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A review of groundwater–surface water interactions in arid/semi-arid wetlands and the consequences of salinity for wetland ecology

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ABSTRACT

In arid/semi-arid environments, where rainfall is seasonal, highly variable and significantly less than the evaporation rate, groundwater discharge can be a major component of the water and salt balance of a wetland, and hence a major determinant of wetland ecology. Under natural conditions, wetlands in arid/semi-arid zones occasionally experience periods of higher salinity as a consequence of the high evaporative conditions and the variability of inflows which provide dilution and flushing of the stored salt. However, due to the impacts of human population pressure and the associated changes in land use, surface water regulation, and water resource depletion, wetlands in arid/semi-arid environments are now often experiencing extended periods of high salinity. This article reviews the current knowledge of the role that groundwater–surface water (GW–SW) interactions play in the ecology of arid/semi-arid wetlands. The key findings of the review are as follows:

1. GW–SW interactions in wetlands are highly dynamic, both temporally and spatially. Groundwater that is low in salinity has a beneficial impact on wetland ecology which can be diminished in dry periods when groundwater levels, and hence, inflows to wetlands are reduced or even cease. Conversely, if groundwater is saline, and inflows increase due to raised groundwater levels caused by factors such as land use change and river regulation, then this may have a detrimental impact on the ecology of a wetland and its surrounding areas.
2. GW–SW interactions in wetlands are mostly controlled by factors such as differences in head between the wetland surface water and groundwater, the local geomorphology of the wetland (in particular, the texture and chemistry of the wetland bed and banks), and the wetland and groundwater flow geometry. The GW–SW regime can be broadly classified into three types of flow regimes: (i) recharge—wetland loses surface water to the underlying aquifer; (ii) discharge—wetland gains water from the underlying aquifer; or (iii) flow-through—wetland gains water from the groundwater in some locations and loses it in others. However, it is important to note that individual wetlands may temporally change from one type to another depending on how the surface water levels in the wetland and the underlying groundwater levels change over time in response to climate, land use, and management.
3. The salinity in wetlands of arid/semi-arid environments will vary naturally due to high evaporative conditions, sporadic rainfall, groundwater inflows, and freshening after rains or floods. However, wetlands are often at particular risk of secondary salinity because their generally lower elevation in the landscape exposes them to increased saline groundwater inflows caused by rising water tables. Terminal wetlands are potentially at higher risk than flow-through systems as there is no salt removal mechanism.
4. Secondary salinity can impact on wetland biota through changes in both salinity and water regime, which result from the hydrological and hydrogeological changes associated with secondary salinity. Whilst there have been some detailed studies of these interactions for some Australian riparian tree species, the combined effects on aquatic biodiversity are only just beginning to be elucidated, and are therefore, a future research need.
5. Rainfall/flow-pulses, which are a well-recognized control on ecological function in arid/semi-arid areas, also play an important, though indirect, role through their impact on wetland salinity. Freshwater pulses can be the primary means by which salt stored in both the water column and the underlying sediments are flushed from wetlands. Conversely, increased runoff is also a commonly observed consequence of secondary salinity, and so, wetlands can experience increased surface water inflows that are higher in salinity than under natural conditions. Moreover, changes in rainfall/flow-pulse regimes can have a significant impact on wetland GW–SW interactions. It is possible that in some instances groundwater inflow to a wetland may become so heavy that it could become a major component of the water balance, and hence, mask the role of natural pulsing regimes. However, if the groundwater is low in salinity, this may provide an ecological benefit in arid/semi-arid areas by assisting in maintaining water in wetlands that become aquatic refugia between flow-pulses.
6. There has been almost no modelling of GW–SW interactions in arid/semi-arid wetlands with respect to water fluxes, let alone salinity or ecology. There is a clear need to develop modelling capabilities for the movement of salt to, from, and within wetlands to provide temporal predictions of wetland salinity which can be used to assess ecosystem outcomes.
7. There has been a concerted effort in Australia to collect and collate data on the salinity tolerance/sensitivity of freshwater aquatic biota and riparian vegetation. There are many shortcomings and knowledge gaps in these data, a fact recognized by many of the authors of this work. Particularly notable is that there is very little time-series data, which is a serious issue because wetland salinities are often highly temporally variable. There is also a concern that many of the data are from very controlled laboratory experiments, which may not represent the highly variable and unpredictable conditions experienced in the field. In light of these, and many other shortcomings identified, our view is that the data currently available are a useful guide but must be used with some caution.

KEY WORDS groundwater–surface water interactions; wetlands; salinity; ecology

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INTRODUCTION

Background

Estimates of the extent of wetland systems globally are uncertain, due in part to confusion over what constitutes a wetland and the difficulties of delineating and mapping habitats with variable boundaries (Finlayson and D'Cruz, 2005). This is particularly pertinent in arid/semi-arid areas where the majority of wetlands are temporary. What is certain though, is that a large percentage of wetlands have been lost in the last century and that ongoing degradation and loss is occurring worldwide (Williams, 1999). Whilst there are many causes, including drainage and land clearance, they are all related to agricultural, urban, and industrial development associated with human population pressure (Finlayson and D'Cruz, 2005).

As reviewed by Sophocleous (2002) there has been increasing attention given to the interactions between groundwater and surface water (GW–SW). Similarly, the review of Danielopol *et al.* (2003) highlights the linkages between groundwater and ecosystems and the ever-increasing human-induced pressures on groundwater systems that have flow-on ecological impact. In the case of wetlands, the majority of the GW–SW research related to wetland ecology appears to have been in temperate and tropical environments. Wetlands in arid/semi-arid areas have all the problems of temperate and tropical areas, i.e. pollution, drainage, eutrophication, and changes to hydrological regime, including surface water impoundment and diversion, and groundwater extraction. Available surface water is declining and the extraction of groundwater beyond natural recharge rates is occurring, lowering the water table, and causing degradation of groundwater-dependent ecosystems (e.g. Mudd, 2000). Wetlands in arid/semi-arid areas are also prone to salinization due to human-induced changes to the hydrological cycle which result in increases in recharge that lead to rises in saline groundwater (e.g. Allison *et al.*, 1990) and its increased movement into wetlands. The African and Australian continents have the largest arid/semi-arid areas and the largest salinized areas in the world (Ghassemi *et al.*, 1995). Paradoxically, the arid/semi-arid areas contain some of the world's largest river systems (for example, the Colorado, Nile, and Murray-Darling River systems) as the source of the rivers are from wetter areas (Williams, 1998a). Also, some of the most important wetlands of the world are in the arid/semi-arid zone including the Okavango Delta (Botswana), the Kafue Flats (Zambia), the Hadejia-Jamaare (Nigeria), and the Prairie Potholes (North America). However, this is not reflected in the degree of knowledge of arid zone wetlands or in their conservation status (Kingsford, 1997).

While the general role of wetlands in the hydrological cycle has been well documented (e.g. Bullock and Acreman, 2003), the level of knowledge in arid/semi-arid environments is still fairly poor, particularly in relation to GW–SW interactions. In arid/semi-arid areas, where rainfall is variable, wetland ecosystems provide vital habitat for unique biota in an otherwise dry environment. Due to the temporary nature of many wetlands, and the resultant variability of physico-chemical factors, the biota have evolved unique features and life-cycle adaptations that enable them to persist over dry intervals (e.g. use of deep channel segments as aquatic refugia, Walker *et al.*, 1995; Sheldon *et al.*, 2002; Hamilton *et al.*, 2005). Arid/semi-arid wetlands show faunal diversity as high as, or greater than that in many temperate and tropical wetlands (Williams, 1998a,b). This is due to the evolutionary path (sea → rivers → river pools → temporary fresh wetlands) in which the biota in arid zones have evolved.

Recent developments in hydrological research have seen surface water and groundwater increasingly being treated as part of the same system (Winter, 2001; Hayashi and Rosenberry, 2002; Sophocleous, 2002). While recent ecological literature has identified the importance of multi-disciplinary studies (i.e. ecohydrology or hydroecology; Hannah *et al.*, 2004), it has not traditionally focused on the role that groundwater plays in wetland environments. Whilst this is changing (e.g. Carter, 1986; Hunt *et al.*, 1996, 1999; Kehew *et al.*, 1998; Raisin *et al.*, 1999; Winter, 1999) there is still very little literature relating to saline groundwater environment and their impact on wetlands in arid/semi-arid areas. Most studies of the impact of salinity on water bodies have concentrated on water supply impacts (e.g. Konikow and Person, 1985; Allison *et al.*, 1990), although ecological impacts of salinity have been studied in Australia since the mid-1960s (e.g. Bayley and Williams, 1966; see also the review of Hart *et al.*, 1991).

This review aims to bring together the state of knowledge of hydrological processes, GW–SW interaction, and the role of groundwater in wetlands of arid/semi-arid areas. Whilst this is a review of research literature worldwide, most of the literature on the ecological impact of salinity is from Australia where research in this area is more advanced due to the extent of salinization in that country. However, it is expected that many of the concepts developed from the Australian experience will apply to arid/semi-arid wetlands in other areas of the world that are influenced by groundwater.

Scope of the review

This review is concerned only with wetlands in arid/ semi-arid environments. These regions receive low (<500 mm yr^{-1} in winter rainfall areas and <800 mm yr^{-1} in summer rainfall areas) and variable annual rainfall, and are characterized by potential evapotranspiration that is far greater than the precipitation (ratio of mean annual precipitation to mean potential evapotranspiration <0.5; UNEP, 1992). Extreme climatic variability and subsequent hydrological fluctuations are typical in these regions. The climatic variability occurs seasonally, interannually, and over longer time frames. Consequently, the arid/semi-arid areas are subjected to frequent and severe droughts and infrequent but significant floods. Climate variability and subsequent fluctuating hydrology are key drivers of ecology in arid/semi-arid environments.

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The wetlands of interest in this review are naturally occurring inland shallow (<5 m), standing (lentic) freshwater wetlands of arid/semi-arid environments covering the spectrum of inundation from permanent to various temporary states. Herein, we refer to wetlands as permanent and temporary as per Williams (1998a). Permanent wetlands contain water all year round except during an extended drought. Temporary includes intermittent wetlands, which have a wet or dry annual cycle, and episodic, which fill unpredictably.

This review is confined to naturally occurring (not constructed) freshwater wetlands that are subject to salinization induced by human activity (secondary salinity), as opposed to naturally occurring primary salinity which occurs in endhorheic systems (closed basins). Whilst it is recognized that chemical elements other than salt may be toxic in wetlands, for instance pH, dissolved oxygen, or the concentration of specific ions (e.g. Zalizniak *et al.*, 2006), salinity is the focus of this review. Of interest here are the increases in salinity, which change natural freshwater wetlands (total dissolved salts, TDS, of less than 1000 mg l^{-1}) into saline wetlands. It is also recognized that there are other environmental factors that impact on ecology including temperature, nutrients, and turbidity. While all may be affected by groundwater, the focus of this review is on two aspects, water regime (surface water and groundwater) and water quality (specifically salinity).

Organization of the review

The review is comprised of two major parts. The first is concerned with determining how GW–SW interactions impact on wetland salinity. This includes descriptions of the key groundwater processes, identification of the key controls on GW–SW interactions in wetlands, discussion of the processes of wetland salinization, understanding the contribution of groundwater to wetland water and salt balances, and a discussion of modelling approaches used for describing GW–SW interactions in wetlands. The second part of the review is concerned with the ecological responses to changes in wetland salinity. This is comprised of a summary of the available Australian salt tolerance data, identification of the knowledge gaps and other issues associated with this data, an assessment of the combined impacts of salinity and changes in water regime, and a discussion of the effects of GW–SW interaction on the pulse events that drive ecological functions in wetlands. The final section of the article is an overall summary of the important conclusions that have been drawn from the review.

GW–SW INTERACTIONS AND WETLAND SALINIZATION

Key groundwater processes

Hayashi and Rosenberry (2002) provided an excellent description of the fundamental concepts of GW–SW interaction and the implications for ecology. To provide the necessary background, some of the information they present is summarized here in the context of arid/semi-arid wetlands. For those unfamiliar with groundwater and salinity processes we define some key terms in Table I.

Groundwater systems are dynamic three-dimensional flow-fields where movement of groundwater is driven by potential gradients (usually described by hydraulic heads) from areas where water is added to the aquifer (recharge) to areas where it is lost from the aquifer (discharge). The flow-fields can be comprised of different sizes and depths and can overlie one another (Figure 1). Local flow systems are the most dynamic and the shallowest, and therefore, have the greatest interaction with surface water bodies. An example of a local flow system is shown in Figure 2 where a typical wetland is incised within a floodplain riparian zone which is the transition between the wetlands (and rivers) and surrounding upland areas. Because the shape of the water table often replicates the shape of the land surface, it is generally shallow

Table I. Definitions of some key groundwater and salinity terms.

Term	Definition
Aquifer	Saturated permeable soil or geologic strata that can transmit significant quantities of groundwater under a hydraulic gradient.
Capillary rise	Upward movement of groundwater through the soil caused by the surface tension of water in soil pores.
Discharge	Loss of water from an aquifer (i) to the atmosphere by evaporation, springs and/or transpiration, or (ii) to a surface water body (in the case of rivers it is generally referred to as base flow) or the ocean, or (iii) by extraction.
Groundwater	Sub-surface water in soils and geologic strata that have all their pore spaces filled with water (i.e. are saturated).
Hydraulic gradient	Change in hydraulic head in an aquifer with either horizontal or vertical distance, in the direction of groundwater flow.
Hyporheic zone	Saturated zone of mixing between groundwater and surface water.
Primary salinity	Natural soil and/or water salinization resulting from a limited capacity to drain salt and water from the landscape.
Recharge	Addition of water to an aquifer, most commonly through infiltration of a portion of rainfall, surface water, or irrigation water that moves down beyond the plant root zone to an aquifer.
Secondary salinity	Soil and/or water salinization caused by human-induced activities such as land use change.
Vadose or unsaturated zone	Zone between land surface and the water table within which the moisture content is less than saturation (except in the capillary fringe).
Water table	Level of groundwater in an unconfined aquifer. The soil pores and geologic strata below the water table are saturated with water.

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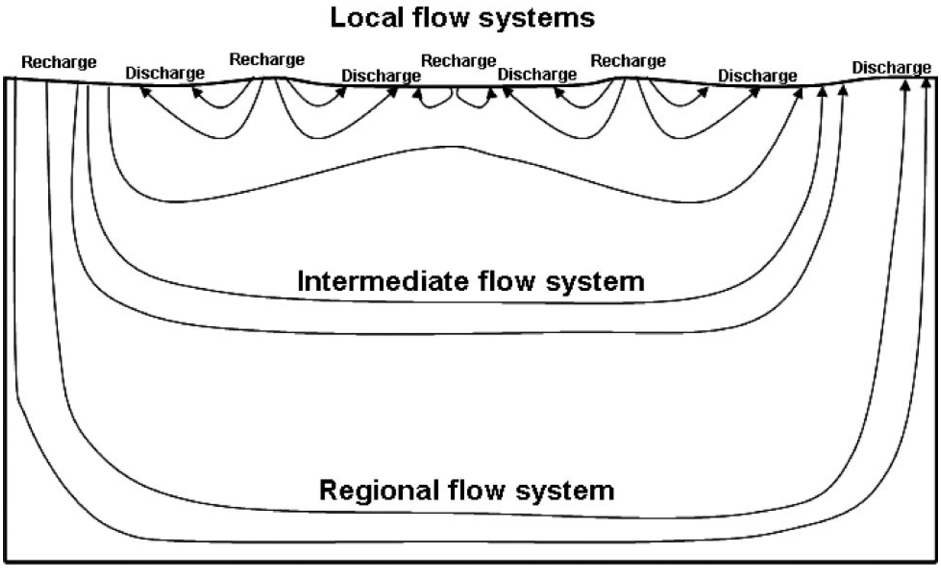

Figure 1. Groundwater flow systems can occur at local, intermediate, and regional scales. Areas of recharge and discharge are shown. Most discharge of groundwater into wetlands is from local flow systems (derived from a similar Figure in Toth (1963)).

beneath the riparian zone and deeper below the upland areas.

The flow of groundwater between the riparian zone and the wetland (via the hyporheic zone) will depend on the relative elevations of the water table beneath the riparian zone and the surface water in the wetland. Amoros and Bornette (2002) point out that GW–SW interactions can be very dynamic in the short term as a result of varying river and wetland water levels (Figure 3). In the long term, groundwater exchange directly affects the ecology of surface water by sustaining stream base flow and moderating water level fluctuations of groundwater-fed water bodies such as lakes and wetlands (Hayashi and Rosenberry, 2002). This is particularly the case in arid/semi-arid environments, where surface water regimes are vulnerable to rainfall variability and/or river regulation and abstraction activities. Therefore, the persistence of wetlands can be dependant, either completely or partially, on contributions from groundwater. Groundwater can, therefore, be a major component of water balance of wetlands in arid/semi-arid areas. Indeed, wetlands can be completely groundwater dependant, with no surface expressions of water (for example, the mound springs of the Great Artesian Basin in central Australia; Mudd, 2000). Conversely, if groundwater is saline, as it commonly is in arid/semi-arid areas, then it may have a detrimental impact on wetland ecology.

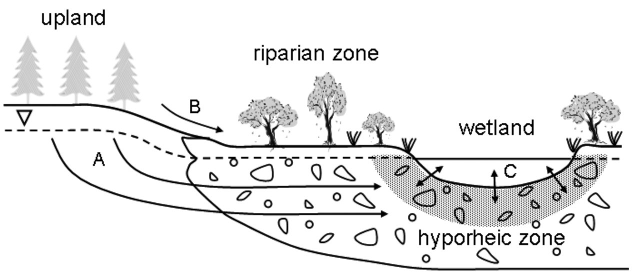

Figure 2. Schematic cross-section of a wetland, hyporheic zone (shaded), riparian zone, and upland. Major pathways of water exchange are indicated by (A) groundwater flow, (B) overland flow, and (C) hyporheic exchange (derived from a figure in Hayashi and Rosenberry (2002)).

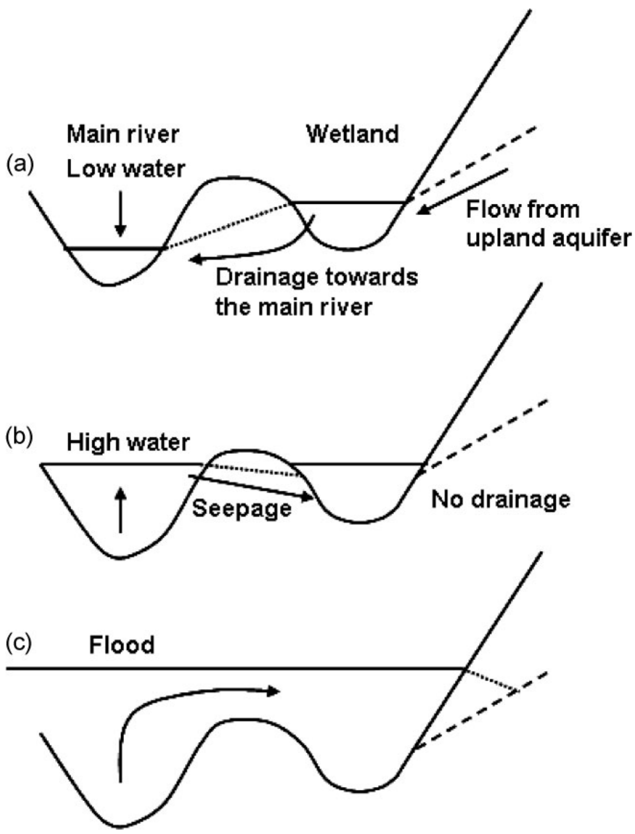

Figure 3. Schematic illustration of the short-term dynamics of GW–SW connectivity in relation to river stages: (a) (low-water stage), the wetlands may be supplied by an upland aquifer or prior flood; (b) (high-water stage), the wetlands are supplied by river infiltration into the alluvial aquifer and possibly by river backflow through a surface channel connection; (c) (flood), the wetlands are supplied by overbank flow (derived from a figure in Amoros and Bornette, 2002).

Controls on GW–SW interactions in wetlands

GW–SW interactions of wetlands are strongly controlled by the relative surface water and groundwater heads and these can vary significantly over the short term (e.g. Rosenberry and Winter, 1997). Over the long term, changes in GW–SW interactions will occur when there are changes in the heads driven by factors such as climate change (e.g. Wurster *et al*., 2003), modifications to the management of the uplands and/or riparian zone (i.e. land use change such as clearing of native vegetation for dryland agriculture, irrigation, forestry, urban development, etc., e.g. Allison *et al*., 1990; Doble *et al*., 2006), and changes in the flow regimes of the river due to regulation, channelization, upstream water abstractions, etc. (e.g. Walker, 1992; Walker *et al*., 1992; Walker and Thoms, 1993; Jolly, 1996). Changes that lead to rises in water tables can result in continual movement of groundwater into ephemeral wetlands. The life cycles of many species in arid/semi-arid wetlands require periods of drying which may be lost if there is continual movement of groundwater into a wetland.

The movement of groundwater into and out of wetlands is often strongly governed by local geomorphology. Most wetlands occur at low points in the landscape where heavy-textured soils are commonplace due to alluvial depositional processes. If the hydraulic conductivity of these clays and silts are lower than that of the underlying aquifer then they can impede groundwater movement between the aquifer and the wetland. If the soils are very high in sodium (i.e. as a result of primary or secondary salinity) then the impedance can be further exacerbated because these soils can disperse and swell when wetted with low-salinity surface water, leading to significant reductions in hydraulic conductivity (e.g. Jolly *et al*., 1994). Conversely, if a wetland has bed materials that are of high permeability (i.e. relic gravels), then there will be active exchange between the surface water and groundwater. While the papers of Huggenberger *et al*. (1998) and Lamontagne *et al*. (2005) are concerned with rivers rather than wetlands, they are good examples of the role that local geomorphology, combined with fluctuating head differences between the water body and the groundwater, can play in controlling the rates of exchange of groundwater and surface water.

Wetland and groundwater flow geometry are also important controls on the exchange of groundwater, as demonstrated by a series of theoretical and field studies by Townley and Davidson (1988); Nield *et al*. (1994); Townley and Trefry (2000); Smith and Townley (2002) and Turner and Townley (2006). These studies have highlighted that GW–SW interactions in wetlands can be broadly classified into four types of flow regimes (Figure 4): (i) connected losing wetland—surface water from the wetland is lost (i.e. recharges) to the underlying aquifer; (ii) disconnected losing wetland—similar to (i) except that leakage of surface water from the wetland is slow enough so that there is an unsaturated zone beneath the wetland; (iii) flow-through wetland—gains water (i.e. receives discharge) from the groundwater in some parts of the wetland and loses water (i.e. recharges) it in other parts; and (iv) gaining wetland—gains water (i.e. receives discharge) from the underlying aquifer. However, it is important to note that individual wetlands may temporally change from one type to another depending on how the surface water levels in the wetland and the underlying groundwater levels change over time.

Wetland salinization

In many arid/semi-arid areas there are naturally high concentrations of salts stored in soil and groundwater systems due to factors such as low relief, little or no surface drainage, and high rates of evapotranspiration (Herczeg *et al*., 2001). The salts can originate from rock weathering, airborne oceanic aerosols transported inland by rainfall (referred to as cyclic salts), connate water trapped in sediments, which were deposited in earlier geological times (i.e. from previous sea water transgressions), or aeolian clays (referred to as parna; Butler, 1956). This natural storage of salt in soils and groundwater is referred to as primary salinity.

As described above, land use/management changes in the uplands/riparian zone and/or changes in river management can lead to modifications to groundwater flow regimes. This, in turn, can lead to the mobilization of the stored salts which can lead to increased salinization of soils and surface water bodies such as rivers, lakes, and wetlands. This human-induced movement of salt through the landscape is referred to as secondary salinity and occurs in many arid/semi-arid countries, for example, Argentina, Australia, Egypt, India, Iran, Pakistan, and South Africa (Ghassemi *et al*., 1995).

The salinity in wetlands of arid/semi-arid environments will vary naturally due to high evaporative conditions, sporadic rainfall, groundwater inflows, and freshening after rains or floods. However, wetlands are often at particular risk of secondary salinity because of their generally lower elevation in the landscape which exposes them to increased saline groundwater inflows caused by rising water tables (Cramer and Hobbs, 2002). In these situations, salt accumulates in the bed of the wetland and in the water column unless there is sufficient low-salinity flushing flows. Wetlands that become terminal as a result of

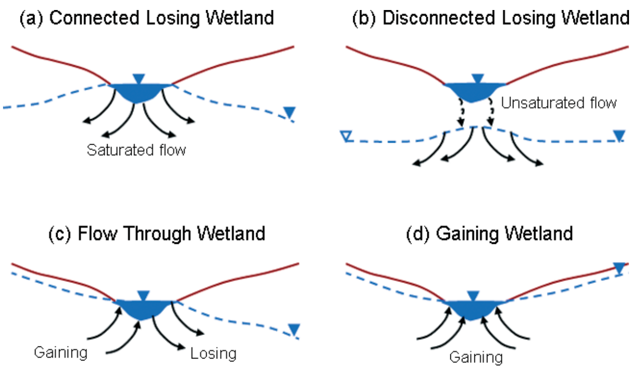

Figure 4. Conceptual groundwater flow paths to and from a (a) connected losing; (b) disconnected losing; (c) flow-through; and (d) gaining wetland.

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the changes in surface hydrology are potentially at higher risk than flow-through systems as there is no salt removal mechanism (Cramer and Hobbs, 2002). Increased runoff is also a commonly observed consequence of secondary salinity, consequently, wetlands can experience increased surface water inflows which are often higher in salinity than under natural conditions. Lakes Toolibin, Towerrinning, and Warden, and the Coomalbidgup Swamp in southwestern Australia are notable examples of wetlands that have been impacted by secondary salinity (Froend *et al*., 1987; Froend and McComb, 1991; Froend and van der Moezel, 1994; Froend *et al*., 1997; Wallace, 1997; Davis and Froend, 1999; Halse *et al*., 2003; Marimuthu *et al*., 2005).

Wetland water and salt balances

Wetlands have historically been described by their surface water regime (generally characterized by water depth through time) and relates to the duration of inundation, seasonality, rate of rise, frequency, inter-flood level, and variability. The contribution from groundwater is progressively being included into the characterization of the water regime of wetlands. Hayashi and Rosenberry (2002) refer to the hydroperiod of ephemeral wetlands as being determined by climatic factors (precipitation and evaporation), amount of surface runoff and input/output from groundwater exchange.

The water and salt balance of a wetland with groundwater exchange is described by the following (Figure 5):

$$P + S_I + G_I = \mathrm{ET} + S_O + G_O + \Delta S \qquad (1)$$

$$PC_P + S_I C_{SI} + G_I C_{GI} = S_O C_{SO} + G_O C_{GO} + \Delta S \Delta C_S \qquad (2)$$

where P is precipitation, S_I is surface water inflow, G_I is groundwater inflow, ET is evapotranspiration, S_O is surface water outflow, G_O is groundwater outflow, ΔS is change in water storage, C_P is salinity of precipitation, C_{SI} is salinity of surface water inflow, C_{GI} is salinity of groundwater inflow, C_{SO} is salinity of surface water outflow, C_{GO} is salinity of groundwater outflow, and ΔC_S is the change in salinity of the water storage. Note that the salinity of ET is zero as salt is left behind during evaporation (and that we have ignored dry deposition and windblown additions/losses of salt). The groundwater inputs and outputs are generally considered one of the most difficult components of the wetland water balance to characterize because they tend to be very small, compared to surface water inputs and rainfall (Hunt *et al*., 1996, 1998 and Hunt *et al*., 1999 provide good summaries of methods for measuring groundwater exchange with wetlands). This difficulty in quantifying groundwater inputs and outputs is further complicated by the possible variations in the surface water connection between wetlands and surface water bodies.

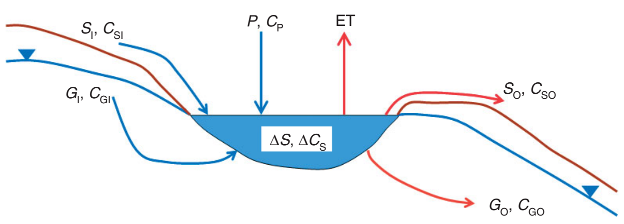

Figure 5. Schematic of the components of the water and salt balance of a wetland.

The majority of literature on the groundwater components of wetland water balances concerns studies in temperate areas (e.g. Gilvear *et al*., 1993; Rosenberry and Winter, 1997, Hunt *et al*., 1999; Raisin *et al*., 1999) and they generally only consider water balances. Indeed, there is a dearth of relevant wetland water and salt balance studies in arid/semi-arid areas. One exception is the study of a prairie wetland in Saskatchewan (Canada) by Hayashi *et al*. (1998a,b). They showed that the cycling of chloride between the wetland and the adjacent uplands by both surface water and groundwater pathways was highly dynamic. Another exception is the study of Marimuthu *et al*. (2005) which attempted to unravel the complex GW–SW interaction processes for a series of coastal dune wetlands in the southwest of Western Australia, and found that the water balance of the wetlands system could not be treated as a single water body, as was perceived from bathymetric data. The study is interesting because it illustrates the value in supplementing traditional hydraulic methods with hydrochemistry when investigating complex wetlands systems and their interactions with groundwater. Although they did not assess salt balances, Wurster *et al*. (2003) demonstrated that the water balance of groundwater-fed wetlands can be dramatically altered by changes in groundwater conditions in the surrounding areas. They studied the disappearance of more than 100 interdunal wetlands in the Great Sand Dunes National Monument in Colorado (USA), and concluded that these wetlands were in fact ephemeral features that disappeared for several years during dry periods when regional water table levels decline. The wetlands then returned during prolonged wet periods when water tables rise and they may then persist for several decades.

Wetland GW–SW modelling

Modelling of the interaction of groundwater with lakes has been an active area of research for over 30 years (e.g. the seminal work of Winter, 1978, 1983). While most of the early studies were site-specific, more recent work has concentrated on developing generic relationships between the geometry of water bodies and the lake/wetland–aquifer interactions (e.g. Townley and Davidson, 1988; Nield *et al*., 1994; Townley and Trefry, 2000; Smith and Townley, 2002). A shortcoming of these approaches is that they generally do not adequately consider the fact that most lakes and wetlands contain bottom sediments, which have different hydraulic characteristics to the aquifer. As described above, heavier-textured bank/bed materials can have a significant control on GW–SW interactions. Another limitation is that they assume steady-state conditions, and these rarely hold for most arid/semi-arid wetlands as they typically undergo cycles of wetting and drying resulting in transient GW–SW interactions. In recent years, the focus of groundwater–lake/wetland interaction modelling has shifted back to site-specific transient studies using traditional numerical modelling approaches (e.g. Restrepo *et al*., 1998; Crowe *et al*., 2004) and newer analytic element techniques (Haitjema, 1995) and link-node approaches (Walton *et al*., 1996). Hunt *et al*. (2003) compare the use of the first two of these techniques. It is important to note that all these studies deal with water flow only. The use of fully coupled groundwater flow and salinity transport modelling in relation to wetland and river ecology has only recently commenced (e.g. Langevin *et al*., 2005; Bauer *et al*., 2006a,b; Zimmermann *et al*., 2006). These numerical models are extremely complex and require large amounts of data to parameterize reliably, and so they are unlikely to see widespread management use.

The groundwater modelling approaches described above cannot simulate the unsaturated zone processes within and around wetlands. These are very important in terms of ecological responses, particularly in relation to vegetation growth, decomposition, and nutrient release. This shortcoming has recently been addressed by a number of authors (e.g. Bradley and Gilvear, 2000; Joris and Feyen, 2003; Dekker *et al*., 2005) who have been using one- and two-dimensional saturated–unsaturated flow models to simulate both the saturated and unsaturated GW–SW processes in and around various European wetlands. While the results of these studies are specific to temperate wetlands, and considered only the movement of water and not salt, the general approaches should have relevance for wetlands in arid/semi-arid areas.

Another modelling approach is box-type models such as FEUWAnet (Dall'O' *et al*., 2001) which simulates the spatial heterogeneity and temporal variation of lateral (from catchment areas to water body) and vertical (from vegetation canopy to groundwater) water fluxes of riparian wetland ecosystems. This model consists of multiple boxes representing various water storage compartments (soil, groundwater, open water, etc.) connected by a network of hydraulic resistances. While FEUWAnet was developed for temperate riparian wetlands in northern Germany for the purpose of assessing the effectiveness of riparian systems in controlling the fluxes of non-point pollution discharging to open water bodies, the concepts should also be applicable to arid/semi-arid wetlands, and in principle, could be extended to modelling salt movement as well. Other box-type models of wetland catchment groundwater movement includes those of Whigham and Young (2001) and Krasnostein and Oldham (2004), although the former does not include interactions with groundwater.

Summary

The limited field studies conducted suggest that in arid/semi-arid areas the interactions between wetlands and groundwater are highly dynamic, are both temporally and spatially complex, and often extend beyond the surface water boundaries of the wetland. In areas where groundwater is low in salinity, it has beneficial impacts on wetland ecology, which can be diminished in dry periods when groundwater levels, and hence, inflows to wetlands are reduced or even cease. Conversely, if groundwater is saline, and inflows increase due to raised groundwater levels caused by factors such as land use change and river regulation, then this may have a detrimental impact on the ecology of a wetland and its surrounding areas.

There has been very little modelling of GW–SW interactions in arid/semi-arid wetlands with respect to water fluxes, let alone movement of salt. However, in temperate regions there has been a reasonable amount of modelling of water exchange between wetlands, their catchments and groundwater; the studies highlighted above are a sample of this literature. While the results of these studies are generally site-specific, the principles and approaches have potential application in arid/semi-arid areas. In addition, there is a clear need to develop modelling capabilities for the movement of salt to, from, and within wetlands. While fully coupled flow and transport modelling has commenced, it is highly specialized with significant data requirements, and so we conclude that box-type modelling may be a more realistic approach that can be used to aid the water and salinity management of wetlands.

ECOLOGICAL RESPONSES TO CHANGES IN SALINITY AS A CONSEQUENCE OF THE CHANGES IN SURFACE WATER AND GROUNDWATER REGIMES

As described above, climate variability and subsequent fluctuating hydrology are the key drivers of ecology in arid/semi-arid environments. Whilst numerous studies have examined the relationship between wetland biota and water regime (e.g. Casanova and Brock, 2000; Warwick and Brock, 2003), there have been few studies of ecological response to the combination of changing water regime and salinity (Brock *et al*., 2005).

In this section, the available literature on ecological responses to increases in wetland salinity that occur as a consequence of changes in surface water and groundwater regimes caused by secondary salinity is reviewed. First, the available Australian salinity tolerance literature for wetland biota is highlighted, and we discuss a range of limitations and other issues associated with the use of this data and knowledge. This is followed by a summary of what is currently known of the combined impact of salinity and changes in water regime on arid/semi-arid wetland ecology. Finally, the impact that changes in GW–SW interactions may have on hydrological pulse events, which are key drivers of wetland ecology in arid/semi-arid areas are discussed.

Available Australian salinity tolerance data, knowledge gaps, and other issues

Due to the significant impact that secondary salinity is having on ecology in Australia there have been a number of key studies and reviews that have summarized the salinity tolerance of freshwater aquatic biota and riparian vegetation (e.g. Hart *et al*., 1990, 1991, 2003; Williams *et al*., 1990; Niknam and McComb, 2000; James *et al*., 2003; Kefford *et al*., 2003, 2004a, 2005, 2006; Nielsen *et al*., 2003a; Horrigan *et al*., 2005, 2007; Pinder *et al*., 2005; Sim *et al*., 2006a,b). These studies and reviews show that there are data available for many taxa of native plants and animals, with the notable exceptions of micro-algae, frogs, platypus, and tortoises for which there is little or no data (Hart *et al*., 1991). We do not intend to present summaries of the salinity tolerances of species/genera as these are already available in these reviews (e.g. Niknam and McComb, 2000) and have comprehensive summary tables of the known glasshouse and field salinity tolerances of Australian native tree species). Instead, we discuss the key knowledge gaps in the available salinity tolerance data and understanding, with a particular focus on a number of issues in relation to arid/semi-arid wetlands.

Field versus laboratory studies of salinity tolerance. In theory, laboratory experiments can be used to unravel the highly complex interactions between ecology and changing water regime and salinity regimes. However, it is now becoming clear that these types of studies are not always representative of the highly variable and unpredictable conditions experienced in the field. Controlled field experiments, such as that of Marshall and Bailey (2004), are rarely undertaken due to the difficulty and expense involved. As a result, most field knowledge is in the form presence/absence (or abundance) data based on the salinity range and maximum salinity (commonly referred to as the maximum field distribution, MFD) in which a species was observed in the field, rather than growth changes with increasing salinity and lengths of time that salinity levels remain elevated. There is often potential for false absences and high sampling biases because of uneven numbers of observations across salinity categories. There is also very little time-series data, and this is a serious issue given that wetland salinities are often highly temporally variable due to changes in surface water inflows and outflows, evapoconcentration, and fluctuations in groundwater inputs, and losses.

In the case of riparian vegetation most of the current knowledge on the salinity tolerance of species is derived from laboratory and glasshouse studies (Niknam and McComb, 2000). One of the problems in utilizing and comparing data from these studies is the lack of uniformity in the treatments tested (differing salinity levels, lengths of waterlogging, study durations, response measurements, etc.). Moreover, in recent times, it has become clear that these types of studies, in which the salinity, irrigation, nutrition, and energy are generally kept constant or are closely controlled, are often not representative of the highly variable conditions experienced in the field. Furthermore, the majority of these studies use individual juvenile plants (up to 1 year old), and so the observed responses are unlikely to be representative of mature communities of plants. Also, the salinity of surface water often differs considerably from both soil and groundwater salinities. Thus, aquatic and emergent vegetation which inhabit wetland sediments or hyporheic zones may experience quite different salinities to those indicated by the surface waters. Deeply rooted riparian vegetation may avoid high soil salinity by utilizing groundwater where it is less saline. It is difficult to accurately replicate these complex field processes in glasshouse and laboratory experiments.

In the case of emergent and submerged or floating aquatic vegetation, glasshouses and laboratory experiments can provide an indication of sub-lethal effects of salinity on vegetation. In these studies, it has been demonstrated that profound growth reductions can occur at considerably lower salinities when compared to those which result in mortality. The sub-lethal responses to salinity are often characterized by reductions in plant biomass, height, flowering, shoot numbers, leaf proliferation, and leaf size. These effects may be apparent at salinities as low as 1000 mg l^{-1} (James and Hart, 1993). Leaf production is often slowed, and in some cases premature leaf senescence is induced (e.g. Warwick and Bailey, 1997, 1998). Visual symptoms of salt stress include leaf burn, wilting, or chlorosis.

In the case of aquatic animals, Kefford *et al*. (2004b) compared laboratory-derived acute salinity tolerance (the concentration level that is lethal to 50% of individuals; LC_{50}) of freshwater macroinvertebrates and fish from southeastern Australia (Victoria) with the maximum salinity at which they have been recorded alive in nature (i.e. their MFD). They found that the MFD of freshwater macroinvertebrate taxa were correlated with their acute (72 h) direct transfer LC_{50} salinity values, and was best for common macroinvertebrates because the high number of field observations led to good estimates of MFD. Relative to macroinvertebrates, direct transfer LC_{50} values from both adult and early life-stage freshwater fish were found to provide a poorer estimate of the MFD values. However, slow transfer (slow increase in salinity over several days to allow fish to acclimatize) LC_{50} provided a better estimate of the MFD for adult freshwater fish. It was thought that because salinity changes in field situations are often slow, short-lived species may not experience large changes during their life, whereas longer-lived and more mobile species may be able to acclimatize and survive in areas where salinity levels would be lethal in their early life-stages.

In a more recent study on the salt sensitivity of stream macroinvertebrates in northeastern Australia (Queensland), Horrigan *et al*. (2007) also found that acute lethal tolerances (72 h LC_{50}) were significantly correlated with maximum field conductivities. However, in contrast to the study of Kefford *et al*. (2004b), they found that the majority of taxa had an LC_{50} higher than the maximum conductivity observed in the field. They speculated that this was either because the salt tolerance under natural conditions may be considerably lower, or because the LC_{50} values represent overestimates because they are the values at which 50% of the test population are able to survive over a relatively short timeframe (72 h), or because there were very few high-salinity (EC > 12 mS cm^{-1}) sites sampled due to their rarity in Queensland.

Overall, there is a paucity of studies which compare laboratory and field-based tolerances. There is clearly a need for further research to reconcile the inconsistencies between the various approaches and to continue to develop robust methodologies that account for the highly variable and unpredictable conditions experienced in the field. From our perspective, there is little need for further studies of salinity tolerance that are based only on laboratory experiments. In our view, the research focus needs to move away from purely correlative studies towards more process-based science in order to more fully understand the physiological effects of time varying the salinity on biota, including the interactions with other stressors and perturbations.

Acclimatization of biota to salinity. Acclimatization to salinity has been demonstrated to enhance salinity tolerance in trees (Heth and MacRae, 1993). Pinder *et al.* (2005) also came to the conclusion that the freshwater invertebrate fauna in the wheat belt of western Australia (an area with naturally high soil, groundwater, and stream salinities) may be comparatively salt tolerant, and that this tolerance provides a buffer against the effects of mild salinization. James *et al.* (2003) are of the view that the acclimatization ability of aquatic organisms is not just dependent on inherent morphological and life-history strategies, but also on the nature of the disturbance (i.e. the rate, duration, periodicity, and seasonality of salinization). They suggest that when salinity slowly increases, some organisms can acclimatize and tolerate such incremental increases ($<$50% of the initial concentration). However, mortality is likely when sudden large increases ($>$100% of the initial concentration) occur.

Resilience of biota to salinity. Resilience is the capacity of a system damaged by disturbance to return to its prior state if the disturbance is removed. Many wetland biota have some natural resilience and adaptive strategies to cope with salinity and dynamic hydrology. As noted by Hart *et al.* (2003), the resilience of most freshwater biota is a function of the use and availability of refugia. They give the example that with salinization of wetlands, biota such as insects may leave for less saline wetlands and then recolonize the affected wetland later if the salinity drops (i.e. returns to its prior state). If however, the salinization of the wetland persists, then the system does not recover and the original species are lost and replaced by a reduced set of more tolerant species (i.e. moves permanently to an alternative state). Hart *et al.* (2003) argue that while resilience is a useful theoretical concept, there is currently insufficient knowledge to measure a system's resilience and to use this to set thresholds for particular disturbances. However, they believe that this knowledge is beginning to be generated, the study of Davis *et al.* (2003) being one example. Another recent example is the study of Strehlow *et al.* (2005) which found evidence that the onset of secondary salinity may decrease the resilience of macrophyte-dominated systems over time and drive them towards benthic community-dominated systems.

Life-stages and salinity tolerance. As summarized by Nielsen *et al.* (2003a), the current understanding of sub-lethal effects and sensitive life-stages is very poor. The limited evidence available suggests that juvenile life-stages are more sensitive than those of adults and that the reproductive capacity of adults may be impaired by elevated, but sub-lethal, salinity levels. Presence of a species at a particular level of salinity does not necessarily indicate that it can complete its life-cycle at that salinity (Kefford *et al.*, 2004b). Indeed, even the long-held assumption that as salinity increases an adult will experience no direct effect until a threshold is reached (Hart *et al.*, 1991) is being challenged (e.g. Kefford and Nugegoda, 2005). This has important implications for the long-term structure, function and sustainability of populations and communities, in that, whilst elevated salinity levels may not be lethal for adults they may not be able to reproduce, and/or there is no recruitment to the population. For aquatic biota, Skinner *et al.* (2001); Brock *et al.* (2003); Nielsen *et al.* (2003a,b) and Brock *et al.* (2005) point out that dormant life-stages (such as eggs, seeds, spores, and asexual propagules of aquatic organisms) are important reservoirs of biodiversity in semi-arid areas, and the juvenile zooplankton and seedlings that emerge from this bank (reservoir) may be more sensitive than adult life-stages to increasing salinity. However, in a recent macroinvertebrate study carried out by Kefford *et al.* (2007), a diversity of responses was observed, with some of the species having similar salinity tolerances in all life-stages, while the eggs and hatchlings of other species had salinity tolerances that ranged from 4 to 88% of those in older life-stages. These authors concluded that on the basis of present knowledge it is still difficult to generate simple rules of thumb to approximate the sensitivity of young life-stages of freshwater macroinvertebrates based on their dominant stage's tolerance.

Interactions between salinity and other environmental stressors. As discussed in James *et al.* (2003), the interactions between salinity and other environmental stressors and perturbations such as changed water regimes, eutrophication, turbidity, temperature, etc. have been rarely studied. Moreover, salinity can also have indirect effects on pH, dissolved oxygen, and nutrient balances of plants, which may be as significant as the direct ion effect of salt alone. There is also a very limited understanding of the impacts of salinity on species' interactions, food-web structures, and the structure and integrity of communities.

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One relevant study is that of Timms and Boulton (2001) who showed the interplay between salinity, turbidity, and water regime in determining invertebrate composition in arid zone wetlands. In particular, they found that whilst species' richness varied amongst wetlands, it was assemblage composition that more clearly differentiated wetland types. This was despite the variable responses to salinity, turbidity, and water regime that different taxa exhibited. They concluded that it was not just salinity that was dictating thresholds of tolerance that distinguish different assemblages.

Another recent study which highlighted complex interactions between ecology, salinity, water regime, and turbidity is that of Strehlow *et al.* (2005). They carried out detailed time-series sampling of water depth, water quality, submerged macrophyte biomass and macroinvertebrate richness, and abundance in six wetlands in southern western Australia over an 18-month period which encompassed a complete wetting and drying cycle. They found that high turbidity occurred when salinity was highest due to wind-induced sediment resuspension in shallow water. They also found that very shallow wetlands were able to support aquatic plant communities and suggested that depth may be affecting these plant communities indirectly by regulating the salinity and turbidity. The responses of invertebrate communities over time varied from site to site, and the differences in the species present at each wetland suggested there was high specificity of fauna in response to the prevailing salinity and hydrological regime. They concluded that a change in ecological regime may be a more important threshold for determining the impacts of secondary salinity on ecology, rather than the increase in salinity alone.

Combined impacts of salinity and changes in water regime

The onset of secondary salinity not only increases the salinity of wetlands, but can also impact on their water regime through increased groundwater inflows which increase water depths and extend periods of inundation (i.e increases hydroperiod) (Cramer and Hobbs, 2002). Because salinity potentially reduces plant height, increases in water depth will compound growth reductions imposed by salinity. Furthermore, increased water depths can result in waterlogging of fringing vegetation, and increasing salinity and waterlogging can act synergistically to reduce plant growth. In this section, we summarize a number of studies where the combined effects of changes in surface water regime and salinity have impacted on wetland ecology.

A large number of intensive field and modelling studies on the floodplains of the lower River Murray in Australia have examined the interaction between groundwater, surface water, salt accumulation, water use, and growth of riparian vegetation (*Eucalyptus camaldulensis* and *E. largiflorens*) which commonly fringe arid/semi-arid wetlands in southeastern Australia (e.g. Jolly *et al.*, 1993; Thorburn and Walker, 1993, 1994a,b; Thorburn *et al.*, 1993, 1995; Mensforth *et al.*, 1994; Jolly, 1996; Jolly and Walker, 1996; Taylor *et al.*, 1996; Akeroyd *et al.*, 1998; Slavich *et al.*, 1999a,b; Doble *et al.*, 2006; Holland *et al.*, 2006; Overton *et al.*, 2006). Accumulation of salt in floodplain soils occurs naturally in the lower River Murray region, and prior to river regulation was mitigated by leaching from frequent floods which inundated the floodplains. Over the long term, there was a salt balance in the soil that enabled the development of long-term stable vegetation communities. However, over the last 70–80 years, the surface and groundwater hydrology of the floodplains has been dramatically altered due to the impact of river regulation and the development of large irrigation areas on the higher areas adjacent to the floodplains. Salt is now accumulating in floodplain soils at an increased rate due to increased groundwater discharge caused by raised water table levels and point source saline discharge from adjacent irrigation areas. These problems are further exacerbated by less frequent leaching of the accumulated salt in the soils by large floods, the frequency and duration of which have been greatly reduced by river regulation. In addition to having severe impacts on the health of the adult populations of these species, the high soil salinity and lack of flooding has reduced recruitment (George *et al.*, 2005).

In the upper southeast region of South Australia, Mensforth and Walker (1996) studied the growth of another species commonly found fringing arid/semi-arid wetlands in Australia (*Melaleuca halmaturorum*). This study highlighted how this species can dynamically alter its water use and source throughout time in response to fluctuating saline shallow groundwater and surface water availability. They found that these trees used groundwater from the soil surface at the end of winter in response to groundwater rise and inundation of the soil profile. During summer they used water from deeper in the soil profile in response to salt accumulation in the surface soils. At the end of summer, although there were high salt concentrations near the soil surface, the soil was generally moist and roots were extracting water from below the saline zone. Winter rainfall quickly recharged the groundwater, leached salt from the soil profile, and caused the moderately saline groundwater to rise to the soil surface. Waterlogging caused the roots near the soil surface to die. Subsequent evapotranspiration then caused the water table to drop quickly. The roots began to grow, drying the soil until the concentration of salts in the soil solution was too high for more water to be extracted. The roots once again began to die back at the soil surface due to the high salinity. This sequence of events occurred over a period of 12 months (Figure 6).

Davis *et al.* (2003) have pointed out that as secondary salinity generally occurs as a result of rising water tables, the most immediate impact on wetland ecology is the often increased water depth and loss of seasonal wetting and drying cycles, rather than the effects of higher salinity alone. They cite oral histories which suggest that in the wheat belt wetlands of western Australia, fringing, emergent, and freshwater aquatic vegetation dies within ~5 years of the onset of secondary salinity, often from

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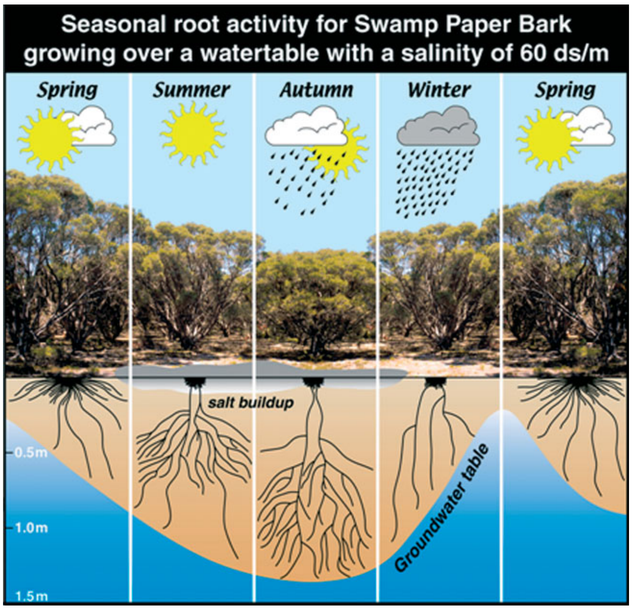

Figure 6. Seasonal root activity and depth of water extraction of *Melaleuca halmatorurum* (Figure based on findings of the study of Mensforth and Walker (1996)).

waterlogging rather than salt *per se*. They also cite Halse *et al*. (1993) who believe that secondary salinity in this region has changed wetland plant communities from those dominated by woody species to those dominated by submerged species, with major consequences for fauna, particularly waterbirds, reliant on emergent plants. Davis *et al*. (2003) provide the case example of Toolibin Lake in the southwest of western Australia, in which permanent inundation over prolonged periods has resulted in the death of wetland tree communities and the prevention of recruitment. Toolibin Lake is the last remaining freshwater wetland in the region with extensive stands of *Casuarina obesa*, *Melaleuca* sp. and *Eucalyptus rudis* (Froend *et al*., 1987). This vegetation association is typical of the naturally occurring wetland vegetation of this area prior to rises in groundwater induced by clearing for agriculture. Measurements of soil salinity and the calculation of percentage inundation from tree elevation and observations of tree vigour and xylem pressure potential response indicated that tree deaths in the *Melaleuaca* sp. and *C. obesa* were due to increased levels of salinity. Death and low vigour in *E. rudis* were attributed to both increasing salinity and prolonged inundation (Froend *et al*., 1987). Secondary salinization has had a greater effect on the lake margin species than on those inhabiting the environments of the lake bottom or the uplands region, which are unaffected by inundation. The lake is an important breeding area for waterbirds as extensive dense thickets of *C. obesa* and *Melaleuca* sp. occur through much of the inundated area. Live vegetation in the lake is important for providing suitable nesting sites, and the fresh/brackish water is of sufficiently high quality for growth of emergent vegetation and is suitable for young birds. The periodic drying of the lake also allows persistence of the trees growing on the lake bed. Toolibin Lake has been the subject of remediation including short- to medium-term engineering measures to decrease salinity within the lake, and long-term rehabilitation measures within the catchment (Froend *et al*., 1997; Wallace, 1997). Another wetland in the southwest of western Australia that has been affected by secondary salinity and changes in water regime is Lake Towerrinning. By the late 1980s, it was highly salinized and eutrophic and had lost its fringing vegetation and contained little aquatic life (Froend and McComb, 1991). It also has been the subject of engineering works aimed at reducing salinity levels.

Brock *et al*. (2005) conducted a laboratory study of the effects of salinity and water regime on aquatic biota in sediments from seven wetlands in the Murray-Darling Basin in southeastern Australia. Their experiments used germination of aquatic plant seeds at five salinity levels (<300, 1000, 2000, 3000, 5000 mg l^{-1}) and two water levels (damp/waterlogged and flooded). They also studied the emergence of zooplankton eggs at the same five salinity levels. For sediments from four of the wetlands, they found that there was decreasing species richness and abundance of biota germinating or hatching as salinity increased above 1000 mg l^{-1}, and that this trend was more marked when sediments were damp rather than flooded. For the other three wetlands, results were more variable. The lack of consistency of responses raises questions about transferability of results between wetlands. Notwithstanding this issue, they concluded that there was greater loss of diversity for plants germinating from seed-banks at the edges of wetlands where plants are not completely submerged than for those in submerged conditions. They suggested that transpiration and evaporation at the exposed soil surface and ion exclusion mechanisms in plant roots could cause localized increases in salinity in the root zone under damp conditions (i.e. the fringe of the wetland), whereas, in flooded conditions (i.e. the wetland itself), constant submergence could prevent or ameliorate accumulation of salts. Overall, Brock *et al*. (2005) concluded that their 'results suggest that the effects of salinity on plants germinating from a seed bank will be more pronounced at wetland edges or in temporary wetlands where water levels fluctuate, than from the same seed bank germinating in permanently flooded areas of wetlands'. A possible implication of this is that if secondary salinity also leads to greater wetland water depths then these may in part offset the impact of the increasing salinity on aquatic vegetation. Clearly, further studies are required to determine if this is indeed the case and whether the results of Brock *et al*. (2005) apply more generally than just the small number of wetlands they studied.

In a recent study of seven saline wetlands in southwest western Australia, Sim *et al*. (2006c) found that the changes in ecological regimes in saline wetlands was driven by the combined effects of salinity and water regime on species' life histories and competitive abilities. In particular, they found that macrophytes were powerful competitors with the ability to germinate and establish

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under a range of salinities, turbidities, and water depths, and were favoured by seasonal drying.

In summary, it is clear that secondary salinity can impact on wetland biota through changes in both salinity and water regime, which result from the hydrological changes caused by secondary salinity. Whilst there have been some detailed studies of these interactions for some Australian riparian tree species, as indicated by Brock *et al.* (2005), the combined effects on aquatic biodiversity are only just beginning to be elucidated.

Pulse events and groundwater–surface water interactions

Climate variability and subsequent fluctuating hydrology are key drivers of biogeochemical cycles and ecology in arid/semi-arid environments (Austin *et al.*, 2004; Chesson *et al.*, 2004; Huxman *et al.*, 2004; Schwinning *et al.*, 2004; Schwinning and Sala, 2004). Rainfall and flow-pulse events drive hydrological fluctuations in wetlands which in turn lead to physiological, morphological, and life-history traits that facilitate survival and growth of biota in the water-limited variable environments of arid/semi-arid regions. For example, in the case of vegetation in arid areas there is a widely cited paradigm, the 'pulse-reserve' conceptual model that depicts a direct relationship between rainfall, which triggers pulses of plant growth, and reserves of carbon and energy (Reynolds *et al.*, 2004). The pulse paradigm has also been applied to rivers and floodplains by Junk *et al.* (1989) who developed the flood-pulse concept based mainly on large tropical lowland systems with predictable overbank flood-pulses of long duration. This concept was then extended by Tockner *et al.* (2000) to encompass temperate floodplains located anywhere along a river corridor, and to include floodplain expansion-contraction cycles occurring below bankfull (i.e. 'flow-pulse' vs 'flood-pulse'). Walker *et al.* (1995) discussed the shortcomings of the flood-pulse concept in relation to lowland rivers in arid/semi-arid areas (the concept is not easily applied where the pulse is variable, and does not account for the effects of river regulation), but concluded that the concept could be adapted to these environments. Puckridge *et al.* (1998) also concluded that the flood-pulse concept could also be extended to encompass the complexity and diversity of hydrological patterns in large rivers in arid zones. Amoros and Bornette (2002) highlight the role of lateral (river to wetlands) and vertical (GW–SW interactions) connectivity in relation to hydrological pulsing that drives the functioning of floodplain ecosystems. From these and many other studies it is clear that the timing and duration of river flow-pulses are major factors responsible for composition, structure, and function of floodplain wetlands communities. Indeed, the life cycles of many wetland biota are directly related to flow-pulses in terms of timing, duration, rise, and fall of flood waters (e.g. fish breeding cycles; Bayley, 1991). Clearly, changes in climate and land management, and regulation of rivers will have significant impacts on rainfall/flow-pulse regimes, and hence, wetland ecology.

In addition to rainfall/flow-pulses directly controlling ecological function they also have an important indirect role through their impacts on wetland salinity. Freshwater pulses can be the primary means by which salt stored in both the water column and in the underlying sediments are flushed from wetlands. Conversely, as discussed above, increased runoff is also a commonly observed consequence of secondary salinity, and wetlands can experience increased surface water inflows which are often higher in salinity than when under natural conditions. Moreover, changes in rainfall/flow-pulse regimes can have significant impact on wetland GW–SW interactions. Because groundwater is generally the primary source of salt in wetlands, and because this is in part controlled by head differences between the surface water in a wetland and the underlying groundwater, any changes in wetland surface water regimes due to changes in rainfall/flow-pulsing regimes will also have salinity implications for wetlands. This is exacerbated in the case of wetlands located in areas experiencing secondary salinization, as water tables underlying wetlands are rising over time (Cramer and Hobbs, 2002), further increasing groundwater inflows, and hence, movement of salt into wetlands. It is possible in some instances that the groundwater inflow to a wetland may become so large that it could become a major component of the water balance (e.g. Raisin *et al.*, 1999), and hence mask the role of natural pulsing regimes. On the positive side, if the groundwater is low in salinity it may provide an ecological benefit in arid/semi-arid areas by assisting in maintaining water in wetlands that become aquatic refugia between flow-pulses (Hamilton *et al.*, 2005).

CONCLUSIONS

1. GW–SW interactions in wetlands are highly dynamic, both temporally and spatially. Groundwater that is low in salinity has a beneficial impact on wetland ecology, which can be diminished in dry periods when groundwater levels, and hence, inflows to wetlands are reduced or even cease. Conversely, if groundwater is saline, and inflows increase due to raised groundwater levels caused by factors such as land use change and river regulation, then this may have a detrimental impact on the ecology of a wetland and its surrounding areas.
2. GW–SW interactions in wetlands are mostly controlled by factors such as differences in head between the wetland surface water and groundwater, the local geomorphology of the wetland (in particular, the texture and chemistry of the wetland bed and banks), and the wetland and groundwater flow geometry. The GW–SW regime can be broadly classified into three types of flow regimes: (i) recharge—wetland loses surface water to the underlying aquifer; (ii) discharge—wetland gains water from the underlying aquifer; or (iii) flow-through—wetland gains water from the groundwater in some locations and loses it in others.

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However, it is important to note that individual wetlands may temporally change from one type to another depending on how the surface water levels in the wetland and the underlying groundwater levels change over time in response to climate, land use, and management.

3. The salinity in wetlands of arid/semi-arid environments will vary naturally due to high evaporative conditions, sporadic rainfall, groundwater inflows, and freshening after rains or floods. However, wetlands are often at particular risk of secondary salinity because their generally low position in the landscape exposes them to increased saline groundwater inflows caused by rising water tables. Terminal wetlands are potentially at higher risk than flow-through systems as there is no salt removal mechanism.
4. Secondary salinity can impact on wetland biota through changes in both salinity and water regime, which result from the hydrological and hydrogeological changes associated with secondary salinity. Whilst there have been some detailed studies of these interactions for some Australian riparian tree species, the combined effects on aquatic biodiversity are only just beginning to be elucidated, and are therefore, a future research need.
5. Rainfall/flow-pulses, which are a well-recognized control on ecological function in arid/semi-arid areas, also have an important indirect role through their impact on wetland salinity. Freshwater pulses can be the primary means by which salt stored in both the water column and in the underlying sediments are flushed from wetlands. Conversely, increased runoff is also a commonly observed consequence of secondary salinity, and so wetlands can experience increased surface water inflows that are higher in salinity than when under natural conditions. Moreover, changes in rainfall/flow-pulse regimes can have significant impact on wetland GW–SW interactions. It is possible in some instances that the groundwater inflow to a wetland may become so large that it could become a major component of the water balance, and hence, mask the role of natural pulsing regimes. However, if the groundwater is low in salinity this may provide an ecological benefit in arid/semi-arid areas by assisting in maintaining water in wetlands that become aquatic refugia between flow-pulses.
6. There has been almost no modelling of GW–SW interactions in arid/semi-arid wetlands with respect to water fluxes, let alone salinity or ecology. There is a clear need to develop modelling capabilities for the movement of salt to, from, and within wetlands to provide temporal predictions of wetland salinity which can be used to assess ecosystem outcomes.
7. There has been a concerted effort in Australia to collect and collate data on the salinity tolerance/sensitivity of freshwater aquatic biota and riparian vegetation. There are many shortcomings and knowledge gaps in these data, a fact recognized by many of the authors of this work. Particularly notable is that there is very little time-series data, which is a serious issue because wetland salinities are often highly temporally variable. There is also a concern that many of the data are from very controlled laboratory experiments which may not represent the highly variable and unpredictable conditions experienced in the field. In light of these, and many other shortcomings identified, our view is that currently the data are a useful guide, but must be used with some caution.

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