
A framework for understanding the hydroecology of impacted wet meadows in the Sierra Nevada and Cascade Ranges, California, USA

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Abstract Meadows of the Sierra Nevada and Cascade mountains of California, USA, support diverse and highly productive wet-meadow vegetation dominated by sedges, rushes, grasses, and other herbaceous species. These groundwater-dependent ecosystems rely on the persistence of a shallow water table throughout the dry summer. Case studies of Bear Creek, Last Chance, and Tuolumne meadow ecosystems are used to create a conceptual framework describing groundwater-ecosystem connections in this environment. The water requirements for wet-meadow vegetation at each site are represented as a water-table-depth hydrograph; however, these hydrographs were found to vary among sites. Causes of this variation include (1) differences in soil texture, which govern capillary effects and availability of vadose water

and (2) elevation-controlled differences in climate that affect the phenology of the vegetation. The field observations show that spatial variation of water-table depth exerts strong control on vegetation composition and spatial patterning. Groundwater-flow modeling demonstrates that lower hydraulic-conductivity meadow sediments, higher groundwater-inflow rates, and a higher ratio of lateral to basal-groundwater inflow all encourage the persistence of a high water table and wet-meadow vegetation, particularly at the margin of the meadow, even in cases with moderate stream incision.

Keywords Ecohydrology · Groundwater dependent ecosystem · USA · Water table · Wetland

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Introduction

Wet meadows are productive and diverse ecosystems that are common in the Sierra Nevada and Cascade ranges of California, USA. The health of these ecosystems is inextricably linked to the shallow groundwater flowing beneath the meadow (Ratliff 1985). The Sierra Nevada and Cascade foothills begin at ~300 m elevation, and peaks rise to over 4,000 m elevation, resulting in a wide range of climates and ecological communities. Most precipitation falls between November and March, primarily as snow at elevations above 1,500 m. There are strong gradients in annual average precipitation, which range from ~20 to 200 cm due to topography-induced, orographic effects, with higher precipitation totals occurring on the western slope as well as a gradient of increasing precipitation from south to north.

Because little precipitation occurs during the warm and dry summer, wet-meadow vegetation relies on shallow groundwater during the growing season. For this reason, wet meadows are classified as groundwater-dependent ecosystems (Boulton 2005; Murray et al. 2003). The source of the groundwater can be local infiltration and recharge in the meadow, watershed scale groundwater discharge to the meadow, or recharge from a stream to the meadow. Identification of the groundwater source is

critical to understanding hydroecologic function and groundwater controls on vegetation patterning, yet heterogeneity and transient conditions within the groundwater flow system can make this determination difficult (Carter 1986; Hunt et al. 1996, 1999; Owen 1995). Extensive monitoring of the water-table configuration (Cooper et al. 2006; Patterson and Cooper 2007; Hammersmark et al. 2008; Loheide and Gorelick 2007) and natural geochemical and isotopic-tracer techniques (Rains and Mount 2002; Atekwana and Richardson 2004; Hunt et al. 1997, 1998; Huth et al. 2004; Matheny and Gerla 1996; Komor 1994) have proven effective for identifying the source of water feeding riparian ecosystems.

Meadows throughout the Sierra Nevada and Cascade Ranges of California have experienced important changes in vegetation and hydrology since the 1850s when European settlers first began to use the land for mining, ranching, and logging. In general, these activities altered hydrologic patterns and processes of ecosystems, either inadvertently or intentionally, often resulting in a lower water table. Because of the tight connection between the vegetation and the groundwater systems, the lowering of the water table typically results in a shift from native wet-meadow vegetation to more xeric vegetation. Four common anthropogenic mechanisms for these ecohydrologic shifts are logging, road and railroad construction, ditching/channelization, and overgrazing (SNEP 1996; Trimble and Mendel 1995; Belsky et al. 1999; Clary and Webster 1990). It is important to recognize that natural changes to the meadow hydrologic regime (Germanoski and Miller 2004; Wakabayashi and Sawyer 2001) and changes to the climatic regime may also cause shifts in vegetation composition and patterning.

Vegetation changes alter the functioning of the meadow and may further change the meadow hydrologic regime. The causes and effects of these ecosystem changes have been described for individual sites (Cooper et al. 2006; Loheide and Gorelick 2005, 2006, 2007; Patterson and Cooper 2007; Hammersmark et al. 2008; Hammersmark 2008), but a comparison of these studies raises several important questions.

First, Hammersmark (2008), Loheide and Gorelick (2007), and Cooper et al. (2006) all present water-table hydrographs associated with wet-meadow vegetation, showing that wet-meadow vegetation is highly correlated with a shallow water table in the Sierra Nevada and Cascade mountains. Yet, comparison of these hydrographs does not reveal a single threshold vegetation hydrograph that could be used to predict the presence or absence of wet-meadow vegetation at all three sites. What is the cause of this apparent difference in water requirements?

Second, Loheide and Gorelick (2007) note strong longitudinal vegetation patterning associated with stream incision; however, this phenomena was observed at neither the site investigated by Cooper et al. (2006) nor that investigated by Hammersmark (2008). What differences in process might help reconcile these conflicting observations?

The purpose of this article is to synthesize the results of case studies of three wet-meadow complexes in the Sierra

Nevada and Cascade mountain ranges, Bear Creek, Last Chance watershed, and Tuolumne Meadows (Fig. 1), to answer these questions and identify hydroecological processes that are consistent among meadows as well as those that differentiate meadow function across geographic, geologic, elevation, climatic, and land-use gradients. Using examples from these case studies, the following will be discussed: (1) the linkages between wetland vegetation and the groundwater system, (2) the watershed scale drivers of meadow hydroecology, (3) the drivers of meadow hydroecology within meadow systems, and (4) the implications of ecosystem-groundwater interactions on restoration/rehabilitation planning and efficacy as called for by Bernhardt et al. (2005), Palmer and Bernhardt (2006), and the US Department of Agriculture (USDA 2001).

In this article, the focus is on the water requirements of wet-meadow groundwater-dependent ecosystems and the development of a conceptual framework for understanding the physical processes and conditions necessary to support these ecosystems. This conceptual framework allows one to interpret apparent inconsistencies as well as commonalities in the form and function of meadow systems. This provides a scientific basis for land managers and restoration practitioners who need to understand how processes at unstudied meadows might relate to findings from intensely monitored research sites elsewhere in the region.

Study site descriptions

Bear Creek Meadow

Bear Creek Meadow is a low-gradient alluvial floodplain situated at the bottom of the 218 km² Bear Creek watershed (Table 1). Located at the northwestern margin of the Fall River Valley near the intersection of the Modoc Plateau and the Cascade Range, the meadow is 2.3 km² in size, at 1,010 m elevation. The Fall River Valley is fed by large springs discharging from permeable volcanic rocks (Meinzer 1927; Grose 1996; Rose et al. 1996) and is underlain by fine-grained lacustrine deposits with hydrologically important clay lenses in the meadow that are overlain by 0.5–2 m of deltaic sands and gravels and 1–3 m of floodplain silty loam soils (Grose 1996; NRCS 2003). The local climate is semi-arid; the meadow receives annual average precipitation of 510 mm mostly as rainfall, while higher elevation areas receive higher precipitation totals largely as snow.

Hydrologic inputs to the meadow include intermittent surface-water inflow from Bear Creek, perennial spring discharge from the Fall River springs, precipitation, and seasonal shallow subsurface recharge from an adjacent irrigated pasture. The Fall River spring system is fed by precipitation, which falls on the Medicine Lake Highlands, perches on low-permeability lacustrine deposits, flows south through fractured basalt and discharges at the downstream end of the meadow (Rose et al. 1996), and forms the headwaters of the Fall River and several short perennial tributaries.

Prior to rehabilitation, Bear Creek Meadow's channels were degraded due to channelization and heavy utilization

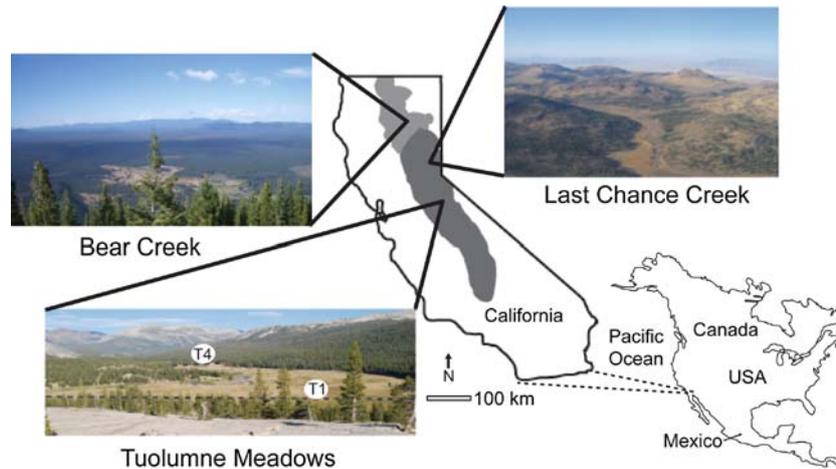


Fig. 1 Map showing sites and location of Sierra Nevada (dark grey) and Cascade ranges (light grey) within California, USA, as well as photos of the meadow systems discussed in the text. Labels T1 and T4 show the location of transects discussed in the text

as livestock pasture (Spencer and Ksander 2002, Table 1). By the mid 1990s, Bear Creek's main channel had incised and widened to the extent that it was completely disconnected from its floodplain in all but the largest flood events. This channel degradation led to a lowered water table and a conversion of wet and moist meadow vegetation dominated by *Carex nebrascensis*, *Carex athrostachya*, *Juncus balticus*, *Juncus covillei* and *Juncus nevadensis* to annual grasses more typical of upland environments, for example *Poa bulbosa*, *Bromus tectorum* and *Bromus japonicus*.

The meadow was rehabilitated in 1999 using a "pond-and-plug" meadow re-watering strategy, where incised stream channels were intermittently filled with plugs of locally derived alluvial material, and the unfilled, incised

channel segments were left as ponds. The new 3.6-km channel was constructed, using remnant channels where possible, with a meandering riffle-pool morphology (Rosgen 1996, 1997; Benoit and Wilcox 1997) with reduced width, depth, and cross-sectional area (Poore 2003). The average depth at riffles was reduced from 2.69 m to 0.89 m, and average bankfull capacity was reduced from 61.7 to 5.35 m³/s (Hammersmark et al. 2008), resulting in more frequent bankfull conditions. These modifications resulted in substantial changes to the meadow hydrologic regime, including: (1) higher groundwater levels and volume of subsurface storage, (2) increased frequency of floodplain inundation and decreased magnitude of flood peaks, (3) decreased baseflow and annual runoff; and (4) increased evapotranspiration

Table 1 Comparison of hydrologic characteristics of study sites

	Bear Creek	Last Chance	Tuolumne
Elevation (m asl)	1,010	1,680–1,820	2,600
Watershed area (km ²)	218	250	186
Study site size	2.3 km ²	~21 km length of continuous meadow system	1.6 km ²
Precipitation (mm)	510	410	1,000
Meadow sediment texture	Silty-clayey loam soil (1–3 m) above sand and gravel layer (0.5–2 m) overlaying lacustrine sediments of the Fall River Valley	Predominantly silts and minor sand and gravel	Sand and gravel
Bedrock geology	Fractured basalt with low-permeability lacustrine deposits underlying the Fall River Valley	(1) Tertiary volcanics: rhyolitic flows including some ash and tuff beds, (2) Miocene pyroclastic deposits consisting of andesitic mudflows, breccias, conglomerate and tuffs and (3) Mesozoic granite (Durrell 1987; Lydon et al. 1960)	Predominately granite, with complex fractures near Soda Springs; lateral glacial moraines along valley
Extent and cause of degradation	Severe channelization and straightening for agricultural reclamation (1960s); three decades of heavy grazing (Spencer and Ksander 2002)	Severe incision due to logging and grazing; local effects of road and railroad construction	Moderate channel widening due to extensive sheep grazing during the late 1800s
Restoration/rehabilitation	Pond-and-plug	Pond-and-plug and check dam	None

(Hammersmark et al. 2008). The presence of wet-meadow vegetation was favored by rehabilitation practices because the mean spring and summer depth to the water table was decreased by 1.20 and 0.34 m, respectively, because the water table rose above pre-rehabilitation levels.

Last Chance Watershed, Plumas National Forest

Last Chance Watershed (250 km²) is located in the Feather River Basin on the eastern slope of the Sierra Nevada in the rain shadow of the mountain crest at an elevation of 1,680–2,350 m (Table 1). It is located in a semiarid environment with mean annual precipitation of 410 mm. Most precipitation occurs as snow during the winter with runoff and recharge occurring during spring snowmelt. The bedrock of the study area contains volcanic flows, pyroclastic deposits, and granitics described in Table 1 and mapped in Fig. 2 (Durrell 1987; Lydon et al. 1960). Given these lithologies, the hydraulic conductivity (K) of the granite bedrock is likely much less than that of the Miocene pyroclastics; the Tertiary rhyolites likely have a K value intermediate to these two lithologies (Freeze and Cherry 1979). The riparian floodplains consist of silty Quaternary alluvial and lacustrine deposits and collectively form one of the longest continuous meadow systems in the Sierra Nevada.

Wet meadows are classified as groundwater-dependent ecosystems because of their reliance on shallow groundwater during the dry summer growing season. However, stream incision, primarily from grazing, logging, and road and railroad construction, has lowered the water table resulting in aridification of soils in portions of the meadows. In the Last Chance watershed, a reduction in water availability caused a succession from native wet-meadow vegetation to xeric vegetation (Wilcox 2005; Loheide and Gorelick 2005, 2007). Because of extensive restoration efforts, the Last Chance study area has been designated as a demonstration watershed, in which pond-and-plug and check dam rehabilitation sites exist (FRCRM 2004). Pond-and-plug rehabilitation, as described earlier, involves the filling in of incised gullies with sediment excavated for ponds alongside the stream, and check dam rehabilitation includes the installation of low profile drop structures that assist grade control, raise stream water levels, and create small aquatic scour pools on incised streams.

Stream incision results in lowering of the water table and sagebrush (*Artemisia tridentata*) encroachment, which has important hydrological and biogeochemical consequences (Berlow et al. 2002; Elmore et al. 2003; Houghton et al. 1999; Schimel et al. 2001). Woody shrubs can modify streamflow, runoff, recharge, and the ratio of plant transpiration to total evapotranspiration due to changes in evaporative leaf area, volume of root systems and the duration of physiological activity (Huxman et al. 2005). Loheide and Gorelick (2005) have used forward-looking infrared thermal imagery to map and quantify restoration/rehabilitation-induced changes in evapotranspiration at this site using an evapotranspiration-mapping

algorithm (ETMA; Loheide and Gorelick 2005). ETMA provides evapotranspiration estimates of 1.5–4 mm/day for xeric dry land grasses and 5–6.5 mm/day for wet-meadow vegetation (Loheide and Gorelick 2005). Stream incision induces vegetative changes, decreases evapotranspiration rates, and alters the balance of meadow hydrologic processes. Loheide and Gorelick (2007) formalized the linkages between the hydrologic and vegetation changes with a coupled groundwater-vegetation model in an archetypical meadow, based on characteristics of meadows in the Last Chance watershed, which predicted the development and widening of observed swaths of xeric vegetation near channels as the depth of incision increased.

Tuolumne Meadows, Yosemite National Park

Tuolumne Meadows in Yosemite National Park is one of the largest high-elevation meadows in the Sierra Nevada. The meadow is located at 2,600 m elevation and has a drainage area of 186 km², with a mean annual precipitation of 1,000 mm (Table 1). The basin is largely composed of granitic rocks, with metavolcanics on the east. Lower elevations are blanketed with glacial till, which serve as important local groundwater aquifers. The soils of the basin are thin, rocky, and have limited water storage capacity.

Tuolumne Meadows was heavily used as summer pasture for thousands of sheep and cattle each year in the late 1800s, which appears to have resulted in damage to the vegetation. This type of utilization and impact occurred throughout the southern Sierra Nevada (Ernst 1949; Dull 1999). One of the most apparent issues in the meadow today is the invasion of lodgepole pine (*Pinus contorta*), a species that occurs primarily in upland forests. Tree invasion into meadows has been a well researched topic in the Sierra Nevada, Cascade Range and Rocky Mountains in the western US (Vale 1981a, b; Vankat and Major 1978; Millar and Woolfenden 1999; Cunha 1992; Franklin and Mitchell 1967; Patten 1963; Vale 1978). Tree invasion has been blamed on hydrologic changes due to road construction and dewatering, climate change, and heavy livestock grazing which disrupted the meadow sod (Cunha 1992). Cooper et al. (2006) focused on analyzing Tuolumne Meadows to determine what hydrologic factors have influenced the meadow vegetation, and the data collected during that study as well as during the summer of 2007 are discussed here.

Methods

Field methods: water-table depth and vegetation classification

At Bear Creek Meadow, Last Chance watershed, and Tuolumne Meadows, 28, 44, and 73 hand-augered monitoring wells, respectively, were installed across the meadow to characterize water-table depth and its influence on vegetation patterns. At all three sites, some wells were

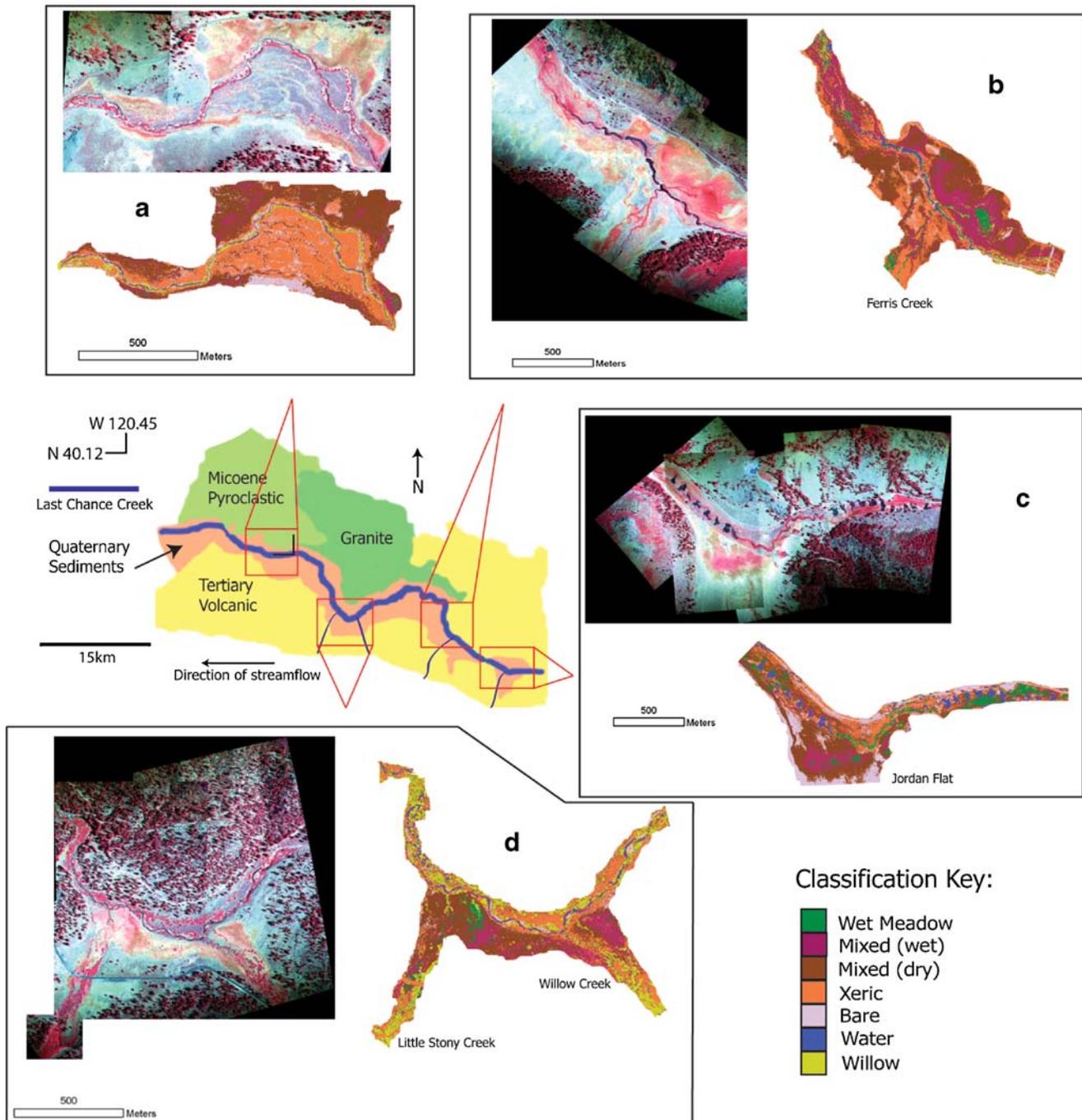


Fig. 2 Geologic map (*center left*) showing location of paired color infrared mosaics (*images*) and vegetation classification (*maps of meadows only*) at four meadows along Last Chance Creek. **a** Asymmetric vegetation patterning with wet-meadow vegetation to the north of the channel and xeric vegetation and abandoned stream channels to the south. **b** Effects of check-dam rehabilitation efforts showing large expanse of dominantly wet-meadow community nearly two decades after project completion. **c** Effects of pond-and-plug rehabilitation efforts with wet meadow and mixed vegetation appearing near the ponds only 1 year after project completion. **d** Wet-meadow vegetation supported by groundwater funneled through the Willow Creek and Little Stony Creek tributary meadows

equipped with continuously recording pressure transducers while others were measured by hand approximately every two weeks during the summer months. At Bear Creek, Hammersmark (2008) sampled vegetation in 128 plots, each 4 m², distributed along 15 transects, and used two way indicator species analysis (TWINSPAN; Hill 1979; McCune and Mefford 1999), to classify the

herbaceous vegetation of the restored meadow. In Tuo-lumne Meadows, a vegetation plot 20 m² in area centered on each well was used to characterize vegetation composition and coverage by species. Vegetation was classified using TWINSPAN (Gauch 1982). In the Last Chance watershed, Loheide and Gorelick (2007) collected vegetation data in 1-m² plots centered on each well and

classified these data into four groups ranging from wet meadow to xeric upland. These data were not originally collected for this cross-site comparison, and further discussion of portions of the data sets can be found in Hammersmark et al. (2008), Hammersmark et al. (2008), Loheide and Gorelick (2007), and Cooper et al. (2006).

Remote sensing methods

For this study, color infrared (CIR) imagery was used to map vegetation in the Last Chance watershed and to determine the hydroecologic processes that led to the observed vegetation patterning. CIR imagery of Last Chance Creek was collected from a helicopter in August 2005 using a RedLake MS4100 multi-spectral camera collecting red, green, and near infrared wavelengths. CIR imagery is valuable for identifying vegetation because healthy, mesic vegetation reflects near infrared electromagnetic radiation to a much greater extent than xeric communities.

CIR data were exported to image processing software (ENVI 4.4) for analysis. 88 CIR images were georeferenced to a digital orthoquadrangle of the Last Chance region and mosaiced. For visualization purposes, the near infrared, red, and blue data are displayed as red, blue, and green, respectively, to produce a false color image. Four example CIR mosaics are displayed in Fig. 2. Maximum likelihood classifications of the four regions of Last Chance were performed using image-processing software to create maps of vegetation cover. Seven regions of interest including open water, bare soil/sand, xeric vegetation, wet-meadow vegetation, mixed-meadow vegetation primarily wet, mixed-meadow vegetation primarily dry, and willows were selected as end members for the maximum likelihood classification. Wet-meadow species in Last Chance include sedges and rushes (e.g. *Carex angustata*, *Carex douglasii*, *Carex nebraskensis*, *Juncus balticus*) whereas xeric vegetation communities include sagebrush and dryland grasses (e.g. *Artemisia tridentata*, *Hordeum jubatum*, *Poa secunda* ssp. *secunda*, *Elymus elymoides*). The vegetation classification has only been applied to the meadows for which it is intended, and the surrounding hillslopes are masked out in the classification images. While this classification should be considered qualitative as the vegetation has not been analyzed on the ground, the data clearly show detailed spatial patterns that cannot be obtained using limited point vegetation analysis.

Analytical and numerical modeling techniques

Meadow aquifers are often fed by groundwater discharge into the meadow system from the hillslopes, which helps to support wet-meadow-vegetation communities (Fig. 3). In order to close the hydrologic budget of the meadow aquifer, the magnitude of the groundwater flux must be accounted for accurately. This water may enter the meadow vertically as a basal flux (N) as well as inflow from the hillslope boundary as lateral flow (Q_x). Both Loheide and Gorelick (2007) and Hammersmark et al. (2008) have recently performed hydrologic modeling

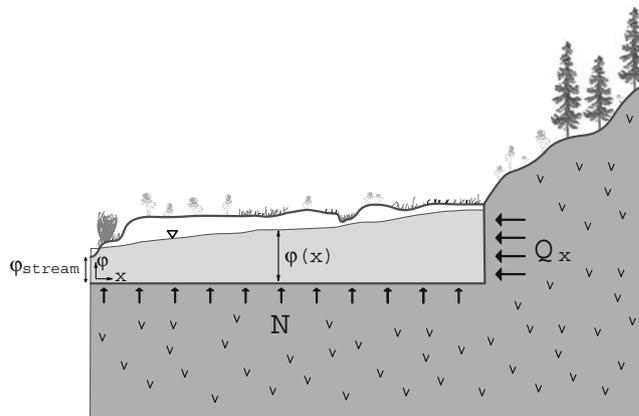


Fig. 3 Conceptual model of regional groundwater flow to the meadow system, which drains towards the stream if the water level in the stream (ϕ_{stream}) is lower than that in the aquifer. This water may enter the meadow vertically through underlying bedrock as a recharge (or accretion) flux (N) as well as from the hillslope boundary as a lateral inflow. The light grey region represents the model domain

studies on meadows and have accounted for regional groundwater flow to the meadow system with the goal of predicting vegetation patterning. At Bear Creek, Hammersmark et al. (2008) simulated discharge to the meadow predominately as a flux which entered the margin of the meadow. In an archetypical meadow representative of Last Chance watershed meadows, Loheide and Gorelick (2007) simulated regional groundwater flow as a basal flux to the meadow. This paper builds on these studies to discuss how the partitioning of this flux between the vertical discharge through the base of the aquifer and the horizontal discharge through the aquifer margin will affect the configuration of the meadow water table and the associated vegetation patterning.

One-dimensional, unconfined, steady-state groundwater flow in aquifers can be approximated using the Dupuit-Forchheimer assumptions (Bear 1972; Haitjema 1995). Analytical solutions were presented by Bear (1972, 1979) for the two extreme cases in which groundwater discharges to the meadow either uniformly as a basal flux (N) or as a lateral flux at the meadow margin (Q_x). For this study, both lateral and basal groundwater discharges are significant, and groundwater drains toward the stream with a head of ϕ_{stream} . Thus, the following solution was developed, which describes the distribution of the hydraulic head, $\phi(x)$, in the meadow aquifer, ($0 < x < L$), which has a uniform hydraulic conductivity (K):

$$\phi(x) = \sqrt{\phi_{\text{stream}}^2 - \frac{2Q_x}{K}x + \frac{N}{K}(2L - x)x} \quad (1)$$

Note, Q_x must have a negative sign to enter the meadow and flow to the left using the coordinate system defined in Fig. 3. If groundwater use by vegetation (ET_G) is to be considered, then N should be replaced by the quantity ($N - ET_G$). It is important to note that the Dupuit-Forchheimer approximation cannot simulate the development of seepage

faces, which may result in overprediction of the depth to the water table near the channel using Eq. (1).

Four scenarios, called A, B, C, and D, were considered to assess the relative importance of: (1) a meadow's hydraulic conductivity, (2) the rate of groundwater flow feeding the meadow, and (3) the partitioning of groundwater flow between basal and lateral fluxes on the position of the water table. In all cases, ϕ_{stream} was set to 2.5 m, and the length of the meadow (L) between the stream and the margin was 100 m. In each scenario, an equivalent inflow of water to the meadow was simulated as occurring 100% as a basal flow, 100% as a lateral flow, or a 50/50% mix of basal and lateral flows. In cases A and B, the high hydraulic conductivity cases, K was set to 10^{-3} m/s, whereas a value of 10^{-4} m/s was used for cases C and D. In cases A and C, the low groundwater inflow cases, the total inflow per unit width of meadow was 5×10^{-6} m²/s. For 100% lateral inflow, $Q_x = 5 \times 10^{-6}$ m²/s and for 100% basal inflow $N = 5 \times 10^{-8}$ m/s. For the high groundwater inflow cases (B and D), these rates were doubled so that the total inflow per unit width of meadow was 1×10^{-5} m²/s.

The magnitude and partitioning of groundwater flow from hillslopes between lateral and basal inflows affects water-table position within the meadow as described by Eq. (1); however, this partitioning is controlled by watershed-scale geologic features, soil hydrologic properties, rainfall and snowmelt rates, and evapotranspiration characteristics of the hillslope vegetation. Two-dimensional, steady-state groundwater flow modeling was used to assess the pattern of discharge to the meadow systems. COMSOL Multiphysics (Comsol 2005), a general purpose finite element modeling environment which has been used for hydrologic applications (e.g. Cardenas and Wilson 2007; Loheide 2008) was used to simulate four cases (I-IV) discussed later. These simulations model a transect from the meadow stream to the ridgetop through the domain illustrated in Fig. 4, which consists of bedrock and meadow sediment subdomains. A

constant inflow rate is specified as the upper boundary condition. A head is specified at the location of the stream within the meadow. No flow boundaries are specified at the lateral boundaries beneath the stream and beneath the ridge top based upon symmetry arguments.

Results and discussion: the groundwater-wet-meadow-vegetation connection

Direct use of groundwater by wet-meadow vegetation

Wet-meadow vegetation relies on shallow groundwater for support throughout the dry summer. Evidence of this dependency and direct use of groundwater by phreatophytes can often be seen as diel water-table fluctuations in detailed water level records collected from wells screened across the water table in environments with a shallow water table (White 1932; Meyboom 1967; Gerla 1992; Loheide et al. 2005; Butler et al. 2007; Loheide 2008). This reliance has been observed as diel water-table fluctuations in meadows alongside Bear Creek and Last Chance Creek (Fig. 5). These records reveal diel water-table fluctuations that show a decline in water-table elevation during the daylight hours, while plant roots extract water from the phreatic zone for transpiration, followed by a recovery period of rising water-table elevation during the night when transpiration is near zero. These water-table fluctuations appear to be a virtually ubiquitous feature when the water table is within the range between the land surface and the maximum rooting depth in wet-meadow ecosystems. If there is ponding on the land surface, water level records are controlled by surface-water processes and generally do not show the typical diel water-table fluctuations, though the pattern can propagate into surface-water flows through the influence this process exerts on surface-water/groundwater interactions (Bond et al. 2002). Conversely, as the water table drops toward the bottom of the root zone, the diurnal fluctuations become

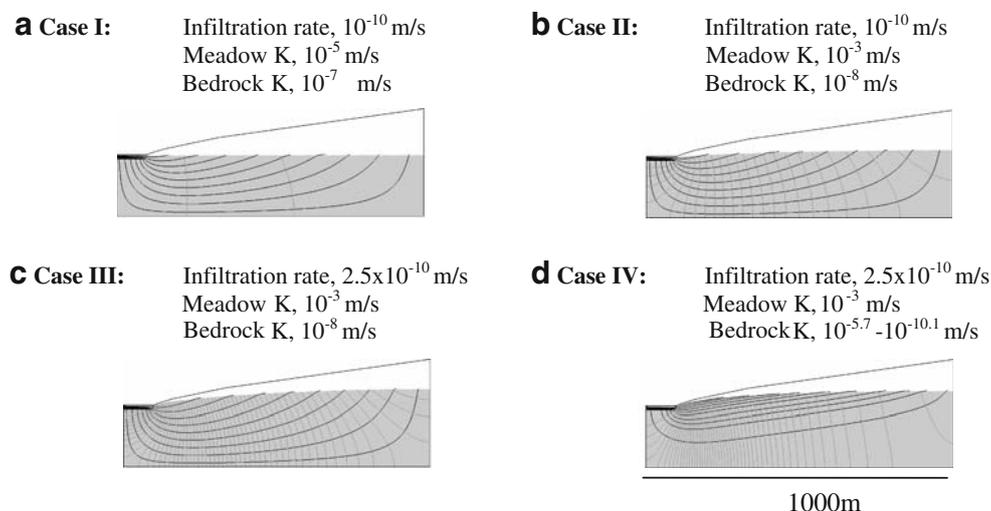


Fig. 4 Regional groundwater flow to the meadow system represented as a cross-sectional flownet through the watershed with *darker lines* representing flowpaths and *lighter lines* representing equipotentials. Cases I-IV are described in the text and illustrate the geologic control of the watershed on the magnitude of groundwater discharging to the meadow as well as the proportion entering as basal and marginal influges

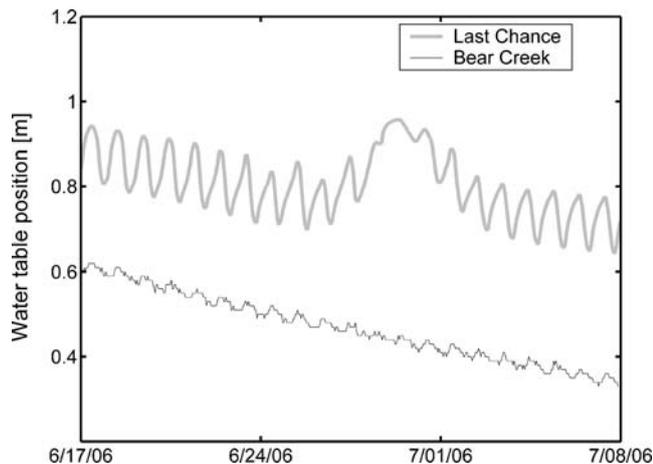


Fig. 5 Evapotranspiration-induced diel water-table fluctuations which demonstrate the groundwater and ecosystem connection in wet-meadow environments. Water-table position is measured from an arbitrary datum

mutated and disappear (Butler et al. 2007; Lott and Hunt 2001). Under these conditions, the vegetation must rely on the limited water available within the vadose zone and may result in early senescence of the vegetation if conditions become too dry.

In Fig. 5, the magnitude of the diel fluctuations differs from site to site. While the amplitude of the fluctuation is indicative of the rate of groundwater consumption (White 1932; Loheide 2008), much of the difference between the sites is due to the water-storage properties of the soil, which is characterized by the readily available specific yield (Meyboom 1967; Gerla 1992; Lott and Hunt 2001; Loheide et al. 2005). Coarse-grained sediments result in smaller observed water-table fluctuations when compared with fine-grained sediments, even for the same root-water uptake rate. This is the primary reason the water-table fluctuations are smaller in the loamy sediment in the vicinity of the

observation well at Bear Creek than the large fluctuations observed at the well located in silty sediment of Last Chance watershed. Evapotranspiration (ET)—driven fluctuations were not observed at most sites in Tuolumne Meadows because groundwater fluctuations were dominated by snow-melt-driven stream discharge variations (Lundquist et al. 2005; Loheide, University of Wisconsin, and Lundquist, University of Washington, unpublished data, 2007).

The data in Fig. 5 were recorded for a 3-week period beginning in mid-June 2006. On 27–28 June, cloudy conditions occurred, and a small amount of precipitation was recorded in the Last Chance watershed (less than 4 mm at the two weather stations). These overcast conditions resulted in lower solar radiation, cooler air temperature, and higher humidity, all of which combined to create much lower potential ET rates. In addition, the small amount of water that infiltrated into the soil provided an additional temporary reservoir of water in the vadose zone that was available to the vegetation. Both the lower potential ET and the greater contribution of soil water to the vegetation resulted in much lower vegetative groundwater consumption during these days. This resulted in a slight rise in the water table, which is likely a result of the reduced groundwater component of ET and the complex interactions that occur between the vadose zone, the capillary fringe, and the water table during rain events (Heliotis and DeWitt 1987). This example indicates that diurnal water-table fluctuations result from groundwater use by vegetation, but do not result from vegetative use of vadose water.

Wet-meadow vegetation communities: observed vegetation patterns in relation to groundwater flow systems

The vegetation classification of Hammersmark (2008) resulted in four community types being identified for Bear

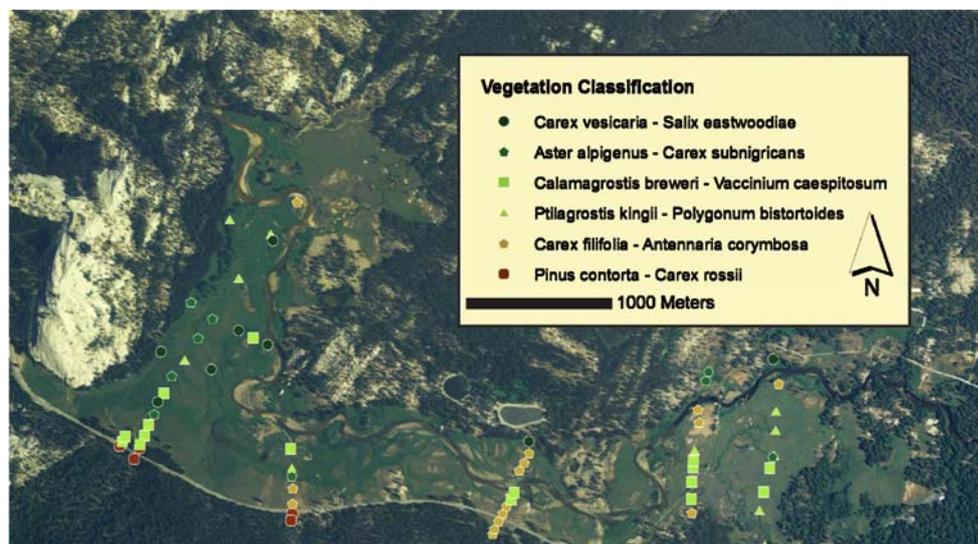


Fig. 6 Aerial imagery of Tuolumne Meadows showing vegetation composition at well locations. Vegetation patterning does not show strong and persistent longitudinal patterns but rather patches that show relationships with abandoned meander channels. The aerial imagery is courtesy of the USDA National Agriculture Imagery Program (2007)

Creek Meadow, which were arranged in three distinct hydrologic groups based on summary hydrologic variables calculated for the growing season (May–August) such as average water-table depth ($\overline{wtd} \pm \text{standard deviation}$), minimum water-table depth, maximum water-table depth, range of water-table depth, and number of days the water-table depth is within 30 cm of the soil surface. Differences between community means for each variable were tested with analysis of variance and Tukey-Kramer honest significant difference (SAS Institute 2004). The *Poa pratensis-Bromus japonicus* ($\overline{wtd} = 119.4 \pm 44.4\text{cm}$) community type was the driest, the *Carex nebrascensis-Juncus balticus* ($\overline{wtd} = 60.3 \pm 12.6\text{cm}$) and *Downingia bacigalupii-Psilocarpus brevissimus* ($\overline{wtd} = 58.5 \pm 19.8\text{cm}$) community types were intermediate and the *Eleocharis macrostachya-Eleocharis acicularis* ($\overline{wtd} = 18.4 \pm 28.0\text{cm}$) community type was the wettest (Hammersmark 2008). The distribution of these communities in the meadow is patchy; however some patterns were observed. The *Poa pratensis-Bromus japonicus* community dominated the upper third of the meadow even in plots 2 to 20 m from the stream margin, while in the lower two-thirds of the meadow, this community type was limited to locations >100 m from the stream margin. The *Carex nebrascensis-Juncus balticus* community type was found near the stream in the lower two-thirds of the meadow. The *Downingia bacigalupii-Psilocarpus brevissimus* community type was limited to the bottoms and margins of channels and swales, which were intermittently or seasonally inundated. The *Eleocharis macrostachya-Eleocharis acicularis* community type was limited to depressions on the floodplain, which were inundated in the early growing season. Importantly, there was no clear longitudinal zonation of vegetation communities, except those related to abandoned channels, which are the currently low-lying swales discussed above.

In Tuolumne Meadows, the vegetation analysis resulted in six plant communities. The *Carex vesicaria-Salix eastwoodiae* community occurred in oxbows along the Tuolumne River that had seasonal flooding and deep standing water. The *Aster alpigenus-Carex subnigricans*, *Ptilagrostis kingii-Polygonum bistortoides*, and *Calamagrostis breweri-Vaccinium caespitosum* communities are the main herbaceous wet-meadow communities. The *Carex filifolia-Antennaria corymbosa* and *Pinus contorta-Carex rossii* communities are found in uplands within or on the edge of the meadow. The distribution of these communities can be seen in Fig. 6, which shows vegetation composition at the well locations overlain on aerial photography. The imagery does not show clear and persistent longitudinal patterning, but rather shows that the position of abandoned river meanders plays an important role in the vegetation patterning, likely due to differences in both sediment texture and topography.

The relationship between groundwater depth and vegetation patterning can be understood by comparing vegetation along water-table transects. For example, the *Carex vesicaria* dominated community occurred in depressions along transect 1 (e.g. 800–850 m in Fig. 7a). The upland communities were located near the road

between 0 and 100 m distance along this transect, where the depth to the water table is the greatest. From 100 to 1,000-m distance along the transect, level meadow areas were dominated by the *Aster alpigenus-Carex subnigricans* community, while communities dominated by *Ptilagrostis kingii* and *Calamagrostis breweri* occurred on raised surfaces that had slightly deeper summer water tables.

Several water sources supply Tuolumne Meadows: the Tuolumne River supplied by its entire watershed, small tributary streams from sub-watersheds, and groundwater from local hillslope aquifers. Along transect 1 (Fig. 7a), vegetation in the region from 800 m to the river is hydrologically connected to and supported by the river. The region between 0 and 800 m is supported by groundwater from local hillslope moraines and bedrock, and the groundwater flow direction is toward the river.

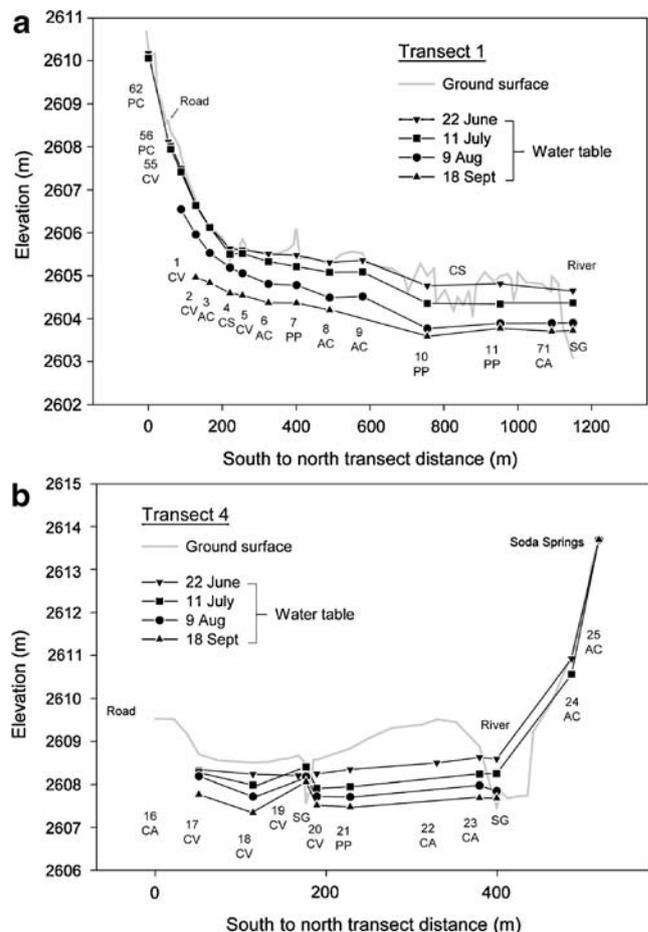


Fig. 7 Groundwater measurements on four dates in 2006 for water level and vegetation monitoring transects **a** T1 and **b** T4 shown on the photograph of Tuolumne Meadows in Fig. 1. The letters beneath the well numbers indicate the vegetation composition as follows: *Carex vesicaria-Salix eastwoodiae* (CS), *Aster alpigenus-Carex subnigricans* (AC), *Ptilagrostis kingii-Polygonum bistortoides* (PP), *Calamagrostis breweri-Vaccinium caespitosum* (CV), *Carex filifolia-Antennaria corymbosa* (CA) and *Pinus contorta-Carex rossii* (PC). Modified from Cooper et al. (2006)

Groundwater supports most areas within Tuolumne Meadows, and the four wet-meadow community types dominated by *Carex vesicaria*, *Aster alpigenus*, *Ptilagrostis kingii*, and *Calamagrostis breweri*, occupy different landscape positions and landforms where suitable summer water-table depths occur. Inundation and saturation to the surface persists longest in *Carex vesicaria* dominated areas and for shorter periods in the *Aster alpigenus*, *Ptilagrostis kingii*, and *Calamagrostis breweri* dominated areas.

Figure 2 shows a geologic map of the Last Chance watershed with paired CIR and vegetation classification at four sites (Fig. 2a–d). The vegetation classification grades from wet-meadow communities dominated by sedges and rushes to xeric vegetation communities dominated by dryland grasses and sagebrush. The typical vegetation pattern observed in meadows with incised channels in Last Chance watershed was described by Loheide and Gorelick (2007), and consists of xeric vegetation in approximately symmetric swaths around incised channels and more mesic and hydric vegetation toward the meadow margin. Figure 2 shows sites that deviate from that strongly longitudinal and symmetric vegetation pattern. Figure 2a shows a highly asymmetric vegetation pattern with a narrow swath of xeric vegetation adjacent to an incised channel to the north which grades into a mesic vegetation community. This is in contrast with a very extensive region of xeric vegetation with only narrow strips of mesic vegetation in remnant channels and at the meadow margin to the south of the channel. Figure 2d shows xeric vegetation to the north of Last Chance Creek and wet-meadow vegetation to the south where two tributaries join Last Chance Creek. Figure 2b and c show the effects of check dam and pond-and-plug rehabilitation, respectively. These vegetation patterns will be used as examples to help illustrate meadow hydroecologic function in the following sections.

Water requirements of wet-meadow communities

The presence of ET induced water-table fluctuations discussed in the previous section indicates groundwater consumption by transpiring plants, and the near ubiquity of these fluctuations in wet meadows indicates that wet-meadow vegetation relies on a shallow water table in the Sierra Nevada and Cascade ranges. Many authors, who have presented this water requirement as either a time-invariant threshold depth to the water table or as a threshold water-table hydrograph that varies through the growing season, have shown that water-table depth is highly correlated with vegetation community type in wet-meadow systems, indicating that local hydrology is the most important factor determining vegetation community type and distribution (Allen-Diaz 1991; Stromberg et al. 1996; Castelli et al. 2000; Darrouzet-Nardi et al. 2006; Dwire et al. 2004; Hammersmark 2008; Kluse and Allen Diaz 2005; Loheide and Gorelick 2007; Martin and Chambers 2001 and 2002; McKinstry et al. 2004; Patterson and Cooper 2007; Sala and Nowak 1997; Steed

and DeWald 2003). While water availability is likely the primary driver of this observed relationship, the underlying physiological reason for this correlation may also be related to drivers associated with water-table position such as soil redox potential (Dwire et al. 2006), thermal influences on biotic processes (Ratcliff and Harding 1993), soil moisture (Stringham et al. 2001), and pedological development and soil chemistry (Chambers et al. 1999). However, it is also important to note that more than one plant community type might exist under the same physical conditions, but one community type prevails simply because it established first at the exclusion of the other community type.

Because strong relationships between water-table depth and vegetation type have been observed in many wet-meadows, Allen-Diaz (1991) noted the potential for predicting changes in vegetation patterning and composition based on water-table configuration. Loheide and Gorelick (2007) and Hammersmark et al. (2008) have pursued this approach based on water requirements they determined specifically for their meadow systems, while Rains et al. (2004), Springer et al. (1999), and Baird et al. (2005) have pioneered the approach in other riparian environments. Henszey et al. (2004) found that for the riparian grasslands in Nebraska, mean growing season water-table depth is not the most important predictor of vegetation type, but rather short-term high water level metrics such as the 7-day moving average water level high and the 10% cumulative frequency curve, were more influential in determining vegetation type.

In the Sierra Nevada and Cascade Ranges, riparian water-table hydrographs follow a very regular pattern: first, the hydrographs reach a maximum elevation, most often at the land surface during the peak of snowmelt, which may be maintained for several weeks to months. Then the water-table drops as meadow groundwater drains to streams and plants consume water. The period of high water, the rate of water-table decline, and the ultimate depth of water at the end of the growing season (i.e., total range of water-table depth) all influence the type of vegetation found at a site. The persistence of wet-meadow vegetation is constrained by two hydrologic features: (1) the early-growing season moisture conditions must be sufficiently wet to cause waterlogged and anaerobic conditions which wet-meadow vegetation can tolerate but is inhospitable to competing upland vegetation communities and (2) sufficient moisture must remain during the late-growing season to support plant growth and reproduction. Like Henszey et al. (2004), Hammersmark (2008) found that mean water-table depth was not the most robust predictor of species presence, but rather minimum (shallowest) water-table depth and the number of days that the water table was within 30 cm of the soil surface were the summary variables most strongly correlated with the different communities. Because of the strong seasonality of climate in the region, all of these features can be captured in a vegetation threshold hydrograph approach as proposed by Loheide and Gorelick (2007). These thresholds describe the maximum water-

table depth required by a vegetation community as it varies throughout the growing season. They are determined empirically, by obtaining the water-table depth hydrographs from several wells located in a given vegetation community for representative years (typically at least one wet year and one dry year). This threshold can then provide an envelope of groundwater hydrographs which are suitable for a given vegetation type. A similar red-yellow-green water-table regime suitability approach has been proposed by the Environment Agency in the UK (Wheeler et al. 2004). While these threshold approaches appear to provide a robust prediction of vegetation community at sites where extensive data are available, little is known about the transferability of these water requirement relationships from site to site. The effectiveness of these threshold approaches, as well as hydrologic metrics used to determine jurisdictional wetlands, is dependent on their ability to characterize whether the extent and duration of the hydrologic wet period is aligned with the growing season. A framework is proposed which may be useful for predicting how elevation, which corresponds to growing season length, and soil texture, which controls capillary rise, may affect wet-meadow water requirements. On average, phenologic stages of wet-meadow vegetation (Ratliff 1983) are reached later in the year at higher elevations, due to later snow melt and cooler temperatures. Even though there is a delay in the onset of the growing season associated with cooler temperatures at higher elevations, a high water table is still required during the early portion of the growing season because it makes conditions undesirable for competing upland plants. In addition, shallow groundwater may need to persist until mid-summer to nurture wet-meadow vegetation through the critical reproductive stages in a low elevation meadow, whereas similar vegetation at high elevation exposed to similar soil and nutrient conditions may require shallow groundwater through late-summer. This elevation variation in water requirements is represented schematically in Fig. 8a as a shift to the right for a conceptual vegetation threshold hydrograph (Loheide and Gorelick 2007) that is expected for a wet-meadow community at increasingly higher elevation.

The late-season portion of the vegetation threshold hydrograph required to support wet-meadow vegetation also varies from site to site because of differences in soil texture and the resulting capillary rise. Fine-grained soils have a larger capillary fringe, resulting in larger volumes of soil water above the water table, much of which may be accessible to plants even though the water table itself is below the root zone. There are two sources from which plants can extract water under these conditions. First, they may deplete the finite volume of water stored in the vadose zone directly. Second, by extracting this water, they lower the matric potential in the vadose zone and create an upward gradient which drives water flow from the water table into the vadose/root zone above. These capillary effects tend to be greater in finer-grained soils with low values of α and β in the Van Genuchten (1980) model of soil water retention (Carsel and Parrish 1988).

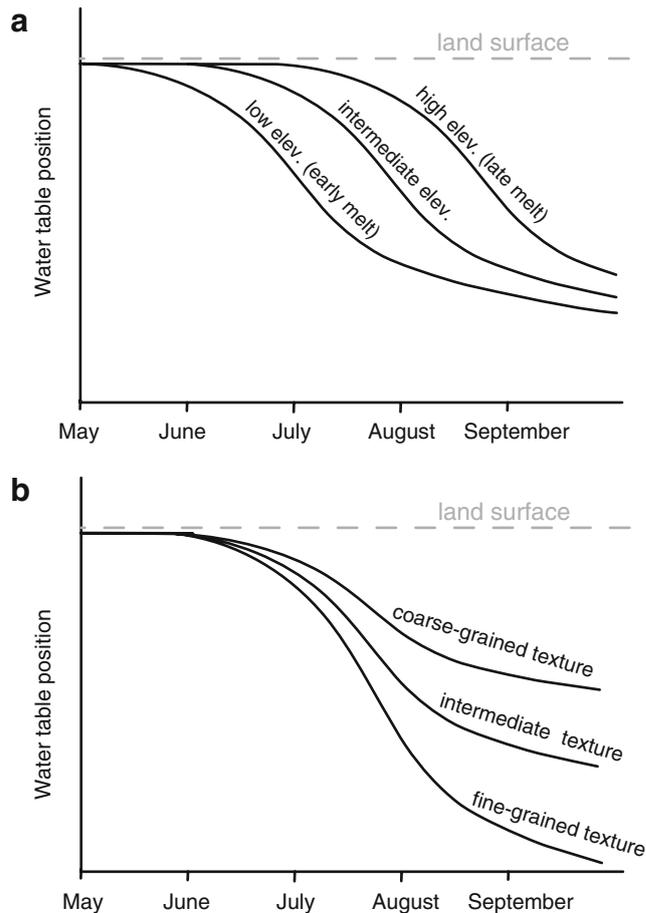


Fig. 8 Proposed shifts in the vegetation threshold hydrograph required to support a wet-meadow vegetation community at **a** different elevations and **b** in soils of various textures

For these two reasons, loamy and silty soils have more available water in the vadose zone just above the water table, and can support wet-meadow vegetation with a slightly deeper water table. This effect on the vegetation threshold hydrograph is depicted conceptually in Fig. 8b as a downward extension of the vegetation threshold hydrograph as soil texture fines from sands and gravels to silt sized-particles. None of the study sites had clay soils, which do not typically support meadow vegetation in the Sierra Nevada and Cascade Ranges, so this soil type was not considered. Figure 9 shows multi-year average water-table hydrographs collected from shallow wells sited within wet-meadow communities from the three study areas. The hydrograph for Last Chance watershed represents the mean of water level records from 2004 and 2005 from seven wells in wet-meadow vegetation plots based on data from Loheide and Gorelick (2007). The hydrograph for Bear Creek represents the mean of simulated water level records from 2004–2006 for 47 plots in the *Carex nebrascensis*-*Juncus balticus* wet-meadow community from Hammersmark (2008). The hydrograph for Tuolumne Meadows represents the mean of eight water level records from wells sited in the *Aster alpigenus*-*Carex subnigricans* wet-meadow community type for 2006 and 2007.

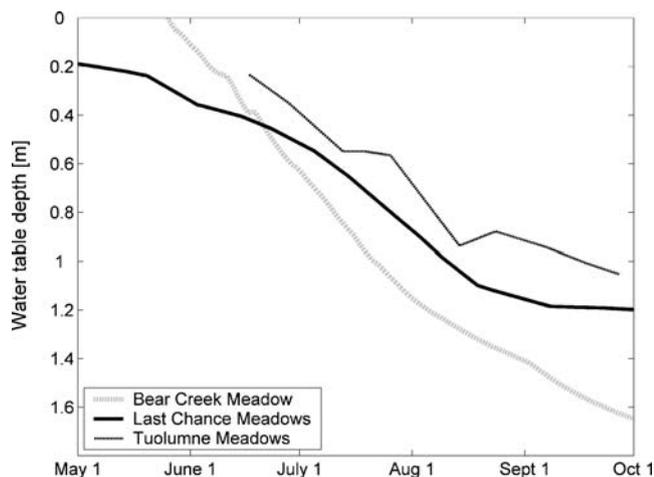


Fig. 9 Observed mean water-table depth hydrograph (multi-year average) for sedge and rush dominated wet-meadow communities at Bear Creek, Last Chance, and Tuolumne Meadows

While the observations are limited, they appear to be consistent with the predicted effects of soil texture and elevation on vegetation threshold hydrographs. First, Fig. 9 shows a general shift to a higher water table at later dates (shift to the right) as elevation increases from Bear Creek, to Last Chance, to Tuolumne Meadows. Second, the shallowest late season water-table depths are found at the site with the coarsest soil, Tuolumne Meadows. Bear Creek, with silty-clayey loam soils, has the deepest mean hydrograph, and Last Chance, with predominantly silts, has an intermediate hydrograph, even though a large soil textural difference is not evident between the sites. It is unclear whether the slightly higher clay content at Bear Creek could account for the downward stretching of the water-table hydrograph that was observed.

To support the hypothesized elevational and sedimentological effects on the vegetation threshold hydrograph, additional data and study are required. First, the mean observed hydrograph for a vegetation community is not the vegetation threshold hydrograph for the community. The actual water-table depth observed at a site could be substantially higher than the minimum, or threshold, required for that vegetation community. Second, the records available from only three sites over 2- to 3-year periods are not sufficient to determine the long-term average water-table hydrographs given the large interannual climatic variability of the Sierra Nevada and Cascade ranges. Although the interannual variability of water-table depth and timing is large, each of the study sites included data from at least one water year (2004 and 2007) ranked among the driest quartile, with earliest snowmelt, within the past 90 years, and at least one year (2005 and 2006) ranked among the wettest quartile, with latest snowmelt, within the past 90 years, based on 90-year records from the Merced River at Happy Isles, which are highly correlated with California-wide snowpack characteristics (Peterson et al. 2000). Thus, while the durations of observations were short, they do sample the known variability in regional climate.

Despite these caveats, the limited comparisons made in Fig. 9 indicate that the hypotheses proposed in Fig. 8 may provide a useful framework for transferring vegetation threshold hydrographs between sites. Predicting these vegetation threshold hydrographs at degraded sites where original data cannot be collected is critical to designing restoration/rehabilitation projects that will meet the water requirements of desired vegetation. Further evaluation of this framework in controlled greenhouse studies where sufficient replicates can be performed and true thresholds can be assessed is required to validate these hypotheses.

Modeling insights on geologic controls of groundwater discharge to meadows: implications for vegetation patterning

While groundwater flow in meadows is transient, responding to seasonal patterns and hydrologic events, several generalizations can be made from the steady-state analysis presented here. Results from the analytic model described by Eq. (1) are presented for the four cases (A–D) considered in Fig. 10. As demonstrated by Haitjema and Mitchell-Bruker (2005), the water table does not always mimic surface topography. Figure 10a and b show that if the hydraulic conductivity is large relative to the groundwater inflow rate (cases A and B), the resultant water table is very flat. Because the water table is flat, spatial patterns in the depth to the water table (land elevation minus water-table elevation) are controlled by topographic variability rather than the subtle water-table gradient. The ecohydrologic consequence of this is that vegetation patterning, which can be predicted with depth to the water table, is topographically controlled.

High hydraulic-conductivity meadow sediment and relatively gradual hydraulic gradients exist at Tuolumne Meadows and Bear Creek, as horizontal transport is controlled by lower sand and gravel layers. Figure 7b shows the topography and water level measurements along a transect crossing the Tuolumne River in Tuolumne Meadows. Sites 17, 18, 19, 20 along this transect are dominated by *Calamagrostis breweri* and *Vaccinium caespitosum* (Cooper et al. 2006), a vegetation community which is characteristic of wet meadows (Ratliff 1982), whereas site 21 is vegetated with a grassland community which has high canopy coverage of *Ptilagrostis kingii*, *Danthonia intermedia*, and *Antennaria corymbosa*. The higher ground between site 21 and 23 is occupied by a xeric (dry meadow) community which is dominated by *Artemisia tridentata* and also includes *Carex filifolia*, *Antennaria corymbosa*, *Muhlenbergia filiformis* and *Solidago multiradiata*. On the opposite side of the river, groundwater levels are controlled by discharge associated with Soda Springs, and *Aster alpigenus*, *Muhlenbergia filiformis*, *Dodecatheon alpinum*, and *Juncus balticus* are the dominant species present at Soda Springs. Because of the high hydraulic conductivity of the sands and gravels in this portion of Tuolumne Meadows, the water table perpendicular to the Tuolumne River is relatively flat.

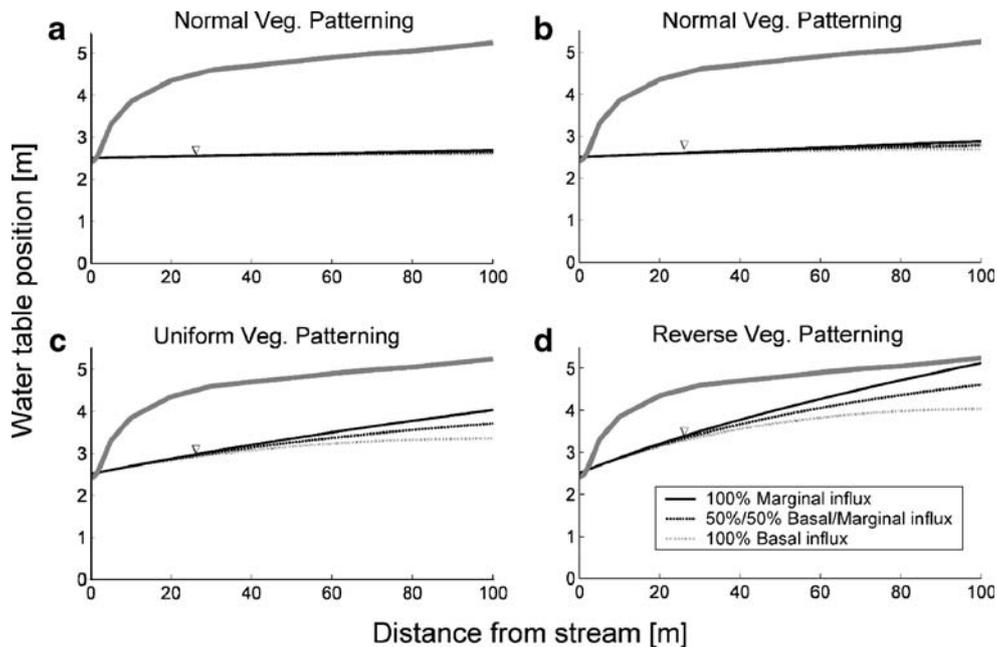


Fig. 10 Water-table position as predicted by the steady state model represented by Eq. (1) for the case with a stream with a stage of 2.5 m at the left side of the domain ($x=0$ m) and a meadow margin at the right side of the domain ($x=100$ m). **a** and **b** represent cases A and B, respectively, with sediments of high hydraulic conductivity ($K=10^{-3}$ m/s), whereas **c** and **d**, cases C and D, respectively, represent meadows with sediments of lower hydraulic conductivity ($K=10^{-4}$ m/s). **a** and **c** represent cases with lower groundwater inflow, whereas the right two panels represent cases with higher groundwater inflow to the meadow. Although the lines in **a** and **b** overlap, each panel shows three lines representing the inflow as completely a basal influx, as completely a marginal influx, and as a mixed influx

The topographic high near the stream creates a greater depth to the water table and results in a drier vegetation community in this region.

Similarly, local topographic features are very important to the resulting mosaic of vegetation distribution. Remnant channels/swales are common at Bear Creek, Tuolumne Meadows, and Last Chance watershed such as those seen to the south of the stream in Fig. 2a, through Tuolumne Meadows in Fig. 6, and between 780 and 880 m in Fig. 7a. These depressions provide locations with shallower depth to groundwater, and thus favor hydric, and in some cases vernal pool, species assemblages.

On the other hand, meadows with sediments of lower hydraulic conductivity (cases C and D) relative to regional groundwater discharge to the meadow result in water tables that slope strongly toward incised stream channels (Fig. 10c and d). If the topography of the meadow is relatively flat, then the water-table position, which is related to distance from the stream as shown by Eq. (1), is the primary determinate of water-table depth and vegetation patterning. As demonstrated by Loheide and Gorelick (2007) for an archetype meadow, this is clearly the case in silty sediments such as those found in the Last Chance watershed. As illustrated in Fig. 10, when the water table slopes strongly toward the incised channel (because the stream is incised and the hydraulic conductivity is low), the greatest depth to the water table occurs just outside of the incised meander belt, resulting in a swath of xeric vegetation near the channel, whereas more mesic and hydric vegetation occurs near the margin of the meadow. This distinctive vegetation patterning caused by stream

incision resulting in swaths of meadow degradation is shown in Fig. 2a and d as well as in Loheide and Gorelick (2007). While this pattern is typically somewhat symmetrical on both sides of the incised channel, Fig. 2a shows a highly asymmetric case where a very wide swath covering almost the entire meadow exists to the south of the deeply incised channel (~ 3 m), whereas a very narrow xeric swath quickly transitions to mixed mesic vegetation to the north. A large difference in hydraulic conductivity of the meadow sediments (higher to the south) could result in the flatter and deeper water table which is inferred to the south; however, there is no evidence that the sediments differ on opposite sides of the channel. Rather, a major geologic contact between relatively high- K Miocene-aged pyroclastics and lower- K , Tertiary-aged, rhyolitic volcanics occurs beneath the meadow shown in Fig. 2a. This geologic difference results in greater groundwater discharge from the northern hillslopes resulting in a higher water table and a wetter vegetation community on the north side of the channel compared with the meadow to the south. Comparison of Fig. 10c and d shows that even a factor of two increase in groundwater discharge to the meadow can appreciably raise the water table in the meadow, particularly near the margin (~ 1 m increase).

Elsewhere along Last Chance Creek, a contrast in vegetation community types can be seen on opposite sides of the meadow in Fig. 2d. The north side of the meadow is bounded by a granitic hillslope with very low hydraulic conductivity and little groundwater discharge. As a result, groundwater in the meadow drains nearly completely to the deeply incised channel, and xeric vegetation domi-

nates. On the south side, the forested hillslopes have developed on Tertiary volcanics. While these rocks did not result in high groundwater discharge to the meadow in Fig. 2a, this geologic unit is the source of all perennial streams within the watershed.

These valleys, whether perennial or ephemeral, convey groundwater toward the main stem channel. Thermal remote sensing similar to that presented by Loheide and Gorelick (2006) identified groundwater discharge to the main stem of Last Chance from several of these tributary meadows (unpublished data). Remote-sensing-based vegetative analysis of the Last Chance watershed indicates that no fewer than nine tributary meadows with wet-meadow vegetation funnel groundwater from the regions of the watershed with Tertiary volcanic bedrock. Examples are Doyle Crossing (Loheide and Gorelick 2005), Jordan Flat (shown in Fig. 2c) and the confluences of Little Stony Creek (ephemeral) and Willow Creek (perennial) to Last Chance (shown in Fig. 2d). These tributaries result in a large lateral influx (large Q_x in Fig. 3) into the main-stem meadow, which supports a high water table and wet-meadow vegetation, as well as supplying baseflow to the main stem channel even during times when there is no surface contribution.

The example of tributary groundwater contributions to main stem meadows is a clear example of lateral groundwater inflow, but regional groundwater flow can also reach the meadow as a basal flux. Loheide and Gorelick (2007) assumed that basal groundwater inflow was the primary inflow of groundwater to the meadow and estimated the magnitude of this flux based on measured vertical hydraulic gradients and estimates of sediment hydraulic conductivity. On the other hand, Hammersmark et al. (2008) determined that groundwater flow to Bear Creek Meadow occurred as lateral flow from an adjacent irrigated area along a portion of the meadow margin. Similarly, as reported by Patterson and Cooper (2007), shallow lateral groundwater flow at Drakesbad Meadow in Lassen Volcanic National Park (California) was the primary source of groundwater inflow and was disrupted by road conditions.

The authors recognize that the end member cases of only basal or lateral inflow may not be common, and it may be more typical that a meadow will receive water from a combination of both sources. The model presented in Eq. (1) is able to provide insight into how partitioning of groundwater inflow between basal and lateral fluxes affects water-table position. Plots a–d of Fig. 10 illustrate the difference in water-table position for each of the four cases. In all cases, lateral inflow results in a higher water-table position at the meadow margin than an equivalent inflow of water distributed as a uniform basal flux. This result occurs because the flux at all locations is Q_x in the lateral inflow case, whereas the flow decreases from $N \times L$ to 0 from $x=0$ to $x=L$ in the case of a basal flux, as the discharge to the meadow occurs uniformly between the channel and the meadow margin. Because the flux goes toward zero as x increases in the basal inflow case, the gradient required to move water through the meadow

aquifer toward the stream is less than that of the lateral inflow case at all positions greater than $x=0$, and in fact, the hydraulic gradient goes to zero at $x=L$ in the basal inflow case. Because the lateral inflow results in a higher water table near the meadow margin, lateral inflow is more likely to result in wet-meadow vegetation than an equal amount of basal inflow.

Four scenarios were used to determine the effects of inflow rates and bedrock and meadow hydraulic conductivity values on the distribution of groundwater discharge to meadows. The results and parameters for these scenarios are given in Fig. 4. In case I, a low inflow rate and a high bedrock K value was simulated as a base case. This simulation showed that while the majority (~70%) of discharge to the meadow occurred through the base of the meadow, a non-negligible portion of groundwater also entered the meadow horizontally at the meadow bedrock interface.

In case II, the same inflow rate was simulated as in case I, but both a higher meadow hydraulic conductivity and lower bedrock hydraulic conductivity was simulated. While the contrast between meadow and bedrock conductivity changes by three orders of magnitude in a way that encourages more groundwater discharge to the margin of the meadow, the difference is less than 10% and would not be a primary factor in most geologic settings.

In case III, the same values of bedrock and meadow hydraulic conductivity are simulated, but the inflow rate is increased by a factor of 2.5. While this change causes a 150% increase in groundwater discharge to the meadow, it has very little effect on the partitioning of groundwater inflow to the meadow between the lateral and basal fluxes.

In case IV, the same inflow rate and meadow hydraulic conductivity is simulated, but a hydraulic conductivity of the bedrock decreases from $10^{-5.7}$ m/s at the top point of the cross section shown in Fig. 4 to $10^{-10.1}$ m/s at the base. This decrease is based on a linear decrease of the log of the hydraulic conductivity and is intended to represent a decrease in hydraulic conductivity with depth often observed when fracture aperture decreases due to the increasing pressure with depth. In this case, most of the groundwater flow to the meadow is lateral flow rather than a basal flux. At Bear Creek, a decrease in hydraulic conductivity with depth occurs as the lacustrine sediments are encountered and likely encourages a greater percentage of the discharge to enter the meadow as a lateral, rather than basal, flux. This analysis shows that under reasonable geologic conditions, either lateral or basal groundwater inflow may dominate even in watersheds with relatively uniform geology.

The analysis above assumes relatively homogenous geologic characteristics. However, in most watersheds of the Sierra Nevada and Cascades, geologic heterogeneity and locations of fractures and faults also play a considerable role in determining groundwater flow paths and the distribution of groundwater discharge areas. In fact, mesic and hydric vegetation communities, often associated with springs and surrounded by more xeric vegetation, are the primary indication of the location of these discharge areas.

Springs and associated vegetation of this type are found at each of the three sites considered. For example, springs at Bear Creek Meadow support areas dominated by the *Carex nebrascensis*–*Juncus balticus* wet-meadow community. In the Last Chance watershed, discharge areas such as these exist on slightly raised topography relative to the surrounding xeric meadow and supports small patches (~3 m diameter) of willows, sedges, and rushes. At Tuolumne Meadows in Yosemite, Soda Springs supports wet-meadow vegetation as discussed earlier and shown in Fig. 7b.

Management and restoration implications and conclusions

Every meadow in the Sierra Nevada and Cascade ranges is unique, and no research site will provide a perfect analogue to guide land managers and restoration practitioners in understanding the hydroecology of a specific site. The purpose of this paper has been to use three intensively studied meadows to describe the general hydroecology of meadow systems and suggest a framework that might help to explain (1) how vegetation water requirements vary along elevational and soil textural gradients and (2) how hydrogeologic characteristics influence the groundwater flow system and vegetation patterning of a meadow.

Wet-meadow vegetation patterning and ecology is tightly linked to hydrologic patterns and processes in the Sierra Nevada and Cascade ranges (Allen-Diaz 1991; Castelli et al. 2000; Darrouzet-Nardi et al. 2006; Dwire et al. 2004; Hammersmark 2008; Kluse and Allen Diaz 2005; Loheide and Gorelick 2007; Martin and Chambers 2001, 2002; McKinstry et al. 2004; Patterson and Cooper 2007; Sala and Nowak 1997; Steed and DeWald 2003). The high seasonality of precipitation in this environment results in the driest portion of the year corresponding with the summer growing season, when vegetation water consumption is greatest. Wet meadows form where a shallow water table during the summer fulfills the water requirements of this groundwater-dependent ecosystem.

Humans have disrupted the hydrologic regime of these ecosystems both intentionally through channelization, stream straightening, drainage efforts, and culvert construction and unintentionally through feedbacks associated with grazing, logging, road and railroad construction, and anthropogenic climate change. These hydrologic alterations have resulted in unanticipated vegetation changes and degraded ecosystem function throughout the meadow systems of the region. All of these commonly cited mechanisms of meadow degradation have one thing in common—each alters the hydrology of the meadow in a way that lowers the water table and triggers a succession to xeric plant species. These altered meadows have insufficient duration of soil saturation within the root zone of plants to be classified as jurisdictional wetlands, under the Clean Water Act (Environmental Laboratory 1987). In addition, the drying of surface soils leads to altered vegetation composition, and meadows can be

dominated by plants which are not typical of wetlands. Thus, many former wetland communities would fail to meet the three parameters required to be considered jurisdictional wetlands, and they would not be regulated by the US government. However, restoration would reverse this process, and many restored and rehabilitated meadows would once again meet the jurisdictional requirements for wetlands.

A critical feature of any restoration or rehabilitation effort must involve restoring the hydrologic processes that allow the existence and persistence of a shallow water table throughout the growing season. Both pond-and-plug and check-dam rehabilitation efforts have proven effective in raising the water table and encouraging reestablishment of wet-meadow vegetation as shown in Fig. 2b and c, respectively, although other methods that attempt true restoration may be more suitable in other areas.

The vegetation threshold hydrograph is a simple method for quantifying and visualizing the water requirements of wet-meadow vegetation communities as they vary with time through the growing season. The best technique for determining these water requirements is to monitor water levels on-site or in nearby meadows for several years to determine the range of suitable groundwater regimes for the vegetation community of interest, in the same watershed, at a similar elevation, with similar soil and nutrient conditions. Unfortunately, there are rarely available resources to follow this approach, and the best alternative is to use the most appropriate data available in the literature.

It appears that these vegetation hydrographs should be shifted upward for sites with coarser textured soils and downward for sites with finer textured soils to account for differences in capillarity compared to a reference site. In addition, it is suggested that the vegetation threshold hydrographs should be shifted to the left for lower elevation sites and to the right for higher elevation sites when compared to the reference site. While this paper does not provide a quantitative measure of the magnitude of these shifts, it does provide a useful conceptual framework for understanding how and why a vegetation threshold hydrograph at one site may differ from that at another location.

The steady-state analytical model developed here is not intended to predict water-table elevation within a specific meadow at a specific time, as these systems experience transient conditions, which, as evidenced by the vegetation threshold hydrographs, are an important determinant of vegetation composition. However, this model could be used as a screening tool to compare processes among sites. It is obvious that, if all other things are equal, meadows receiving higher groundwater inflow will have a higher water table and be more likely to support wet-meadow vegetation. In addition, the hydraulic conductivity of the meadow sediments ranges over orders of magnitude and is important in determining the drainage to the stream in meadow systems. Sites with low hydraulic conductivity are more likely to have steeper groundwater gradients toward the stream, resulting in longitudinal vegetation patterning with a deeper water table and xeric vegetation near the channel and a shallow water table and

mesic or hydric vegetation near the meadow margin. Lastly, this model shows that marginal groundwater inflow raises the water table near the margin of the meadow more than an equivalent basal flux feeding the meadow.

Land-managers and restoration practitioners should work to include both of these groundwater inflow processes in their conceptual and physical models of meadow function. Numerical modeling indicates that for watersheds with relatively uniform bedrock hydraulic conductivity, a good rule of thumb is that approximately 70% of the regional groundwater flow entering a meadow occurs as basal flux; however, this value will be reduced if the hydraulic conductivity of the bedrock decreases with depth. Though interflow through soil layers was not considered here, this process could also increase the percentage of water feeding the meadow at the meadow margin.

To understand observed hydroecologic changes, predict future trends, and implement restoration or rehabilitation efforts to prevent or reverse ecosystem degradation in meadow systems (Wright and Chambers 2002; Klein et al. 2007; Loheide and Gorelick 2007; Hammersmark 2008), it is imperative to: (1) quantify the water requirements of wet-meadow vegetation communities, and (2) identify the inflows of water to the meadow and to understand the physical and geologic controls on these processes. The framework presented here identified elevation and edaphic gradients as the primary variables for understanding how vegetation water requirements are expected to differ among sites. The rate and distribution of regional groundwater flow feeding a meadow system, the degree of stream incision, and the hydraulic properties of the meadow sediment are identified as the primary factors influencing groundwater flow in a particular meadow. Recognition of how these factors differ among meadow systems and the effect they have on meadow hydroecology provides resource managers and restoration practitioners with a means for transferring results from reference sites that have been more intensively studied to systems in which they are working.

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