ECOHYDROLOGICAL CONTROL OF DEEP DRAINAGE IN ARID AND SEMIARID REGIONS

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Abstract. The amount and spatial distribution of deep drainage (downward movement of water across the bottom of the root zone) and groundwater recharge affect the quantity and quality of increasingly limited groundwater in arid and semiarid regions. We synthesize research from the fields of ecology and hydrology to address the issue of deep drainage in arid and semiarid regions. We start with a recently developed hydrological model that accurately simulates soil water potential and geochemical profiles measured in thick (>50 m), unconsolidated vadose zones. Model results indicate that, since the climate change that marked the onset of the Holocene period 10 000–15 000 years ago, there has been no deep drainage in vegetated interdrainage areas and that continuous, relatively low (< −1 MPa) soil water potentials have been maintained at depths of 2–3 m. A conceptual model consistent with these results proposes that the native, xeric-shrub-dominated, plant communities that gained dominance during the Holocene generated and maintained these conditions. We present three lines of ecological evidence that support the conceptual model. First, xeric shrubs have sufficiently deep rooting systems with low extraction limits to generate the modeled conditions. Second, the characteristic deep-rooted soil–plant systems store sufficient water to effectively buffer deep soil from climatic fluctuations in these dry environments, allowing stable conditions to persist for long periods of time. And third, adaptations resulting in deep, low-extraction-limit rooting systems confer significant advantages to xeric shrubs in arid and semiarid environments. We then consider conditions in arid and semiarid regions in which the conceptual model may not apply, leading to the expectation that portions of many arid and semiarid watersheds supply some deep drainage. Further ecohydrologic research is required to elucidate critical climatic and edaphic thresholds, evaluate the role of important physiological processes (such as hydraulic redistribution), and evaluate the role of deep roots in terms of carbon costs, nutrient uptake, and whole-plant development.

Key words: deep drainage; ecohydrology; groundwater recharge; xeric shrubs.

INTRODUCTION

Understanding the distribution and state of water in the vadose (unsaturated) zone of arid and semiarid regions requires the integration of hydrological and ecological research. A primary focus of vadose-zone hydrology is quantifying groundwater recharge and pollutant transport, which depend critically on factors that control deep drainage. For our purposes, deep drainage is defined as the downward movement of water across the bottom of the root zone. Our analysis pertains to interdrainage uplands and does not apply to washes and topographic depressions that are subject to inun-

dation and exhibit considerably different water transport dynamics (e.g., Scanlon and Goldsmith 1997, Nimmo et al. 2002*a*). In humid to mesic environments, deep drainage and groundwater recharge are generally considered equivalent, but this may not be true in arid and semiarid regions, where vadose zones are commonly thick and thus lag times between deep drainage and groundwater recharge can be long (Scanlon et al. 1997). In these regions, deep vertical water fluxes are influenced by factors such as long-term climate change and concomitant trends in vegetation structure.

A fundamental aspect of ecology in arid and semiarid regions is that the lack of water imposes limitations on plant growth (Noy-Meir 1973). We might therefore expect that plants would be under a strong selective pressure to maximize soil water extraction and that inter-

actions among plants would be largely governed by access to soil water. Since deep drainage water is not available to the plants, it is a measure of biological response to a resource-limited environment. Improved understanding of deep drainage processes is intimately linked to a commensurate understanding of relevant biological processes.

Because human populations are currently rising in arid and semiarid regions, and use of groundwater is increasing, understanding the interactions between plant processes, soil water fluxes, deep drainage, and groundwater recharge is especially important. Further, these regions are often chosen for hazardous waste disposal, on the assumption that deep drainage is negligible over the long term and therefore buried wastes will not threaten groundwater quality for many generations to come (Reith and Thompson 1992).

Recent research suggests that deep drainage and groundwater recharge do not occur in many arid and semiarid landscapes, which challenges previously accepted estimates of widespread, low rates of deep drainage and groundwater recharge in arid and semiarid regions. In this paper, we describe this research and analyze the potential function of xeric vegetation in this context. We then synthesize research undertaken from a variety of perspectives to describe critical soil-vegetation characteristics and potential biological mechanisms involved in controlling deep drainage over long time scales. Finally, we discuss important gaps in our understanding of deep drainage processes and opportunities for future ecohydrological research.

Evidence for a Revised View of Deep Drainage in Arid Semiarid Regions

The most definitive and generalizable hydrological data have been collected at interdrainage sites characterized by thick, unconsolidated, vadose zones that receive little or no net lateral water input. Our focus is on widely dispersed arid-to-semiarid environments in the western United States. The current vegetation communities typically contain a dominant or codominant woody shrub component such as *Larrea tridentata* (creosote bush), *Artemisia tridentata* (big sagebrush), or *Atriplex confertifolia* (shadscale).

Analyses of soils in these regions typically indicate abrupt reductions in deep drainage coincident with the late-Pleistocene–early-Holocene transition 10 000–15 000 years ago (Scanlon 1991, Phillips 1994). At that time, a relatively cool, moist, regional climate that supported mesic woodland vegetation transitioned to a warmer, drier climate similar to that which supports current xeric shrub plant communities (Benson et al. 1990, Morrison 1991). The strongest evidence for reduced deep drainage at this juncture comes from depth profiles of measured soil pore-water chloride (Cl⁻) concentrations. Atmospherically deposited Cl⁻ is a useful environmental tracer that generally behaves as a conservative solute (Allison and Hughes 1983). Chloride
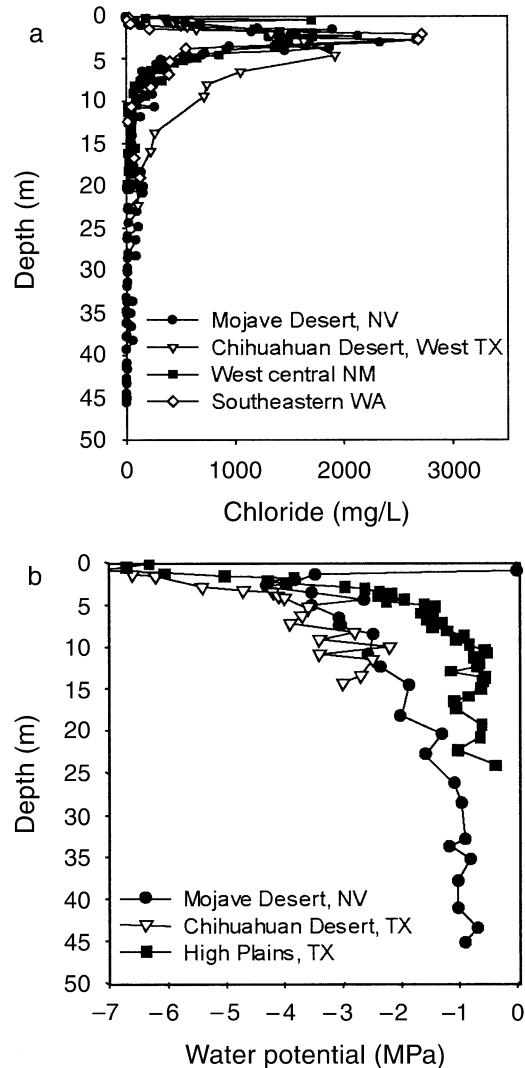

FIG. 1. Vadose zone (a) chloride profiles and (b) water potential profiles measured in semiarid and arid environments (from Walvoord et al. 2002). State abbreviations: NV, Nevada; TX, Texas; NM, New Mexico; WA, Washington.

profiles from semiarid interdrainage regions typically exhibit characteristic "bulges," with high concentrations in the upper 10 m and more dilute concentrations at greater depths (Fig. 1a). A mass balance argument applied to Cl⁻ (e.g., Allison and Hughes 1983) yields typical bulge inventories equivalent to 10 000–15 000 years of atmospheric deposition, which are consistent with low (~1 mm/yr) deep drainage rates during the Holocene. The low concentrations measured below the bulge reflect greater pre-Holocene deep drainage in which Cl⁻ was transported downward more rapidly. The consistency of these observed Cl⁻ profiles across geographic location and edaphic conditions have led some to suggest that vegetation is a key factor controlling deep drainage (Phillips 1994).

TABLE 1.   Input parameters for the one-dimensional multi-phase flow and transport simulations depicted in Figs. 2 and 3.

Property	Value
Water table depth	50 m
Root zone depth	2 m
Porosity	30%
Intrinsic permeability	1×10^{-12} m^2
van Genuchten parameter α	10.0 m^{-1}
van Genuchten parameter n	1.4
Residual volumetric water content	2%
Maximum volumetric water content	29%
Geothermal gradient	30°C/km

This scenario of low deep-drainage rates has been generally accepted in recent years. However, Walvoord et al. (2002) pointed out that relatively recent soil water-potential measurements (e.g., Scanlon et al. 1997) contradict that scenario. These measurements reveal an upward soil water-potential gradient (Fig. 1b) below the root zone, rather than the downward gradient required to support low deep drainage rates. In addition, multiyear soil psychrometry data from vegetated desert soils indicate large seasonal fluctuations in water potentials in the upper few meters, but very low (-2 to -6 MPa) and relatively invariant water potentials below depths of 2–5 m (Andraski 1997, Scanlon et al. 1999, 2003). Soil water potentials in this range are too low to support the previously assumed low rates of deep drainage.

To resolve both Cl$^-$ and soil water-potential data, Walvoord et al. (2002) proposed a conceptual model of deep vadose-zone hydrodynamics for arid-semiarid environments that incorporates the role of xeric vegetation. In this model, continuous, low (< -1 MPa) soil water potentials were established and continuously maintained at the base of the root zone at the outset of the Holocene. This represents an important distinction from previous models that are based on equilibrium or unit-gradient soil water-potential gradients. They tested this conceptual model using FEHM (finite element heat and mass transfer; Zyvoloski et al. 1997), which simulates processes of liquid and vapor water flow and solute transport under nonisothermal conditions using numerical solutions to the differential equations that

govern those processes. Model results indicate that characteristic Cl$^-$ bulge and soil water potential profiles (e.g., Fig. 1) were approximated by implementing the proposed conceptual model (Walvoord et al. 2002).

In order to illustrate modeling results, we performed FEHM simulations subject to representative vadose zone properties (Table 1) and initial and boundary conditions (Table 2). The system initially maintains a steady-state 10 mm/yr downward flux to represent Pleistocene climate and vegetation conditions. Then, a 10 kyr drying trend, simulated by imposing a low sub-root zone soil-water potential boundary condition (-4 MPa at 2 m depth) reflects the drier, warmer conditions and xeric vegetation of the Holocene. The simulated Cl$^-$ and water potential profiles that develop over the latest 10-kyr period (Fig. 2) resemble the characteristic shape and magnitude of observed profiles (Fig. 1). Elimination of regular solute flushing past the root zone subsequent to 10 kyr results in shallow Cl$^-$ accumulation, and Cl$^-$ moves downward by concentration-driven diffusion to produce a Cl$^-$ peak (Fig. 2a). The simulated fixed low water potential maintained at the base of the root zone creates a drying front that moves slowly downward, resulting in the type of curved water potential profile often observed (Fig. 2b). Other conceptual models were tested, but none were found that reproduced both the observed Cl$^-$ and soil-water potential profiles. For example, if increased aridity and 100% evaporation from near the soil surface are assumed, simulated soil water potentials are much greater than those observed (profile for bare soil in Fig. 2b).

It could be hypothesized that Holocene deep drainage and consequent downward transport of Cl$^-$ occurred during rare episodic periods of exceptionally high precipitation. If this were the case, current measurements may not reflect conditions during critical periods of deep drainage, and therefore present a misleading picture of deep drainage processes. Such events would necessarily result in greatly increased soil water potentials with a downward gradient. The model results we present (Fig. 2b) and in Walvoord et al. (2002), however, argue against such processes during the Holocene because thousands of years are required to generate the currently observed soil water potential profiles after such deep wetting events.

TABLE 2.   Initial and boundary conditions for the one-dimensional multiphase flow and transport simulations depicted in Figs. 2 and 3.

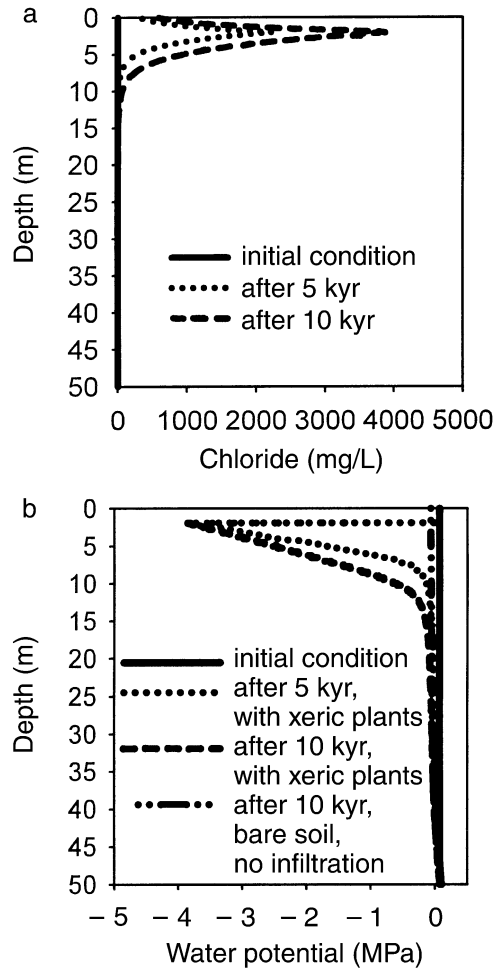| Condition	Initial value	Final value
Deep drainage	10 mm·m^{-2}·yr^{-1}	NA
Precipitation	NA	200 mm·m^{-2}·yr^{-1}
Water potential at water table	0.1 MPa	0.1 MPa
Fixed water potential at 2 m	NA	-4 MPa
Surface chloride flux	70 mg·m^{-2}·yr^{-1}	70 mg·m^{-2}·yr^{-1}
Chloride concentration in porewater	7 mg/L	NA
Surface temperature	18°C	18°C
Water table temperature	19.5°C	19.5°C

Note: NA = not applied.

a

b

FIG. 2. Model-predicted (a) chloride profiles and (b) water potential profiles for simulation times since the initial Pleistocene conditions and establishment of xeric shrub communities. Also shown in panel (b) is the modeled profile for a bare soil with evaporation = precipitation (i.e., no infiltration), illustrating the importance of plant water uptake in generating observed soil water potential gradients.

The emergent picture of soil water movement in deep, unconsolidated, arid and semiarid vadose zones that is consistent with both measured data and simulations is illustrated in Fig. 3. In it, deep percolation was completely eliminated during the Holocene, and there is a very slow upward movement of soil water, mostly as vapor, in response to vegetation-generated low soil water potentials at the base of the root zone. At intermediate depths (20 m in Fig. 3), liquid water flux is downward, reflecting the continued drainage of Pleistocene-age water. Thus, there is simultaneous groundwater recharge and negative deep percolation. Upward vapor flux is continuous through the profile and dominates under the very dry conditions in the upper 33 m of the profile.

The role of vegetation is central to the conceptual model of Walvoord et al. (2002) and the description of

soil water dynamics illustrated in Fig. 3. The conclusion from the analyses summarized above is that climate change early in the Holocene and coincident establishment of xeric shrub vegetation resulted in the establishment of low soil water potentials at the base of the root zone that were maintained over thousands of years.

If verified, this conceptual model raises some intriguing ecological questions concerning water relations and the long-term functioning of arid and semiarid ecosystems. Below, we link these recent advances in hydrologists' understanding of deep drainage to current ecological understanding of the structure and function of root systems and of vegetation change in arid and semiarid environments.

CHARACTERISTICS OF XERIC VEGETATION
NECESSARY FOR CONTROL OF DEEP DRAINAGE

The validity of the conceptual model and supportive FEHM simulations described above, in which native xeric vegetation is assumed to control deep drainage, requires, at a minimum, that the dominant or codominant plant species have two characteristics. First, the roots of those plants must extend to depths of 2–3 m with sufficient density to effectively extract all downward-percolating water within those depths. Second, those plants must be able to generate and maintain relatively low soil water potentials (< -1 MPa) at depths of 2–3 m for very long periods.

Although surveys of the depth and lateral extent of roots show wide variation in root system structure across different plant functional groups and habitats,
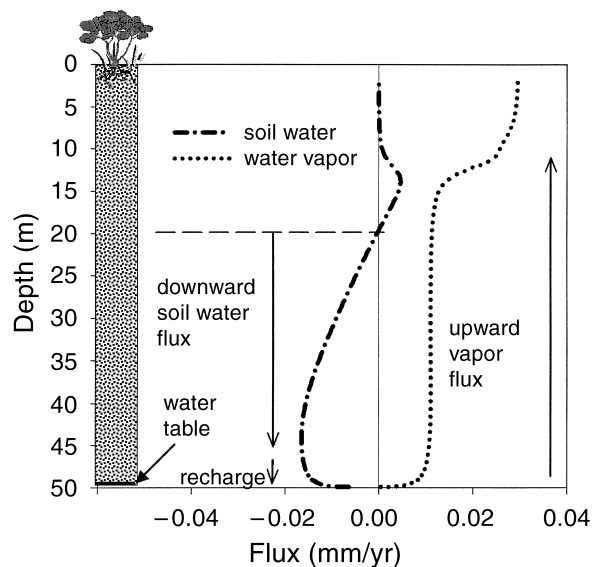

FIG. 3. Model-predicted soil water (liquid) and water vapor fluxes for depths below the root zone 10 kyr subsequent to the establishment of xeric vegetation. These fluxes are consistent with the Cl⁻ and soil water potential profiles in Fig. 2. Negative values indicate downward fluxes.

generalizations about the root zone as a whole can be made on an ecosystem basis (Canadell et al. 1996, Jackson et al. 1996). For example, root densities generally decrease exponentially with depth, less steeply in arid than in more mesic environments (Jackson et al. 1996). Schenk and Jackson (2002*b*) found that maximum rooting depths of xeric shrubs are ~5 m, and that most individual shrubs had maximum rooting depths of ~1.8 m. In some cases, maximum rooting depth may be much greater (Phillips 1963, Canadell et al. 1996). Herbaceous plants in the same environment had shallower rooting depths. The most extensive survey and analysis of root data to date showed that rooting depths tend to increase with mean annual precipitation, and that rooting depths tend to be greater in sandy as opposed to clayey or loamy soils (Schenk and Jackson 2002*a*).

The maintenance of relatively low soil water potentials at depth depends upon the range of water potentials over which plants can take up water. During extended drought, the depth of maximum water uptake shifts down towards regions of higher soil water potential. Water uptake can continue as long as hydraulic continuity is maintained from the soil through the xylem, which is a function of the physical limits on plant water uptake and transport (Tyree and Sperry 1989). Hydraulic failure can occur as a result of xylem cavitation if xylem pressure falls below structurally defined limits or if soil hydraulic conductance at the root–soil interface falls to zero due to high rates of plant water extraction or desiccation (Sperry et al. 1998, 2002). Thus, xylem structure, soil texture, and relative carbon allocation to root and leaf area influence the limit to plant water extraction. However, cavitation vulnerability of the xylem, and root xylem in particular, frequently defines the minimum soil water potential where uptake and transpiration can occur (Fig. 4; Sperry et al. 2002). Extraction limits vary widely among species, with exceptionally low values (−4 to −9 MPa) among critical deep-rooted species such as *A. confertifolia*, *A. tridentata*, *L. tridentata*, *Prosopis glandulosa*, and *Juniperus osteosperma* (Linton et al. 1998, Jackson et al. 2000, Pockman and Sperry 2000, Sperry and Hacke 2002, Sperry et al. 2002).

The actual soil water potentials developed by these plants under field conditions depends, among other things, on edaphic conditions, such as texture (Sperry et al. 1998). Simulations indicate that the soil water potential maintained at the root zone base must be less than −1 MPa in order to generate the observed Cl− bulge and upward potential gradients (Walvoord et al. 2004). The low extraction limits measured for critical xeric shrub species indicates that those plants are physiologically capable of developing and maintaining the low potentials observed in the field (Andraski 1997, Scanlon et al. 1999, 2003) and proposed in the conceptual model (Walvoord et al. 2002).

Thus, it appears that the two plant characteristics required for control of deep drainage—deep roots and
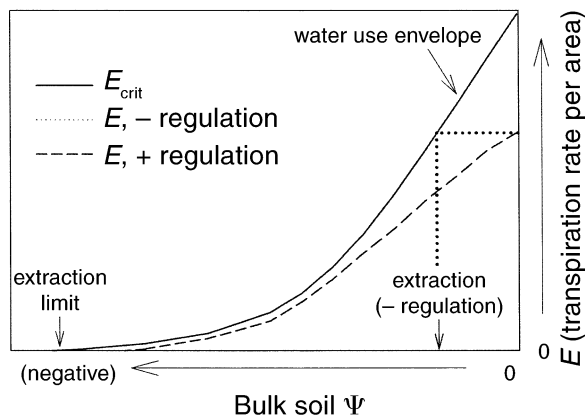

FIG. 4. Water extraction limits for plant roots. The water use envelope, E_{crit}, is the maximal permissible transpiration rate at a given soil water potential, such that any rate higher than this would lead to complete xylem embolism and set the hydraulic conductance of the soil–plant continuum to zero. The dotted line (E − regulation) shows a hypothetical transpiration function in the absence of stomatal control. In this case, transpiration remains maximal until E_{crit} is exceeded and transpiration drops to zero. The dashed line (E + regulation) illustrates how real plants regulate transpiration to avoid loss of hydraulic conductivity. The absolute extraction limit is where E_{crit} itself goes to zero. (This figure is from Sperry et al. [2002] with permission of the publisher.)

low extraction limits—are found in dominant or co-dominant xeric species in the region. While this indicates that the conceptual model is plausible, it does not address the question of how low soil water potentials could be maintained during the highly variable short- and long-term climatic inputs that occur over a large area for very long periods. For them to be maintained, soil water status at depths of 2–3 m in vegetated arid and semiarid vadose zones must be effectively buffered, in a hydrologic sense, from climatic variations that impact near-surface soil conditions.

HYDROLOGIC BUFFERING CAPACITY

To understand how these systems may be buffered from long-term climatic variations and short-term weather extremes, it is important to consider the combined soil–plant system. The following water balance equation provides a framework within which the fundamental relationships between precipitation inputs, soil storage, and deep drainage may be viewed (e.g., Rodriguez-Iturbe 2000). For our purposes, the water balance equation can be written as follows:

$$D_{D} = I - (A_{ET} + \Delta S) \qquad (1)$$

where D_{D} is deep drainage, I is water input (rain or snowmelt), A_{ET} is combined evaporation and transpiration, and ΔS is the change in root-zone water storage. Runoff and runon are not represented in Eq. 1 because they are small relative to the other terms on an annual basis at the upland sites we discuss. All of these terms are expressed as units of length per time (e.g., mm/yr).

The relative magnitudes of the terms partly explain how the soil–plant system is buffered against the high-input events that occur occasionally.

For deep drainage to occur in Eq. 1, I must be greater than $A_{ET} + \Delta S$. In arid and semiarid regions, the soil water content of the root zone typically returns to approximately the same low value at some point within each year (e.g., Seyfried et al. 2001; Schwinning et al., *in press*), so that the year-to-year change in soil water storage is effectively zero. Therefore, for there to be deep drainage within a given year, I must at least be greater than the soil storage capacity (C, mm), which is the maximum value of ΔS for a given time interval. The storage capacity can be calculated as

$$C = P_S \times D \times A_W \qquad (2)$$

where P_S is the soil porosity (volumetric fraction), D is the effective rooting depth (mm), and A_W is the water available to plants expressed as a volumetric fraction of the porosity. The importance of rooting depth is evident. Choosing fairly conservative (sandy loam) estimates of 0.45 for P_S and 0.24 for A_W (Rawls et al. 1982), C is equal to 324 mm for a 3-m rooting depth, which is greater than the mean annual precipitation for most of the region. In this case, generation of D_D would require a time period during the year in which I is 324 mm greater than A_{ET}.

In arid and semiarid regions, large amounts of stored water are not likely to persist. Annual potential evapotranspiration greatly exceeds annual precipitation throughout the region (Smith and Nowak 1990) so that plant uptake of water is generally limited by plant characteristics and the amount of precipitation (or I). In general, plant response to elevated precipitation and resultant soil water storage is to increase transpiration, or A_{ET} (Ehleringer 1995). Annual net primary productivity, and therefore transpiration, of water-limited systems is strongly and often linearly related to annual precipitation (Le Houérou 1984, Le Houérou et al. 1988). As a consequence, relatively wet years tend to be balanced by relatively high A_{ET}.

Ultimately, there are limits to how much transpiration can be generated from sparse semiarid vegetation. It is possible that multi-year trends in annual precipitation (e.g., a decade of wetter than average winters) could overwhelm the buffering capacity of the resident soil–plant system. In this case, transpiration may be increased by slower plant community-level responses that increase longer term transpiration and C. Long-term monitoring of desert vegetation dynamics has shown that wetter-than-average winters appear to promote the expansion of deep-rooted shrubs (Goldberg and Turner 1986, Turner 1990, Brown et al. 1997). Thus, the potential for increased deep percolation during wet decades may be countered by an increase in the density of plants, a concomitant increase in the density of deep roots, and possibly an increase in the depth of the root zone as well.
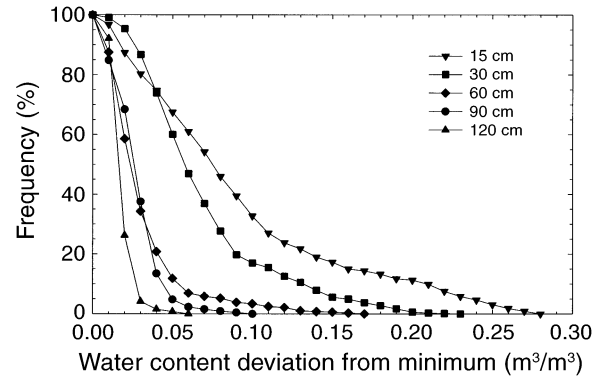

FIG. 5. Frequency (expressed as the percentage of total measurements) with which biweekly soil water content measurements exceeded the minimum measured value by the amount shown on the x-axis for five measurement depths in a sagebrush steppe ecosystem. Given a measurement error of 0.01–0.02 m^3/m^3, these data indicate that depths of 60 cm or greater rarely receive water inputs, and when they do, they are not retained long. See Seyfried et al. (2001) for information on data collection and site information, including weather during the measurement period.

This analysis indicates that the combination of high storage capacity relative to precipitation and plant response to wet conditions may effectively buffer deep (2–3 m) soil water content and potential from exceptional weather and climatic trends in deep-rooted xeric plant communities, thereby enabling them to maintain the low soil-water potentials proposed in the conceptual model. This implies that deep roots are maintained during very dry periods because the transition from dry to wet conditions may be abrupt. More perplexing biological questions are related to how and why plants invest the carbon required to maintain these roots during drought periods. The fact that xeric shrub species from a broad geographic and genotypic spectrum exhibit similar rooting structures suggests that there must be some adaptive significance to these characteristics.

Adaptive Significance of Deep Roots

The growth and maintenance of plant structure, including deep roots, requires a carbon expenditure that should be balanced by the carbon gains facilitated by the presence of that structure. The issue surrounding the carbon economy of deep roots is whether there is enough extractable water in deep soil layers to support the root biomass necessary to extract it.

We illustrate this problem (Fig. 5) with soil water content data collected at 2-wk intervals over a 31-yr period (with a 1-yr gap) in a semiarid *A. tridentata* community in southwest Idaho (Seyfried et al. 2001). Given the length of record, these data represent the soil water regime at depths of 15, 30, 60, 90, and 120 cm under the current climate and vegetation. As noted previously, water content at each depth returned to approximately the same value in late summer each year. We note the frequency of measured deviations from the

minimum measured value, which approximates the amount of plant-available water. Since measurements were evenly spaced throughout the year, the frequencies represent the proportion of time a given amount of soil water was plant available. Measurement error varied somewhat over time with different instruments, but was generally between 0.01 m^3/m^3 and 0.02 m^3/m^3. Thus, a value of 0.05 m^3/m^3 represents a significant change in soil water content over the minimum.

We find that water content in the upper two depths was usually more than 0.05 m^3/m^3 above the minimum, about 70% of the time. In contrast, 60 cm measurements exceeding 0.05 m^3/m^3 occurred only 17% of the time, while the 90 and 120 cm depths did so only 9% and 1% of the time, respectively. In addition, no water content change was observed at 60, 90, or 120 cm for a full decade within the 31-yr measurement period. Yet when water did infiltrate to those depths, it returned rapidly to the minimum value. We attribute this reduction in water content to plant uptake processes, as opposed to drainage, for the following reasons: (1) roots were observed in a nearby characterization pit to a depth of 173 cm; (2) observed water contents correspond to matric potentials of <-1.5 MPa (e.g., 0.06 m^3/m^3 for sandy loam texture at 120 cm), which is much lower than would be achieved by drainage; and (3) the relatively rapid rate of decrease, in less than one season, is indicative of active uptake rather than drainage. These data are consistent with the conceptual model and indicate that some deep roots are maintained, at some expense of carbon, in soil volumes that rarely receive water and therefore contribute little additional carbon assimilation to the plant.

A partial explanation for this apparently ineffective carbon expenditure is that the costs associated with growing and maintaining a root structure at that depth may be low. Deep roots have relatively long lifetimes (Eissenstat and Yanai 1997), and their exposure to root predators probably declines rapidly with depth (although see Freckman and Virginia 1989). There is also some evidence that roots may adjust their basal respiration downward during unfavorable conditions (Holthausen and Caldwell 1980). In addition, the sparse root networks observed in deep soils may be simply a basic infrastructure from which absorbing roots grow during rare, wetter conditions. Numerous experiments have demonstrated that root growth and root absorption rates accelerate in regions of higher resource supply and after rain (North and Nobel 1991, BassiriRad et al. 1999). In cold desert shrubs, the depth of maximal root growth shifts seasonally, presumably tracking regions in the soil where water is most easily extracted at the time, in terms of both temperature and water content (Fernandez and Caldwell 1975). This root growth, which for some shrubs has been shown to account for more than 75% of the annual biomass production (Caldwell et al. 1977), is dedicated primarily to the relatively fine, short-lived roots that are responsible for most water uptake.

Recent observations of the passive redistribution of water through plant roots (e.g., Burgess et al. 1998) indicate that deep roots may provide advantages to the plant other than the direct uptake of soil water. This phenomenon was initially identified as hydraulic lift (Richards and Caldwell 1987), reflecting the observed upward movement of water from relatively moist subsoil to relatively dry surface soil layers following the soil water potential gradient. Subsequent studies have confirmed that hydraulic lift occurs in a variety of xeric species (e.g., Yoder and Nowak 1999) and is one component of the larger phenomenon of hydraulic redistribution whereby root systems can facilitate water redistribution across the rooting zone in either the upward or downward direction (Burgess et al. 1998).

Hydraulic redistribution appears to be a water conservation mechanism for perennial, woody shrubs that has substantial adaptive significance and is most effective when deep roots are present (Ryel et al. 2003b). For example, one of the potential benefits of deep roots is an enhanced ability to survive during long droughts (Smith et al. 1997). When the surface soil is relatively moist after pulses of rainfall, water redistributed downward to deep roots is placed out of reach of other, shallow-rooted plants. The immediate effect is to slow shrub transpiration because the overall net soil water potential is reduced, but as dry conditions persist, this water becomes slowly available to the shrub, allowing it to function during extended drought.

Paradoxically, downward hydraulic redistribution of water in deep-rooted plants may increase the long-term uptake of shallow soil water. This is especially critical because most soil nutrients within the root zone, including N, are concentrated near the soil surface. As the surface soil dries out during dry periods, water stored in deep roots becomes available for transpiration and may also be redistributed back to shallow roots, enabling them to function even when the soil is dry and to rapidly take advantage of small precipitation events (Ryel et al. 2003b). This also serves to keep xylem vessels water-filled and leaves hydrated, enabling deep-rooted plants to return to positive carbon balances quickly after rain. In contrast, more shallow-rooted plants whose xylem vessels embolize and leaves abscise during drought would first have to grow new roots, new leaves, and possibly even new wood.

Downward hydraulic redistribution of water would appear to contradict the conceptual model assumption of a continuously maintained, low soil-water potential. Few data have been collected to date, but a recent study of hydraulic redistribution in *A. tridentata* showed that, while downward hydraulic redistribution caused an increase in soil water potential at depths as great as 1.5 m, soil water potentials at 1.8, 2.4, and 3.0 m were constant and less than -2.5 MPa, even though roots were observed to a depth of 3.4 m (Ryel et al. 2003a).

These continuous, low soil water potentials at depth are consistent with the conceptual model.

Deep roots may also confer advantages during periods with unusually wet winters. By virtue of their greater access to water, deep-rooted plants may remain active longer and thus continue growth and nutrient uptake, possibly near the soil surface (through hydraulic redistribution) at the possible expense of more shallow-rooted plants. This activity, combined with greater plant recruitment during wetter periods, may be responsible for the previously noted increases in deep rooted shrubs during unusually wet winters (Goldberg and Turner 1986, Turner 1990, Brown et al. 1997).

EXTENT OF VEGETATIVE CONTROL OF DEEP DRAINAGE IN SEMIARID REGIONS

We have shown that there is considerable biological evidence in support of the conceptual model proposed by Walvoord et al. (2002). Recall that the hydrologic data consistent with the conceptual model were collected in deep, unconsolidated material in relatively dry environments and do not necessarily apply to all upland arid and semiarid locations. In fact, there is considerable evidence suggesting that there is deep drainage and groundwater recharge in upland semiarid environments. In the following section, we consider the conceptual model as a point of departure for assessing the conditions that may lead to deep drainage in upland arid and semiarid landscapes. Using Eqs. 1 and 2 as a framework, we describe three landscape characteristics in which deep drainage has been documented and propose that, where these characteristics are found, deep drainage is most likely to occur. These landscapes are important both in terms of assessing water supply and quality.

The importance of the water-storage capacity of the soil (C) as a buffering mechanism was emphasized previously. A common characteristic of areas in which C may be greatly reduced is the presence of fractured bedrock close to the soil surface (overlying soils are less than 1–1.5 m deep). The same xeric shrub species are often found to be dominant on these soils. Although the hydraulic properties of rock formations are highly variable, rock fractures commonly accommodate substantial water flows (Nimmo et al. 2002b). The presence of fractured rock does not necessarily reduce the rooting depth, but it may greatly reduce both P_S (which may effectively be the fracture volume) and A_W, especially where the rock imbibes little water. Thus, where soils are shallow and bedrock is fractured, storage is greatly reduced and the probability of deep drainage greatly increased. Deep drainage and groundwater recharge have been observed in semiarid regions underlain by basalt (Stephenson and Zuzel 1981), fractured tuff (Newman et al. 2001), and limestone (Jackson et al. 1999, Bellot et al. 2001). Most watersheds include some areas in which soils are shallow to bedrock. In sloping terrain, deep drainage in fractured rock

may not result in direct groundwater recharge but in lateral subsurface flow.

Flow in fractured rock may be considered a special case of preferential flow (flow of water down macropores or through water-repellent soils), which temporarily reduces the effective storage capacity of the soil and is not considered in Eq. 1 or Eq. 2. Most examples of preferential flow in unconsolidated material come from relatively humid regions (e.g., Beven and German 1982), where preferential flow is seen in relatively moist soils. Preferential flow associated with shrubs has been documented in arid and semiarid regions (e.g., Seyfried 1991, Devitt and Smith 2002). However, the strong soil water potential gradient away from preferential flow paths in dry, unconsolidated soils tends to absorb flow and minimize its impact below depths of 50–100 cm (Phillips 1994). Nonetheless, this appears to be an important consideration in some semiarid locations (Petheram et al. 2002).

A second characteristic of areas in which deep drainage has been documented is the absence or significant reduction of native xeric shrub vegetation. The replacement vegetation is usually composed of relatively shallow-rooted, often annual, grasses and forbs. This effectively reduces C and A_{ET}, resulting in the penetration of water below the root zone and deep drainage. This effect has been documented in semiarid regions where vegetation has been removed (Gee et al. 1994), where native shrubs have been replaced with annual grasses (Link et al. 1990, Kremer and Running 1996), and where intensive grazing has reduced shrub populations (Aguiar et al. 1996). The deep-drainage-producing effect of these vegetation changes is especially critical at hazardous material storage sites, because creation of the site almost invariably disturbs the native vegetation, which can be extremely difficult to reestablish.

The third, and probably most obvious, characteristic of areas in which deep drainage has been documented in semiarid regions is relatively high water input (I in Eq. 1). The effectiveness of input water in generating deep drainage is dependent on the timing as well as the amount of inputs relative to evaporative demand, so that winter precipitation and snowmelt are more likely to produce deep drainage than equal amounts of summer precipitation. Near Santa Fe, New Mexico, USA, where the mean annual precipitation is ~360 mm/yr, measured Cl^- profiles in sediments yield Cl^- inventories of 6700–8800 years (Anderholm 1994). This is somewhat lower than inventories from drier parts of New Mexico (e.g., Phillips 1994), indicating a transitional environment in terms of deep drainage. Inventories from nearby, higher elevation sites with slightly more precipitation (400 mm/yr) tend to be lower—as low as 1000 years (Newman 1996), indicating that there has been substantial deep drainage during the Holocene.

Very limited data collected to date (see also Walvoord and Phillips [2004]) indicates that the climatic

transition to an environment with Holocene deep drainage tends to be accompanied by a vegetation change to woodland vegetation. In New Mexico, for example, the transitional environment is not vegetated with xeric shrubs, but piñon-juniper woodland at the dry end and ponderosa pine at the moist end. The generality of this observation will not be known without further investigation.

Implications for Future Research

We have shown that the conceptual model presented by Walvoord et al. (2002) is plausible in that, given climatic and edaphic constraints, native xeric vegetation may be capable of generating and maintaining low soil-water potentials and eliminating deep drainage. In an attempt to identify possible biological mechanisms involved and their potential adaptive significance, we have synthesized research from different disciplines carried out for different purposes to address the question of deep drainage. This unique synthesis of information yields an ecohydrological, as opposed to a merely hydrological or ecological, perspective. The hydrological constraints imposed by the conceptual model present an opportunity for more focused ecohydrological research—both to examine biological responses to a water-limited environment (which necessarily involves a close look at belowground processes) and to manage semiarid regions in a way that achieves a sustainable water supply and good water quality.

Better and more focused research of this kind will require the development and testing of more realistic and more comprehensive models in conjunction with process oriented research. Ideally, such models would incorporate explicit mechanistic descriptions of hydrological transport processes, including hydraulic redistribution, as well as explicit, semi-mechanistic descriptions of root proliferation in variable environments. Prediction of root growth and distribution may be based on cost–benefit models (e.g., Kleidon and Heiman 1998, Schwinning and Ehleringer 2001, van Wijk and Bouten 2001). Desert plants have recently been shown to take up nutrients from at least 3 m depth (Jackson et al. 2002). Thus, it may be important for the models to include the distributions of macronutrients, such as N and P, and temperature as factors modifying the responses of plants to water availability (Ehleringer et al. 1998). In this context, recent research has shown that, in addition to a conservative tracer like Cl^-, mobile plant nutrients (NO_3^-) may be transported through the root zone in arid and semiarid upland soils (Walvoord et al. 2003). Future research could potentially address critical knowledge gaps by addressing questions such as:

1) What are critical environmental thresholds associated with changes in deep drainage such as may have occurred at the outset of the Holocene?

2) What are the carbon costs and associated aboveground responses related to the development and maintenance of deep roots?

3) What are the short-term plant responses and long-term plant community responses to precipitation changes?

4) What are the impacts of hydraulic redistribution on deep drainage and interspecies dynamics?

5) How can variable upland recharge areas be incorporated into the larger watershed context that includes ephemeral and intermittent stream flow? and,

6) What is the role of nutrient supply and distribution in controlling root growth, distribution and function in arid and semiarid environments?

Finally, it is important to search for deeper patterns or generalizations that may emerge from ecohydrologic research. It has been suggested by Rodriguez-Iturbe (2000) and others that there may be "global properties" or "hidden order" in the stochastic space–time interactions between climate, soil, and vegetation. These may provide a basis for unifying and simplifying a field that would otherwise produce a limitless set of complex process representations derived from local cases. Consider, for example, the surprising degree of uniformity found in Cl^- and soil water potential profiles within a large region containing variable climatic, soil and vegetative characteristics (Phillips 1994). This may be linked to observed variations in plant rooting depth and extraction limits across variable soil conditions (Schenk and Jackson 2002b, Sperry and Hacke 2002). Perhaps there are ecohydrological constraints, as yet undefined, that produce this uniformity.

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