

Phreatophytic Vegetation and Groundwater Fluctuations: A Review of Current Research and Application of Ecosystem Response Modeling with an Emphasis on Great Basin Vegetation

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ABSTRACT / Although changes in depth to groundwater occur naturally, anthropogenic alterations may exacerbate these fluctuations and, thus, affect vegetation reliant on groundwater. These effects include changes in physiology, structure, and community dynamics, particularly in arid regions where groundwater can be an important water source for many plants. To properly manage ecosystems subject to changes in depth to groundwater, plant responses to both rising and falling groundwater tables must be understood. However, most research has focused exclusively on riparian ecosystems, ignoring regions where groundwater is avail-

able to a wider range of species. Here, we review responses of riparian and other species to changes in groundwater levels in arid environments. Although decreasing water tables often result in plant water stress and reduced live biomass, the converse is not necessarily true for rising water tables. Initially, rising water tables kill flooded roots because most species cannot tolerate the associated low oxygen levels. Thus, flooded plants can also experience water stress. Ultimately, individual species responses to either scenario depend on drought and flooding tolerance and the change in root system size and water uptake capacity. However, additional environmental and biological factors can play important roles in the severity of vegetation response to altered groundwater tables. Using the reviewed information, we created two conceptual models to highlight vegetation dynamics in areas with groundwater fluctuations. These models use flow charts to identify key vegetation and ecosystem properties and their responses to changes in groundwater tables to predict community responses. We then incorporated key concepts from these models into EDYS, a comprehensive ecosystem model, to highlight the potential complexity of predicting community change under different fluctuating groundwater scenarios. Such models provide a valuable tool for managing vegetation and groundwater use in areas where groundwater is important to both plants and humans, particularly in the context of climate change.

Groundwater is an important source of water for plants and humans, especially in arid and semiarid regions. In those regions, shallow water tables support

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a greater density of vegetation than in areas with deep water tables by providing additional water for plant growth and transpiration. In the Great Basin-Mojave Desert region of the United States, groundwater recharge is tightly coupled to precipitation (Harrill and Prudic 1998), and thus, water tables fluctuate naturally with drought and wet cycles as well as seasonally (Ganskopp 1986, Nelson and others 1990). The need for fresh water for drinking, irrigation, and other uses has created an increasing demand for groundwater, particularly in fast-growing cities such as Las Vegas and Reno, Nevada (Harrill and Prudic 1998, Simon 1998, Ward 2002). Because extraction may decrease

groundwater levels, vegetation in this region may experience more frequent, rapid, and extended groundwater table declines and fluctuations than in undisturbed systems. Similar scenarios exist in other semiarid regions of the world, e.g., Australia (Hatton and others 1998, Groom and others 2001), South Africa (Le Maitre and others 1999), China (Zhu and others 2004), and the Mediterranean (Bernaldez and others 1989, Puidefábregas and Mendizabal 1998). Thus, understanding the relationship between vegetation and groundwater dynamics becomes crucial to managing and maintaining healthy ecosystems while providing water for human needs.

It is widely recognized that a decrease in groundwater depth can be detrimental to vegetation if the change separates roots from their water source. It may not be widely recognized that an increase in groundwater can also be detrimental, because flooding produces anoxic conditions that also lead to water stress. Although a wealth of information exists on the effects of groundwater level declines on riparian vegetation (Kelliher and others 1980, Brothers 1984, McGlothlin and others 1988, Smith and others 1991, Stromberg and others 1993, Grantham 1996, Stromberg and others 1996, Scott and others 1999, Rood and others 2000a, Stromberg 2001, Horton and others 2001), comparatively little research has been conducted on the effects of fluctuating water tables (Mensforth and Walker 1996, Shafroth and others 2000).

After a review of available literature, we develop two conceptual models synthesizing processes affecting vegetation under fluctuating groundwater and identify information gaps. We further incorporate key concepts into an ecosystem model to highlight the complexity of interacting factors that can result in different outcomes, even in a simplified system. We begin the review with a discussion of the term "phreatophyte," which is commonly used for vegetation that can access groundwater.

Literature Review

Phreatophytes

"Phreatophytes consume groundwater" is a common definition that lacks utility, because all plants will consume groundwater if it is within the reach of their roots. For example, Meinzer (1927), who first used the term, stated that the distinction between vegetation that does or does not use groundwater becomes more difficult when going from arid to mesic zones, and that species dependent on groundwater in arid regions can thrive without it in mesic regions. Thus, a phreatophyte

grows where precipitation is insufficient for long-term survival and, consequently, it requires groundwater in that specific environment. Riparian and wetland species growing in desert environments represent good examples. However, other species that are common in arid regions frequently also grow where they can access groundwater. In contrast to riparian species, these species tolerate water stress better and may not require groundwater for long-term survival. Rather, they grow more vigorously in the presence of groundwater due to the increased water availability. *Artemisia tridentata*, *Chrysothamnus nauseosus*, and *Sarcobatus vermiculatus* commonly occur in the Great Basin region of the United States and represent examples of such species. Because of the range of vegetation using groundwater in arid regions, discussing the effects of fluctuating groundwater on "phreatophytic" vegetation cannot be general and simplified. So, although it may be safe to state that wetland species cannot survive in arid sites without access to groundwater, the fate of more drought-stress-tolerant species may range from minor biomass losses to significant dieback. For the purpose of this article, we will refer to the latter species as *xeric phreatophytes* to distinguish them from the more water-stress-sensitive wetland and riparian species.

Responses to Declining Water Tables

Declining water tables decrease the accessibility of a permanent water source and can therefore result in water stress. They also leave behind aerated soil profiles at field capacity that become available for new root exploitation. If groundwater severely restricts the active rooting zone, this scenario will benefit vegetation (e.g., Martin and Chambers 2001). Up to a limit, deeper water tables will also increase the soil volume available for storage of precipitation and hydraulically lifted water, which can significantly increase plant water use and growth (Jackson and others 2000). Furthermore, high groundwater tables may interact with saline soil layers to reduce vegetation health. In semiarid areas, salts can accumulate in soils, particularly if evapotranspiration, which leaves dissolved solutes behind, is high. Rainwater may partially leach these salts to deeper layers or to shallow groundwater tables. If groundwater is high, this may limit the rooting zone to the saline soil layers or introduce saline water to the rooting zone, thus reducing growth (Sorenson and others 1991, Rengasamy and others 2003). Thus, declining water tables can benefit vegetation although the literature contains comparatively few examples of positive responses. In the remaining sections, we focus on detrimental effects of declining water tables

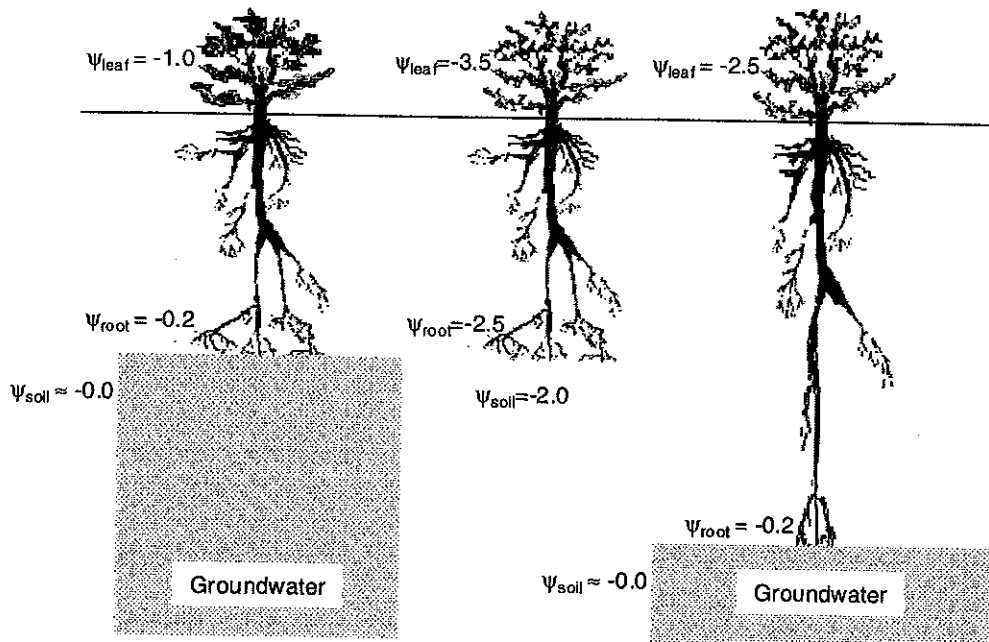


Figure 1. Idealized schematic of plant water relations under different groundwater regimes (high, none, and deep groundwater). Water transport from soil to roots to leaves into the atmosphere is driven by a water potential (ψ , MPa) gradient. The amount of water moving through the plant (F , kg s^{-1}) can be calculated using an ohm's law analog (Tyree and Ewers 1991): $F = -k(\psi_{\text{leaf}} - \psi_{\text{soil}})$, where k is the hydraulic conductance ($\text{kg s}^{-1} \text{MPa}^{-1}$) of the entire plant including the soil-root interface. Therefore, for leaves to receive water, their water potential has to be more negative than that of the soil, which leads to decreasing ψ_{leaf} as soils dry out. Also, as the pathway of water transport becomes longer, k decreases, resulting in lower ψ_{leaf} as well.

beginning with the direct effects, mitigating factors, indirect effects, and finally confounding factors.

Direct effects of water stress. Declining water tables can decrease plant-available soil water in areas where groundwater is within the rooting zone (Scott and others 1999). Water deficits stress growing vegetation and lead to numerous physiological changes. As transpiration occurs at the leaf surface, water is pulled up from the soil into roots and through xylem conduits in plants. Water in xylem is under tension and, therefore, xylem pressure is negative (Figure 1). With a decrease in available soil water, xylem tension increases and leaf water potential becomes more negative (Tyree and Ewers 1991). However, plants can tolerate decreasing water potentials only up to a tissue- and species-specific threshold, beyond which xylem cavitation occurs (Sperry and others 1998). Beyond this threshold, emboli form and block all water movement through the cavitated xylem. Consequently, the amount of water transported to leaves decreases, which causes stomatal closure, a reduction in photosynthesis, and, if enough xylem cavitates, branch and crown mortality (Leffler and others 2000, Sperry and Hacke 2002, Sperry and others 2002, Cooper and others 2003). A partial loss of leaves and branches under drought, however, may

facilitate plant survival because it reduces whole plant water needs (Rood and others 2000a, Horton and others 2001, Davis and others 2002).

Desert shrubs can tolerate low soil water conditions and survive leaf water potentials to -12.0 MPa because they have cavitation-resistant xylem (Hacke and others 2000, Pockman and Sperry 2000). Xeric phreatophytes in the Great Basin can tolerate water potentials ranging from -4 to -9 MPa, suggesting variable degrees of water stress tolerance in these species (Branson and others 1988, Donovan and others 1996). In contrast, less drought-tolerant species, such as riparian trees and shrubs, cannot tolerate water potentials this low. Shoot water potentials beyond which xylem cavitation will occur for *Populus fremontii* and *Salix gooddingii* lie around -1.5 MPa (Tyree and others 1994, Pockman and others 1995, Pockman and Sperry 2000, Horton and others 2001). As a consequence of high vulnerability to xylem cavitation, riparian trees will experience branch or crown mortality when cut off from groundwater (Segelquist and others 1993, Pezeshki and others 1998, Lines 1999, Scott and others 2000, Shafroth and others 2000, Horton and others 2001). On the other hand, phreatophytic shrubs can survive significant water table drawdowns, but may lose some branches and

leaf area (Groeneveld and others 1994). Thus, large differences in their ability to withstand water stress exist among species utilizing groundwater in arid regions. Therefore, generalizing from riparian to other vegetation types may not be valid. Knowledge of species-specific differences in their ability to withstand low water potentials becomes key to understanding the degree of vegetation damage under water stress.

Redistribution of roots. Plant roots can remain in contact with a declining water table if the rate of decline does not exceed potential root growth rate. Moist, aerated soil layers left behind by falling water tables will facilitate root proliferation with depth. Most relevant studies have investigated riparian trees because seedlings often establish during periods of subsiding floodwater and roots must elongate to maintain contact with the falling water table (Mahoney and Rood 1998, Shafroth and others 1998, Stromberg 2001). Roots of *Populus*, *Salix*, and *Tamarix* seedlings may grow 1–13 mm/day (Fenner and others 1984, Braatne and others 1996, Horton and Clark 2001). As a consequence, *Populus* seedlings stay in contact with groundwater at declines of up to 20 mm/day, whereas 40 mm/day declines cause reduced growth and declines greater than 40 mm/day cause death (Mahoney and Rood 1992, Segelquist and others 1993, Kranjcec and others 1998, Rood and others 2000b, Horton and Clark 2001). In a mature *Populus deltoides* stand with a rapid and sustained water table decline (≥ 1 m) over 1 week, leaf desiccation and branch dieback occurred within 3 weeks and 88% of trees died within 3 years (Scott and others 1999). In the same study, stands that experienced gradual water table declines of ~ 0.5 m over 1 year showed no measurable effect, most likely because roots were able to maintain contact with groundwater. Thus, the rate of water table declines may be just as important to vegetation health as the absolute change in water table.

Maximum root growth rates of arid shrub and grass species range between 3 and 15 mm/day (Fernandez and Caldwell 1975, Harris 1977, Roundy 1985, Simanton and Jordan 1986, Salih 1998), whereas maize roots can grow up to 60 mm/day (Kramer 1969). The shrub and grass root growth rates are similar to those of riparian tree seedlings after a declining water table and, thus, roots of xeric phreatophytes may follow a declining groundwater table as well (Groeneveld 1990). However, because these plants can tolerate water stress better than riparian species, constant contact with groundwater may be less crucial, and moist soil layers left behind by declining water tables may prove sufficient to sustaining biomass. However, because research on these species is limited, their tolerances to

differing rates and amount of groundwater declines remain unclear.

Alternate sources of water. Vegetation can adjust to declining water tables by utilizing water from other sources. In general, root water extraction rates will be highest where the combination of hydraulic conductivity, soil water potential, and root density leads to the lowest amount of energy expenditure (Adiku and others 2000). Therefore, plants use shallow soil moisture preferentially if it is abundant and switch to groundwater or deeper soil layers as shallow layers become dry (Thomas and Sosebee 1978, Smith and others 1991, Flanagan and others 1992, Dawson and Pate 1996, Smith and others 1997, Zencich and others 2002, Chimner and Cooper 2004), although some riparian tree species may rely solely on groundwater (Snyder and Williams 2000). Consequently, the effects of declining groundwater on vegetation should be less severe during years of high precipitation.

There are, however, limits to utilizing shallow soil moisture if shallow roots have lost their ability for water uptake after dry conditions. For example, the desert shrubs *Chrysothamnus nauseosus* and *Artemisia tridentata* differ in their uptake of shallow and deep soil water during summer (Donovan and Ehleringer 1994, Lefler and others 2004). *Artemisia tridentata* will access shallow soil water after summer precipitation events, whereas *C. nauseosus* continues to use deeper soil water (Flanagan and others 1992, Donovan and Ehleringer 1994). *A. tridentata* retains active roots in shallow, dry soil at the cost of lower leaf water potentials, allowing water uptake after rains. In contrast, *C. nauseosus* maintains higher water potentials by keeping active roots mostly in wetter, deeper soils (Sperry and Hacke 2002, Lefler and others 2004). Thus, although both of these dryland shrubs occur in similar habitats in the Great Basin, differences in morphology and physiology would cause each species to be uniquely affected by declines in groundwater even in the presence of summer precipitation.

Hydraulic lift. As groundwater drops, the amount of water available to roots in deeper soil layers declines as well, but hydraulic lift may provide supplemental moisture in the upper soil layers. Hydraulic lift occurs when transpiration ceases (usually at night) and water moves from deeper and wetter to shallower and dryer soil layers via plant root systems (Caldwell and others 1998). The driving force for this water movement is heterogeneous soil water potential within the rooting zone. Substantial amounts of water can be lifted overnight, contributing up to half of the following day's transpiration due to higher available soil moisture (Richards and Caldwell 1987, Jackson and others

2000). Furthermore, shallow-rooted herbaceous species incapable of utilizing deep soil water may benefit from the increased water availability in shallow layers in periods of stress (Dawson 1993, Stromberg and others 1996). This process occurs in a number of species and ecosystems (Stromberg and others 1996, Caldwell and others 1998, Yoder and Nowak 1999, Burgess and others 2000, Peñuelas and Filella 2002, Moreira and others 2003) and can increase the effectiveness of water uptake in large-scale areas with shallow aquifers (Caldwell and others 1998, Jackson and others 2000). As such, this process could mitigate the effects of decreasing groundwater levels as long as roots maintain contact with the saturated zone.

Water transport capacity and biomass production limitation. Two factors may limit the ability of plants to maintain constant groundwater use under falling water tables. The first factor relates to the physics of water transport. With an increase in the path length, resistance to water transport increases proportionally (Tyree and Ewers 1991). Other factors being equal, this increased resistance will result in a proportional decrease in water transport capacity and, consequently, transpiration. Alternatively, plants can maintain transpiration rates by decreasing leaf water potentials, which would increase the driving force for water flow and compensate at least partially for the increased resistance (Figure 1). However, this mechanism is limited in its effectiveness because decreasing leaf water potentials over a species-specific threshold will cause xylem cavitation and tissue death (Sperry and others 1998). As a second alternative, plants can increase the amount and/or efficiency of conducting roots accessing deeper water sources. Larger diameter conducting tissues in deep roots (Pate and others 1995, McElrone and others 2004) represent an increase in transport efficiency because of a strong relationship between diameter and resistance (Tyree and Ewers 1991).

The second factor potentially limiting constant groundwater uptake under falling water tables is biological and species specific. Obviously, if the depth to water or capillary fringe exceeds the maximum rooting depth of a species, groundwater is eliminated as a water source. Because herbaceous plants have, on average, shallower maximum rooting depths than shrubs and trees (Schenk and Jackson 2002), this is a greater factor for herbaceous species. However, even if the depth to water does not exceed the maximum rooting depth of a species, there may be limits to the amount of roots that can be produced at increasing depths. Because deep roots have a longer transport path, increasing the uptake and transport capacity in deep layers requires a

greater biomass investment than in shallow layers. As a consequence, the increased biomass cost of deep roots may limit their proliferation. The importance of this factor is difficult to evaluate because of the almost complete lack of data on deep root distributions (>2 m) in all phreatophytic plants under either constant or fluctuating water tables. This problem is obviously related to the ability to obtain samples from deep enough soil cores or pits. So, although some root data for xeric phreatophytes have been published (Branson and others 1976, Groeneveld 1990), they are insufficient to determine water uptake limitations as a function of groundwater depths.

Although definitive root data are lacking, indirect data on groundwater uptake with depth are more abundant. Evapotranspiration of xeric phreatophytic shrub and grass systems decreases with increasing depth to water (Lee 1912, Robinson 1958, Nichols 1994). Furthermore, plants growing in areas with comparatively deeper groundwater are of shorter stature and have smaller leaves and lower leaf water potentials, indicating greater water stress and lower aboveground productivity (Meinzer 1927, Harr and Price 1972, Chaney 1981, Sharifi and others 1982, Stromberg and others 1993). All these studies indicate an increasing cost of utilizing deeper water sources that changes in anatomy and allocation cannot completely overcome, thus resulting in reduced aboveground biomass.

Confounding factors. The severity of water stress that plants experience during a declining water table partially depends upon other factors, such as rainfall amounts, soil type and hydraulic conductivity, depth, rate, and duration and timing of water decline, and historical stability of the groundwater table (Shafroth and others 2000). The effects of declining groundwater are more severe in media with large pore size (gravel and sand) than those with small pore size (silt and clay) because of the lower water-holding capacity of gravel and sand (Shafroth and others 1998, Scott and others 1999). Thus, moist soil layers left behind by falling water tables get depleted faster in coarse texture soils. Furthermore, the height of the capillary fringe depends on soil texture decreasing in height from clay, silt, sand, and gravel soils (Dragun 1988). Therefore, in different areas subjected to declining groundwater, the water status of vegetation may differ significantly depending on soil type.

Falling water tables might have less harmful effects on plants when coinciding with a dormant stage. During periods of dormancy, plants have significantly lower water and nutrient requirements than during periods of active growth because the former period

involves a pronounced decline in metabolic activities such as photosynthesis and respiration (Harris and Campbell 1981, Smith and Nowak 1990). Thus, water table declines during dormancy may have little effect if the water table recovers before the vegetation breaks dormancy. Conversely, more significant effects would be expected during peak transpiration in summer.

One of the primary confounding factors in arid rangelands is grazing. The amount of damage to a plant due to grazing depends upon individual species' physiological and morphological characteristics and also varies with season and the intensity, frequency, and duration of grazing (Pieper and Donart 1978, Briske and Richards 1995, Brown 1995, Dahl 1995). Generally, grazing affects vegetation by reducing photosynthetic surfaces and root growth as the plant tries to re-establish root:shoot ratios (Schuster 1964, Mohammad and others 1982, Svejcar and Christiansen 1987, Briske and Richards 1995). In periods of declining water levels, light grazing may temporarily benefit vegetation by lowering leaf biomass and water requirements (Mohammad and others 1982, Martin and Chambers 2002). However, because grazing reduces root growth, this decreased water uptake capacity will result in severe plant damage if heavy grazing and water stress coincide (Sosebee and Wan 1988, Chambers and Norton 1993). To date, little research is available on the interaction of grazing and fluctuations in the groundwater table on xeric phreatophytic vegetation.

Responses to Rising Water Tables

Rising water tables can saturate a plant's rooting zone, and the resulting anoxia places stress on growing vegetation because of lacking oxygen required for aerobic respiration. In response to anoxia, plant roots switch to anaerobic metabolism. This may initially cause an accumulation of toxic end products and cell damage (Drew 1997). Roots that cannot tolerate extended periods of anoxia usually die. As a consequence of decreased root functioning and death, water transport capacity decreases. Therefore, whole-plant responses may resemble symptoms of drought stress, including the closure of stomata and a decrease in photosynthetic activity (Cronk and Fennessy 2001).

Flood-tolerant species have developed a number of adaptations that allow them to cope with periods of soil saturation and anoxia, primarily by increasing oxygen supply to roots (Kozlowski 1997, Mitsch and Gosselink 2000, Cronk and Fennessy 2001, Kozlowski 2002). However, these structural and physiological adjustments are mainly observed in wetland vegetation, which is adapted to extended periods of flooding

(Kozlowski 1997, Keddy 2000). Morphological adaptations to saturated soils have been documented in only a few dryland plant species (Groeneveld and Crowley 1988).

Biomass production. Because rising water tables can decrease the soil rooting zone and cause death of existing roots, negative effects on aboveground growth may result as well. For example, periods of high runoff resulted in an increase in water tables, which triggered a decrease in aboveground biomass, root death, and mortality of xeric phreatophytes (Ganskopp 1986, Nelson and others 1990). Even species considered phreatophytic showed root mortality under flooding (Groeneveld 1990) and complete mortality when entire root systems were submerged for prolonged periods (Groeneveld and Crowley 1988).

Significantly lower biomass and tillering was observed in *Poa pratensis* when grown in areas with shallow water tables (7 to 32-cm depth) than when grown in areas with deeper water tables (31 to 69-cm depth) (Martin and Chambers 2001). Similarly, *Populus* seedlings grew faster under slowly declining water tables than under saturated conditions (Segelquist and others 1993). Three days of flooding caused chlorosis and a halt in root growth in *Lepidium latifolium*, an exotic perennial that grows in areas with shallow water tables in the western United States (Chen and others 2002). After 7 days of flooding, plants started to develop adventitious roots that grew horizontally, but after 50 days of flooding plants had 80% less total biomass than plants that were not flooded. Thus, even species that have high water requirements show negative responses to increasing or very high water tables.

Redistribution of roots. Phreatophytic vegetation adjusts its root growth to the level of the water table and, therefore, prolonged increases or declines in groundwater will cause root growth redistribution to maintain water uptake in unsaturated zones above the water table (Jarrell and Virginia 1990, Oosterbaan and Nabuurs 1991, Segelquist and others 1993, Scott and others 2000, Martin and Chambers 2002). For example, *Populus* roots remain above the permanent water level under constant or small annual fluctuations but penetrate deeper under larger fluctuations (Lines 1999, Shafroth and others 2000). However, frequent fluctuations of water tables cause repeated occurrences of anoxia, which create an obstacle for deep root formation (Martin and Chambers 2002). Root growth of riparian meadow plants (*Poa pratensis*, *Carex nebrascensis*, and *Salix lemniai*) was minimal within or at the surface of the water table and increased in depth as water tables declined (Svejcar and Trent 1995, Martin and Chambers 2002). The increase of root activity at lower

water tables was due to an increase in soil aeration (Martin and Chambers 2001), indicating that anoxia can limit root growth even for some wetland species. Finally, *Atriplex torreyi* and *Chrysothamnus nauseosus* displayed lateral root development and shallower rooting depth in flooded than in aerated soils (Groeneveld and Crowley 1988). These studies suggest that phreatophytes have limited tolerances to prolonged flooding of their roots, which result in limited rooting depths and, potentially, death of entire communities.

Formation of aerenchyma. Because saturated soils are detrimental to plant health due to lower oxygen availability, mechanisms that enhance oxygen transport can increase plant resistance to anoxia stress. Aerenchyma are porous tissues that act as an internal gas-transport system by decreasing the resistance to flow of oxygen and other gases in plants (Cronk and Fennessy 2001). This lowered resistance allows oxygen to reach waterlogged roots more easily than without the presence of aerenchyma (Drew 1997). Aerenchyma formation is common in stems and roots of flood-tolerant vegetation, but only a few upland species that grow in arid and semiarid regions have been shown to exhibit this adaptive strategy. The xeric phreatophytes, *Atriplex torreyi* and *Chrysothamnus nauseosus*, survived 6 months of flooding by growing new roots with aerenchyma (Groeneveld and Crowley 1988). However, in the same study, *Sarcobatus vermiculatus* failed to survive the continuously flooded conditions, although it can develop aerenchyma. The extent to which dryland species can form aerenchyma and survive extended flooding of part or all of their root zone is a research area that deserves attention in the future.

Dormancy. Dormancy reduces the oxygen requirement of roots and consequently roots may also survive waterlogging if they are dormant before the water table rises (Coutts and Nicoll 1990). Dormant roots of *Picea sitchensis* and *Pinus contorta* cuttings survived 1 month of waterlogging, whereas actively growing root tips died (Coutts and Philipson 1978). After the soil was drained, dormant root tips began growing once again. Furthermore, in a saturated medium, inactive roots of *Picea sitchensis* survived to a depth that was 18 cm greater than the maximum depth of survival for actively growing roots (Nicoll and Coutts 1998).

Flooding may also induce root dormancy (Coutts and Philipson 1978, Mensforth and Walker 1996). For example, *Melaleuca halmaturorum* was able to maintain a matrix of dormant roots throughout the soil profile to rapidly utilize available water, creating a successful adaptive response to growth under seasonal variations in the groundwater table (Mensforth and Walker 1996). Thus, in temperate areas, the time of year that

the water table rises will also significantly impact plant survival because flooding that occurs while plants are dormant rarely causes problems (Drew and Stolzy 1996). However, because of the timing of spring runoff, which often drives seasonal fluctuations in water tables, high water tables coincide with active growth in natural systems (Ganskopp 1986, Shafroth and others 2000).

Conceptual Models of Vegetation Responses to Water Table Changes

Based on the literature, it is difficult to draw definitive conclusions on how fluctuating water tables in water-limited environments affect vegetation. This is largely due to both positive and negative effects involved in both rising and dropping water tables and species differences in stress tolerance. Using available data, we have compiled conceptual models of vegetation responses to increasing and decreasing groundwater expressed as shifts in productivity and standing biomass.

Figure 2 represents a simplified summary of the biomass responses of phreatophytic vegetation to decreasing water tables. The outcome can range from no observable change to the loss of entire communities, depending on the interaction of biological and physical properties. For example, even if the vegetation cannot produce new roots at sufficiently high rates to maintain contact with the water table (first decision in flowchart), as long as precipitation is above average or soils have a high water-holding capacity, the effects of a dropping water table will be delayed or possibly avoided. Conversely, if the vegetation is exposed to additional stresses such as low precipitation, herbivory, or disease, then the consequences will be more severe.

At the second decision point, the relative change in depth to groundwater will determine how well root systems can transport water from a greater depth. Obviously, if the groundwater depth exceeds the maximum rooting depth of a species, groundwater is lost as a direct water source. Groundwater may still be available via hydraulic lift of deeper-rooted species. However, even if a species can still tap into groundwater, the transport limitations discussed above may reduce water availability and cause a reduction in aboveground biomass.

As with declining groundwater, rising water tables can have a wide range of possible outcomes (Figure 3). Key to predicting outcomes with sufficiently large changes in groundwater levels depends on whether root systems can tolerate and/or morphologically

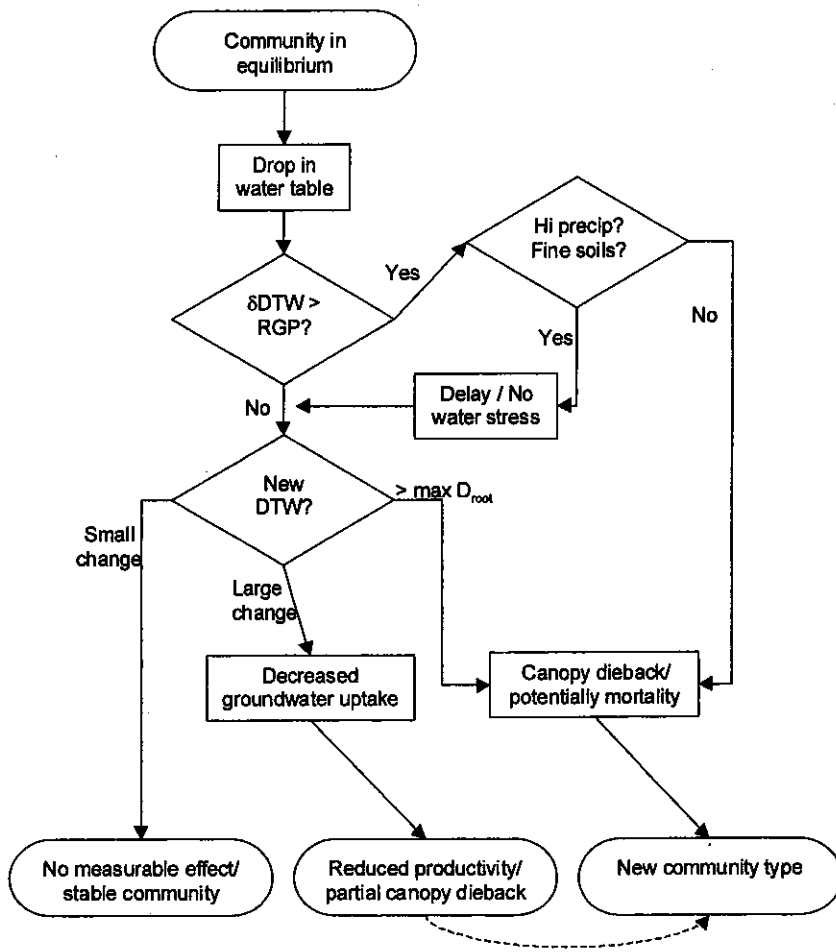


Figure 2. Simplified conceptual model of the effects of a dropping water table on a community that was in equilibrium with and using groundwater as a significant source of water. DTW refers to the depth to groundwater, δ DTW to the rate of increase in depth to groundwater, RGP to the potential root growth rate, $\max D_{\text{root}}$ to the maximum potential rooting depth, and dashed arrow to potential long-term routes. Refer to the text for further explanations.

adapt to anoxic conditions. Desert shrubs and other upland species will experience root mortality in the anoxic zone (Lunt and others 1973) and, depending on the extent of the flooding, entire plants may die (Ganskopp 1986, Nelson and others 1990). At the other extreme, species that are highly adapted to flooded conditions will experience comparatively few negative effects from submerging parts of their root systems (Keddy 2000). More difficult to evaluate are effects on xeric phreatophytes because of very limited data on their root system responses to flooding. These species may tolerate anoxia longer than flood-intolerant species (Ganskopp 1986), but ultimately their roots die as well (Groeneveld 1990).

After the initial root loss, plants may recover if they either have a sufficiently large rooting volume available above the anoxic zone or if they are able to grow new modified roots that can tolerate anoxic conditions (Groeneveld and Crowley 1988). If a plant has sufficient resources available, root regrowth will occur above the anoxic zone, although some aboveground

biomass loss may occur. If too much of the root zone is flooded and the plant loses a significant portion of roots, death may follow. Some plants, while unable to endure extended flooding, may tolerate anoxia for a short period. Thus, the ultimate effect of increasing water tables on vegetation is strongly dependent on the degree of root flooding, length of flooding, and species-specific ability to tolerate anoxic conditions.

Although these two models conceptualize changes that occur with opposing directions of groundwater movement, common factors determine the extent of vegetation stress: the relative change in the depth to groundwater and the associated changes in functional root biomass and water uptake capacity. If plants are exposed to frequently rising and falling groundwater, the stress to vegetation may be compounded over that expressed in either conceptual model because of the constant need to readjust root systems to new water levels. The ultimate outcome of fluctuating groundwater levels is difficult to judge, however, because frequency, timing, duration, species-specific traits, and

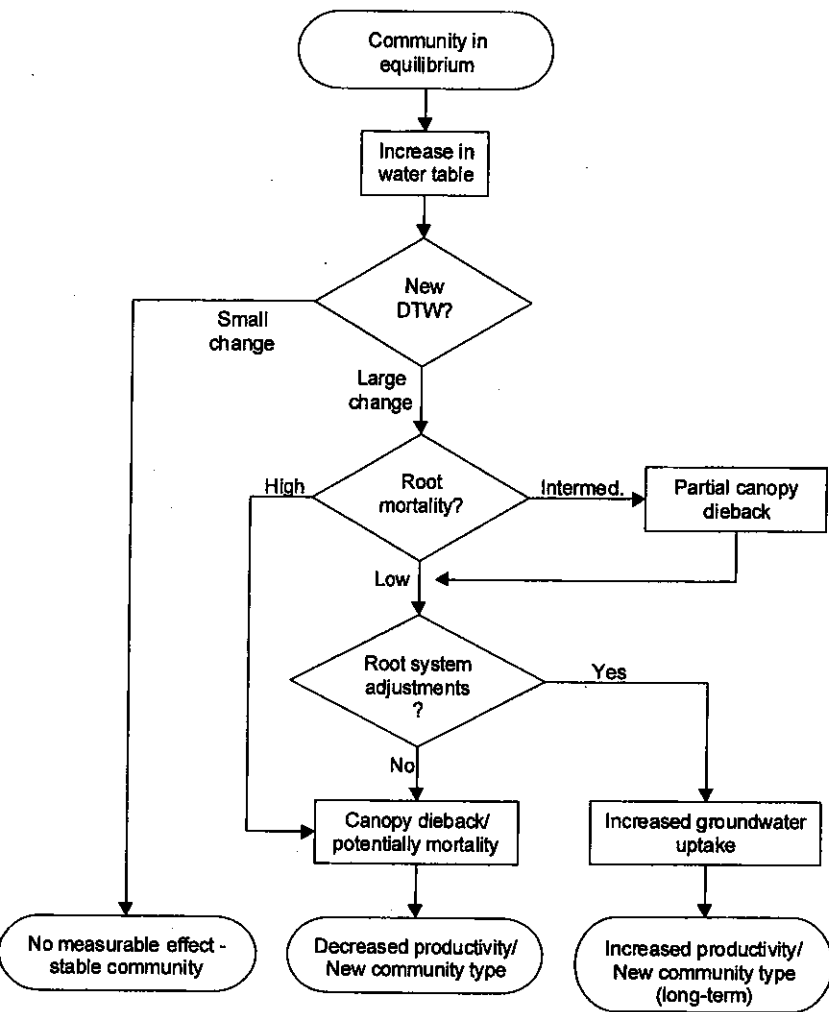


Figure 3. Simplified conceptual model of the effects of a rising water table on a community that was in equilibrium with and using groundwater as a significant source of water. DTW refers to the depth to groundwater. Refer to the text for further explanations.

seemingly unrelated factors such as grazing and disease will all affect how severely root systems and water uptake capacity are compromised. Because so many confounding factors exist, predictions of the effects of groundwater fluctuations are best conducted using ecological models with the capacity to accurately assess the simultaneous effects of all stressors on vegetation health and productivity.

Application of Conceptual Models

To demonstrate the complexity of fluctuating groundwater even in a simplified system, we used the EDYS model (Childress and McLendon 1999, Childress and others 2002), which projects the dynamics of soil, plant, animal, water balance, and landscape features over decades (Childress and others 1999a, 1999b). Soils are implemented in layers where water is extracted based on root densities and availability and recharged by precipitation and groundwater. Under

equal water availability over the entire soil profile, plants will preferentially extract water from the upper layers. Plants are represented as biomass components: trunk, stem, leaves, seeds, and coarse and fine roots in discrete soil layers. Based on their potential growth rate and water use efficiency, plants take up nitrogen and water on a daily time-step. If insufficient resources are available, each species receives amounts proportional to their root biomass in a given layer. Thus, the main mechanism for belowground competition is root allocation as a function of depth, which is species specific in the initial model setup, and absolute root biomass. New fine root growth is allocated preferentially to soil layers where a species is able to obtain needed resources (mostly water and nitrogen), thus allowing root proliferation in high resource soil layers. Coarse root biomass is allocated such that water transport capacities are in balance with fine root water uptake. Because of increased physical resistance of water transport from

deeper layers, we currently implement a linear decrease in water uptake capacity of fine roots with depth. For woody species, we set the water uptake capacity at 1 m depth at 100% and decrease it linearly to 40% at 10 m. Similar logic is applied to the fibrous root system of grasses, except that the 40% threshold is at 5 m because of their lower maximal rooting depth. These values are estimates based on the analysis of Nichols (1994) and Lee (1912), who suggest that phreatophytic transpiration rates steeply decline with depth to water, probably due to both increased resistance of water transport and fewer roots with depth.

For this application, we parameterized EDYS for Owens Valley, California, which has a range of different phreatophytic and nonphreatophytic vegetation communities. We ran the model for 15 years for a simple 30 × 30-m plot without any herbivory or disturbance. The initial species composition was an artificial community with *Atriplex torreyi*, *Chrysothamnus nauseosus*, *Distichlis spicata*, and *Sporobolus airoides*, which are representative dominants in Owens Valley. We used a constant precipitation regime composed of months that represented the long-term monthly totals for the Bishop Airport National Weather Service station. These months were annually repeated for the 15-year model runs. To show the effect of abiotic factors, we used two actual soil types in Owens Valley: Shondow-Hessica Association, a loam derived from mixed sources that has around 45% sand and 18% clay in the upper layers, and Hesperia-Cartago Complex, a sand derived from granite that has around 92% sand and 2% clay in the upper layers. We used constant 1- and 4-m depths to the water table, water table depths increasing from 1 to 4 m or decreasing from 4 to 1 m over 3 months in model year 7, and levels fluctuating between 1 and 4 m on an annual basis. These scenarios were used in separate model runs to demonstrate the effects of different groundwater regimes.

Model results presented here are intended to demonstrate how different species traits and groundwater depths interact and should not be viewed as absolutes due to some uncertainty in model parameterization. On the loam soil, species showed different responses depending on the groundwater regime and the relative competitiveness of the species (Figure 4, top panel). *C. nauseosus* results show the commonly expected responses to the different groundwater scenarios: high groundwater levels (1 m, shift from 4 to 1 m) resulted in the highest biomass because of close proximity of a permanent water source and associated high water uptake and growth. Deeper water tables (4 m, shift from 1 to 4 m) reduced water availability due to initially low root biomass near the groundwater table. This

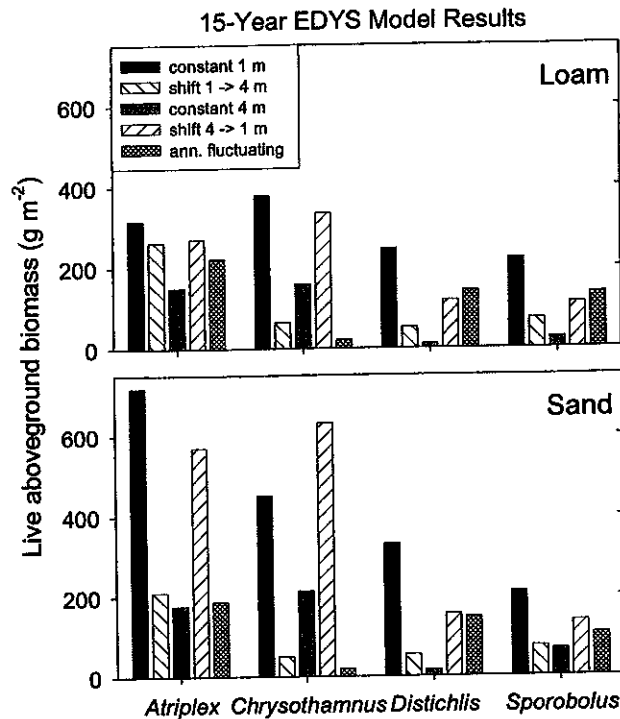


Figure 4. Model results after 15-year runs for two different soil types and five depth-to-groundwater scenarios. Groundwater shifts from 1 to 4 m (and vice versa) occurred in year 7 over a 3-month period, while "annually fluctuating" stands for groundwater that fluctuated between 1 and 4 m annually. The species represent two shrubs (*Atriplex torreyi*) and (*Chrysothamnus nauseosus*) and two grasses (*Distichlis spicata* and *Sporobolus airoides*).

slowed biomass production and root proliferation near the water table and consequently resulted in lower biomass. Finally, under the annually fluctuating water table, the effective rooting zone was restricted to 1 m due to root mortality, which resulted in low final biomass. The other species showed similar patterns, although the fluctuating water table was less detrimental than for *C. nauseosus*. This difference was most likely due to different rooting depth profiles. The grasses did most poorly under the constant 4-m scenario because of their shallower root distributions and lower water uptake capacities at this depth. In separate model runs with lower initial grass biomass, the *A. torreyi* was the most competitive species under all groundwater regimes, resulting in the highest individual species biomass values (results not shown). Therefore, the effects of different groundwater regimes on vegetation will depend on the species composition and the relative competitiveness of the species, which relates to growth potential and root distribution in the current model setup.

In the sandy soil, shrubs performed better, especially with shallow water tables (Figure 4, bottom panel). Deeper precipitation penetration resulted in available soil moisture being present in deeper layers only. This deeper water resource was better exploited by the shrubs over time, which led to deeper soil root proliferation and greater groundwater use. In contrast, the lower water-holding capacity of the sand resulted in lower total biomass for the sand versus the loam plot under the fluctuating and drop-to-4-m scenarios.

Overall, the model produced results that we would expect based on the reviewed literature, e.g., lower biomass with deeper water tables, especially for shallow-rooted grasses, species differences related to their root distributions, and differences depending on environmental conditions such as soil types. Unfortunately, direct comparisons to published studies are not possible due to lacking data. Finally, these highly simplified model scenarios highlight the potential complexity of predicting vegetation change as a function of fluctuating groundwater levels due to the interaction of the physical environment (soil, precipitation), competition, and species-specific traits.

Discussion

Humans consume increasing amounts of water in semiarid and arid areas worldwide and struggle to balance human and ecosystem water requirements (e.g., Hatton and others 1998, Puigdefábregas and Mendizabal 1998, Le Maitre and others 1999, Zhu and others 2004). As in the Great Basin, knowledge about vegetation groundwater needs and physiological and ecological responses to altered groundwater regimes remains insufficient to allow for science-based management in many nonriparian ecosystems (Hatton and others 1998, Le Maitre and others 1999). Thus, managers need both more information about vegetation/groundwater interaction and tools to evaluate different water extraction strategies.

Our current knowledge suggests that three factors drive aboveground vegetation responses to changes in groundwater levels: 1) drought and anoxic stress tolerance; 2) changes in the size and distribution of the active root system; and 3) associated changes in the water uptake capacity. In addition, a number of confounding factors may modify vegetation responses. These include soil texture, timing and rate of change in groundwater, herbivory, and disease. Finally, climate change may affect precipitation amount and temporal distribution and thus groundwater recharge in these ecosystems. This could further increase conflicts between human consumption and ecosystem require-

ments. The only way human impacts on such complex systems can be addressed and mitigated is by modeling. Models like EDYS allow the evaluation of different management and climate change scenarios, which provide a way to determine better management practices.

Currently, the biggest challenge to predicting and modeling vegetation responses to changing water tables relates to uncertainties in quantitatively assessing the decisions in the flowcharts. For example, how large must a change in groundwater table be before it manifests itself in a change in community biomass? How great are growth-form or species-to-species differences in this regard? Significant data gaps are particularly evident with respect to the following:

- deep root distributions (>2 m) in the presence of groundwater;
- root elongation rates in response to declining water levels;
- the degree of physical limitations to water transport from deep layers;
- the importance of hydraulic lift for phreatophytic species as a function of groundwater depth; and
- the response of xeric phreatophyte roots to partial flooding of their root systems.

Additional data to answer these and other questions will greatly improve model accuracy for predicting the effects of natural and human-exacerbated fluctuations of groundwater in ecosystems with shallow water tables. Consequently, increased research efforts in these ecosystems are crucial for their management and health.

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