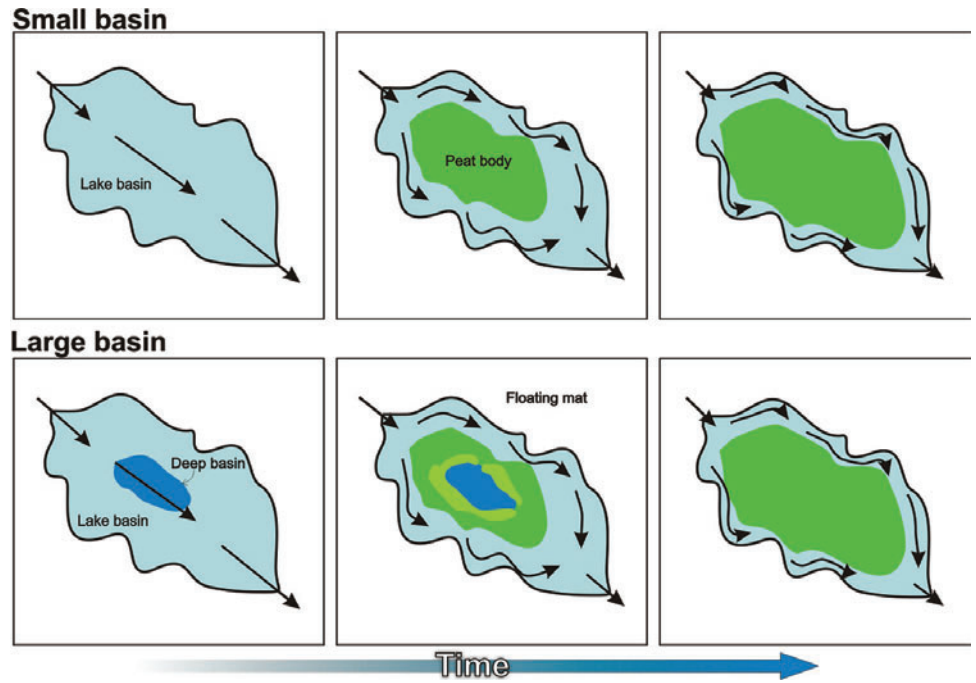


Figure 32—General illustration of the development of two fens formed in basins of different size over time. Arrows indicate principal direction of surface water. The main peat body in the small basin is formed on the basin floor, while a floating peat mat is found during the developmental sequence in the larger basin (re-drawn from Moore and Bellamy 1974).

While successional processes have been extensively studied in peatlands elsewhere (Bauer and others 2003; Campbell and others 1997; Glaser and others 2004a; Heinselman 1970; Vandiggelen and others 1996), this subject has received little study within Region 2. In boreal regions, several successional stages have been described related to peatlands, with wetlands proceeding from pond to marsh, to rich fen, to poor fen, and finally to bog (Muller and others 2003). The widespread application of this successional model, the classical hydrosere, has been questioned for boreal wetlands (Klinger 1996), and it is probably not applicable to many Region 2 fens.

Allogenic processes such as regional changes in climate or isostatic uplift have been hypothesized to be the dominant control on the development of peatlands in boreal and subarctic regions (Glaser and others 2004a, 2004b). Other studies have stressed autogenic processes as key drivers of peatland development (Muller and others 2003). Each process is important, with the relative dominance of each likely varying among individual wetlands and over time (Vitt 1994). In addition, there may be a threshold effect in the relationship between climate and peatland development, whereby climate variables such as precipitation only limit peat accumulation and successional processes past some threshold, with autogenic factors controlling peatland development when climate conditions are wetter (Muller and others 2003).

There are few examples of successional sequences for Region 2 fens. A general successional pattern for basin fens in the Southern Rocky Mountains was presented by Cooper (1990), where open-water aquatic communities dominated by *Nuphar lutea* and *Potamogeton gramineus* proceed through a *Menyanthes trifoliata-Carex utriculata* stage, into a *C. limosa* stage and, ultimately, to a *C. utriculata-C. canescens* community. There is some applicability of this model to other basin fens, like those in Prospect Basin in the San Juan Mountains of Colorado; however, it will not be applicable to sloping fens and more research is needed to characterize the range of variation in successional processes.

Fen Classification and Gradients _____

A number of classification schemes have been applied to wetlands, with varying degrees of utility for peatlands. The criteria used to classify features vary among classification systems. Examples include dominant vegetation, hydrologic characteristics, geomorphic setting, and water chemistry. Each approach has strengths and weaknesses depending on the application.

Classifications based on vegetation are available for many regions. At broad scales, vegetation is well suited to mapping from aerial photographs and other remotely sensed data; however, most geospatial datasets lack sufficient detail to effectively differentiate the vegetation types found in fens. An example of a vegetation classification is the National Vegetation Classification System used by Natural Heritage programs (Comer and others 2003a, 2003b).

Classifications developed for all wetland types such as the Cowardin system used by the National Wetlands Inventory program are of limited utility for discriminating peatlands or among peatland types (Cowardin and others 1979). Under the Cowardin system, all fens fall within the palustrine system and, depending upon their vegetation, may be placed in the moss-lichen, forested, emergent, or scrub-shrub class. Fens in Region 2 would generally be classified as either (1) palustrine, emergent, persistent, with a saturated water regime and organic soils, or (2) palustrine, scrub-shrub with a saturated water regime and organic soils.

Another widely used classification scheme for wetlands is the Hydrogeomorphic (HGM) approach (Brinson 1993a; Cooper 1998a). HGM emphasizes physical variables in classification, specifically geomorphic setting and hydrologic regime. Because these characteristics are such important drivers of ecological processes in wetlands, they provide a robust framework from which to evaluate the ecological functions of individual wetlands. The original framework was intended to be augmented by publication of regional guides; however, relatively few of these have been prepared (Hauer and others 2002a, 2002b), and none deal specifically with fens in the region.

A preliminary classification of Colorado wetlands using the HGM approach was prepared for Colorado and three subclasses were identified relevant to fens. The Depressional 1 subclass includes mid- to high-elevation basins with peat soils as well as lake fringes that may or may not support peat accumulations. Wetlands in the Slope 1 HGM subclass include alpine and subalpine fens and wet meadows on saturated, non-calcareous substrates, while those placed in the Slope 2 subclass include Subalpine and montane fens and wet meadows on saturated calcareous substrates (Carsey and others 2003; Cooper 1998a). Johnson (2005) developed an HGM classification for wetlands within Summit County, Colorado, based on edaphic, hydrologic, and geomorphic characteristics as part of a landscape analysis of cumulative impacts to wetlands.

A variety of other classification systems have been developed specifically for peatlands. For example, Moore and Belamy (1974) classified peatlands based on processes of hydrologic characteristics, identifying three main categories: rheophilous, transition, and ombrophilous. Rheophilous peatlands are influenced by groundwater from outside the immediate watershed; transition peatlands are influenced by groundwater derived only from the immediate watershed; and ombrophilous peatlands are not influenced by groundwater (Moore and Belamy 1974). Subdivisions within these groups are made on the basis of whether flow is intermittent or continuous and whether flows occur on the peat surface or underneath a floating vegetation mat. As noted earlier, ombrophilous systems do not occur in Region 2 because evapotranspiration rates are too great and precipitation is insufficient to support them.

Although the original classification system developed for Scandinavian peatlands referred to species richness, pH is often used to differentiate peatland types (Figure 33), because pH is often strongly correlated with other water chemistry characteristics and vegetation composition (Cooper and Andrus 1994; Windell and others 1986). Bogs and poor fens are highly acidic, while pH values greater than 8 have been reported from extreme rich fens in Colorado (Johnson and Steingraeber 2003). Cation concentrations in peatlands are generally assumed to vary along pH gradients, with low concentrations of cations such as calcium and magnesium at low pH values (Figure 33). However, many studies have demonstrated that the two can often vary (Bragazza and Gerdol 2002).

The majority of fens in the region would likely be described as transitional or moderately rich fens based on water quality and floristic criteria (Cooper and Andrus 1994; Johnson and Steingraeber 2003). While the main hydrological distinction between peatland types is between ombrotrophic bogs and minerotrophic fens, research suggests that, when gradients in chemistry and vegetation composition are included, the primary division among peatlands should be between acidic *Sphagnum*-dominated bogs and poor fens and alkaline, brown-moss-dominated rich fens (Vitt 1994).

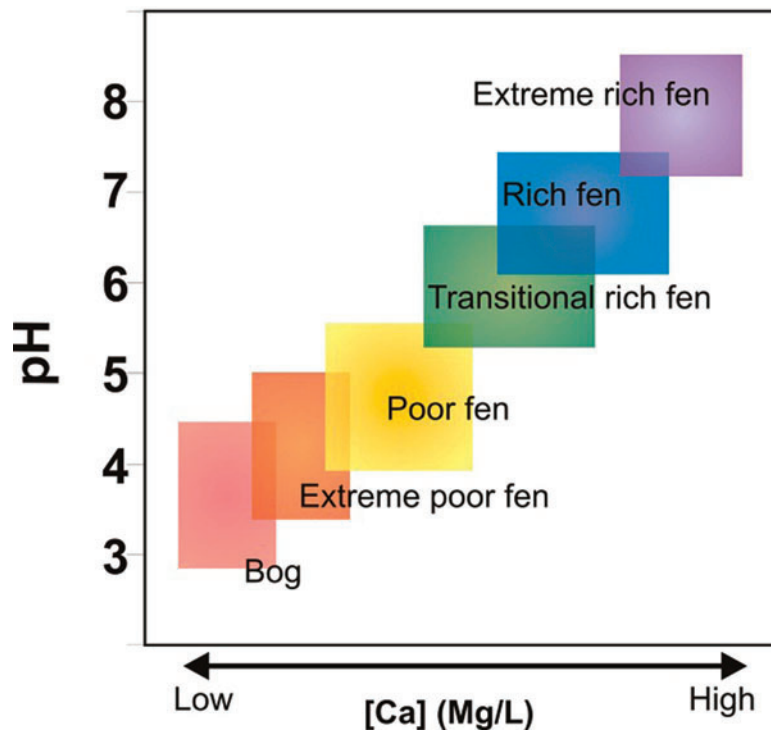


Figure 33—General relation between pH and Ca^{2+} concentrations characteristic of different peatland types. Note that the actual relationship between variables can vary widely.

The most rare fen types in the region are iron fens and extreme rich fens. Both represent extreme physiochemical environments and support species that are either very rare or completely unknown from other fens in the region. Iron fens are found in a limited number of sites in Colorado and the Black Hills (Cooper 2003; Glisson 2003). The reduction of pyrite in groundwater entering these fens produces highly acidic conditions, and poor fen species such as *Sphagnum angustifolium*, *S. fuscum*, *S. balticum* and *Drosera rotundifolia* occur (Cooper and others 2002; Wolf and others 2006). Iron fens are unusual in having very low pH and supporting vegetation typical of ombrotrophic bogs and poor fens, but with mineral ion concentration more typical of rich fens (Cooper 2003). For example, water in the Redwell iron fen in Colorado was found to have conductivity of 304 μS and very high levels of lead, zinc, cadmium, iron, aluminum, yet it had a pH of only 3.5 (Rocchio and others 2003).

Most mountain ranges in the region are dominated by igneous and metamorphic rock. However, a handful of areas such as the Mosquito Range in Colorado and the Gros Ventre Range in Wyoming are composed of calcareous bedrock, such as limestone and support extreme rich fens (Figure 34) (Cooper 1996).



Figure 34—Aerial photo (A) and close-up shots of High Creek fen (B and C), an extreme rich fen in central Colorado. White areas in panel A are accumulated magnesium and sodium salts.

These are among the rarest fen types in North America, having only been described in small portions of California, the Great Lakes region, Iowa, Alaska, and Canada (Johnson and Steingraeber 2003). These fens have extremely high calcium and magnesium concentrations and pH values greater than 7.0. Due in part to their unique chemical characteristics, these fens support a range of species and communities found nowhere else in Region 2 (Cooper 1996; Cooper and Sanderson 1997; Johnson 2003; Lesica 1986).

Fen Vegetation in the Region ---

Fens may be floristically rich, supporting numerous rare species and community types. For example, fens harbor over 10 percent of the state plant species of special concern in Wyoming; while on the Shoshone National Forest, they support 26 percent of the state species of concern (Heidel and Laursen 2003b). Many regionally rare species have circumboreal affinities and are at or near the edge of their range in Region 2 (Gage and Cooper 2006a, 2006b; Hulten 1968; Weber 2003).

Natureserve (2006) recognizes approximately 20 fen vegetation associations, the majority of which occur as part of the Rocky Mountain Subalpine-Montane Fen ecological system (CES306.831). A variety of additional classifications have been developed outside of the National Vegetation Classification System as part of site-specific studies of fens (Cooper 1990a; Cooper 1996; Cooper and Andrus 1994; Cooper and others 2002; Johnson 1996; Johnson 2003). Vegetation in fens is typically dominated by species of *Carex*, *Juncus*, *Eleocharis* and *Calamagrostis* (Windell and others 1986) (Table 22), and while a variety of herbaceous dicots also inhabit fens, overall cover is generally low. Clonal sedges such as *Carex utriculata* and *C. aquatilis* are among the most common dominants, although a wide variety of other sedges also occur. Communities dominated by grasses and rushes are less common and are often most prevalent along fen margins, particularly where fens abut other wetland types such as wet meadows. Examples of common species are *Calamagrostis canadensis*, *Calamagrostis stricta*, and *Juncus arcticus*.

Although the cover of herbaceous dicots is typically low, some species such as *Menyanthes trifoliata* are dominants in certain community types. Common dicots include *Pedicularis groenlandica*, *Caltha leptosepala*, and *Polygonum bistortoides*. Shrub-dominated communities, sometimes referred to as carrs, are also common in montane and subalpine environments. The most common shrub species in the region are *Salix planifolia*, *S. wolfii* and *Betula nana*. In contrast to boreal regions, ericaceous shrubs are often a minor component of vegetation in Region 2 peatlands. Forested fens (“treed fens”) are also widely distributed in subalpine environments, although these appear to be less common than in boreal regions (Johnson 1996, 1997). The most common overstory dominants in treed fens are *Picea engelmannii*, *P. glauca* and *Pinus contorta*, which have genotypes that can tolerate the saturated conditions found in fens.

Table 22—Fen vegetation associations recognized under the National Vegetation Classification System in Colorado, Wyoming, Nebraska, South Dakota, and Kansas (NatureServe 2003; NatureServe 2005).

NVCS ID	Association Name
CEGL001562	<i>Carex utriculata</i> Herbaceous Vegetation
CEGL001806	<i>Carex buxbaumii</i> Herbaceous Vegetation
CEGL001810	<i>Carex lasiocarpa</i> Herbaceous Vegetation
CEGL001811	<i>Carex limosa</i> Herbaceous Vegetation
CEGL001825	<i>Carex simulata</i> Herbaceous Vegetation
CEGL001831	<i>Dulichium arundinaceum</i> Seasonally Flooded Herbaceous Vegetation
CEGL002739	<i>Ledum glandulosum</i> Shrubland (Cohen and others 2003)
CEGL002898	<i>Carex aquatilis</i> - <i>Sphagnum</i> spp. Herbaceous Vegetation
CEGL002899	<i>Betula nana</i> / <i>Sphagnum</i> spp. Shrubland
CEGL002900	<i>Kobresia myosuroides</i> - <i>Thalictrum alpinum</i> Herbaceous Vegetation
CEGL002901	<i>Kobresia simpliciuscula</i> - <i>Trichophorum pumilum</i> Saturated Herbaceous Vegetation
CEGL002922	<i>Carex utriculata</i> Perched Wetland Herbaceous Vegetation
CEGL005887	<i>Betula nana</i> / <i>Carex</i> spp. Shrubland
CEGL002189	<i>Betula pumila</i> - <i>Salix</i> spp. prairie fen shrubland
CEGL001188	<i>Salix candida</i> / <i>Carex utriculata</i> Shrubland
CEGL002383	<i>Carex lasiocarpa</i> - <i>Calamagrostis</i> spp.-(<i>Eleocharis rostellata</i>) Herbaceous Vegetation
CEGL002390	<i>Carex interior</i> - <i>Eleocharis elliptica</i> - <i>Thelypteris palustris</i> Herbaceous Vegetation
CEGL002041	<i>Carex pellita</i> - <i>Carex</i> spp.- <i>Schoenoplectus tabernaemontani</i> Fen Herbaceous Vegetation
CEGL002267	<i>Carex prairea</i> - <i>Schoenoplectus pungens</i> - <i>Rhynchospora capillacea</i> Herbaceous Vegetation
CEGL002268	<i>Carex</i> spp.- <i>Triglochin maritima</i> - <i>Eleocharis quinqueflora</i> Marl Fen Herbaceous Vegetation

Fens in the region also support extensive bryophyte cover. *Sphagnum* spp.-dominated fens are uncommon in Region 2 compared to boreal regions, and are largely restricted to acidic peatland types such as iron fens and some nutrient poor fens. *Sphagnum* species can also occur in microenvironments, such as on hummock tops, in more minerotrophic peatlands (Figure 35) (Johnson 1996; Zoltai and Johnson 1985). Although *Sphagnum* species are most common in very acidic peatlands, some species, for example *S. contortum*, can be found with rich fen indicators (Janssens and Glaser 1986). Many of the *Sphagnum* species found in the region occur in just one or a few locations (Cooper and others 2002). More commonly in Region 2, bryophyte communities are dominated by brown-moss species in the genera *Drepanocladus*, *Aulacomnium*, and *Tomentypnum*, which are characteristic of rich fens.

Species diversity varies among fen types and is typically lowest in nutrient-poor systems such as poor fens or in microsites characterized by either extremely wet or acidic conditions. While fens with very acidic or alkaline pH often support low species richness, they are important for regional biodiversity, supporting species that are rare elsewhere in Region 2 (Cooper and others 2002; Cooper and Sanderson 1997; Rocchio 2006b). The most important factors influencing patterns of plant occurrence and distribution differ among species and life forms (i.e., moss vs. sedge) (Gignac 1994). For example, vascular plant distribution appears to be influenced more by nutrient levels, while mosses respond more to gradients of acidity and cation concentration (Chee and Vitt 1989).



Figure 35—Bryophyte-dominated hummocks in fen, Rocky Mountain National Park, Colorado (photo: E. Gage).

The relative importance of environmental variables also differs depending on the range of peatland types being analyzed. For example, water and peat chemistry are typically the primary factors segregating habitat types when the peatlands that fall along the full pH range are compared, while water table depth gradients assume primacy when acidity-alkalinity gradients are more narrowly defined (Belland and Vitt 1995; Bragazza and Gerdol 1999; Cooper and Andrus 1994; Vitt and others 1995). For example, the wettest microsites (e.g., floating mats, pools, and water tracks) may support species such as *Carex lasiocarpa* or *C. limosa*, while species such as *C. utriculata*, *S. planifolia*, and *Calamagrostis canadensis* are common along fen margins (Bragazza and Gerdol 1996; Cooper and Andrus 1994; Slack and others 1980). Often, vegetation responds to complex gradients comprised of several physiochemical variables. For instance, the mire margin-mire expanse gradient described for many peatlands is thought to include several ecological factors related to the degree of minerotrophy, peat aeration, and hydrology (Bragazza and others 2005; Wheeler and Proctor 2000).

Vertical zonation of vegetation is common in fens with well-developed microtopography. Different *Sphagnum* spp. often occupy distinct niches on hummocks or peat mounds (Figure 36) (Andrus and others 1983; Mulligan and Gignac 2001; Vitt and others 1975). Species often segregate along gradients of water table and water chemistry and are thought to be shaped in part by competitive interactions among species (Bragazza 1997). Although more extensively studied for *Sphagnum* species, brown-moss species also show distinct niche separation (Kooijman and Bakker 1995; Kooijman and Hedenas 1991).

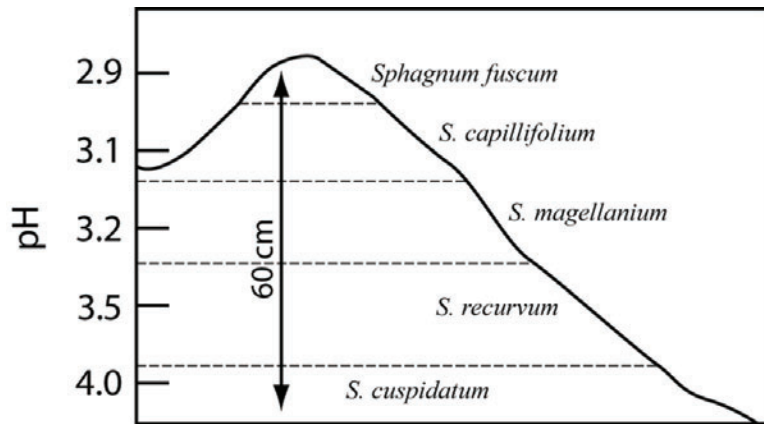


Figure 36—Relationship of five *Sphagnum* species to pH along a hummock-hollow complex in a northern Michigan peatland (re-drawn from Vitt et al. 1975).

Vegetation composition can vary widely among fens, even those located in close proximity to one another. Such differences can be caused by differences in fen morphology, hydrology, and chemistry, as influenced by age and geomorphic setting (Cooper 1996; Cooper and Andrus 1994; Cornwell and Grubb 2003; Locky and Bayley 2006). For instance, although located in the same watershed and geological setting, five different fens in the San Juan Mountains of Colorado had little overlap in the dominant communities present in each fen (Cooper and Arp 2002). In general, moderate rich fens share more species in common with extreme rich fens than with poor fens, although the three fen types are separated by surface water pH, calcium, magnesium, and conductivity (Chee and Vitt 1989).

Diversity within individual communities is often low, as many fen dominants are clonal and form relatively uniform stands. However, species diversity within entire fens can be high, particularly where significant structural complexity in the form of fallen trees, strings, flarks, or ponded water is present. Fen age may also be a contributing factor; older fens may act as refugia, supporting vegetation once more widespread in the region (Cooper and Arp 2002). Vegetation patterns in fens often exhibit distinct zonation patterns. Complex gradients broadly structure vegetation patterns in relation to the morphology and hydrology of the wetland (Cooper 1996; Cooper and Andrus 1994; Johnson 1997). The patterns of vegetation structure, as well as the relative importance of environmental processes on vegetation, vary depending on the scale evaluated (Hajkova and others 2004).

Among the most important factors influencing patterns of species distribution and abundance are variation in water table elevation, pH, degree of minerotrophy, water temperature, and substrate type (Bragazza and Gerdol 1999; Cooper 1990a; Johnson and Steingraeber 2003). Complicating interpretation, the particular gradients of greatest importance for vascular species and bryophytes can differ (Bragazza and Gerdol 1996; Gerdol 1995; Hajkova and Hájek 2004). In addition to within fen variability, vegetation can widely differ among fens in the same watershed. Differences may be the result of variation in relative age, hydrologic regime, and geomorphic setting of fens.

HRV of Fens in Region 2

Overview of anthropogenic impacts

Humans have altered fens in a number of ways. These activities and their associated impacts can be broadly grouped into on-site and off-site impacts, although hydrologic modifications can be in both groups. The extent and magnitude of anthropogenic impacts to fens varies widely geographically and by fen type. Some impacts (e.g., peat mining) are locally severe but affect a relatively small area of fen, while others (e.g., atmospheric deposition of pollutants) may be more widespread but are subtle in their ecological effects (Chimner and others 2010).

Peat mining—Peat mining, including pre-mining drainage, is the most severe site-level impact to a fen because the entire peat body, vegetation, and soil seed bank are removed (Figure 37). Peat extracted from fens in the region comprise a small portion of the total national supply, as most commercial peat originates in Canada (Crum 1988). However, because the total area of fens in the region is so small, impacts from even small peat mining operations can be significant. In addition to changing the substrates available for plant growth, peat mining may cause significant hydrologic changes. Fens are typically drained using ditches prior to mining (Crum 1988), resulting in lower water table elevations and the oxidation of any peat that remains (Laiho 2006). The harvesting of peat reduces water storage capacity and the ability of fens to trap pollutants and often results in negative effects on water quality (Cooper 1990b).



Figure 37—Fen in the Mosquito Range of Colorado mined for peat. Note that even after more than two decades, almost no plants grow from natural colonization in the mined area (Photo: D. Cooper).

In Colorado, it is estimated that 200 to 500 acres of fen have been impacted by peat mining, representing less than 1 percent of the total fen area in the state (USDI FWS 1997). No estimates are available for other states in the region. While the total area of fen impacted is not large, most of the mining has occurred in just a few areas and many ecologically significant fens have been impacted. For example, High Creek fen in South Park, Colorado (the best representative of an extreme rich fen in the southern Rocky Mountains) was partially mined prior to its purchase by The Nature Conservancy (Cooper and MacDonald 2000; Johnson and Steingraeber 2003; Sanderson and March 1996).

Mineral extraction—Lode mining represents one of the most significant environmental impacts in Region 2 (Limerick and others 2005; Wohl 2005). Although mining within fens is uncommon, instances of direct impacts have been documented (Figure 38). Direct effects include peat removal, plant mortality, changes to community structure, and alteration of groundwater flow paths.

More important to fens on a regional scale are the indirect effects of mining operations in watersheds where fens occur. The most important of these are changes in the quality and quantity of surface water and groundwater entering fens. Frequently, the water draining from waste-rock piles, mill tailings, and mine adits has very low pH and elevated concentrations of heavy metals due to the exposure of sulfide minerals (e.g., pyrite). These effects on water quality often persist long after the cessation of mining activities (Balistrieri and others 1999; USDA FS 1995).



Figure 38—Mining within an iron fen, near Ophir, Colorado (Photo: R. Chimner).

Generically referred to as acid rock drainage, mine-contaminated waters can negatively impact aquatic organisms as well as a variety of ecosystem processes such as plant production and decomposition. Research in Colorado fens found significant differences in the decomposition rate of *Carex aquatilis* between pristine and acid rock drainage-affected fens. Decomposition rates in pristine wetlands were comparable with boreal rich fens, while those in polluted fens were more similar to poor fens and bogs (Arp and others 1999).

Direct hydrologic modifications—Direct hydrologic modification is one of the most widespread impacts to fens, although no statistics are available on the extent of such modifications. Fens have been ditched and drained for a variety of purposes, most of which are secondary in nature such as to increase forage production and accessibility for livestock. In addition, ditching typically precedes other activities such as peat mining or real estate development (Crum 1988; USDI FWS 1997).

The most direct impact to fens from ditching is lowering of the water table, the effects of which can persist long after the ditches are abandoned. Ditches through Big Meadows fen in Rocky Mountain National Park, Colorado, were still effectively intercepting and diverting water nearly 75 years after abandonment (Cooper 1990a; Cooper and others 1998). The resulting lower water tables facilitated invasion of the fen by *Deschampsia cespitosa*, a native grass common in wet meadows but not fens (Cooper and others 1998). Similar effects may also promote invasions by non-native species (Figure 39) and a reduction in the suitability of habitat for species found in wet microsites such as *Carex limosa* (Gage and Cooper 2006b). Changes to hydrologic regimes can result in the loss of fen obligates and changes in the successional trajectory of impacted wetlands (Jukaine and others 1995).

Drainage of fens also impacts the processes of peat accumulation and carbon storage. Effects include increased CO₂ flux from peat decomposition, an effect exacerbated by enhancement of decomposition by the addition of easily decomposable material from root exudation (van Huissteden and others 2006). Drier conditions in fens can cause a shift from net accumulation of carbon to loss through oxidization (Chimner and Cooper 2003). Such changes may eventually result in the complete loss of the peat body.

In addition to ditching, groundwater pumping may deplete aquifers and represent an additional threat to groundwater-dependent wetlands like fens (Chimner and Cooper 2003). For example, groundwater pumping at Crane Flat in Yosemite National Park was lowering the water table in an adjacent fen (Cooper and Wolf 2006). Hydrologic modifications such as streamflow diversion may reduce the amount of water entering fens, deleteriously affecting vegetation and ecological processes (Chimner 2000; Chimner and Cooper 2003).

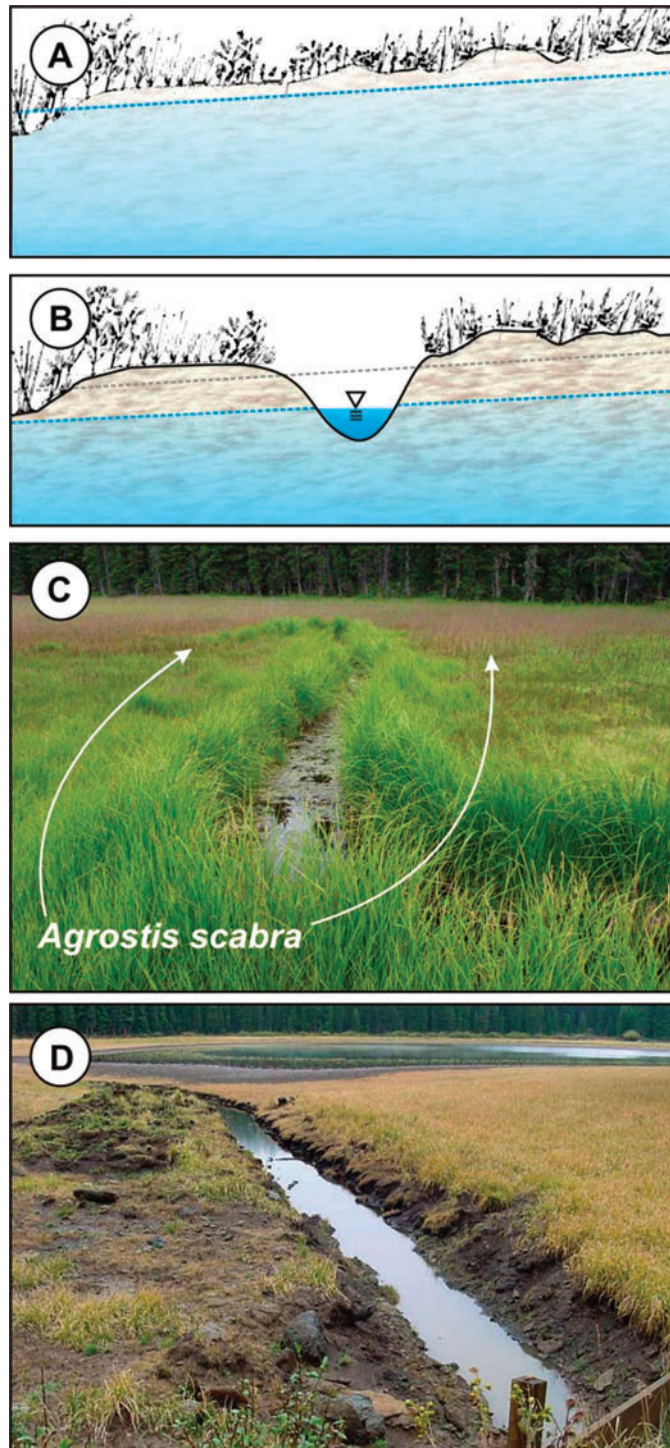


Figure 39—Diagram illustrating water table in a hypothetical fen before (A) and after (B) ditching. The Grand Mesa National Forest, Colorado fen pictured in panel (C) has been ditched, lowering the water table and facilitating invasion by the non-native *Agrostis scabra*, the reddish vegetation in the back of the photograph (photo: D. Cooper). Panel (D) is a photograph from another fen on the Grand Mesa National Forest, Colorado, that has recently been ditched (photo: G. Austin).

Livestock—Although widely examined in other riparian areas (Marlow and Pogacnik 1986; Parsons and others 2003; Roath and Krueger 1982; Vavra and others 1994), livestock impacts on fens are little studied in Region 2. Anecdotal evidence suggests that livestock spend little time foraging in wet areas like fens. However, fen species can be a significant source of forage for livestock (Catling and others 1994; Hermann 1970), especially late in the summer or during extended drought.

The most obvious impact to fens from livestock is direct plant mortality, either through consumption or hoof action. The effect is not likely experienced equally by all plant life forms. For example, species with rhizomes may be selected against and taprooted and short-lived species favored under heavy grazing pressure. Among clonal species, plant architecture may influence response (Martin and Chambers 2001). Some studies have shown that species with fast spreading clonal organs such as stolons are favored by grazing, as they can effectively colonize gaps such as hoof prints (Stammel and Kiehl 2004; Stammel and others 2003).

Since establishment and recruitment from seed is thought to be relatively rare in fens, species incapable of rapid vegetative growth may be more vulnerable to trampling impacts. However, disturbance from livestock may positively benefit some species by creating germination niches for seeds (Smith and others 2003; Stammel and others 2003). However, the negative effects of soil compaction and altered patterns of water and light availability on diversity probably outweigh positive effects such as the promotion of subordinate species; overall, livestock use appears to negatively affect species richness in fens (Stammel and Kiehl 2004). Additional changes include shifts in the relative dominance of species through effects on the competitive ability of plants (Ausden and others 2005; Martin and Chambers 2001; Smith and others 2003). Trampling has been linked to decreases in moss cover and richness and increases in bare peat (Arnesen 1999; Rawes and Hobbs 1979).

Additional effects associated with livestock include hummock development, as rhizomes of clonal sedges are broken by hooves (Figure 40). Waterlogged peat soils are highly susceptible to displacement and hoof punching, and recovery time of sites to pre-disturbance conditions can be decades to centuries long (Middleton 2002; Smith and others 2003). Trampling may increase the amount of bare peat, leading to increases in surface runoff and erosion (Pellerin and others 2006). Livestock can also affect fens through the addition of nitrogen via urine and feces (Blank and others 2006).

As with cattle, native ungulates can have a significant effect on fens. Elk, moose, and deer, for example, can alter nitrogen availability through urine and feces inputs (Frank and Evans 1997). However, the greatest impact from native ungulates is likely trampling. For example, trampling by deer destroyed surface vegetation and increased the area of bare peat in Quebec peatlands (Pellerin and others 2006).

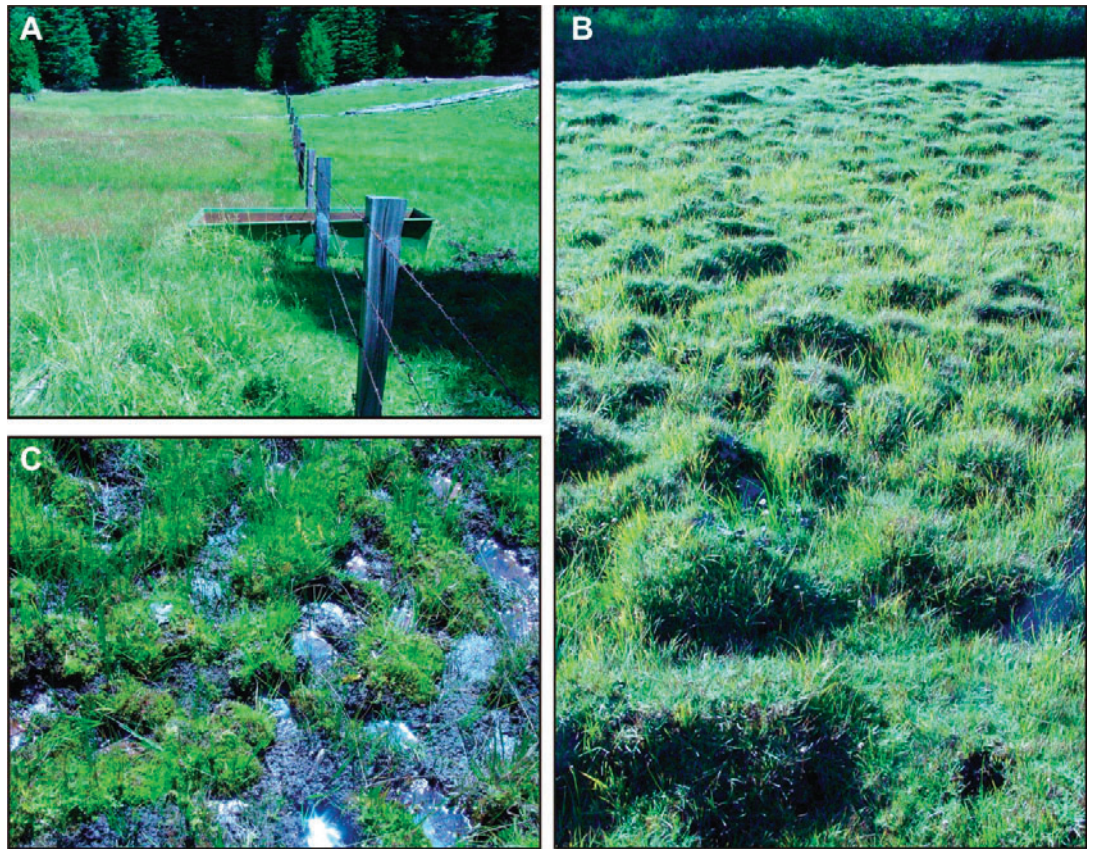


Figure 40—Fen subjected to livestock herbivory. Note difference in vegetation at (A) fenceline, (B) hummock formation, and (C) hoof prints in peat body (photos: D. Cooper).

Presumably, where ungulate populations have remained within their historical range of variation, impacts to fens have been modest and localized. Where populations have exceeded their HRV, as has been documented in several areas in the region (Coughenour and Singer 1996; Lubow and others 2002; Singer and others 1998), impacts may be more significant.

Water development projects—Most of Region 2 has experienced water resource development, including stream diversions and storage reservoirs in the mountains and plains. As noted earlier, stream diversions affect many of the region’s streams, reducing surface water inputs to fens as well as the amount of water entering aquifers necessary to support wetlands. Construction of storage reservoirs are an additional direct impact. Because fens occur in topographic low points, impoundments may lead to their flooding (Figure 41). No statistics are available to evaluate the extent of historical impacts to fens.

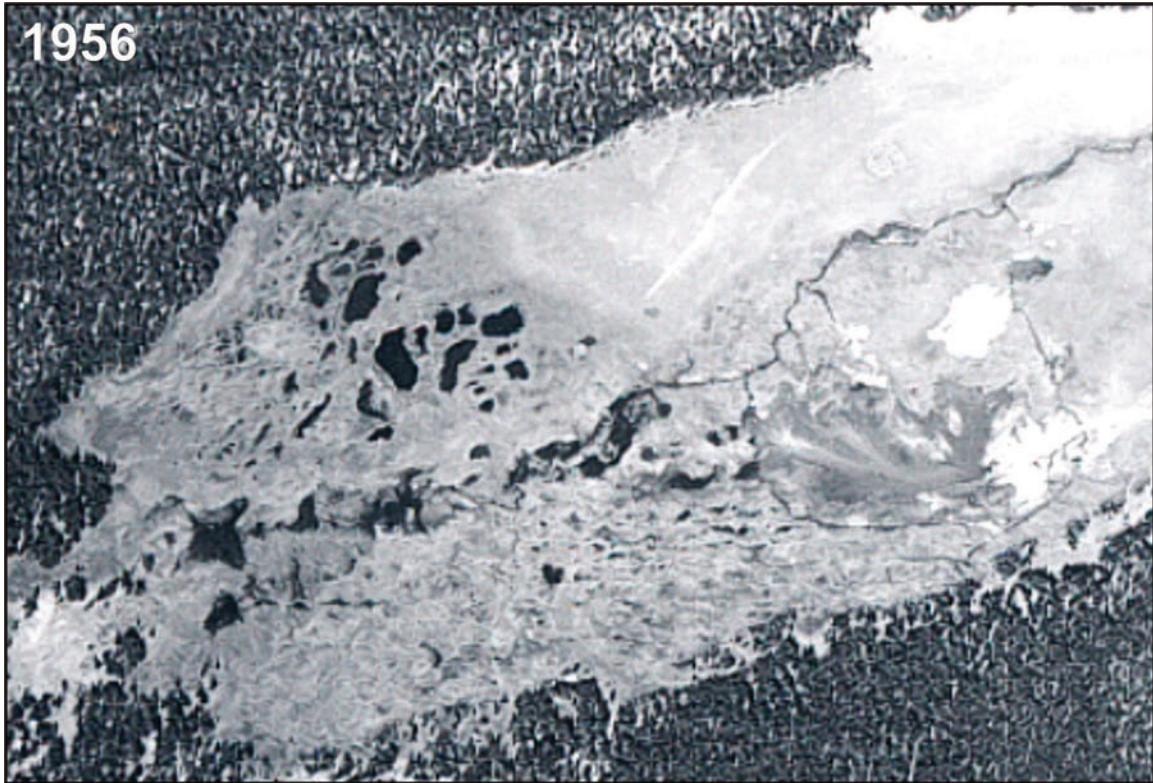


Figure 41—Fen in 1956 and in 2004 following construction of Left Hand Reservoir, Boulder County, Colorado, illustrating impacts from water resource developments. Note that in the 1956 photograph, the fen had already been ditched and mined in the bottom left part of the photo.

Roads and transportation infrastructure—Roads and related infrastructure can directly and indirectly impact fens. Where roads are constructed through wetlands, they can directly impact vegetation and hydrologic processes (Forman and Sperling 2002). In addition, transportation infrastructure can indirectly affect fens through changes in watershed-scale hydrologic processes. Culverts and ditches associated with roads and trails can alter natural drainage patterns, reduce interception and infiltration rates due to the removal of vegetation and soil compaction, and alter the hydrologic response of basins to annual snowmelt runoff and storm events (Jones and others 2000). Typical hydrologic responses involve more rapid overland flow and hydrograph responses to precipitation events, potentially causing erosion or increases in the sediment flux to affected fens.

Roads may impact fens by degrading water quality, thereby negatively impacting plant species that are dependent on specific water chemistry (Panno and others 1999; Wilcox 1986a, 1986b). Specific pollutants include combustion by-products and oil from vehicles, as well as chemicals used for dust abatement. Road salt used for de-icing may negatively impact fen species, particularly bryophytes (Pugh and others 1996; Wilcox and Andrus 1987). At sufficient concentrations, runoff can cause significant decreases in species richness, evenness, and abundance (Richburg and others 2001). Although reliable statistics regarding road abundance are available, there are no data from the region specifically examining the relationship between roads and fen function.

Roads may indirectly affect fens by facilitating the spread of exotic plant species. Disturbances from road construction or maintenance create sites conducive to the establishment of many exotics, while vehicles and increased human traffic can serve as dispersal agents for weed propagules (Gelbard and Belnap 2003; Parendes and Jones 2000). Off-highway vehicle (OHV) trespass onto fens occurs in many National Forests, disturbing fen vegetation and causing ruts that are capable of intercepting sheet flow on the surface of fens. OHV use in or near wetlands may also affect fens by contributing pollutants from inefficient combustion and engine emissions (Havlick 2002). Although such impacts may only affect a small number of fens, the effects are slow to heal.

Exotic species—Although a variety of exotics can invade wetlands, fens are not conducive to aggressive exotics such as Canada thistle (*Cirsium arvense*) or introduced pasture grasses such as timothy (*Phleum pratensis*). These species are more characteristic of wet meadows and typically only invade fens following hydrologic alterations, such as ditching. Under conditions of excessive nutrient loading, native species such as *Calamagrostis canadensis* or *Typha latifolia* can overtake wetlands, including fens, forming monotypic stands and reducing community diversity (Drexler and Bedford 2002; Zedler and Kercher 2004).

Beaver trapping—Beavers may influence the form, function, and successional dynamics of some fens (Chadde and others 1998). In low-gradient landscapes, beavers may initiate fen formation by creating ponds that are subsequently invaded by sedges and bryophytes. They can also influence landscape-level patterns of diversity by maintaining a mosaic of wetlands in different successional stages (Chadde and others 1998; Mitchell and Niering 1993). Although their importance to riparian ecosystems is widely recognized, few studies have examined the influence of beavers on fens in Region 2, making estimation of the potential impacts of trapping impossible. Presumably, the widespread trapping that occurred in many watersheds at least indirectly affected some fens by removing a major source of hydrologic variability from the landscape.

Logging—Timber harvest, like fire, has the potential to affect fens largely through indirect changes to surrounding landscapes. Reduced interception and infiltration can alter surface runoff from basins, evapotranspiration rates, and snow accumulation patterns. For example, the amount of precipitation reaching the forest floor increased by approximately 40 percent, and peak snowpack water equivalent increased by more than 35 percent following canopy removal in a subalpine watershed in Colorado (Stottlemeyer and Troendle 1999, 2001). Annual and peak stream flows in logged watersheds generally increase following harvest (Troendle and King 1987), although how such changes affect fens is difficult to predict considering the importance of groundwater recharge and discharge processes on fens. Because fens in Region 2 form only in physically stable locations with limited erosion and mineral sediment deposition, where large increases in sediment yields result from upland vegetation removal, fens can be negatively impacted.

In subalpine watersheds, the main hydrologic pathway for snowmelt is subsurface flow (Stottlemeyer and Troendle 1999). By changing basic hydrologic processes, timber harvest can result in changes to meltwater chemistry (Stottlemeyer and Troendle 1999). For example, increases in the content of Ca^{2+} , NO_3^- , and NH_4^+ in meltwater and the seasonal flux of K^+ , Ca^{2+} , SO_4^{2-} , NO_3^- , and HCO_3^- increased following logging in Colorado. Within decades of harvest, hillslope hydrological processes returned to near pre-harvest levels (Troendle and King 1985). Whether fens respond to changes of this type is unknown. Since many fens are over 10,000 years old, overall effects at the landscape scale are likely limited.

Atmospheric deposition of pollutants—The atmospheric deposition of pollutants occurs throughout the world and is a major research focus for many scientists. Of particular concern are nitrogen and sulfur emissions that originate from vehicles and industrial as well as agricultural activities. Intensification of agricultural practices, including the introduction of commercial fertilizers and increases in the number of livestock in confined feedlots has occurred over the last 60 years (Baron and others 2000). Other activities contributing to changes in the N cycle include: biomass burning, land clearing and land cover conversion, and the drainage of wetlands, which are a major N sink due to the process of denitrification (Vitousek and others 1997).

Oxidization of sulfur and nitrogen compounds in emissions leads to the formation of nitric acid and sulfuric acid, which can contribute to the acidification of lakes, streams, and wetlands (Battarbee and others 1990; Charles 1990; Moore 2002). In the Colorado Front Range, nitrogen emissions have increased dramatically during the Twentieth Century, driven by a growing population and intensive agricultural activities (Baron and others 2000). Many catchments in areas with high-deposition may be nitrogen saturated (Bowman and others 2006), suggesting an increasing role for nitric acid in the acidification of surface waters and wetlands. In addition, because nitrate is a mobile anion capable of moving through soils to streams and groundwater, it can pull cations with it, depleting the soil of minerals such as calcium (Vitousek and others 1997).

A range of ecological responses to atmospheric deposition of pollutants can occur, including changes in soil fertility, vegetation type, and acidification of lakes, streams, and wetlands (Vitousek and others 1997). Studies in calcareous fens in central Europe have documented increases in plant biomass and compositional shifts to more generalist species following N additions (Pauli and others 2002). Effects and response thresholds likely differ between vascular species and bryophytes. For example, in Canadian bogs and fens, the response of individual species varied but overall, moss productivity increased in response to nitrogen deposition, while productivity of *Betula pumila* and *Ledum groenlandicum*, shrub species also examined, was unchanged (Li and Vitt 1997; Vitt and others 2003). Nitrogen enrichment can alter microbial community composition in peatlands (Gilbert and others 1998), although this has not been analyzed for Region 2 fens.

Using interpolated maps of pollutant concentrations such as nitrate and sulfate, Nanus and others (2003) found an increasing spatial trend in the concentration and deposition of pollutants from north to south in the region. The authors identified hot-spots of atmospheric deposition such as northern Colorado, where the highest nitrate (2.5 to 3.0 kg/ha N) and sulfate (10.0 to 12.0 kg/ha SO₄) deposition rates were observed. Research comparing ecosystem processes and properties on opposite sides of the Continental Divide in the Colorado Front Range found significant differences between the eastern side, which is subject to elevated N deposition from urban, agricultural, and industrial sources, and the western side, which experiences lower deposition rates. Soil percent N is higher and C:N ratios lower east of the Divide, while lake NO₃ concentrations are also significantly higher on the east side, which drives changes in diatom community composition toward eutrophic communities (Baron and others 2000; Rueth and Baron 2002). High nitrogen deposition has also been documented in the Park Range and Medicine Bow Mountains—an area supporting a high density of fens.

Cumulative effects—Cumulative effects include any ecosystem changes that are influenced by multiple land use activities (Reid 1993). In many instances, more than one anthropogenic factor has affected fens directly or indirectly. As groundwater-fed wetlands, the hydrologic function of fens is particularly dependent on surrounding watershed processes, and factors well outside the immediate boundaries of fen can significantly influence hydrologic and ecological processes (Siegel 1988). Many individual ecological stressors act synergistically; thus, evaluating the effects of single factors in isolation may not adequately capture the true impacts to fens (Preston and Bedford 1988). For example, some research suggests that the impacts of nitrogen deposition may be exacerbated by grazing (van der Wal and others 2003).

Abundance, distribution, and condition of fens across Region 2 landscapes

No rigorous, quantitative studies of fen abundance and distribution have been conducted for contemporary landscapes across the entire region, let alone for historical landscapes. While estimates of the status and trends in wetland area have been conducted (Dahl 1990; Dahl 2000; Dahl and Johnson 1991), data are not specific to fens and are too coarse to make strong inferences about changes in fen abundance or distribution. Estimates have been developed for smaller land areas. For example, in Colorado, the area occupied by peatlands was estimated at approximately 100,000 acres or 10 percent of Colorado's total wetland areas (USDI FWS 1997). More rigorous inventories of peatland area have been conducted on individual National Forests, usually at the scale of eighth level watersheds, but too few data are available to extrapolate to the entire region.

Because peat accumulation rates are so slow, it is reasonable to assume that fen area and spatial distribution did not vary in the centuries preceding Euro-American settlement of the region. Unlike forest cover types, which may change over decades or centuries in response to disturbance, fens are relatively permanent and stable landscape features. The HRV of the number of fens or their cumulative area was narrow as few fens were created or lost through natural processes. Although quantitative data are not available to compare current versus historical patterns, rates of fen loss may be outside of the HRV for many portions of the region due to anthropogenic activities. Total fen abundance in more remote wilderness areas is likely within the HRV, but intensively used areas like the Nebraska Sandhills have likely experienced significant fen loss.

Fen condition and ecological processes—With the exception of a few well-studied fens, the functioning and condition of fens in Region 2 is poorly understood. Basic inventories of fens are lacking for the majority of the region, and data on fen condition are largely unavailable, at least at landscape and regional scales. Several approaches have been developed for wetland functional analysis and condition assessment, although their applicability within the region and to fens vary. HGM functional assessments have been developed for wetlands in portions of Colorado, Nebraska, and adjacent states (Arp and Cooper 2004; Hauer and others 2002a; Hauer and others 2002b), although regional HGM guidebooks for fens have not been developed. Because actual data on wetland impacts are lacking at the landscape scale, broad-scale assessments have largely relied on surrogates such as indices of road density and land use/land cover data to infer disturbance (Johnson 2005). Several new approaches are being developed for site-level assessment; however, these projects are largely in the pilot phase and at present, relatively few wetlands have been evaluated (Faber-Langendoen and others 2006; Rocchio 2006b, 2006c).

Results from a fen inventory and condition assessment in the San Juan Mountains of Colorado documented a range of disturbances to fens (Chimner and others 2010). The most common types of disturbances were associated with recreational and large mammal (native and livestock species), followed by roads and real estate development. While some disturbances such as ditching are uncommon, they have a more severe impact on fens. Ten percent of the fens sampled were highly disturbed, while the majority of fens (80 percent) were judged to be in either good or excellent condition.

Vegetation composition and structure—Because fens vary widely in floristic composition and only a small percentage have been botanically inventoried, it is impossible to assess, in general, the potential departure of vegetation attributes from historical conditions. Declines in species richness have been documented in response to disturbances (Golinski 2005; Soro and others 1999), however, the specific response depends on the nature and severity of the disturbance and type of fen being impacted. Because of the slow rate of peat accumulation, recovery from particularly severe disturbance may be exceedingly slow. In Colorado, significant impacts to vegetation composition, species richness, and vegetative cover were documented in response to peat mining, even many years after the cessation of the disturbance (Johnson 2003). A study in Sweden found that vegetation composition in mined peatlands was still significantly different from undisturbed wetlands even after 50 years (Soro and others 1999). Similar results were reported by Cooper and MacDonald (1998), who found that Colorado fens subjected to peat mining had only 30 species compared with 122 species in unmined reference areas, and that even after 40 years, the sedges and willows that dominated the undisturbed sites were largely absent on the mined sites.

In the Nebraska Sandhills, disturbed fens often have lower species diversity and fewer community types than pristine fens (Borgmann-Ingwersen 1998; Steinauer and others 1996). However, species richness in disturbed sites may not be different. For example, some hydrologically modified fens may be invaded by exotic and upland species. In such cases, the relatively unchanged species richness may obscure more significant impacts to biodiversity resulting from the loss of rare species.

Although data are largely lacking, we assume that many fens have been affected by the extensive land use changes in the region. In Ontario, Canada, land uses within approximately 250 to 300 m of a wetland boundary affected plant diversity (Houlahan and others 2006). With the exception of wilderness areas, most National Forests support extensive road networks (McGarigal and others 2001), some of which may have affected vegetation in fens.

A variety of anthropogenic factors can impact the diversity and spatial arrangement of community types within an individual fen. Microsite diversity is a primary factor influencing species diversity in fen communities. Thus, anthropogenic impacts that reduce habitat diversity may strongly impair fen biodiversity. Hydrologic modifications, such as ditches, may eliminate pools and water track features, which often support distinct species assemblages. Drier conditions created by ditches promote the invasion of facultative meadow species such as *Deschampsia cespitosa* (Cooper 1990a). Historically, willows were removed from riparian areas, meadows, and fens (Patterson and Cooper 2007; Peinetti and others 2002b). The presence of shrubs creates unique microsites for herbs and bryophytes, and may offer protection from native herbivores and livestock.

Fens subject to intensive agricultural uses like haying are likely well out of the HRV for fen structural characteristics. This would probably include most fens in the Sandhills, where wide expanses of vegetation have been disturbed by ditching and haying. One researcher characterized the aerial view of disturbed Sandhills fens as smooth, monotypic expanses of grasses and sedges in contrast to relatively undisturbed areas that exhibited distinct patchiness (Borgmann-Ingwersen 1998). With the exception of fens managed by the Nature Conservancy, nearly all known fens are on private lands. Presumably, they are subject to intensive use, including ditching, heavy cattle grazing, and the introduction of non-native species such as pasture grasses (Borgmann-Ingwersen 1998).

Hydrologic regimes — Because fen formation and the maintenance of peat require stable hydrologic regimes, one of the most significant impacts to the functioning of fens is through direct hydrologic alteration. Ditches are common in many fens, even in remote areas such as National Parks and wilderness areas (Cooper 1990a, 1998b; Patterson 2005). The effects of disturbance on hydrologic regimes are well documented and include increases in seasonal water table fluctuations, a reduction in the mean summer water table, and elimination of wet microhabitats such as hollows and lawns (Golinski 2005).

In addition to direct hydrologic impacts, dewatering of fens via ditching can allow the invasion of burrowing animals such as pocket gophers and voles. The activities of these small animals may create preferential flow paths capable of further dewatering of peat body and hastening peat loss due to oxidation (Figure 42). Without active hydrologic restoration, such changes may be irreversible.

Stable hydrologic regimes are necessary for peat accumulation, and a water table decline will, over time, result in peat oxidization. Because fens vary widely in geomorphic setting and hydrologic functioning, and few long-term hydrologic data are available for different fen types, it is difficult to generalize about the likely response of fens to past climatic fluctuations. The HRV for key climatic factors important to fen hydrologic regimes and carbon accumulation dynamics such as the amount and seasonality of precipitation, timing of spring snowmelt, and temperature is broad and includes both extended periods of both wet and cool conditions and extended dry periods (Blasing and others 1988; Cook and others 1999; Woodhouse 2003; Woodhouse and Overpeck 1998).

Fens surely vary in their sensitivity to climatic fluctuations (Winter and others 2001). Fens supported by several aquifers or with large contributing watersheds may be more resilient to major climate shifts than fens with smaller watersheds. In contrast, fens formed in more marginal settings, such as those found in association with isolated springs on hill slope locations, may experience alternating periods of carbon accumulation and loss.

Indirect changes to fen hydrologic processes can occur as a result of structural changes to surrounding uplands. For example, the reduction in forest fire frequency surrounding McIntosh Fen on the Black Hills National Forests has led to increased tree cover and reduced groundwater flow into the fen (Glisson 2003).

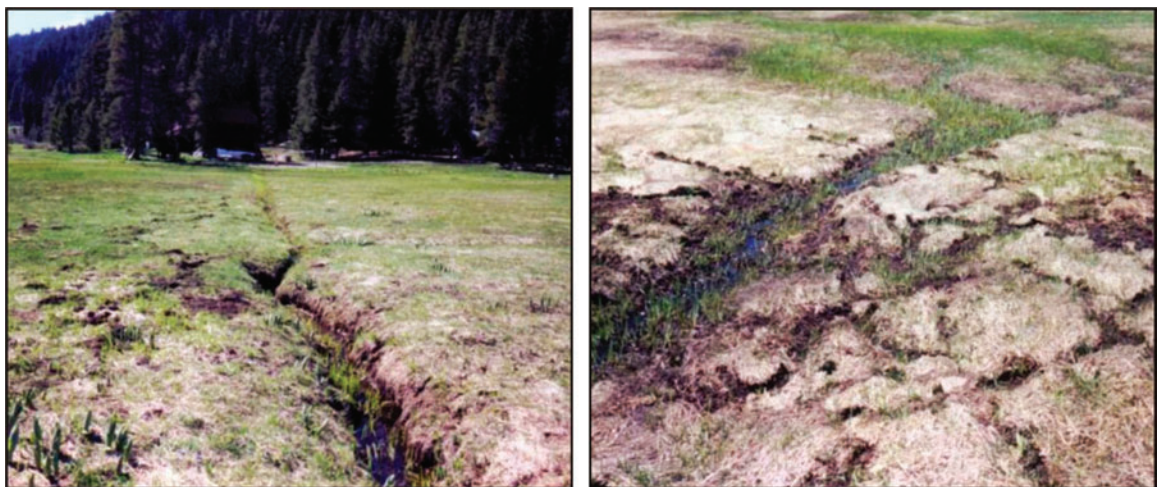


Figure 42—Fen dewatered by installation of a ditch during the early Twentieth Century (left panel) and subsequently invaded by pocket gophers, resulting in a proliferation of new channels, further degrading the integrity of the peat body (right panel), Drakesbad Meadows, Lassen Volcanic National Park, California (photos: D. Cooper).

Where key ecological processes in surrounding uplands have significantly departed from their HRV, effects on fens may also be expected to occur, although there are insufficient data to be conclusive.

Peat accumulation—Several studies in the region have examined the stratigraphy and age structure of peat deposits (Chimner and others 2002; Cooper 1990a). However, no studies have attempted to place these patterns into a regional context. There are several methodological issues with the dating of peat profiles, including temporal discontinuities, spatial variability in the basal depth and age of peat deposits, and the high cost of ^{14}C dating samples. These often prevent the collection of large datasets, which would be useful in developing and calibrating peat accumulation models at regional scales.

A variety of models describing peatland dynamics have been developed in other regions (Belyea and Malmer 2004; Belyea and Warner 1996; Frolking and others 2001; Korhola 1992; Robinson 2006); however, most are not applicable to Region 2 because they focus on ombrotrophic bogs. Many models of peat accumulation over time incorporate the effects of environmental change on plant productivity but ignore the botanical composition of peatland communities. However, at times scales of decades to centuries, changes in plant communities are probably an important determinant of the response of fens to climate—both historically and into the future (Bauer 2004).

In a study from Europe, Aurela and others (2004) found that inter-annual variation of fen carbon balances was tied to variations in the duration of the snow-free period. Research in the western United States suggests that snowmelt is occurring earlier (Cayan and others 2001), and while current climate conditions may not have yet departed from the HRV, if climate predictions are accurate, it is reasonable to expect further increases in the snow-free period.

Water chemistry—Fens in Region 2 occur in a wide range of chemical environments, from highly acidic iron fens on one end to extreme rich fens on the other. However, these fen types are rare, and the majority of fens are classified as transitional rich fens with intermediate pH values and ion concentrations (Cooper 1990a; Cooper and Andrus 1994). With the exception of some microsites such as hummocks, there is little evidence to suggest that fens in Region 2 become successively more ombrotrophic through time, as has been documented for many boreal peatlands. In boreal regions, minerotrophic fens may develop into ombrotrophic bogs due to autogenic processes; however, Region 2 fens have a relatively stable water chemistry environment through time and do not appear to follow the same developmental trajectory. If this is true, it is not meaningful to consider a range of historical variability with regard to water chemistry at the site level. At landscape and regional scales, the question is whether the relative proportion of fen types has fluctuated over time. Since fens in the region owe their chemical characteristics primarily to hydrogeological setting and groundwater flow processes and because these processes change little over time, the answer appears to be no.

While there was likely little variability in water chemistry historically, anthropogenic disturbances have probably altered some key fen chemical characteristics at both local and landscape scales. For example, water chemistry differed widely between disturbed and undisturbed fens on eastern Vancouver Island, with higher specific conductivity and cation concentrations observed in disturbed compared to undisturbed peatlands, which were attributed to altered drainage and changing land uses (Golinski 2005)

An additional anthropogenic impact without historical analogue is the increasing deposition of nitrogen in many portions of Region 2. Because the phenomenon is so recent relative to the age of fens, it is difficult to predict the effects of N enrichment on fen species and ecological processes. However, the variability in deposition rates alone across the region appear to represent a departure from historical patterns.

Management Opportunities and Constraints _____

Management opportunities

Increasingly, both managers and scientists are recognizing the important ecological functions provided by fens. However, as we have made clear in this assessment, there are many gaps in our knowledge of fens. More broad-scale assessments of fen distribution and abundance are needed. A variety of approaches should also be used in these assessments, including aerial photographs or other remotely sensed data (e.g., hyperspectral satellite imagery) to identify and map fens.

We also need detailed assessments of fens at the site level. Basic hydrology, water chemistry, and vegetation analyses are necessary to develop realistic models of fen vegetation dynamics and to understand and evaluate the effects of management activities on fens. Such studies may appear prohibitively expensive or complicated at first glance; however, installation of even a few groundwater monitoring wells can yield invaluable data.

More detailed studies relating geomorphology, peat stratigraphy, hydrologic regimes, and community composition are important for developing an understanding of the origin and development of fens in the region. Also needed are more studies examining the physiochemical and hydrologic drivers of fen formation and development as well as fen sensitivity to anthropogenic disturbance. Improved approaches for restoring degraded fens are also needed. The development of effective restoration techniques would provide managers useful tools to approach impaired fens.

Restoration

Given the degraded condition of many fens in the region, there are numerous opportunities for restoration. Processes for evaluating options for restoration should incorporate ecological, technical, economic, and social aspects (Brooks and others 2006). Because of the complexity of these variables, there is no single approach for prioritizing restoration goals. However, there are several practices that can facilitate efficient use of limited resources and help ensure successful restoration outcomes.

First of all, a reliable inventory and assessment of the planning area is essential, as this allows for consideration of all restoration options and selection of sites with the greatest potential benefit and likelihood of success. It is useful to include reference sites when developing design standards for restoration projects (Cole and others 2006). These can be used to help formulate realistic restoration targets and specific design criteria for projects. Once a decision to implement a project has been made, a conceptual plan for restoration must be prepared that is based on the information collected during the site selection process. The proposed project should be mapped in both plan and profile views with the intended hydrologic source clearly identified (Brooks and others 2006). Restoration plans should specify the particular species and techniques to be used in planting and should identify areas where colonization by seed is to be relied upon or where containerized plantings or plugs will be installed. Post-construction monitoring protocols should also be part of any restoration plan (Brooks and others 2006).

Since hydrologic regime is such an important factor in the functioning of fens, every effort must be made to accurately identify all potential water sources and to explicitly formulate desired hydrologic outcomes. Hydrologic processes should be addressed at the earliest stages of project development, as the ultimate success or failure of a project will depend on successfully restoring water sources. Often, hydrologic restoration can be accomplished once the extent and nature of hydrologic modifications are known. For example, wetland hydrology can be restored to drained fens by plugging ditches to return the water table to its original elevation using soils or sheet metal check dams (Figure 43) (Cooper and others 1998; Patterson 2005). Because organic soils typically subside after drainage, caution should be exercised when planting as water tables may rise above the soil surface, killing newly planted vegetation (Ewing and Vepraskas 2006).

If disturbed fens retain suitable hydrologic regimes following disturbance, asexual propagules present in the fen may allow for some degree of recovery. For example, Johnson (2000) found that in areas with intact wetland hydrologic regimes, seeds played a minor role in revegetation, and that most new growth originated from vegetative structures. However, where significant drainage has occurred, sexual reproduction was found to be the dominant mode of plant establishment. In another experiment, of eight species seeded, only one, *Triglochin maritima*, germinated and established seedlings (Cooper and MacDonald 2000).



Figure 43—Ditch in Big Meadows, Rocky Mountain National Park in 1989 (left panel), prior to hydrologic restoration by National Park Service personnel using sheet metal check dams (center panel). The same area in 2006 (right panel) (photos: D. Cooper).

Seedlings, rhizome transplants, and stem cuttings of woody species such as willows are all potential approaches that should be evaluated for possible inclusion in revegetation plans, as each differs with respect to likely survival patterns in relation to hydrologic regimes (Cooper and MacDonald 2000).

Seedbanks are likely important following disturbance. Many graminoid species that are common in fens exhibit delayed germination, allowing for the formation of soil seedbanks (Leck and Schutz 2005; Schütz 1998; van den Broek and Beltman 2006). Some research also suggests that the spores of some bryophytes may remain viable for several years. Sunderg and Rydin (2000) found that under suitable conditions, the spores of some *Sphagnum* species can form a persistent spore bank with a half-life of between 1 and 20 years and with individual spore capsules capable of persisting for several decades or even centuries (Sundberg and Rydin 2000). Several soil seedbank studies have shown that woody plants may be absent or poorly represented in soil seed banks (McGraw 1987; Patterson 2005; Rossell and Wells 1999).

Transplantation of soils from relatively pristine fens to heavily disturbed sites may promote colonization of desired species. In a Colorado fen, replacement of the upper 10 cm of native soil significantly speeded revegetation by supplying viable sexual and asexual propagules (Johnson 2003). It may be possible to reestablish some fen species, even if the complete loss of the peat body occurs. For example, Amon and others (2005) documented the production of peat composed of brown-mosses within three years of revegetation of gravel substrates on top of a buried fen. The authors also reported that naturally derived plugs were established most successfully while plants that established from seed produced the fewest survivors (Amon and others 2005). Where fens have been buried, the fill material should be removed and the sites should be revegetated using plantings grown in green houses from locally collected seed. For woody plants like willows, stem cuttings can be planted. This approach has been used successfully for large-scale fen restoration near Telluride, Colorado (Cooper, unpublished data).

Direct seeding of wetland plant species for fen restoration has generally produced poor results (Cooper and MacDonald 2000); however, because direct seeding is relatively inexpensive, it continues to be used for many restoration projects. The germination requirement of seeds are species specific (Isselstein and others 2002; Tallowin and Smith 2001), leading to unpredictable results from seeding. Irrigation may facilitate germination and seedling establishment, while shading inhibits germination. Higher soil temperatures may improve germination rates. To ensure genotypes are well adapted to local site conditions, seeds should be collected from the area where restoration will occur. All seed should be cleaned and screened to remove the non-seed materials like fruiting bracts, floral parts, awns, scales, and perigynia (Dunne and others 1998). Many seeds require stratification under wet and cold conditions or temperature fluctuations mimicking natural diurnal rhythms to break dormancy. Seed stratification can be done in the lab or by dispersing seeds in the fall and allowing them to overwinter in the field.

Because of the sensitivity of peat soils, broadcast seeding is generally the preferred method of seeding. Hydroseeding is not appropriate, as the mulch, binder, and seed/seedlings may be washed away prior to germination and seedling establishment (Colorado Natural Areas Program 1998). Although the best depth to incorporate seeds varies by species, general guidelines are to plant to a minimum depth of 0.7 cm and a maximum depth of 1.3 cm for most small seed mixes, while a minimum depth of 1.5 cm and a maximum depth of 2.6 cm may be more appropriate for mixes containing larger seeds (Dunne and others 1998). Natural seed rain cannot generally be relied upon since many fen species are not capable of seed dispersal over large distances, particularly where surface water flow is interrupted (Bakker and others 1996). Some species, such as willows, can be effectively established from natural seed rain if appropriate water table depths are present (Cooper and Andrus 1994).

Plugs and bare root stock are other possible techniques that can be used in fen restoration (Pfadenhauer and Grootjans 1999). For example, *Kobresia simpliciuscula*, *Carex utriculata*, and other species were successfully established at a peat mined fen in Colorado from rhizomes collected from undisturbed areas (Cooper and MacDonald 2000). However, this approach is time consuming and is only suggested for relatively small restoration areas. Plants grown from field-collected seed in greenhouses have been successfully used in many restoration projects. This approach may be appropriate for *Carex aquatilis*, *C. utriculata*, *Calamagrostis canadensis*, *Carex vesicaria*, and *Scirpus pungens*, among others. This approach can be expensive relative to broadcast seeding but typically results in much higher plant survival. Once plants are established, they can provide localized centers of seeds for future plant establishment, as well as vigorously growing rhizomes that can spread over large areas. Planting densities of 2 to 4 plants/m² have been used, and for rhizomatous species, a planting density of even 1 plant/m² or lower could be used to introduce the desired species over large areas or to supplement other plant propagation approaches such as direct seeding.

Management constraints

Constraints on the management of fens can be divided into several categories. Resource constraints include access to funding to develop management and restoration goals. It is often useful to identify several likely funding scenarios when developing management objectives to help keep focus on realistic restoration options and to identify at what point attainment of project goals are not possible if resources are limiting. Political constraints are an additional factor that should be considered. It is usually best to identify and engage all potential stakeholders early on in planning, as this may prevent problems further down the road.

An external constraint that may have significant effects on fens that is outside the control of managers is regional climate changes. Where managers rely on harsh winters to control overabundance of elk populations, moderate climatic conditions predicted under some regional climate models may allow significant increases in elk herds, thereby increasing impacts to fens (Wang and others 2002). Surface temperature increases and the resulting increase in evapotranspiration rates may lead to lower water tables in fens, altering peat accumulation processes and species composition (Hogg and others 1992). Since soil temperature is a major factor affecting organic matter decomposition, warming may accelerate decomposition processes (Domisch and others 2006). Models of climate change indicate that temperatures will increase and precipitation seasonality will shift over the coming decades in the Rocky Mountains, leading to earlier spring runoff, lower summer and fall flows, decreased snowpack, and an increase in the proportion of precipitation falling as rain versus snow (Cooper and others 2006; Knowles and others 2006).

Increased ultraviolet-B (UV-B) radiation caused by reductions in the amount of stratospheric ozone could affect fens via effects on plant carbon allocation and root exudation, which in turn, could impact microbial communities. For example, research by Rinnan and others (2006) using experimental microcosms found that when *Eriophorum angustifolium*, a widespread fen species, was exposed to enhanced UV-B radiation simulating a 15 percent reduction in ozone, there was an increase in the concentration of root exudates in the rhizosphere and in the ratio of roots to shoots. Such responses may alter the belowground biomass distribution of the fen plants, leading to changes in the net efflux of root exudates (Rinnan and others 2006) and altered peat accumulation rates.

7. Historical Range of Variation for Region 2 Salt Flats

Definitions and Concepts of Salt Flats

Salt flats are wetlands characterized by high salt concentrations. As with other wetland types, the terminology used to describe these ecosystems is often ambiguous or imprecise, with different terms applied regionally. Other terms used to describe salt-affected wetlands are inland salt marsh, salt pan, sabhka, and playa. The key characteristic defining the wetlands discussed in this chapter is the presence of high soil salt concentrations. As described in subsequent sections, highly saline soils impose a significant environmental stress on plants and relatively few plant species are able to tolerate these conditions. Generically referred to as halophytes, plant species tolerant of highly saline environments form distinct plant communities and are important for delineating salt flats in the field. Some terms, like playa, also include non-saline wetlands and are not considered salt flats in this report. As with all wetlands, hydrologic regime is a key variable controlling the structure and function of salt flats; however, it is the presence of high salt concentrations that most clearly distinguishes salt flats from other ecosystem types.

Geomorphic Setting and Principal Ecological Drivers

Geomorphic setting

Salt flats most commonly occur in arid and semi-arid landscapes where evapotranspiration exceeds precipitation throughout the year (Aschenbach 2006). However, saline wetlands are also abundant in more humid regions such as the prairie pothole region of the northern Great Plains (Last and Ginn 2005; Lieffers 1984). There are no reliable statistics describing the contemporary distribution of salt flats in Region 2. Estimates of salt affected soils have been developed within individual states and maps showing the distribution of saline soils may be found on some county soil surveys. More than 400,000 ha of soils are classified as salt affected in Kansas (Aschenbach 2006). Salt flats are generally restricted to the Great Plains, although saline ecosystems also occur at high elevations in intermountain basins. For example, Ungar described halophytic communities occurring in South Park, Colorado, at elevations greater than 3000 m (Ungar 1974b).

A variety of factors influence the accumulation of salts in soils and salt flat ecosystems can occur in several geomorphic settings. Within Region 2, salt flats most commonly occur associated with terminal sump basins or along the margins of ponds or lakes where evaporation may lead to the accumulation of high soluble salt concentrations (Ungar 1974b). Salt mobilization from edges can be rapid and influenced by lateral groundwater flow through surface sediments (Arndt and Richardson 1993). Halophytic communities also occur in association with discrete saline springs (Bolen 1964; Joeckel and Clement 1999, 2005). Anthropogenic features such as reservoirs or ditches also support salt flats, often in landscape settings that did not historically support such communities (Peck and Lovvorn 2001; Skarie and others 1986).

Key drivers and ecological processes

Climate—Climate is a primary driver of wetland formation and wetland functional characteristics, although the variables of greatest importance vary among wetland types. Variables of particular importance to salt flats are temperature and annual precipitation, particularly as they influence processes of evapotranspiration. The dominant form of precipitation at lower elevations, where the majority of salt flats occur, is rain. The frequency and magnitude of precipitation events is highly variable spatially and temporally, resulting in cyclical patterns of relative wetness and dryness. Most commonly studied in relation to freshwater marshes, these cycles also influence the function of salt flats (Kantrud and others 1989a; van der Valk and Davis 1978).

Climate can affect salt flat formation and function in several ways. The main hydrological input in many salt flats, particularly playa-type ecosystems, is direct precipitation and surface runoff from surrounding areas. Because of their reliance on precipitation, inter-annual and decadal fluctuations in precipitation are major drivers of hydrologic function and vegetation dynamics in these ecosystems.

At broad temporal scales, climate influences geomorphic processes. For example, the formation of landforms such as dunes appears to have been episodic, driven by shifts towards drier and warmer climatic conditions (Forman and others 2001; Muhs and Holliday 1995). The expansion and retreat of glaciers, the key process forming many saline wetlands in the northern Great Plains outside of Region 2, was driven by large shifts in precipitation and temperature (Krimmel 2002; Munroe 2003; Munroe and Mickelson 2002).

Salt accumulation may affect microclimatic processes, including site evapotranspiration rates. A study in a playa found that high osmotic pressure and the presence of salt crusts caused most absorbed radiation to be partitioned to sensible heat (Malek and others 1990). Higher air temperatures above the wetland raised potential evapotranspiration (ET), and while evaporation rates of the two sites were similar following rainfall events, playa ET rates were quickly reduced as the osmotic potential increased.

Geology— At both local and regional scales, geologic setting is a primary driver of salt flat accumulation processes and salt flat functioning. Excluding anthropogenic sources, soluble salts can originate from either marine or lithogenic sources, with the importance of each varying among sites (Waisel 1972). Because of the region's continental setting, marine salt sources such as windborne sea spray are not factors influencing the formation of Region 2 salt flats, although fossil marine salt deposits do occur in some locations. Bedrock salt sources, created from the weathering of rock, are the most important source of salts in Region 2. The amount of soluble salts and the dominant ionic species present (e.g., sodium, calcium, sulfate, and chloride) can vary widely among different rock types. For example, sandstones typically contain little chloride, while limestone contains high amounts of chloride and sulfur relative to most shales (Waisel 1972).

The composition of parent materials in watersheds and aquifers supporting salt flats influences processes of salt accumulation. Saline soils are typically associated with sedimentary rock formations. For example, in Colorado, soil and water in areas formed from Mancos shale on the Colorado Plateau are often highly saline (Wagenet and Jurinak 1978; Whittig and others 1982). Because of low ion concentrations and slow weathering, ecosystems with high salt concentrations are rare in landscapes dominated by igneous or metamorphic rocks.

Parent material also influences salt flat formation through effects on local and regional hydrologic processes. Processes such as groundwater recharge and discharge vary as a function of the transmissivity of bedrock layers and the arrangement of geological strata. For example, salt marshes and springs are common in river valleys of central Kansas and are usually associated with the Dakota Formation, which can include permeable sandstones and less permeable siltstones and shales with high storage. Because of variation in the configuration of strata, hydraulic conductivity of the underlying aquifer ranges from less than 10 ft/day to more than 50 ft/day (Macfarlane and others 1989).

Eolian processes can influence the form and function of salt flats and wind erosion has influenced the formation of playas, many of which support halophytic communities (Hovorka 1995). Salt crusts formed in salt-affected soils are easily mobilized and transported by wind (Blank and others 1999) and have been shown to influence solute concentration in groundwater in arid and semi-arid areas. On the southern high plains, approximately 4.5×10^5 kg of chloride is estimated to be removed annually from the basin floor of a relatively small (4.7 km²) saline lake (Wood and Sanford 1995). The transport of dust is temporally variable and influenced by seasonal patterns of soil moisture and wind intensity. Dust transport is typically limited to brief periods, separated by long periods of inactivity, and peaks during winter months when winds are moderately strong, precipitation is at a minimum, and vegetation is senescent (Stout 2003).

Glaciation is a major factor influencing the formation of saline wetlands in some regions such as the prairie pothole region of the northern Great Plains (Dodd and Coupland 1966; Keller and Vanderkamp 1988), and while continental glaciers did reach parts of present-day South Dakota, no USFS lands in Region 2 were overlain by continental ice sheets. Pleistocene valley glaciers did affect many high mountain areas in the region, an important factor in the formation of some wetland types such as fens. However, with the exception of some intermountain valleys, saline wetlands rarely occur outside of the Great Plains because geological and climatic factors are not conducive to their formation.

Hydrologic regime—Hydrologic regime is the key factor controlling vegetation composition and soil development in all wetlands, including salt flats. Because high salinity is the primary feature used to differentiate salt flats from other wetland types, there is considerable variability in hydrologic characteristics among them. Some salt flats have hydrologic regimes similar to marshes. Their water levels may fluctuate widely both seasonally and among years, with extended periods of deep inundation alternating with periods where surface water may be completely absent. Many salt flats are associated with lacustrine features such as lakes, ponds, and reservoirs with widely fluctuating water levels.

Sources of water to salt flats are precipitation, surface water, and groundwater. The importance of each can vary among wetlands and temporally within individual ecosystems. The main hydrologic inputs to salt flats occurring in closed basins are precipitation and surface runoff (Cooper and Severn 1992). Salt flats may also be influenced by the groundwater, either through direct discharge in discrete springs or through capillary movement of water from seasonally high water tables (Bolen 1964; Joeckel and Clement 2005; Riley 2001).

High-velocity surface flows resulting from precipitation runoff may affect salt flats but are less important to geomorphic and ecological processes than in riparian ecosystems. In many wetlands, spatial and temporal patterns of salt accumulation in near-surface groundwater and surface water are dynamic and closely linked with discrete recharge events (Arndt and Richardson 1993). The frequency and magnitude of water table fluctuations are strong drivers of processes of salt accumulation and removal from soils, and are influenced by the amount and timing of precipitation events and by the presence of groundwater.

Anthropogenic factors, particularly irrigated agriculture, are responsible for salination in many areas of the semi-arid West. Stock ponds and other water storage features across Region 2 have likely led to an increase in lacustrine and lacustrine fringe wetlands in much of the region (Figure 44a). Saline seeps may form where slopes naturally break and water tables are near the surface. Contact salinity occurs where a permeable water-bearing surface layer that is thinning out above a less permeable layer (e.g., clay) forces groundwater flow close to the soil surface. Farming practices can allow water to move out of the root zone into the subsoil, dissolving and accumulating salts in transit, and salt flats commonly

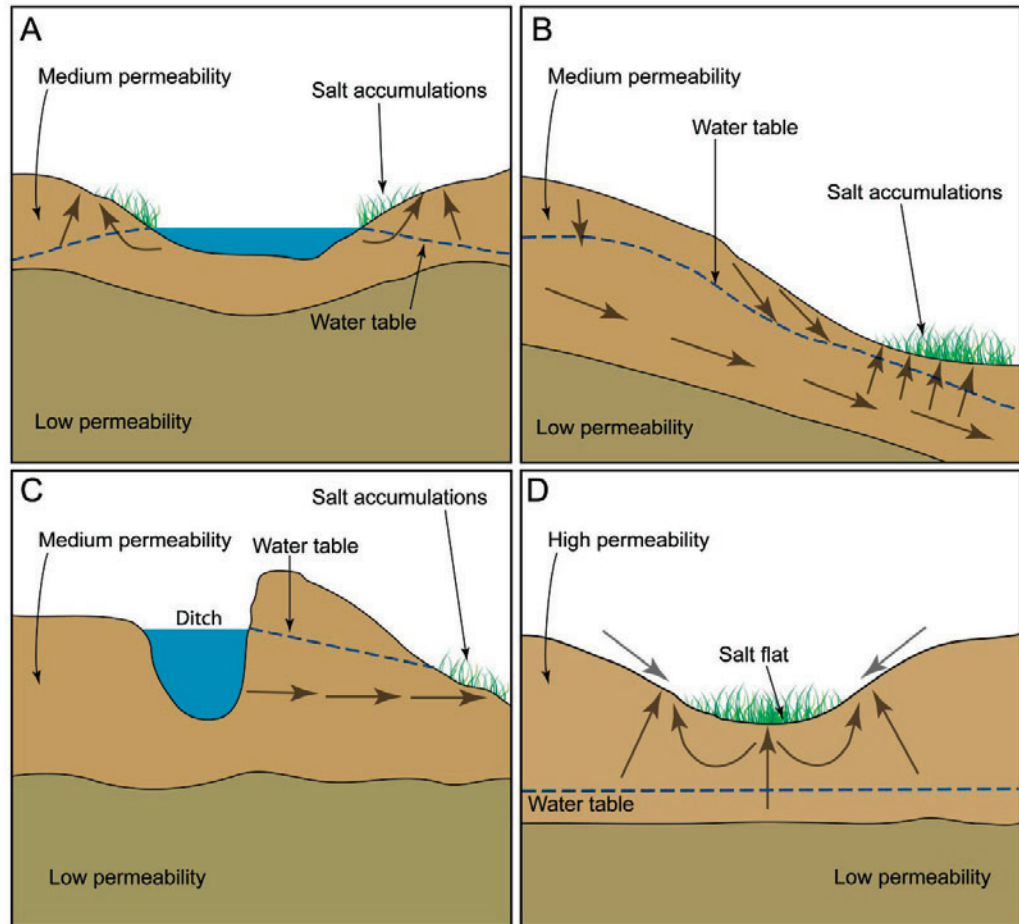


Figure 44—Schematic illustrations of different hydrogeomorphic settings for salt flats. Lacustrine fringe creates salt accumulation where ponds dry seasonally or where the surface water supported water table is close to the soil surface (A), break in slope (B) where groundwater discharges to near the soil surface, downstream of a ditch (C) where groundwater reaches to near the soil surface, and perched water table (D) where capillary water reaches the soil surface (modified from Alberta Agriculture and Food 2004).

occur adjacent to irrigation ditches (Figure 44b, c). Salt flats may also form where layers of low permeability create a perched water table, with evaporation leading to salt precipitation. For example, saline seeps are more common in western than eastern South Dakota in part because much of the subsoil consists of bedded shale material with low permeability (Millar 2003) (Figure 44d).

The chemical composition of aquifers can vary. In Canada, researchers documented several subsurface water types with distinctive ionic composition and salt concentration (Last and Ginn 2005). Fluctuations in water table depth and precipitation events create temporal variation in salt accumulation (Riley 2001). There are large differences in the hydrologic functioning of saline wetland types. For example, while wetlands in the San Luis Valley of Colorado share many attributes with playas of the Southern High Plains or central California (Bolen and others 1989; Fort and Richards 1998; Smith 2003), they are not hydrologically isolated and precipitation fed; rather, they are connected to a large subsurface aquifer (Groeneveld and Or 1994).

Water and soil chemistry—Considerable variation may exist in the geochemistry of salt flats. The most common salts are sulfates, carbonates, bicarbonates, and chlorides of calcium, magnesium, sodium, and potassium (Table 23). The concentration and composition of the dominant ions in soil and water varies spatially among and within individual wetlands, as well as over time (Last 1989a). As salt flats dry, salt crusts develop on the soil surface. Specific evaporites that are formed along the margin and bottom of salt flats may include mirabilite, thenardite, and bloedite (Last 1989a). Sodium sulfate occurs as thenardite (Na_2SO_4) above 32 °C and mirabilite ($\text{Na}_2\text{SO}_4 \cdot 10\text{H}_2\text{O}$) at cooler temperatures. Volume increases and solubility decreases when thenardite changes to mirabilite, often creating salt heaving (USDA NRCS 1999).

Table 23—Salt compounds and their constituent cations/anions found in salt flats.

Salt compound	Cation (+)	Anion (-)	Common name
NaCl	sodium	chloride	halite (table salt)
Na_2SO_4	sodium	sulfate	Glauber's salt
MgSO_4	magnesium	sulfate	epsom salts
NaHCO_3	sodium	bicarbonate	baking soda
Na_2CO_3	sodium	carbonate	sal soda
CaSO_4	calcium	sulfate	Gypsum
CaCO_3	calcium	carbonate	calcite (lime)

A standard measure of salinity used by the NRCS in soil taxonomy is electrical conductivity (EC), generally measured in decisiemens per meter (dS/m) or Millimhos per centimeter (mmhos/cm) (U.S. Department of Agriculture 1999). The NRCS recognizes five salinity classes based on EC, including non-saline (0 to 2 mmhos/cm), very slightly saline (2 to 4 mmhos/cm), slightly saline (4 to 8 mmhos/cm), moderately saline (8 to 16 mmhos/cm), and strongly saline (greater than 16 mmhos/cm) (USDA NRCS 1999). The concentration of ions can vary widely in relation to local and regional geological and hydrological factors.

The main classifiers of soils in salt flats are salinity, alkalinity, and sodicity. Salinity refers to the concentrations of both total soluble salts and exchangeable sodium, which is usually measured by EC (Shainberg 1975; Ungar 1974b), although most studies do not explicitly consider alkalinity or sodicity. Sodicity refers specifically to soil Na^+ abundance. Sodium adsorption ratio (SAR)—calculated from the concentrations of sodium, calcium, and magnesium in a saturated extract—is typically used to measure the sodicity of a soil. The sodium adsorption ratio is calculated from the concentrations (in milliequivalents per liter) of sodium, calcium, and magnesium in the saturation extract (USDA NRCS 1999):

$$\text{SAR} = (\text{Na}^+) / \sqrt{((\text{Ca}^{2+} + \text{Mg}^{2+}) / 2)}$$

High exchangeable sodium occurs in sodic soils and has a significant influence on the physical and chemical properties of a soil. The presence of large quantities of Na^+ ions leads to loss of soil structure because of the weak attraction of Na^+ ions to the soil colloids allows for clay dispersion, which clogs soil pores, decreasing hydraulic conductivity and infiltration. Sodic soils have high levels of exchangeable sodium but low levels of total salts.

Sodic soils may impact plant growth by specific sodium toxicity, nutrient deficiencies or imbalances, high pH, and soil structure changes resulting from dispersion of clay particles. Sodic soils may be hard when dry, limiting water intake and plant growth is typically poor (Davis and others 2003). Sodium problems are most pronounced on soils with high clay contents, particularly where clays with high shrink-swell potential are present, such as in the basins and plains of Wyoming.

The pH in salt flats may range from approximately 7.0 to over 10.0 and may be barren of vegetation in the most alkaline sites (Winters and others 2005). Soils in arid and semiarid areas may become alkaline if there is insufficient precipitation to leach cations (e.g., Ca^{2+} and Mg^{2+}) from soils. In alkaline sites, carbonic acid (H_2CO_3) that is formed from microbial and root respiration may form bicarbonate and carbonate ions. The pH of soil and water may reduce the availability of essential elements necessary for plant growth. Typically, plants growing in soils with high pH have reduced stomatal conductance and leaf nutrient concentrations of iron, calcium, manganese, and zinc (Brady 1996; Haukos and Smith 1996).

Disturbance processes—The role of disturbance in salt flat dynamics is largely unstudied in the region, although disturbance is likely a major environmental gradient affecting salt flat vegetation (Walker and Wehrhahn 1971). Disturbance in salt flats may include periodic high water periods, which can drown plants, as well as multi-year droughts, which lead to high plant mortality. As wetlands dry, evaporation increases salt concentrations, which eventually exceed plant tolerances. Halophytes in coastal salt marshes often exploit patches created by disturbance and are restricted to salt-stressed microsites because of their inability to compete with turf-forming perennial species (Bertness 1992; Shumway and Bertness 1992); however, it is unknown whether similar processes are important in inland ecosystems.

Disturbances from animals may be locally important to salt flats. Livestock and native ungulates can trample salt flat plants, causing plant mortality. Birds, particularly geese, can be disturbance agents in salt marshes. For example, geese can destroy salt marsh plants and expose bare sediments by grubbing for grass roots and rhizomes in the spring. Increased evaporation later in summer from disturbed sediments can cause increased soil salinities that adversely affect remaining plants (Srivastava and Jefferies 1996).

Fire can also influence salt flats, although the specific importance of fire probably varies widely. Because salt flats are relatively discreet and isolated, ignitions within salt flats are probably very rare and any fires affecting them likely originate in surrounding ecosystems. The incidence of fire varies as a function of the fire regimes of surrounding community types. Smith and Kadlec (1985) found in a study of Utah marshes that vegetation regrowth was rapid following fire in communities dominated by *Typha* spp, *Scirpus lacustris*, and *S. maritimus* but was very limited in more saline sites dominated by *Distichlis spicata* (Smith and Kadlec 1985).

Salt flat soils with high clay contents can shrink and swell, forming large crack networks (Hovorka 1995). Salt efflorescence and precipitation features may be formed, which can create complex microtopography. Goodall and others (2000) described thick crusts, with high relief (>10 cm) and a blocky morphology and thin crusts, with low relief and a blister-like appearance. Working in the northern Great Plains, Last (1989b) described four basic types of salt occurrences: surface crusts and hardgrounds, massive and bedded salts, deposits associated with springs, and subsurface and groundwater-related accumulations. Soil deformation and crust formation may kill seedlings but it can also create microsites that facilitate seed entrapment and germination (Fort and Richards 1998).

Salt flat development and succession—Because of the extreme environment, salt flats are species poor—limited to halophytes. Succession in saline ecosystems may occur slowly because of a limited species pool of adapted species and may consist of successive species replacements with the same or similar species. Where hydrology and salinity are stable, communities may reach a sort of edaphic climax; however, these characteristics often vary widely.

Over broad time scales, primary successional patterns may be driven by long-term changes in water levels and flood frequency. The margins of saline lakes, for example, may experience a cyclical pattern of species invasion and retrogression. Long-term evolution of salt flats varies based on climatic and geological factors. Wetlands in the northern Great Plains are young, originating within the last 10,000 years, in contrast to the much older playas of southwestern United States (Last 1989b).

Seasonal fluctuations in soil salinity are an important factor driving vegetation dynamics, and life stages of a species may differ strikingly in their salinity tolerance. Many species will only germinate during periods of lower salinity (Riley 2001), although some species (e.g., *Hordeum jubatum*) will germinate at salinities higher than those considered favorable to growth and reproduction (Badger and Ungar 1989; Egan and Ungar 1999).

Salt Flat Classification and Gradients ---

Under the hierarchical classification scheme used by the National Wetlands Inventory program, salt flats are placed into either the Lacustrine or Palustrine system (Cowardin and others 1979). The Lacustrine system includes wetlands situated in a topographic depression or dammed river channel, that exceed 8 ha in area, and that have less than 30 percent total cover from trees, shrubs, or persistent emergent vegetation. Also included are wetland and deepwater habitats less than 8 ha in area that have active wave-formed or bedrock shoreline features along their boundary, features not generally found in Region 2. Palustrine wetlands are less than 8 ha in size, have more than 30 percent vegetation cover, lack active wave-formed or bedrock shoreline features, and have water levels less than 2 m at their deepest location (Cowardin and others 1979). The majority of salt flats would be placed into the Palustrine system using the Cowardin (1979) classification scheme.

Under the Cowardin (1979) classification, a variety of modifiers can be applied to wetlands. Modifiers include water regime, soil type, and water chemistry parameters such as pH and salinity. Among non-tidal wetlands, water regimes are defined in terms of the frost-free period and include, from wettest to driest, the following categories: permanently flooded, intermittently exposed, semi-permanently flooded, seasonally flooded, saturated, temporarily flooded, and intermittently flooded. Because our definition of salt flats in this assessment is based on salinity rather than hydrologic characteristics, salt flat examples of many of the Cowardin water regime types can be found, although most salt flats would fall under the saturated, temporarily flooded, and intermittently flooded categories. The Cowardin classification system also uses the artificially flooded modifier to describe wetlands in which the amount and duration of flooding is controlled by means of pumps or siphons in combination with dikes or dams, although wetlands within or resulting from leakage from man-made impoundments and irrigated pasture lands supplied by diversion ditches or artesian wells are not included (Cowardin and others 1979).

The Cowardin (1979) system also includes water chemistry modifiers related to salinity, which range from fresh to hypersaline (Table 24). As we define them in this assessment, salt flats include wetlands classified from oligosaline to hypersaline under the Cowardin system. Notably, salinity in an individual wetland can vary widely over time and with the degree of flooding.

Under the HGM approach (Brinson 1993a; Cooper 1998a), salt flats can be described as mineral flats, depressional, or slope wetlands. The original framework was intended to be augmented by publication of regional guides; however, relatively few of these have been prepared (Hauer and others 2002a). None deals with the entire range of saline wetlands, although some types are covered in existing guides (Stutheit and others 2004).

Table 24—Salinity modifiers used in the National Wetland Inventory program (Cowardin and others 1979).

Inland modifiers	Salinity (parts per thousand)	Approximate specific conductance (μ Mhos at 25° C)
Hypersaline	>40	>60,000
Eusaline	30.0-40	45,000-60,000
Mixosaline	0.5-30	800-45,000
Polysaline	18.0-30	30,000-45,000
Mesosaline	5.0-18	8,000-30,000
Oligosaline	0.5-5	800-8,000
Fresh	<0.5	<800

Several subclasses relevant to salt flats were identified in a classification of Colorado wetlands using the HGM approach (Cooper 1998): subclass D2—encompassing low-elevation basins with permanently or semi-permanently flooded hydrologic regimes such as reservoir and lake margins and marshes; subclass D3—low-elevation basins acting as sumps for water moving from mountains or as depressions in irrigated slopes; subclass D4—low-elevation sites with temporarily flooded hydrologic regimes and poorly developed vegetation; and subclass D5—Intermittently flooded low elevation basins that are not flooded annually or are largely barren of vegetation. The F1 subclass include mineral soil flats at low-elevation (Table 25) (Carsey and others 2003; Cooper 1998a). In practice, ordination data used to delineate HGM subclasses can be problematic as some species occur in multiple categories. Distinguishing between slope and mineral flat wetlands can be particularly difficult.

Table 25—Primary HGM subclasses described by Cooper (1998) relevant to salt flats.

HGM Subclass	Description	Common species
Depressional 4	Temporarily flooded low-elevation basins flooded for short periods in the spring and early summer.	<i>Polygonum lapathifolium</i>
Depressional 5	Intermittently flooded low-elevation basins that are not flooded annually or are largely barren of vegetation.	<i>Xanthium strumarium</i>
Flats 1	Middle to low-elevation sites on mineral saline soil (due to evaporation) with a seasonal high water table near the ground surface and occasionally shallow standing water.	<i>Suaeda calceoliformis</i> , <i>Puccinellia nuttalliana</i> , <i>Sarcobatus vermiculatus</i>
Slope 2	Subalpine and montane fens and wet meadows on saturated calcareous substrates.	<i>Eleocharis quinqueflora</i> , <i>Kobresia simpliciuscula</i> , <i>Carex simulata</i>
Slope 4	Low-elevation meadows with a seasonal high water table near the ground surface. May occur on floodplains or near springs.	<i>Hordeum jubatum</i>

Under the National Vegetation Classification System used by Natural Heritage programs, salt flats may be mapped or classified under the InterMountain Basins Playa, Inter-Mountain Basins Mixed Salt Desert Scrub, Eastern Great Plains Wet Meadow Prairie and Marsh, or North American Arid West Emergent Marsh ecological system (Comer and others 2003b). A variety of associations have been described, with regional variation in specific species depending on the available species pool (Table 26).

Salt Flat Vegetation in the Region

Salt flats typically have sparse plant cover, due to high pH and salt concentrations, although wetlands may support high aquatic invertebrate and algae production when inundated (Winters and others 2005). Soil moisture and salt concentration gradients are the primary edaphic factors affecting plant distribution in saline areas (Rogel and others 2001a, 2001b), although other factors affect species composition and distribution in salt flats, including hydrologic regime, plant competition, pH, nutrient status, and seed bank response to wet and dry cycles (Dix and Smeins 1967; Stewart and Kantrud 1972; van der Valk and Davis 1978).

Table 26—Primary vegetation associations related to salt flats in Colorado (Carsey and others 2003).

Element code	Scientific name	Common name
Mineral flats 1		
CEGL001770	<i>Distichlis spicata</i> Herbaceous Vegetation	Inland saltgrass Herbaceous Vegetation
CEGL001779	<i>Muhlenbergia asperifolia</i> Herbaceous Vegetation	Alkali muhly Herbaceous Vegetation
CEGL001799	<i>Puccinellia nuttalliana</i> (= <i>airoides</i>) Herbaceous Vegetation	Nuttall's alkaligrass Herbaceous Vegetation
	<i>Sarcobatus vermiculatus</i> /Barren ground Shrubland	Black greasewood/Barren ground Shrubland
CEGL001363	<i>Sarcobatus vermiculatus</i> / <i>Distichlis spicata</i> Shrubland	Black greasewood/Inland saltgrass Shrubland
CEGL001843	<i>Schoenoplectus maritimus</i> (= <i>Bolboschoenus maritimus</i>) Herbaceous Vegetation	Cosmopolitan bulrush Herbaceous Vegetation
	<i>Scirpus nevadensis</i> (= <i>Amphiscirpus nevadensis</i>) Herbaceous Vegetation	Nevada bulrush Herbaceous Vegetation
CEGL001588	<i>Spartina gracilis</i> Herbaceous Vegetation	Alkali cordgrass Herbaceous Vegetation
CEGL001685	<i>Sporobolus airoides</i> Southern Plains Herbaceous Vegetation	Alkali sacaton Southern Plains Herbaceous Vegetation
	<i>Suaeda calceoliformis</i> Herbaceous Vegetation	Pursh seepweed Herbaceous Vegetation
	<i>Triglochin maritimum</i> - <i>Triglochin palustris</i> Herbaceous Vegetation	Seaside arrowgrass-Meadow arrowgrass Herbaceous Vegetation
Depressional 4/5		
CEGL001798	<i>Hordeum</i> (= <i>Critesion</i>) <i>jubatum</i> Herbaceous Vegetation	Foxtail barley Herbaceous Vegetation

Plants have a range of physiological and life history adaptations to saline environments and vary in their tolerance to these conditions (Glenn and others 1999). The main physiological stresses experienced by plants in saline soils are related to alteration of their osmotic balance. Plants accumulate organic acids intracellularly to compensate for high levels of external soluble salts (Shainberg 1975; Ungar 1974a, 1974c). Effects can include reduced transpiration rates and plant water availability, while excessive ion concentrations may reduce uptake of essential mineral nutrients, constraining plant growth (Shainberg 1975). Other adaptations include: lower selectivity against leaf sodium uptake; the ability to isolate sodium from metabolically active tissues; and among some perennial species, accumulation of salt in older leaves, which are shed at the end of each year (Shainberg 1975; Ungar 1974c). High conductivities affect stomatal conductance and water use, thereby affecting photosynthetic rate. Affected plants may exhibit a variety of phenotypic responses, including differences in leaf morphology and branching pattern. Additionally, the ramets of some clonal salt flat species may be physiologically integrated. Vegetatively reproducing species such as *Juncus arcticus*, *Salicornia rubra*, and *Triglochin* spp. may be able to out compete disturbance-dependent annuals (Riley 2001).

The germination of seed for many halophytes occurs in response to seasonal fluctuations in salinity levels. Seeds that germinate early may be more resistant to increased salinity later in the season because of greater stored food reserves (Foderaro and Ungar 1997). Persistent soil seed banks allow for rapid colonization when more favorable salinities are present and are considered important in maintaining populations of halophytes in many wetlands (Badger and Ungar 1994; Egan and Ungar 2000; Gul and Weber 2001). For example, *Distichlis spicata* responds to short-term salt marsh disturbance with rapid colonization of bare patches from a persistent seed bank and vegetative spread (Bertness and Ellison 1987).

Obligate halophytes are plants with optimal growth at moderate or high salinity that are incapable of growth at low salinity. However, true obligate halophytes are rare, and many species are facultative (Barbour 1970). Many halophytes are in the families Chenopodiaceae and Asteraceae, although grasses (Poaceae) are also common.

Species diversity is typically low in salt flats (Riley 2001; Rocchio 2006a; Windell and others 1986), although distinct patterns of plant zonation often occur. In Colorado's San Luis Valley, wide hydrologic and salinity gradients occur over an elevation range of less than 2.5 m (Cooper and Severn 1992). Pondweed and other aquatic species dominate playas that are regularly flooded, while the margins of wetlands or mineral flat sites may be dominated by succulent dicots such as *Suaeda calceoliformis* and *Salicornia* spp. Monocots may include *Puccinellia airoides*, *Spartina gracilis*, *Hordeum jubatum*, *Triglochin* ssp., *Sporobolus airoides*, *Muhlenbergia asperifolia*, and *Distichlis spicata* (Redmann 1972). Salt-tolerant, phreatophytic shrubs such as *Sarcobatus vermiculatus* commonly occur adjacent to wetter communities (Cooper and others 2006; Rocchio 2004, 2006a).

HRV of Salt Flats in Region 2 ---

Overview of anthropogenic impacts

Because plant cover and productivity are low in salt flats and only salt-tolerant taxa occur (Dodd and Coupland 1966; Ungar 1966), salt flats are rarely utilized by people. As a result, many salt flats have been spared anthropogenic impacts affecting other wetland types. Hydrologic modifications can result from both on-site and off-site impacts. Some impacts, such as livestock trampling, may be locally severe, but probably affect a relatively small number of sites, while others may be more widespread and subtle in their ecological effects. Unlike fens, no broad-scale analyses have been conducted to examine the relative importance of different impacts on salt flats in the region.

Mineral extraction— There are documented examples of historical and contemporary human exploitation of the salt accumulated in saline ecosystems. “Salt licks” in the eastern half of the United States were a significant local to regional source of commercial salt well into the Nineteenth Century. Salt springs and efflorescences in Nebraska were known to Euro-Americans as early as 1835, and by the late 1850s, they had become the main impetus for the settlement of the area (Joeckel and Clement 1999). That these operations failed within 30 years suggests that overall levels of exploitation are not great in the region. Similar “salt works” occur in South Park, Colorado, just southwest of Antero Reservoir. South Park was called Bayou Salado by early explorers due to the broad expanses of salt on the soil (Simmons 1992).

Oil and gas extraction— Soil salinization can occur associated with oil and gas production since salt water, consisting primarily of sodium chloride (NaCl) is often encountered during drilling operations. While water may be reinjected into disposal wells or deposited in on-site reserve pits, contamination can occur from accidental spills or lateral subsurface movement of reserve pit brine (Aschenbach 2006). Contamination from brine spills can result in the death of vegetation and reduced forage production on rangelands or crop yields on agricultural lands. Common halophytes occurring in salt flats can be used in bioremediation of soils contaminated by brine spills. For example, one study found that nearly all species evaluated reduced soil salinity significantly compared with paired control plots, indicating that establishment of salt-accumulating halophytes on salt-affected sites can sufficiently remediate the soil to the point where it can be returned to agricultural productivity or where other native plants can invade and become established (Keiffer and Ungar 2002).

Regions such as the Powder River basin in Wyoming have seen a large increase in coal bed methane (CBM) development. Because water permeates coal beds and maintains the pressure needed to trap methane within the coal, CBM production requires that water first be drawn off, lowering the pressure so gas can flow out of the coal and into the well bore. Commonly this water is saline and poses a disposal issue since surface disposal can affect streams and other habitats and subsurface reinjection increases the cost of production (USDI GS 2000).

Hydrologic modifications—As with other wetland types, hydrologic modifications are likely the single greatest factor altering salt flats. Hydrologic alterations can be on-site in origin or can result from actions off-site. Specific causes of alteration include direct ditching to bring water to or away from an area, seepage from features such as stock ponds and irrigation ditches, and direct application of irrigation water. Modifications may obstruct drainage, preventing water from flowing to existing sites, or they may result in increased drainage, flushing of salts, or a change of vegetation away from halophytes. Roads, culverts, and collection structures all can alter hydrology and may act to either increase or decrease salt flat vegetation.

Agriculture—Cultivation is possibly the most drastic type of disturbance capable of overriding other natural gradients (Walker and Coupland 1968). Alterations of hydrologic regimes through drainage and land use practices were identified as one of the main factors affecting floristic composition in the Rainwater Basin (Stutheit and others 2004). Irrigation is the most common anthropogenic cause of salinity. As water is removed from the soil by ET, salt in soil solution may become 4 to 10 times greater than irrigation water within 3 to 7 days (Chapman 1975). In much of the West, the dominant salts present in irrigation water are chlorides; sulfates; carbonates; and bicarbonates of calcium, magnesium, sodium, and potassium.

Livestock—Palatability of halophytes varies among species. *Distichlis spicata* (saltgrass) can be a salt-tolerant forage crop, although it requires more selection and breeding (Bustan and others 2005). The palatability of some salt flat species changes through development. For example, *Atriplex* spp. may provide good forage when plants are young, but old leaves become unpalatable because of increased concentrations of sodium, chloride, and oxalate (Waisel 1972). Although forage and seed products from halophytes can replace conventional ingredients in animal feeding systems, there are restrictions on their use due to high salt content and anti-nutritional compounds present in some species (Glenn and others 1999). *Distichlis spicata* is grazed readily by livestock (Bustan and others 2005). Livestock effects on plant diversity may depend on salinity. In more productive grasslands, grazing may increase plant diversity; however, in arid or very saline environments, diversity often is unchanged or can decrease (Milchunas and others 1988). For example, herbivores in tallgrass prairies on poor soils reduced plant diversity, whereas those on rich soils increased diversity (Olf and Ritchie 1998). Livestock may promote salinization in some settings by encouraging the formation of salt crusts through changes to evaporation rates following trampling (Lavado and others 1993; Lavado and Taboada 1987). Livestock and large native ungulates can also affect habit through impacts to soil structure. Trampling can cause soil compaction and reduced infiltration (Daniel and others 2002).

Exotic species—A number of exotic species may occur in salt flats. The success of many Eurasian exotics is due in part to the ability of many to tolerate saline soils. Salt flats are susceptible to invasion by exotic perennial species like *Cardaria latifolia* and non-native annuals such as *Chenopodium glaucum*. Other common exotics are *Salsola* spp., *Cirsium arvense*, *Bassia hyssopifolia*, and *Kochia scoparia* (Rocchio 2006a).

Atmospheric deposition of pollutants—Practices including the use of commercial fertilizers, increases in the livestock numbers, and manufacturing and transportation growth have led to increases in nitrogen deposition (Baron and others 2000). Although unstudied in Region 2 salt flats, possible ecological responses to atmospheric deposition of pollutants can include changes in soil fertility and shifts in vegetation composition (Vitousek and others 1997). Pollutants such as SO₂ may influence salt flat vegetation through both fertilizing and toxic effects on vegetation depending on SO₂ concentration, duration of exposure, plant species, and environmental factors such as light, temperature, and nutrient regime (Milchunas and others 1981). One study found that the biweekly addition of nitrogen to a salt marsh led to an increase in plant biomass and cover, but no reduction in diversity (Traut 2005). Dominant species such as *Salicornia virginica*, *D. spicata*, and *Triglochin concinna* thrived with the additional nitrogen, but did not displace subdominant species, suggesting that competitive exclusion does not occur (Traut 2005).

Abundance, distribution, and condition of salt flats across Region 2 landscapes

Relatively few data are available as a baseline in evaluating possible changes in salt flat conditions or abundance. Available data include NRCS soil surveys, which list soils by series and describe their suitability for agriculture, among other uses. In soil surveys, map units are typically assigned a capability class, which is the broadest category in the land capability classification system. Class codes from 1 to 8 are used to indicate increasing limitations of soils. Map units can be assigned subclass codes; for example, class “s” is made up of soils that have soil limitations within the rooting zone, such as shallowness of the rooting zone, stones, low moisture-holding capacity, low fertility that is difficult to correct, and salinity or sodium content (USDA NRCS 2005). Such information can be used to identify areas of high salinity. Soil series descriptions in surveys often list depth to water table, which, in conjunction with salinity information, could be used to map salt flats.

Direct hydrologic alteration, especially from agricultural activities, is likely the most significant anthropogenic impact. Agricultural impacts were by far the greatest contributor to wetland loss during the late Eighteenth to the late Twentieth Century (Dahl 1990). Changes in the quality, quantity or timing of surface and groundwater flow into salt flats is also common due to indirect hydrologic alterations of surrounding landscapes, for example due to roads, storm water and

irrigation outflows, groundwater pumping, or plowing that changes the direction of surface water runoff (Cooper and others 2006; Richter and others 1996). In addition to probable loss of many salt flats, anthropogenic activities have created salt flats in novel landscape conditions. Features such as stock watering ponds and water storage reservoirs, irrigation ditches and canal-fed wetlands, and roadside ditches have expanded the distribution of salt flats.

Only a small fraction of salt flats in the region have been evaluated botanically, so it is impossible to confidently assess departures in vegetation attributes from historical conditions. Although declines in species richness have been documented in response to disturbances for other ecosystems, too little research has been completed in salt flats to make generalizations, although we assume that many salt flats have been altered as a result of land use changes. Hydrologic regimes have been extensively modified, although few data are available. Where longer-term data are available, for example, in Colorado's San Luis Valley, data demonstrate changes in hydrologic process such as water table depth and inundation frequency (Cooper and others 2006). Chemical changes have also occurred, directly in response to factors like atmospheric nitrogen deposition and indirectly due to altered salt transport and deposition patterns from irrigation.

Management Opportunities and Constraints _____

Management opportunities

Although wetlands are generally recognized as providing important ecological functions, salt flats are not necessarily widely valued. This is due, in part, to their low productivity and diversity and to the negative impact of high salinity on activities such as agriculture. Little information is available on the functions and ecological services provided by salt flats. However, the important role of many saline wetlands as bird habitat has been demonstrated, providing an incentive for preservation of playas. More regional assessments of salt flats should be conducted. Possible tools include aerial photographs or other remotely sensed data to identify and map wetlands and salt affected ecosystems (Cooper and others 2006; Farifteh and others 2006; Metternicht and Zinck 2003). Site-level assessments of salt flat hydrology, water chemistry, and vegetation relationships are also needed. Modest investments of time and money for installation of groundwater-monitoring wells and other environmental sensors can provide valuable data.

Restoration

Little research has been directed at restoring salt flats—more is known about methods to alleviate certain types of salinity, such as adding gypsum to leach sodium from soils (Davis and others 2003; Davis and others 2003; Skarie and others 1987). The restoration of inland salt-affected wetlands has received relatively little attention. Notable exceptions are studies of the salt-affected communities of Cheyenne Bottoms, Kansas. The Nature Conservancy restored native plant communities subject to grazing and former cropland by reestablishing sheet flow across disturbed areas. Results were mixed, indicating the difficulty of restoring heavily disturbed plant communities (Kindscher and others 2004).

As previously discussed, a key first step in any wetland restoration project is to gain an understanding of hydrologic regimes driving the ecological function of a site. Any control structures (e.g., drainage tiles or ditches) need to be identified and removed. Proper selection of species is important, particularly for salt flats, since the salt tolerance of different species varies widely (Table 27) and ecotypic variation should also be considered (Aschenbach 2006). Seeds for restoration can be collected in the field, stratified, germinated, and grown into seedlings for use in restoration projects. A benefit of such an approach is the ability to place species directly into the physical environments where they will perform best. Soil texture and chemistry measurements are essential.

Table 27—Summary of the hydrologic and salinity tolerances of a variety of wetland species in relation to salinity and hydrologic regime.

Salinity	Hydrologic regime		
	Perennial saturation/ stable water table	Seasonal saturation/moderate deep flooding/ fluctuating water table	Seasonal saturation/ no flooding/fluctuating water table
Fresh <2 mS/cm	<i>Calamagrostis canadensis</i> , <i>Carex aquatilis</i> , <i>Carex aurea</i> , <i>Carex norvegica</i> , <i>Carex</i> <i>raymondii</i> , <i>Carex rostrata</i> , <i>Carex utriculata</i> , <i>Eleocharis</i> <i>acicularis</i> , <i>Equisetum arvense</i> , <i>Glyceria striata</i> , <i>Menyanthes</i> <i>trifoliata</i> , <i>Muhlenbergia</i> <i>glomerata</i> , <i>Poa palustris</i>	<i>Beckmania syzigachne</i> , <i>Calamagrostis</i> <i>canadensis</i> , <i>Calamagrostis</i> <i>inexpansa</i> , <i>Carex utriculata</i> , <i>Eleocharis palustris</i> , <i>Equisetum arvense</i> , <i>Glyceria borealis</i> , <i>Glyceria grandis</i> , <i>Glyceria striata</i> , <i>Juncus balticus</i> , <i>Phragmites australis</i> , <i>Poa palustris</i> , <i>Scirpus microcarpus</i> , <i>Scirpus pungens</i> , <i>Scirpus validus</i> , <i>Typha latifolia</i>	<i>Deschampsia cespitosa</i> , <i>Equisetum arvense</i> , <i>Juncus balticus</i>
Moderately saline 2- 15 mS/cm	<i>Calamagrostis inexpansa</i> , <i>Carex utriculata</i> , <i>Kobresia</i> <i>simpliciuscula</i> , <i>Muhlenbergia</i> <i>glomerata</i>	<i>Beckmania syzigachne</i> , <i>Calamagrostis</i> <i>inexpansa</i> , <i>Eleocharis palustris</i> , <i>Juncus balticus</i> , <i>Phragmites australis</i> , <i>Scirpus pungens</i> , <i>Scirpus validus</i> , <i>Scolochloa festucaeae</i> , <i>Sparganium</i> <i>eurycarpum</i> <i>Spartina pectinata</i> , <i>Typha latifolia</i>	<i>Calamagrostis inexpansa</i> , <i>Juncus balticus</i> , <i>Puccinellia</i> <i>nuttalliana</i> , <i>Spartina gracilis</i>
Saline 15- 45 mS/cm	<i>Triglochin maritima</i> , <i>Triglochin palustris</i>	<i>Juncus balticus</i> , <i>Phragmites australis</i> , <i>Spartina pectinata</i> , <i>Triglochin maritima</i>	<i>Juncus balticus</i> , <i>Spartina</i> <i>gracilis</i> , <i>Puccinellia nuttalliana</i> , <i>Triglochin maritima</i>
Hypersaline >45 mS/cm	<i>Triglochin maritima</i>		<i>Puccinellia nuttalliana</i> , <i>Spartina gracilis</i>

Because many salt flat species are represented in the soil seed bank (Badger and Ungar 1990), direct placement of soils to restoration areas could potentially be used for establishing plant cover. Seed bank assays should be conducted to assure that the correct species are present in the soil. Typically, only the upper soil horizons contain viable seed. Depending on the proximity of restoration areas to other wetlands, natural seed rain may be effective.

Management constraints

Management constraints can include lack of funding to develop management and restoration goals and insufficient information on the nature of the resource. Legal and political constraints are often imposed by issues involving wetlands because of water rights, so it is best to identify potential stakeholders early in planning. Constraints outside the control of managers include regional climate change and changes in surrounding land use.

8. Historical Range of Variation for Region 2 Wet Meadows

Definitions and Concepts of Wet Meadows

Wet meadows are the most widespread wetland type in Region 2, occurring from the plains to the alpine zone. Although wet meadows as a class are variable in vegetation, geomorphic setting, and hydrologic function, they differ from other wetland types in several ways. Wet meadows lack the perennial high water tables and organic soils found in fens, the large seasonal and inter-annual water table fluctuations characteristic of marshes, the high salt concentrations of salt flats, and the direct influence of high energy surface water flows characterizing riparian ecosystems. Wet meadows are typically highly productive and have historically been heavily utilized. Since the arrival of Euro-Americans, wet meadows have been commonly managed for livestock forage and hay production. Although wet meadows are abundant, particularly in intermountain basins and on the plains, it is one of the least studied wetland types.

Geomorphic Setting and Principal Ecological Drivers

Geomorphic setting

Considering that wet meadows span all elevations and ecoregions in Region 2, it is not surprising that they occur in a variety of geomorphic settings. However, wet meadows have seasonally saturated conditions and most are supported, in part, by groundwater and are found in landscape settings where groundwater levels are near the soil surface. Wet meadows may form in topographic low positions, such as around lakes and ponds (Figure 45). In these settings, marshes may occupy the deepest portion of the basin, with wet meadows on the margins. Such zonation among wetland types is common in wetlands in the Great Plains such as the Nebraska Sandhills and prairie pothole region (Johnson and others 1987; Kantrud and others 1989a; Seabloom and others 1998).

Wet meadows may also occur adjacent to riparian communities (Figure 45). In these settings they may be hydrologically connected to the stream but lack the influence of flooding that characterizes the active riparian zone. At higher elevations, the area of wet meadow surrounding riparian zones increases relative to the area of the active riparian influence. This is due to the greater groundwater inputs and smaller streams, which affect a smaller area with overbank flooding relative. In the alpine, wet meadows often occur in saddles (Walker and others 2001).

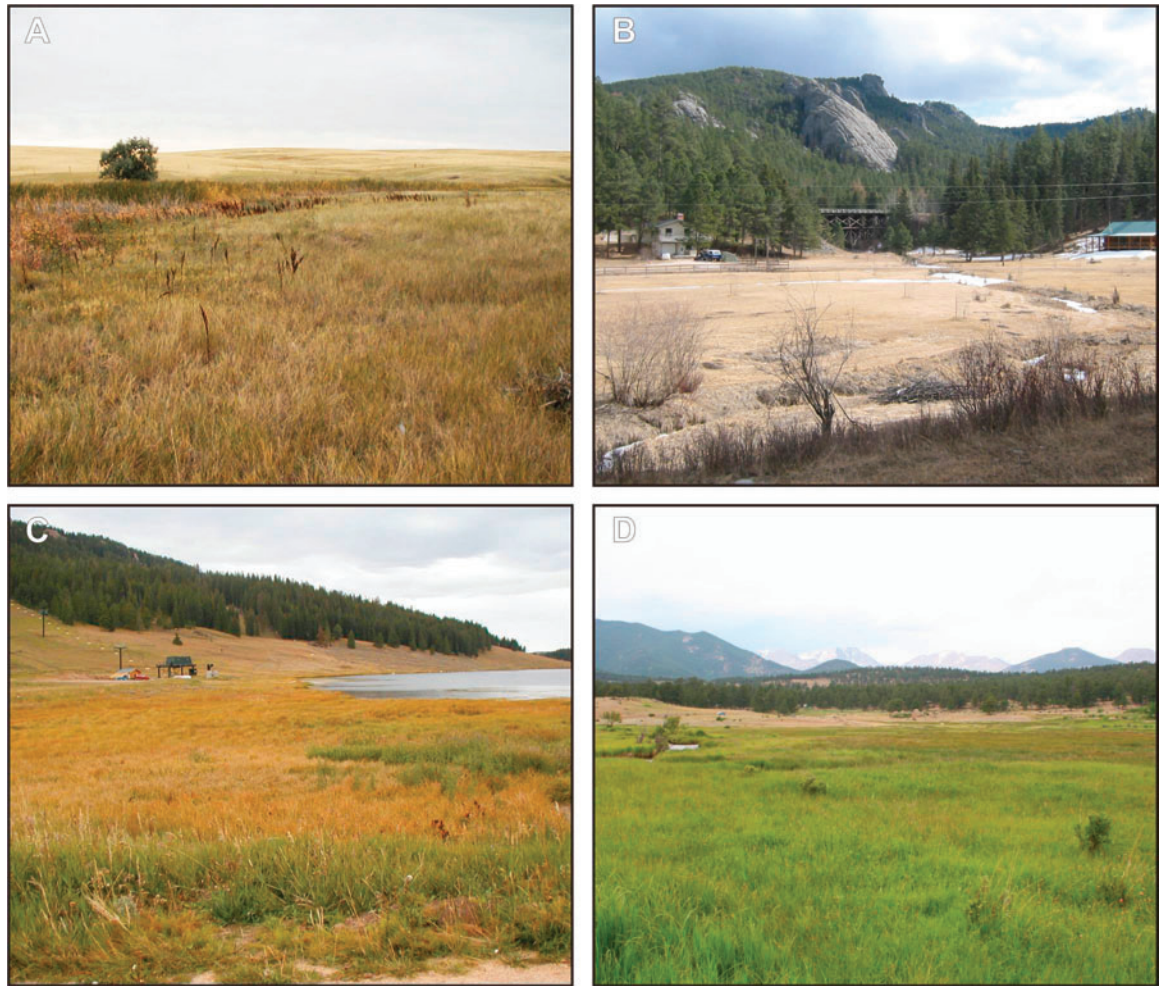


Figure 45—Wet meadows from across the region: (A) Oglala National Grassland (Nebraska), (B) Black Hills National Forest (South Dakota), (3) Bighorn National Forest, (Wyoming), and (4) Rocky Mountain National Park (Colorado).

Key drivers and ecological processes

Climate—Wet meadows exist along nearly the entire elevation gradient in Region 2. Because of this, it is difficult to generalize about the influence of climate on wet meadows. The prevalent precipitation type (rain versus snow) and the direct importance of precipitation to the hydrologic functioning and vegetation of wet meadows varies widely. Snow and rain differentially influence processes of infiltration and surface water runoff and affect groundwater recharge. Consequently, the proportion of a watershed with a snow- versus rain-dominated precipitation regimes can substantially influence the abundance and function of wet meadows. At low elevations, most precipitation falls as rain, although the amount and seasonality varies across the region. At higher elevations, snow and rain-on-snow precipitation regimes become dominant, and the cooler and wetter climate can support more wetlands, including wet meadows.

Temperature is the primary factor determining the length of the growing season. Mean temperatures generally decline with increasing elevation. However, rugged topography and the resulting processes of cold air drainage can create a great deal of spatial variability in temperatures. Site aspect is also important, particularly in subalpine and alpine areas where the growing season length is controlled in large part by the timing of snowmelt. In a study of alpine tundra wet meadow soils in Colorado, researchers found that temperatures were relatively stable near freezing for much of the spring and autumn, and water availability was limited by freezing rather than by drying (Costello and Schmidt 2006).

In the alpine zone, strong and variable winds and complex topography create highly heterogeneous patterns of snow accumulation. The timing of snow melt varies, with snowmelt arriving early in windward and ridge top locations (Billings and Bliss 1959). Wind-driven redeposition of snow creates substantial local variation in the amount of effective precipitation. Because the timing and duration of spring thaw determines the fraction of this precipitation that ultimately passes into the soil, direct measurements of precipitation may poorly reflect the effective precipitation affecting a site (Taylor and Seastedt 1994). For plants, the timing of key phenological events (e.g., the initiation of growth) is related to snowmelt patterns, resulting in differences among communities (Walker and others 1995).

Geology—A number of geologic factors affect the distribution and function of wet meadows across the region. Differences among watersheds in lithologic characteristics influence the composition and concentration of ions in groundwater as well as characteristics such as porosity and permeability. Because wet meadows may be supported by inputs of groundwater, the mineralogy of watersheds can influence water chemistry, biota, and ecological processes.

Geomorphic history is also important. Pleistocene glaciation in mountainous areas of Region 2 strongly influenced the configuration of many contemporary landscapes (Richmond 1960; Thornbury 1965; Wright and Porter 1983). Large wetland complexes supporting extensive wet meadows are common in broad, glaciated valleys (Windell and others 1986). For example, large wetland complexes on both the east and west side of the Continental Divide of Colorado's Front Range in Rocky Mountain National Park support marshes, fens, riparian shrublands, and wet meadows (Cooper 1990a; Cottrell 1993).

Hydrologic regime—Hydrologic regime is the primary factor distinguishing wet meadows from other wetlands types and is an important influence on biota and geochemical functioning of wet meadows. Wet meadows occur in sites where soils are seasonally saturated, but perennially high water tables or seasonally deep water do not occur. In montane and subalpine watersheds, wet meadows frequently occur in stream valleys as part of larger wetland complexes. However, unlike riparian ecosystems, wet meadows do not experience high-velocity surface flows or sediment deposition from fluvial processes. Relative to marshes, wet meadows have stable water tables and do not experience deep inundation.

Mean water tables are lower in wet meadows than the threshold required for deep peat formation—the main characteristic that defines fens.

Sources of water to wet meadows include direct precipitation, surface water, and groundwater, with the relative importance of each varying among individual wetlands. Wet meadows receive a portion of their annual water budget through direct precipitation. The amount is generally scaled to wetland area, although in alpine and subalpine areas where extensive drifting of snow may occur, the relationship may not hold. Overall, precipitation is likely the least important direct contributor to hydrologic regimes in wet meadows in the Rocky Mountains. Direct surface water inputs to wet meadows are generally limited to sheet flow following extreme precipitation events or during spring snowmelt. Channelized flows generally do not occur in wet meadows, although wet meadows are often found in close proximity to streams. While the overall frequency of flooding in wet meadows is low, wetlands in settings such as wide, low-gradient alluvial valleys may be periodically flooded due to the activities of beaver.

For most wet meadows, groundwater is the most important hydrologic input; however, there is considerable variability in the size and characteristics of aquifers. Wet meadows in the Nebraska Sandhills may be supported by regional aquifers, while small and local hillslope aquifers support wet meadows in montane environments (Winter and others 2001). High early summer water tables maintained by snowmelt occur in both fens and wet meadows. The hydrologic distinction is that in wet meadows, the aquifer provides less stable groundwater flows and the water table may drop in the middle to late summer. The water table in wet meadows may drop to 1 m or more below the soil surface in July and August. In fens, with the exception of dry years, the summer water table remains within approximately 20 to 40 cm of the soil surface (Chimner and Cooper 2003; Chimner and others 2002; Cooper 1990a).

Water and soil chemistry—The chemical properties of wet meadow soils are closely related to both hydrologic regimes and plant species distributions. Water and soil pH and the concentration of cations and nutrients vary among wet meadows. Site-level variables such as soil particle size distribution, organic matter content, and groundwater source influence soil chemistry, as do watershed-scale characteristics such as the mineral composition of meadow soils and surrounding landscapes. For instance, where relatively soluble minerals are dominant, groundwater may contain abundant dissolved solids, while areas composed of relatively insoluble minerals will have lower concentrations of ions. The pH in wet meadow soils can vary widely but is typically neither extremely acidic nor basic. Wet meadows in the Nebraska Sandhills, for example, ranged from 5.9 to 7.6 (Kapustka and others 1988).

Most wet meadows have relatively fine-textured soils that are dark in color with high organic matter content. Anaerobic conditions lead to the formation of hydric soil indicators such as mottles and oxidized root channels, and these features can be used to delineate wet meadows from dry meadows, particularly where vegetation has been disturbed. Nutrients are generally more abundant than in adjacent uplands—a factor contributing to the high primary productivity seen in many wet meadows.

The dominant forms and abundance of nutrients varies among wet meadows. For example, subalpine meadow soils in Colorado had low NO_3^- concentrations, likely the result of assimilation and denitrification in anoxic meadow soils (Clow and Sueker 2000). Variation in microbial processes is highly related to soil moisture. For example, the topographic soil moisture gradient found in alpine areas is a fundamental control of nitrogen turnover patterns among communities (Fisk and others 1998).

When present in a watershed, beavers can significantly affect biogeochemical pathways by shifting element storage from vegetation to sediments and soils. The fundamental control over subsequent alterations of biogeochemical pathways is the occurrence of anaerobic conditions from waterlogged soils. As ponds fill, sediments accumulate substantial standing stocks of chemical elements that are available for vegetation growth. Short-term hydrologic variations can cause shifts in the aerobic-anaerobic boundary in the upper soil layers of wet meadows, enhancing nitrogen cycling and nitrogen availability for plant growth in both active and abandoned ponds (Pinay and Naiman 1991).

Disturbance processes—Wet meadows are subject to a range of natural and anthropogenic disturbances. Relative to riparian areas or marshes, abiotic disturbances such as floods are less important, while biotic disturbances from animals are of greater ecological significance. Data describing disturbance frequency, magnitude, or return interval from wet meadows are largely non-existent in the region. Unlike forests, where dendrochronological approaches to reconstructing disturbance processes are available, inferences about disturbances in wet meadows must be made from anecdotal accounts and case studies, often from research conducted outside of the region.

The role of fire in wet meadow dynamics is poorly understood. Wet meadows in Region 2 occur as relatively small, discrete patches set within other cover types. Ignitions in wet meadows are likely rare and fires affecting them originate from outside of the wetland's boundaries. Because fire regimes vary widely within the region in response to factors such as cover type, physiography, and climate, it is impossible to generalize on fire regime parameters for wet meadows other than to say that, historically, most wet meadows would have burned on some time scale. Fire in wet meadows may cause direct plant mortality, influencing community composition, and may favor herbaceous species over woody ones

(DeBenedetti and Parsons 1984; Jacobson and others 1991). Indirect effects may include increased water, sediment, and nutrient flux from surrounding hill slopes (Anderson and Menges 1997).

Disturbance caused by animals are locally important in many wet meadows. Native ungulates such as deer, elk, and bison, as well as domestic livestock such as sheep and cattle can have important effects on the abiotic and biotic environment in wet meadows. Because of their high productivity, wet meadows are attractive to grazers, and have a long evolutionary history of herbivory. In conifer-dominated montane areas, meadows may provide the most significant resource of graminoid vegetation. Large animal effects can include plant mortality from herbivory or trampling. In addition, animals may alter soil chemistry and nutrient availability through the deposition of urine and feces (Frank and Evans 1997). Historically, significant local impacts to vegetation likely occurred but because of variable population density and migratory behavior, the effects of native ungulates on wet meadows at broad spatial or temporal scales was not likely great.

Small mammals such as pocket gophers can have a significant influence on wet meadows. Through their burrowing and foraging, they can affect patterns and rates of soil development, nutrient availability, microtopography, demography and abundance of plant species, and plant diversity (Ellison and Aldous 1952; Huntly and Inouye 1988; Ward and Keith 1962). For example, erosion measurements in a Colorado alpine ecosystem indicated long-term susceptibility of gopher-disturbed soils to redistribution by water and/or wind (Sherrod and Seastedt 2001). Research in Arizona found that pocket gophers can act as a keystone herbivore by limiting aspen invasion of meadows (Cantor and Whitham 1989). Small soil disturbances can also be important for the establishment of many species. For example, cohorts of invading sagebrush seedlings in California meadows were preferentially associated with gopher mounds (Berlow and others 2002). Other mammals that may influence wet meadows are voles (Austin and Pyle 2004; Howe and Lane 2004) and marmots (del Moral 1984).

Although most important in riparian ecosystems, beavers may create disturbances important to wet meadows. Beavers are a major geomorphic driver of meadow formation and landscape dynamics in some montane and subalpine areas. In low-gradient glacial valleys, which often support wetland complexes with both riparian and wet meadows ecosystems, beaver dams may cause channel avulsions flooding surrounding wet meadows (Cooper and others 2006). Abandoned beaver ponds may develop into wet meadows or marshes depending on resulting water table characteristics. At broad spatial scales, the activities of beaver can create a complex, heterogeneous pattern of wetland types, including wet meadows, marshes, and riparian ecosystems, thereby increasing landscape patterns of species richness (Wright 2002).

In many mountain watersheds, spatial and temporal variability in the location and duration of beaver ponds is a major factor influencing the hydrologic, geochemical, and community-level characteristics of wetland complexes (Cooper and others 2006; Westbrook and others 2006). Beavers can also be important drivers of vegetation structure and composition, acting directly through their selection of species for food and dam construction and indirectly through their hydrologic effects (Baker and others 2005a; Barnes and Mallik 2001; Naiman and others 1988).

Post-disturbance recovery to natural and anthropogenic disturbances varies. Alpine areas are, in general, slower to recover than sites at lower elevations (Ebersole 2002). Individual species also vary widely in their response to disturbance. Some species respond positively or even require disturbance in order to persist. An example is *Spiranthes dulivialis*, a diminutive orchid found in riparian areas and adjacent wet meadows at low elevations and listed by the USFWS as threatened under the Endangered Species Act (Sipes and Tepedino 1995). Management practices employed to promote the species in some areas include active mowing. Mowing is also used in Europe to promote species diversity (Grootjans and others 2002; Vinther and Hald 2000).

Wet meadow development and succession — Successional patterns vary because a wide range of wet meadow vegetation types exists. Alpine communities often do not exhibit well-defined successional sequences. The relative abundance of species following disturbance remains nearly constant in some sites following disturbance, while at others, one or more species may increase in relative abundance over time (Ebersole 2002). In subalpine and montane meadows, researchers have described successional shifts towards increased shrub dominance (Langenheim 1962), although many meadows show no such trend and appear to be physiognomically stable. The mechanisms driving different successional trajectories among meadows are complex. For example, abandonment and drainage of beaver ponds may result in the formation of meadows, which may persist for decades as graminoid-dominated patches that resist conifer invasion despite close proximity to seed sources (Terwilliger and Pastor 1999).

Wet Meadow Classification and Gradients _____

Wet meadows have been classified in a number of ways. Specific criteria used by different classification approaches to differentiate wetland classes include dominant vegetation, hydrologic characteristics, geomorphic setting, and water chemistry. Under the Cowardin classification used by the National Wetland Inventory, all wet meadows fall within the palustrine system, and depending upon their vegetation, are placed in the emergent or scrub-shrub class. However, fens and salt flats may be identically classified, reducing the utility of NWI maps for analyzing individual wetland classes like wet meadows.

The Hydrogeomorphic (HGM) approach used to classify wetlands (Brinson 1993a; Cooper 1998a) emphasizes physical variables such as geomorphic setting and hydrologic regime in classification. Several subclasses relevant to wet meadows were identified in a preliminary classification of Colorado wetlands using HGM (Table 28). Wet meadows in Slope Subclasses 1 and 2 (S1/2) may be dominated by woody or herbaceous species (Carsey and others 2003). Slope Subclass 1 wetlands are very common and widespread in mountainous portions of Colorado, and similar ecosystems are found in Wyoming. Slope Subclass 2 wetlands occur on calcareous substrates and have higher concentrations of mineral ions (e.g. Ca²⁺). These are less common since most Rocky Mountain ranges are composed of igneous or metamorphic rocks. Wetlands in Slope Subclasses 3 and 4 (S3/4) includes wet meadows at middle elevations in the mountains. Similar wetlands also occur in Wyoming and the Black Hills. Slope 4 wetlands occur at lower elevations but have a seasonally high water table that supports herbaceous or occasionally shrub associations (Carsey and others 2003).

Stewart and Kantrud (1971) classified wetlands in the prairie pothole region into one of seven classes based on water permanence, quantity, and quality, as well as the vegetation communities present. Ephemeral ponds are often wet for only a few weeks each year, and vegetation is dominated by facultative wetland plants such as *Poa pratensis*, *Anemone canadensis*, and *Symphoricarpos* spp. Wetlands in the temporary pond class support wet meadow communities in the deepest part of the basin and are usually fringed by the low prairie zone along meadow margins. Common species include *Poa palustris*, *Carex lanuginosa*, *Juncus balticus*, *Eleocharis* spp, *Hordeum jubatum*, *Calamagrostis stricta*, *Spartina pectinata*, and *Mentha arvensis*. In this classification, a shallow marsh zone occurs in the center of seasonal ponds and lakes, surrounded by wet meadows and wet prairie. The deepest portion of semi-permanent ponds and lakes support a deep marsh zone, followed by the shallow marsh zone, and lastly a wet meadow zone (Stewart and Kantrud 1971).

Table 28—HGM subclasses relevant to wet meadows in Colorado (Carsey and others 2003).

HGM	Subclass description	Common species
Slope 1	Alpine and subalpine fens and wet meadows on saturated non-calcareous substrates.	<i>Carex aquatilis</i> var. <i>stans</i> , <i>Carex scopulorum</i>
Slope 2	Subalpine and montane fens and wet meadows on saturated calcareous substrates.	<i>Eleocharis quinqueflora</i> , <i>Kobresia simpliciuscula</i> , <i>Carex simulata</i>
Slope 3	Wet meadows at middle elevations in the mountain ecoregion with a seasonal high water table near the ground surface.	<i>Juncus balticus</i> var. <i>montanus</i>
Slope 4	Low elevation meadows with a seasonal high water table near the ground surface. May occur on floodplains or near springs.	<i>Carex nebrascensis</i>
Depressional 1	Lake fringes without peat soils.	<i>Carex utriculata</i>

Wet Meadow Vegetation in the Region

Because wet meadows occur over such broad environmental gradients, they are highly variable in species composition and are one of the most diverse and productive ecosystem types in Region 2. Comer (2003) identified four primary ecological systems in Region 2 relevant to wet meadows (Table 29). More than 18 wet meadow vegetation associations are recognized by NatureServe (NatureServe 2005), although this likely misses some associations in the region (Table 30). Some meadow species have large elevation ranges and considerable ecotypic variation. For example, *Deschampsia cespitosa* and *Poa pratensis* occur from low elevations to the alpine (Pearcy and Ward 1972) and may occur in wet meadows in some zones but not in others.

Some community types are very common. For example, wet meadows dominated by *Juncus balticus* are found widely throughout the western United States, occurring from low to middle elevations. Shrubs are typically absent or their cover is low in wet meadows, however *Dasiphora fruticosa* commonly occurs in montane wet meadows with *Juncus arcticus*. The species is resistant to drought and can persist or expand in response to drought or disturbance such as grazing. Introduced perennial sod-forming grasses such as *Agrostis stolonifera* are often co-dominants (NatureServe 2005), particularly at lower elevations. In the Nebraska Sandhills, vegetation is dominated by introduced cool-season grasses and legumes, along with native sedge and *Juncus* species, in contrast to upland sites that are dominated by native, warm-season grasses (Volesky and others 2004).

Communities dominated by *Schoenoplectus pungens* are common at low elevations and, like *Juncus balticus* communities, are easily identified at a distance by their dark green to black colors. The community occurs adjacent to ponds, lakes, or low-gradient streams. Shrubs and trees are usually absent. *Carex*-dominated communities are also common. For example, wet meadows dominated by *Carex nebraskensis* occur throughout much of the West from as low as 1000 to over 2800 m above sea level (NatureServe 2005). Other common species are *Carex praegracilis*, *Calamagrostis stricta*, *Deschampsia cespitosa*, *Eleocharis palustris*, *Glyceria striata*, *Juncus balticus*, and *Schoenoplectus pungens*. Common wet meadow associations in the alpine zone include those dominated by *Carex scopulorum*, *Pedicularis groenlandica*, *Caltha leptosepala*, and *Rhodiola integrifolia*. Communities typically occur down-slope of snow banks. Wet meadows are most common in the lower alpine zone, although some rare associations occur at the base of rock glaciers at higher elevations (Walker and others 2001).

Table 29—Ecological systems relevant to wet meadows in Region 2 (Comer and others 2003b).

Ecological systems	Hectares	% Area
Eastern Great Plains Wet Meadow Prairie and Marsh	138,843	0.1
Western Great Plains Riparian/Western Great Plains Floodplain	1,488,930	1.3
Rocky Mountain Subalpine-Montane Riparian Shrubland	475,655	0.4
Rocky Mountain Subalpine Mesic Meadow	884,960	0.8

Table 30—Graminoid-dominated wet meadow alliances and vegetation associations in Region 2 (Nature-Serve 2005).

Alliance	Association	Code
<i>Calamagrostis canadensis</i>	Seasonally Flooded Herbaceous Alliance <i>Calamagrostis canadensis</i> Western Herbaceous Vegetation	CEGL001559
<i>Carex (rostrata, utriculata)</i>	Seasonally Flooded Herbaceous Alliance <i>Carex rostrata-Carex lacustris-(Carex vesicaria)</i> Herbaceous Vegetation <i>Carex utriculata</i> Herbaceous Vegetation	CEGL002257 CEGL001562
<i>Carex aquatilis</i>	Seasonally Flooded Herbaceous Alliance <i>Carex aquatilis-Carex</i> spp. Herbaceous Vegetation	CEGL002262
<i>Carex atherodes</i>	Seasonally Flooded Herbaceous Alliance <i>Carex atherodes</i> Herbaceous Vegetation	CEGL002220
<i>Carex buxbaumii</i>	Seasonally Flooded Herbaceous Alliance <i>Carex buxbaumii</i> Herbaceous Vegetation	CEGL001806
<i>Carex nebrascensis</i>	Seasonally Flooded Herbaceous Alliance <i>Carex nebrascensis</i> Herbaceous Vegetation	CEGL001813
<i>Carex pellita</i>	Seasonally Flooded Herbaceous Alliance <i>Carex pellita-Calamagrostis stricta</i> Herbaceous Vegetation	CEGL002254
<i>Carex</i> spp.- <i>Plantago eriopoda</i>	Temporarily Flooded Herbaceous Alliance <i>Calamagrostis stricta-Carex sartwellii-Carex praeegracilis-Plantago eriopoda</i> Saline Herbaceous Vegetation	CEGL002255
<i>Carex</i> spp.	Seasonally Flooded Herbaceous Alliance <i>Carex diandra</i> Wet Meadow Herbaceous Vegetation	CEGL002549
<i>Deschampsia caespitosa</i>	Saturated Herbaceous Alliance <i>Deschampsia caespitosa-Caltha leptosepala</i> Herbaceous Vegetation	CEGL001882
<i>Eleocharis palustris</i>	Seasonally Flooded Herbaceous Alliance <i>Eleocharis palustris</i> Herbaceous Vegetation Marsh	CEGL001833
<i>Glyceria borealis</i>	Semipermanently Flooded Herbaceous Alliance <i>Glyceria borealis</i> Herbaceous Vegetation	CEGL001569
<i>Juncus balticus</i>	Seasonally Flooded Herbaceous Alliance <i>Juncus balticus</i> Herbaceous Vegetation	CEGL001838
<i>Phalaris arundinacea</i>	Seasonally Flooded Herbaceous Alliance <i>Phalaris arundinacea</i> Western Herbaceous Vegetation	CEGL001474
<i>Schoenoplectus pungens</i>	Semipermanently Flooded Herbaceous Alliance <i>Schoenoplectus pungens</i> Herbaceous Vegetation	CEGL001587
<i>Spartina pectinata</i>	Temporarily Flooded Herbaceous Alliance <i>Spartina pectinata-Carex</i> spp. Herbaceous Vegetation <i>Spartina pectinata-Schoenoplectus pungens</i> Herbaceous Vegetation	CEGL001477 CEGL001478

Hydrologic regime is generally the most important factor influencing vegetation patterns and dynamics in wet meadows, although in alpine tundra, patterns of snowpack accumulation and melt-out strongly control vegetation zonation (Billings and Bliss 1959). Individual species vary in their response to water table gradients, with some species (e.g., *Juncus arcticus*) capable of growing along a wider range of water table depths than others (Dwire and others 2006). In a study evaluating the response of 63 riparian grassland species to hydrologic variation, the best plant-frequency response curves were obtained by using the growing season 10 percent cumulative frequency water level, followed closely by the growing season seven-day moving average high water level, suggesting that high water levels may be more influential than mean, median, or low water levels. (Henszey and others 2004).

Water table dynamics are also important drivers of community-level characteristics such as species richness and total plant cover. For instance, Dwire and others (2006) found that wet meadow communities dominated by sedges (*Carex* spp.) had lower species richness and diversity compared to dry meadow communities, which supported a mixture of grasses and herbaceous dicots. In their study, species richness and total plant cover were negatively correlated with mean water table depth and positively correlated with mean redox potential at 10-cm and 25-cm depths (Dwire and others 2006). In the wettest wet meadow communities, obligate hydrophytes tolerant of seasonal flooding, shallow water table depths, and anaerobic soil conditions generally dominate. In contrast, competition and other biotic interactions likely play a greater role in determining species composition and vegetation structure in the more diverse moist and dry meadow communities (Dwire and others 2004).

Most wet meadows exhibit seasonal declines in their water table. This is particularly true of wet meadows in subalpine and alpine areas that receive significant hydrologic inputs from snow. The magnitude of water table fluctuations varies widely, and drawdown may or may not create moisture stress for plants. In alpine areas, average moisture values for wet meadows at the end of the growing season are still higher than for mesic meadows in the beginning of the season, and other factors such as release from snow, solar radiation, and soil nutrients generally limit production (Billings and Bliss 1959; Ehleringer and Miller 1975; Taylor and Seastedt 1994). At lower elevations, the drop in water tables may be more significant and may result in decreased plant physiological performance (Svejcar and Riegel 1998).

Although the main variable driving species responses and interactions within wet meadows is the water table, direct and indirect effects of disturbances such as livestock grazing can also play a role. For example, *Carex nebrascensis* and *Poa pratensis* commonly co-occur in meadows throughout the West, but have maximum expression at different water tables. *Poa pratensis* is capable of more rapidly responding to disturbances that remove neighbors and increase available space than *C. nebrascensis*, suggesting that grazing may alter the relative competitive ability of the two species in favor of *Poa pratensis* (Martin and Chambers 2001).

Temperature represents an additional variable influencing vegetation, particularly at higher elevations. Temperature is strongly influenced by slope position and aspect, particularly in rugged terrain. Soil temperatures within meadows may also vary along water table gradients. For example, sites in wet meadows were cooler than those in the dry and mesic meadow types and sagebrush vegetation types (Castelli and others 2000).

Some research suggests that, relative to marshes and salt flats, few meadow species form persistent seed banks (Bekker and others 1998). However, this may not be true for all wet meadows. The dense vegetation cover, dominance by perennial and clonal species, and relatively low disturbance frequency do not favor this life history attribute as strongly as in more environmentally stochastic ecosystems like marshes. Certainly, many species do exhibit some form of seed dormancy but, overall, seed banks appear to be less crucial to vegetation dynamics in wet meadows (Adamus 1996). Small-scale disturbances may be important for the establishment of many wet meadow species. For example, some studies have found that hoof prints may provide opportunities for plant establishment, although other studies have not observed this effect (Stammel and Kiehl 2004). Likewise, soil disturbance from small mammals like pocket gophers can provide microsites amenable for plant establishment (Ellison and Aldous 1952; Huntly and Inouye 1988; Sherrod and Seastedt 2001).

HRV of Wet Meadows in Region 2 ---

Overview of anthropogenic impacts

The extent and magnitude of anthropogenic impacts to wet meadows varies across the region, with some landscapes, such as the Nebraska Sandhills, subject to high degrees of modification, and others, including most alpine areas, relatively unimpacted by direct anthropogenic impacts. Anthropogenic impacts to wet meadows include both on-site and off-site impacts, although some stressors such as hydrologic modifications can fall into both groups. The effects of some stressors are locally severe but only affect a small fraction of the wet meadows in the region. Others, such as the aerial deposition of pollutants, may affect large areas but have subtle ecological effects. Landscape and regional analyses of the relative importance of different stressors is lacking, although strong inferences can be made from knowledge of the dominant contemporary and historical land uses in the region.

Livestock—Livestock use is widespread in wet meadows and is a dominant land use in many portions of the region (Crowley 1975). Wet meadow species are an important source of forage, although the digestibility and nutrient value of native species varies. Some sedges have relatively high crude protein and acid-pepsin digestibility levels, while others are poor forage (Catling and others 1994; Hermann 1970). In addition to their direct effects, hay production for livestock use has one of the most pervasive and significant effects on wet meadows.

The purposeful introduction and promotion of non-native pasture grasses has shifted the composition of many wet meadows outside of the HRV.

Livestock can have significant effects on wet meadows, including direct effects such as herbivory and trampling and indirect impacts such as nutrient enrichment from urine and feces. Specific effects vary depending on the seasonality, intensity, and duration of grazing, and the effects differ among livestock species. Among the possible impacts is alteration of species composition (Belsky and others 1999). In alpine areas, sheep have been shown to shift the floristic composition of meadows, with species such as *Polygonum bistortoides*, which are eaten by sheep during the early part of the season, decreasing in abundance (Bonham 1972). Sheep grazing during the Nineteenth Century has been identified as a major cause of change to meadows in the Sierra Nevada (Dull 1999). Season-long grazing by cattle has apparently been responsible for decreasing production and retarding plant succession in montane meadows in Idaho (Leege and others 1981). In the Nebraska Sandhills, stocking rate did not affect the frequency of dominant species, but the frequency of legumes and *Poa pratensis* was higher in grazed pastures (Volesky and others 2004). Defoliation of taller grasses and sedges by grazing also altered the vertical structure of wet meadows, creating a more open canopy and allowing shorter-stature species to increase. The stocking rate affected more response variables than grazing frequency (Volesky and others 2004).

Grazing can affect soil physical and chemical characteristics. Grazed meadows had higher extractable Na^+ , Ca^{2+} , Mg^{2+} , and NO_3^- ; higher pH; and lower K^+ and NH_4^+ than sites where cattle grazing was excluded. Grazing effects were most pronounced at the forest edge, likely because of the spatial transfer of nutrients via urine and feces (Blank and others 2006).

Where populations of native ungulates have exceeded their HRV, including several areas in Region 2 (Coughenour and Singer 1996; Lubow and others 2002; Singer and others 1998), impacts may be similar to those from livestock. Native ungulates such as elk can cause plant mortality from trampling and herbivory and can alter nitrogen availability through urine and feces inputs (Frank and Evans 1997). In Yellowstone, the net mineralization of soil nitrogen was higher outside of exclosures than inside (Frank and Groffman 1998). Elk can affect the physical properties of soils by increasing bulk density (Binkley and others 2003). Where ungulate populations have remained within their HRV, the likely impacts to wet meadows have probably been localized.

Agriculture—Many wet meadows in the Great Plains are adjacent to actively cultivated land. Activities related to farming such as pesticide and fertilizer applications can affect adjacent wet meadows. These chemicals can reach wet meadows through processes of surface water runoff, groundwater flow, or aerial deposition. Surface soils in the wet meadow zones of wetlands surrounded by cultivated land had phosphorus concentrations 2.5 to 6 times greater than those surrounded by uncultivated grasslands (Freeland and others 1999). Subsoils also

differed, with higher organic matter content and concentrations of phosphorus and NO_3^- in the wetland surrounded by cultivated land. Cultivated wetland basins also typically have higher erosion rates than those surrounded by intact grasslands (Freeland 1997).

Hay production is very common throughout the region, pursued as a feed source for livestock during the dormant season. Hay production is most common on private lands. Harvest dates in wet meadows are dependent upon the water table since equipment cannot access hay until after the water table has dropped sufficiently below the soil surface. For example, normal harvest dates for wet meadows in the Sandhills range from mid-June to mid-August (Reece and others 1994; Volesky and others 2004).

Throughout the West, there is widespread use of irrigation for hay production (Smeal and others 2005). Many irrigated meadows were sown with cool season pasture grasses, thereby altering the species composition and functional characteristics of meadows. Irrigated pastures are significant contributors of phosphorus to streams and aquifers, with much of the phosphorus coming from applied fertilizers (Bush and Austin 2001). In nutrient addition experiments in meadows near Gunnison, Colorado, White et al (2003) found that the loadings of both P and NH_4^+ were significantly greater when fertilizer was applied in the early or late spring as opposed to in the fall. The authors suggested that producers of hay in mountain meadows should apply fertilizer in the fall to improve hay yields and reduce impacts to water quality (White and others 2003).

Exotic species—A number of exotic species regularly invade wet meadows. These include noxious weeds, such as *Cirsium arvensis* and *Phalaris arundinacea*, and pasture grasses purposefully introduced to the region for livestock forage. Examples of the latter are *Poa pratensis*, *Dactylis glomerata*, and *Phleum pratense*. Native species such as *Juncus balticus* and *Dasiphora fruticosa* may increase with hydrologic or physical site disturbances such as overgrazing. Vegetation types that are rich in native species are often highly vulnerable to invasion by nonnative plant species and are hotspots of exotic species richness (Stohlgren and others 1997, 1999).

Hydrologic modifications—Hydrologic modifications are one of the most common and significant impacts to wet meadows in the region. Actions can either increase the amount of water reaching a site, for example through irrigation or streamflow augmentation, or decrease water, as with flow diversion, ditching or groundwater pumping. Impacts can also be separated into those that occur on-site (e.g., ditching) and those that occur off-site (e.g., upstream flow diversion).

Many wet meadows occur along with riparian areas as part of wetland complexes. Although wet meadows do not experience regular flooding, water levels in many wet meadows are controlled, in part, by fluctuations in stream stage.

As a consequence, activities that affect streamflow such as upstream diversions or impoundments may alter hydrologic processes and the hydrologic function of wet meadows. As an example, stabilized flow regimes and reduced spring floods due to upstream water developments have reduced the area of wet meadow along the Platte River (Niemuth and others 2004).

Changes in vegetation commonly occur when hydrologic regimes have been significantly altered. In southeastern Wyoming, researchers evaluated changes in montane meadow vegetation following flow augmentation and found that after two years of elevated surface and groundwater levels, herbaceous vegetation had shifted toward more hydrophytic species. For example, the biomass of *Carex* spp. increased from 337 to 456 g/m² in wet meadows (Henszey and others 1991).

Groundwater pumping is an additional factor potentially affecting wet meadows, at least at local scales. A cone of depression is formed around the well during pumping, often creating a significant decline in water tables in the vicinity of pumps (Cooper and Wolf 2006). This may lead to moisture stress in vegetation and, if severe enough, eventually to shifts in species composition (Cooper and others 2006). As discussed previously, the application of irrigation water can also alter soil properties and available moisture, leading to shifts in vegetation composition.

Roads and transportation infrastructure—Transportation infrastructure such as roads, culverts, and ditches can affect the function of wet meadows. Impacts can be direct, such as when a road bisects a wetland, or indirect, through changes to hill slope processes in contributing watersheds (Forman and Sperling 2002). Transportation infrastructure can alter natural drainage patterns, reduce interception and infiltration rates due to the removal of vegetation and soil compaction, and alter the hydrologic response of basins to annual snowmelt runoff and storm events (Jones and others 2000). Roads can also contribute chemical pollutants, although there is no evidence to suggest that this is a widespread stressor for wet meadows in the region.

Beaver trapping—In low-gradient landscapes, the dam building activities of beavers are important drivers of hydrologic function and geomorphic development. The loss of beaver from trapping or habitat degradation can lead to significant changes in hydrology and vegetation (Cooper and others 2006; Peinetti and others 2002b; Westbrook and others 2006). Presumably, these impacts have at least indirectly affected wet meadows by reducing hydrologic variability and rates of patch creation (Johnston and Naiman 1990a).

Atmospheric deposition of pollutants—Increased atmospheric loading of pollutants such as nitrogen and sulfur has been well documented in much of Region 2 (Baron and others 2000; Fenn and others 2003b). Hotspots of elevated deposition typically occur downwind of large metropolitan centers or significant agricultural operations. A variety of ecological responses to nitrogen deposition

have been documented (Baron and others 2000; Fenn and others 2003a; Rueth and others 2003), but data specific to wet meadows is lacking.

Research in a Montana grassland exposed to elevated concentrations of sulfur and nitrogen found significant increases in leaf area at low SO₂ concentrations but not at high levels, suggesting a fine balance between fertilization and toxicity (Milchunas and others 1981). Research in Canadian bogs and fens examining the response of species to nitrogen deposition found that the response varied among species (Li and Vitt 1997). However, the transferability of such studies is questionable considering the different soil, hydrologic, and biogeochemical environment of wet meadows. The applicability of responses observed in more arid grasslands to wet meadows is also unknown.

Cumulative effects—Multiple landscape stressors can affect ecological processes in wet meadows. Because of their dependence on groundwater, wet meadows are sensitive to changes in surrounding watershed processes (Siegel 1988). Ecological stressors can act synergistically and unpredictably (Holling 2001). For example, roads may provide a conduit for the dispersal of seeds from exotic species and they may create disturbance conducive for their establishment. Wet meadows typically have low to moderate sediment fluxes, and actions in the surrounding watershed that affect the quality and quantity of ground or surface water may affect wet meadow function. Watershed properties are critical variables for analysis in common wetland condition assessments (Faber-Langendoen and others 2006; Hauer and others 2002b; Richter and others 1996; Rocchio 2006c) and should be part of any cumulative effects assessment approach.

Abundance, distribution, and condition of wet meadows across Region 2 landscapes

No region-wide inventory of wet meadows has been conducted in Region 2. While nearly the entire region has been mapped as part of the NWI program, only a fraction of maps have been digitized, much of the data is outdated, and it's not possible to separate wet meadows from other palustrine wetlands. As a result, no reliable statistics exist for wet meadow area across the contemporary landscape, let alone historical landscapes.

Estimates are available for portions of Region 2. For example, wet meadows were estimated to comprise approximately 10 percent of the 4.8 million-ha Nebraska Sandhills region (Volesky and others 2004). In their analysis of GAP vegetation data, Comer and others (2003) presented a value of 1,023,803 ha (0.9 percent of the Region 2 area) for the main Ecological System types they identified for wet meadows in Region 2. However, it is not possible to perfectly cross-walk from Ecological System type to the classification system used in this assessment.

There are insufficient historical data to characterize trends in wet meadow condition. Estimates from the USFWS in its “Status and Trends” publications (Dahl 2000; Dahl and Johnson 1991; Tiner 1984) are too imprecise to make specific quantitative estimates of wetland loss for wet meadows. It is likely that the pattern of change in wet meadow area has varied across the region. In general, higher rates of wetland loss would be expected on the Great Plains, particularly in sites suitable for crops such as the eastern part of the region. Wetland losses in mountain regions are likely smaller as more area is under public land management, mostly in National Parks or USFS wilderness areas.

While many wet meadows have been destroyed, others have been created as a result of anthropogenic activities. Examples include wet meadows created by irrigation of former non-wetlands, ditching and draining of fens, or fringe wet meadows formed around ponds and reservoirs. On balance, though, the likely trend for all of Region 2 has been toward a net loss of wet meadows since Euro-American settlement.

A separate set of questions can be asked regarding historical changes in the condition or integrity of wet meadows. Historical vegetation and hydrology data are largely unavailable, particularly at broad landscape or regional scales. Anecdotal information such as historical photographs do provide limited evidence of change, such as a transition from herbaceous dominated communities to shrub dominated ones, but it is not possible to confidently extrapolate to broader areas from such limited information.

Wet meadows are highly susceptible to invasion by a variety of non-native species. Although they are among the most diverse and productive ecosystems in the region, wet meadows also support many exotics (Stohlgren and others 1997, 1999). In addition to the accidental and incidental spread of non-native species, many wet meadows have been planted to Eurasian pasture grasses, completely changing the composition of communities from historical conditions. *Poa pratensis* has been increasing in western montane meadows, although it is unknown whether this is a result of grazing, decreased water tables, or competitive effects (Kluse and Allen-Diaz 2005).

In addition to altered species composition, the vegetation structure of many wet meadows has been altered due to the invasion of woody species. Tree and shrub invasion has increased in mountain meadows in many portions of the west within the last century (Miller and Halpern 1998). There has been widespread establishment of trees in mountain meadows of the Pacific Northwest, Sierra Nevada, and Rocky Mountains (Dyer and Moffett 1999; Jakubos and Romme 1993; Millar and others 2004; Schauer and others 1998), although there is still considerable uncertainty regarding the precise cause. Climate change and grazing have been identified as possible causes. Some research suggests that in the absence of disturbance, dense herbs will prevent germination of seeds. Berlow and others (2002) concluded that, while sagebrush expansion is traditionally associated with increased meadow aridity, sagebrush exhibits the greatest potential

for seedling germination, growth, and survival in mesic sites and that potential spread is dependent on the confluence of exposed soil, a nearby seed source, and reduction of aboveground herb biomass such as through grazing (Berlow and others 2002). In contrast, shrub cover in many wet meadows has declined as a result of anthropogenic activities. Willows have been removed from many wet meadows throughout the West, often to create pasture for livestock (Patterson 2005; Peinetti 2000).

Wet meadows supported by several aquifers or with large contributing watersheds may be less sensitive to climate shifts than wetlands with smaller watersheds or that formed in more marginal settings. Indirect and direct changes to wet meadow hydrologic processes have occurred in many wetlands throughout the region; however, the data are insufficient to quantitatively assess potential changes. Where key ecological processes in surrounding uplands have significantly departed from their historical range of variability, effects on wet meadows may be expected to occur.

Management opportunities and constraints

Management opportunities—Landscape assessments of wet meadows are needed, because of the lack of sufficient data to establish contemporary benchmarks, let alone to make historical reconstructions. Possible data tools include aerial photographs or other remotely sensed data to identify and map wetlands. Normalized Difference Vegetation Index (NDVI) values derived from satellite data hold promise for remote sensing of wet meadows. Researchers in alpine areas of Colorado compared NDVI values with snow depth and soil moisture values and found a trend of increasing value from barren to fellfield to dry meadow to snowbed to moist meadow to wet meadow (Walker and others 1993). Researchers in Oregon analyzed the spectral signature of meadows using a temporal series of five Landsat thematic mapper (TM) images and found that the sequence of scenes provided ample resolution to differentiate most of the meadow plant communities identified in previous field studies. The authors suggested that the technique also may be useful to detect the location and spread of species with distinctive vegetative or floral phenologies (Ager and Owens 2004).

Site-level assessments of wet meadows examining basic hydrology, water chemistry, and vegetation relationships are also needed. Relatively little money or time is needed for installation of a few shallow groundwater-monitoring wells. Several tools have been developed to assess wetland condition. Methods such as the Vegetation Index of Biological Integrity, Floristic Quality Assessment, and Ecological Integrity Scorecards vary in detail but all offer potential for landscape-scale assessment work (Faber-Langendoen and others 2006; Lopez and Fennessy 2002; Rocchio 2006c). In addition to improving our understanding of landscape-scale patterns of wet meadow condition, such studies would be useful to identify sites for restoration. Also needed are studies evaluating approaches for restoring degraded sites.

Restoration—The ecological integrity of many wet meadows in the region has been degraded. Whether through hydrologic alteration or invasive species, many wetlands no longer provide the ecological functions they once did. Restoration provides a means of recouping lost ecological functions. Before conducting a wetland restoration project, it is critical to understand site hydrology. Drainage tiles, ditches and water diversions need to be identified and removed, as these will prevent success in later stages if not addressed first.

For vegetation establishment, it is important to select the proper species since the hydrologic preferences of species varies. A variety of approaches are available for establishing vegetation, including the use of plugs, bare root stock, or containerized stock (Steed and DeWald 2003; Steed and others 2002). In addition, seeds can be collected in the field, stratified in a greenhouse, and germinated and grown into seedlings for use in restoration projects. This approach allows placement of species directly into the physical environments where they will perform best. The choice of specific methods should be made carefully. Additional techniques should be evaluated for vegetation management. For example, fire has been used to as a management tool for some wet meadows. Prescribed burns can be used to slow woody plant invasion into meadows or to set back invasive species (Debenedetti and Parsons 1979; 1984).

Management constraints—Constraints include lack of information regarding the extent and condition of wet meadow resources. Political, economic, and regulatory issues may also come into play when formulating management plans. A long-term issue outside the control of managers is regional climate change. Changing temperatures and precipitation patterns predicted under some global climate change scenarios (US EPA 1998b, 1998c; Wagner 2003) will likely affect the composition and function of wet meadows by shifting the competitive balance among species. The boundaries between wet meadows and adjacent ecosystems (mesic and dry meadows, uplands, different wetland types) may shift, making it difficult to predict net effects on wet meadow area.

9. Conclusions

The ecosystem types forming the basis of this assessment—fens, marshes, wet meadows, salt flats, and riparian areas—differ in vegetation composition, key functional characteristics, and underlying drivers. Given this natural variability and the large extent of the assessment area, it is not surprising that the data needed to quantitatively assess many important metrics are lacking. As a result, the value of this assessment lies not in a spatially explicit definition of the HRV for any particular part of Region 2, but rather in a conceptual overview of how wetland and riparian ecosystems are structured and function and the myriad ways Euro-Americans have altered them. The information presented here is best used as a basis for developing more specific hypotheses regarding possible changes in the HRV at the scale of individual Forests and Grasslands. Although it is possible to make some generalizations, readers are cautioned to evaluate the specific circumstances in their particular Forest or district.

At broad scales, climate, hydrology, and geomorphic processes are key factors influencing the natural abundance and distribution of wetland and riparian types. Wetlands are generally more abundant in cooler and moister climates, where groundwater and precipitation are more abundant, and in complex geomorphic settings, such as glaciated mountain valleys. Patterns in the general distribution of wetlands are also evident in the distribution of specific wetland types. Groundwater-dependent wetlands such as fens and wet meadows are typically more abundant at higher elevations, while more hydrologically variable marshes and salt flats occur at lower elevations.

Recognizing the functional differences among wetland types is important for developing an understanding of how humans may have affected wetlands and riparian ecosystems. Hydrologic processes are critically important to wetland and riparian areas. As a consequence, when evaluating human impacts, particular attention must be paid to the various ways in which anthropogenic activities may affect hydrologic function. For example, where hydrologic modifications like dams are present in a watershed, it is likely that downstream riparian areas have been altered. Other important anthropogenic impacts are grazing and the introduction and spread of exotic species. Both are responsible for changing the character of many wetlands and riparian areas in the region.

In preparing of this assessment, we identified several major information and research needs. One of the most critical information gaps relates to the condition or integrity of wetlands and riparian areas at landscape and regional scales. By leveraging recent advances in technology such as remote sensing and by developing improved field evaluation methods such as Indices of Biotic Integrity (IBI), it is possible to develop more rigorous and quantitative estimates of the condition of wetlands and riparian areas across Region 2 (Faber-Langendoen and others 2006; Karr 1999; Rocchio 2006c). Site-level hydrologic data are

essential for identifying and quantifying possible deviations from historical conditions (Richter and others 1998, 2003). Taken together, broad-scaled and local assessments can provide a means of identifying impaired ecosystems and prioritizing restoration efforts.

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