DISSERTATION

HYDROLOGY AND CONSERVATION OF INTERMOUNTAIN WETLANDS

Submitted by

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In partial fulfillment of the requirements

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY JOHN SANDERSON ENTITLED HYDROLOGY AND CONSERVATION OF INTERMOUNTAIN WETLANDS BE ACCEPTED AS FULFILLING IN PART THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

HYDROLOGY AND CONSERVATION
OF
INTERMOUNTAIN WETLANDS

To protect biodiversity in the arid intermountain valleys of the western U.S., hydrology and biology must be integrated in wetland management. This dissertation takes a step in that direction for Colorado's San Luis Valley. The dissertation has three major components: (1) an investigation of evapotranspiration (ET) from five intermountain wetlands, (2) an assessment of current and simulated hydrologic conditions in an intermountain playa wetland complex, and (3) research on factors, including flooding, that govern the distribution of plant species in this playa complex.

In intermountain valleys, ET is the primary means of water loss. In order to improve its estimation, ET was measured in five herbaceous wetlands using the Bowen ratio energy balance method. Annual ET and the ground water component of ET (ET_g) were calculated, and the relationship of ET_g to water table depth was determined and compared to existing models. The calculated decrease in annual ET_g with water table decline to 1.0 m was as little as 30% of previous predictions. This study also demonstrated that the relationship of ET_g to water table depth differs markedly between ground water and surface water wetlands.

A resulting model of ET was applied at an intermountain playa, where current hydrologic function was compared to the historical (natural) flow regime. No quantitative approach had been previously been used to assess how hydrologic alteration has affected these ecosystems. The simulated unaltered (i.e., natural) hydrologic regime differed substantially from current conditions with respect to depth, variability, and frequency of flooding, on both an intra-annual and inter-annual basis.

The altered hydrologic regime of intermountain wetland ecosystems appears to have significant biological effects. For example, hydrologic alterations were implicated in a decrease in density of the rare plant *Cleome multicaulis* from 55.6 to 0 stems/m^2 over five years. Also, this study provided inferential evidence that abiotic factors, including inundation as affected by hydrologic alteration, are a major determinant of vegetation zone distribution across the entire elevation gradient of this playa. Given the importance of abiotic factors, restoration of a natural flow regime can be expected to contribute significantly to restoring ecological function.

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CHAPTER 1

DISSERTATION OVERVIEW:

HYDROLOGY AND CONSERVATION OF INTERMOUNTAIN WETLANDS

INTRODUCTION

The scarcity of water in the intermountain western U.S. and its implications for society were recognized early in the settlement of the region (Powell 1879, Siebenthal 1910). Nearly another century passed before it was widely recognized and accepted that water scarcity and consequent anthropogenic development of this resource also had profound implications for water-dependent ecosystems. These ecosystems, including rivers and wetlands, are important and prominent features of western landscapes, despite the relatively small surface area they cover. For rivers, considerable work has been done to elucidate ecological consequences of water manipulation (see Poff et al. 1997). Less work has been done to understand loss and change of ecological function that result from an altered hydrologic regime in wetlands.

In the intermountain West, the most extensive wetland ecosystem complexes occur in hydrologically closed basins (Snyder 1962). These basins are common in western Utah (e.g., the Great Salt Lake region), throughout Nevada (e.g., Stillwater marshes), and in eastern California (e.g., Owens Valley), but also occur farther north (e.g., Oregon's

Malheur Basin) and east (e.g., Colorado's San Luis Valley). George Wheeler, an officer in the U.S. Army, surveyed the San Luis Valley (SLV) of southern Colorado in the 1870s, describing the "San Luis marshes" (Wheeler and Humphreys 1878), an apparently year-round feature across about 125 km^2 of land, and seasonally extending nearly 100 km from north to south. The SLV still contains Colorado's most extensive wetland ecosystems (Walton-Day 1996).

As in many intermountain basins, extensive wetlands occur in the SLV despite the low precipitation and the high evaporative demand resulting from warm summer temperatures (July mean = 17°C) and high insolation (Western Regional Climate Center 2005). Average potential evapotranspiration and precipitation in the middle of the SLV, at Center, Colorado, are 1200 mm/yr and 180 mm/yr, respectively (Western Regional Climate Center 2005). The primary supply of water to the SLV wetlands is snowmelt runoff from adjacent mountains, where up to 1500 mm of precipitation fall each year (Western Regional Climate Center 2005). The large annual influx of water to the basin, combined with the large disparity between precipitation and evaporation, has important implications for the hydrologic regime of wetlands and organisms that inhabit wetlands.

Evapotranspiration (ET) is the primary means of water loss in both the valley as a whole (Emery et al. 1973, Huntley 1979) and in individual wetlands (Sanderson this dissertation Chapter 3). ET losses affect the availability of water for wildlife breeding and foraging (Shjeflo 1968), the salinity of water and soil surfaces (Williams 2002), and the extent and duration of soil anoxia (Ponnamperuna 1972). All of these factors can influence wetland vegetation (Mitsch and Gosselink 2000). Also, although wetlands cover a relatively small percentage of the total land area in the SLV, they account for a disproportionately high percentage of total evapotranspiration. This is because wetland ET rates are between 2.5 and 5 times higher than ET rates for non-wetland communities (Laczniak et al. 1999).

In arid regions, evapotranspiration is a particularly important component of hydrologic models. Such models are being used throughout the West to predict impacts of anthropogenic developments and natural events on water supplies (e.g., RGDSS 2005). Models can potentially play an important role in conservation of wetlands by providing insights into current conditions and potential future impacts of water development and climate change. For example, in the prairie pothole region, Poiani et al. (1996) used a combination hydrologic-vegetation model to predict changes in wetland vegetation in response to global climate change. In some cases, these models have potential to be used to elucidate historical conditions in a wetland, thus serving as a reference for restoration efforts (Sanderson this dissertation Chapter 3).

Ultimately, it is not the frequency, extent, depth, and duration of flooding *per se* that interests ecologists and conservation biologists, it is the effect of the hydrologic regime on the structure and function of water dependent ecosystems. For example, plant community composition and distribution in wetlands is a function of physical factors (e.g., soil anoxia) and/or biotic interactions (e.g., competition, herbivory). Both sets of factors are mediated by the hydrologic regime. Additionally, plant communities are inextricably linked to all other ecosystem functions and components, such as primary productivity, biodiversity, food web dynamics, and nutrient cycles.

Achievement of conservation objectives in the San Luis Valley and throughout the western U.S. requires understanding linkages between hydrologic regimes and wetlands.

Also, since most intermountain wetlands are currently altered from their historical condition, restoration of hydrologic regimes may be required to optimize conservation actions. Unfortunately, few minimally impacted reference sites exist, and there is generally very limited information about pre-settlement conditions.

For my dissertation, I have conducted research on both the hydrology and plant community ecology of intermountain playas in the SLV in an attempt to understand current hydrologic conditions, to simulate a natural flow regime, and to determine primary factors governing plant distribution in these wetlands. In this present Chapter, I outline the context of my work. Chapters 2, 3 and 4 constitute the main body of the work; they are manuscripts prepared for submission to peer-reviewed journals. In Chapter 5, I synthesize the entire body of work.

In Chapter 2, I test existing models of the ground water component of evapotranspiration (ET) in wetlands as it relates to water table elevation, and I formulate an improved model. The improved model is based on the most extensive data set in the region, collected during six years from two surface water and three ground water wetlands. My results illustrate that the decrease in annual ET_g with water table decline to 1.0 m is substantially less than previously assumed, and demonstrate that the relationship of ET_g to water table depth in wetlands differs markedly between ground water and surface water wetlands.

In Chapter 3, I investigate current and historical hydrologic function of an intermountain playa wetland in Colorado's San Luis Valley, where there has been much discussion but no quantification of historical conditions in wetlands. Current hydrologic conditions are quantified, and a water-budget model is developed to simulate an unaltered hydrologic regime. The simulated unaltered hydrologic regime indicates that the natural flow regime would differ substantially from current conditions with respect to depth, variability, and frequency of flooding.

In Chapter 4, I provide evidence that physical factors are a major determinant of vegetation zone composition and distribution across the entire elevation gradient at Mishak Lakes. This result contrasts with results of studies in coastal salt marshes and other wetlands, where competitive interactions govern the distribution of vegetation zones at the high end of the elevation gradient.

Finally, in Chapter 5, I conclude the dissertation by integrating my findings and summarizing their potential role in conservation of wetland ecosystems in the intermountain west.

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CHAPTER 2

EVAPOTRANSPIRATION FROM WETLANDS IN AN ARID INTERMOUNTAIN BASIN

ABSTRACT

To improve modeling of the ground water component of evapotranspiration (ET) in wetlands as it relates to water table elevation, daily ET was measured using the Bowen ratio energy balance method during 1999-2005 in five herbaceous wetlands in an arid intermountain valley of Colorado. Three of the wetlands were supplied by ground water, and two were supplied by surface water. In ground water wetlands, maximum single day actual ET (ET_a) ranged from 8.1 to 9.6 mm/d, and minimum mid-summer ET_a ranged from 3.2 to 3.9 mm/d. In surface water wetlands, maximum single day ET_a ranged from 4.8 to 9.1 mm/d, and minimum mid-summer ET_a ranged from 1.2 to 4.0 mm/d. The ground water component of ET_a (ET_g) was calculated, and the relationship of annual ET_g to mean annual water table depth (WTD) was investigated and compared to existing ET_g-WTD models. For ground water wetlands with mean annual WTD < 1.0 m, ET_g decreased exponentially as WTD increased ($r^2 = 0.82$, CV = 5%, $p<0.001$). Compared to the findings in this study, all but one existing model over-estimate ET_g at WTD = 0.1 m, by as much as 49%. At WTD = 1.0 m, existing models under-estimate ET_g by as much as 44%. This study indicates that ET_g would decrease 222 mm as WTD increases from 0.1 to 1.0 m; existing models predict decreases from 256 to 741 mm. In surface water wetlands, ET_g was strongly dependent on water supplies. In contrast to existing models, ET_g was 0 mm in surface water wetlands when there were sufficient water inputs to meet ET demand, independent of WTD. When inputs did not meet ET demand, ET_g was positive though highly variable at WTD up to 1.66 m. This study offers substantial improvements to existing models of ET_g by illustrating that the decrease in annual ET_g with water table decline to 1.0 m is substantially less than previously assumed. This study also demonstrates that the relationship of ET_g to water table depth in wetlands differs markedly between ground water and surface water wetlands.

INTRODUCTION

Evapotranspiration (ET) constitutes the dominant water loss from many different types of wetlands (Drexler et al. 2004). This is especially true in semi-arid and arid regions, where ET is a critical component of water budgets (Winter 1992) and potential ET (ET_p) can be up to 30 times annual precipitation (Mifflin 1988). In the hydrologically-closed basins that are common in the intermountain western US (Snyder 1962), virtually all water loss is through evapotranspiration (Huntley 1979).

Despite the extreme water deficit in intermountain basins, many wetlands occur here (Walton-Day 1996), and for most wetlands, most water loss is through ET (Bidlake 2000). The amount of water lost as ET can be influenced by short-term and long-term variation in the presence of surface water and by fluctuations in water table depth. This variation can be produced by stream diversions, ground water pumping, changes in precipitation, and climate change (Cooper et al. 2006). Although wetlands cover a relatively small proportion of the landscape in arid regions, because they have high ET rates, they may account for a disproportionately high percentage of ET when compared to upland areas (Laczniak et al. 1999).

Accurate estimation of ET is required when modeling the water budget of individual wetlands (e.g., Poiani and Johnson 1993, Sanderson this dissertation Chapter 3) and of entire basins (Devitt et al. 2002, CDSS 2005). A variety of models and methods have been developed for estimating ET under conditions where water is not limiting, otherwise known as potential ET (ET_p) (Winter et al. 1995, Rosenberry et al. 2004, Drexler et al. 2004). Among the models are those derived from theoretical principles (e.g., Penman 1948, Penman 1963, Monteith 1965), others that are based on empirical relationships (e.g., Blaney and Criddle 1950, Thornthwaite 1948), and still others that are theoretically based but contain significant empirical components (e.g., Priestley and Taylor 1972).

Several models of ET_p have been applied successfully to wetlands (Drexler et al. 2004, Rosenberry et al. 2004) after calibration to an independent measure of actual ET (ET_a) (Souch et al. 1996, Jacobs et al. 2002). Calibration may be required for a variety of reasons. When water is not limiting, ET_a can be greater than or less than theoretical ET_p depending on vegetation canopy characteristics such as leaf surface area, plant height and roughness, albedo, and total plant cover (Peacock and Hess 2004), which all vary throughout the growing season. ET_a generally falls to less than ET_p when water becomes limiting as surface water disappears, water tables decline, and soil moisture decreases (Jacobs et al. 2002). Independent measurements of ET_a to which ET_p is calibrated are performed using a variety of field methods (Drexler et al. 2004), among which the Bowen ratio energy balance method (BREB) is among the most common and robust (Winter et al. 1995, Rosenberry et al. 2004).

The role of increasing water table depth (WTD) in reducing ET_a relative to ET_p has received considerable attention (Nichols 2000, Jacobs et al. 2002, Cooper et al. 2006). Potential effects of WTD on ET_a are important to understand because where the water table depth is shallow, a large majority of ET_a may come from the shallow aquifer (73 to nearly 100% in parts of Nevada; Lacsniak et al. 1999). As such, the ground water component of ET_a (known as ET_g) can be a critical component of hydrologic models used to estimate water storage in shallow aquifers. Since ground water models such as MODFLOW (Harbaugh et al., 2000; McDonald and Harbaugh, 2003) estimate WTD, the existence of a relationship between ET_g and WTD would allow a straight-forward means for estimating ET_g across large areas.

Several researchers have proposed models that relate ET_g to WTD (Emery 1970, Emery 1991, Harmon 2000, Nichols 2000). These models are based on relatively few studies, from a narrow range of vegetation types. In addition, the ET_g-WTD relationships in these models for wetlands are based on few data points (Emery et al. 1973), and comprehensive data for wetlands in semi-arid and arid regions has only recently been collected (Laczniak et al. 1999, Laczniak et al. 2001, Reiner et al. 2002, DeMeo et al. 2003). More data are needed to assess where existing ET_g-WTD models apply and whether they need to be modified or even discarded.

One gap in our current understanding of ET_g in wetlands is how the ET_g-WTD relationship varies for sites supplies primarily by ground water versus surface water. Throughout the intermountain region of the US, where concerns over ground water supply are great and increasing, substantial areas of wetlands are supplied primarily by ground water. In ground water wetlands, a large proportion of ET_a may be ground water. In other wetlands, surface water may be sufficient to satisfy ET_a, and ET_g may be zero despite the presence of a high water table and productive hydrophytic vegetation.

The primary objectives of this study were to quantify ET_a and ET_g in different intermountain wetland types, and to investigate how ET_g rates vary as a function of WTD. Specifically, I asked:

- What is the magnitude of total annual ET_a and ET_g in wetlands of an intermountain basin in Colorado?
- How does ET_g change as WTD changes?
- Does this relationship differ between ground water and surface water wetlands?

To accomplish these objectives and answer these questions, daily ET_a was measured during six years in five wetlands in the San Luis Valley, Colorado (Figure 2.1). Measured ET_a was used to calibrate the Priestley-Taylor ET_p model (Priestley and Taylor 1972), and the calibrated model was used to estimate daily ET_a for days when measured data were unavailable. Annual ET_g was then calculated, and annual ET_g-WTD relationships were analyzed and compared to existing models, with emphasis on differences between ground water and surface water wetlands.

STUDY AREA

Regional setting

The San Luis Valley (SLV) is a high elevation intermountain basin covering ~8400 km^2 in southern Colorado (Figure 2.1; Huntley 1979). The valley floor averages ~2350 m elevation, and has little topographic relief. Mountains rise above 4000 m in the Sangre de Cristo range to the east and the San Juan range to the west. In the SLV, summers are warm (July mean = 17°C), winters are cold (January mean = -9°C), and insolation is high all year (Doesken and McKee 1989, Western Regional Climate Center 2005).

Orographic effects result in high mountain precipitation and low valley-floor precipitation. Mean annual precipitation at Wolf Creek Pass (elevation 3290 m, Figure 2.1) is 1153 mm; on the SLV floor at Center, Colorado (elevation 2350 m, Figure 2.1) it is 177 mm (Western Regional Climate Center 2005). Despite the aridity on the SLV floor, it contains Colorado's highest concentration of wetlands (Walton-Day 1996), which result from the abundant snowfall in the mountains contributing copious surface water runoff to the valley.

The years of this study (1999-2005) spanned a range of climatic conditions. In the late 1990s, the second-longest sustained wet period on record and the most drought-free period since 1890 were just ending (McKee et al. 2000). Several months of moderate drought occurred in 2000, followed by a wet period from late 2000 through July of 2001. A severe drought lasted from the second half of 2001 through 2004. High snowmelt runoff and moderate rainfall followed the winter of 2004-2005, but water levels did not return to 2000 levels.

The study sites represent the major wetland types that occur in the San Luis Valley. Three wetlands receive no surface water inflow; the primary source of water to these wetlands is a water table with 1 m of the ground surface. These ground water wetland sites include one fen with peat soils (Alamosa NWR) and two wet meadows (Higel and Rito Alto). The other two wetlands (Bulrush and Mishak Lakes) are intermountain playas, shallow (<1.25 m deep) basins supplied by surface water from ephemeral streams. In the absence of stream inflow, the water table beneath these wetlands is > 1 m below the ground surface. Uplands surrounding all of the sites are dominated by greasewood (*Sarcobatus vermiculatus* (Hooker) Torrey) and rabbitbrush (*Ericameria nauseosa* (Pallas ex Pursh) Nesom & Baird). Species names follow USDA (2005).

Ground water wetlands

Alamosa NWR

The Alamosa National Wildlife Refuge site (Alamosa NWR; Figure 2.2a) is located on the margin of the broad Rio Grande floodplain. The primary water source is ground water flowing from shallow sandy alluvium of the SLV floor, termed the Alamosa formation (Siebenthal 1910). The water table is near the soil surface each spring through ~July 1, and declines rapidly over about 6 weeks to ~0.8 m below ground surface where it remains until mid-October (Figure 2.3a). The upper 1.4 m of soil is partially decomposed organic matter (i.e., peat). The dense vegetation at the site is dominated by grasses and grass-like species, mostly sedges (*Carex* spp.) that are ~0.5 m tall (Table 2.1). The site has significant microtopographic relief with hummocks up to 0.2 m high.

Higel

The Higel site (Figure 2.2b) is located on the edge of the broad Rio Grande floodplain. Water levels remain within ~0.4 m of ground surface throughout the summer, supported by irrigation ditches on the upper floodplain margin (Figure 2.3a). Mean daily water table depths do not necessarily represent short-term water table dynamics, because the water table can fluctuate up to 0.20 m daily. Soil water content in silt loam soils remain close to saturation all summer. The vegetation, which reaches ~0.6 m, is dominated by grasses and grass-like species (especially *Carex simulata* Mackenzie, but also *Juncus balticus* Willd., *Hordeum jubatum* L., and others; Table 2.1). There are also several broad-leaved species present such as *Argentina anserina* (L.) Rydb. The site has significant microtopographic relief, with hummocks up to 0.30 m high. Hollows at the site fill with water while hummocks remain above the water table reaches the ground surface. Many hollows lack vegetation, although bare ground at the site is < 5% of the total surface cover.

Rito Alto

The Rito Alto site (Figure 2.2c) is located ~5 km west of the Sangre de Cristo Mountains on the floodplain of Rito Alto, a small creek that flows from the mountains. The water table at the site is supported primarily by regional ground water flow, although it also responds to high creek discharge and large, local rain events. During most study years, the seasonal water table high occurred before or in April, and then declined through summer. During July and August the water table occasionally rose following short periods of heavy summer thunderstorms (Figure 2.3a). Soils are silt loam in texture, with high organic matter content in the upper 5 cm. The dense vegetation is dominated by the grass-like species *Juncus balticus* and *Carex simulata* to ~0.5 m high, and several broad-leaved species are also present (Table 2.1).

Surface water wetlands

Bulrush

The Bulrush site (Figure 2.2d) is a 100 ha terminal playa on a distributary of Sand Creek located ~5 km west of the Sangre de Cristo Mountains. There is high inter- and intra-annual variability of inflowing surface water and ground water depth (Figure 2.3b). No outflow occurs at this site. Flooding to a depth of 0.24 m was recorded in 1999, but no flooding occurred in 2003 or 2005, the years of ET measurements. Soils are sandy clay loam in texture. When flooded in 1999, the bulrush (*Schoenoplectus tabernaemontani* (K.C. Gmel.) Palla) that dominates site vegetation grew in dense stands to >1.5 m (Table 2.1). During dry years the stems grew to <1.0 m tall and in sparse stands, and weedy species colonized portions of the site.

Mishak Lakes

The Mishak Lakes site (Figure 2.2e) is part of a complex of 280 ha of shallow (1.25 m depth) interconnected basins ~25 km east of the San Juan mountains. Mishak Lakes receives ~80% of its water from a single creek (Russell Creek). When sufficient water flowed into this wetland complex, as it did during years when ET was measured (1999-2001), surface water outflow occurred (Sanderson this dissertation Chapter 3). Little net infiltration of surface water occurred (Kappen 2004). In a typical year, surface water reached ~ 0.5 m deep in May, after which water levels steadily declined and the ponds dried by the end of July (Figure 2.3b). After basins dried, WTD increased rapidly to >1.0 m. Soils at Mishak Lakes are largely sandy loam in texture. Vegetation is a near-monoculture of the grass-like species *Eleocharis palustris* (L.) Roemer & J.A. Schultes that is ~0.5 m high (Table 2.1). The *Eleocharis* has relatively low (< 30%) total cover; between stems of *Eleocharis* is either water (when there is standing surface water) or bare soil and litter from the previous years vegetation.

METHODS

Field measurements

Daily ET_a was measured using the Bowen Ratio energy balance (BREB) method (Tanner 1960, Fritschen and Simpson 1989, Moncrief et al. 2000, Drexler et al. 2004). Data were collected using a micrometeorological system from Radiation Energy Balance Systems Inc. (REBS Inc., Bellevue, WA). Platinum resistance elements were used to measure temperature in the atmosphere and in the cavity where humidity was measured. Humidity was measured with a hydroscopic polymer capacitance chip. Humidity and temperature sensor pairs were vertically separated by 1 m. To remove bias between sensors, their positions were exchanged every 15 minutes using an automated system. Net radiation (R_n) was measured with a REBS, Inc. Q*7.1 net radiometer deployed and leveled ~2.5 m above the ground surface and oriented due south. For settings without surface water, soil heat flux (G) was measured using two heat flow transducers buried 5 cm below the ground surface, and two 10 cm-long soil temperature probes buried at an angle to measure heat storage in the top 5 cm of soil. For conditions with surface water, temperature sensors were suspended in the water column, and soil heat flux plates were positioned at the soil surface. Measurements were made every 15 seconds, and averaged and stored on a datalogger every 15 minutes. ET_a was calculated at 30-min intervals and summed over each 24-hour period.

Requirements for fetch (the upwind distance to which the uniform vegetation extends) at three sites (Alamosa NWR, Higel, and Bulrush) exceeded the generally accepted minimum fetch to upper sensor ratio of 100:1 (Stannard 1993, Moncrief et al. 2000). At Rito Alto and Mishak Lakes, minimum fetch-to-height ratio was met in and near the direction of the prevailing wind, but was less in other directions.

The BREB method failed under specific combinations of available energy, temperature gradient, and vapor pressure gradient (Ohmura 1982, Perez et al. 1999), and during advective inversions (Verma et al. 1978). Failures were identified in the data set, and 30-min ET values were interpolated from temporally proximate values. These failures typically occurred around sunrise or sunset, when ET_a is low, and they generally lasted for only one or two 30-min intervals, so it is expected that they did not introduce significant error in daily ET_a totals.

Water table depth was measured using a Druck 1-5 psi water level sensor. Precipitation was measured using an unshielded Texas Instruments 20.3 cm tipping-bucket rain gage with a sensitivity of 0.254 mm. Beginning in 2001, soil water content was measured by time domain reflectometery using Campbell Scientific CS615 probes at 0-30 cm. Probes were calibrated in the lab for each specific soil using known soil water contents.

Modeling

A primary objective of this work was to improve estimates of ET_g as a function of WTD. Because existing models of this relationship express ET_g as an annual total (Emery 1970, Huntley 1979, Hearne and Dewey 1988, Emery 1991, Harmon 2000), I used measured and modeled daily values of ET_a to calculate annual totals (Figure 2.4). Measured daily ET_a was available for 55 - 88% of the growing season (Apr 15 - Oct 15) for 10 of 14 calculations of annual ET_g; it was available for 7 – 33% of the growing season for the remaining 4 calculations (Table 2.2). It is expected that annual totals for years with a greater percentage of measured ET_a values are more accurate.

Calibrating the Priestley-Taylor ET_p model

When measured values were not available, daily ET_a (in mm) was modeled using Priestley-Taylor ET_p (also in mm; Priestley and Taylor 1972) calibrated to water-limiting conditions as:

$$ET_a = f(\text{water}) * ET_p \tag{1}$$

where f(water) was a calibration function (no units) consisting of water-limiting factors (Jacobs et al. 2002). The Priestley-Taylor model was chosen because it has been widely demonstrated to produce a reasonable approximation of ET_a under a variety of well-watered conditions (e.g., Priestley and Taylor 1972, Jacobs et al. 2002, Rosenberry et al. 2004). ET_p was calculated as:

$$ET_p = 1.26\left(\frac{s}{s+\gamma}\right)\frac{(R_n - G)}{\lambda} \tag{2}$$

where s is the slope of the saturated vapor pressure-temperature curve (mb / °C), γ is the psychrometric constant (mb / °C), R_n is net radiation (MJ / m^2 / d), G is change in heat stored in surface soil or water (MJ / m^2 / d), and λ is the latent heat of vaporization (MJ / kg). ET_p includes only energy terms and assumes unlimited water supply.

Water-limiting variables considered were season, water table depth (WTD), soil water content, cumulative precipitation, and year. Season, which was assumed to represent changes in leaf area, was expressed as a log-normal function with the form:

$$\text{season} = \frac{1}{\mathrm{x} * \mathrm{s} * \sqrt{2\pi}} * \mathrm{e}^{\left(-\frac{1}{2} * \left(\frac{\ln(x) - \mathrm{m}}{\mathrm{s}}\right)^2\right)} \tag{3}$$

where x is day-of-year, and m and s are constants (5.44 and 0.533, respectively) determined through iteration so that season ranges from 0 (no green leaves) on April 15 and October 15 to 1 (full canopy) on June 22 (summer solstice). The changing value of season represents seasonal changes in leaf area, plant cover, surface roughness, and other plant canopy-related factors that affect ET (Peacock and Hess 2004). Soil water content was volumetric water content in the upper 30 cm ($\mathrm{cm}^3/\mathrm{cm}^3$). Cumulative precipitation was the sum of weighted daily precipitation for the previous seven days calculated as:

$$\text{cumulative precipitation} = \sum_{i=1}^{7} (D - i) * e^{\left(\frac{1-i}{2}\right)} \tag{4}$$

where D is the day for which ET is being modeled, so that, for example, (D -1) is the amount of precipitation on previous day and (D – 7) is the amount one week ago. Using this formula, yesterday's precipitation was weighted more heavily than the day before yesterday, and so on until seven days previous, beyond which the effect of precipitation was negligible. Cumulative precipitation was square-root transformed before use in model development.

A calibration function was developed for each site using multiple linear regression, with the dependent variable being the ratio $\mathrm{ET_a}/\mathrm{ET_p}$ and the independent variables being the water-limiting variables described above. Values of $\mathrm{ET_a}$ were those measured during the growing season (Apr 15-Oct 15). Values of ET_p were calculated using on-site daily means of temperature, net radiation (R_n) and energy storage (G). Available daily values were randomly split into two equal-sized data sets, and one data set was used for model development. The best regression model was selected using a stepwise procedure with α_{entry} and $\alpha_{exit} = 0.05$ (SAS Institute 2003). WTD and soil water content in particular were, in some instances, highly correlated. Because WTD was of primary interest, preference was given to WTD during model development when WTD and soil water content were equally good predictors.

Model fit was evaluated using a cross-validation approach. Data withheld during the model development step were used to calculate goodness-of-fit statistics. Statistics included a coefficient of determination (r^2) of modeled and measured values of ET_a, a coefficient of variation (CV) calculated as the standard error of the model divided by the mean of the measured values of ET_a (Stannard 1993), and a mean-bias error defined as the mean difference between modeled and measured values (Kaygusuz 1999). Also, slopes of best-fit lines through modeled versus measured ET_a were calculated to assess deviation from unity; deviation from unity indicates that the error in the modeled value varies as a function of the size of the value, possibly causing systematic under- or over-estimation of daily ET_a.

Developing models of available energy (R_n-G)

For days lacking on-site measurements, available energy (R_n-G) for use in the Priestley-Taylor ET_p equation was modeled as a function of variables measured at a regional weather station. Total solar radiation (Q_s) can be used to model R_n-G with reasonable results (Stewart and Rouse 1976). However, changes in plant cover alter the relationship between Q_s and R_n-G by changing albedo and surface temperatures, so the season function (equation 3) was also used to model R_n-G. Yesterday's precipitation was also considered for models of R_n-G, because our data suggest that where vegetation is sparse (such as the Bulrush site) rain wets the soil, temporarily making it darker and lowering its albedo relative to dry soil.

Development and validation of the R_n-G model were done using the same cross-validation approach described for the ET_a model. On-site data were used for the dependent variable and weather station data for the independent variables. Weather station data were obtained principally from the CoAgMet Ctr01 station at Center, Colorado (Colorado Climate Center 2005). Precipitation data from the Alamosa NOAA weather station (NOAA 2005) and the Blanca, Colorado CoAgMet station were used when they were the nearest stations with available data.

Estimate of annual ET_a and ET_g

Annual ET_a was calculated by summing daily ET_a (measured where available; otherwise estimated using calibrated P-T ET_p model) for the entire growing season (Apr 15-Oct 15), and then adding modeled winter ET_a (Figure 2.4). Winter ET_a measurements from Rito Alto (at least seven days in all months, measured in winters of 2001-02 and 2003-04) were used to calculate mean monthly ET_a from Oct 16-Apr 14, and these means were applied to all sites. This approach is acceptable because winter ET_a rates are similar across sites in winter, when solar radiation is low, plants are leafless, frozen soils inhibit capillary movement of ground water to the surface, and frontal rather than convective weather patterns prevail. Because winter ET_a represents ~10% of annual totals, even large inaccuracies in winter totals would not cause substantial errors in annual totals.

Annual ET_g was calculated by subtracting precipitation from ET_a (Laczniak et al. 1999; Reiner et al. 2002, DeMeo et al. 2003, Cooper et al. 2006). This calculation rests on the assumption that surface water flow is negligible, which should be the case given the rough surface of the sites (constraining runoff) and the small magnitude of most precipitation events (so infiltration capacity is rarely exceeded). The assumption about surface water flows to or from the site likely does not hold for Mishak Lakes, the only site with surface influx of water other than precipitation; at Mishak Lakes, estimated annual stream inflows (Sanderson this dissertation Chapter 3) were assumed to contribute to ET_a.

RESULTS

Patterns of daily ET_a

All three ground water wetlands shared a characteristic overall pattern of daily ET_a during the growing season (Figure 2.5a-c). In late spring and early summer, when water tables were highest, daily ET_a increased in response to seasonal increases in solar radiation and leaf area. ET_a rose quickly following leaf emergence in late April, and it remained high during June and July. Maximum single day ET rates ranged from 8.1 mm/d at Rito Alto to 9.6 mm/d at Higel. Minimum mid-summer (the two weeks centered on the summer solstice) rates ranged from 3.2 mm/d at Alamosa NWR to 3.9 mm/d at Higel. ET_a decreased steadily from August through early October as solar radiation decreased, water tables declined, and soil moisture was depleted. Leaf senescence typically occurred by mid-October, and mean daily ET_a decreased to less than 1 mm/d.

In surface water wetlands, patterns of daily ET_a differed between the two surface water wetlands studied, based on two years of growing-season measurements at Bulrush and three years at Mishak Lakes. At Bulrush, which did not have surface water in either 2003 or 2005, the water table was deep through May, and ET_a climbed slowly from April 15 through early June (Figure 2.6a), reaching a maximum of 4.8 mm/d. In contrast, Mishak Lakes was inundated at the beginning of each growing season, and ET_a rose rapidly in the early growing season to a late June maximum of 9.1 mm/d (Figure 2.6b), nearly matching the measured rates at Higel (Figure 2.5b). Minimum mid-summer (the two weeks centered on the summer solstice) rates ranged from 1.2 mm/d at Bulrush to 4.0 mm/d at Mishak Lakes.

Models of ET_a

For ground water wetlands, Priestley-Taylor (P-T) ET_p generally provided good estimates of ET_a ($r^2 = 0.73$ to 0.86; coefficient of variation, CV = 14 to 24%) (Figure 2.7, left column). At Alamosa NWR and Rito Alto, P-T ET_p tended to overestimate ET_a across the range of measured values. At Higel, P-T ET_p overestimated at low values and underestimated at high values. Slopes of P-T ET_p versus measured ET_a were 26 to 35% less than unity.

Calibrating ET_p improved estimates for all sites ($r^2 = 0.87$ to 0.92; CV = 9 to 12%) (Figure 2.7, right column). Slopes of calibrated ET_p versus measured ET_a were only 6 to

11% less than unity. Calibration functions included season and WTD for Alamosa NWR and Rito Alto, but only season for Higel (Table 2.3).

For surface water wetlands (Bulrush and Mishak Lakes, mean annual WTD = 1.56-1.66 m and 0.34-0.62 m, respectively), P-T ET_p was a poorer estimator of ET_a than for ground water wetlands ($r^2 = 0.36$ and 0.62, for Bulrush and Mishak Lakes, respectively; Figure 2.8, left column). At Bulrush, P-T ET_p greatly overestimated daily measured ET_a (CV = 126%; Figure 2.8a). Calibrating ET_p for water availability improved the fit for both sites ($r^2 = 0.76$-0.87; CV = 12-25%; Figure 2.8, right column). The calibration function for Mishak Lakes was similar to that for ground water sites, but the function for Bulrush differed substantially from all others (Table 2.3). Calibrated ET_p at Bulrush, which had the deepest water table, yielded the poorest fit to measured ET_a when compared to all other sites.

Modeled daily ET_a using off-site energy flux data (i.e., regional weather station data) compared acceptably well to measured ET_a ($r^2 = 0.70$-0.84, CV = 15-25%, slopes = 0.81-0.91; Table 2.4). The model for Bulrush produced the greatest average error in daily estimates (CV = 25%, versus 15-18% for the other sites). Mishak Lakes yielded the poorest fit of modeled to measured ET_a ($r^2 = 0.70$). All sites underestimated daily ET_a at low values and overestimated at high values, but slopes for ground water sites were about 10% closer to unity than surface water sites (slopes = 0.78 – 0.82 for ground water sites versus 0.70 - 0.71 for surface water sites).

Modeling daily ET_a when on-site data were not available was possible because available energy (R_n-G) at each site was significantly related to solar radiation as measured at Center ($p < 0.001$, Table 2.5). Thus, ET_p could be calculated even when on-site energy flux data were missing.

Annual ET

At ground water sites, where mean annual WTD was ≤ 1.0 m (i.e., water table within 1.0 m of the ground surface), calculated annual ET_a ranged from 751 mm (Rito Alto in 2005) to 994 mm (Higel in 2005) (Table 2.6), corresponding to mean WTDs of 1.01 m and 0.12 m, respectively. Annual ET_g at ground water sites ranged from 629 mm (Rito Alto in 2004 and 2005) to 873 mm (Higel in 2005).

At surface water sites, annual ET_a ranged from 352 mm (Bulrush in 2003) to 892 mm (Mishak Lakes in 2005), corresponding to mean annual WTDs of 1.66 and 0.62 m, respectively. ET_g at these sites ranged from 0 mm (Mishak Lakes, 1999-2001) to 571 mm (Bulrush in 2005) (Table 2.6). At Mishak Lakes annual stream inflows to the wetland complex in combination with on site precipitation supplied 36% more surface water to the wetland than was consumed by annual ET_a (Sanderson this dissertation Chapter 3). ET_g was estimated to be 0 mm at Mishak Lakes during all years because (i) the entire ET_a demand was met by surface water, (ii) most or all of the 36% excess inflows were lost from the wetland as surface water outflows (Sanderson this dissertation Chapter 3), and (iii) there is little net recharge at Mishak Lakes (Kappen 2004). At Bulrush, ET_g in 2005 (466 mm) was 172% greater than ET_g in 2003, even though mean WTD was only 0.10 m higher in 2005.

Annual ET_g was significantly related to WTD for ground water wetlands. The best-fit curve for the nine annual values for ET_g from ground water wetlands is:

$$ET_g = 642.0 * WTD^{-0.139} \qquad (r^2 = 0.81, p < 0.001) \qquad (5)$$

This curve indicates that ET_g decreases exponentially as WTD increases, similar to the shape of the curve suggested by Emery (1970, 1991) (Figure 2.9). However, the magnitude of ET_g estimated differs from existing curves. At mean annual WTD = 0.12 m (the highest recorded during this study), equation 5 yields annual ET_g = 864 mm; values yielded by existing models at WTD = 0.12 are both higher and lower, differing from this study by -28% (Emery 1991) to +49% (Emery 1970) (Table 2.7). At mean annual WTD = 1.01 m (the lowest seen during this study for ground water wetlands), equation 5 yields annual ET_g = 642 mm; values yielded by existing models at WTD = 1.01 are all lower, differing from this study by -15% (Emery 1970) to -44% (Emery 1991).

The magnitude of the decrease in ET_g and the decrease as a percentage of ET_g at WTD = 0.12 also differ substantially between thus study and existing models. This study indicates that in ground water wetlands, ET_g declines 222 mm (26%) as the WTD drops from 0.12 to 1.01 m depth. Existing models indicate greater decreases in ET_g as water tables decline, ranging from 256 mm (41%; Emery 1991) to 741 mm (58%; Emery 1970).

DISCUSSION

Annual ET_g versus WTD

The results of this study indicate that the relationship between ET_g and WTD is not as simple as has been previously proposed (Emery 1970, Huntley 1979, Hearne and Dewey 1988, Emery 1991). This relationship differs for ground water and surface water wetlands, in contrast to models that have been applied irrespective of water source or vegetation cover (Emery 1971, Emery 1991). Among ground water wetlands, ET_g has a consistent relationship with WTD, while among surface water wetlands, it does not.

This study offers substantial improvements to existing models of ET_g by illustrating that the decrease in annual ET_g with water table decline to 1.0 m is substantially less than previously assumed. This study also demonstrates that the relationship of ET_g to water table depth in wetlands differs markedly between ground water and surface water wetlands.

ET_g versus WTD in ground water wetlands

For ground water wetlands, the results presented here corroborate the oft-proposed relationship of decreasing ET_g as the water table declines. However, the magnitude of ET_g estimated by existing models is too high when the water table is very near the ground surface (within ~0.1 – 0.2 m), and too low when the water table is ~1.0 m below the surface (Figure 2.9). The most-recently proposed model (Harmon 2000) estimates a value ET_g at WTD = 0.12 m that is 23% greater than this study's estimate, and at WTD = 1.01 Harmon's model estimates a value of ET that is 40% less than this study's estimate. At WTD = 0.12 m, the highest over-estimate by an existing model is 49% greater than this study's estimate (Emery 1970). At WTD = 1.01 m, the greatest under-estimate is -44% (Emery 1991).

Because of the pattern of over- and under-estimates of ET_g, existing models predict a substantially larger decrease in ET_g as the water table declines than my data indicate. An important consequence of this difference is that existing models would predict higher ET "salvage"—i.e., the amount that ET_g would be reduced if the water table were drawn down—than would actually occur. Compared to this study, existing models overestimate salvage by 15 to 234%, with three of four existing models estimating at least 99% more salvage than this study. The most-recent model (Harmon 2000) estimates a decrease in ET_g of 681 mm as WTD changes for 0.12 to 1.01 m, thus estimating salvage that is 459 mm (207%) greater than the estimate from this study.

Our results suggest that the magnitude of ET_g decrease as a function of water table decline is less than previously predicted because soil moisture does not become strongly limiting as long as the water table is within ~1.0 m of the ground surface. During this study, soil water content in all ground water wetlands remained above 0.20 cm^3/cm^3, even when WTD was at 1.20 m depth, suggesting significant capillary movement of water from the water table to the upper soil horizons. This finding is consistent with other studies that have found that capillary movement of water through fine textured soils can be high and can influence root zone soil water content (Andersen 2005), even up to WTD of 2.5 m (Chimner and Cooper 2004). It also suggests that wetland plants in the study area have deep root systems that can acquire large amounts of water even when the water table is 1.0 m below the ground surface.

Existing models likely are inaccurate due to a lack of data for wetland sites that vary with respect to hydrology and vegetation (Harmon 2000). For example, steep decreases in ET_g as a function of WTD are based on only open water ET and ET_g from a single vegetation type (saltgrass, *Distichlis spicata* (L.) Greene) (White 1932, Blaney et al. 1938, Blaney and Criddle 1962, Robinson and Waananen 1970, Dylla et al. 1972). Saltgrass is not a typical wetland plant because it often grows in alkaline soils where, despite a shallow water table, surface soil water content and plant productivity can remain low (J. Sanderson, pers. obs.). It differs in many ways from the highly productive sedges (*Carex* spp.), rushes (*Juncus balticus*), and emergent vegetation that dominate many intermountain wetlands in the western US. ET_g estimates from this study, which are based on ET_a measurements in a variety of wetland types, suggest that saltgrass is a poor representative of wetland vegetation in general.

ET_g versus WTD in surface water wetlands

My data indicate that the ET_g-WTD relationship in surface water wetlands differs from the relationship for ground water wetlands. Unlike in ground water wetlands, estimated ET_g in surface water wetlands is highly variable. The variability in ET_g arises from the variability in water supply to surface water wetlands in intermountain valleys, which is driven by basin wide precipitation patterns, especially winter snow in the mountains adjacent to the valleys. Inter-annual surface water inflows to intermountain basin wetlands may vary by >300 % (Sanderson this dissertation Chapter 3). When surface water inflows are sufficient to meet ET_a demand, ET_g can be 0 mm, or ET_g can be less than 0 mm, indicating ground water recharge (de Meo et al. 2003). For example, at Mishak Lakes, which was inundated by stream inputs for part of every year of this study, there was no estimated ET_g despite the mean annual water table being within 1 m of the ground surface (WTD < 1.0). All existing models predict $ET_g > 0$ mm when WTD < 1.0 m.

When drought prevails and snowmelt provides insufficient inflows to wetlands yet water tables still approach the ground surface (e.g., at Bulrush), some ET_a is satisfied by ground water, thus ET_g is > 0 mm. For example, at the Bulrush site, which was not inundated during the study period, ET_g was > 0 mm despite a mean annual water table that was more than 1.5 m below the ground surface (WTD > 1.0 m). The relatively high ET_g in 2005 occurred because the water table rose abruptly to within 0.35 m of the ground surface, saturating the soil well within the root zone of the plants that dominate the site. Although rare, increasing ET_g with increasing WTD has been reported elsewhere. Scott et al. (2004) measured a significant decrease in ET_g from a mesquite stand despite a slight rise in the mean water table, probably as a consequence of a drought induced decrease in leaf area.

In surface water wetlands, ET_g can also vary considerably for a given WTD. For example, at the Bulrush site ET_a was 172% higher in 2005 than in 2003 (443 vs 163 mm, respectively), despite mean water tables that were nearly identical (1.56 m and 1.66 m, respectively). Bulrush annual values are variable because of the large and rapid fluctuations in water table beneath the site that, in 2005, caused a large increase in near-surface soil water content, yet the water table spike did not persist long enough to change greatly the annual mean water table. Higher soil water content subsequently led to higher ET_a and ET_g.

The relationship between the variability of the hydrologic regime and ET_g of surface water wetlands is difficult to predict with the current state of knowledge. For example, during long drought periods water tables drop and seepages losses from streams may be great, and surface water wetlands may remain dry despite high runoff (Wurster et al. 2003), as occurred in 2005 at the Bulrush site. ET_g in this case would be > 0 mm.

Consecutive years of moderate runoff could also occur, possibly resulting in extensive flooding and causing ET_g to be ≤ 0 mm.

Role of vegetation in ET_g

The results from this study improve on existing models of ET_g versus shallow WTDs in part because a variety of common wetland types were investigated. Most previous researchers applied a single ET_g-WTD relationship to all vegetation types, irrespective of hydrologic dynamics and variability in vegetation type, growth, and physiology. The data presented herein suggest that, for a given WTD, non-saline wetlands use ground water at a much higher rate than the halophytic vegetation (especially saltgrass) and non-hydrophytic vegetation used to develop existing ET_g-WTD relationships (White 1932, Blaney et al. 1938, Eakin 1960, Blaney and Criddle 1962, Robinson and Waananen 1970, Dylla et al. 1972, Nichols 1994). Harmon (2000) was the first to explicitly propose different ET_g-WTD relationships for different classes of vegetation types in the SLV. However, at WTD greater than 0.6 m, his curve for hydrophytic vegetation is nearly identical to Emery (1991), indicating the influence of data from non-hydrophytic vegetation on the formulation of the hydrophytic curve.

Water availability is a critical determinant of vegetation composition, and vegetation strongly influences ET_g. As water use changes continue in intermountain basins of the western US, vegetation will also continue to respond dynamically, in both the short- and long-term. In the short-term, species dominance, leaf area, and stomatal conductance can respond to a changing water table, thus changing within-season ET rates. In the long term, changes in water availability may trigger changes in site vegetation composition, cover, and rooting characteristics. For example, Cooper et al. (2005) documented floodintolerant shrubs invading intermountain playa basins formerly dominated by wetland grasses and other non-woody species after a water table decline of 1.6 m. These upland shrubs have different water acquisition and use patterns than the hydrophytic vegetation they replaced, because they are deeply rooted and can access deep water tables, yet they have low productivity and low leaf area (Cooper et al. 2006). ET, water table position, and vegetation type are critically inter-related (Ridolfi et al. 2006), and efforts to predict changes in ET_g must consider both short- and long-term changes in other closely-related factors.

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Table 2.1. Location and major characteristics of wetland sites studied.

Wetland	**Type**	**Dominant vegetation**	**Vegetation height (m)**	**Water table elevation (m)***	**Location†**
Ground water wetlands					
Alamosa NWR	Peatland	*Carex simulata* Mackenzie and *C. aquatilis* Wahlenb.	0.50	0.0 to -0.90	37.4100° N 105.7496° W
Higel	Wet meadow	*Carex simulata* Mackenzie and *Juncus balticus* Willd. var. *montanus* Engelm.	0.60	0.0 to -0.40	37.5384° N 105.9839° W
Rito Alto	Wet meadow	*Carex simulata* Mackenzie and *Juncus balticus* Willd. var. *montanus* Engelm.	0.50	-0.24 to -1.20	38.0393° N 108.815° W
Surface water wetlands					
Bulrush	Intermountain Playa	*Schoenoplectus tabernaemontani* (K.C. Gmel.) Palla	1.0-2.0**	+0.35 to -1.89	37.7301° N 105.7581° W
Mishak Lakes	Intermountain Playa	*Eleocharis palustris* (L.) Roemer & J.A. Schultes	0.50	+0.65 to -1.26	37.9147° N 105.9872° W

* Relative to ground surface; positive is above the ground surface, negative is below.

† NAD1983 Datum

** Height of Bulrush varies considerably depending on amount of water supplied to the wetland. During the years of this study (2003 and 2005), plants did not exceed 1.0 m.

Table 2.2. Percent of growing season days that were measured for each site/year combination.

Site	Year	% of days measured
Alamosa NWR	2003	33
	2005	76
Higel	2003	78
	2005	76
Rito Alto	2001	82
	2002	64
	2003	88
	2004	78
	2005	72
Bulrush	2003	67
	2005	55
Mishak	1999	7
	2000	10
	2001	29

Table 2.3. Models used to calibrate Priestly-Taylor potential evapotranspiration (ET_p) to measured actual evapotranspiration (ET_a). WTD is water table depth. "7 d ppt" is cumulative weighted precipitation over the previous seven days. See text for complete explanation of independent variables. See the right column of figures 6 and 7 for fit statistics.

Site	**Variables included**	**Parameter estimate ± 1 s.e.**	**p-value**
Ground water wetlands			
Alamosa NWR	Intercept	1.14 ± 0.085	
	season	-0.30 ± 0.100	0.003
	WTD	-1.02 ± 0.13	<0.001
	season*WTD	1.50 ± 0.18	<0.001
Higel	intercept	0.75 ± 0.027	
	season	0.44 ± 0.035	<0.001
Rito Alto	intercept	0.85 ± 0.042	
	season	0.38 ± 0.026	<0.001
	WTD	-0.29 ± 0.041	<0.001
Surface water wetlands			
Bulrush	intercept	-356.2 ± 40.4	
	soil moisture	0.73 ± 0.32	0.023
	7 d ppt	0.054 ± 0.011	<0.001
	year	0.18 ± 0.020	<0.001
Mishak Lakes	intercept	0.31 ± 0.069	
	season	0.83 ± 0.071	<0.001
	WTD	-0.11 ± 0.29	0.001

Table 2.4. Statistics for modeled actual evapotranspiration (ET_a) versus measured ET_a using modeled available energy (R_n-G) and off-site regional weather station data. r^2 is the coefficient of determination, CV is the coefficient of variation, and MBE is mean bias error (in mm).

Site	r^2	CV (%)	MBE	slope
Alamosa NWA	0.84	16	0.0	0.80
Higel	0.80	15	0.0	0.82
Rito Alto	0.75	17	0.0	0.78
Bulrush	0.76	25	-0.1	0.71
Mishak Lakes	0.70	18	+0.1	0.70

Table 2.5. Models of available energy (R_n-G) as a function of off-site data. "1 d ppt" is total rainfall on the previous day. See text for complete explanation of independent variables. r^2 is coefficient of determination of modeled versus measured (Rn-G), and MBE (in MJ/m^2/day) is the mean bias error of the model.

Site	**Variables included**	**Parameter estimate ± 1 s.e.**	**p-value**	**model r^2**	**model MBE**
Ground water wetlands					
Alamosa NWR	Intercept	2.78 ± 0.85		0.79	0.14
	solar radiation	0.37 ± 0.037	<0.001		
	season	3.36 ± 0.72	<0.001		
Higel	intercept	1.76 ± 0.58		0.56	-0.25
	solar radiation	0.50 ± 0.023	<0.001		
Rito Alto	intercept	2.57 ± 0.49		0.64	-0.04
	solar radiation	0.36 ± 0.022	<0.001		
	season	3.20 ± 0.42	<0.001		
Surface water wetlands					
Bulrush	intercept	3.24 ± 0.76		0.64	-0.32
	solar radiation	0.33 ± 0.031	<0.001		
	season	2.02 ± 0.65	0.003		
	1 d ppt	0.76 ± 0.24	0.002		
Mishak Lakes	intercept	2.90 ± 1.01		0.76	-0.23
	solar radiation	0.49 ± 0.040	<0.001		

Table 2.6. Annual estimated actual evapotranspiration (ET_a) and the annual estimated ground water component of evapotranspiration (ET_g) for all sites and all years. Ground water wetland sites are AL = Alamosa National Wildlife Refuge, HI = Higel, RA = Rito Alto. Surface water wetland sites are BU = Bulrush and MI = Mishak. WTD = water table depth.

Site	Year	WTD (m)	ETa (mm)	Precipitation (mm)	ETg (mm)
AL	2003	0.39	882	158	724
AL	2005	0.40	891	131	760
HI	2003	0.12	987	155	832
HI	2005	0.13	994	121	873
RA	2001	0.68	897	221	676
RA	2002	0.87	845	110	735
RA	2003	0.91	804	205	599
RA	2004	0.96	809	180	629
RA	2005	1.01	751	122	629
BU	2003	1.66	352	189	163
BU	2005	1.56	571	128	443
MI	1999	0.39	868	1199*	0
MI	2000	0.62	892	1258*	0
MI	2001	0.34	872	1232*	0

* includes surface water inflows per unit area of wetland. The majority of inputs in excess of ET were lost from wetland as surface water outflow (Sanderson this dissertation Chapter 3).

Table 2.7. Estimates from existing models and the current study of the ground water component of evapotranspiration (ET_g) in the San Luis Valley with mean water table depth (WTD) = 0.12 and 1.01 m, the range encountered during this study. ET_g values are in mm. Percentages in parentheses show the difference from this study.

	Estimated ET_g				Decrease
	@WTD = 0.12 m		@ WTD = 1.01		in ET_g
This study	864		642		222
Emery 1970	1286	(+49%)	545	(-15%)	741
Emery 1991	618	(-28%)	362	(-44%)	256
Huntley 1979	930	(+ 8%)	488	(-24%)	442
Hearne and Dewey 1988	945*	(+ 9%)	n/a		
Harmon 2000	1065	(+23%)	384	(-40%)	681

* for water table within 0.60 m of the ground surface (i.e., WTD < 0.60 m).

Figure 2.1. Study area and site locations.

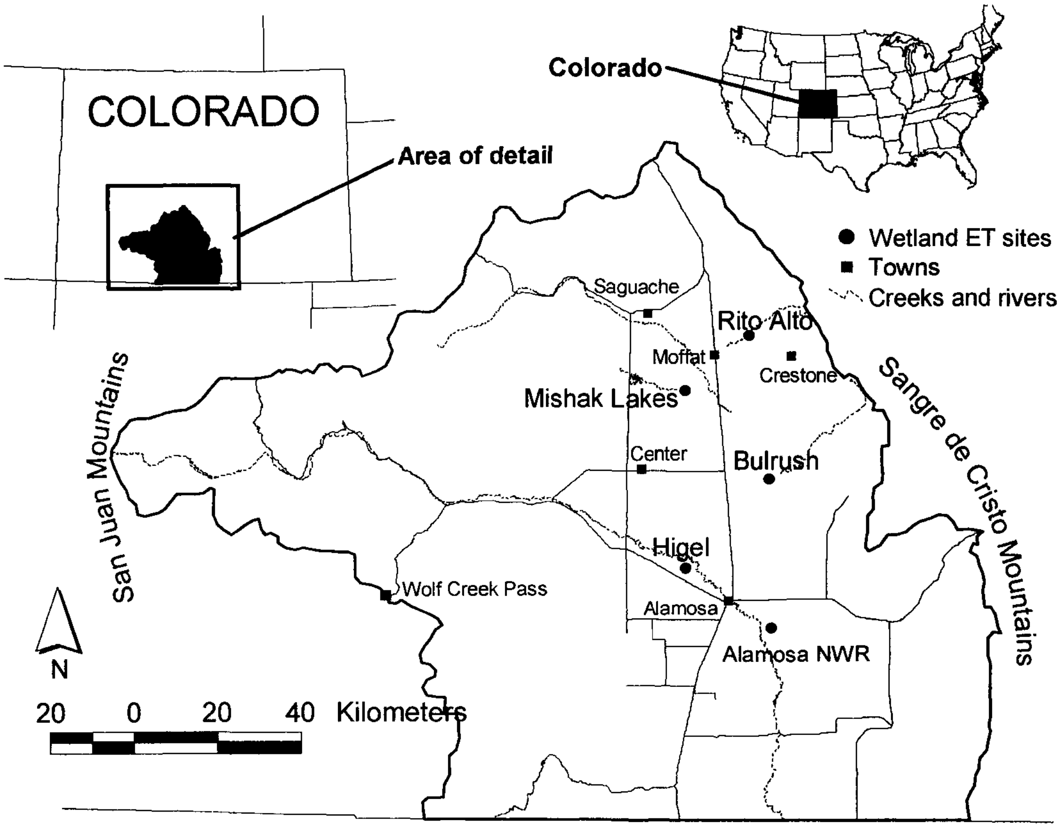
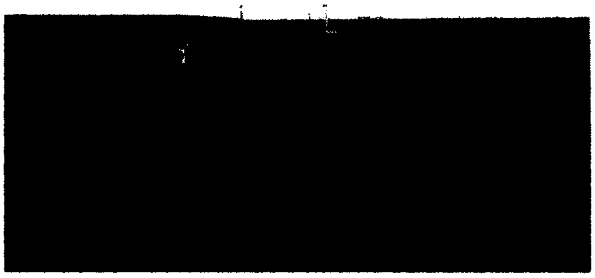


Figure 2.2. Photos of wetland study sites. Wetlands supplied primarily by ground water are (a) through (c). Wetlands supplied primarily by surface water in most years are (d) and (e). The sets of equipment shown are the Bowen Ratio Energy Balance stations. The highest pieces of equipment are ~2.5 m above the ground surface.

(a) Alamosa NWR



(d) Bulrush

(b) Higel

(e) Mishak Lakes

(c) Rito Alto

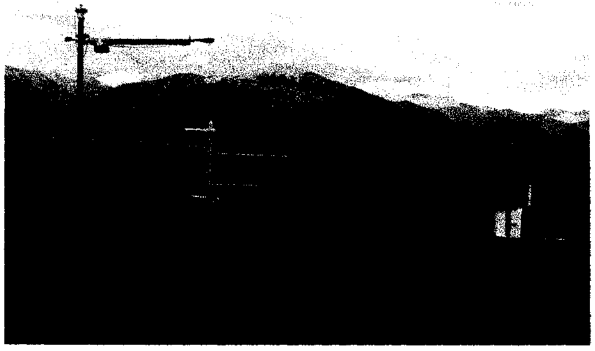


Figure 2.3. Representative patterns of growing season water table position for (a) ground water wetlands and (b) surface water wetlands. Among ground water wetlands, Alamosa NWR is a peatland, and Rito Alto and Higel are wet meadows. Among surface water wetlands, Bulrush and Mishak Lakes are intermountain playas. Multiple years are shown for sites where pattern was highly variable between years.

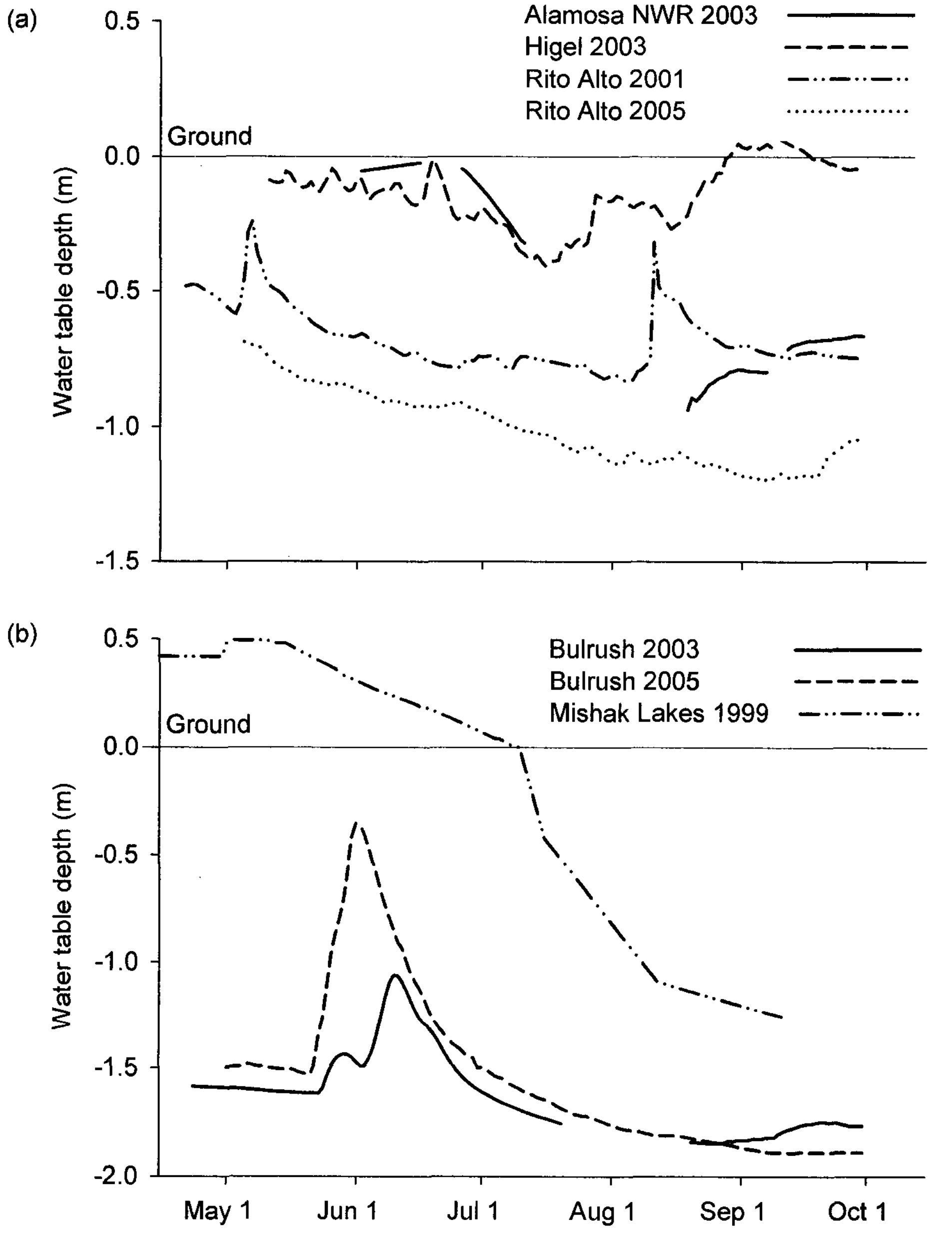
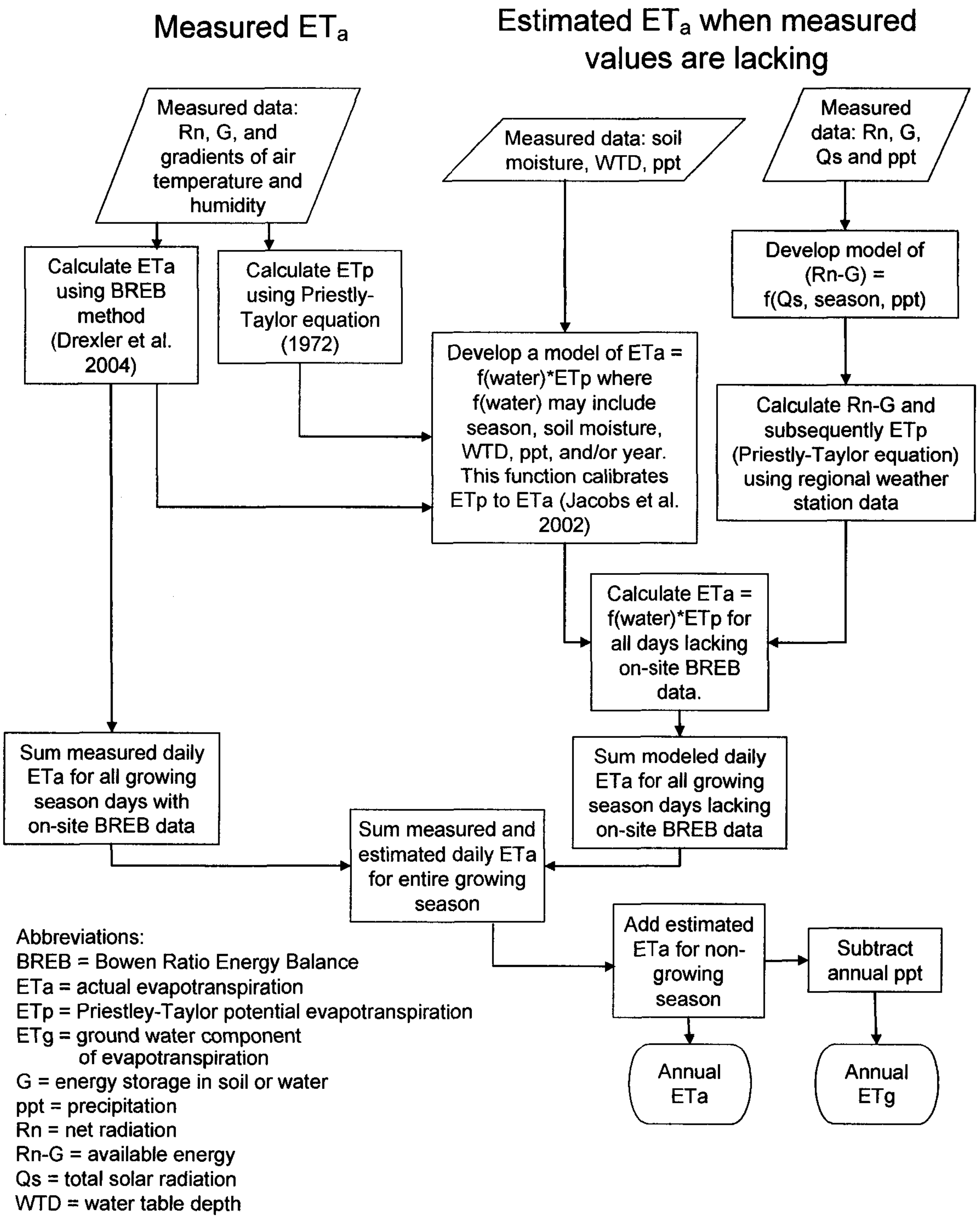


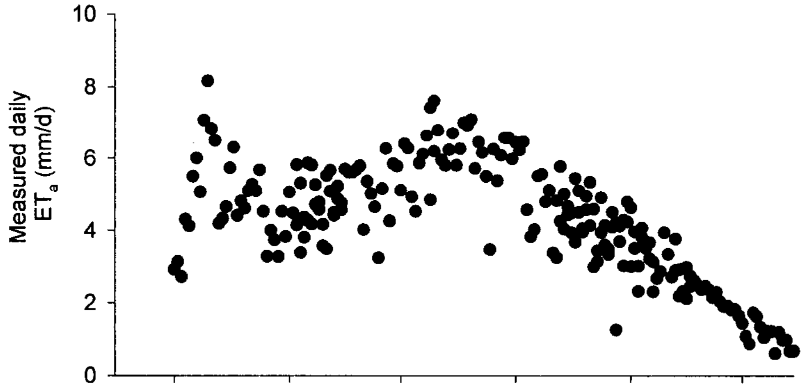
Figure 2.4. Steps followed for estimating annual actual evapotranspiration (ET_a) and the ground water component of evapotranspiration (ET_g). Growing season is Apr 15-Oct 15.



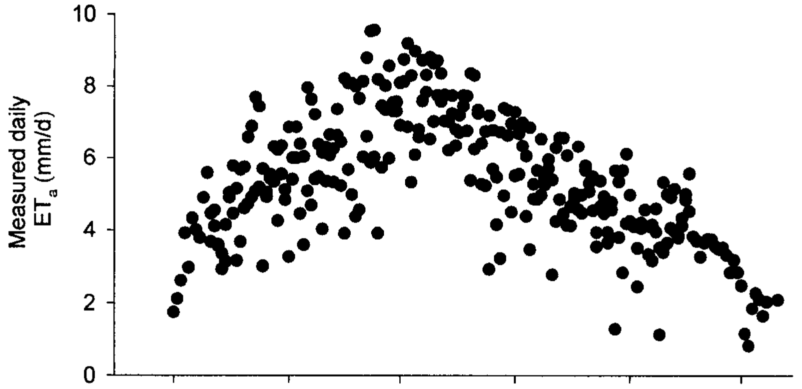
Abbreviations:
BREB = Bowen Ratio Energy Balance
ETa = actual evapotranspiration
ETp = Priestley-Taylor potential evapotranspiration
ETg = ground water component of evapotranspiration
G = energy storage in soil or water
ppt = precipitation
Rn = net radiation
Rn-G = available energy
Qs = total solar radiation
WTD = water table depth

Figure 2.5. Measured daily actual evapotranspiration (ET_a) in ground water fed wetlands. Alamosa NWR (a) is a peatland; Higel (b) and Rito Alto (c) are wet meadows. The number of years of data for each figure is: (a) two, (b) two, and (c) five. Some daily values are missing in all years for all sites (see Table 2.2).

(a) Alamosa NWR



(b) Higel



(c) Rito Alto

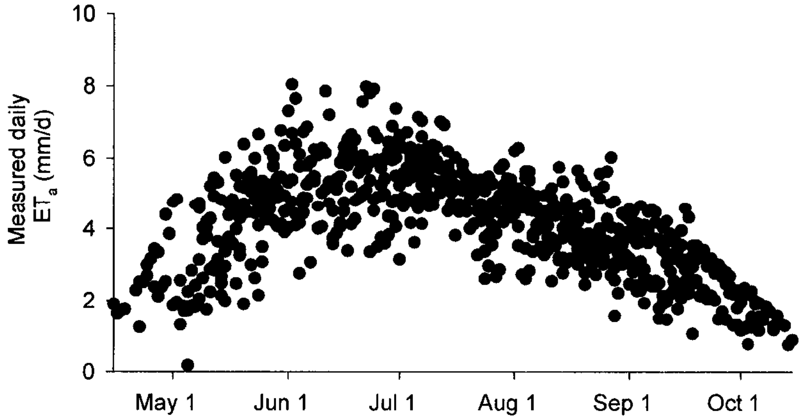
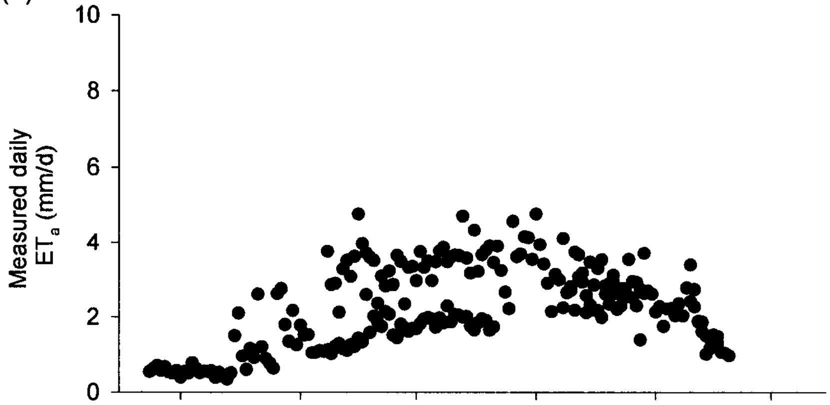


Figure 2.6. Measured daily actual evapotranspiration (ET_a) in surface water wetlands. Bulrush (a) and Mishak Lakes (b) are intermountain playas. The number of years of data for each figure is: (a) two, and (b) three. Some daily values are missing in all years for all sites (see Table 2.2).

(a) Bulrush



(b) Mishak Lakes

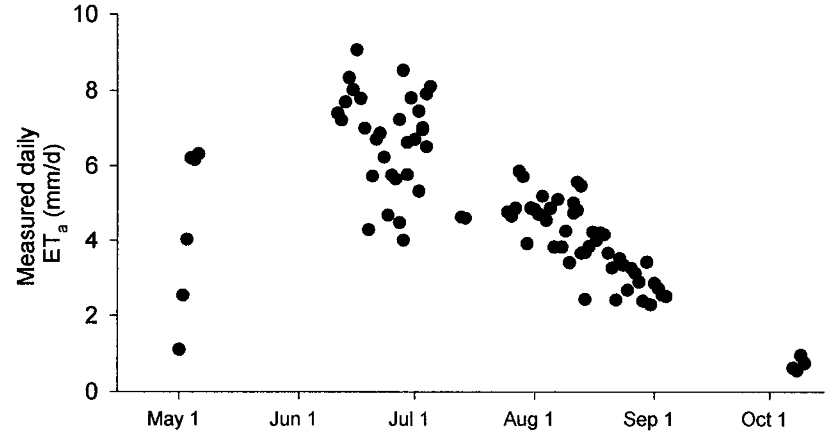
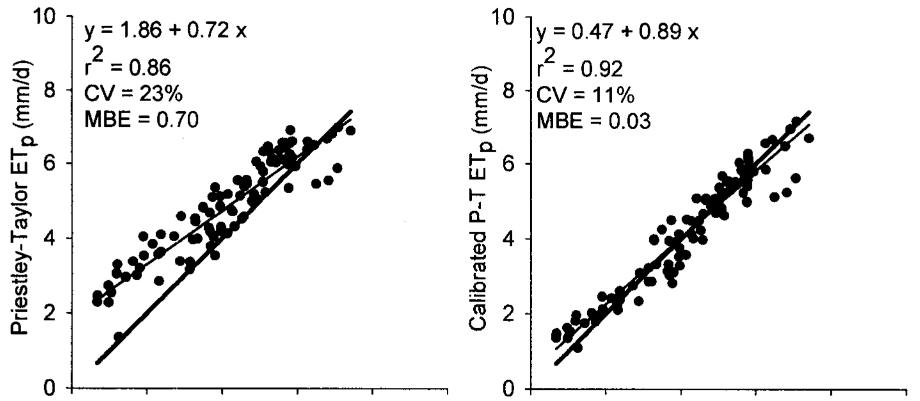
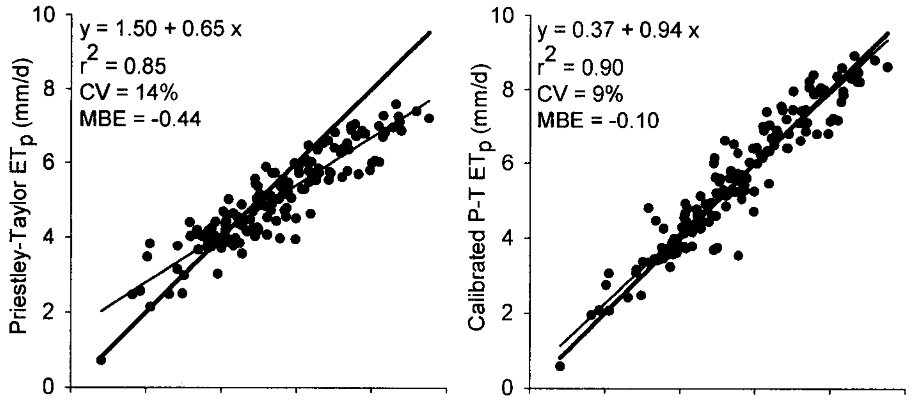


Figure 2.7. Priestley-Taylor potential evapotranspiration (P-T ET_p) (left) and calibrated P-T ET_p (right) for wet meadows. r^2 is the coefficient of determination, CV is the coefficient of variation, and MBE is the mean bias error. The light line through the data points is the least-squares best fit. The heavy line shows the 1:1 relationship.

(a) Alamosa NWR



(b) Higel



(c) Rito Alto

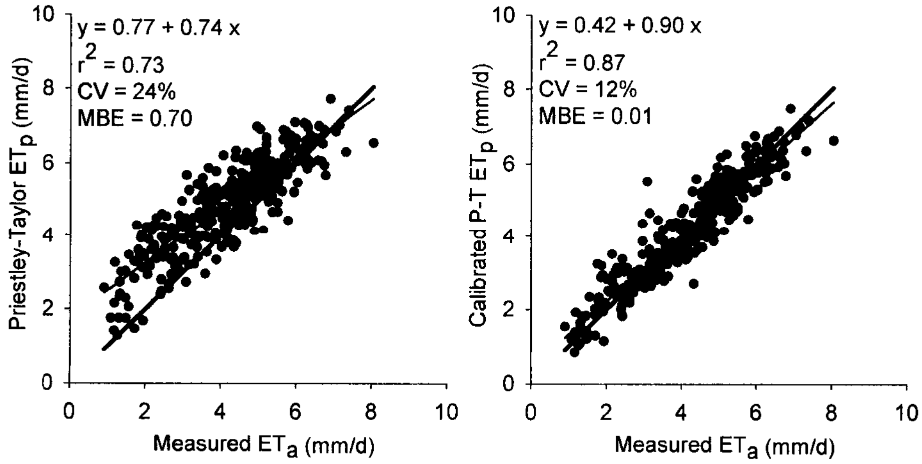
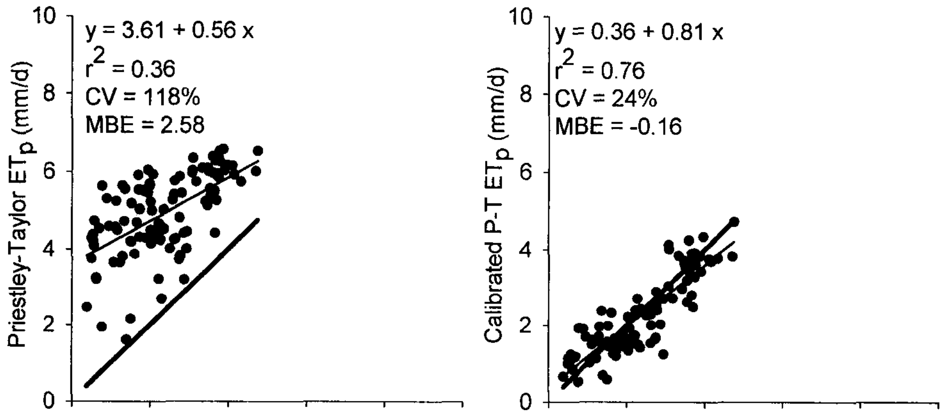


Figure 2.8. Priestley-Taylor potential evapotranspiration (P-T ET_p) (left) and calibrated P-T ET_p (right) for intermountain playas. r^2 is the coefficient of determination, CV is the coefficient of variation, and MBE is the mean bias error. The light line through the data points is the least-squares best fit. The heavy line shows the 1:1 relationship.

(a) Bulrush



(b) Mishak Lakes

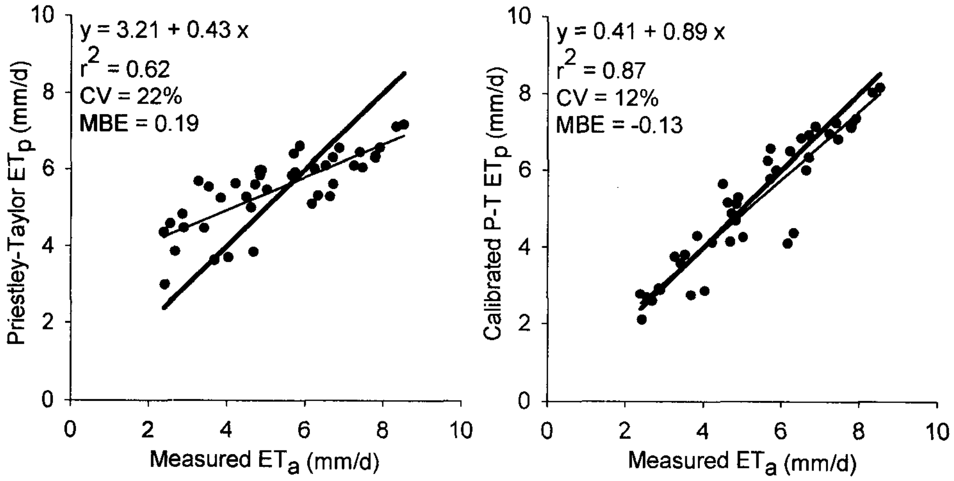
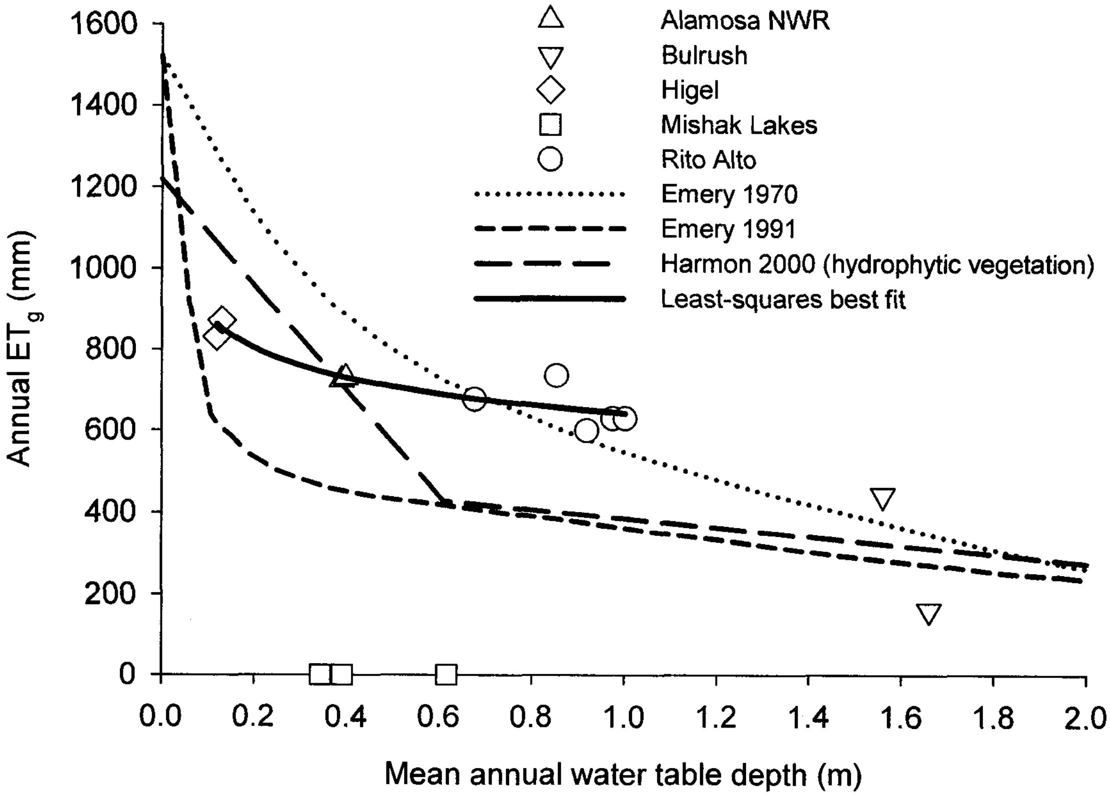


Figure 2.9. Total annual ground water component of evapotranspiration (ET_g) as a function of mean annual water table depth (WTD) for all sites and years, plus 3 existing models for comparison. The solid line shows the least-squares fit to the 9 values for ground water wetlands.



CHAPTER 3

THE SIMULATED NATURAL HYDROLOGIC REGIME OF AN INTERMOUNTAIN PLAYA CONSERVATION SITE

ABSTRACT

An intermountain playa wetland preserve in Colorado's San Luis Valley was studied to assess how its current hydrologic function compares to its historical natural flow regime. Current hydrologic conditions were quantified, and on-site effects of off-site water use were assessed. A water-budget model was developed to simulate an unaltered (i.e., natural) hydrologic regime. The model was validated and subjected to a sensitivity analysis. From 1999-2005, observed stream inflows accounted for ≥80% of total annual water inputs. No ground water discharged to the wetland. Evapotranspiration (ET) accounted for ≥69% of total annual water loss. The simulated natural hydrologic regime differed substantially from current altered conditions with respect to depth, variability, and frequency of flooding. During 1998-2002, observed monthly mean surface water depth was 65% lower than under simulated conditions. Observed monthly variability in water depth range from 129% greater (May) to 100% less (September and October) than simulated. As observed, the wetland dried completely (i.e., was ephemeral) in all years; as simulated, the wetland was ephemeral in 2 of 5 years. For the period 1915-2002, the simulated wetland was inundated continuously for as long as 16 years and 9 months. The

large differences in observed and simulated surface water dynamics resulted from differences between altered and simulated unaltered stream inflows. The maximum and minimum annual total stream inflows observed from 1998-2005 were 3.1 x 10^6 m^3 and 0 m^3, respectively, versus 15.5 x 10^6 m^3 and 3.2 x 10^6 m^3 under simulated conditions. The maximum simulated inflow was 484% greater than observed. These data indicate that the current hydrologic regime of this intermountain playa differs significantly from its natural hydrologic regime, which has important implications for planning and assessing conservation success.

INTRODUCTION

The protection of biodiversity in rivers, lakes, and wetlands requires that water flows and flooding resemble historical patterns (Baron et al. 2002, Postel and Richter 2003, Acreman and Dunbar 2004). This is because natural flow regimes (Poff et al. 1997) create a particular range of conditions of habitat availability, water quality, nutrient cycling, substrate composition, insect and fish life cycle transitions, seed dispersal, plant growth, and the maintenance of biodiversity (Postel and Richter 2003). Worldwide, the frequency, intensity, and duration of flooding in many freshwater ecosystems have been profoundly altered by water regulation, diversion and augmentation for agriculture, mining, human water supply, energy production, flood control, and wildlife management (Poff et al. 1997, Bunn and Arthington 2002, Acreman and Dunbar 2004). Alteration of hydrologic systems has been particularly intense west of the 100th meridian, where there are nearly 15,000 dams > 2 m high (U.S. Army Corps of Engineers 1996) and tens of thousands of surface water diversions (Lytle and Merritt 2004).

Hydrologic alterations can change habitat characteristics, and consequently can have short- and long-term effects on species, populations, and communities (Richter et al. 1996, Poff et al. 1997, Lytle and Poff 2004). For example, in snowmelt river ecosystems (Poff 1996) variability in flow is needed to maintain natural dynamics of populations and to facilitate and mitigate species interactions (Poff et al. 1997, Baron et al. 2002). Among aquatic invertebrates, specialized species often survive while other species may be eliminated during prolonged low-flows (Williams and Hynes 1977) and periodic drying (Williams 1987). Among plants, species differ in their flood tolerance, so flood flows influence the composition, structure, and distribution of plant communities (Postel and Richter 2003).

Assessing ecological changes resulting from hydrologic alterations requires characterizing the hydrologic regime. For rivers, there are at least 171 hydrologic indices that have been used to characterize stream flow regimes (Olden and Poff 2003). These indices are based on stream flow records (Richter et al. 1996), which are available for many rivers dating back to the 19th century. Such extensive data sets, however, are rarely available for wetlands. Where data are limited, hydrologic models can be used to simulate historical flooding patterns (Fennema et al. 1994). Models are valuable tools for examining past or future water dynamics in wetlands over long time scales (Sturtevant 1998, Poiani et al. 1995).

In intermountain valleys of the western U.S., hydrologic conditions appear to have changed substantially over the past 150 years, yet there are few data available for assessing the exact nature of these changes. For example, in the San Luis Valley (SLV), a high valley covering 8400 km^2 of southern Colorado (Figure 3.1, Huntley 1979), a 19th century map created by a U.S. Army surveyor (Wheeler 1877) shows extensive marshes in the northern SLV. Wheeler and Humphreys (1878) describe the "San Luis swamp" extending nearly 100 km down the middle of the Valley. Water flows supporting these wetlands came under the influence of intensive agriculture by 1879. Large-scale water development projects were in place in the SLV by 1884, and intensive development of surface water and ground water continued through the 20th century (Table 3.1). Stream flows were not systematically recorded on even the largest river in the SLV, the Rio Grande, until 1890 (U.S. Geological Survey 2005), and records for smaller streams and aquifers were limited or nonexistent through the first several decades of water development. As such, historical flooding patterns in SLV wetlands are not easily characterized.

The re-construction of natural flow regimes is important because wetlands in the SLV have significant conservation value (Neely et al. 1993). One important SLV wetland complex is Mishak Lakes (ML), a preserve owned by The Nature Conservancy (Figure 3.1). Wheeler (1877) clearly shows ML as an extensive wetland complex. Oral histories (Warner 1998) and local 4th generation ranchers (J. Werner pers. comm.) describe greater inflows to ML and more extensive flooding in the early- to mid-1900s than in the recent past. Water from streams that historically supplied ML was appropriated as early as 1868 (CDSS 2005), and flow to ML was reduced (U.S. Bureau of Reclamation 1979).

The overall objective of this study was to assess how off-site water use has altered hydrologic functioning of ML, and to describe the hydrologic regime in the absence of alterations (i.e., the natural hydrologic regime). The first goal was to quantify patterns of water fluxes and inundation, including stream inflows and outflows, precipitation, evapotranspiration, and ground water fluxes, as well as depth and timing of flooding across the wetland. The second goal was to re-construct the ML historical hydrologic regime using the limited data available in a water budget model. The model was used to compare current conditions in 1998-2002 to conditions over the same period in the absence of flow alterations (simulated conditions). The model was also used to simulate historical hydrologic patterns in ML from 1915 through 2002.

STUDY AREA

Regional Setting

The San Luis Valley (Figure 3.1) is similar to many intermountain valleys of the western U.S. (Mifflin 1988). The valley floor has little topographic relief, averaging 2350 m elevation. Summers are warm (July mean = 17°C), winters are cold (January mean = -9°C), and insolation is high all year (Doesken and McKee 1989, Western Regional Climate Center 2005). Mountains rising above 4000 m in the Sangre de Cristo range to the east and the San Juan range to the west create orographic effects that result in low precipitation on the valley floor (177 mm at Center, CO, elevation 2350 m) and high precipitation in the mountains (1153 mm at Wolf Creek Pass, elevation 3290 m) (Western Regional Climate Center 2005).

Mountain precipitation falls mostly as snow, which melts in late spring and provides abundant water to the valley floor. Most of the snowmelt water enters two large aquifers, a near-surface unconfined aquifer (0 to ~30 m below ground surface) and a confined aquifer (~30 m to ~1200 m below ground surface) (Hanna and Harmon 1989). The aquifers are separated by a series of discontinuous clay layers that extend across most of the valley, but taper out near the valley margins (Emery 1971, Emery et al. 1971). Snowmelt recharges the confined aquifer by infiltrating along the margins at the base of the mountains. The confined aquifer also receives ground water originating in the mountains to the west (Huntley 1979). The unconfined aquifer likewise is recharged by snowmelt, but it additionally receives upward leakage from the confined aquifer (Siebenthal 1910, Emery et al. 1973).

The Mishak Lakes Wetland Complex

Mishak Lakes is a 283 ha complex of shallow, interconnected playa basins (37.925 N, 105.993 W, NAD83 datum; Figure 3.2). The site has little topographic relief. The bottoms of the deepest basins are approximately 1.1 m below adjacent dry shrublands, and the valley floor drops less than 3 m over nearly 5 km from NW to SE.

Soil and subsoil strata influence hydrologic processes by storing water and restricting water fluxes. Soils at ML are mostly sandy loams, with approximately 40% porosity. A laterally consistent low permeability (clay) layer occurs near the bottom of the deepest basins (Kappen 2004), without which the wetland likely would not retain water. Beneath this clay is a series of alluvial layers ranging from silts to gravels, continuing to about 22 m where additional clay layers indicate the top of the confined aquifer.

A 19th-century survey map (Wheeler 1877), surface geomorphology, and local anecdotes are among the evidence that indicates two streams historically flowed into ML: Russell Creek and Werner Arroyo (Figure 3.2). Russell Creek is supplied primarily by Russell Springs, a group of artesian springs originating on the eastern slope of the San Juan Mountains about 11 km west of Mishak Lakes. At the beginning of the 20th century

Russell Springs consisted of about 25 springs that drained into Russell Lakes, a complex of shallow lakes and wetlands 3 km east of the springs (Siebenthal 1910). Russell Springs average discharge decreased from 0.10 m^3s^{-1} in 1936 (Powell 1958) to 0.026 m^3s^{-1} in 1970, likely as a result of withdrawals from the confined aquifer (Emery et al. 1973). Flow from these springs is now supplemented by an average of ~0.35 m^3s^{-1} from artesian wells at Russell Lakes (Leonard Rice 1998). Werner Arroyo historically conveyed snowmelt from the San Juan Mountains to ML. Recently, however, there has been no evidence of flow into ML via the Werner Arroyo. As recently as 50 years ago, springtime peak discharge of 0.60 m^3s^{-1} or greater occurred in Werner Arroyo a short distance above Mishak Lakes (A. Davey, J. Werner, pers. obs.).

Six distinctive plant communities occur at ML, and are described elsewhere (Cooper and Severn 1992, Sanderson this dissertation Chapter 4). Extensive stands of spikerush (*Eleocharis palustris*) dominate the wetland basins, and are the largest known occurrence of this plant community in Colorado (Sarr and Sanderson 1998). The wetlands also support a small population of *Cleome multicaulis*, a rare plant with few occurrences outside the SLV (Spackman et al. 1997). The upland shrub community adjacent to the wetlands is dominated by shrubs (*Sarcobatus vermiculatus* and *Chrysothamus nauseosus*) that are supported in part by a water table within 2 m of the ground surface (Cooper et al. 2006).

METHODS

Description of the hydrologic regime

Data collected under current conditions (1998-2005) and output from a simulation model were used to assess how off-site water use currently alters water dynamics at the ML conservation site, and to determine how patterns of flooding would appear in the absence of hydrologic alteration. Patterns of flooding were described within years and between years using a set of hydrologic indices (Olden and Poff 2003). Values for the hydrologic indices were calculated for current and simulated conditions for 1998-2002, and also for simulated conditions for 1915-2002. For the 1998-2002 period, medians were compared using the Wilcoxon-Mann-Whitney test (Zar 1999), and dispersion was compared using Levene's test of homogeneity of absolute differences from the group mean (SAS Institute 2003).

The hydrologic indices used were similar to available hydrologically and ecologically relevant indices that are commonly used to characterize stream flow (Richter et al. 1996, Olden and Poff 2003). The indices (Table 3.2) reflect the five fundamental characteristics of hydrologic regimes: magnitude, timing, frequency, duration, and rate of change (Richter et al. 1996). Since existing indices are most relevant to lotic ecosystems, a distinct set of indices were developed for intermountain playas that are believed to reflect ecologically relevant aspects of these wetlands.

Field data collection

To characterize the current hydrologic conditions at ML, water levels in the major plant communities and water fluxes to and from the wetland complex were quantified.

Data on fluxes included stream inflows and outflows, ground water discharge and recharge, evapotranspiration, and precipitation. During the latter years of this study, ground water recharge was investigated in more detail by Kappen (2004) using ion concentrations and stable isotopes of water.

Surface water fluxes were measured at 2 inflow locations and 2 outflow locations (Figure 3.2). Inflow locations included the artesian-supplied stream (Russell Creek) and the snowmelt-supplied stream (Werner Arroyo). Outflow locations were located on the southeast end of the complex. A stage-discharge relationship was developed for these points using float measurements of velocity at multiple stage elevations (Dunne and Leopold 1978). Daily stage elevation was recorded at the Russell Creek inflow location during water years 1999 and 2000, and at the wetland outflow locations during water year 2000. No surface flow was observed in Werner Arroyo.

Ground water fluxes were investigated using a network of wells placed in 40 locations across the wetland complex in intersecting, perpendicular transects (Figure 3.2). Wells were placed in all dominant plant communities and at all major topographic breaks. Wells were constructed using 32 mm diameter PVC pipe, with a 0.5 m-long slotted section (screen) at the bottom. Holes were hand-augered to approximately 1 m below the water table (2-3 m below the ground surface). After wells were installed, the hole outside the well pipe was backfilled with sand and gravel for the length of the slotted section, and bentonite was placed above the slotted section to restrict surface water flow down the pipe. All locations were surveyed to within 0.02 m. Water levels were measured weekly to biweekly during the growing season in 1998-2000 and monthly during late fall, winter, and early spring. During 2001-2005, a subset of 15 wells around a central basin (Figure

3.2) was measured at infrequent intervals, ~6 times per year. Continual (15 min avg) surface water and ground water levels were recorded at three locations during several intervals of 3 weeks to 6 months in 1999 and 2000. The depth of surface water at each well location was also measured.

Evapotranspiration (ET) and precipitation at Mishak Lakes were measured during multiple intervals of 3 days to 5 months during 1999 to 2001 in the *Eleocharis palustris* plant community. ET was measured using the Bowen Ratio Energy Balance method (Tanner 1960, Moncrief et al. 2000) with a micrometeorological system (Radiation and Energy Balance Systems, Inc., Bellevue, WA, see Fritschen and Simpson, 1989).

Precipitation was measured simultaneous with ET measurements using a Texas Electronics 525 20.3 cm tipping rain gauge. Additional precipitation data were obtained from the National Weather Service Cooperating Site in Center, CO, which is 20 km from ML (Figure 3.1) and receives similar amounts of precipitation based on an isohyetal map of average annual precipitation (Doesken et al. 1984).

Wetland Simulation Modeling

The fluxes in the water-budget model used to simulate the natural flow regime at ML included artesian-supplied and snowmelt-supplied stream inflows (Q_{in}), seepage into the ground (Q_{seep}), evapotranspiration (Q_{ET}), precipitation (Q_{ppt}), and stream outflows (Q_{out}) (Figure 3.3a). None of these historical fluxes is known with certainty, and all are estimated as described below. Model water fluxes were used to calculate surface water volume present in wetlands in any given month (Figure 3.3b), and surface water volume was then used to calculate water depth based on the basin's depth-to-volume relationship.

Programming for the simulation was done in Excel 2002-Visual Basic for Applications (Microsoft, Inc. 2002).

The model was based on a simple accounting procedure (Figure 3.3, Poiani and Johnson 1993). Surface water storage was calculated for each month as:

$$S_{surface} = S_{surface\ (previous)} + Q_{in} + Q_{ppt} - Q_{ET} - Q_{seepage} - Q_{out} \qquad (1)$$

Surface water storage ($S_{surface}$) was assumed to be zero at the beginning of the simulation (Oct 1914). $S_{surface}$ was increased by inflows from artesian-supplied Russell Creek and snowmelt-supplied Werner Arroyo (Q_{in}), and precipitation directly on the wetland (Q_{ppt}). $S_{surface}$ was decreased by ET (Q_{ET}) and seepage ($Q_{seepage}$). After accounting for ET and seepage, any surface water in excess of the maximum $S_{surface}$ was assigned to stream outflow (Q_{out}).

The complexity of the actual ML basins was reduced to a single, circular basin that retained the actual volume ($\sim 1.53 \times 10^6$ m^3) and area (283 ha) of the entire wetland complex (Figure 3.3a). The slope of the bottom of the model basin was set equal to the slope of the actual central basin. The sides of the model basin were vertical, which roughly corresponds to the abrupt transition of typical basin to adjacent non-wetland areas. The height of the vertical sides was set to achieve the actual wetland volume.

Inflows

Simulated inflows to ML included those from Russell Creek and Werner Arroyo. Russell Creek inflows were calculated as Russell Springs flow minus ET losses at historical wetlands upstream of ML. Russell Springs were assumed to flow at 0.14 m^{3}s^{-1} (Powell 1958, A. Davey pers. comm.). No inter- or intra-annual variation of spring flow was assumed, which is consistent with the minimal variation observed in the absence of deep ground water withdrawals (A. Davey pers. comm.). ET losses in wetlands below Russell Springs were based on a wetland area at Russell Lakes of 176 ha. The area of this historical wetland was estimated by first assuming that the Russell Lakes wetland area is directly proportional to artesian flows. Next, current wetland area was measured on USGS 1:24000 quadrangles. Finally, historical wetland area was calculated by multiplying current wetland area by the ratio of estimated historical to current artesian flows.

When mean daily ambient temperatures were less than 0 °C, warm artesian water froze on the surface soon after emerging from a spring or well, and it did not appear in Russell Creek until weeks later when temperatures rose above freezing. Temperatures below 0 °C prevailed in December and January. Intermittent warm periods occurred in February, and by April temperature on most days was above freezing. In the model, frozen December and January artesian flows were apportioned to February, March, and April based on typical proportions of temperatures greater than 0 °C in each month.

Werner Arroyo inflows were estimated based on irrigation diversion records (1951-2002, CDSS 2005), and on flow in Saguache Creek (1912-2002, US Geological Survey 2005), which supplies water to Werner Arroyo. All reported diversions from Werner Arroyo were summed by month, and it was assumed that this volume of water would have reached ML if it had not been diverted. To estimate Werner Arroyo monthly flows for the period prior to diversions, I paired monthly flows in Werner Arroyo with those in Saguache Creek. Using even-year data, monthly Werner Arroyo flows were modeled as a function of monthly Saguache Creek flows. The model was validated using odd-year data (for modeled vs. actual flows $r^2=0.85$, $p < 0.001$). This method was used to extend monthly Werner Arroyo flow estimates back to 1915.

Inflows from precipitation were estimated using monthly mean values from 1983 through 2002 from the National Weather Service Cooperating Site in Center, CO. Total inflows due to precipitation were calculated as monthly precipitation multiplied by total actual wetland area.

Outflows

Evapotranspiration losses were modeled by using measured evapotranspiration to calibrate potential evapotranspiration (ET_p). ET_p can provide reasonable estimates of ET_a. However, actual wetland sites differ from assumed theoretical conditions, so ET_p often provides better estimates if it is calibrated to a particular site (Jacobs et al. 2002, Rosenberry et al. 2004). ET_p was calculated using the Jensen-Haise method (McGuinness and Bordne 1972) as:

$$ET_p = (0.014*T-0.37)*K{\downarrow}*25.4 \qquad (1)$$

where:

ET_p = daily potential evapotranspiration (mm)

T = temperature (°F)

$K{\downarrow}$=incoming solar radiation (langleys)

Mean monthly T and $K{\downarrow}$ were obtained for 1994-2002 from the CoAgMet weather station in Center, Colorado (Colorado Climate Center 2005). When compared to measured ET_a, ET_p consistently underestimated ET_a. A better fit was achieved through a linear calibration (Rosenberry et al. 2004), where $ET_a = 0.902^* ET_p + 0.660$ ($r^2 = 0.90$, $p < 0.01$).

Seepage from the basin was set at a constant 3.8 mm d^{-1} as calculated by Kappen (2004) using isotopic methods, except for December through February when seepage was set to 0 mm d^{-1}. This rate is consistent with basin floor seepage rate estimates of 3.2-5.3 mm/d by Wood et al. (1997) in semi-arid southern high plains playas.

Model Validation

The accuracy of the simulation was assessed by comparing model output to observations from water years 1999 and 2000 and to historical aerial photos. For the 1999-2000 period, modeled stream inflows were adjusted to observed values. For comparisons with aerial photos, surface water depth was estimated using known basin topography and patterns of surface water observed in photos from November 1941, September 1955, July 1966, and June 1993.

The model was tested for its sensitivity to the magnitude of inflow in Werner Arroyo, magnitude of inflow in Russell Creek, and seepage. Werner Arroyo inflow and Russell Creek inflow were varied +/-20% (Fennema 1994). Seepage was varied to 3.2 and 5.3 mm/d, the minimum and maximum estimated by Wood et al. (1997). Also, adjustments to all three parameters were made simultaneously. Mean monthly depth and variation from all eight sensitivity runs were compared to the "baseline" simulation, i.e., the model run without varied parameters, using mean difference of the sensitivity run from observed and simulated.

RESULTS

Observed hydrologic conditions

Inflows and outflows and surface water depths

Artesian flows via Russell Creek contributed approximately 2.6 x 10^6 m^3 and 3.1 x 10^6 m^3 of water to ML in 1999 and 2000, respectively, which represented approximately 80% and 93% of inputs to the wetlands in 1999 and 2000, respectively (the remaining inputs were precipitation). Russell Creek flow at the inlet to ML began as early as November and as late as March, peaked in April or May, and abruptly ceased at the beginning of the growing season (late May or early June). After the cessation of flow, the creek did not respond to rain events up to 15.2 mm. The timing of peak flow occurred 1-4 months before peak flow in the Saguache Creek, the source of Werner Arroyo, the snowmelt-supplied source of inflow to ML (Figure 3.4a). Werner Arroyo did not flow during the years of this study.

Surface water was not present at the deepest point in the wetland complex for at least one month during all years of this study (Figure 3.4b). The pattern of flooding was governed by Russell Creek flow and evapotranspiration. Water depth peaked in April or May, around the time of peak flow in Russell Creek. After the cessation of inflow, water depth declined from 0.65 to 0.00 m over the following three months.

Outflow from the ML complex occurred only in 1999 and 2001 during one or two months of spring; from 2002 through 2005, there was not sufficient water to fill the basins completely, and no outflow occurred. In the years outflow occurred, it accounted for approximately 20-31% of the total water loss from ML.

Russell Creek inflows to ML were apparently altered by water withdrawal from the confined aquifer. Changes to the confined aquifer were evident beginning in 2002, which was a year of severe drought, and the first of three consecutive drought years. Between 1998 and 2003, increased withdrawals for irrigation and diminished recharge reduced hydraulic head ~4.4 m in the confined aquifer that supports Russell Springs (Figure 3.5). The decline in hydraulic head corresponded to reduced artesian flow to Russell Creek, less inflow into ML, and lower surface water depths (Figure 3.5).

Surface water - ground water interactions

There is limited surface water – ground water interaction at ML. A low permeability (vertical hydraulic conductivities ~3.6×10^{-10} m/s) clay stratum of at least 12 cm underlying the wetland basins restricts movement of surface water to the shallow, unconfined aquifer (Kappen 2004). The piezometric surface 1.5 m beneath the bottom of the basin was as much as 0.75 m lower than the surface water level, and this large downward gradient persisted while the basins remained flooded. Neither ion concentrations nor isotopic data between April 23 and May 20, 2003 indicated ground water recharge by surface water (Kappen 2004). Water did, however, move through macropores in the dried clays of the basin bottoms as the basins initially flooded (prior to April 23), causing mixing of surface and ground water, and creating a ground water mound beneath the basins that persisted while surface water was present (Kappen 2004); this mound dissipated during the several weeks following the disappearance of surface water. Most of the water that contributed to the ground water mound apparently returned to the surface as evapotranspiration, resulting in little net ground water recharge (Kappen 2004).

Evapotranspiration and precipitation

During the years of this study, ET was the greatest component of water loss from the wetland complex. In 1999 and 2000, ET accounted for 82% and 69%, respectively, of the annual water budget. The highest measured daily ET rate was 9.1 mm/d in mid-June. Monthly ET rates are highest in June and July when water availability, insolation, and temperatures were highest (Figure 3.6). Throughout the year, ET was several times higher than precipitation, with the possible exception of the winter months, when both were low (Figure 3.6).

Simulated versus observed hydrologic conditions

Within-year surface water patterns

A comparison of observed (altered) conditions to simulated (unaltered) conditions for 1998-2002 indicates that under a natural hydrologic regime ML had higher mean (Figure 3.7) and median (Table 3.3) monthly surface water depths and greater variability of these depths. Observed monthly median water depths were 16% (Apr; $p = 0.09$) to 100% (Sep, Oct, Nov; $p = 0.09$, 0.01, and 0.02, respectively) lower than simulated medians. Median monthly absolute differences from the monthly mean depth (average variability) were 129% greater than simulated in May ($p = 0.17$), and 100% less than simulated in September ($p < 0.01$) and October ($p = 0.05$). Significant differences ($p < 0.05$) between observed and simulated were found for water depth and/or variability for June through

December, when median observed monthly depths were 0.00-0.11 m, versus 0.49-0.74 m for simulated conditions. The range of average variability during these months was 0.00-0.15 m (observed) and 0.14-0.32 m (simulated). The full range of observed depths during this period was 0.00-0.19 m (observed) and 0.00-0.85 m (simulated). During August and September, when wetland foraging habitat is critical to many migrating shorebirds, surface water was observed in only one month of one year, with a depth of 0.04 m. Under simulated conditions, surface water was present during August and September in 3 of 5 years, with a median depth of 0.60 m.

Simulated conditions for 1998-2002 also indicated greater duration of surface water during the growing season and throughout the year when compared with observed conditions (Table 3.3), although these differences were not significant ($p > 0.05$), perhaps due to small sample size ($n = 5$). From May through September (the growing season), the median duration for which simulated wetlands contained surface water was 5.0 months versus 3.0 months for observed conditions. A similar pattern occurred on an annual basis: simulated wetlands contained surface water for an average of 9.5 months per year versus 7.0 months under observed conditions.

Simulated conditions for 1915-2002 (Table 3.4) were generally similar to simulated conditions for 1998-2002 (Table 3.3), but 1998-2002 experience greater water depths but shorter periods of inundation. Simulated median monthly water depths from 1998-2002 averaged 6% greater than for 1915-2002, but were as much as 32% greater (November). The simulation of 1915-2002, when compared to the simulation of 1998-2002, indicates longer duration of surface water being present each year (10.4 vs. 9.5 months) and May-

September (4.6 vs. 3.8 months), and longer periods with surface water depth > 70% capacity (3.8 vs. 2.4 months).

Between-year variability

Observed and simulated surface water patterns also differed between years, with simulated conditions having relatively more years where wetland capacity is achieved, fewer years when surface water dries completely, and more years with surface water present in August and September (Table 3.3). During 1998-2002, as observed, surface water reached 70% of capacity in 4 of 5 years versus 5 of 5 years under simulated conditions. The annual minimum depth observed was 0 m in 5 of 5 years, versus 3 of 5 years as simulated, and no surface water was present in August and September in 5 of 5 years (observed) versus 3 of 5 years (simulated). For the 1915-2002 simulation, these indices were similar to the 1998-2002 simulation (Table 3.4): surface water reached 70% of capacity in 87% of the years, annual minimum depth was greater than 0 m in 55% of years, and the wetlands contained surface water in August and September in 67% of years.

Simulated conditions also provided insights into dynamics that occur on a longer time scale, although no comparison with observations was possible. The simulation indicates that ML contained surface water continuously for 16 years and 9 months (1915-1931), suggesting possible long periods of perennial function. In contrast, the simulated wetlands also remained dry for as long as 6 months in several years. The longest period of ephemeral function (at least one month of each year was dry) under simulated conditions was 7 years.

Inflows

The large differences in observed and simulated surface water dynamics resulted from differences between altered (observed) and simulated unaltered (natural) stream inflows. For 1998-2002, the maximum annual total stream inflows observed was 3.2 x 10^6 m^3 versus 8.4 x 10^6 m^3 under simulated conditions (163% greater). In 2005, there was no observed inflow to the wetlands; in contrast, for 87 years of simulated natural conditions, the minimum inflow was 3.2 x 10^6 m^3, roughly equal to the relatively wet conditions observed during water years 1999 and 2000 (Figure 3.8).

Werner Arroyo, the snowmelt stream, was the largest contributor to the differences between observed and simulated inflows. Under simulated conditions, Werner Arroyo contributed on average 60% of the inflows to ML.

Model performance

Simulated water depths coresponded closely to observed basin depths when Werner Arroyo and Russell Creek inflows were set to observed values (Figure 3.9). For 1999 and 2000, under simulated and observed conditions surface water was present beginning in late fall or early winter, maximum depth was reached in spring, and surface water depth was back to 0 m by late summer. The simulated maximum depth was greater and occurred earlier than under observed conditions. This difference may have occurred because of inflow over-estimates in the model resulting from a Russell Creek stage-discharge relation that was not calibrated at the highest recorded stage. Also, the duration of surface water under simulated conditions was less than observed, possibly because of modeled mid- to late-summer seepage rates that were greater than actually occurred.

Simulated surface water conditions also corresponded to conditions recorded in aerial photos. For 1941, 1955, and 1966, simulated depths are within 0.1 m of estimated actual depths (Table 3.5). For 1993, the simulated depth is 0.39 m greater than the estimated actual depth.

Results of the sensitivity analysis suggest that conclusions regarding simulated versus observed conditions are robust. Specifically, for seven of eight sensitivity runs where important model parameters were increased or decreased, simulated mean water depth and average variability were much greater than observed. For June through December (when significant differences were found between simulated and observed), mean water depth was 194-692% of observed. Simulated average variability was 179-266% of observed. Only one sensitivity simulation (creek inflows reduced 20% and seepage increased 39%, simultaneously) yielded a mean depth and average variability near observed values (no difference in the mean and 67% greater variability).

DISCUSSION

Current altered hydrologic regime

The current hydrologic regime at ML is affected by off-site water use on multiple spatial and temporal scales. The high likelihood that there are multiple factors affecting surface waters at ML follows directly from the interconnected character of all components of the hydrologic system (Winter et al. 1998). The most proximate and immediate alteration arises from diversions of water out of the two streams that historically conveyed water to this wetland complex; there are at least 25 potential diversion points along Russell Creek and at least 30 along Werner Arroyo (CDSS 2005). These diversions alter both quantity and timing of inflows to ML. Even during years of highest total inflow, artesian-supplied Russell Creek declined suddenly at the beginning of the agricultural growing season (late May or early June) and flow did not resume until November 1 or later, after the growing season had ended. The greatest alteration of inflows has been in snowmelt-supplied Werner Arroyo, which no longer reaches ML. Simulated flows indicate that on average only one-third of historical inflows (both streams combined) now reach this wetland complex. Inflows currently peak in late March or early April. In contrast, snowmelt streams typically have peak flows around June 1 (Poff 1996) and continue to flow, although with lower water levels, through the summer. As modeled, Werner Arroyo peaked later and flowed during more months of the year when compared to observed conditions. Wheeler (1877) appears to corroborate the simulated character of Werner Arroyo by showing the stream as a solid line (i.e., perennial) connecting Saguache Creek to ML.

ML may be unusual for an intermountain playa because, on average, approximately 33% of its historical stream inflows—and 100% of its current stream inflows—originated as artesian flow. These artesian flows are likely the reason why ML contained water in most years despite the loss of its snowmelt inflows. Artesian sources flow throughout the winter when agricultural demand for water is minimal, potentially providing water to ML from late fall through early spring.

Dependence on artesian flow makes ML vulnerable to hydrologic alterations in the confined aquifer over hundreds of square-kilometers and cumulatively many years.

Because of it low storativity (0.008, no units), the confined aquifer can experience large and widespread hydraulic changes when water is withdrawn from the aquifer (Emery et al. 1973). When drought occurs, recharge to the aquifer decreases and ground water withdrawals for irrigation increase. As a result, there is a decline in the pressure head in the confined aquifer that supports artesian flows. Declining artesian flows during Colorado's recent severe drought (Colorado Water Conservation Board 2004) decreased flows in Russell Creek, and there was a steady year-to-year decline in depth and duration of flooding in ML from 2001-2004. In 2005, ML did not flood despite above average snowmelt runoff, indicating that changes in the confined aquifer can affect these wetlands even after the severity of the drought has lessened. Given the large size of the confined aquifer (3600 km^2 in extent and several km deep in some areas; Emery et al. 1973), many years of above-average precipitation will be required for artesian flows to rise to the levels seen at the beginning of this study.

ML may also be affected by water table declines in the unconfined aquifer resulting from shallow ground water withdrawals. Crouch (1985) showed a general decline in water table levels due to the combined agricultural use of unconfined aquifer water in the area. This decline is expected to increase due to continuous withdrawals as part of the Closed Basin Project (U.S. Bureau of Reclamation 1987), which is predicted to cause a permanent water table drawdown of up to 0.60 m on the eastern edge of the Mishak Lakes complex (Leonard and Watts 1989). Although the low-permeability clay underlying ML (Kappen 2004) would likely prevent significant increases in seepage from wetland basins, a lower water table may increase seepage from streams that transport water tens of kilometers across the valley floor (Wurster et al. 2003).

Simulated unaltered (natural) hydrologic regime

Simulation of surface water patterns at Mishak Lakes indicated that an unaltered hydrologic regime would differ substantially from the current hydrologic regime at this intermountain playa complex, as is the case in many hydrologic systems of western U.S. (Hauer and Lorang 2004, Rood et al. 2005). Under historical conditions, it is likely that mean water depths were greater, periods of flooding were longer, and the range and the variability of water depths were greater than under the current hydrologic regime. Model results also indicated that water depths from July through November were relatively unpredictable in comparison with current conditions. For example, water was predictably absent by the end of the growing season of every year during this study, whereas under simulated conditions water was present in August and September in most years. However, simulated wetlands were also dry at this time on average 1 of every 3 years. This type of dynamic and unpredictable variation may be essential to maintain (Haukos and Smith 2003) or restore (Scoppettone et al. 2005) biodiversity.

Conservation Implications

Although there are no long-term records documenting the historical biota of ML or other SLV wetlands under natural flow conditions, it is likely that alterations to hydrologic conditions have significant implications for native plants and animals. For example, hydrologic alterations can diminish reproductive success of amphibians (Semlitsch 2002) such as the locally-abundant *Pseudacris triseriata* and *Bufo* spp. Greater duration of surface water generally increases amphibian reproductive success

(Semlitsch 2000), but flooding that lasts more than 2 years can diminish success by allowing the accumulation of a diverse array of aquatic larval predators (Van Buskirk 1988; Werner and McPeek 1994, Adams 2000). Thus, generally long periods of flooding at ML suggested by the simulation (11.1 months per year) interspersed by periodic drying (on average 45% of years) may make it valuable amphibian habitat. This semi-permanent character of flooding at ML may promote species diversity (Kolozsvary and Swihart 1999). Under current conditions, however, ML often dries completely by mid-summer and periodically does not even flood, which likely diminishes amphibian populations (Semlitsch 2002). This type of change to habitat is likely common throughout the western U.S., where extensive ephemeral wetlands are no longer or only rarely inundated, while many small wetlands are permanently flooded (Blaustein and Kiesecker 2002).

The dominant emergent vegetation at ML, *Eleocharis palustris*, responds dynamically to surface water depths, as does vegetation in many wetlands that have high variability in patterns of flooding and drying (Poiani and Johnson 1993). Vegetation changes in turn can affect distribution of aquatic macroinvertebrates (Severn 1992), amphibian oviposition (Semlitsch 2002), and foraging patterns of shorebirds (Helmers 1992). Certain halophilic species, including the rare plant *Cleome multicaulis* (Spackman et al. 1997), may experience more sustainable populations under a variable hydrologic regime. Soils that are too consistently wet will promote the growth of tall vegetation that may outcompete *C. multicaulis*, yet soils that are too dry may interfere with plant growth and seed bank maintenance (Riley 2001).

Water-dependent species and communities are often adapted to particular hydrologic regimes (Baron et al. 2002, Lytle and Poff 2004). Impacts to the hydrologic regime in basins of ML may result from alterations to streams many kilometers from the wetlands and withdrawals in the confined aquifer at distances of tens of kilometers. Demands on water in intermountain valleys of the western U.S. are still present and growing (see 1986 and 1996 in Table 3.1). These demands can have large effects on wetland ecosystems. Effective conservation of wetland-dependent species in this context must consider the potential effects on all water sources (ground water discharge, streamflow, runoff, etc.) and sinks (ET, seepage, outflow, etc.) so that water can be managed appropriately for specific wetland types (Winter et al. 2001).

Models such as the one developed for this study can be useful tools for assessing both changes in water sources and sinks (Fennema et al. 1996) and the biological consequences of these changes. They can also be used to guide restoration of hydrologic regimes. I expect that results of this simulation will be used as one measure of conservation success at ML, and that the model will be used to develop quantitative goals for re-creation of potentially critical aspects of the natural hydrologic regime.

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Table 3.1. A brief history of water in the San Luis Valley (SLV). Where no source is indicated, information is from the U.S. Bureau of Reclamation (2005).

Year	**Historical occurrence**
Pre-European settlement	"numerous streams . . . maintained shallow lakes and wetlands over much of this area" and "marshes and ponds supported a diverse and relatively easily harvested group of . . . fish, edible insects, waterfowl" (Button 1982)
1848	John C. Frémont enters the valley in search of a rail route through the Rockies (Richmond 1990). Expedition member Ben Kern describes an area near Mishak Lakes as a "low place of long grass weeds & cattails" (Simmons 1990).
1851	In 1851, New Mexican settlers founded the first town in Colorado, San Luis. By 1852, first irrigation systems developed.
1853	John Gunnison searches for rail route. While in the SLV, adjusts route, having been warned of extensive marshes. Lieutenant Beckwith describes extensive marshes east of Mishak Lakes (Simmons 1990).
1877	Wheeler creates a map of the SLV (Wheeler 1877).
1879	145,000 sheep and 35,000 head of cattle in the valley.
1884	The Rio Grande canal completed, moving ~30,000 ac-ft of water each year from the Rio Grande to the northern part of the SLV.
1887	Artesian aquifer in the SLV discovered. By 1891, an estimated 2,000 flowing wells tapping the aquifer (Carpenter 1891), increasing to 3000 by 1910 (Siebenthal 1910) and 7000 by 1958 (Powell 1958).
1938	Rio Grande compact of 1938 is signed, establishing regulations concerning the quantity and quality of water leaving Colorado.
1970s	Inexpensive center-pivot irrigation allows large-capacity wells (>1600 $m^3 d^{-1}$) in the SLV's unconfined aquifer to increase from 2,800 in 1967 to 3,800 in 1979; water tables in some areas dropped substantially (Crouch 1985).
1986	As part of an interstate agreement, Colorado begins pumping shallow ground water out of northern part of the SLV and delivers it to the Rio Grande river; planned $1.23 x 10^8 m^3 yr^{-1}$; actually averaging ~$2.96 x 10^7 m^3 yr^{-1}$.
1986	American Water Development Inc. files for the right to pump and sell $2.46 x 10^8 m^3 yr^{-1}$ of ground water for export from the SLV. The plan is later defeated in court.
1996	Stockman's Water Company announces plans to pursue the right to pump $1.85 x 10^8 m^3 yr^{-1}$ of ground water from the SLV to the Denver area
2002	Driest year on record for the SLV.

Table 3.2. Summary of indices used to characterize surface water patterns at Mishak Lakes. "Depth" refers to surface water depth at the deepest point in the wetland complex.

Hydrologic regime characteristics	**Indices**
Magnitude	1) Mean monthly depth
	2) Mean annual maximum depth
	3) Mean annual minimum depth
	4) Mean depth in Aug and Sep
Duration	5) Mean number of months per year with surface water
	6) Mean number of months per growing season (May-Sep) with surface water
	7) Mean number of months per year with depth > 70% of capacity*
Timing	8) Month annual maximum depth is reached
	9) Month annual minimum depth is reached
Frequency	10) % of years that depth of flooding reaches 70% of capacity
	11) % of years when annual minimum depth > 0 m (i.e., wetlands do not dry completely)
	12) % of years with surface water present in Aug and Sep
Rate of change	13) Change in flooding depth per month (m) between maximum and minimum depth

* 70% of capacity (surface water depth = 0.60 m) is the approximate level at which outflow from the wetland begins, and the level at which the dominant emergent vegetation is eliminated.

Table 3.3. Comparison of indices for observed and simulated conditions, 1998-2002. "Average variability" is the mean absolute difference from group mean. For comparison of medians, a Wilcoxon 1-way non-parametric comparison was performed. For average variability, a Levene's test was performed on the absolute deviations from group means. Indices are described in Table 3.2. n = 5. "Mag." is the magnitude of the difference; 'insuff.' indicates that insufficient data were available to calculate p-value.

	Observed		**Simulated**		**Deviations of obs. from sim.**	
	Median	Average variability	Median	Average variability	Median Mag./% (p-value)	Average Variability Mag./% (p-value)
Magnitude (m)						
1) Depth						
Oct	0.00	0.00	0.55	0.15	-0.55 / -100 (0.02)	-0.15 / -100 (<0.05)
Nov	0.05	0.07	0.49	0.16	-0.45 / -90 (0.02)	-0.09 / -57 (0.14)
Dec	0.15	0.15	0.50	0.15	-0.35 / -70 (0.02)	<0.01 / 3 (0.92)
Jan	0.27	0.15	0.51	0.15	-0.24 / -47 (0.07)	0.01 / 5 (0.92)
Feb	0.40	0.09	0.66	0.11	-0.27 / -40 (0.10)	-0.02 / -15 (insuff.)
Mar	0.52	0.04	0.65	0.11	-0.13 / -21 (0.19)	-0. 06 / -59 (insuff.)
Apr	0.64	0.08	0.76	0.06	-0.12 / -16 (0.09)	0.02 / 30 (0.59)
May	0.62	0.19	0.86	0.08	-0.24 / -28 (0.15)	0.11 / 129 (0.17)
Jun	0.35	0.15	0.80	0.14	-0.45 / -56 (0.03)	0.01 / 5 (0.92)
Jul	0.11	0.07	0.74	0.27	-0.64 / -86 (0.10)	-0.20 / -75 (<0.05)
Aug	0.00	0.01	0.65	0.35	-0.65 / -100 (0.09)	-0.34 / -96 (<0.01)
Sep	0.00	0.00	0.56	0.32	-0.56 / -100 (0.01)	-0.32 / -100 (<0.01)

2) Mean annual max	0.64	0.12	0.86	0.02	-0.22 / -25 (0.20)	0.09 / 461 (0.02)
3) Mean annual min	0.00	0.00	0.21	0.19	-0.21 / -100 (0.05)	-0.19 / -100 (<0.01)
4) Mean Aug-Sep depth	0.00	0.01	0.60	0.33	-0.60 / -100 (0.02)	-0.33 / -98 (<0.01)
Duration (number of months)						
5) Months per yr with surface water	7.0	2.9	9.5	2.7	-2.5 / -26 (0.23)	0.15 / 6 (0.21)
6) Months with surface water May-Sep	3.0	0.9	5.0	1.4	-2.0 / -40 (0.21)	-0.56 / -39 (0.23)
7) Months per yr > 70% capacity	2.0	0.7	2.0	1.3	0.0 / 0 (0.40)	-0.56 / -44 (0.32)
Timing (Jan = 1, Dec = 12)						
8) Month annual max depth is reached	4.0	0.5	5.0	0.6	-1.0 / -20 (0.24)	-0.16 / -25 (0.45)
9) Month annual min depth is reached	8.0	0.9	9.0	1.4	-1.0 / -11 (0.25)	-0.56 / -39 (0.23)
Frequency (%)						
10) % of yrs where max depth > 70% capacity	80	n.a.	100	n.a.	-0.20 / -20 (n.a.)	n.a.
11) % of yrs where min depth > 0 (never dry)	0	n.a.	60	n.a.	-0.60 / -100 (n.a.)	n.a.
12) % of yrs with surface water in Aug & Sep	0	n.a.	60	n.a.	-0.60 / -100 (n.a.)	n.a.
Rate of change (m month^{-1})						
13) From annual max to min depth	0.21	0.04	0.09	0.08	0.13 / 146 (0.10)	-0.05 / -56 (0.12)

Table 3.4. Values for hydrologic indices based on simulation of 1915-2002 (87 years). Indices are described in Table 3.2. n.a. = not applicable.

	Mean	Median	Avg. variability
Magnitude (m)			
1) Depth			
Oct	0.44	0.54	0.31
Nov	0.41	0.48	0.30
Dec	0.47	0.49	0.24
Jan	0.48	0.49	0.23
Feb	0.67	0.65	0.16
Mar	0.66	0.64	0.15
Apr	0.75	0.83	0.12
May	0.75	0.86	0.13
Jun	0.70	0.86	0.20
Jul	0.61	0.76	0.26
Aug	0.53	0.65	0.29
Sep	0.46	0.60	0.32
2) Mean annual max depth	0.80	0.86	0.09
3) Mean annual min depth	0.29	0.00	0.29
4) Mean Aug-Sep depth	0.49	0.62	0.31
Duration			
5) Months per yr with surface water	10.4	11.0	1.6
6) Months with surface water May-Sep	4.6	5.0	0.6
7) Months per yr > 70% capacity*	6.7	6.0	3.9
Timing (Jan = 1, Dec = 12)			
8) Month annual max depth is reached	3.8	4.0	1.1
9) Month annual min depth is reached	9.7	11.0	1.7
Frequency			
10) % of yrs where max depth > 70% capacity	87	n.a.	n.a.
11) % of yrs where min depth > 0 (never dry)	55	n.a.	n.a.
12) % yrs with surface water in Aug & Sep	67	n.a.	n.a.
Rate of change (m month^{-1})			
13) From annual max depth to min depth	0.10	0.05	0.08

Table 3.5. Comparison of actual historical water depths estimated from aerial photographs and simulated water depths.

Date	Actual depth (m)	Simulated depth (m)	Difference (m)
Nov 1941	0.78	0.72	+0.06
Sep 1955	0.02	0.00	+0.02
Jul 1966	0.62	0.54	+0.08
Jun 1993	0.47	0.86	-0.39

Table 3.6. Mean monthly water level and average variability for observed (Obs.), baseline simulation (Sim.), and eight sensitivity analysis simulations. Included in comparison are those months for which a significant difference was detected between baseline simulation and observed for central tendency and dispersion (June through December). "WA" = Werner Arroyo. "RC" = Russell Creek. "+20%" and "-20%" indicate a 20% increase and decrease to flow in WA and RC. 'Seep' = Seepage rate in mm/d. 'Average variability' is the mean absolute difference from the mean monthly depth. Values are in meters.

	Obs.	Sim.	WA+20%	WA-20%	RA+20%	RA-20%	Seep=3.2	Seep=5.3	WA+20% RA+20% Seep=3.2	WA-20% RA-20% Seep=5.3
Mean depth	0.09	0.54	0.61	0.30	0.58	0.37	0.60	0.26	0.65	0.09
Average variability	0.06	0.22	0.23	0.18	0.23	0.23	0.22	0.18	0.22	0.10

Figure 3.1. The watershed of the San Luis Valley and the location of Mishak Lakes. Solid lines within the valley are major roads.

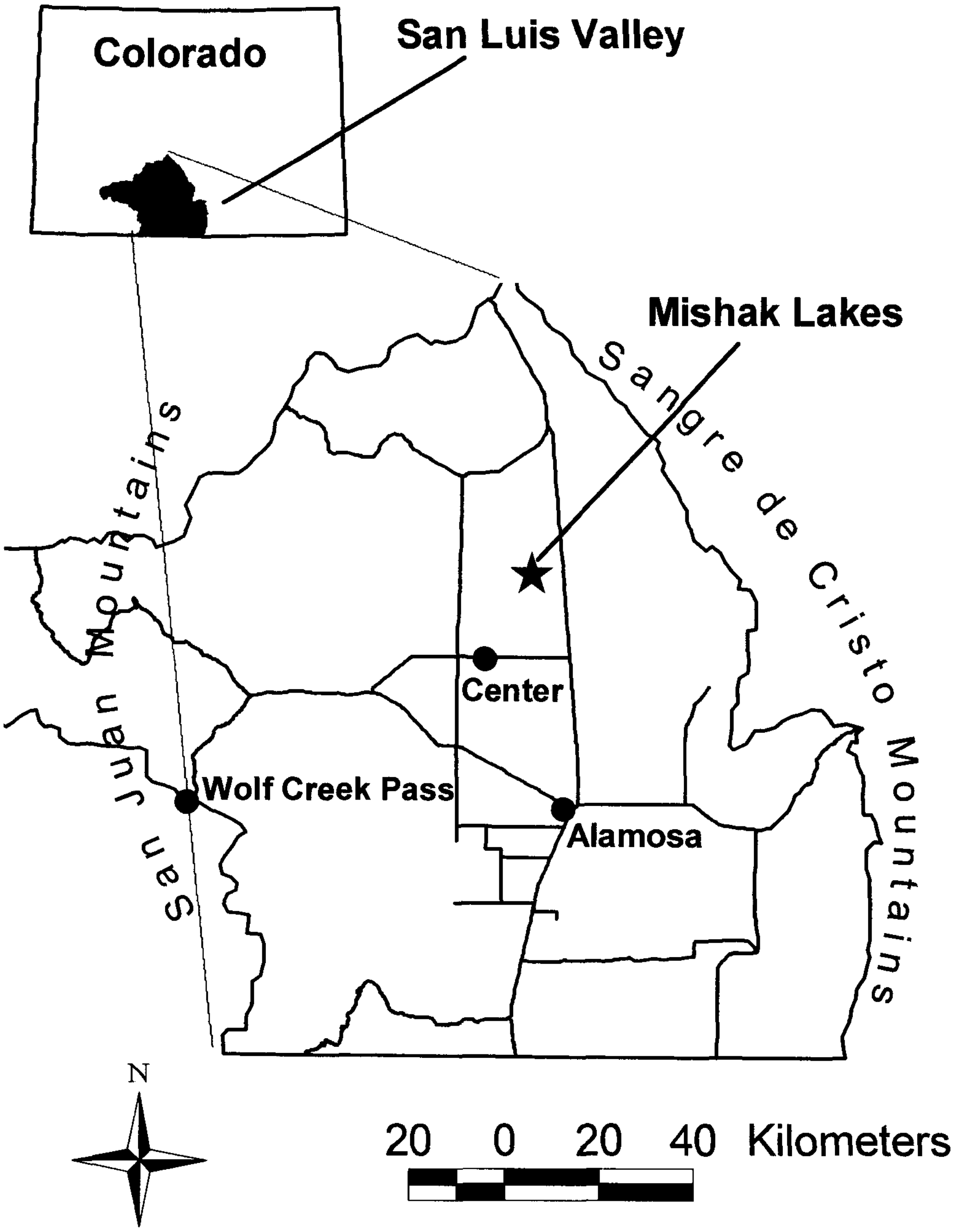


Figure 3.2. The Mishak Lakes complex, with sampling locations indicated. Gray indicates wetlands.

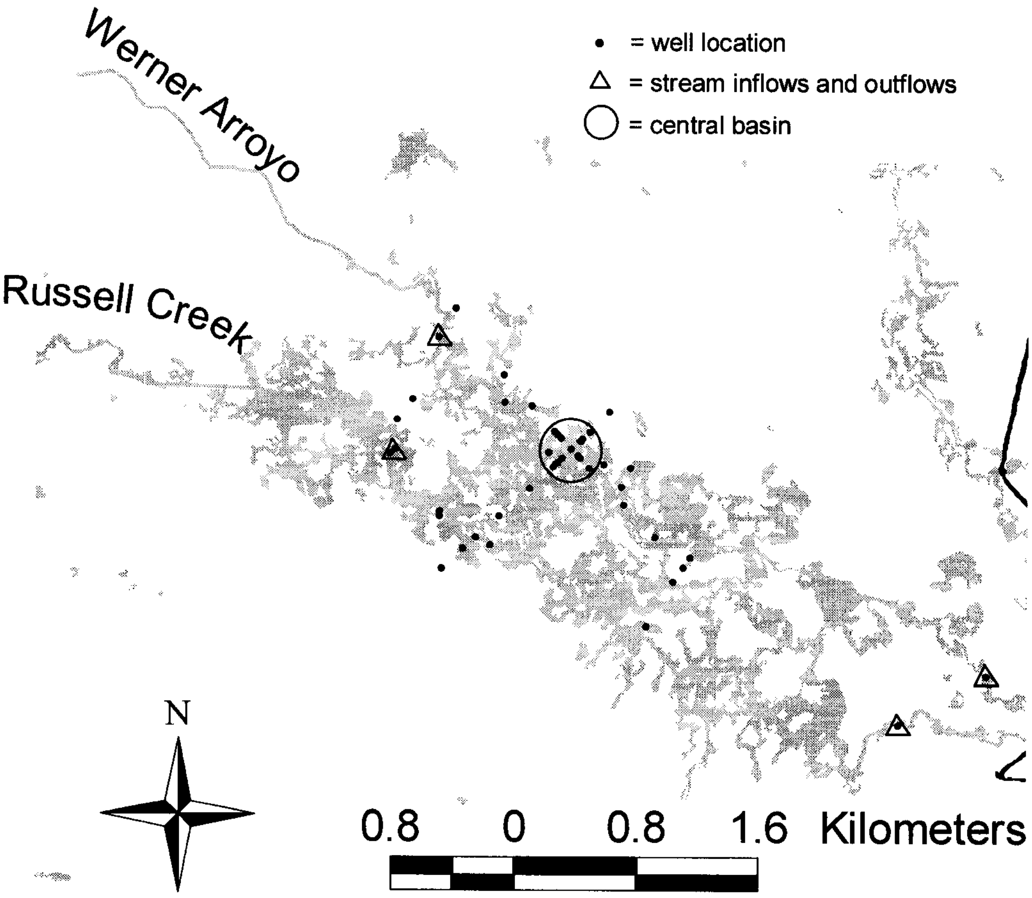
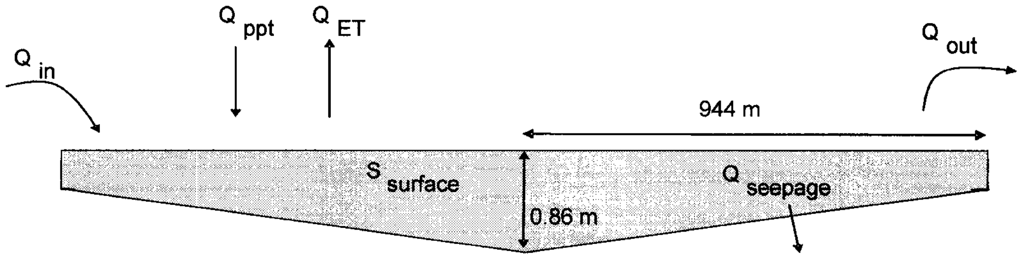


Figure 3.3. (a) Model basin and flow components.



Total wetland area = 283 ha
Maximum volume = 1.53 x 10^6 m^3

Not to scale.

Key:
Q_{in} = artesian- and snowmelt-supplied inflows
Q_{ppt} = precipitation on wetland
Q_{ET} = evapotranspiration
$Q_{seepage}$ = seepage losses
Q_{out} = surface water outflows
$S_{surface}$ = surface water storage

(b) Flow diagram of surface water calculations in simulation model.

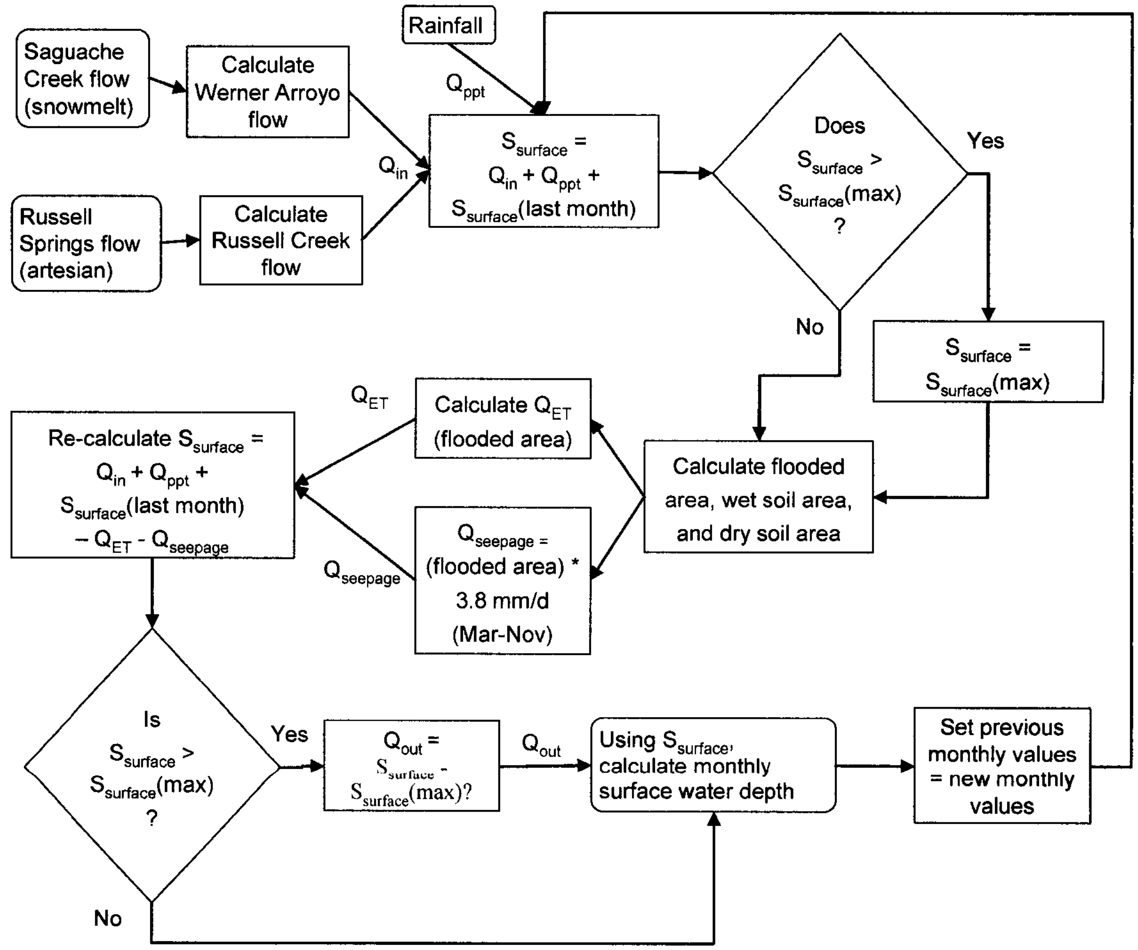


Figure 3.4. (a) Monthly inflow from artesian-supplied Russell Creek, and discharge from snowmelt-supplied Saguache Creek, the source of Werner Arroyo (which formerly flowed into Mishak Lakes). (b) Surface water levels at the deepest point in the Mishak Lakes wetland complex. Data for (a) and (b) are from water year 1999.

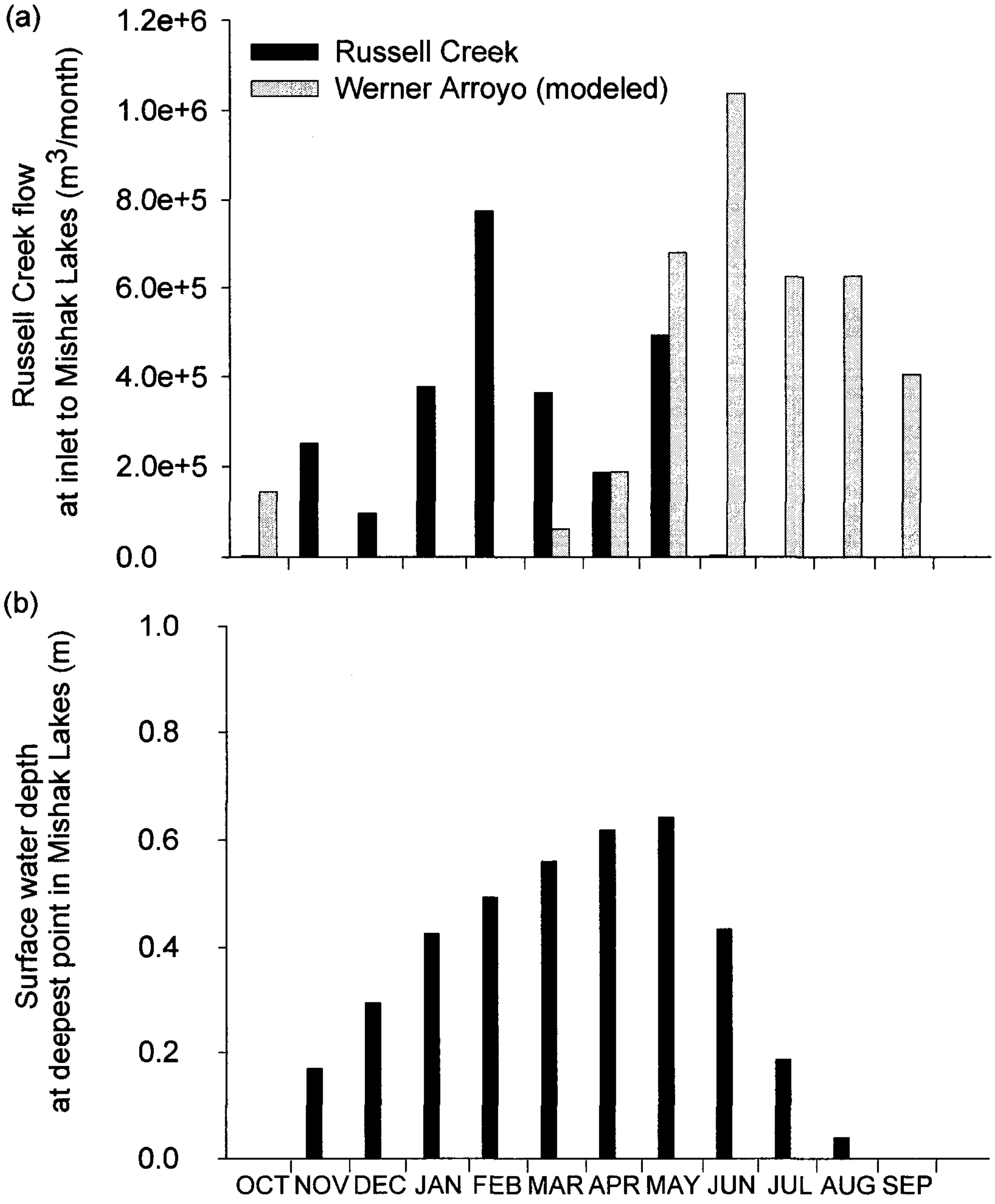


Figure 3.5. (a) Maximum observed water depth at Mishak Lakes, and (b) hydraulic head in four confined aquifer wells near the source of Russell Creek. Positive values for hydraulic head indicate flowing wells. Key to well USGS well identifiers: A = 375310106050001, B = 375310106021501, C = 375918106063601, D = 375255106084401.

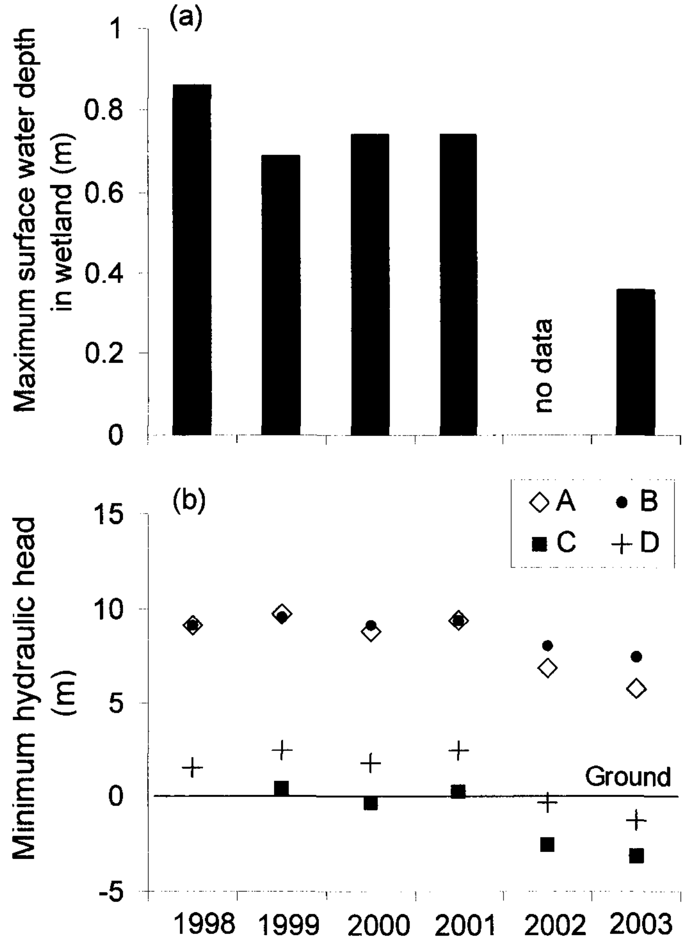


Figure 3.6. Monthly evapotranspiration and precipitation at Mishak Lakes. Evapotranspiration was estimated with the Jensen-Haise model calibrated to daily values measured during 1998-2001 (assumed negligible in Dec, Jan, and Feb). Precipitation is monthly means from 1973-2004 at Center, Colorado, located 15 km southwest of Mishak Lakes.

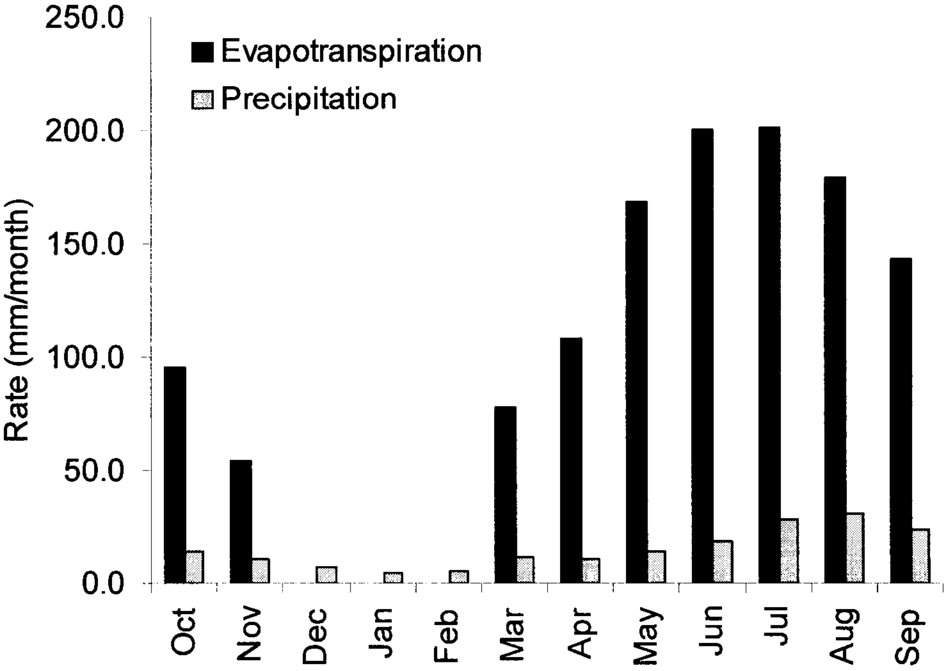


Figure 3.7. (a) Observed monthly water depths at Mishak Lakes for 1998-2002 under current, altered conditions, and (b) simulated monthly depths based on re-constructed, unaltered inflows. Points show mean water depth at the deepest location in the wetland across all years. Bars show range. n = 5 except for observed Oct-Dec n=4, Jan n=4, Feb-Mar n=2.

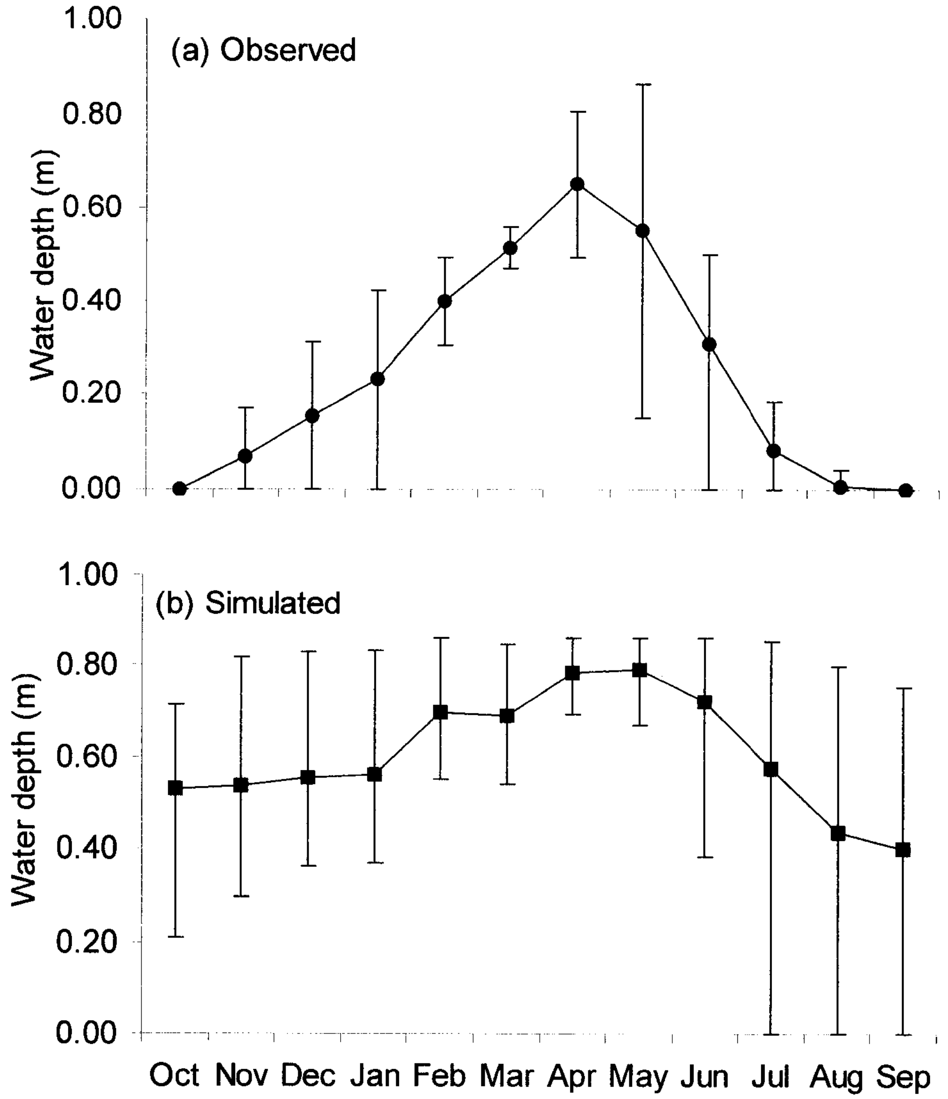


Figure 3.8. Simulated total annual inflows to Mishak Lakes. Line at 3.2 x 106 m3 is approximate 1999 and 2000 total observed inflow.

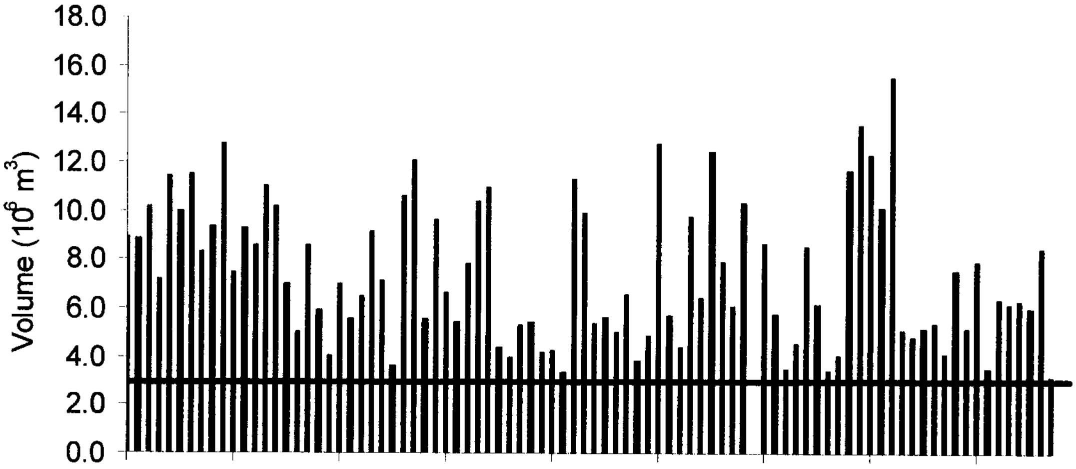
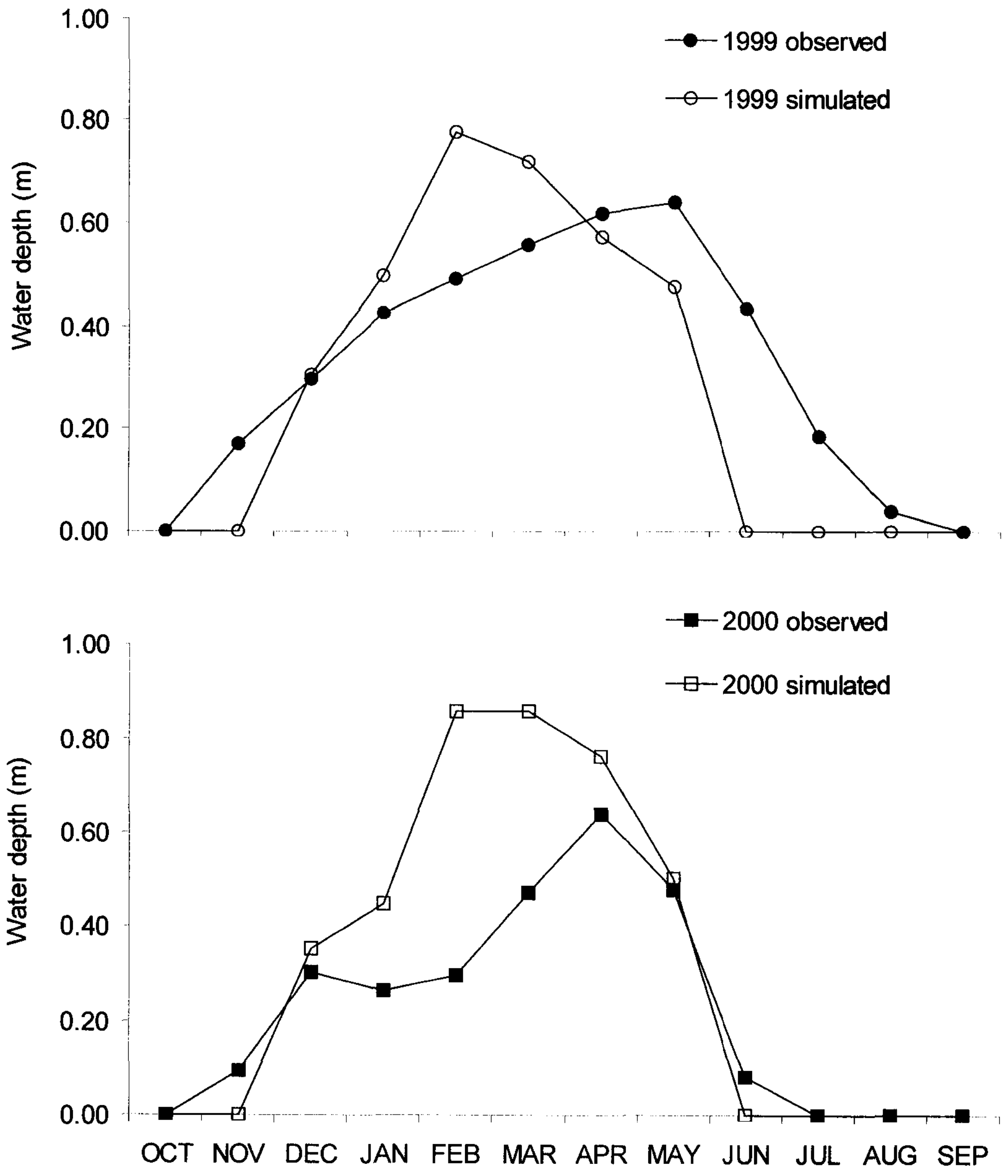


Figure 3.9. Observed and simulated water depths in Mishak Lakes for 1999 and 2000 given current altered inflows.



CHAPTER 4

OPPOSING ENVIRONMENTAL GRADIENTS, NOT COMPETITION, CONTROL VEGETATION ZONATION IN AN INTERMOUNTAIN PLAYA

ABSTRACT

Vegetation zonation was investigated at an intermountain playa wetland (Mishak Lakes) in the San Luis Valley (SLV) of southern Colorado. Plant composition and abiotic conditions were quantified in six vegetation zones, and in areas supporting *Cleome multicaulis*, a rare plant with its center of distribution in the SLV. Reciprocal transplants were performed to test the importance of abiotic versus biotic factors in governing zonation. Abiotic conditions differed significantly among several vegetation zones. Prolonged inundation led to anaerobic soils in the *Eleocharis palustris* and the submerged aquatics zones, on the low end of the site's 1.25 m elevation gradient. On the high end of the gradient, soil salinity and sodicity (a measure of exchangeable sodium) were high in the *Distichlis spicata* zone (electrical conductivity, EC = 5.3 dS/m, sodium absorption ratio, SAR = 44.0) and extreme in the *Sarcobatus vermiculatus* zone (EC = 21 dS/m, SAR = 274). Transplanted species produced maximum biomass in the zone where they originated, not in any other higher or lower vegetation zone. The greatest overall effect of transplantation occurred for *E. palustris*, which experienced a ≥ 77% decline in

productivity when transplanted to other zones. This study provides evidence that physical factors are a major determinant of vegetation zone composition and distribution across the entire elevation gradient at Mishak Lakes. Patterns at Mishak Lakes arise from counter-directional stress gradients: a gradient from anaerobic to well-oxygenated from basin bottom to upland and a gradient from extremely high salinity to low salinity in the opposing direction. Because abiotic conditions dominate vegetation zonation, restoration of the altered hydrologic regime of this wetland to a natural hydrologic regime may be sufficient to re-establish many of the historical biodiversity functions provided by these wetlands.

INTRODUCTION

Zonation of plant species is a conspicuous feature of many wetlands (Stewart and Kantrud 1971, Vince and Snow 1984, Mitch and Gosselink 2000). In coastal salt marshes, vegetation zones tend to occupy a characteristic vertical range in relation to sea level (Adam 1990, Davy and Costa 1992). Early researchers attributed this pattern to tidal influences such as salinity and anoxia (Vince and Snow 1984), based on correlations between plant distributions and soil properties (e.g., Gray and Bunce 1972). Cooper (1982) asserted that there was general agreement that edaphic rather than biotic factors are principal determinants of vegetation zonation. Implicit in this assertion is the assumption that the physical conditions associated with each zone represent the preferred or optimal habitat of the species that occupy that zone (Vince and Snow 1984).

The problems with such an assumption were famously demonstrated in the rocky intertidal zone in the 1960s (Connell 1961, Paine 1966), and since then have been addressed by several authors for vegetation zones in several wetland types (freshwater plant communities: Grace and Wetzel 1981, Wilson and Keddy 1985; mangroves: Rabinowitz 1978), including salt marshes (Snow and Vince 1984, Bertness and Ellison 1987). These studies led to the generally accepted idea that in less stressful habitats, better competitors dominate, and poorer competitors are displaced to more stressful habitats (Keddy 1989, Levine et al. 1998). In coastal salt marshes, several researchers have found evidence supporting this idea by demonstrating that salt marsh plants from stressful habitats generally grow as well or better in less stressful habitats (Snow and Vince 1984, Bertness and Ellison 1987, Bertness 1991a, b, Pennings and Callaway 1992, and others). These researchers have concluded that, in coastal salt marshes, biotic interactions tend to be most important in determining the upper, landward limit of plant distributions, and physiological tolerance of the effects of tidal submergence tend to determine lower limits of vegetation zones (Little and Kitching 1996, Raffaelli and Hawkins 1996, Bertness 1999, Castillo et al. 2000, Rand 2000).

Understanding factors determining species distributions may inform efforts to preserve and restore wetland ecosystems by allowing prediction of changes in plant composition and distribution (Crain et al. 2004). Throughout the intermountain west, important abiotic factors governing wetland ecosystems, especially hydroperiod, have been dramatically altered by damming of rivers and streams, surface water diversions, and ground water withdrawals, and have likely had ecological consequences (Poff et al. 1997). In intermountain playa wetlands, the relationship between abiotic factors and plant zonation has not been studied. If physical factors are primary determinants of vegetation zone composition and distribution, a passive approach to vegetation restoration following hydrologic restoration could suffice. On the other hand, if biotic factors, including competition (Ewanchuk and Bertness 2004), dispersal (Rabinowitz 1978), herbivory (Pigott 1969), or founder effects (Costa et al. 2003) have important consequences, more active efforts toward restoration may be warranted.

Intermountain playas, a type of wetland in the intermountain region of the western U.S., share several characteristics with coastal salt marshes. Both wetland types have distinctive vegetation zonation, species composition overlaps at both the generic level (e.g., *Juncus* spp.) and the species level (e.g., *Distichlis spicata*), and each contains habitats with extreme levels of salinity and anoxia.

The directions of the salinity and aerobic-anaerobic gradients differ markedly between intermountain playas and coastal salt marshes. In coastal salt marshes, where the primary water supply is the ocean, anaerobic conditions decrease significantly and salinity increases significantly moving from landward to seaward (Bertness and Ellison 1987). As such, the zones of greatest anoxia coincide with zones of highest salinity. In contrast, intermountain playas are fed primarily by fresh water that originates in nearby mountains. Thus, redox potential in inundated areas of playas can indicate anaerobic conditions while salinity remains low. At the same time, intermountain playas frequently occur in areas with shallow water tables, where capillary movement of ground water with high concentrations of dissolved minerals can transport salts to the soil surface from depths greater than 2 m (Chimner and Cooper 2003). High evapotranspiration leads to significant salt accumulation on the surface, often resulting in a white crust. As a result, well oxygenated soils even short distances from inundated playas can have extremely high salt concentrations. Because of the counter-directional stress gradients at Mishak

Lakes (a gradient from anaerobic to well-oxygenated from basin bottom to upland and a gradient from extremely high salinity to low salinity in the opposing direction), I hypothesized that tolerance of these stresses (sensu Grime 2001) would be the primary pattern-forming mechanism at this wetland complex.

The overall objective of this study was to quantify the vegetation distribution and composition and associated abiotic factors in the major vegetation zones at an intermountain playa complex in the San Luis Valley, Colorado, and to assess experimentally the role of abiotic versus biotic factors in governing the composition of these zones. The vegetation and abiotic factors were also quantified in areas that support *Cleome multicaulis*, a rare plant with the center of its global distribution in the San Luis Valley (Spackman et al. 1997), to better understand how habitat conditions my affect the conservation of this species.

Study Area

The San Luis Valley (SLV) is a high intermountain valley covering about 8400 km^2 of southern Colorado (Figure 4.1, Huntley 1979). The valley floor has little topographic relief, averaging 2350 m elevation. Mountains rising above 4000 m in the Sangre de Cristo Range to the east and the San Juan Range to the west dominate the weather. In the SLV, summers are warm (July mean = 17°C), winters are cold (January mean = -9°C), and insolation is high all year (Doesken and McKee 1989, Western Regional Climate Center 2005). Orographic effects result in high mountain precipitation and low valley-floor precipitation. Mean annual precipitation at Wolf Creek Pass (elevation 3290 m, Figure 4.1) is 1153 mm, whereas on the valley floor at Center, Colorado (elevation 2350 m, Figure 4.1) it is 177 mm (Western Regional Climate Center 2005). Despite the aridity on the valley floor, the SLV contains Colorado's highest concentration of wetlands (Walton-Day 1996), which result from the abundant snowfall in the mountains contributing copious spring runoff to the valley.

The field site was Mishak Lakes (ML), a preserve owned by The Nature Conservancy of Colorado. ML is a complex of uplands and shallow, interconnected basins that includes about 287 ha of wetlands and 842 ha of upland (37.925 N, 105.993 W, NAD83 datum; Figure 4.1). The site has little topographic relief. The deepest basins are approximately 1.25 m below adjacent uplands, and the valley floor drops less than 3 m over nearly 5 km from NW to SE.

A single stream, Russell Creek, which originates at a series of artesian wells and springs, currently supplies ≥ 80% of the water the floods ML (Sanderson this dissertation Chapter 3). Approximately 69-100% of the water lost from ML is through evapotranspiration (ET; Sanderson this dissertation Chapter 3). The only significant loss other than ET is surface water outflow, which does not occur in all years. There is no ground water discharge to the wetlands (Sanderson, this dissertation Chapter 3), and a laterally consistent low permeability (clay) layer occurs near the bottom of the deepest basins, inhibiting downward seepage (Kappen 2004). The upland areas surrounding the wetland basins are underlain by a shallow (<2 m) water table.

Six distinctive vegetation zones occur at ML (Table 4.1; Cooper and Severn 1992). From the highest to lowest topographic position, these are:

1) *Sarcobatus vermiculatus* (greasewood),
2) *Distichlis spicata* (saltgrass),

3) *Juncus balticus* (Baltic rush), often co-dominated by *Distichlis spicata*,
4) Annuals, dominated by the non-native a7nnual *Polygonum aviculare* (prostrate knotweed) and the native annual *Plagiobothrys scouleri* (Scouler's popcornflower),
5) *Eleocharis palustris* (common spikerush),
6) Submerged aquatics, dominated by *Zannichellia palustris* (horned pondweed) and *Potamogeton pectinatus* (sago pondweed).

Species names follow USDA (2005). Authorities for all species are shown in Tables 4.2.

METHODS

Vegetation zone composition and distribution

Vegetation zones were mapped across the entire wetland in 1996 using aerial photographs and on-the-ground surveys. A Geographic Information Systems (GIS) data layer was created and then used to calculate the area of each of the six zones. In the deepest basin in the wetland complex, several hundred ground locations were surveyed with a total station to create digital elevation model (DEM) with accuracy of ~0.05 m. Boundaries between vegetation zones were also surveyed, and relative elevations between vegetation zones were calculated.

To quantify species composition, three 3 x 5 m randomly-selected plots were establish in each of the six dominant vegetation zones, for a total of 18 plots among all zones. A 3.6 m^2 area in the middle of each plot was excluded to avoid trampled vegetation during measurement of abiotic factors, thus each plot contained 11.4 m^2. Plant species present and canopy coverage were determined using a point-intercept sampling methodology (Floyd and Anderson 1982) in July of 1998-2000. Plots in the topographically lowest locations were sampled again in 2001 because species cover had changed substantially since the beginning of the study. The presence of numerically rare species that were in the plot but not detected by the point-intercept method were also recorded (Snow and Vince 1984).

In addition to data collected in each vegetation zone, similar data were also collected in three plots that contained high densities of the rare plant *C. multicaulis* at the beginning of the study (1998). In these plots, the number of *C. multicaulis* stems per plot was counted in July during 1998-2004 (2003 not included).

To determine objectively the vegetation zone where *C. multicaulis* occurs, Jaccard's coefficient (Krebs 1999) was calculated to quantify species similarity between plots with *C. multicaulis* and plots within each vegetation zone. Jaccard's coefficient (J) was calculated as:

$$J = [A/(A + B + C)]*100 \qquad (1)$$

where A = the number of species found in *C. multicaulis* plots and vegetation zone plots being compared, B = the number of species in vegetation zone plots but not in *C. multicaulis* plots, and C = the number of species in *C. multicaulis* plots but not in vegetation zone plots. The multiplier 100 in (1) allows Jaccard's coefficient to be expressed as a percentage ranging from 0% for no similarity (i.e., no shared species) to 100% for complete similarity (i.e., every species occurs in both sets zones).

Environmental Factors

Water table location was measured in two observation wells installed in each plot. Wells were constructed with 3.2 cm (1.25 in) PVC, and they were installed with a hand-augur. One well was fully screened in the upper 0.6 m of soil (to record water table level in the root zone). The other well had a 0.5 m screen located 1-2 m below the ground surface. Bentonite was placed above the screen to restrict the flow of surface water down the pipe. The location of each well was surveyed to within 0.02 m. During 1998-2001 water levels were measured every two weeks between April 15 and October 15 (the growing season), and monthly outside this period. Water depth was measured through 2004 at the deepest point in the wetland and in plots containing *C. multicaulis*.

Redox potential (E_h) was measured at 0.15 m and 0.35 m soil depth in two plots of each vegetation zone following methods described in Faulkner *et al.* (1989). Probes were built by welding platinum directly to a single-strand copper wire, and the junction was sealed with shrink-tube and epoxy. Probes were installed in triplicate at each depth. Redox potential was measured every two weeks during the growing season in 1998-1999, and the three readings at each depth were averaged to yield a single value (D'Amore et al. 2004). Redox readings were adjusted by +244 mV to base the redox potential on the standard hydrogen reference electrode (Faulkner et al. 1989).

Soil texture, pH, electrical conductivity (EC), and sodium adsorption ratio (SAR) in the upper 0.10 m of each plot were analyzed. Two soil subsamples were taken at random locations in each vegetation plot and were mixed to yield one sample per plot. Soil particle size distribution was determined using the hydrometer method (Sheldrick and

Wang 1993). Soil pH, EC, and water-soluble salts were determined using aqueous extraction techniques (Janzen 1993). Sodium absorption ratio, a measure of relative sodium status, was calculated as $[Na^+]/[(Ca^{2+} + Mg^{2+})/2]^{0.5}$ (Janzen 1993)

Reciprocal transplants

Reciprocal transplants were implemented to assess the growth potential of dominant species in each of four vegetation zones (Bertness and Ellison 1987): *Eleocharis palustris*, the annuals, *Juncus balticus*, and *Distichlis spicata*. Transplants were done in all possible combinations among these four zones for a total of 16 separate experiments, each with its own control. *Sarcobatus vermiculatus* (a shrub with roots exceeding 10 m) and *Zannichellia palustris* (an aquatic species without roots) were not transplanted.

Following Bertness and Ellison (1987), twenty units (0.25 x 0.25 x 0.25 m) of substrate (plants and soil) were reciprocally transplanted in all combinations (Figure 4.2), with five replicates of four treatments. Treatments were:

(i) control—plot marked in origination zone, but no manipulation done.

(ii) *in situ* transplant—block lifted from ground, rotated 90°, and placed back in the same location (origination zone).

(iii) transplant without competition—block placed in destination zone. Above ground parts of all neighboring plants removed twice per month to minimize competition from plants in the destination zone.

(iv) transplant with competition—block placed in the destination zone, neighbors left in place.

Units were transplanted in July 1999, after surface water had sufficiently dropped. In August 2000, all above-ground vegetation was harvested in one 0.10 x 0.10 m patch in the middle of each experimental unit, dried to a constant mass at 105 °C, and weighed.

Statistical analysis

Results were compared using one-way ANOVA in SAS (SAS Institute 2003). The Scheffé test was used for multiple comparisons. For the comparison of environmental factors among communities, the level of α for calculating the test statistic was set at 0.10 because of the relatively small sample size (three replicates per zone). For the transplant experiment, where there were five replicates, α was set at 0.05.

RESULTS

Vegetation zones

The vegetation zones at ML are highly intermixed across an area of 1215 ha (Figure 4.3). At the time of mapping (1996), wetland vegetation occurred in an extensive upland zone dominated by the phreatophytic shrub *Sarcobatus vermiculatus*, which covered 839 ha (69.1% of the site, Table 4.1). *Eleocharis palustris* was the most extensive herbaceous zone, covering 113 ha (9.3% of the total area), followed by the *Juncus balticus* zone and the *Distichlis spicata* zone, both of which also covered more than 5% of the site. The submerged aquatic zone dominated by *Z. palustris* covered 42 ha (3.4% of the site). Areas dominated by the annuals *Polygonum aviculare* and *Plagiobothrys scouleri* were subsumed into other zones during the mapping process because they occurred in patches smaller than the minimum mapping unit. The area covered by the annual zone was estimated to be less than 1% of the study area.

Across the wetland, one vegetation zone yielded to another over relatively small elevation changes, illustrating the importance of small differences in water elevation relative to ground surface. Only 1.25 m of elevation separated the dry, saline *S. vermiculatus* zone from the *Z. palustris* submerged aquatic zone, and there were three additional zones between these two zones (Figure 4.4). The *Juncus balticus* and *D. spicata* zones shared a similar elevation range along the edges of wetland basins, from 0.70 to 1.15 m above the bottom of the deepest basins. The annuals zone occurred in a very narrow (< 0.10 m) elevation band between the *E. palustris* and *D. spicata* zones on slopes that are nearly flat. The lower edge of the *E. palustris* occurred only 0.20 m above the bottom of the basin.

Twenty-four species were recorded among all of the plots (Table 4.2), but most vegetation zones had low diversity, as measured by richness and evenness. The most species rich zone was the *J. balticus* zone, with 13 species. The *D. spicata* zone contained, on average, 10 species, but cover was uneven; only the dominant (*D. spicata*) occurred with > 2% average cover. Overall, 13 species (54%) occurred with ≤ 1% cover, and additional four species (17%) occurred with >1% but ≤ 5% cover. Four of the six vegetation zones contained only one species with > 5% cover.

The composition of the submerged aquatics zone changed over the course of this study. In 1998, plots in the submerged aquatic zone were dominated by *Z. palustris* and *Potamogeton pectinatus*, while the emergent species *E. palustris* occurred at <1% cover.

After two years of maximum water levels being 0.18 m lower than 1998 levels, *E. palustris* cover in these plots had increased to 16% (Table 4.3).

Cleome multicaulis plots

Plant species similarity between plots containing *C. multicaulis* and plots of vegetation zones ranged from 0 to 69% (Table 4.4). Plots containing *C. multicaulis* had high similarity to the *D. spicata* zone (69% similarity) and the *J. balticus* zone (61% similarity), whereas similarity between the *D. spicata* zone and the *J. balticus* zone was 44%. Similarity between *C. multicaulis* and all other zones was low (6% for the *S. vermiculatus* zone; 0% for the annuals zone, the *E. palustris* zone, and the submerged aquatics zone).

Numbers of *C. multicaulis* decreased after 1998, from many hundreds of stems per plot to its disappearance from all plots (Figure 4.5a). The majority of the decline occurred between 1998 and 1999, after a decrease in maximum water depth of 0.18 m (Figure 4.5b). In 2003 and 2004, inflows to ML were down substantially, as were maximum water levels, and few to no *C. multicaulis* were seen anywhere in the wetland complex. No data were collected in 2002.

Environmental factors

During 1998-2000, when most of the environmental data were collected, temporal patterns of water levels in the wetland were similar (Figure 4.6). Water levels rose abruptly following inflows to the wetland that began around November 1. Maximum water levels occurred in April or May, followed by a steep decline through the end of

July. After July, well water levels continued a gradual decline to the low water point in late September, and then rose gradually into the fall.

When water levels were at their maximum, surface water was present in three vegetation zones: annuals, *E. palustris*, and submerged aquatics. In the annual zone, water depth reached a maximum of 0.02 m, and surface water was gone by mid May. The maximum water depth in the submerged aquatics zone ranged from 0.68 to 0.86 m during 1998-2000. No surface water was recorded in even the deepest basins after early August.

Maximum water levels relative to ground surface differed significantly among several vegetation zones (Figure 4.7a). The greatest difference in mean maximum water level was between the submerged aquatics zone (0.60 m above ground surface) and the *S. vermiculatus* zone (1.63 m below ground surface) (mean difference = 2.23 m, df = 14, $p < 0.001$). The maximum water level in the *S. vermiculatus* zone was significantly lower than all other zones (mean = -1.63 m, df = 14, $p \leq 0.001$ to 0.03). Among zones other than the *S. vermiculatus* zone, no maximum water level differed from the adjacent zones (df = 14, $p \geq 0.30$ to 0.99).

The patterns of minimum redox potential as a function of vegetation were similar at the 0.15 and 0.35 m soil depths, although mean values of E_h were about 90 mV lower for the 0.35 m than for the 0.15 m depth (Figure 4.7b). From the topographically highest zone (*S. vermiculatus*) down to the annuals zone, there were no differences in minimum redox potential (df = 18, p = 0.99). None of these zones experienced anaerobic conditions, based on a threshold for reducing (anoxic) conditions of E_h = 200 mV (Ponnamperuma 1972, D'Amore et al. 2004). Only the *E. palustris* and the submerged aquatics zones experienced anaerobic conditions, although minimum redox potential in *E. palustris* at 0.35 m did not differ significantly from the four topographically higher zones (df = 18, $p \geq 0.27$ to 0.71). The submerged aquatic zone was significantly more reduced than all other zones at 0.15 and 0.35 m (df = 18, $p \leq 0.001$ to 0.02)

Soils were, in general, saline, sodic, and alkaline (Table 4.5). Soils ranged from borderline saline (mean EC = 2 dS/m in the *E. palustris* and annual zones) to extremely saline (mean EC = 21 dS/cm in the *S. vermiculatus* zone). Similarly, soils ranged from borderline sodic (SAR avg. = 10 in the *E. palustris* zone) to extremely sodic (SAR avg. = 274 in the *S. vermiculatus* zone). All soils were alkaline, with average pH values ranging from 8.2 to 9.8. The *S. vermiculatus* zone had pH and sodicity that were significantly higher than all other zones (df = 14, for pH $p < 0.02$, for sodicity $p<0.09$), except *D. spicata* (for pH $p = 0.12$, for sodicity $p = 0.15$) and *C. multicaulis* (for pH $p = 0.37$, for sodicity $p = 0.23$). Otherwise, salinity, sodicity, and alkalinity did not differ among zones. Soil textures varied little among zones (Figure 4.8); they were, on average, sandy loams (Soil Survey Staff 2006).

Reciprocal transplant experiments

Reciprocal transplants of sod blocks among zones showed that maximum biomass production for dominant species always occurred in the origination zone, as opposed to the destination zone (Figure 4.9; see Figure 4.2 for definition of origination and destination zones). In no case did biomass production increase upon transplantation, and for several species biomass production decreased significantly. Also, in no case was there a significant difference between competition and no competition treatments. No conclusions could be drawn about the production of *J. balticus* in other vegetation zones, because even *in situ* transplantation of *J. balticus* caused an 80-100% decrease in biomass production relative to sod blocks that were not transplanted (Figure 4.9a).

When compared to *in situ* transplantation, the greatest overall effect on biomass production of transplantation to other vegetation zones occurred for *E. palustris*, an obligate hydrophyte that can grow in both slightly saline and non-saline environments (Aronson 1989). When compared to *in situ* transplants, *E. palustris* biomass was reduced by 77%, 99%, and 88% when transplanted without competition to annual, *D. spicata*, and *J. balticus* zones, respectively (for all tests, ANOVA $p<0.001$, df=16, k=4; Figure 4.9b).

The effect on biomass production in *D. spicata* differed according to the direction of the transplantation (Figure 4.9c). *D. spicata* biomass production was reduced by 93% when compared to the *in situ* transplants when transplanted without competition into the *E. palustris* zone (ANOVA $p<0.001$, df=16, k=4). When transplanted to the annual zone and the *J. balticus* zone, biomass production did not differ from in situ transplants ($p > 0.05$).

The smallest effect of transplantation occurred for the annuals (Figure 4.9d). Biomass production did not differ among treatments for transplantation to the *D. spicata* and *J. balticus* zones (ANOVA $p = 0.09$ for *D. spicata*, $p = 0.05$ for *J. balticus*, df=16, k=4). There was, however, a distinct pattern of less biomass production in the competition treatments versus the no competition treatment (92% less biomass in competition treatments for both *E. palustris* and *J. balticus* zone), but this reduction was not significant. Upon transplantation to the *E. palustris* zone, biomass production was lower than the *in situ* treatment but it did not differ from the control.

DISCUSSION

Vegetation zonation and the primacy of abiotic factors

This study provides evidence that physical factors are the major determinant of vegetation zone composition and distribution across the elevation gradient at Mishak Lakes, in contrast to results from coastal salt marshes (Snow and Vince 1984, Bertness and Ellison 1987, Crain et al. 2004). In contrast to studies conducted in other wetland types, no dominants from one vegetation zone were more productive in another vegetation zone. Instead, the data suggest that the most prevalent zonation patterns at ML are produced by the dominant's ability to tolerate one or more high stress condition.

The conclusion that abiotic factors determine plant zonation appears particularly on the most stressful ends of the abiotic gradients. In the *S. vermiculatus* shrublands surrounding the wetlands, the extreme soil salinity and the widely recognized halophytic nature of the few species that grow in the shrublands (Shreve 1942) suggest that most species are excluded from this zone. Species diversity was also low in the *E. palustris* zone, where anaerobic conditions prevail, and perennials transplanted into this zone grew poorly.

An exception to the control by abiotic factors may occur at the boundaries between *D. spicata* and *J. balticus*, which share the same elevation band. These two zones also share many of the same species. On average, the abiotic conditions under which they occur do not differ markedly, with soils that are only slightly saline and not anaerobic. However, despite the failure to detect significant abiotic differences, plots of *D. spicata* that do not contain *J. balticus* appear to have lower mean water tables and higher soil salinity than plots dominated by *J. balticus* (0.61 vs. 0.05 m below ground surface and 5.3 vs. 2.4 dS/m, respectively). With greater soil moisture and lower soil salinity, *J. balticus* cover appears to increase substantially while *D. spicata* cover decreases, suggesting that under the more benign conditions present in *J. balticus* zone, *J. balticus* is a superior competitor. This conclusion is consistent with findings in coastal salt marshes where *J. gerardii* is the competitive dominant (Bertness 1991a).

Results also indicate that the distribution of the annuals zone may not be restricted by abiotic factors across several vegetation zones. Instead, annuals may act as fugitives (Hutchinson 1951), colonizing bare patches yet giving way to tall perennials under appropriate conditions. Bare patches commonly form near the annual high water mark, where low salinity and wet, anaerobic conditions give way to high salinity and dry, aerobic conditions. Annual biomass production after transplanting neither decreased nor increased, indicating a broad tolerance of habitat conditions. However, the "with competition" treatment, although not significantly different ($p > 0.05$), suggests lower annual biomass production when among tall perennials such as *J. balticus* and *E. palustris*. Low production may occur because *P. aviculare* is as a weedy annual (Whitson et al. 1992) that germinates better with more available light (Baskin and Baskin 1990). In Atlantic salt marshes, it is *D. spicata* that acts as a fugitive (Bertness and Ellison 1987).

Several factors not addressed in this study could also influence the long-term distribution and composition of vegetation zones in these wetlands. For example, soil salinity in intermountain playa complexes is strongly influenced by hydrologic patterns. Increased anthropogenic demand for water and the concomitant reduced frequency of flushing in the wetland (Sanderson this dissertation Chapter 3) could lead to increased salinity levels and associated changes in the biota (Nielsen et al. 2003). Possible changes in vegetation include decreased species diversity and an expansion of the distribution of extreme halophytes across the wetland complex. Such changes have already occurred in other parts of the San Luis Valley (Cooper et al. 2006). On the other hand, restoration of a natural hydrologic regime (Sanderson this dissertation Chapter 3) may lead to greater frequency and degree of flushing, as well as anaerobic conditions that are more extensive and more extreme.

The control of vegetation zonation by abiotic factors results from stressful habitat conditions across the wetland, including extreme salinity in areas that do not flood and strongly anaerobic soils in areas that do flood. Plants growing in high salinity areas are simultaneously subjected to very low precipitation (average 180 mm/yr) and high evaporative demand. In regularly flooded areas, anaerobic conditions vary considerably within and between years.

Plant diversity and *Cleome multicaulis* habitat

Plant diversity (richness and evenness) is low at ML. This finding was expected given that plant species numbers generally decrease as abiotic stresses increase along natural gradients (Grime 1973, Keddy 1989, Huston 1994, Grime 2001). Observational studies indicate such a relationship for salinity and flooding gradients (Grace and Pugesek 1997), and Gough and Grace (1998) observed a decrease in species diversity after experimentally increasing salinity and flooding.

Although vegetation diversity is low at ML, some areas of the *D. spicata* and *J. balticus* vegetation zones support the globally rare but locally abundant plant *Cleome multicaulis*. *C. multicaulis* appears to strike a balance between moisture and salinity, although it has a broad range of tolerance with respect to both factors (Riley 2001). It also does poorly in competition with adjacent highly productive vegetation (Riley 2001), which suggests why *C. multicaulis* is often found in saline habitats that limit productivity of potential competitors.

C. multicaulis declined over the latter years of this study, simultaneously with the declines in water supplies to ML. This response was consistent with Riley's (2001) conclusion that insufficient soil moisture was the most likely cause of seed mortality. *C. multicaulis* is not sensitive to soil moisture changes induced by precipitation (Riley 2001). Therefore, surface and ground water supplies to wetland are critical to the viability of this species.

Cleome multicaulis may experience more sustainable populations under a variable hydrologic regime. Soils that are too consistently wet will promote the growth of tall vegetation that outcompete *C. multicaulis*, yet soils that are too dry interfere with plant growth and seed bank maintenance (Riley 2001). Historical variation in water depths, which included both wet and dry conditions, would prevent either condition from creating a long-term limitation on *C. multicaulis* populations.

The question remains as to why *C. multicaulis* does not occur in otherwise available habitat. Riley (2001) found little difference between plots containing *C. multicaulis* and abiotically similar areas that did not contain plants. Her work did, however, reveal an apparent tolerance by *C. multicaulis* of soils with high pH where many other species may be unable to grow, suggesting that avoidance of competition is a primary strategy for this species.

Lack of seed dispersal may partially explain the absence of *C. multicaulis* in otherwise apparently suitable habitat. *C. multicaulis* seed is water borne, although it may also be transported in the hooves of large ungulates (Riley 2001). The lack of connectivity among wetlands may inhibit dispersal (Riley 2001). Sanderson (pers. obs.) noted that all stands of *C. multicaulis* at ML are near the inlet to the wetland complex, suggesting that seed transport from upstream was responsible for establishment of these stands. As such, reductions in flow to ML may affect seed transport to the wetland and subsequent population dynamics of *C. multicaulis*.

The primary important of abiotic conditions at Mishak Lakes suggests that restoration of the altered hydrologic regime of this wetland (Sanderson this dissertation Chapter 3) to a natural hydrologic regime (Poff et al. 1997) may be sufficient to re-establish many of the wetland's historical biodiversity functions, including connecting wetlands across the landscape and supporting viable populations of the rare plant *Cleome multicaulis*. Since the pattern of stress gradients is common in wetlands of arid valleys, this hydrology-based approach to wetland restoration may have broad application to wetlands throughout the intermountain region of the western U.S.

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Table 4.1. Area of vegetation zones at Mishak Lakes. Annuals are estimated to be less than 1% of the total area, and were subsumed into other communities.

Vegetation zone	**Area (ha)**	**% of area**
Sarcobatus vermiculatus	839	69.1
Juncus balticus	113	9.3
Distichlis spicata	89	7.3
Annuals	--	--
Eleocharis palustris	132	10.9
Submerged aquatic	42	3.4
Total area:	**1215**	

Table 4.2. Species composition in the six major vegetation zones at Mishak Lakes in 1998, as well as plots containing *Cleome multicaulis*. In all cases n=3. Values are average (constancy), where average is mean percent cover and constancy is the number of plots in which the species occurs. A '+' indicates presence in the plot with <1% cover.

	Vegetation zone						
Species	*Sarcobatus vermiculatus*	*Distichlis spicata*	*Juncus balticus*	Annuals	*Eleocharis palustris*	Submerged aquatics	*Cleome multicaulis*
Sarcobatus vermiculatus (Hooker) Torrey	22 (3)	–	–	+ (1)	–	–	–
Distichlis spicata (L.) Greene	5 (3)	48 (3)	24 (3)	–	–	–	53 (3)
Eleocharis acicularis (L.) Roemer & J.A. Schultes	1 (1)	–	–	–	–	–	–
Sporobolus airoides (Torrey) Torrey	–	2 (1)	–	–	–	–	–
Muhlenbergia asperifolia (Nees & Meyen ex Trin.) Parodi	–	2 (1)	18 (3)	–	–	–	+ (1)
Juncus balticus Willd. var. *montanus* Engelm.	–	1 (1)	28 (3)	–	–	–	5 (2)
Hordeum jubatum L.	–	+ (3)	3 (3)	+ (2)	–	–	–
Chenopodium glaucum L.	–	+ (2)	+ (2)	1 (1)	+ (2)	–	–
Suaeda calceoliformis (Hooker) Moquin	–	+ (2)	–	–	–	–	3 (3)
Scirpus nevadensis S. Watson	–	+ (1)	–	–	–	–	–
Atriplex patula L.	–	+ (1)	1 (2)	–	–	–	+ (1)
Pyrrocoma lanceolata (Hooker) Greene	–	+ (1)	+ (3)	–	–	–	1 (2)
Argentina anserina (L.) Rydberg	–	–	+ (1)	1 (1)	–	–	–
Cleome multicaulis DC.	–	–	–	–	–	–	10 (3)
Polygonum aviculare L.	–	–	–	28 (3)	–	–	–
Chamaesyce glyptosperma (Engelm.) Small	–	–	+ (1)	–	–	–	–
Lepidium virginicum L.	–	–	+ (1)	–	–	–	–
Pascopyrum smithii (Rydberg) A. Löve	–	–	+ (1)	–	–	–	–
Plagiobothrys scouleri (Hooker & Arnott) I.M. Johnston	–	–	–	+ (1)	–	–	–
Ranunculus cymbalaria Pursh	–	–	+ (2)	–	–	–	–
Schoenoplectus pungens (Vahl) Palla	–	–	–	–	+ (1)	–	–
Eleocharis palustris (L.) Roemer & J.A. Schultes	–	–	1 (2)	1 (3)	42 (3)	+ (2)	–
Stuckenia pectinatus (L.) Boerner	–	–	–	–	–	4 (3)	–
Zannichellia palustris L.	–	–	–	–	–	28 (3)	–

Table 4.3. Average percent cover of species in plots that consisted almost exclusively of submerged aquatic species at the beginning of the study. A "+" indicates presence in the plot with <1% cover.

Year	**1998**	**1999**	**2000**	**2001**
Ranunculus trichophyllus Chaix	--	11	--	+
Eleocharis acicularis (L.) Roemer & J.A. Schultes	+	--	--	--
Eleocharis palustris (L.) Roemer & J.A. Schultes	+	1	16	15
Stuckenia pectinatus (L.) Boerner	4	1	--	--
Zannichellia palustris L.	28	75	85	78

Table 4.4. Jaccard's coefficient for comparisons of plots containing *Cleome multicaulis* and plots from vegetation zones. Jaccard's coefficient ranges from 0%, indicating no similarity (i.e., no shared species) to 100% for complete similarity (i.e., every species occurs in both sets of plots).

Zone being compared to *C. multicaulis* plots	**Jaccard's coefficient (%)**
Sarcobatus vermiculatus	6
Juncus balticus	61
Distichlis spicata	69
Annuals	0
Eleocharis palustris	0
Submerged aquatic	0

Table 4.5. Physical parameters by vegetation zone. Different letters indicate significant differences ($p<0.10$, Scheffé test). Values are $\bar{x} \pm se$. $n = 3$. Saline soils (EC > 2 dS/m) are those in which plant growth is limited by large quantities of soluble salts. Sodic soils ($\mathrm{SAR} = \frac{[\mathrm{Na}^+]}{[[\mathrm{Ca}^{2+} + \mathrm{Mg}^{2+}]/2]^{1/2}} > 15$) have high exchangeable sodium. Highly alkaline soils ($\mathrm{pH} \geq \sim 8.5$) often have problems with water percolation. Definitions are from Bohn et al. (1985).

	Vegetation zone						
Soil parameter	*Sarcobatus vermiculatus*	*Distichlis spicata*	*Juncus balticus*	Annuals	*Eleocharis palustris*	Submerged aquatics	*Cleome multicaulis*
Electrical conductivity (dS/m)	a 20.9 ± 9.7	a 5.26 ± 0.41	a 2.4 ± 0.54	a 1.94 ± 0.42	a 2.00 ± 0.19	a 3.11 ± 0.32	a 5.43 ± 1.48
Sodium Absorption Ratio (SAR)	b 274.3 ± 125.1	ab 44.0 ± 6.7	a 20.3 ± 4.2	a 13.6 ± 1.5	a 10.1 ± 2.4	a 20.5 ± 1.9	ab 65.3 ± 22.3
pH	b 9.80 ± 0.28	ab 8.57 ± 0.12	a 8.18 ± 0.23	a 8.25 ± 0.13	a 8.22 ± 0.35	a 8.42 ± 0.17	ab 8.86 ± 0.35

Figure 4.1. The watershed of the San Luis Valley and the location of Mishak Lakes. Solid lines within the valley are major roads.

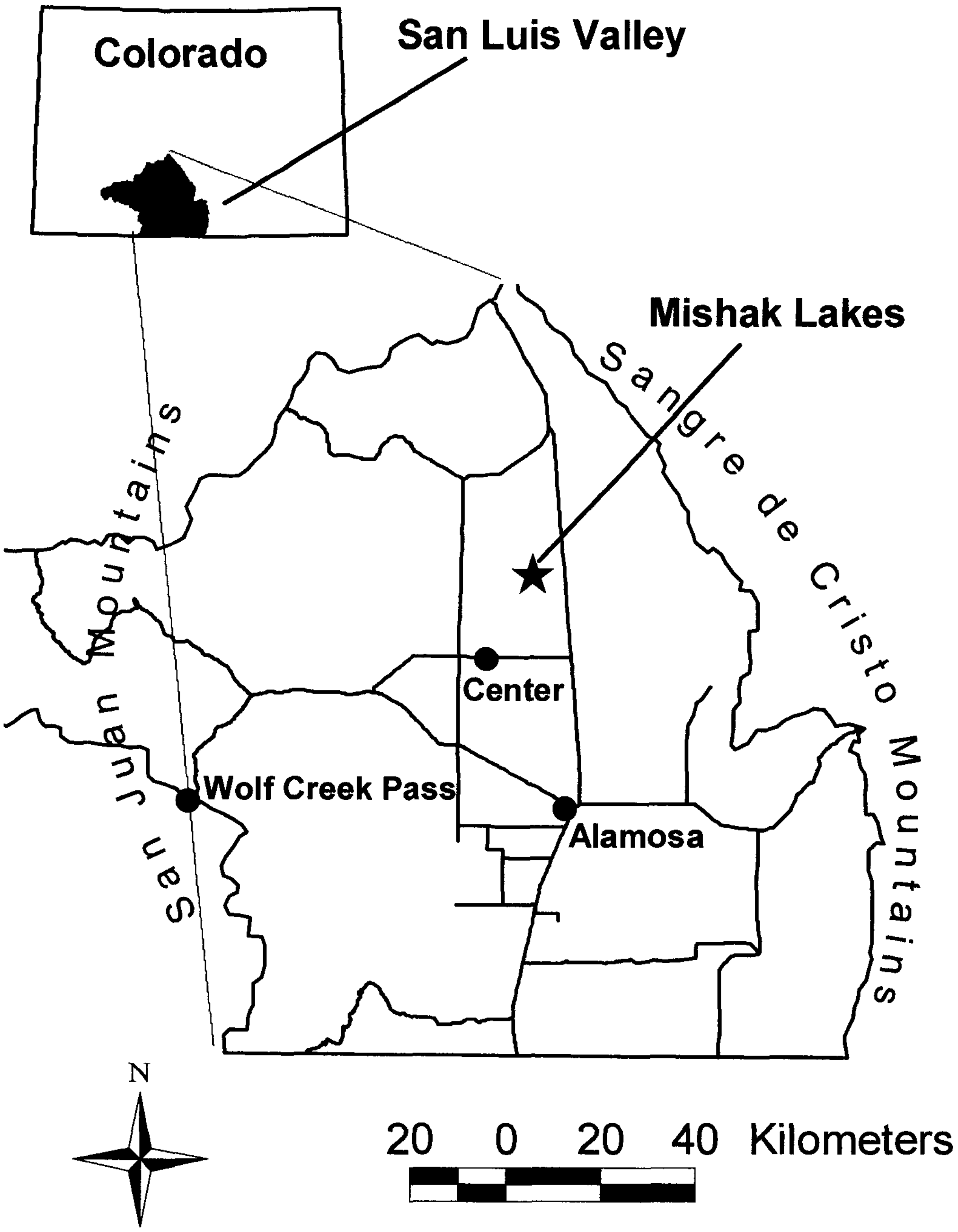


Figure 4.2. Representative layout of reciprocal transplant experiment. One replicate only is shown (total number of replicates was 4). Squares represent the 0.25 x 0.25 x 0.25 m blocks of sod that were the experimental units. Text inside the units are the treatments (see *Methods* for full description). Only one direction of one reciprocal transplant is shown (identical treatments were done in the opposite direction), and only one pair of zones is shown (reciprocal transplants were done among all pair-wise combinations of four zones).

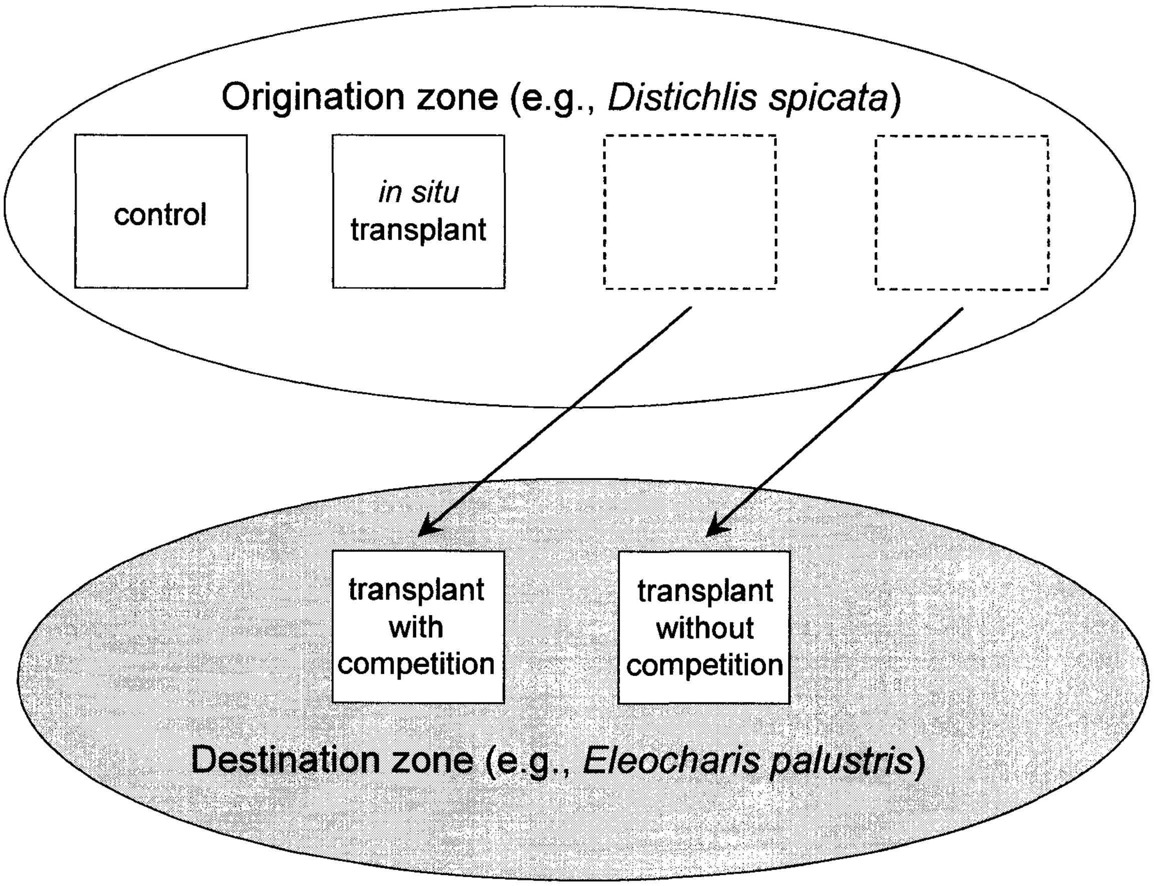


Figure 4.3. Map of vegetation zones at Mishak Lakes. Zones were delineated using aerial photos taken in 1988, and were verified using ground-truthing.

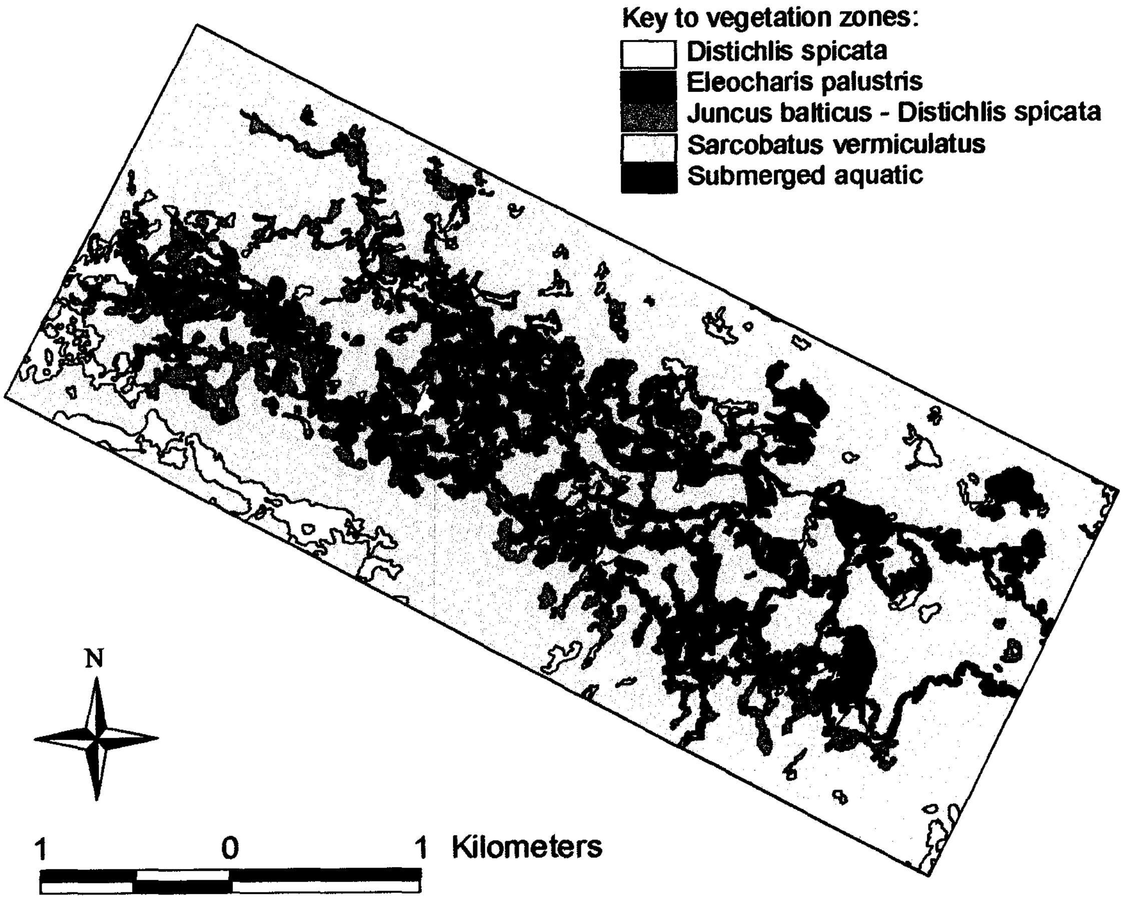


Figure 4.4. Cross-sectional view of vegetation zone positions along a transect through the deepest basin in the wetland complex. Horizontal bars mark upper and/or lower limits of plant communities. Note: vertical scale is greatly exaggerated relative to the horizontal scale.

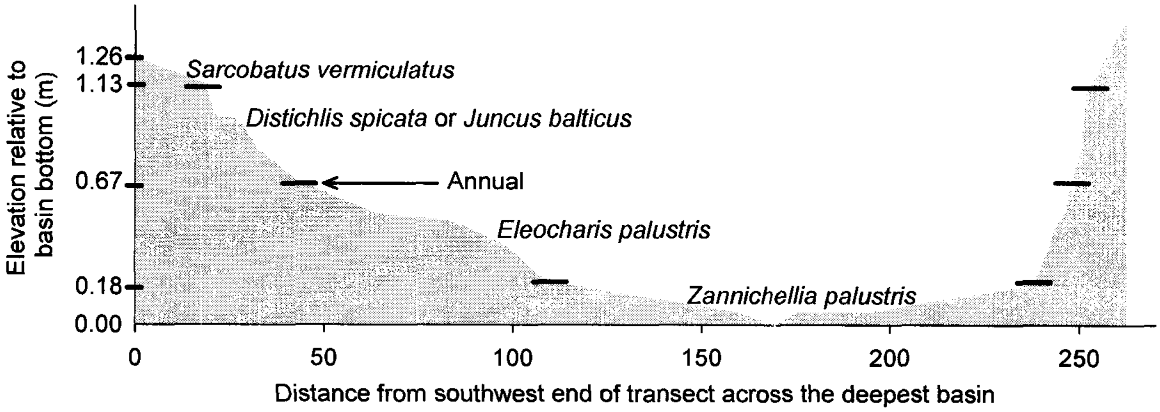


Figure 4.5. (a) *C. multicaulis* density and (b) maximum water depth in wetland. Bars in the top chart show $\bar{x} \pm se$ (n=3). Bars in the bottom chart show maximum recorded depth in the deepest basin of the wetland complex (n=1).

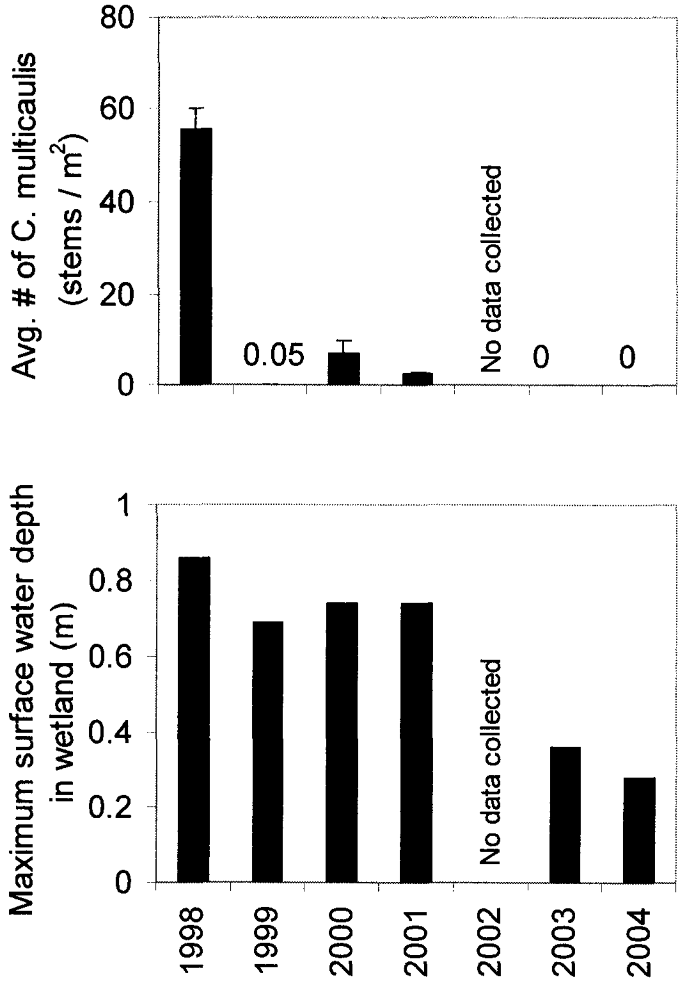


Figure 4.6. Typical water level pattern in the middle of the deepest basin in the wetland complex. The data shown are from water year 1999; no data were collected between data points shown.

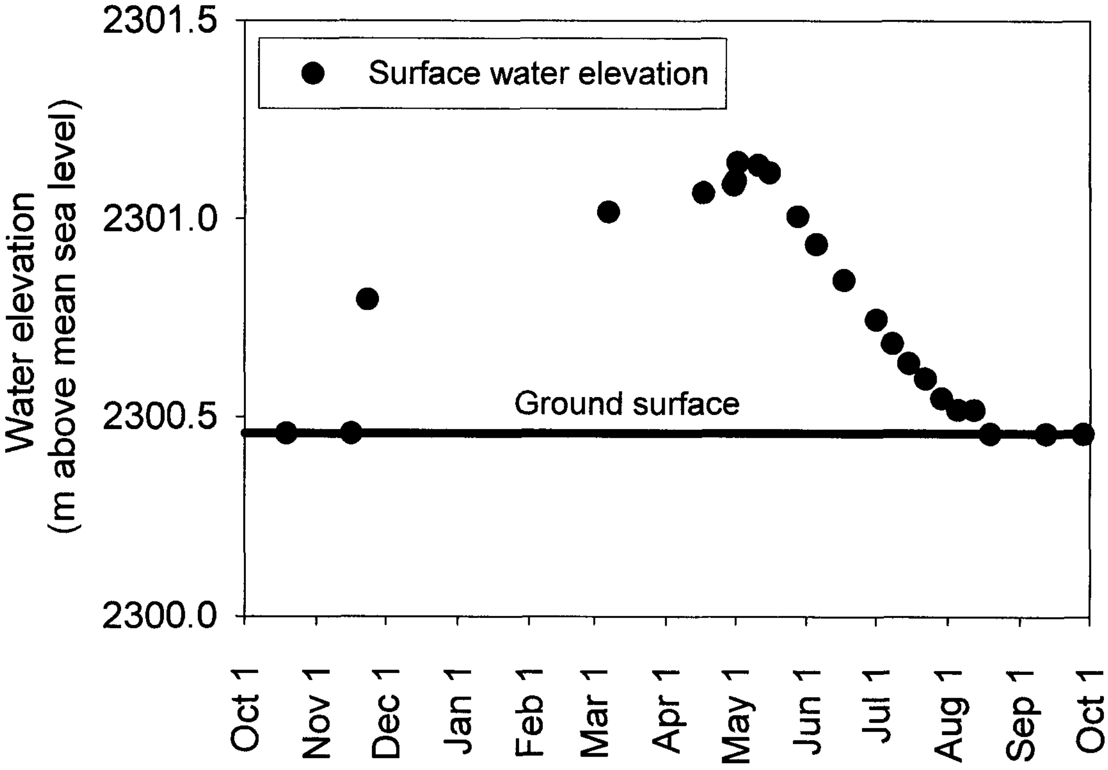


Figure 4.7. (a) Minimum redox potential and (b) maximum water levels in vegetation zones. Bars show $\bar{x} \pm se$ (n = 4 for redox; n = 3 for maximum water level). Different letters indicate significant differences (p<0.10, Scheffé test). Redox potentials were compared only within each depth, not between depths.

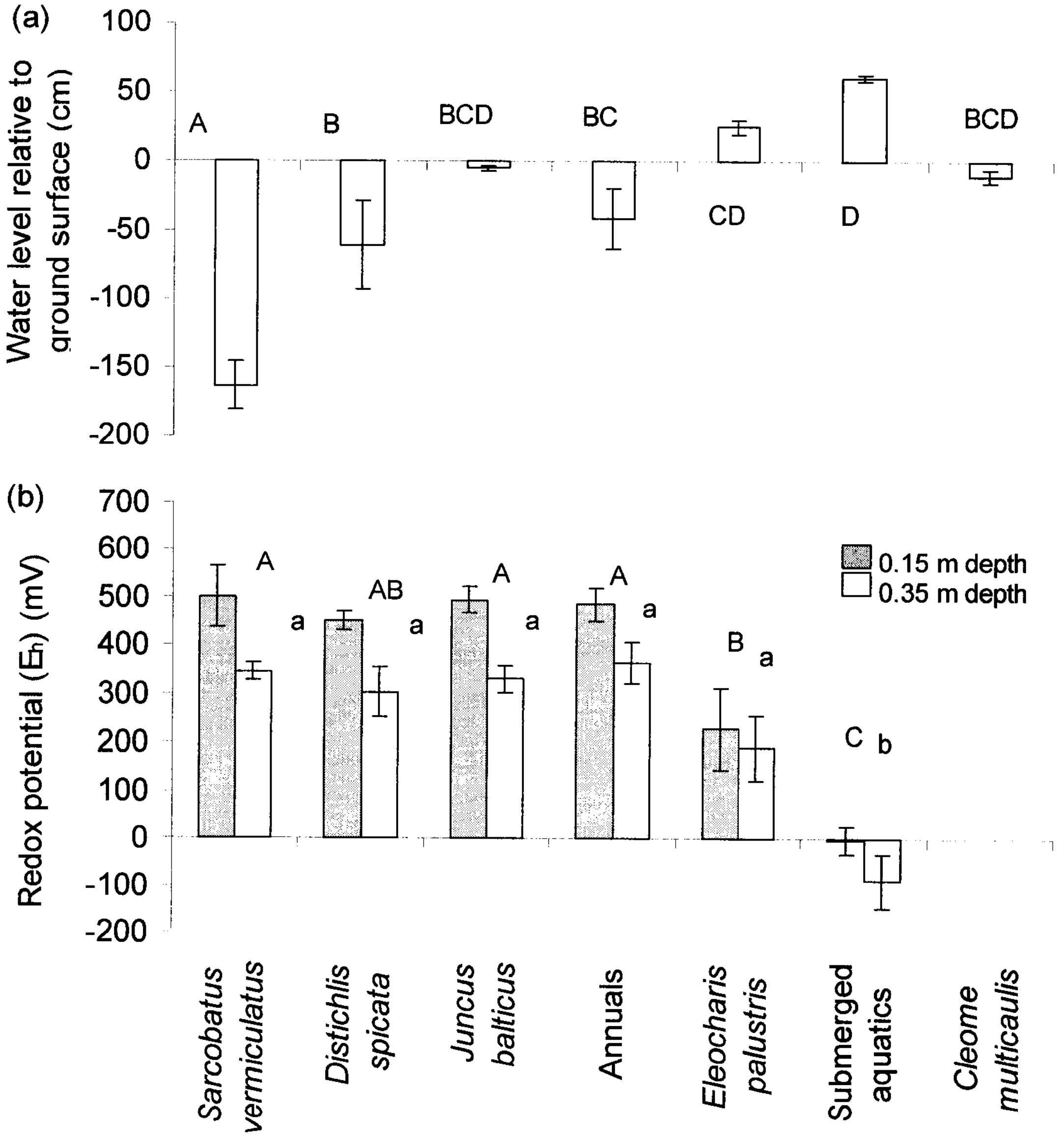


Figure 4.8. Percent sand, silt, and clay in soils of each vegetation zone.

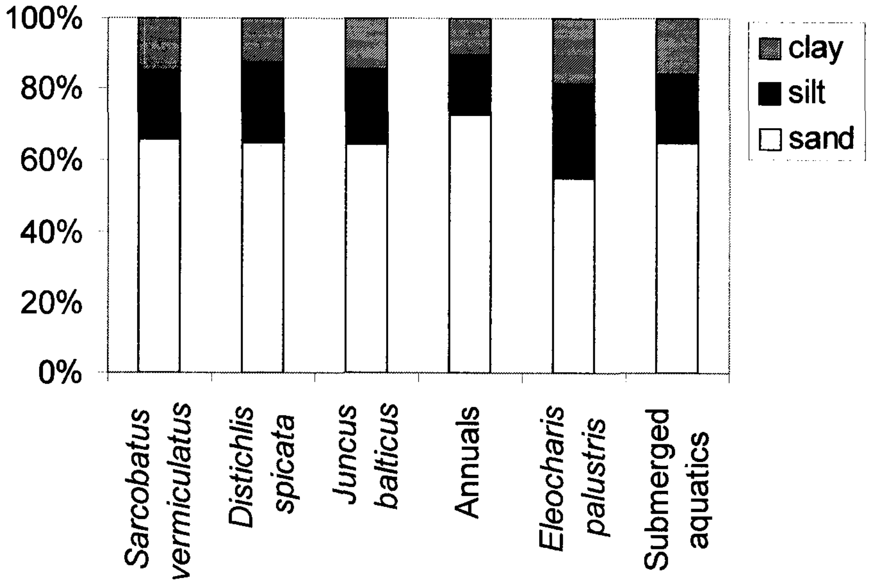
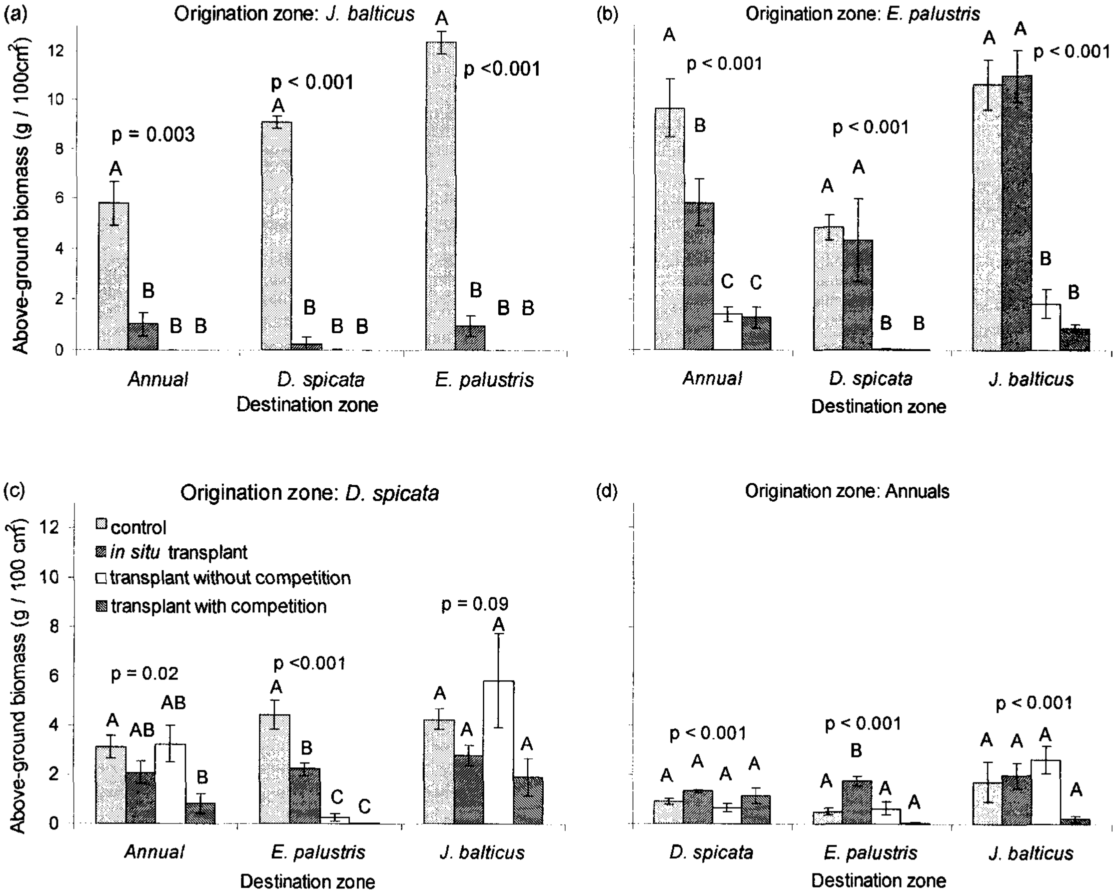


Figure 4.9. Above-ground biomass following reciprocal transplants for (a) *D. spicata*, (b) *J. balticus*, (c) annuals (*Polygonum aviculare* and *Plagiobothrys scouleri*), and (d) *E. palustris*. Bars show $\bar{x} \pm se$. ANOVA p-value is shown above each experiment. Different letters indicate significant differences ($p<0.05$, Scheffé test).



CHAPTER 5

INTEGRATING HYDROLOGY AND BIOLOGY TO ACHIEVE CONSERVATION GOALS

This dissertation has combined hydrological and biological investigations—ranging from evapotranspiration to plant zonation—to address questions of water management and wetland ecosystem conservation in Colorado's San Luis Valley (SLV). The streams and wetlands in the SLV contain species (e.g., *Cleome multicaulis*) and ecosystems (e.g., intermountain playas, interdunal wetlands) of high conservation concern (Sarr and Sanderson 1998). Throughout intermountain valleys of the western U.S., water-dependent species and ecosystems are threatened by unsustainable water use on a local scale as well as by proposals to export water from the region on a large scale. In order for biodiversity to be protected effectively for posterity, it is critical that hydrology and biology be integrated in the management of these types of wetland systems.

Because intermountain valleys have a dry, sunny climate (Doesken and McKee 1989), any discussion of hydrology necessarily includes evapotranspiration (ET), since ET is the primary means of water loss in both the valleys as a whole (Emery et al. 1973, Huntley 1979) and in individual wetlands (Sanderson this dissertation Chapter 3). Chapter 2 of this dissertation presents evapotranspiration (ET) research that substantially improves prediction of the ground water component of ET (ET_g) for ground water wetlands, where ET_g can be modeled as a function of water table depth (WTD). This research illustrated that as WTD increases to 1.0 m below the ground surface, the decrease in ET_g is substantially less than previously assumed. Consequently, ET "salvage"—the amount of water that can potentially become available by reducing ET through water table drawdown—is likely much smaller than previously predicted. This study, which was based on a much larger data set and variety of wetlands than were previous studies, indicated that ET_g would decrease 222 mm as WTD increased from 0.1 to 1.0 m; existing models estimate salvage 15 to 234% larger, with three of four existing estimating at least 99% more salvage than this study (Emery 1970, Emery 1991, Huntley 1979, Harmon 2000).

This study also demonstrated that the relationship of ET_g to WTD in wetlands differs between ground water and surface water wetlands. In surface water wetlands, ET_g was strongly dependent on water supplies. In contrast to existing models, ET_g was 0 mm in surface water wetlands when there were sufficient water inputs to meet ET demand, independent of WTD. When inputs did not meet ET demand, ET_g was positive though highly variable at WTD up to 1.66 m. Because the relationship of ET_g to WTD differs in ground and surface water wetlands, wetlands will have to be considered by type when hydrologic models are developed to predict their function under varying scenarios.

This improved understanding of how ET_g responds to WTD changes can inform a variety of hydrologic models. Some models using ET_g-WTD relationships are currently being used to predict impacts of anthropogenic developments and natural events on water supplies (e.g., RGDSS 2005). Other models can also potentially play an important role in conservation of wetlands, by providing insights into current conditions and facilitating prediction of future impacts of water development and climate change (e.g., Poiani et al. 1996).

In chapter 3 of this dissertation, I used a conceptually simple hydrologic model and available historical data to demonstrate that the current hydrologic function at Mishak Lakes--an intermountain playa in Colorado's San Luis Valley--differs markedly from its historical natural flow regime. This wetland complex is governed by surface water dynamics. Under current hydrologic conditions (WY 1998-2005), stream inflows accounted for ≥80% of total annual water inputs. No ground water discharged to the wetland. ET accounted for ≥69% of total annual water loss, and most of the remaining water loss was through surface water outflow.

The simulated hydrologic regime (e.g., historical conditions in the absence of hydrologic alteration) indicated that natural flow regime would differ substantially from current conditions. Simulated wetland was wetter and more variable in late summer and fall, while being more consistently flooded near maximum depth in late spring and early summer. During 1998-2002, observed monthly mean surface water depth was 65% lower than under simulated depths. Standard deviations of observed monthly water depths were as much as 177% greater (in May) and 100% less (in September) than simulated. During the growing season, the simulated wetland contained surface water for 46% longer than observed.

Inter-annual variation under simulated unaltered conditions also differed from observed. As observed, the wetland dried completely (i.e., was ephemeral) in all years; as simulated, the wetland was ephemeral in 2 of 5 years. For the period 1915-2002, the simulated wetland was inundated continuously (i.e., was perennial) for as long as 16 years and 9 months.

The large differences in observed and simulated surface water dynamics resulted from differences between altered (observed) and simulated unaltered (natural) stream inflows. For 1998-2002, the maximum annual total stream inflows observed was 3.2×10^6 m^3 versus 8.4×10^6 m^3 under simulated conditions (163% greater). In 2005, there was no observed inflow to the wetlands; for 87 years of simulated natural conditions, the minimum inflow was 3.2×10^6 m^3, roughly equal to the relatively wet water years 1999 and 2000.

The simulated historical conditions are all consistent with anecdotes from the SLV, which contain references to extensive wet areas. Ben Kern of the 1848 Fremont expedition passed through an area in the north central part of the valley that he described as a "low place of long grass weeds & cattails" (Hafen and Hafen 1960). Lt. Beckwith of the 1853 Gunnison expedition described the area east of Mishak Lakes as extensive marshlands (Richmond 1990). Wheeler (1877) showed extensive marshes across about 125 km^2 of land, and seasonally extending nearly 100 km from north to south.

Much existing research suggests that altered hydrologic conditions may have significant ecological impacts, and, as a result, native species and ecosystems may be threatened by hydrologic alterations. At Mishak Lakes, there are many species that may be affected by altered hydrologic conditions. For example, a decrease in maximum flooding depth may inhibit growth and reproduction of the rare plant *Cleome multicaulis* (Riley 2001). A decrease in the density of *C. multicaulis* from 55.6 to 0 stems/m^2 was observed during 1998 to 2002. The majority of this decline occurred between 1998 and 1999, after a decrease in maximum water level of 0.18 m. In addition to decreases in maximum flooding depth, there are other important hydrologic alterations that may affect a variety of native flora and fauna at Mishak Lakes. For example, decreased duration of flooding may limit survivorship of amphibians and reduced frequency of fall flooding may eliminate use of the wetlands during fall bird migration.

The degree to which decreased variability in flooding patterns may also affect spatial and temporal patterns of plant community distribution was investigated by examining factors that may govern plant species distribution in the intermountain playa Mishak Lakes. This investigation found evidence that physical (abiotic) factors—including flooding and associated anaerobic soil conditions—are the major determinants of vegetation zone composition and distribution across the elevation gradient at Mishak Lakes. Descriptive work showed that abiotic conditions differed significantly among several vegetation zones. Significant abiotic stressors included anaerobic soil conditions at the low end of the 1.25 m elevation gradient and extreme soil salinity and sodicity (a measure of exchangeable sodium) at the high end of the gradient. In wetland basins, prolonged inundation led to anaerobic soil conditions in the *Eleocharis palustris* and the submerged aquatics zones. At the other end of the elevation gradient, soil salinity and sodicity were high in the *Distichlis spicata* zone (EC = 5.3 dS/m, SAR = 44.0) and extreme in the *Sarcobatus vermiculatus* zone (EC = 21 dS/m, SAR = 274).

Experimental work demonstrated that transplanted species experienced maximum biomass production in the zone where they originated, as opposed to any other higher or lower vegetation zone. When compared to *in situ* transplantation, the greatest effect of transplantation to other vegetation zones had the occurred for *E. palustris*, which experienced biomass reductions $\geq 77\%$ when transplanted to the annual, *D. spicata*, and *J. balticus* zones, respectively (ANOVA, $p<0.001$, df=16, k=4).

Conclusions about the primary influence of abiotic factors in Mishak Lakes contrasts with results from coastal salt marshes. In coastal marshes, competitive interactions govern the distribution of vegetation zones at the higher end of the elevation gradient (Snow and Vince 1984, Bertness and Ellison 1987, Crain et al. 2004). This contrast appears to occur because at Mishak Lakes, patterns of vegetation zonation arise from counter-directional stress gradients: a gradient from anaerobic to aerobic conditions from basin bottom to upland and a gradient from extremely high salinity to low salinity in the opposing direction. Since abiotic factors appear to be the primary, proximate cause for plant species distribution at Mishak Lakes, restoration of ecological function should occur following the restoration of hydrologic conditions.

Altered hydrologic conditions are now the norm in the San Luis Valley and throughout the intermountain valleys of the western U.S. In these areas rivers and wetlands are important and prominent features of the landscapes despite the relatively small surface area they cover. Altered hydrologic conditions have significant and often detrimental consequences for native species and ecosystems (Poff et al. 1997). If conservation of water-dependent ecosystems in these regions is to occur, it is critical that hydrology and biology be integrated (Strange et al. 1999), and that this integration be applied to conservation problems.

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