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Integrated modelling of ecohydrological processes along ephemeral rivers

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To Mirka

Zusammenfassung

Über eine Milliarde Menschen in 110 Ländern der Welt leben in ariden Gebieten, welche etwa ein Drittel der Erdoberfläche ausmachen. In zwanzig afrikanischen Ländern befinden sich über neunzig Prozent der landwirtschaftlich genutzten Fläche in diesen vulnerablen Trockengebieten. Dies verdeutlicht die soziale, ökologische und ökonomische Dimension dieser Gebiete.

Aride Gebiete sind durch ein Defizit an pflanzenverfügbarem Wasser geprägt, was das Gedeihen von Ökosystemen hemmt. Außerdem unterliegen die Niederschlagsereignisse großen räumlichen und zeitlichen Schwankungen, weshalb Oberflächengewässer selten sind und die Infiltrationsraten zu gering sind, um einen oberflächenhaltigen Grundwasserspeicher zu etablieren. Allerdings führen die gelegentlichen Flutereignisse entlang von sogenannten Trockenflüssen zur Entstehung von Grundwasserreservoirs, von denen sich flussnahe Wälder mit Wasser versorgen. Die ökologische und sozio-ökonomische Bedeutung dieser Wälder wird durch den oftmals verwendeten Begriff "lineare Oase" widergespiegelt. Trockenflüsse befinden sich in fast allen ariden Gebieten der Welt, bekannt sind Beispiele aus Israel (Negev Wüste), Namibia (Namib Wüste), Australien (Simpson Wüste) und der Arabischen Halbinsel (Wadis). Trockenflüsse führen nur zeitweise Wasser und der Oberflächenabfluss kann sehr stark innerhalb einer Saison und mehrerer Jahre schwanken. Anhand der Hydrogeologie ist eine Unterscheidung in zwei Typen möglich: Der erste Typ umfasst Flüsse, die durch große, mit Sedimenten gefüllte Becken fließen. Der Grundwasserspeicher ist ausgedehnt, aber zu oberflächenfern, um von Pflanzenwurzeln erreicht zu werden. Die Infiltration während der Fluten in das Flussbett ist im Wesentlichen durch die maximale Infiltrationsrate limitiert. Dieser Typ kommt vor allem in der Mitte von Wüsten vor, wie z.B. die Kalahari oder die Sahara Wüste. Der zweite Typ umfasst Flüsse, die durch kleine, mit fluviatilen Sedimenten gefüllte Becken fließen. Die geringe Größe des Alluviums ermöglicht die Ausbildung eines oberflächennahen Grundwasserspeichers, der von Pflanzenwurzeln erreicht werden kann. Die Infiltration der Fluten in das Flussbett ist sowohl durch die maximale Infiltrationsrate als auch durch den Grundwasserflurabstand limitiert. Dieser Typ kommt vor allen in den Randgebieten von Wüsten vor, wie z.B. die Namib Wüste.

Die Kopplung zwischen der Wasserressource und der Pflanzengesellschaft ist selten so stark ausgeprägt wie entlang von Trockenflüssen. Ökohydrologische Rückkopplungen können sowohl die Wasserverfügbarkeit als auch die Artenzusammensetzung beeinflussen. Die Nutzung der Ressourcen Wasser und Vegetation durch den Menschen kann die Intensität der Rückkopplung noch verstärken. Das verdeutlicht, dass ein klares Verständnis über ökohydrologische Prozesse entlang von Trockenflüssen notwendig ist, um beide Ressourcen (Wasser und Vegetation) nachhaltig zu nutzen. Allerdings sind die meisten ariden Gebiete schwer zugänglich und befinden sich in schlecht entwickelten Ländern, was zu begrenzter Information über das Öko- und Hydrosystem führt. Modelle können dazu beitragen, den geringen Informationsgehalt effektiv zu nutzen, indem Annahmen getestet und Hypothesen erstellt werden. Des Weiteren können virtuelle Experimente durchgeführt werden, deren reale Umsetzung kosten- und zeitintensiv wäre. Validierte Modelle können auch die Arbeit von Entscheidungsträgern unterstützen, indem potenzielle zukünftige Systemzustände aufgezeigt werden.

Die vorliegende Arbeit beschäftigt sich mit einer ökohydrologischen linearen Oase inmitten eines ansonsten ausgesprochen trockenen Gebietes entlang des Kuiseb River, einer der am umfangreichsten genutzten Trockenflüsse Namibias. Entlang des Flussverlaufs wird Oberflächen- und Grundwasser für die Trinkwasserversorgung, die Landwirtschaft und den Bergbau genutzt. Des Weiteren ist das Ökosystem entlang des mittleren und unteren Kuiseb Lebensgrundlage für das Volk der Topnaar. Insgesamt werden jährlich etwa 30 000 Menschen und zehntausende Touristen durch das Kuiseb Einzugsgebiet mit Wasser versorgt. Das Ziel der vorliegenden Arbeit ist es, ein integratives Modellkonzept zu entwickeln, um das mechanistische Verständnis der steuernden ökohydrologischen Prozesse entlang des Kuiseb River zu erhöhen (Kapitel 2 und 3) und es für ein nachhaltiges Wasserressourcenmanagement anzuwenden (Kapitel 4 und 5). Eine große Herausforderung stellt dabei der Mangel an Informationen und die damit verbundene Unsicherheit über das Öko- und Hydrosystem dar. Das liegt daran, dass aride Gebiete im Allgemeinen schlecht zugänglich und Monitoring-Systeme schlecht entwickelt sind. Die vorliegende Arbeit konzentriert sich im Wesentlichen auf drei Arten von Unsicherheit: (1) Das Parametrisieren eines Populationsmodells kann schwierig werden, wenn Langzeitdaten über Pflanzenarten fehlen. Dieses Parametrisierungsproblem wird gelöst, indem ein einfach zu beobachtendes qualitatives Muster - die langjährige Koexistenz von drei Baumarten entlang des Kuiseb River – genutzt wird, um das Populationsmodell zu kalibrieren. (2) Eine weitere Unsicherheit ergibt sich aus der Stochastizität der Flutereignisse, die dazu führt, dass die Flutzeitreihen zwar stochastisch identisch, aber ihre Realisierungen verschieden sind. Aus diesem Grund wird jede Parameterkombination nicht nur mit einer sondern mit 100 stochastisch identischen Flutreihen hinsichtlich des Koexistenzmusters geprüft, was schließlich zu einer Quantifizierung der Parametrisierungsunsicherheit führt. (3) Die Unsicherheit der Parameter, die das Flutregime beschreiben. Entlang von Trockenflüssen sind oftmals nur wenige Daten über den Oberflächenabfluss vorhanden. Dies liegt zum einen an der schwer zugänglichen Lage in infrastrukturell schwachen Regionen und zum anderen am zeitweiligen Charakter der Flutereignisse, was das Messen von langen Zeitreihen unmöglich macht. Der Einfluss dieser Unsicherheit auf die Robustheit und Bedeutung von Managementstrategien, die sowohl das Grundwasser als auch die Vegetation regulieren, wird in dieser Arbeit untersucht, ohne dabei die vorangegangenen Unsicherheiten zu vernachlässigen.

Der erste Teil der Arbeit konzentriert sich auf die Kopplung der Vegetationsstruktur und dem Wasserkreislauf im Modell. In Kapitel 2 wird das ökohydrologische Modellkonzept unter Berücksichtigung der verfügbaren Information über den mittleren Kuiseb entwickelt, dessen Pflanzengemeinschaft von drei Baumarten dominiert wird. Das konzeptionelle Modell integriert die Dynamik von Ökologie und Hydrologie auf saisonaler Zeitskala. Es basiert auf einem ökologischen Populationsmodell und einem hydrologischen Speichermodell. Um entscheidende Prozesse in der Dynamik der Pflanzengemeinschaft und ihrer Reaktion auf das hydrologische System zu berücksichtigen, wird die pflanzliche Biomasse in grüne und Reservebiomasse unterteilt. Die grüne Biomasse beschreibt alle Pflanzenorgane, die Photosynthese durchführen, wohingegen die Reservebiomasse alle Organe abdeckt, die photosynthetisch inaktiv sind. In diesem Modell gibt es pflanzenverfügbares Wasser sowohl im ungesättigten oberen Alluvium als auch im darunter liegenden Aquifer. Beide Speicher werden von stochastischen Flutereignissen gesteuert, welche durch ein "fractional autoregressive moving average model" (FARIMA) erzeugt werden. Dabei werden Zeitreihen generiert, die sowohl Kurz- als auch Langzeitstrukturen aufweisen, wie sie in vielen hydrologischen Zeitreihen zu beobachten sind. Populationsmodell und hydrologisches Speichermodell sind über Wachstum, Mortalität und Transpiration der Biomassen miteinander gekoppelt. Sowohl Wachstum als auch Mortalität hängen von der Wasserverfügbarkeit ab. welche das Flutregime durch (Dauer. Intensität. Wiederkehrsintervall) und der Konkurrenz mit anderen Arten kontrolliert wird. Die Wasserspeicher werden neben der Flut auch von der Transpiration beeinflusst, welche von der Dynamik der grünen Biomass gesteuert wird.

Wie bereits erwähnt, wird das Parametrisierungsproblem in Kapitel 2 gelöst, indem ein einfach zu beobachtendes qualitatives Muster (Koexistenz) genutzt wird, um das Populationsmodell zu kalibrieren. Um geeignete Parameterkombinationen zu finden, die zu dem beobachteten Muster führen, wird die Methode des "Latin Hypercube Sampling" verwendet. Dabei fließen weitere, bereits beobachtete, qualitative Informationen in das wie die artspezifische maximale Wurzeltiefe, Wachstumsraten Modell ein. der Reservebiomasse und die Transpirationsraten pro grüne Biomasse. Die musterorientierte Kalibrierung erweist sich zwar als zielführend, um sowohl die Modellstruktur als auch den Parameterraum einzuschränken, allerdings gibt es immer noch mehrere Modellvariationen und zahlreiche Parameterkombinationen, die die Modellierung einer Drei-Arten-Koexistenz ermöglichen. Diese Unsicherheit in der Modellstruktur und Parametrisierung wird durch die gesamte Arbeit hinweg berücksichtigt, indem weiterführende Simulationen als Ensembleläufe für alle möglichen Parameterkombination ausgenutzt werden.

Die Modellvarianten unterscheiden sich in ihrer Struktur, insbesondere in der Stärke der Kopplung von Ökologie und Hydrologie. Prozesse, die zu Koexistenzmechanismen wie Nischenteilung oder Gleichgewichten zwischen Wachstum und Mortalität führen, sind unterschiedlich implementiert. So kann sowohl die Phänologie der Pflanzen (hier Zeitpunkt des Laubabwurfs) als auch die Sensitivität gegenüber der Flut für alle Arten gleich, artspezifisch oder eine Kombination aus beiden sein. In Kapitel 3 werden die vier möglichen Modellvarianten hinsichtlich ihrer Fähigkeit, die beobachtete Koexistenz zu modellieren, untersucht. Im Ergebnis sind drei Modelle dazu in der Lage, allerdings, nur eines davon (Model C) ist mit zwei weiteren beobachteten ökohydrologischen Mustern konsistent. Diese sind zum einen der artspezifische Zugang zur Wasserressource (ungesättigter Boden oder Grundwasser) und zum anderen die artspezifische Sensitivität gegenüber der Intensität der Flutereignisse. Die strukturellen Unterschiede der Modellvarianten werden in Kapitel 3 als Grundlage genommen, um den Einfluss von Koexistenzmechanismen auf die Schwankungen von hydrologischen Variablen wie die Transpiration und den Grundwasserflurabstand zu untersuchen. Die Ergebnisse lassen vermuten, dass die artspezifische Reaktion auf die Flutintensität als Umweltstörung zwar zu erhöhten Schwankungen führt, diese aber erst durch die artspezifische Phänologie verstärkt werden, da der artspezifische Zeitpunkt des Laubabwurfs zu zeitlichen Schwankungen in der Wasseraufnahme durch Pflanzen führt und damit zu erhöhten Schwankungen der Transpiration und des Grundwasserspiegels. Die Mittelwerte der hydrologischen Größen sind jedoch für alle Modellvarianten ähnlich, was darauf rückzuführen ist, dass zwar das ökologische Teilmodell geändert wurde, aber nicht das hydrologische. Daraus kann geschlussfolgert werden, dass die Mittelwerte hydrologischer Größen wie Transpiration und Grundwasserflurabstand im Wesentlichen vom hydrologischen Teilmodell gesteuert werden. Die Stärke der kurzzeitigen Schwankungen von hydrologischen Flüssen (Transpiration) und Zustandsvariablen (Grundwasserspiegel) hingegen wird vom ökologischen Teilmodell beeinflusst und hängt vom Koexistenzmechanismus ab.

Die Unsicherheit über die Parameter des stochastischen Flutregimes wird im zweiten Teil der Arbeit aufgegriffen und untersucht, wie sie sich auf die Robustheit von Managementstrategien auswirkt. Dabei wird insbesondere auf die Bedeutung von Managementstrategien, die sowohl das Grundwasser als auch die Vegetation regulieren, eingegangen. Die im ersten Teil der Arbeit berücksichtigte Unsicherheit in der Modellstruktur und der Parametrisierung wird weiterhin beachtet und für weiterführende Untersuchungen verwendet. In Kapitel 4 wird eine Vielzahl von Managementstrategien bezüglich ihrer Robustheit unter der Unsicherheit des zukünftigen Flutregimes untersucht. Die Robustheit einer Strategie bezieht sich darauf, ob sie es ermöglicht, sowohl den Grundwasserspeicher mit einer gewissen Versorgungssicherheit zu nutzen als auch die natürliche Ökosystemstruktur (Koexistenz) zu erhalten. Dafür wird die "Information-Gap Decision Theory" verwendet. Das Model C aus Kapitel 2 und 3 wird als Systemmodell genutzt, da es als einziges alle drei am Kuiseb River beobachtete Muster (Koexistenz, artspezifischer Wasserzugang und Sensitivität gegenüber der Flutintensität) konsistent reproduziert. Da die Managementstrategien hinsichtlich zweier Kenngrößen untersucht werden, sind zwei Grenzwerte für deren Performance notwendig - einer für die ökologische Performance und einer für die Performance der Wasserversorgung. Der erste ist ein relativer deskriptiver Wert, der sich auf die Anzahl von Parameterkombinationen (mögliche Ökosysteme) bezieht, die ohne Management ("natürlicher" Zustand des Systems) Koexistenzmuster reproduzieren können. Der Performancegrenzwert für das die Wasserversorgung hingegen ist ein festgelegter normativer Wert, der die Anzahl der Zeitschritte beschreibt, in denen das Pumpen von Grundwasser möglich ist (hier 95 %). Das Pumpen von Grundwasser wird eingestellt, sobald ein gewisser Grundwasserstand unterschritten wird. Das Unsicherheitsmodell beschreibt den Unsicherheitsraum um die in Kapitel 2 geschätzten Flutparameter (Autokorrelation, gleitender Durchschnitt der Fluthöhe, mittlere Fluthöhe, Langzeitgedächtnis). Dabei variiert der Unsicherheitsraum von 0 bis 100 %, um das Niveau der Unsicherheit identifizieren zu können, bei dem die Performancegrenzwerte gerade noch überschritten werden.

Parameterunsicherheit, hier die der Flutregimeparameter, kann zu besserer oder schwächerer als der erwarteten Performance der Managementstrategien führen. Beide Aspekte werden in

Kapitel 4 berücksichtigt. Die verwendeten Managementstrategien sind dieselben für Kapital 4 und 5. Die Grundwasserentnahmerate und der Flurabstand zum Grundwasser, ab dem das alle Strategien Pumpen eingestellt wird, sind für ebenfalls dieselben. Die Managementstrategien sind in zwei Kategorien eingeteilt. Die erste umfasst rein hydrologische Strategien, in denen die Vegetation zwar nicht direkt reguliert wird, allerdings durch Wassermangel verursachter Pflanzenstress zum Einstellen des Pumpens führt oder zur künstlichen Bewässerung des oberen ungesättigten Bodens. Die zweite Kategorie umfasst gekoppelte öko-hydrologische Strategien, in denen eine Art entweder mit einer konstanten Rate reguliert wird (unflexibel) oder die Art reguliert wird, die das Vegetationssystem zum Zeitpunkt des Managements dominiert (flexibel).

In Kapitel 5 werden die Auswirkungen der Anwendung unterschiedlicher Systemmodelle auf die Planung von Managementstrategien untersucht. Diese Systemmodelle entstammen alle vom selben ökohydrologischen Modellkonzept, entwickelt in Kapitel 2. Sie unterscheiden sich hinsichtlich der ökologischen Merkmale, die den Modellen zu Grunde liegen. Dies betrifft besonders die artspezifische Reaktion auf das Hydrosystem (Flut als Umweltstörung und Wasser als Ressource). Im Ergebnis wird deutlich, dass die Unsicherheit über ökohydrologische Wechselwirkungen die Güte von Managementstrategien mehr beeinflusst als die Parameterunsicherheit des Flutregimes. Außerdem sind Strategien, die sowohl das Grundwasser als auch die Vegetation regulieren, nicht zwingend die beste Lösung hinsichtlich der Nachhaltigkeit, jedoch kann der Anwendungsbereich auf ökohydrologische Systeme eingegrenzt werden, deren Pflanzenarten verschiedene Wasserspeicher nutzen und unterschiedliche Sensitivitäten gegenüber der Flutintensität aufweisen.

Zusammengefasst kann gesagt werden, dass die Modellierung einer Drei-Arten-Koexistenz in einem wasserlimitierten Umweltsystem nicht trivial ist. Die Rückkopplungen zwischen Ökologie und Hydrologie müssen in geeigneter Art und Weise implementiert werden und genügend Freiraum für die Ausbildung von Koexistenzmechanismen einräumen. Da sich zeigte, dass diese einen großen Einfluss auf die Güte der Managementstrategien haben, erwies sich der kontinuierliche Prozess der Veränderung der Modellstruktur und das Vergleichen der Modellergebnisse mit beobachteten ökologischen und ökohydrologischen Mustern als vielversprechende Vorgehensweise, um eine verlässliche Modellstruktur und die damit verbundenen Parametrisierungen zu identifizieren.

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Chapter 1

Introduction

Over a billion people in 110 countries around the world live in arid regions, which constitute one third of the earth's land surface. In twenty African countries more than 90% of productive land sites are located in these vulnerable drylands, illustrating the social, ecological and economic dimension of these areas (Le Houerou, 1996; UNEP, 1992; WRC, 2005).

Arid areas suffer from a deficit of plant available water, hindering the development of prospering ecosystems. Moreover, the precipitation events are highly variable in space and time. The degree of aridity can be indicated by the Aridity Index *AI*, adopted by the United Nations Environment Programme (UNEP, 1992):

$$AI = \frac{P}{PET},\tag{1.1}$$

where *P* is the average annual precipitation and *PET* the is the potential evapotranspiration, both expressed in millimetres. According to *AI* a region is hyperarid (AI < 0.05), arid (0.05 < AI < 0.20), or semiarid (0.20 < AI < 0.50).

Due to the high variability in the precipitation events surface water is rare in arid regions and, consequently, infiltration rates are too low for generating sustainable ground water reservoirs. However, along ephemeral rivers temporary floods allow the establishment of ground water storages, which support riparian forests. These forests are often referred to as linear oases, reflecting the ecological and socio-economic importance of these systems in arid landscapes. Ephemeral rivers are located throughout the world's arid areas (WRC, 2005) and are characterised by temporary surface flow that strongly varies between seasons and years (Seely et al., 2003). In (Jacobson, 1997) ephemeral rivers are defined as systems with measurable discharge occurring less than 10% of the year. The linkage between the water resource and the plant community is crucial along ephemeral rivers. Ecohydrological feedbacks can influence both the water availability and the biodiversity. The use of both resources by humans can enhance the intensity of these feedbacks considerably. Therefore, the sustainable

use of the ecological and water resources clearly requires a well developed understanding of the ecohydrological processes. However, in many arid areas environmental monitoring systems are little developed, leading to limited information about their eco- and hydrosystems (Khazaei et al., 2003). Models can help to deal with the scarce information by testing assumptions, generating hypotheses and conducting virtual experiments, which would be time and costs consuming if implemented in reality. Models may also be used to illustrate options and scenarios in terms of alternative future states of the system, which can then be assessed and compared by decision makers (Baumgartner et al., 2008).

This research discusses an ecohydrological linear oasis through otherwise dry landscapes along the ephemeral Kuiseb River in Namibia. Objective of this research is to develop a model framework that integrates both ecological and hydrological system dynamics to (1) increase the mechanistic understanding of driving ecohydrological processes and (2) apply it for sustainable water resource management along ephemeral rivers. The first objective is critical since the composition of the plant community affects the hydrosystem dynamics and vice versa. However, the modelling of the coexistence of multiple species that belong to the same plant functional type (e.g. trees) is a well-known nontrivial problem (Arora and Boer, 2006; Chesson, 2000; Clark et al., 2007) that is addressed in this research. Objective number two aims at the investigation of management strategies in terms of their ability to sustainably exploit the ground water resource while preserving the natural vegetation structure along the middle section of the Kuiseb River.

The main challenge this research is faced with is a lack of available information and, consequently, the uncertainty for both the eco- and the hydrosystem due to the generally poor accessibility of arid regions and poorly developed monitoring systems. In particular, the research focuses on three types of uncertainty: (1) The parameterisation of the population model is challenging as this requires long-term observation of species abundance that is not available. This parameterisation problem is addressed by using a pattern-oriented model calibration, which adjusts the species parameters in such a way that the resulting parameterisation reproduces the observed three species coexistence pattern along the river course under study. (2) The inherent uncertainty in the occurrence of flood events, which is driven by unpredictable rainfall events. Throughout this study the unpredictability is described with a stochastic process characterised by parameters such as frequency, duration and short/long-term memory of flood events. In order to address the parameterisation problem to this type of uncertainty, for each parameter combination the model runs 100 times with stochastic identical flood realisations, eventually leading to a quantification of the uncertainty

in parameterisation. (3) The uncertainty in parameters describing the (stochastic) flood regimes. This uncertainty arises from the scarce information about the runoff data along ephemeral rivers. The reasons for that are the sparse monitoring system and the temporary character of the flood events hindering the measurement of large time series. The influence of this particular type of uncertainty on the robustness and significance of integrated management strategies is investigated without neglecting the preceding types of uncertainty.

Chapter 1 gives an overview of the geography of ephemeral rivers in general and particularly with regard to the catchments across western Namibia and the Kuiseb River (Section 1.1). Then, a literature review gives overview of the emerging discipline of ecohydrology (Section 1.2) with regard to the feedbacks between ecosystem dynamics and the water cycle. Further, the objectives of the first part of this research (Chapter 2 and 3) are briefly summarised. In Section 1.3, a concise review of approaches that address uncertainty in ecology and hydrology is given. In addition to that, a powerful approach is introduced helping to master information gaps in model parameters that need to be known to make competent management decisions – the information-gap decision theory. Finally, the objectives of the second part of this research (Chapter 4 and 5) are summarised.

Chapter 2 is a published paper and Chapter 3, 4 and 5 are manuscripts written for publication in peer reviewed journals. To keep these chapters readable as standalone papers, they follow the same structure comprising introduction, materials and methods, results, discussion and conclusions. Therefore, some overlaps may exist between the Introduction and Synthesis of this thesis and the respective sections of each paper. The description of the study site in each paper is focused on the particular topic.

1.1 Geography of the ephemeral Kuiseb River

Many ephemeral rivers arise in mountainous regions where the precipitation is higher compared to the average catchment precipitation. Examples are known, among others, for the Zahedan catchment in Iran (Khazaei et al., 2003), the Negev Desert in Israel (Wiegand et al., 1999, 2004), the Kuiseb River in Namibia (Botes et al., 2003; Lange, 2005; Manning and Seely, 2005; Dahan et al., 2008) and many rivers in Australia (Costelloe et al., 2003, 2005). Based on the hydrogeology ephemeral rivers can be divided into two types (Kulls, 2007, pers. com.): (1) Rivers running through sediments accumulated in extensive synclines. The ground water storage involves an extensive area but is too deep to be reached by plant roots. The transmission losses (infiltration through the river bed) are only dominated by the maximum infiltration rates. This type mostly occurs in the middle of deserts like the Kalahari Desert or

the Sahara Desert. (2) Rivers running through sediments accumulated in pools of impermeable bedrocks with low fracture volumes. The ground water storage has lower thickness and can be reached by plant roots. Transmission losses are dominated by both the maximum infiltration rate and the depth to ground water. This type mostly occurs in the peripheral areas of deserts such as the Negev Desert in Israel (Wiegand et al., 1999, 2004), deserts in Australia (Costelloe et al., 2003; Jansen and Brierley, 2004) or in India (Sinha et al., 2006; Sharma and Murthy, 1996), or the ephemeral river catchments across western Namibia (Fig. 1.1).

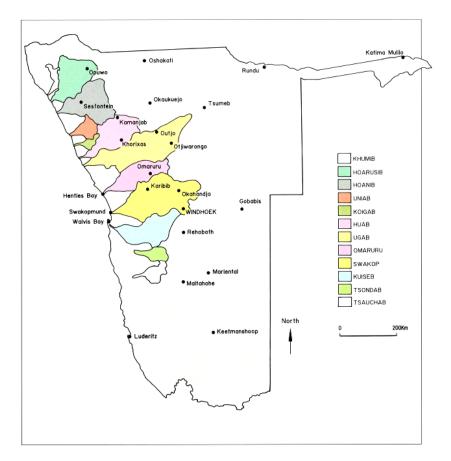


Fig. 1.1. The major ephemeral rivers across western Namibia (after Jacobson et al., 1995).

The ephemeral rivers in Namibia support vegetation and wildlife, both critical to agriculture and tourism, which are two of the major sectors of the Namibian economy (Hoff and Overgaard, 1993; Namibia Trade Directory, 1993). At the same time, these rivers are critical water sources for the most important economic centres of Namibia (Windhoek, Walvis Bay and Swakopmund), indicating the need for appropriate management of both the ecology and the water resource. However, declining ground water tables, changing vegetation

communities and a quickly growing population indicate that current use of resources is not sustainable and will not maintain future development (Jacobson et al., 1995).

The Kuiseb River is one of the most diversely used environments among the ephemeral rivers in Namibia. Along the entire river course surface runoff and ground water are exploited for drinking, farming, and mining (Dahan et al., 2008). Further, the vegetation of the Kuiseb River is essential for the survival of the rural Topnaar community (Moser, 2006). In total, more than 30 000 people and tens of thousands of tourists per year depend directly on the water of the Kuiseb River (Botes et al., 2003).

The Kuiseb catchment can be divided into three parts (Manning and Seely, 2005): In the mountainous area of the *upper* Kuiseb (Khomas Hochland) privately owned farmlands dominate the landscape. Most of the rain falls in the upper catchment and the farmers abstract water from deep boreholes and build small dams to use the surface run off of rare rainfall events. After having passed the escarpment by running through the steep Kuiseb Canyon the river reaches the *middle* part of the catchment, which is dominated by communally owned farmland. The average annual rainfall decreases significantly and is almost zero. However, along the river course a shallow ground water storage has been developed creating a living riparian environment for vegetation. In this area both the Gobabeb Training and Research Centre and the Topnaar community abstract water from the shallow ground water. In the *lower* part of the catchment the Kuiseb River reaches the Atlantic Ocean, but this is only exceptional and occurred only in 10% of the years (over the past 120 years) (Dahan et al., 2008). The lower Kuiseb is dominated by conservation and tourism areas with the main water consumers being the city of Walvis Bay and the mining industry.

1.2 Ecohydrology: Coupling ecosystem dynamic and the water cycle

Ecohydrology is the science that studies the interactions between ecosystems and the hydrological cycle (Rodriguez-Iturbe and Proporato, 2004; Kundzewicz, 2002; Zalewski, 2002). The understanding of the dynamics of coupled ecohydrological systems is essential to assess the impacts of climate change or management strategies on the ecosystem structure in water-controlled environments (Tietjen et al., 2009). The interplay between vegetation and the water cycle occurs at different spatial and temporal scales, reaching from point to regional or hour to annual scales. Such a distinction of scales is important as it naturally suggests different levels of analysis in which only the main interactions may be retained (Rodriguez-Iturbe and Proporato, 2004).

Several studies emerged investigating feedbacks between ecosystem dynamic and the water cycle. For instance, Huxman et al. (2005) and Wilcox and Thurow (2006) investigate the implications of vegetation change (woody plant encroachment, invasive plants) for the water cycle with focus on water yield, carbon cycling and evapotranspiration. In other, more experimental studies, the feedback between ground water fluctuations and riparian ecosystem function (transpiration) is investigated (Loheide et al., 2005; Butler et al., 2007; Scott et al., 1999; Cooper et al., 2006; Cleverly et al., 2006; Lamontagne et al., 2005). The most frequently cited series of papers in the scientific field of ecohydrology is the model framework developed by Rodriguez-Iturbe et al. (2001), Laio et al. (2001b,a) and Porporato et al. (2001). They apply a model which is focused on the plant-soil-climate interface for semiarid climates. It is based on nonlinear, stochastic differential equation of soil moisture dynamics and represents the infiltration from rainfall by a marked Poisson process. The large number of different processes and phenomena that make up the ecohydrological dynamics forced them to introduce simplifying assumptions in the modelling scheme while still preserving the most important features of the dynamics. This ensures analytical tractability and gives insight and increases the understanding of ecohydrological mechanisms on a more general level. For instance, Caylor et al. (2006, 2009) apply the plant-soil-climate interaction to explore a general hypothesis that the spatiotemporal organisation of semiarid ecosystems can be best described through the consideration of an explicit trade-off between resource use (growth) and stress avoidance (survival). Examples for the simplifying assumptions are the neglect of lateral moisture contribution, the soil moisture-root interaction, vegetation dynamics (seed dispersal, intra-specific competition, age structure, etc), and the ground water access by plants. The latter is integrated in studies of Camporeale and Ridolfi (2006) and Ridolfi et al. (2006) to investigate the effects of vegetation-water table feedbacks on the stability and resilience of riparian ecosystems. However, in all these previous studies the different strategies of plant water use are modelled generally for plant functional types (trees, shrubs, grasses). Consequently, these models are not appropriate for investigating the impact of hydrological dynamics (timing and amount of rainfall or flood) on the ecosystem consisting only of species being part of one plant functional type (e.g. trees).

The first part of this research is focused on the feedbacks between the ecosystem structure and the water cycle along the ephemeral Kuiseb River. In particular, it discusses how uncertainty within ecosystem interactions influences transpiration and depth to ground water, and vice versa. It explicitly considers the coexistence of several species belonging to the same plant functional type (trees), the vegetation-groundwater interaction and the trade-off between resource use and stress avoidance.

In Chapter 2, the ecohydrological model framework (storage based hydrological model and population model) is described in detail. The model parameterisation is oriented towards an observed pattern: the coexistence of three tree species along the river course. Pattern oriented modelling is a well established approach in ecological modelling, because patterns contain information on the internal organisation of a system in an integrated form and are often indicators of essential underlying processes and structures (Grimm et al., 2005). The population parameters are found by Latin hypercube sampling of the parameter space, which is constrained qualitatively by plausibility checks and available information such as root depths, growing rates and transpiration rates. To maintain the model mathematical tractable and parsimonious simplifying assumptions are done and stated clearly.

In Chapter 3, another model version for the same system is investigated with regard to its ability to model the observed coexistence pattern. Moreover, further qualitative patterns are considered to better evaluate the reliability of the investigated model versions. These ecohydrological patterns comprise the species specific source of water from the subsurface and ecological traits with regard to the vulnerability to flood events. Further, all model versions that lead to robust coexistence are investigated to detect the influence of coexistence mechanisms on the fluctuations of hydrological variables such as transpiration and depth to ground water. This insight is particularly important when applying the model framework as management support tool under the uncertainty of future flood conditions (see section 1.3 and Chapter 4, 5).

1.3 Deciding under severe uncertainty

Decisions about the management of environmental systems are made in the face of considerable uncertainty. There are a number of forms of uncertainty highlighted in ecological and conservation studies (Regan et al., 2002). There my be uncertainty around estimated parameters leading to questionable model outcomes or there may also be uncertainty about the actual model chosen to represent a system (Chatfield, 1995; Runge and Johnson, 2002). The uncertainty around parameter estimates of the population model is addressed in Chapter 2 and 3 resulting by applying all parameter combinations (potential ecosystems) that lead to the observed coexistence pattern. With regard to management decisions parameter uncertainty can be adverse or favourable, i.e. it entails the possibility of failure or the opportunity for unexpected success (Ben-Haim, 2006). Both aspects are considered in the second part of this

research by applying the info-gap decision theory for management strategies along the Kuiseb River under uncertainty of both the future stochasticity of the flood regime (Chapter 4) and the actual model version (Chapter 5).

In the past, theories have been developed that describe how to deal with imperfect or fragmentary information, e.g. the fuzzy logic theory or probability theory (Chen, 2000). These theories describe linguistic (fuzzy logic theory, (Akter and Simonovic, 2005)) or stochastic (probability theory) uncertainties and quantify them with normalized mathematical functions, e.g. the membership or the probability density function. The fuzzy logic theory tends to simplify purely analytical or numerical models representing complex systems with high heterogeneity and nonlinear behaviour (Bardossy and Duckstein, 1995). It describes the ambiguity of a proposition (linguistic uncertainty) or the possibility (rather than the probability) of the occurrence of an event. On the other hand, in probability theory the lack of information is either quantified in terms of the frequency of recurrence of an event or in terms of an observer's subjective degrees of belief (Mises, 1957; Ben-Haim, 2006). In probabilistic models the parameters are determined from typical rather than extraordinary events. Hence, applying them for management decisions may be acceptable for the majority of events but less optimal for the rare events. However, often and particularly in arid areas, it is the rare events that are critical to the health of environmental systems (Chapter 2; Mandelbrot and Wallis, 1968; Levy et al., 2000) and, hence, these events are of greatest concern to the decision maker (Ben-Haim, 2006).

Another way to describe uncertainty in parameters of process models is the information-gap (info-gap) decision theory of uncertainty which is a non-probabilistic quantification of uncertainty. The procedure by which an info-gap model is formulated is different from the method for specifying a probabilistic model, particularly in the treatment of rare and extreme events (Ben-Haim, 1994, 2004, 2006). Further, contrary to distribution based theories, where probability density or membership functions are applied, in info-gap models the events are organised into clusters. The rules by which the events occur are incompletely known.

In Chapter 4, the info-gap theory is briefly introduced comprising the main elements: system model, performance requirements, uncertainty model, robustness and opportuneness function. Then, the parameter combinations (potential ecosystems) of the most reliable model version (see Chapter 3) are subject to a variety of hydrological and (in)flexible ecohydrological management strategies under uncertainty of the future stochastic flood regime. In particular, the management strategies are investigated in terms of their ability to sustainably exploit the

ground water resource while preserving the vegetation structure (coexistence of three tree species).

In Chapter 5, the consequences for the design of management strategies are assessed, when applying several system models that arise from the same conceptual model framework, but differ in the assumptions on ecological traits of the plant species determining the plants' response to the water resources. Further, the relative importance of ecohydrological feedbacks and uncertainty for the design of sustainable strategies for water extraction along ephemeral rivers is clarified.

Chapter 6 summarises the thesis and shortly presents the findings of the former chapters. Furthermore, it gives recommendations about the management of strongly coupled ecohydrological systems along ephemeral rivers and outlines future perspectives of ecohydrological research.

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Chapter 2

Uncertainty in parameterisation and model structure affect simulation results in coupled ecohydrological models ¹

2.1 Introduction

In semiarid environments water is not only a scarce resource, water availability also varies greatly in timing and magnitude. Both natural ecosystems and people have to adapt to these conditions, and often they share the same water source. Thus, water management of the water source might influence natural ecosystems, but also inversely, the management of vegetation might affect the water fluxes. In order to understand, what implications human development in semiarid regions has, models are required that help investigating the effect of management actions. Such models need appropriate description of both ecological and hydrological processes.

A great deal of work in ecohydrology has already been dedicated to understanding mechanisms, by which a variation in water availability influences vegetation patterns. Much of this work is based on considering single plant species, and comparing expected water stress-levels in different environments. Therefore, these models cannot consider inter-specific competition or coexistence. However, research dealing with biodiversity and species-co-existence suggests that particularly fluctuations of environmental signals might favour co-existence (D'Odorico et al., 2008). Hence certain levels of variance of water availability could also be a driver for maintaining multispecies plant communities. Moreover, diverse ecosystems are thought to be more resilient to disturbance and should thus react differently to extreme conditions than single species ecosystems. Hence coexistence mechanisms might be important ecosystem processes shaping plant-water interactions in water limited environments, which motivates the need for multispecies ecohydrological models. Such a model is developed and applied in this paper.

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Ecological modelling has different approaches to describe multi-species plant communities. One way is spatially explicit individual-based modelling (DeAngelis and Gross, 1992; Grimm and Railsback, 2005), representing a bottom-up approach. Here, plant communities are described as systems of interacting plant individuals responding to their environment. This approach is particularly powerful when specific systems are to be analysed. The respective models, however, are often complex that makes parameterisation a challenge (lots of parameters) and hampers generalization (adjustment to a specific case vs. principle understanding, transferability). To gain principle understanding of the interplay between water resources and vegetation and the response of environmental variability along ephemeral rivers is central for the present study. Therefore, we follow a top-down approach, i.e. we use a multi-species population dynamical model (Kot, 2001) to describe the plant community in an aggregated way but explicitly consider the species' competition for water. The population dynamical parameters summarize all relevant effects caused by processes at the individual scale (e.g. plant growth and mortality, response to disturbances, type and strength of competition, seed dispersal) (Moorcroft, 2003; Frank and Wissel, 2002; Fahse et al., 1998; Heinz et al., 2005; Ovaskainen and Hanski, 2002, 2004). Most ecohydrological models work at the population scale (Rodriguez-Iturbe et al., 2001; Porporato et al., 2001; Camporeale and Ridolfi, 2006; Ridolfi et al., 2000). Direct parameterisation of population models is sometimes impossible as this requires long-term observation of species abundance, which is not always available.

Generally, both population and hydrological models can be developed with varying levels of complexity. In order to keep a coupled model manageable, the level of model complexity needs to be appropriate regarding the desired predicted variable but also regarding the available data. And there has to be a strategy how the model should be parameterised.

In this study, we address this parameterisation problem by using pattern-oriented model calibration, in that we adjust species parameters such that the resulting model reproduces the observed coexistence. Models have been parameterised based on information of presence or absence of plant species before (Laio et al., 2001; Rodriguez-Iturbe et al., 1999). When the existence criterion will be extended to several species it is called coexistence, and also observed coexistence has been used to evaluate (at least qualitatively) the validity of ecohydrological models. In doing so, researchers put their models to a strict test, since modelling coexistence is comparatively difficult (Arora and Boer, 2006; Clark et al., 2007). A given model only allows for coexistence, if its structure and parameters meet strict conditions, which provide for the required relation of trade-offs. A number of mechanisms can be

invoked fostering coexistence in models, such as ecological niches (in time and space) and tradeoffs (Chesson, 2000; Clark et al., 2007). Ecological theory also indicates that the variability of an environmental signal, such as resources or disturbance regimes, influences biodiversity. According to the Intermediate Disturbance Hypothesis (Connell, 1978; Huston, 1979), moderate levels of environmental fluctuations can enhance both biodiversity and resilience (D'Odorico et al., 2008). So far, such studies have dealt with uncorrelated, random environmental signals. Examples are given for random water table (Ridolfi et al., 2007) and climate fluctuations (Rodriguez-Iturbe et al., 1999), or environmental disturbances induced by fires (Higgins et al., 2000; van Wijk and Rodriguez-Iturbe, 2002). However, many hydrologic time series are characterized by auto-correlated and longterm-memory processes (Montanari et al., 1997; Hurst, 1951), particularly in arid environments. This directly leads to the question of the role of this autocorrelation, that is the duration of a disturbance event (water stress, disruptive flood), for the functioning of the ecohydrological system. Moreover, studies usually consider only one consequence of an environmental signal. However, the same signal, for example rain, may interact with the system in multiple ways. A strong rain event might recharge the water storage for plants, but at the same time, the storm might destroy part of the vegetation. Thus the event acts on both, mortality and growth, but possibly not in the same fashion. Such combined effects are not fully understood so far. In this work we wish to investigate both of these issues, based on the example of an ephemeral river in Namibia. This allows for testing the adequateness of the Intermediate Disturbance Hypothesis in the context of ecohydrological systems along ephemeral rivers.

The middle section of the ephemeral Kuiseb River in Namibia is a representative example of an environmental system with ecohydrological feedbacks and need for management. Previous studies indicate that the development of riparian vegetation depends on the subsurface water storage (alluvial aquifer) which is recharged by intermittent floods. At the same time, strong floods lead to uprooting of riparian vegetation and increased mortality. There is negligible rainfall in this part of the river, the floods originate in the upper reach, and depend both on the rainfall regime and small scale farm dams. In this study, we aim to build a model that allows understanding, how the flood regime interacts with the riparian ecosystem and the resulting transpiration loss and aquifer storage. Little data is available regarding the ecosystem. We therefore rely on conceptual models both for ecosystem and aquifer. In order to address structural uncertainty, we select three models, with increasing degree of complexity of the ecological model. We attempt to parameterise these models based on the scarce available information, namely the fact that three species coexist and some knowledge about their maximum transpiration rates and rooting behaviour. Our investigation shows that different coexistence supporting mechanisms can be invoked, depending on the assumed conceptual model. While the distribution of mean hydrologic variables (groundwater level and transpiration) was similar in all models, their variability depended both on the model structure and the parameters sets. This points at the difficulty to parameterise an ecohydrological model in real world applications. However, our model gives clear indications, what measurements are most effective for improving the necessary process understanding.

2.2 Methods and materials

2.2.1 Study site

The study site covers an area of approximately 18 km² and is located in the Kuiseb catchment (~ 15500 km² (Jacobson et al., 1995)) in Namibia (Fig. 2.1). The Kuiseb River arises from the Khomas Hochland (~ 2000 m in elevation) and runs westward through the escarpment into the Atlantic Ocean. The rainy season is during the southern hemisphere summer between January and April (Henschel et al., 2005). Most of the rain falls in the upper reach of the catchment (Khomas Hochland). This study is concerned with the arid middle reach of the Kuiseb River, where rain is exceptional, and water arrives mainly during the floods in the ephemeral river channel. Near this channel, riparian vegetation has established. Although the channel does not contain water for most of the year, it supplies a shallow aquifer with water during times of flood and thus creates a living environment for riparian vegetation. The flood is influenced by upstream farm damns and the ground water table is influenced both by plants and human consumption.

Ecosystem

Vegetation around the river channel consists of 80% of only three coexisting species: Camel Thorn (*Acacia erioloba*), Ana Tree (*Faidherbia albida*) and Wild Tamarix (*Tamarix usneoides*) (Theron et al., 1980). All of them depend on the infiltration of flood water, with slight differences in strategies. Schachtschneider and February (2007) investigated the water use strategies of all three species by using isotope methods. They found that both Camel Thorn and Ana Tree use a mixture of ground- and soil water, and Wild Tamarix uses water from the unsaturated zone, originating from flood and also fog water. The known differences between the three species are in their phenology (time of leaf shedding), maximum transpiration and growth rates (see Table 2.1). Besides supplying vegetation with water, floods in the river channel have also a destructive component. Small trees are usually washed

out by strong floods. The latter makes slow growing trees vulnerable for large floods for longer time.

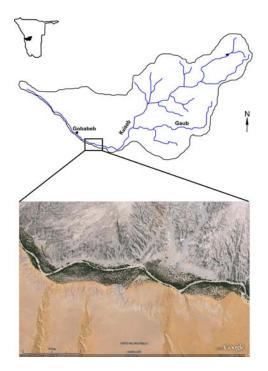


Fig. 2.1. Kuiseb catchment and middle part with dense riparian vegetation.

Table 2.1. Ecology of the three	main tree species a	long the middle part	rt of the Kuiseb River.

	Camel Thorn (<i>A. erioloba</i>)	Ana Tree (F. albida)	Wild Tamarix (T. usneoides)
Leaf Shedding	slightly during dry season ^a	slightly during rainy season ^a	evergreen ^a
Root Depth	up to 60 m ^b	up to 34 m ^c	$shallow^{f}$
Spatial Distribution	along rivers and plains ^a	along rivers ^a	along rivers ^a
Wood Density	1230 kg/m ^{3 h}	560 kg/m ^{3 h}	600 - 700 kg/m ^{3 h}
Maximum Height	16 m ^g	30 m ^e	8 m ^a
Trunk Diameter	0.8 m ^e	2 m ^e	_
Others	-	obligate phreatophyte ^d	often in saline soils ^a

^a(Curtis and Mannheimer, 2005), ^b(Canadell et al., 1996), ^c(Dalpe et al., 2000), ^d(Stave et al., 2005), ^e(Moser, 2006), ^f(Schachtschneider and February, 2007), ^g(Coates Palgrave, 1983), ^e(Timberlake et al., 1999), ^h(Wickens et al., 1995).

Hydrosystem

The study site is located in a hyperarid area with mean annual rainfall less than 20 mm and mean potential evaporation of 1700 to 2500 mm (Botes et al., 2003). The shallow alluvial aquifer consists of sand and is embedded into impermeable granite (Dahan et al., 2008; Morin et al., 2009; Schmidt and Plöthner, 1999) (Fig. 2.2). Its thickness and width vary along the

river. The alluvial aquifer is recharged by temporary floods that are caused by rainfall in the upper Kuiseb catchment (Khomas Hochland). Volume and duration of the resulting floods vary strongly (Fig. 2.3). Larger floods burst over the limits of channel bed, leading to inundation of the river banks. At the same time, about 90% of the floods run dry within the Kuiseb middle section under study here. This shows the comparatively large role of infiltration. The dynamics of flood water infiltration were investigated by Dahan et al. (2008). Their studies show that, during a flood, the water content of the unsaturated layer only increases up to the twofold value of the field capacity and that the infiltration rates across different flood events are very similar. Further, above a certain flood stage threshold, it is the flow duration and not the flood height that controls the recharge amounts.

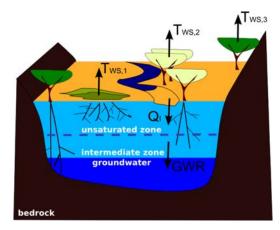


Fig. 2.2. Water balance of an ephemeral river with shallow aquifer. The intermediate zone denotes the layer where saturated and unsaturated conditions alternate frequently. The arrows denote the transpirational demand for each species $T_{WS,i}$ (Eq. 2.11), the infiltration flux Q_I , and the ground water recharge GWR (Eq. 2.6).

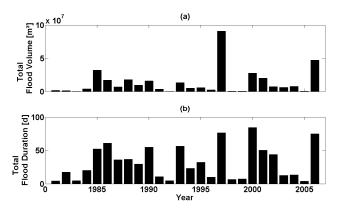


Fig. 2.3. (a) Flood volume and (b) duration at gauging station Schlesien from 1981 to 2006. Data are provided by the Department of Water Affairs (DWA) in Windhoek.

2.2.2 Hydrological model

We modelled the hydrological processes along an ephemeral river with shallow aquifer. Figure 2.2 gives a sketch of the hydrological unit modelled. We modelled a representative river–valley segment of 60 km length and a constant width of 300 m. Hence we considered total fluxes over the entire surface area of the segment, which is $A_{seg} = 18 \text{ km}^2$.

The water balance for this segment is written as

$$\Delta WS(t) = \Delta S_{unsat}(t) + \Delta S_{GW}(t), \qquad (2.1)$$

where $\Delta WS(t)$ is the sum of change in unsaturated ($\Delta S_{unsat}(t)$) and ground water storage ($\Delta S_{GW}(t)$). The storage in the unsaturated and ground water layer was calculated as

$$S_{unsat}(t) = A_{seg} \cdot z_{unsat}(t) \cdot \theta(t) \text{ for the unsaturated storage,}$$
(2.2a)

$$S_{GW}(t) = A_{seg} \cdot h_{GW}(t) \cdot \phi$$
 for the ground water storage, (2.2b)

where $\theta(t)$ is the water content (m³/m³) of the unsaturated zone, which ranges between 0 and porosity ϕ (Table 2.2) and $h_{GW}(t)$ is the ground water level. The depth to ground water $z_{unsat}(t)$ is

$$z_{unsat}(t) = h_{WS} - h_{GW}(t), \qquad (2.3)$$

where $h_{WS} = 15$ m is the total depth of the alluvium. In our simulations we fixed the initial value of ground water depth to $z_{unsat}(t=1) = 5$ m.

The change in unsaturated storage was calculated as

$$\Delta S_{unsat}(t) = I(t) - GWR(t) - T_{unsat}(t), \qquad (2.4)$$

with I(t) denoting the infiltration, GWR(t) the ground water recharge, and $T_{unsat}(t)$ the transpiration from the unsaturated storage. The infiltration to unsaturated soil is based on the results of Dahan et al. (2008) who concluded that infiltration fluxes are limited by a flux-regulating mechanism at the top of the unsaturated zone, independent of the flood height. They suggest a time constant infiltration rate of $Q_I(t) = 1$ cm/h, which is 2400 m³/d*ha. Therefore, the infiltration depends only on flood duration D(t) (Eq. (2.20)) and the specific infiltration flux $Q_I(t)$:

$$I(t) = D(t) \cdot Q_I(t) . \tag{2.5}$$

Table 2.2. Hydrological parameters (for soil and flood shape) used for all model versions (Table 2.4). We used the Hydraulic Properties Calculator of Saxton and Rawls (2006) to estimate the volumetric water content at permanent wilting point (θ_{PWP}), field capacity (θ_{FC}) and the porosity (ϕ). For this study we assumed the soil texture class of the alluvial fill to be sand with an average grain size distribution of 8% gravel, 90% sand, and 2% clay.

Soil	Flood generator (FARIMA)	Value
φ		$0.439 \text{ m}^3 \text{ m}^{-3}$
$ heta_{ m FC}$		$0.061 \text{ m}^3 \text{ m}^{-3}$
$ heta_{ m PWP}$		$0.015 \text{ m}^3 \text{ m}^{-3}$
	Н	0.75
	$\mu_{ ext{Flood}}$	3 269 000 m ³
	$X_1(\lambda)$	0.192
	$\Psi_1(\lambda)$	0.8969

Flood duration is calculated as a function of flood volume in Eq. (2.20) (see section 2.2.3). The ground water recharge depends on the water content $\theta(t)$ of the unsaturated layer:

$$GWR(t) = S_{unsat}(t) - S_{FC}(t) \text{ for } \phi \ge \theta(t) \ge \theta_{FC}(t), \qquad (2.6a)$$

$$GWR(t) = 0 \text{ for } \theta(t) \le \theta_{FC}(t).$$
 (2.6b)

where $S_{FC}(t)$ is the water volume in the unsaturated zone corresponding to the water content at field capacity ($\theta_{FC}(t) = 0.061$). The transpiration is composed of transpiration from unsaturated layer and ground water. The transpiration from the unsaturated layer is the sum of the transpiration from individual species $T_{unsat,i}(t)$:

$$T_{unsat}(t) = \min[(S_{unsat}(t) - S_{PWP}(t)), \sum_{i=1}^{3} T_{unsat,i}(t)], \qquad (2.7)$$

where $S_{PWP}(t)$ is the water volume in the unsaturated zone corresponding to the water content at permanent wilting point ($\theta_{PWP}(t) = 0.015$). For plants where the roots reach the groundwater, transpiration originates from both the unsaturated and the saturated zone. The unsaturated part is calculated as

$$T_{unsat,i}(t) = \frac{V_{unsat,i}(t)}{V_{WS,i}(t)} T_{WS,i}(t) , \qquad (2.8)$$

where $T_{WS,i}(t)$ is the transpirational demand for each species (Eq. 2.11), $V_{unsat,i}(t)$ the water volume in the unsaturated storage and $V_{WS,i}(t)$ is the total water volume (unsaturated and ground water) that can be reached by plant roots of species *i*:

$$V_{WS,i}(t) = V_{unsat,i}(t) + V_{GW,i}(t),$$
(2.9)

where $V_{GW,i}(t)$ is the ground water volume available to plant roots. The water in the unsaturated storage available for transpiration of species *i* depends on its rooting depth $z_{r,i}(t)$:

$$V_{unsat,i}(t) = z_{r,i}(t) \cdot \theta(t) \cdot A_{seg} \text{ if } z_{r,i} \le z_{unsat}(t), \qquad (2.10a)$$

$$V_{unsat,i}(t) = z_{unsat}(t) \cdot \theta(t) \cdot A_{seg} \text{ if } z_{r,i} > z_{unsat}(t).$$
(2.10b)

Note, that for the purpose of keeping the model simple we neglected any age structure in the ecological model (see section 2.2.4). Consequently, the rooting depth does not depend on the age of a (sub)population. The transpirational demand for each species ($T_{WS,i}(t)$) is a linear function of the green biomass $G_i(t)$ (see section 2.2.4) with an upper boundary given by the potential evapotranspiration (PET):

$$T_{WS,i}(t) = \min(PET, Q_{T,i}(t) \cdot G_i(t)).$$
(2.11)

The PET was estimated using the Penman-Monteith Equation for both the flooding and the dry season. The transpiration per green biomass $Q_{T,i}(t)$ of each species is derived from measurements of Bate and Walker (1991) and is summarized in Table 2.3.

	$Q_{T,i}$ [m ³ /t*season]		
Species	Rainy Season	Dry Season	
Camel Thorn	2,423.8	1,434.1	
Ana Tree	3,529.8	2,088.4	
Wild Tamarix	2,517.9	1,489.8	

 Table 2.3. Transpiration rates for each species.

The change in ground water was calculated as

$$\Delta S_{GW}(t) = GWR(t) + Q_{GW}(t) - T_{GW}(t), \qquad (2.12)$$

where $Q_{GW}(t)$ is the ground water flow and $T_{GW}(t)$ the transpiration of all species from ground water Eq. (2.15). The ground water flow is

$$Q_{GW}(t) = Q_{In} + Q_L - Q_{Out}(t) - Q_V, \qquad (2.13)$$

where Q_{In} is the ground water inflow from upstream, $Q_{\text{Out}}(t)$ the ground water outflow downstream, Q_L the lateral ground water inflow, and Q_V the vertical ground water outflow to the bedrock. Q_{In} , Q_L and Q_V are assumed to be constant over time (Table 2.7). $Q_{\text{Out}}(t)$ was calculated by Darcy's Law, as:

$$Q_{Out}(t) = k_f \cdot \Delta h(t) \cdot A_{GW}, \qquad (2.14)$$

with k_f denoting the hydraulic permeability of the ground water layer, $\Delta h(t)$ the hydraulic gradient between the inlet and outlet of the modelled aquifer segment, and A_{GW} the cross-sectional area of the ground water layer. The transpiration of all species from ground water is the sum of individual species transpirations $T_{GW,i}(t)$:

$$T_{GW}(t) = \max[(S_{GW}(t) - S_{PWP}(t)), \sum_{i=1}^{3} T_{GW,i}(t)], \qquad (2.15)$$

$$T_{GW,i}(t) = \frac{V_{GW,i}(t)}{V_{WS,i}(t)} T_{WS,i}(t) , \qquad (2.16)$$

where $V_{GW,i}(t)$ is the ground water that can be reached by plant roots of species *i*.

In the water balance described above, we neglected two processes: precipitation and evaporation. The first is very low at the study site (23.8 mm/year at Gobabeb Research Centre (Schulze, 1969)). The second is only active during flooding, which is only a few days per year. The effective depth of direct evaporation from bare soils was assumed to be 1.5 m and can be considered as non active soil layer above the alluvium.

2.2.3 The stochastic flood generator

The flood volume $V_{\text{Flood}}(t)$ was generated by a fractional autoregressive moving average (FARIMA(p, d, q), $p, q \in N$) model with symmetric α -stable (S α S, $\alpha \in (1,2)$) innovations (Kokoszka and Taqqu, 1995; Stoev and Taqqu, 2004). The FARIMA(p, d, q) model generates time series with both short- and long-term dependence structures that are present in many hydrologic processes (Hurst, 1951; Montanari et al., 1997). We used the algorithm presented in (Stoev and Taqqu, 2004) to generate time series with given short- and long-term memory. The short term dependence structure is determined by the real polynomials X_p and Ψ_q of degree p and q. The autoregressive part of FARIMA is represented by the coefficients of X_p ,

$$\mathbf{X}_{p}(\boldsymbol{\lambda}) = 1 - \chi_{1}\boldsymbol{\lambda} - \chi_{2}\boldsymbol{\lambda}^{2} - \dots - \chi_{p}\boldsymbol{\lambda}^{p}, \qquad (2.17)$$

where $X_1(\lambda) = 1 - 0.192\lambda$ and λ is a random number drawn from a normal distribution with mean 0 and standard deviation 1. The moving average part is represented by the coefficients of Ψ_q :

$$\Psi_q(\lambda) = 1 - \psi_1 \lambda - \psi_2 \lambda^2 - \dots - \psi_q \lambda^q, \qquad (2.18)$$

with $\Psi_1(\lambda) = 1 - 0.8969\lambda$. The long term behaviour is governed by *d* that is an arbitrary fractional real number:

$$0 < d < 1 - 1/\alpha$$
, and $1 < \alpha < 2$. (2.19)

The relationship between d and the Hurst-Exponent H is as follows:

$$H = d + 1/\alpha \,. \tag{2.20}$$

The value of *H* varies between 0 and 1, an *H* of 0.5 means absence of long term memory or white noise. Values lower than 0.5 correspond to negative dependence; however, these are rarely encountered in the analysis of hydrologic data (Montanari et al., 1997). Typical values of *H* range between 0.7 and 0.8 (Hurst, 1951). Hence, for our study, we assumed *H* to be 0.75 (with $\alpha = 1.99$ and d = 0.25), and p = q = 1. The time series were generated with FARIMA(p=1, d=0.25, q=1) and adjusted to the observed mean annual flood volume $\mu_{Flood} = 3269\ 000\ \text{m}^3$, and thus yielding

$$V_{Flood}(t) = e^{(FARIMA(1,0.25,1) + \log(\mu_{Flood}))}.$$
(2.21)

Flood duration was found to be related to flood volume. Therefore we performed a linear regression between the measured flood duration and the corresponding logarithmic flood volumes from 1981 to 2006. The derived best fit ($r^2 = 0.9$) was given by

$$D(t) = e^{\frac{\log V_{Flood}(t) - 10.58}{1.64}},$$
(2.22)

and used in the following to calculate the flood duration.

2.2.4 Ecological model

The ecological model aims to describe the dynamics of the plant community consisting of the three tree species of interest in the river-basin of the Kuiseb in relation to the availability of water as jointly utilized resource. Each tree species is characterized by its biomass in the river-valley segment. In order to address important processes of the plant community dynamics and their response to the hydrological system in an adequate way, biomass of a species is differentiated into green (G) and reserve biomass (R) similarly as (Muller et al.,

2007), who termed R after (Noy-Meir, 1982). The green biomass describes all the parts of a plant, which perform photosynthesis, while the reserve biomass covers all parts of the plant that are not photosynthetically active, like woody parts and roots. The dynamic of G is driven by seasonality (phenology) and short-term water stress. The process of photosynthesis performed by G depends on the availability of water (transpiration, see section 2.2.2) and results in the production of organic carbon, which maintains both green and reserve biomass. The dynamic of R occurs on a longer timescale and reflects the long-term history of the ecohydrological system.

The model is applied at a seasonal time scale, thus dividing the year in two halves: the season when floods occur (southern hemisphere summer) and the dry season. During the seasons, when the plants are photosynthetically active, the green biomass G_i is modelled as

$$G_i(t) = (1 - \varepsilon_i(t)) \cdot G_i(t-1) + w_{G_i}(t) \cdot R_i(t-1), \qquad (2.23)$$

where $G_i(t)$ and $G_i(t-1)$ are the green biomass in this and the previous time step of species *i*, with units of t/ha, $R_i(t-1)$ is the reserve biomass in the previous time step, $w_{G,i}(t)$ is the conversion rate from reserve into green biomass (Eq. 2.26), and $\varepsilon_i(t)$ is the unitless water stress function (Eq. 2.27), ranging from 0 for no water stress to 1 for complete water stress. The latter two terms, $w_{G,i}(t)$ and $\varepsilon_i(t)$, are functions of the available amount of water (Eq. 2.25, 2.26)). The first term of Eq. (2.23), $(1 - \varepsilon_i(t)) \cdot G_i(t-1)$, denotes the leaf shed due to water stress, while the second part, $w_{G,i}(t) \cdot R_i(t-1)$, denotes the growing of leaves on the existing reserve biomass, assuming that the required Carbon of the reserve biomass was already accumulated in the buds during the previous season.

Depending on the complexity of the model, we either assume no phenological differences between the species (model A), or we include the known differences in phenology. In the first case, Eq. (2.23) applies to all species at all times. In the latter case, some species are dormant during a particular season (model B and C). Green biomass during the dormant season was calculated as:

$$G_{i}(t) = (1 - ls_{i}) \cdot (1 - \varepsilon_{i}(t)) \cdot G_{i}(t - 1), \qquad (2.24)$$

where ls_i is the unitless leaf shedding factor and ranges from 0 to 1 of species *i*. $ls_i = 0$ corresponds to no leaf shedding at all, and 1 to complete leaf shed. Usually, leaf shed is not complete, so ls_i takes a value between 0 and 1.

The formation of reserve biomass takes place at the end of each season *t*:

$$R_{i}(t) = fr_{i}(t) \cdot \{ [1 - m_{R,i} \cdot (1 + \varepsilon_{i}(t))] \cdot R_{i}(t - 1) + w_{R,i} \cdot G_{i}(t) \},$$
(2.25)

where $fr_i(t)$ is the unitless flood resistance of species i and ranges from 0 to 1 (Eq. 2.28, see below). It denotes the vulnerability of a given species to being uprooted and washed away by a flood of given magnitude. $fr_i(t) = 0$ corresponds to complete removal of reserve biomass by the flood. In the dry season, $fr_i(t)$ is set to 1. The parameter $m_{R,i}$ denotes the mortality of the reserve biomass, and $w_{R,i}$ the growth rate of reserve biomass. Both are constant over time and unitless. The first part of Eq. (2.25), $[1 - m_{R,i}(1 + \varepsilon_i(t))] \cdot R_i(t-1)$, denotes the amount of reserve biomass remaining after mortality and response to water stress. Note that the total mortality increases when $\varepsilon_i(t) > 0$. The second part, $w_{R,i} \cdot G_i(t)$, corresponds to growth of reserve biomass, based on the photosynthesis performed by the green biomass $G_i(t)$. In our simulations we fixed the initial values of green and reserve biomass to $G_i(t=1) = 0$ t/ha and $R_i(t=1) = 0.1$ t/ha.

In our model, favourable periods of growth in the green biomass *G* can markedly increase the reserve biomass *R*, whereas unfavourable periods reduce *G* fast, but *R* only slowly. In his paper about the multispecies competition in variable environments, Chesson (1994) called this the storage effect, which "is a metaphor for the potential for periods of strong positive growth that cannot be cancelled by negative growth at other times". The storage effect is enhanced by the parameter $w_{R,i}$ (Eq. 2.25).

The three parameters conversion rate $w_{G,i}(t)$, water stress $\varepsilon_i(t)$, and flood resistance $fr_i(t)$ are characteristics of the tree species that are dynamically linked to the hydrosystem. The conversion rate from reserve to green biomass, $w_{G,i}(t)$, is described by a sigmoid function that depends on the water volume in the alluvium that can be reached by the plant roots $(V_{WS,i}(t))$ (see section 2.2.2, Eq. (2.9)) and the total reserve biomass of the ecosystem in the previous

time step
$$(R_{total}(t-1) = \sum_{i=1}^{3} R_i(t-1))$$
:
 $w_{G,i}(t) = \frac{a_i}{1+e^{b_i(c_i - \frac{V_{WS,i}(t)}{R_{total}(t-1)})}},$
(2.26)

where a_i , b_i and c_i are the shape parameters of the sigmoid function, and depend on species *i*. The dependence of $w_{G,i}(t)$ on accessible water volume $V_{WS,i}(t)$ and total reserve biomass R_{total} reflects the intra- and interspecific competition between the three plant species for water, although in an aggregated and non-spatial way.

The water stress function $\varepsilon_i(t)$ was calculated as

$$\varepsilon_i(t) = 1 \text{ for } V_{WS,i}(t) < V_{PWP}, \qquad (2.27a)$$

$$\varepsilon_i(t) = \frac{(V_{WS,i}(t) - V_{Stress,i})^2}{(V_{PWP,i} - V_{Stress,i})^2} \text{ for } V_{PWP,i} \le V_{WS,i}(t) \le V_{Stress,i},$$

$$(2.27b)$$

$$\varepsilon_i(t) = 0 \text{ for } V_{WS,i}(t) > V_{Stress,i}, \qquad (2.27c)$$

where $V_{\text{Stress},i}$ is the water volume in the alluvium reachable by plant roots that leads to water stress in the population of species *i* and $V_{\text{PWP},i}$ is the water volume within the reach of plant roots that is no more extractable by plants. It is species-specific because it depends on the species root depth Eq. (2.9). $V_{\text{Stress},i}$ is also a species-specific parameter: the lower $V_{\text{Stress},i}$ the more drought tolerant is this species.

The flood resistance $fr_i(t)$, describes the capacity of the vegetation to withstand a flood without being uprooted and washed away. It reduces the reserve biomass, which is assumed to be built at the end of season, and only applies during the flood season Eq. (2.25). We modelled it as a linear function of the flood volume (V_{Flood} with unit m³/ha), which was generated by Eq. (2.21).

$$fr_i(t) = 1 \text{ for } V_{Flood}(t) < V_{low,i},$$
 (2.28a)

$$fr_i(t) = f_i \cdot V_{Flood}(t) + g_i \text{ for } V_{low,i} > V_{Flood}(t) > V_{high,i}, \qquad (2.28b)$$

$$fr_i(t) = 0 \text{ for } V_{Flood}(t) > V_{high,i}, \qquad (2.28c)$$

where f_i and g_i are species specific shape parameters. When the flood volume is below $V_{\text{low},i}$ the flood resistance is 1, the flood is minor and the species population does not suffer additional mortality induced by flood. Above the flood volume of $V_{\text{high},i}$ the flood resistance is 0, i.e. the species population is completely washed away.

2.2.5 Model versions

One aim of this study was the analysis of model complexity with regard to model output. Therefore we investigated several model types that differ in complexity regarding the representation of the ecosystem. Since little is known about the ecological parameters in the Kuiseb River, any model would be comparatively simple. We compared three model version of the same area. Table 4 gives an overview about the model differences.

Model Type	Phenology	Flood Resistance	Number of Parameters
A	same for all	same for all	23
В	species specific	same for all	25
С	species specific	species specific	29

Table 2.4. Levels of complexity in model A-C. Phenology and flood resistance can be implemented species specific or same for all species.

In the first model (A) we neglected phenology, all species were evergreen, but differed other traits like maximum transpiration rate. Generally, leaf shed is only partial for all species, thus it suggests itself to neglect seasonal variation. In the second version B, we included the observed species specific phenology of Camel Thorn and Ana Tree (Table 2.1). For this we added two parameters (ls_{Cam} and ls_{Ana}), which increased the degree of complexity (model type B). Finally, in model C, we included more knowledge regarding the difference in flood resistance between species, thus allowing the parameter fr_i to be species specific.

In summary, model type C included the most ecological information, strongest constraints and a mortality that is not only stochastic but also depends on the hydrosystem. In each model application we compared, if the model was able to reproduce the observed coexistence of three species. To achieve this goal we parameterised the models accordingly, as pointed out in the next section.

2.2.6 Parameter sampling

Depending on the model version, the ecological model contained 23-29 parameters. Table 2.5 gives an overview of those parameters together with their physical range. We used Latin hypercube sampling in order to identify parameter sets, which lead to the observed coexistence of three species. This was performed for each model version separately. Only the ecological parameters were calibrated, the hydrological parameters were fixed to the values indicated in Table 2.2.

We constrained the parameter space qualitatively according to the available ecological information summarized in Table 2.1: The root depth was largest for Camel Thorn, followed by Ana Tree and Wild Tamarix. Further, we assumed that the growth rate of reserve biomass can be derived from wood density, that is, the larger the wood density the smaller is $w_{R,i}$. Hence, reserve biomass growth rate was largest for Ana Tree, followed by Wild Tamarix and Camel Thorn. Additionally, we checked the sampled parameter sets for plausibility: For the

shape parameters a_i , b_i , and c_i we allowed only combinations that lead to $w_{G,i}(t) = 0$, if $\frac{V_{WS,i}(t)}{R_{total}(t-1)} \le 0 \text{ in Eq. (2.26)}.$

Parameter	Description	Range
$\theta_{\mathrm{Stress},i}$	Water content leading to water stress	$\{0.016 - 0.06\} \text{ m}^3 \text{ m}^{-3}$
$Z_{r,i}$	Root depth	{3 - 15} m
$W_{R,i}$	Growth rate of reserve biomass	{0 - 1}
a_i	Shape parameter of green biomass growth rate (maximum)	{0 - 1}
b_i	Shape parameter of green biomass growth rate (slope)	{0.001 - 0.03}
c_i	Shape parameter of green biomass growth rate (shift)	$\{1000-15000\}\ m^3/t$
$m_{R,i}$	Mortality of reserve biomass	{0.01 - 0.07}
ls _i	Leaf shedding in model B and C	{0.1 - 0.9}
f_i	Shape parameter of flood resistance (slope)	$\{-10^{-6}10^{-4}\}$
g_i	Shape parameter of flood resistance (intersection with y-axis)	{1.1 - 2.0}
fr _i	Flood resistance in model C	{0.0 - 0.5}
$V_{\rm FR}$	Flood volume that leads to biomass decrease	$\{10^5 - 10^9\}m^3$

Table 2.5. Ecological parameters that were calibrated and their range.

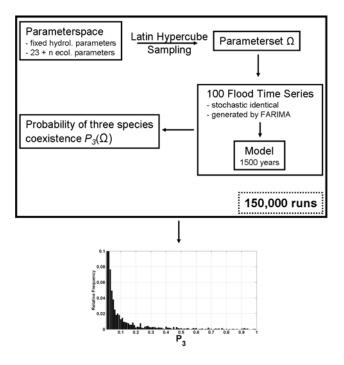


Fig. 2.4. Scheme of the parameter sampling.

The sampling procedure is illustrated in Fig. 2.4. For each sampled parameter set (Ω_{ι}) we run the model 100 times. We than counted the number of runs, where all three species coexisted and defined the probability of coexistence ($P_{3,\iota}$) for the parameter set Ω_{ι} as follows:

$$P_{3,\iota}(\Omega_{\iota}) = \frac{\#B(n=3)}{100},$$
(2.29)

where #B(n=3) is the number of flood realisations that led to coexistence of all three species. $P_{3,t}$ gives an indication how robust the modelled coexistence was. If $P_{3,t}$ is small, the parameter set Ω_t only led to coexistence under very specific flood conditions, while a $P_{3,t}$ near 1 indicates that the parameter set led to coexistence in almost all flood realisations with the same stochastic properties.

We defined coexistence based on the following criterion: The average reserve biomass during the last 1000 years must exceed the reserve biomass necessary to maintain 10 adult individuals of average size of each species. The method for deriving the number of individuals is described in the appendix A.

2.2.7 Analysis of the ensemble models

For analysis of the model results, we used ensemble statistics of hydrological variables of interest and each parameter set Ω_t (with $P_{3,t}$ as indicated). The statistics were only performed on the last 1000 years (2000 time steps) of each simulation, in order to avoid the influence of initial conditions.

The expected ensemble mean for parameter set Ω_t of the variable of interest (for example total ecosystem transpiration) was calculated as follows. We first calculated the time series means of the variable of interest, for each simulation that led to coexistence with the same parameter set Ω_t . Secondly, we calculated the ensemble mean of the obtained set of time averages.

We only calculated the time average for the subset of η_3 simulations, which led to three species coexistence. The statistics was performed on at least $\eta_3 = 10$ simulations. If necessary, additional forward simulations were run in order to obtain 10 simulations with coexistence. Each time average of the variable of interest ($\overline{V}_{i,n}$) is calculated as

$$\overline{V}_{t,\eta} = \frac{1}{2000} \sum_{t=1000}^{t=3000} V_t$$
(2.30)

where V_t is the value of the hydrological variable of interest at time step t, and η the number of the model realisation. This led to a set of η_3 time averages for the variable of interest. Based on this set we calculated the ensemble mean of η_3 realisations, which is

$$\left\langle \overline{V_{\iota}} \right\rangle = \frac{1}{\eta_3} \sum_{\eta=1}^{\eta_3} \overline{V_{\iota,\eta}}$$
(2.31)

We proceeded similarly, to obtain the ensemble average of the coefficient of variation of the hydrologic variable. We calculated the dimensionless coefficient of variation $(CV_{Vi,\eta})$ for the time series:

$$CV_{V_{i,\eta}} = \frac{\sigma_{V_{i,\eta}}}{\overline{V}_{i,\eta}},$$
(2.32)

where $\sigma_{V_{l,\eta}}$ denotes the standard deviation within the time series of the variable of interest. Based on this we calculated the ensemble mean of η_3 realisations, which is

$$\langle CV_{V_{i}} \rangle = \frac{1}{\eta_{3}} \sum_{\eta=1}^{\eta_{3}} CV_{V_{i,\eta}}$$
 (2.33)

2.2.8 Forward simulations with changed flood regime

After finding ensembles of suitable parameter sets, we tested how models behaved for changed flood conditions. For this we selected those parameter sets which led to coexistence, and run them again with changed flood regime. We changed the long term memory of the flood generation algorithm, by decreasing and increasing the Hurst exponent (Eq. 2.20). We grouped the forward simulations into those performed with parameter sets of weak robustness $(0.1 \le P_{3,t} \le 0.5)$ and elevated robustness $(P_{3,t} > 0.5)$.

2.3 Results

Table 2.6 shows in per cent how many of the 150 000 sampled parameter sets led to $P_{3,t} \ge 0.1$ for models A, B and C. In all cases, the number of parameter sets that allowed for coexistence of all species is very small (less than half percent in all cases). Furthermore, coexistence was modelled for more parameter sets in models A and C, compared to B: The total number of parameter sets leading to $P_{3,t} \ge 0.1$ for model A and C was about 20 times (both around 0.2%) larger than model B (0.009%, Table 2.6). Model B was not subject to further investigations because there were no parameter sets leading to elevated robustness of three species coexistence with $P_{3,t} \ge 0.5$.

	Model A	Model B	Model C
Probability of a three	0.26	0.009	0.2
species coexistence [%]			

Table 2.6. Results of parameter sampling over 150 000 parametersets ($P_{3,t} \ge 0.1$).

In Fig. 2.5 we plotted histograms of the achieved probabilities of coexistence ($P_{3,t} \ge 0.1$) for model A and C. These histograms give an impression how robust the modelled coexistence was for the different models. The skewness γ of both histograms indicates that most parameter sets showed little robustness ($\gamma_A = 1.5$ and $\gamma_C = 1.7$). Also, for model A the number of robust parameter sets was larger. For example, consider only parameter sets with $0.1 \le P_{3,t} \le 1$: In model A 14.3% of those had $P_{3,t} > 0.5$, but in model C only 4.2%.

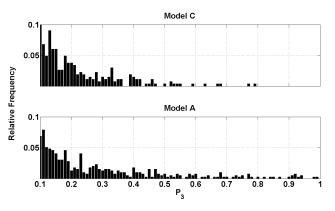


Fig. 2.5. Results of the parameter sampling. Histograms show the relative frequency of parameter sets resulting in $P_3 \ge 0.1$ with model C and A (H = 0.75 for both).

In order to show how models A and C differ hydrologically we compared the distributions of the ensemble means of hydrologic variables for parameter sets (Ω_i) with $P_{3,i} \ge 0.1$. In Fig. 2.6 we plotted histograms of the ensemble average of total transpirations (left) and depths to ground water (right). In model A the transpiration was larger (median 161 mm/year) than in model C (median 148 mm/year). In contrast, the depth to ground water was similar for both models (median A: 7.38 m, C: 7.63 m). The difference for model A and C becomes apparent when comparing the extremes of depth to ground water. In model A the ground water was more often modelled close to the surface (0.25 percentile was 5.93 m) than in model C (0.25 percentile was 6.63 m). The opposite is true for deep ground water tables (0.75 percentile in model A was 11.80 m versus 9.74 m in model C).

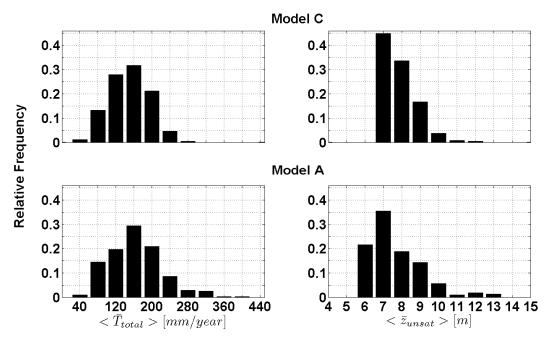


Fig. 2.6. Relative frequencies of ensemble mean total transpiration (left column) (Eq. 2.31) and ensemble mean depth to ground water (right column) of parameter sets with $P_3 \ge 0.1$ for model C (upper row) and model A (lower row).

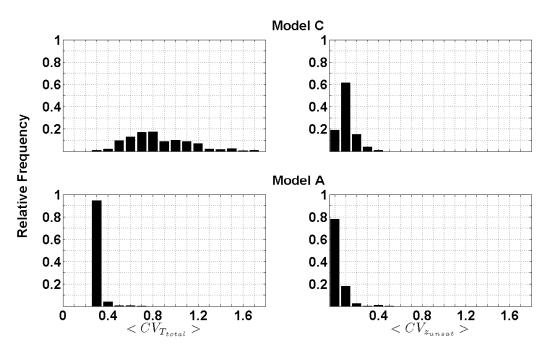


Fig. 2.7. Relative frequencies of ensemble *CV* of total transpiration (left column) (Eq. 2.33) and ensemble *CV* of depth to ground water (right column) of parameter sets with $P_3 \ge 0.1$ for model C (upper row) and model A (lower row).

In Fig. 2.7 we plotted histograms of the ensemble means of CV for total transpiration and depth to ground water. While models A and C differed little with regard to the distributions of the ensemble averages of transpiration and depth to ground water, they were much different with regard to the distributions of the time fluctuations of these variables. In model A the time fluctuation in transpiration was much lower (median 0.258) than in model C (0.799). Less pronounced was the difference in the variation of ground water depth, which was also smaller in model A (median 0.025) than in model C (median 0.084).

Next, we investigated, if increase in robustness was related to similar parameter sets and similar hydrological conditions. In other words, are all robust parameter sets just small variations of a similar model, or are they completely different? For this, we looked at both the modelled hydrology and the difference between parameters. In Fig. 2.8 we plotted the medians of transpirations and ground water depth corresponding to the probabilities of coexistence ($P_{3,t}$).

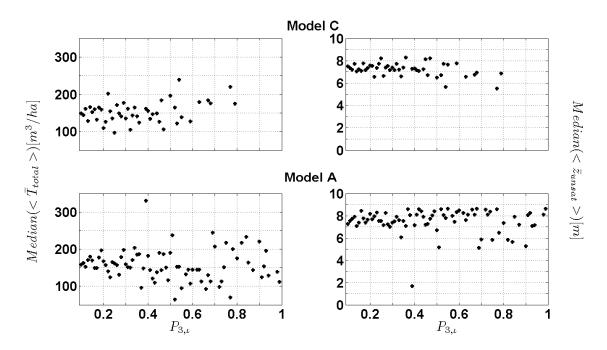


Fig. 2.8. Medians of $\langle \overline{T}_{total} \rangle$ (left column) and $\langle \overline{z}_{unsat} \rangle$ (right column) of parameter sets with $0.1 \le P_{3,t} \le 1$. The bin size of x-axis is 0.01. Results of model C are shown in the upper row and model A in the lower row. The linear correlation coefficients are (line by line): 0.34, -0.38, -0.08, -0.06

In Fig. 2.9 we plotted the medians of CV of transpiration and ground water depth corresponding to the probabilities of coexistence $(P_{3,i})$. Both, Fig. 2.8 and 2.9, suggest that in model C a weak relationship existed between the robustness of the parameter sets $(P_{3,i})$ and transpiration $(r^2 = 0.34)$ and ground water table $(r^2 = -0.38)$. Also, a weak relationship existed

between $P_{3,i}$ and the CV of transpiration ($r^2 = -0.27$) and ground water table ($r^2 = 0.14$). No such relation existed for model A. Fig. 2.10 gives an impression how robustness of the parameter sets was related to the similarity of four parameters in model C: the root depth ($z_{r,i}$), the growth rate of reserve biomass ($w_{R,i}$), the mortality of reserve biomass ($m_{R,i}$), and the shape parameter c_i of the conversion rate from reserve to green biomass. The plots show that no relationship between robustness of the parameter sets and parameter similarity existed. The same holds for model A.

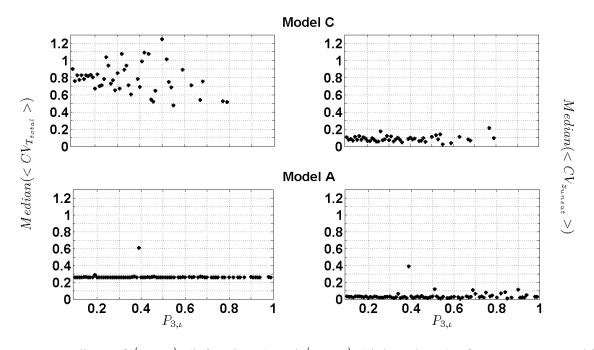


Fig. 2.9. Medians of $\langle CV_{T_{total}} \rangle$ (left column) and $\langle CV_{z_{unsarl}} \rangle$ (right column) of parameter sets with $0.1 \leq P_{3,t} \leq 1$. The bin size of x-axis is 0.01. Results of model C are shown in the upper row and model A in the lower row. The linear correlation coefficients are (line by line): -0.27, 0.14, -0.06, 0.06

In Fig. 2.11 and 2.12 we plotted typical time series of the reserve and green biomass, the flood volume and the depth to ground water. These time series allow insight into the driving coexistence mechanisms in model A and C. In model C the biomass and ground water was more affected by the flood (Fig. 2.12a) than in model A (Fig. 2.11a). In model C, two alternating states existed. One state was associated with high prevalence of Camel Thorn and Wild Tamarix, small floods and deep ground water table (e.g. year 600 - 750 in Fig. 2.12). The other state was associated with high prevalence of Ana Tree and Wild Tamarix, strong floods and shallow ground water table (e.g. year 850 - 1000 in Fig. 2.12). In all parameter sets of model C Ana Tree was characterized by a larger vulnerability to flood disturbance than Camel Thorn and Wild Tamarix (Fig. 2.12b). Model A showed different dynamics. In model

A the green biomass and the ground water remained constant after initial fluctuations (Fig. 2.11). The time series of each species reserve biomass were synchronized with small and frequent disturbances by the flood.

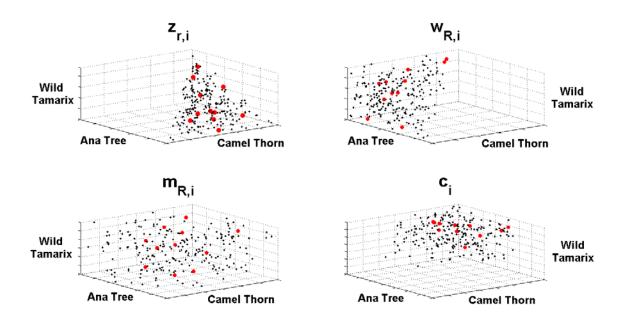


Fig. 2.10. Parameter space of root depths $(z_{r,i})$, growth rates of reserve biomass $(w_{,R,i})$, mortality rates of reserve biomass $(m_{R,i})$ and one of the shape parameters of the conversion rate from reserve to green biomass (c_i) . Black points denote the non robust parameter sets with $0.1 \le P_{3,i} \le 0.5$, and red filled circles denote the robust parameter sets with $P_{3,i} > 0.5$. The axes show the entire parameter space that was sampled in model C. The clustering of $z_{r,i}$, $w_{R,i}$, and c_i is caused by the constraints in parameter space and the plausibility check (see Sect. 2.2.6).

Fig. 2.13 shows how model A and C were affected by a changed long term memory of the flood volume. The relative frequencies refer to the previously identified parameter sets with low robustness ($0.1 \le P_{3,t} \le 0.5$, Fig. 2.13a) and elevated robustness ($P_{3,t} > 0.5$, Fig. 2.13b). In model C decrease of long term memory decreased species coexistence. This effect was even stronger for the robust parameter sets (Fig. 2.13b). In model A three species coexistence was little affected by change of the long term memory of the flood, and independent of the robustness of the parameter sets.

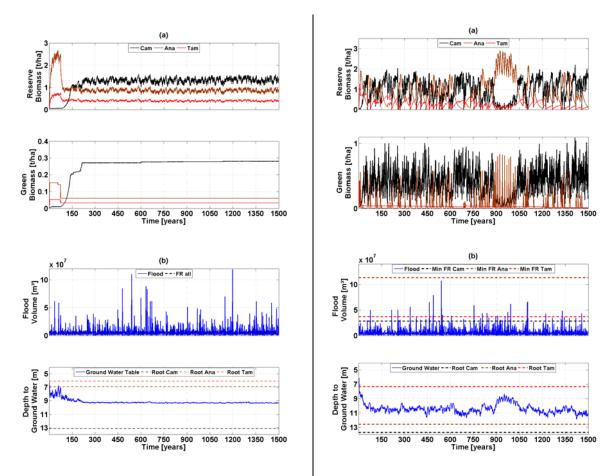


Fig. 2.11. Typical time series of model A: (a) reserve and green biomass, (b) flood volume and depth to ground water.

Fig. 2.12. Typical time series of model C: (a) reserve and green biomass, (b) flood volume and depth to ground water.

2.4 Discussion

We applied three ecohydrological models that differ in the amount of included information, and structure. Differences particularly concerned the functional response of the plant species to the hydrosystem along the ephemeral Kuiseb River. We assessed these models regarding their ability to predict coexistence of the three species as was observed in reality. This strategy of pattern-oriented modelling (see e.g. Grimm et al. (2005) and references therein) has been used to model coexistence before. In our study, only two of the three models allow for robust coexistence of all three species. Further, in both models only few parameter sets reproduce coexistence. This is in line with the classical competition models from ecology (e.g. (Lotka, 1925; Volterra, 1926)). These models also reveal that species coexistence only emerges if certain restrictive conditions are met by the model parameters. As a result, the parameter combinations found to be appropriate are sparse given the entire parameter space.

The comparison between observed and simulated patterns acts as a filter, which allows us to identify, whether a given model structure and parameter combination allows coexistence. In

this study, only models A and C allow for robust coexistence. They describe two different coexistence mechanisms for different levels of detail. In model A, species are found to coexist only, if they have access to different water storages, depending on their root depths (Fig. 2.11b). Camel Thorn has access to deep ground water and does not compete with any other species. On the other hand, the roots of Ana Tree and Wild Tamarix can only reach the unsaturated layer. Hence, only these two species compete for water in the unsaturated layer. Their coexistence is driven by the trade-off between growth rate of reserve biomass (w_{Ri}) and water stress (ε_i), both influencing green biomass and, hence, transpiration demand of the individual species (see Eq. 2.11). Ana Tree, for instance, has the larger growth rate, but is less water stress resistant. Therefore, coexistence in model A is based on both niche partitioning and trade-offs.

In model B this sensible balance is broken, by introducing the (observed) phenology. The phenology of Ana Tree in model B reduces the growth period to one season whereas the direct competitor, Wild Tamarix, is evergreen and uses the water resource all year. This provides Wild Tamarix with an advantage in the competition over Ana Tree. In other words, inter-specific competition is enhanced in Model B with the effect that coexistence of all three species is not possible anymore. This is in accordance with the classical competition theory (see above). Note that this also indicates that integrating more knowledge in a model does not automatically lead to more realistic modelling results. On the other hand, models can give satisfactory results, but maybe for the wrong reason. Effects may be neglected which can play an important role under different management or climatic conditions.

In model C, another coexistence mechanism is enabled, only by allowing for species specific vulnerability to the flood. Thus, as opposed to models A and B, the flood has differential influence both as a water resource and via the destructive impact of the flood; the latter acts directly as an environmental disturbance on the plant species and favours flood resistant species during periods of strong floods. This can compensate the disadvantage of being less competitive than other species in other respects and, hence, can mediate coexistence again. In this case, coexistence results from the combination of niche differentiation and environmental disturbance. The latter fits in the context of the Intermediate Disturbance Hypothesis (Connell, 1978; D'Odorico et al., 2008; Grime, 1973; Huston, 1979). The species specific flood resistance in model C allows for ecological differences in the response to disturbance and outbalances too strong advantages from the differences in the phenology, and thus enhances coexistence (Roxburgh et al., 2004).

Although both models differ in their structure and coexistence mechanisms, the ensemble statistics of mean hydrologic variables like transpiration and depth to ground water are surprisingly similar between models A and C (Fig. 2.6). This is owed to the fact that the hydrological model is the same in both A and C. However, the differences between the two models become apparent, when considering the variation in the time series for both hydrological and ecological variables (depth to ground water, green and reserve biomass) of the system and its sensitivity to environmental change (here: change of the Hurst-Exponent). The more complex model C shows higher variation in the variables, and is more sensitive to environmental change than model A. This is a logical consequence of the modelled coexistence mechanism. In model C, the flood has both indirect (via the hydrosystem as resource) and direct (as disturbance) impacts on the plant species. Thus, both reserve and green biomass of the different species are independently linked to the flood fluctuations. As a result, species abundances change over time, sometimes with a prevalence of the water conserving species, sometimes with prevalence of the water demanding species. Thus, transpiration and the resulting ground water level vary accordingly. In model A, however, the flood influences the ecosystem merely via the reserve biomass (no direct impacts on the green biomass). The reserve biomass is able to act as a buffer and to stabilize the entire system (green biomass, ground water depth).

The results on the influence of the Hurst exponent also give rise to some conclusions on the adequateness of the Intermediate Disturbance Hypothesis (IDH) in ecohydrological systems along ephemeral rivers. The IDH primarily argues with the frequency of the disturbance. Our results indicate, however, that the autocorrelation in the varying water supply and so the duration of related disturbance events (cumulative water stress during dry periods, repeated disruptive floods) are crucial for the impact on species coexistence and resilience as well. In this ephemeral ecosystem, considering solely the frequency would reach too short. The importance of autocorrelation / red noise has also been shown in the context of species survival. Schwager et al. (2006) for instance, showed that autocorrelation can be stabilizing or destabilizing depending on the species' ecological traits.

The results of our study suggest that the assumptions on the functional traits of the species in the plant communities (e.g. regarding resource utilization, flood resistance) and so on the mechanisms of competition / coexistence can influence the modelled hydrology. Furthermore, we find hints that the distribution of mean hydrologic variables in this system is probably driven by the applied hydrological model, whereas the distribution of fluctuations (here: coefficient of variation) is probably driven by the assumed ecological interactions.

Our forward simulations with different Hurst exponents show that not only the stochasticity of the environmental disturbance (the flood) influences the coexistence of the three species, but also the cyclicity of periods with high and low floods (long term memory, see section 2.2.3) plays an important role. Most hydrological processes are characterized by long term memory processes (Montanari et al., 1997), which lead particularly in arid regions to extended periods of unusually small or strong events ("Joseph Effect", (Mandelbrot and Wallis, 1968)). Our model suggests that this hydrologic characteristic might have important influence on ecosystem structure. This finding is in line with other results showing that the fine structure of environmental fluctuations can alter systems dynamics, qualitative trends or ranking orders among scenarios with serious implications for management (Frank, 2005; Schwager et al., 2006). Furthermore, the two models A and C show differences in the sensitivity of species coexistence against a change in the Hurst exponent. While model C reveals a strong sensitivity and a loss of coexistence, model A is found to be rather robust. The reason for this difference is again the buffer capacity of the reserve biomass in absence (model A) and presence (model C) of direct disturbance effects of the flood on the plant species.

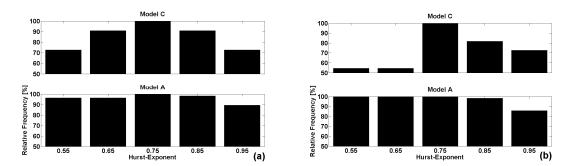


Fig. 2.13. Results of forward simulations. Relative frequency refers to the parameter sets identified by the parameter sampling with (a) $0.1 \le P_{3,t} \le 0.5$, and (b) $P_{3,t} > 0.5$.

The two models A and C can also be interpreted as two types of plant communities which differ in the impact of floods on their species (e.g. indirect only; indirect and direct). But note that both models that successfully modelled robust coexistence are still abstract representations of ecological and hydrological processes along ephemeral rivers. Thus, only limited knowledge of the actual mechanisms is implemented. Such generic models that focus on essential aspects are known to be crucial for integration and analysing consequences of feedback loops when entering new interdisciplinary fields (Baumgartner et al., 2008). This allows formulating new hypotheses, which can then be tested by more complex and structurally realistic models. In our context, additional intra- or interspecific effects (like age

dependent rooting depth) might be active in maintaining the observed coexistence. Potentially, a lot more mechanisms can enhance the three species coexistence like random individual effects or multi dimensional tradeoffs (Clark et al., 2007). Thus, our models are just a subset of possible abstraction, which might all reproduce the observed coexistence. In fact it might be impossible to find the "right" model. The coexistence constraint did not limit the possible parameter space enough to lead to a unique ecohydrologic response. However, our models shed light on possible options. They also give hints towards which variables could be measured to increase the understanding about the involved mechanisms.

2.5 Conclusions

The modelling of three species coexistence in a water limited environment is challenging because feedbacks between ecology and hydrology have to be implemented in an appropriate way. The present study introduced a model that facilitates the investigation of effects of model structure and parameter uncertainty on ecology and hydrology of the water limited system along ephemeral rivers. We applied a range of model versions with a varying degree of included information. Given that only two of three models led to robust three species coexistence, we conclude that the driving coexistence mechanism is defined by the model structure. On the other hand, the robustness check of the parameter sets leading to three species coexistence indicates that the success of the underlying coexistence mechanism is controlled by the combination of the population parameters. Further, depending on the model structure the flood can act as water resource or environmental disturbance or a combination of both. When acting as environmental disturbance the change in long term memory strongly affected the robustness of the parameter sets. Therefore, we conclude that the long term memory of hydrological processes is important in water limited ecosystems. In this study, we applied the same hydrological concept for all model versions and only changed the complexity of the ecological model. Considering that the distribution of average values of transpiration and ground water table were similar but not their distribution of fluctuations, we conclude that the ensemble statistics of average values of hydrologic variables are probably influenced by the applied hydrological model, whereas the ensemble statistics of fluctuations of both are probably controlled by the applied ecological model.

Our study shows that the species composition in the plant community strongly influences the stability properties of the ecohydrological system (e.g. variation in transpiration and ground water depth; variation in reserve and green biomass; sensitivity of species coexistence to

change in the Hurst exponent). This stresses the necessity to consider explicitly species composition and functional interactions in the ecosystem when assessing the impact of climate or land use change on water resources and vegetation along ephemeral rivers. This is particularly important in systems where the floods have direct destructive impacts on the vegetation. Here, models are essential that explicitly take into account such disturbance effects (such as model C). The relative importance of the species composition for understanding ecohydrological systems, however, came only to light through the subsequent process of changing the model structure and comparing their outcomes.

Symbol	Description	Value/Units	Equation
A_{GW}	Cross-sectional area of the ground water layer	m ²	14
A_{seg}	Surface area of the segment under study	18 km^2	2
a_i, b_i, c_i	Shape parameter of green biomass growth rate		26
α	Arbitrary fractional real number	1.99	19
γ	Skewness of a histogram		
$CV_{V_{\iota,\eta}}$	Coefficient of variation of variable of interest		32
$\left\langle CV_{V_{i}} ight angle$	Ensemble mean of $CV_{V_{i,\eta}}$		33
D	Flood duration	d	22
d	Fractional differencing exponent	0.25	20
\mathcal{E}_i	Water stress	{0.0 - 1.0}	27
fr _i	Flood resistance	{0.0 - 1.0}	28
f_{i}, g_{i}	Shape parameter of flood resistance		28
G_i	Green biomass	t ha ⁻¹	23, 24
GWR	Ground water recharge	m ³ ha ⁻¹ season ⁻¹	6
Η	Hurst exponent	0.75	20
η	Number of model realisation	100	30
η3	Number of model realisation leading to three species coexistence	10	30
Δh	Hydraulic gradient in ground water storage	$m m^{-1}$	14
h_{max}	Maximal tree height	m	A2
h_{GW}	Ground water level	m	2
h_{WS}	Total depth of alluvium	15 m	3
Ι	Infiltration into unsaturated storage	m ³ ha ⁻¹ season ⁻¹	5
k_f	Hydraulic permeability of the ground water storage	$m s^{-1}$	14
λ	Random number drawn from normal distribution with mean 0 and standard deviation 1		17, 18
ls _i	Leaf shedding	{0.0 - 1.0}	24
$m_{R,i}$	Mortality of reserve biomass		25
N _{Ind,i}	Number of adult individuals		A1
μ_{Flood}	Average flood volume	3,269,000 m ³	21
$P_{3,t}$	Probability of three species coexistence for Ω_t	{0.0 - 1.0}	29
PET	Potential evapotranspiration	m ³ ha ⁻¹ season ⁻¹	11

Table 2.7. Symbols used in this study, *i* denotes the reference to a species.

Table 2.7	. Continued.
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Symbol	Description	Value/Units	Equation
φ	Porosity	$0.439 \text{ m}^3 \text{ m}^{-3}$	2
Q_I	Infiltration flux	$m^3 ha^{-1} d^{-1}$	5
Ω_ι	Parameter set		29
Q_{In}	Ground water inflow	14.9 m ³ ha ⁻¹ season ⁻¹ (dry) 20.9 m ³ ha ⁻¹ season ⁻¹ (rainy)	13
Q_{GW}	Ground water flow	m ³ ha ⁻¹ season ⁻¹	13
Q_L	Lateral ground water inflow	869.2 m ³ ha ⁻¹ season ⁻¹	13
Q_{Out}	Ground water outflow	m ³ ha ⁻¹ season ⁻¹	14
$Q_{T,i}$	Transpiration flux	$m^3 t^{-1} season^{-1}$	11
Q_V	Vertical ground water outflow	434.6 m^3 ha ⁻¹ season ⁻¹	13
$R_{1,i}$	Reserve biomass of one adult individual		A2
R_i	Reserve biomass	t ha ⁻¹	25
<i>R</i> total	Reserve biomass of all species	t ha ⁻¹	
r _i	Maximal trunk radius	m	
$ ho_i$	Wood density	t m ⁻³	A2
S_{FC}	Water volume in S_{unsat} corresponding to θ_{FC}	$m^3 ha^{-1}$	6
S_{GW}	Ground water storage	$m^3 ha^{-1}$	2
S_{PWP}	Water volume in S_{unsat} corresponding to θ_{PWP}	$m^3 ha^{-1}$	7a
Sunsat	Unsaturated storage	$m^3 ha^{-1}$	2
$\sigma_{V_{1,\eta}}$	Standard deviation of the variable of interest		32
θ	Volumetric water content	$m^{3} m^{-3}$	2
$ heta_{FC}$	Water content at field capacity	$0.061 \text{ m}^3 \text{ m}^{-3}$	6
$ heta_{PWP}$	Water content at permanent wilting point	$0.015 \text{ m}^3 \text{ m}^{-3}$	7
T_{GW}	Transpiration from ground water	m ³ ha ⁻¹ season ⁻¹	15
$T_{GW,i}$	Individual transpiration from ground water	m ³ ha ⁻¹ season ⁻¹	16
T _{unsat}	Transpiration from unsaturated storage	m ³ ha ⁻¹ season ⁻¹	7
T _{unsat,i}	Individual transpiration from unsaturated storage	m ³ ha ⁻¹ season ⁻¹	8
T _{WS,i}	Individual transpirational demand from alluvial storage (unsaturated + groundwater)	m ³ ha ⁻¹ season ⁻¹	11
t	Timestep	season	
V_{Flood}	Water volume of the flood	$m^3 ha^{-1}$	21

Symbol	Description	Value/Units	Equation
V _{GW,i}	Water volume in the groundwater reachable by roots of species <i>i</i>	m ³ ha ⁻¹	16
V _{high,i}	Flood volume that leads to completely washed away population	$m^3 ha^{-1}$	28
$V_{low,i}$	Flood volume that leads to additional mortality	$m^3 ha^{-1}$	28
$\overline{V}_{\iota,\eta}$	Time average of the variable of interest		30
$\left\langle \overline{V_{\iota}} \right\rangle$	Ensemble mean of $\overline{V}_{\iota,\eta}$		31
$V_{PWP,i}$	Water volume in the alluvium where no water is available for roots of species <i>i</i>	m ³ ha ⁻¹	27
V _{Stress,i}	Water volume in the alluvium that leads to water stress of species <i>i</i>	m ³ ha ⁻¹	27
V _{unsat,i}	Water volume in the unsaturated storage reachable by roots of species <i>i</i>	$m^3 ha^{-1}$	9
V _{WS,i}	Water volume in the alluvium reachable by plant roots of species <i>i</i>	$m^3 ha^{-1}$	8
W _{G,i}	Conversion rate from reserve to green biomass		23
W _{R,i}	Growth rate of reserve biomass		25
WS	Alluvial storage (unsaturated + groundwater)	$m^3 ha^{-1}$	1
X_p	Polynomial of degree p (autoregressive)	$X_1(\lambda) = 1 - 0.192\lambda$	17
Ψ_q	Polynomial of degree q (moving average)	$\Psi_1(\lambda) = 1 - 0.8969\lambda$	18
Z _{unsat}	Depth to ground water	m	3
$Z_{r,i}$	Root depth	m	10

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Chapter 3

How do coexistence mechanisms influence the fluctuations of hydrological variables?

3.1 Introduction

The spatial pattern of vegetation is both a cause and effect of variation in water availability in semiarid ecosystems (Rodriguez-Iturbe, 2000). Several ecohydrological studies have dealt with stochastic hydrological inputs and their influence on ecological patterns in semiarid regions. For instance, Rodriguez-Iturbe et al. (1999a,b) explain the stable coexistence of treegrass communities in water limited systems by the stochastic soil water availability and strategies to minimise plant water stress. In other studies, the impact of hydrological changes (flood regime and ground water) on riparian cottonwoods is investigated. Scott et al. (1997, 1999) conclude that the riparian cottonwoods respond to changes in the flood stochasticity (frequency, duration) and to ground water decline. Their results indicate that, to sustain the recent ecosystem structure, a responsible water use management is required.

But also the dynamic of ecosystems can influence the water cycle. For instance, Huxman et al. (2005) and Wilcox and Thurow (2006) investigate how woody plant encroachment and invasive plants affect streamflow and evaporation processes along rivers. In field investigations, Butler et al. (2007) and Loheide et al. (2005) assessed the major controls of riparian phreatophytes on daily ground water fluctuations. Eventually, Caylor et al. (2006, 2009) apply an ecohydrological model framework, developed by Laio et al. (2001a,b), Proporato et al. (2001) and Rodriguez-Iturbe et al. (2001) to investigate the role of tree density, canopy size, and the lateral extension of the root system on spatiotemporal patterns of soil moisture dynamics, plant water uptake, and plant stress.

Many processes, biotic and abiotic, can influence the dynamics of ecosystems. In particular, mechanisms that foster coexistence and the resulting multispecies community shape the

evolution of biomass. However, the modelling of multiple species coexistence is comparatively difficult (Arora and Boer, 2006; Clark et al., 2007). A number of mechanisms can be invoked fostering coexistence in models, such as ecological niches in time and space or trade-offs between processes influencing the growth and mortality of different species (Chesson, 2000; Clark et al., 2007). Further, temporal environmental variation and disturbance might enhance biodiversity and resilience of ecosystems (Arora and Boer, 2006; D'Odorico et al., 2008; Piou et al., 2008; Roxburgh et al., 2004). There has, however, been comparatively little discussion concerning the influence of ecosystem dynamics on fluctuations in hydrological variables. The implications of different coexistence mechanisms for fluctuations in the water cycle are poorly understood.

In a previous study (Chapter 2) we developed an integrated ecohydrological model framework allowing us to investigate structural differences in population dynamics with regard to their ability to model the observed three species coexistence pattern. Conceptually the model is based on a hydrological storage model with stochastical forcing from the flood and an ecological population model. Within this framework we identified two model versions able to reproduce robust three species coexistence. For each version we explicitly considered uncertainty in parameterising the population model by investigating all parameter combinations (artificial ecosystems) that comply with the coexistence pattern. The model concept is the same for all model versions, however, processes leading to particular coexistence mechanisms such as trade-offs or niche partitioning are integrated differently: Time of leaf shedding (phenology) and vulnerability to flood disturbance (flood resistance) are either the same for all species, species specific, or a combination of both. Consequently, four model versions emerge. However, in Chapter 2 we tested only three of them for the ability to reproduce the observed coexistence pattern. In this study, we complete the list of model versions by implementing the flood resistance species specific and the phenology as same for all (all species evergreen). We use the small variations of model versions to investigate the influence of coexistence mechanisms on the fluctuations of hydrological variables such as transpiration and depth to ground water. Eventually, we use, apart from the coexistence pattern, two ecohydrological patterns observed at the study site to prove the reliability of each model version in terms of an application as management tool along the Kuiseb River in Namibia.

3.2 Methods and materials

3.2.1 Study site

The study site is located in the middle reach of the Kuiseb River in Namibia, where rain is exceptional, and water arrives mainly during the flood events in the ephemeral river channel. Although the channel does not contain water for most of the year, it supplies a shallow aquifer with water during times of flood and thus creates a living environment for riparian vegetation. The vegetation mainly consists of three coexisting tree species: Camel Thorn (*Acacia erioloba*), Ana Tree (*Faidherbia albida*) and Wild Tamarix (*Tamarix usneoides*). The known differences between the three species are in their phenology (time of leaf shedding), maximum transpiration and growth rates.

3.2.2 Ecohydrological model

For this study we applied a conceptual ecohydrological model presented in Chapter 2 to investigate the effects of another model version (see section 3.2.3) on the simulation of vegetation structure (probability of three species coexistence (P_3)) and fluctuations of hydrological variables (transpiration, depth to ground water).

The hydrological part of the model is storage based (Eq. 3.1) with stochastical forcing from the flood (Eq. 3.3). The water balance of the system under study is written as

$$\Delta WS(t) = \Delta S_{unsat}(t) + \Delta S_{GW}(t), \qquad (3.1)$$

where $\Delta WS(t)$ is the sum of change in unsaturated ($\Delta S_{unsat}(t)$) and ground water storage ($\Delta S_{GW}(t)$). The actual transpiration $T_{WS,i}(t)$ for each species *i* from $\Delta S_{unsat}(t)$ and $\Delta S_{GW}(t)$ is a function of the green biomass $G_i(t)$ (Eq. 3.4a,b) with an upper boundary given by the potential evapotranspiration (*PET*):

$$T_{WS,i}(t) = \min(PET, Q_{T,i}(t) \cdot G_i(t)), \qquad (3.2)$$

where $Q_{T,i}(t)$ denotes the transpiration rate of each species.

The water storage (Eq. 3.1) is recharged frequently by stochastic flood events. The flood volume of each event ($V_{Flood}(t)$) was generated by a fractional autoregressive moving average (FARIMA(1,0.25,1)) model that generates time series with both short- and long-term dependence structures (Kokoszka and Taqqu, 1995; Stoev and Taqqu, 2004):

where $\mu_{Flood} = 3,269,000 \text{ m}^3$ is the observed mean annual flood volume. The long-term memory is characterised by the Hurst-Exponent *H*, which was 0.75 for this study.

The ecological part of the model is based on a population model. It represents the populations of three dominating riparian plant communities that compete for the water resource. In order to address important processes of the plant community dynamics and their response to the hydrological system in an adequate way, biomass of a species was differentiated into green (G) and reserve biomass (R). In the present paper, we assume that floods take place in the middle of the vegetation period, i.e. after the sprouting of the green biomass but before the feed back to the reserve biomass. Therefore, floods are modelled as additional mortality to the green biomass in the respective year. These assumptions result in the following equations:

$$G_i(t) = (1 - \varepsilon_i(t)) \cdot G_i(t-1) + w_{G_i}(t) \cdot R_i(t-1), \text{ for photosynthetically active season,}$$
(3.4a)

$$G_i(t) = (1 - ls_i) \cdot (1 - \varepsilon_i(t)) \cdot G_i(t - 1)$$
, for photosynthetically dormant season, (3.4b)

$$R_{i}(t) = fr(t) \cdot \{ [1 - m_{R,i} \cdot (1 + \varepsilon_{i}(t))] \cdot R_{i}(t - 1) + w_{R,i} \cdot G_{i}(t) \},$$
(3.5)

where $G_i(t)$ and $G_i(t-1)$ are the green biomass, and $R_i(t)$ and $R_i(t-1)$ the reserve biomass in this and the previous time step, $w_{G,i}(t)$ is the conversion rate from reserve into green biomass, $\varepsilon_i(t)$ represents the water stress, fr(t) is the flood resistance, $m_{R,i}$ denotes the mortality of the reserve biomass, and $w_{R,i}$ the growth rate of reserve biomass.

3.2.3 Model versions

We investigated several model types that differ in complexity regarding the implementation of the time of leaf shedding (phenology) and the vulnerability to flood (flood resistance). Table 3.1 gives an overview about the model differences.

Model Version	Flood Resistance	Phenology
А	same for all	same for all
В	same for all	species specific
С	species specific	species specific
D	species specific	same for all

Table 3.1. Model versions applied in this study.

The flood resistance was implemented either same for all species (Model A and B) or species specific (Model C and D). The same was done for the phenology, which was either neglected (Model A and D - all species evergreen) or species specific (Camel Thorn - leaf shedding during dry season, Ana Tree – leaf shedding during wet season). All model versions were tested towards their ability to model robust three species coexistence ($P_3 > 0.5$). Further, if robust coexistence was given, we investigated the influence of species specific implementation of phenology and flood resistance on the fluctuations of hydrological variables (transpiration, depth to ground water).

3.2.4 Model analysis

We used Latin hypercube sampling in order to identify parameters sets leading to three species coexistence. The parameter sampling procedure is described in detail in a previous study (Chapter 2). One variable of interest for evaluating the different model versions was the probability of three species coexistence P_3 . It gives an indication how robust the modelled coexistence was. If P_3 is small, the sampled parameter set only led to coexistence under very specific flood conditions, while a P_3 near 1 indicates that the sampled parameter set led to coexistence in almost all flood realisations with the same stochastic properties.

Other variables of interest were the ensemble statistics of hydrological variables. Therefore we evaluated the ensemble means of average total transpiration $\langle \overline{T}_{total} \rangle$ and depth to ground water $\langle \overline{z}_{unsat} \rangle$. Further we investigated the time fluctuation of the hydrologic variables by evaluating the ensemble means of the coefficient of variation of total transpiration $\langle CV_{T_{total}} \rangle$ and depth to ground water $\langle CV_{z_{unsat}} \rangle$.

3.3 Results

Table 3.2 shows in per cent how many of the sampled parameter sets led to $0.1 \le P_3 \le 0.5$ (less robust) and $P_3 > 0.5$ (robust) for models A-D. Robust three species coexistence was only modelled for models A, C, and D. Model B led only to less robust coexistence. Further, the total number of less robust parameter sets for models A, C, and D was one order of magnitude larger than for Model B.

Model	Less robust [%]	Robust [%]
А	0.21	0.033
В	0.01	0
С	0.20	0.007
D	0.42	0.038

Table 3.2. Relative frequency of less robust $(0.1 \le P_3 \le 0.5)$ and robust $(P_3 > 0.5)$ parameter sets.

In order to show how the models A, C, and D differ with regard to the water storage layers that are reached by the plant roots we compared typical time series of the depth to ground water for the most robust parameter sets and the corresponding root depths of each species (Fig. 3.1). The order of root depths was qualitatively the same for all three models because we constrained the parameter space according to the available ecological information (see Chapter 2). However, qualitative differences arose when comparing the water storage layers that are reached by roots of Ana Tree and Wild Tamarix (roots of Camel Thorn always reached the ground water). In models A and D the roots of both species were either located in the intermediate zone of the water storage where saturated and unsaturated conditions alternate frequently (Fig. 3.1a, left), or both were located in the unsaturated zone (Fig. 3.1a, middle; Fig. 3.1c, middle, right), or the roots of Wild Tamarix were located in the unsaturated and those of Ana Tree reached the ground water (Fig. 3.1a, right; Fig. 3.1c left). On the other hand, Fig. 3.1b depicts that in Model C the roots of Wild Tamarix were always located in the unsaturated zone, whereas the roots of Ana Tree always reached the ground water.

Next, we investigated, how models C and D differ with regard to species specific flood resistance (fr_i) (for Model A the flood resistance was the same for all species). For this, we plotted typical time series of the flood volume and the corresponding flood volumes where $fr_i = 0$ (Fig. 3.2). In Model C the species with the most elevated flood resistance was always the *Ana Tree* (Fig 3.2 upper row), whereas for Model D the order of flood resistance was different for each parameter set (Fig. 3.2 lower row).

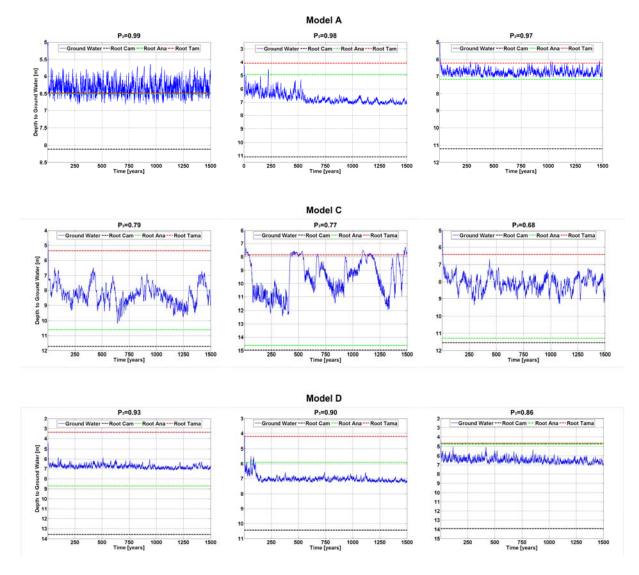


Figure 3.1. Time series of the depth to ground water (z_{unsat}) with corresponding root depths (z_{ri} , black denotes Camel Thorn, green Ana Tree, and red Wild Tamarix) for Model A (upper row), Model C (middle row), and Model D (lower row) and their most robust parameter sets.

In Fig. 3.3 we plotted typical time series of the reserve and green biomass for models A, C, and D. In both models A and D the reserve biomass of the populations was synchronised with disturbances by the flood but with larger fluctuations in Model D. On the other hand, in Model C the reserve biomass was more affected by the flood and two alternating stable states existed (Camel Thorn and Wild Tamarix, Ana Tree and Wild Tamarix).

In order to show how the models A, C, and D differ hydrologically we compared the histograms of ensemble means of CV (Fig. 3.4) of hydrologic variables (total transpiration, depth to ground water). In Model C the time fluctuation of total transpiration was larger (median 0.799) than in models A and D (0.258 and 0.295) (Fig. 3.4, left column). Less

pronounced was the difference in time fluctuation of the depth to ground water for models A, C, and D (median 0.025, 0.084, and 0.036) (Fig. 3.4, right column).

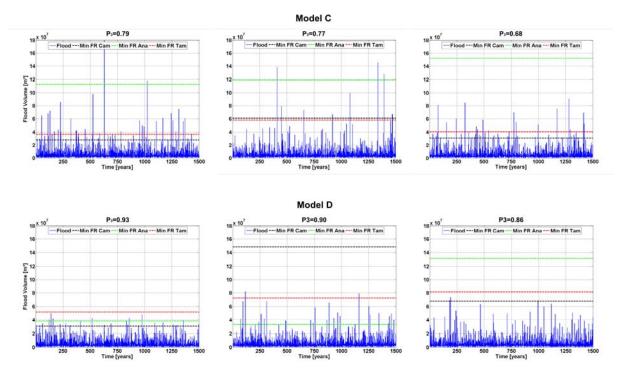


Figure 3.2. Time series of the flood volume (V_{Flood}) with corresponding flood volumes where flood resistances (fr_i , black denotes Camel Thorn, green Ana Tree, and red Wild Tamarix) are zero for Model C (upper row) and Model D (lower row) and their most robust parameter sets.

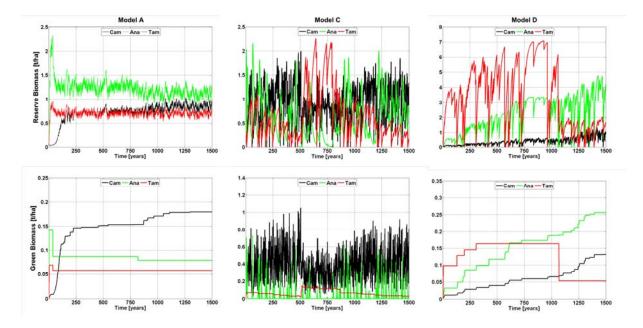


Figure 3.3. Typical time series of the reserve (upper row) and green biomass (lower row) for models A (left), C (middle), and D (right).

Fig. 3.5 shows how models A, C, and D were affected by a changed long term memory of the flood volume (by changing the Hurst-Exponent). The relative frequencies refer to the previously identified less robust ($0.1 \le P_3 \le 0.5$) and robust ($P_3 > 0.5$) parameter sets. In Model A the three species coexistence was little affected by change of the long term memory of the flood (Fig. 3.5, upper row), whereas in models C and D a changed long term memory affected species coexistence for both the less robust and the robust parameter sets (Fig. 3.5, middle and lower row).

3.4 Discussion

We applied an ecohydrological model framework and pattern-oriented modelling to assess different model versions regarding their ability to predict coexistence of three species as was observed in reality. The comparison between the observed and the simulated patterns acts as filter, which allows us to identify, whether a given model version and parameter combination allows coexistence. Further, in this study, two more observed ecohydrological patterns proved to be useful to constrain both the model structure and the parameter combination: (1) The species specific access to the unsaturated soil or the ground water storage. (2) The species specific vulnerability to the magnitude of flood events.

3.4.1 Coexistence pattern

In this study, models A, C, and D allow for robust coexistence (Table 3.2). The coexistence mechanisms in models A and C are described in detail in Chapter 2: In Model A the coexistence is based on both niche partitioning and trade-offs between growth rate and water stress ($w_{R,i}$ and ε_i in Eq. 3.5). This sensible balance is broken in Model B by introducing the phenology, which enhances the inter-specific competition and inhibits robust coexistence. In Model C the species specific flood resistance enables ecological differences in the response to the strength of flood events and compensates too strong advantages from the differences in the phenology, and thus enhances coexistence. In Model D the species specific vulnerability to the flood is integrated but it is not the driving mechanism for coexistence. Rather, it is the non-species specific phenology (all plants evergreen) that leads, similar to Model A, to a trade-off. However, in Model D, the trade-off is between species with low water use efficiency (growth rate) and water stress / flood sensitivity (mortality), and species with high

growth rate und mortality. For instances, a species with low growth rate and low flood sensitivity cannot take advantage of a disruptive flood event that reduces the biomass of a flood sensitive species, because this species compensates the damage by a high growth rate.

Therefore, Model C mostly represents ecosystems whose biomass dynamic is driven by the temporary availability of water that is resource and disturbance at the same time, leading to an allocation of niches, whereas Model A and D represent ecosystems whose biomass dynamic is more driven by the trade-off between water use efficiency and water stress / flood sensitivity of each species.

3.4.2 Ecohydrological patterns

Our results indicate that two other ecohydrological observed patterns can be used to prove the reliability of parameter combinations (which are potential ecosystems of the reality) and model structures with regard to the study site along the Kuiseb River. The first pattern is the water storage from which the three tree species take up the water. It is observed that Wild Tamarix mostly uses water from the unsaturated layer, whereas Camel Thorn and Ana Tree use a mixture of ground and soil water (Schachtschneider and February, 2007). In Model C, for each robust parameterisation, the roots of Wild Tamarix reach the unsaturated layer and those of Ana Tree and Camel Thorn reach the ground water (Fig. 3.1b), whereas Model A and D no such a clear pattern reveal (Fig. 3.1a,c). The second pattern concerns the species specific vulnerability to the magnitude of flood events. The spatial distribution of the three species regarding the distance to the active river channel (Ana Tree close to the active river course (Jacobson et al., 1995)) and their maximum height (Curtis and Mannheimer, 2005; Moser, 2006) indicate that Ana Tree is robust to flood events, whereas Camel Thorn and Wild Tamarix are rather vulnerable. The structure of Model C also supports this pattern by constraining the parameter combinations such that, for all robust parameterisations, the resulting flood resistance of Ana Tree is one order of magnitude larger than those of Camel Thorn and Wild Tamarix (Fig. 3.2a).

This illustrates that the two additional qualitative ecohydrological patterns reveal Model C as the most reliable model version regarding the study site along the Kuiseb River, whereas Model A and D are able to model the coexistence pattern but not the ecohydrological patterns.

3.4.3 Fluctuation of hydrological variables

Although the three models, leading to robust coexistence, differ in their structure and coexistence mechanisms, the ensemble statistics of mean transpiration and depth to ground water are surprisingly similar. This is probably owed to the fact that the hydrological model is the same in all model versions and already discussed in a previous study (see Chapter 2). Differences become apparent when considering the time fluctuations of hydrological variables such as transpiration and depth to ground water (Fig. 3.4) and its sensitivity to environmental change (Fig. 3.5).

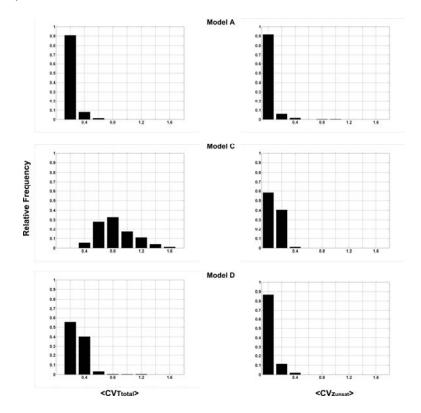


Figure 3.4. Histograms of ensemble means of CV total transpiration (left column) and depth to ground water (right column) of parameter sets with $P_3 \ge 0.1$ for A (upper row), C (middle row), and D (lower row).

The species specific phenology in Model C leads to temporal variability in the green biomass (Fig. 3.3) and, hence, to a temporally heterogeneous plant water uptake. Consequently, the average fluctuations in transpiration and depth to ground water are most elevated for Model C. On the other hand, the green biomass in Model A and D varies only little. The reason for this lies in the particular parameter combinations that comply with the coexistence pattern. The shape parameters of the sigmoid function (Eq. B1) describing the conversion rate from reserve to green biomass ($w_{G,i}$ in Eq. 3.4a) are combined in a manner that the resulting $w_{G,i}$ is

always close to zero and, consequently, the green biomass grows only if the ratio between available water and total reserve biomass (Eq. B1) is large. This, however, is only the case after extraordinary flood events, which refill the water storage and reduce the ecosystem biomass at the same time. This constraint is broken in Model C by introducing the phenology of Camel Thorn and Ana Tree, which allows parameter combinations to comply with the coexistence pattern although the green biomass grows with a rate much larger than zero.

When considering the sensitivity of the model versions against a change in cyclicity of periods with high and low floods (Hurst-Exponent in Eq. 3.3) our previous study is supported by the recent results: Both models with species specific vulnerability to the flood (Model C and D) reveal strong sensitivity against a change in the hydrological conditions and, hence, a loss of coexistence. On the other hand, when neglecting this species specific property (Model A) the found parameter combinations are rather robust against changes of the hydrological long term memory (Fig. 3.5).

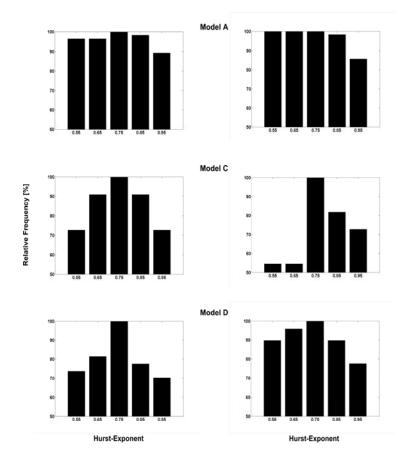


Figure 3.5. Results of forward simulations. Relative frequency refers to the less robust (left column) and robust parameter sets (right column) identified by the parameter sampling (Hurst-Exponent = 0.75) for models A (upper row), C (middle row), and D (lower row).

3.4.4 Implication for management decisions

Integrating more knowledge in a model does not automatically lead to more realistic modelling results. On the other hand, models can give satisfactory results, but maybe for the wrong reason (Arnold et al., 2009). This is important, when applying a model for testing management strategies under the uncertainty of future climatic conditions, e.g. the uncertainty in stochastic flood events. Model A and D give satisfactory results considering the pattern of coexistence. However, they fail when comparing the model outcomes to ecohydrological patterns such as species specific access to the unsaturated soil / ground water storage or the species specific sensitivity to flood events. Model C is the only model version, which supports all three patterns observed along the Kuiseb River. Therefore, from the given model versions and for the application as potential management tool, we suggest Model C to be the most reliable model version along the study of the Kuiseb River.

3.5 Conclusions

The modelling of three species coexistence along the water limited ephemeral Kuiseb River is challenging because ecohydrological feedbacks have to be implemented in an appropriate way. Applying pattern-oriented modelling allows the identification of different model structures and parameter combinations that are potential ecosystems of the reality. The subsequent process of changing the model structure and comparing the outcomes with observed ecohydrological patterns eventually leads to a reliable model structure and corresponding parameter combinations. Nevertheless, less reliable model versions can be investigated with regard to the influence of different underlying coexistence mechanisms to the fluctuations of hydrological variables. Our study emphasises that the species specific response to the flood disturbance enhances elevated fluctuations of hydrological variables such as transpiration and depth to ground water. However, this phenomenon is amplified by integrating the observed phenology, because the species specific time of leaf shedding leads to a temporally heterogeneous plant water uptake. Considering that the model version that integrates both species specific flood resistance and phenology is the only model that complies with three observed qualitative patterns (coexistence and ecohydrological patterns) we conclude that, at this state, Model C is the most reliable model involving the critical processes along the Kuiseb River. This illustrates that qualitative patterns are appropriate to constrain both the model structure and the parameter combinations and, hence, helps to reveal

driving system mechanisms that are essential when applying the model as management support tool.

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Chapter 4

Integrated management strategies for sustainable water use along ephemeral rivers under severe uncertainty of future flood regimes

4.1 Introduction

Water controlled ecosystems are characterised by strong feedbacks between ecological and hydrological processes (Rodriguez-Iturbe and Proporato, 2004). Particularly along riparian corridors of ephemeral rivers flow regulation and water diversions can create different hydrological states (Nagler et al., 2009; Stromberg et al., 2009). As a result, the structure of the vegetation can change as well, for instance towards more tolerant and competitive species (e.g. salt tolerant Tamarix spp. (Gaskin and Schaal, 2002)), or towards a pioneer species dominated ecosystem, or to a changed age structure, or from perennial to annual plant communities (Stromberg et al., 2009). Ecosystems with strong ecohydrological interactions, such as ephemeral rivers, have been subject to investigations in terms of management implications before. Stromberg et al. (1993) applied empirical models using hydrological (depth to ground water) and ecological (structural parameters such as water potential of shoots, canopy height, leaf area index) data to reveal implications for the management of natural resources in riparian ecosystems. They suggest to use the water potential of shoots as warning detector for plant water stress and they emphasise the restriction of water consumption as soon as plant water stress occurs. However, with regard to financial costs and time efforts plant physiological variables are critical to measure in the field. Moreover, if management activities on the water resource have long lasting effects on the ecosystem it is questionable if an abrupt stop of these activities is effective and appropriate to preserve the vegetation structure (e.g. species composition). Such suggestions emphasise the need for models that consider the feedbacks between the water resource and the vegetation structure. Only when ecohydrological feedbacks are explicitly modelled the performance of management strategies can be quantified that consider both the regulation of water extraction

and vegetation structure. Otherwise, when neglecting these feedbacks the fundamental dynamics of water limited ecosystem is omitted and, consequently, management strategies are suggested that are less suitable to sustainably exploit ground water while conserving the natural vegetation structure.

But it is not only the explicit implementation of ecohydrological feedback mechanisms that is important. Particularly in the face of climate change, the management strategies have to be applicable to a wide range of possible flood regimes, i.e. they have to be robust to the uncertainty of future flood regimes. For ecosystems along ephemeral rivers the robustness of management strategies is related to two types of uncertainty: (1) The inherent uncertainty in the occurrence of flood events, which is driven by unpredictable rainfall events. This unpredictability can be described with a stochastic process characterised by parameters such as frequency, duration or short/long term memory of flood events. (2) The uncertainty in parameters describing the (stochastic) flood regimes. This uncertainty arises due to the scarce information about the runoff data along ephemeral rivers because often monitoring systems are rare and the temporary character of the flood events hinders the measurement of large time series. Moreover, even if information about the ephemeral runoff would be sufficient to estimate reliable flood regime parameters it is a weak indicator for future runoff because arid areas are prone to fundamental change of future environmental conditions. If ecosystems along ephemeral rivers are supposed to be managed adequately both types of uncertainty have to be considered explicitly because they influence the robustness of management strategies.

The inherent uncertainty in the flood regime was subject in Chapter 2. We parameterised several model versions within a conceptual ecohydrological model framework by evaluating the ability of each version to reproduce an observed vegetation pattern: coexistence of three tree species. Therefore, we run each parameter combination several times with several realisations of the same flood regime. Here we focus on the uncertainty regarding future flood regimes.

Often there is an information gap between what is known and what needs to be known to make competent management decisions, e.g. under the uncertainty of future flood regimes. One powerful approach to master this challenge is the information-gap (info-gap) decision theory that can quantify this uncertainty and, moreover, facilitates the estimation of the robustness of management decisions under uncertainty. The procedure by which an info-gap model is formulated is different from the method for specifying a probabilistic model,

particularly in the treatment of rare and extreme events (Ben-Haim, 1994, 2006, 2004). Further, contrary to distribution based theories (probability theory or fuzzy logic theory), where probability density or membership functions are applied, in info-gap models the events are organised into clusters (Ben-Haim, 2006). The rules by which the events occur are known incompletely.

Decision-making involves trade-offs (Regan et al 2005). In this study we investigate the trade-off between ecological and human performance requirements that arise when both the ecosystem (especially the vegetation) and people share the same water source along an ephemeral river. We apply a previously tested model version (Model C) developed within an ecohydrological model framework (Chapter 2). The model complies with three qualitative patterns that are observed along the ephemeral Kuiseb River in Namibia: (1) The coexistence of three tree species, (2) the species specific access to the unsaturated soil or ground water storage, and (3) the species specific vulnerability to the magnitude of flood events. Therefore, we believe that, at this state, the applied model version is most reliable model involving critical processes along the Kuiseb River. Further, the model is characterised by a high sensitivity to changes in the duration of disturbance events such as dry periods and disruptive floods (Chapter 3, Fig. 3.5) and fluctuations in hydrological variables are elevated, such as transpiration and depth to ground water (Chapter 3, Fig. 3.4).

The objective of this study is to assess a variety of management strategies regarding their performance under different (artificial) eco-hydrological systems and under uncertainty in the future (stochastic) flood regimes. In particular, we investigate the management strategies in terms of their ability to sustainably exploit the ground water resource while preserving the vegetation structure (coexistence of three tree species). In addition to human and ecological performance, we also consider the robustness and opportuneness of management strategies. The first refers to the greatest level of uncertainty that still meets the pre-determined performance requirements, whereas the second refers to the least level of uncertainty, which entails the possibility of unexpected but potentially favourable performance. We finish the study with some general conclusions on the design of sustainable management strategies in strongly coupled ecohydrological systems.

4.2 Methods and materials

4.2.1 Study site

The study site covers an area of approximately 18 km² and is located in the Kuiseb catchment (~ 15,500 km² (Jacobson et al., 1995)) in Namibia. The Kuiseb River arises from the Khomas Hochland (~ 2000 m in elevation) and runs westward through the escarpment into the Atlantic Ocean. The rainy season is during the southern hemisphere summer between January and April (Henschel et al., 2005). This study is concerned with the arid middle reach of the Kuiseb River, where rain is exceptional, and water arrives mainly during the floods in the ephemeral river channel. Near this channel, riparian vegetation has established. Although the channel does not contain water for most of the year, it supplies a shallow ground water storage with water during times of flood and thus creates a living environment for riparian vegetation. The flood is influenced by upstream farm dams and the ground water table is influenced both by plants and human consumption.

Ecosystem

The ecosystem is a fragile system where species coexistence is linked to the dynamics of the hydrosystem, in particular to the ground water table (Arnold et al., 2009). Vegetation around the Kuiseb River consists to 80% of only three coexisting species: Camel Thorn (*Acacia erioloba*), Ana Tree (*Faidherbia albida*) and Wild Tamarix (*Tamarix usneoides*) (Theron et al., 1980). The known differences between the three species are described in Chapter 2. The riparian forest exists since many decades and is often referred to as linear oasis because it provides food and water for humans and animals in an otherwise arid area (Jacobson et al., 1995), e.g. the rural Topnaar community lives along the middle Kuiseb River and depends on the stability and resilience of the ecosystem by farming with goats and cattle (Moser, 2006).

Hydrosystem

The study site is located in a hyperarid area with little annual rainfall (< 20 mm) and high potential evaporation (1700 to 2500 mm (Botes et al., 2003)). The ground water is recharged by temporary floods that are caused by rainfall in the upper Kuiseb catchment (Khomas Hochland). We estimated the statistical properties of the flood regime such as short/long term memory and average of the flood volume in Chapter 2 by analysing the time series from 1981 to 2006 (Fig. 2.3). However, because of the temporary nature of the floods these estimates, and consequently the resulting flood volume, are highly uncertain. Further, the

flood regime is prone to changes in future caused by climate change and/or human impacts such as the building of upstream farm dams. When managing the ecohydrological system of the middle section along the Kuiseb River the uncertainty in future flood events can lead to failure or unexpected success, which both can be evaluated by using an information gap model.

4.2.2 Information gap model

In this study the uncertainty is related to the parameters characterizing the flood regime, in particular the short/long term memory and the average of the flood volume. However, the processes that modify these parameters are complex and poorly understood due to missing sufficient long term data of the flood regime. Along the Kuiseb River the probability distribution functions that underlie the flood regime parameters are unknown. Hence, the uncertainty cannot be modelled with moments of probability distributions, i.e. we face true Knightian uncertainty (Knight, 1921; Stranlund and Ben-Haim, 2008). Even if plenty information about the past flood regime would be available, it is still prone to changes (e.g. caused by the climate change or human impacts) and so a weak indication of the future (Ben-Haim, 2006). Therefore, we are unable to specify a probabilistic model for the uncertainty in the flood regime parameters and, instead, formulate a non-probabilistic quantification of uncertainty: the info-gap model of uncertainty. It was invented by Ben-Haim (2001) to assist decision-making when there are severe knowledge gaps and when probabilistic models of uncertainty are unreliable, inappropriate, or unavailable (Regan et al., 2005). Info-gap models express uncertainty at two levels (Ben-Haim, 2000): (1) the uncertainty parameter α expresses the information gap between what is known (flood regime parameters estimated in Chapter 2) and what needs to be known (the exact values of future flood regime parameters) for an ideal management decision. The greater α , the greater is the range of possible variation. (2) α is unknown, i.e. the horizon of uncertain variation is unbounded.

Information-gap methodology requires three distinct elements: (1) a system model, (2) a performance requirement, and (3) an uncertainty model (Ben-Haim, 2006; McDonald-Madden et al., 2008). Moreover, since parameter uncertainty may be either pernicious or propitious the three elements can be used to estimate the robustness and the opportuneness of a management decision (Ben-Haim, 2006).

The system model is a mathematical representation of the system under study that produces a measure of management success (performance). It summarizes what the analyst believes to be true and important about the system (Regan et al., 2005). To simulate the ecohydrological processes along the middle section of the Kuiseb River we applied a previously developed model version within a conceptual ecohydrological model framework (Model C from Chapter 2 and Chapter 3), which links ecological and hydrological processes.

The performance requirement or degree of success of a decision can be assessed by a threshold referred to as "reward", which is usually a value below or above which the performance of a decision is unacceptable (Ben-Haim, 2006). When assessing the robustness of a decision the performance of the system model should not fall below the critical reward r_c . On the other hand, when assessing the opportuneness of a decision the performance should exceed the windfall reward r_w . In any case r_w is usually much greater than r_c (Ben-Haim, 2006).

The uncertainty model describes what is unknown about parameters in the system model (Regan et al., 2005). However, in this study the uncertainty refers to the stochastic properties of the flood regime, hence, here the uncertainty model describes what is unknown about the flood regime parameters (Table 4.1).

Flood Parameter	Nominal Value	
\widetilde{d}	0.25	
$\widetilde{\mu}_{\scriptscriptstyle Flood}$	3,269,000 m ³	
$\widetilde{\chi}_1$	0.192	
\widetilde{arphi}_1	0.8969	

Table 4.1. Nominal values of the flood parameters estimated in Chapter 2.

When parameter uncertainty is adverse it entails the possibility of failure. On the other hand, when being favourable it entails the opportunity for sweeping success. Both aspects of uncertainty can be quantified by info-gap decision theory: The robustness function expresses the immunity to failure, while the opportuneness function expresses the immunity to windfall gain. Both functions enable a decision maker to formulate preferences on the options in the light of the uncertainties. Depending on the aversion to failure a decision maker will concentrate more on the robustness or the opportuneness of a decision (Ben-Haim, 2006).

4.2.3 System model

For this study, we applied a previously tested model version (Model C from Chapter 2 and Chapter 3) of an ecohydrological model framework, which differentiates the plant species biomass into photosynthetically active green (G) and inactive reserve biomass (R). We assume that floods take place in the middle of the vegetation period, i.e. after the sprouting of the green biomass but before the feed back to the reserve biomass. Therefore, floods are modelled as additional mortality to the green biomass in the respective year. These assumptions result in the following equations:

$$G_i(t) = (1 - \varepsilon_i(t)) \cdot G_i(t-1) + w_{G,i}(t) \cdot R_i(t-1), \text{ for photosynthetically active season,}$$
(4.1a)

$$G_i(t) = (1 - ls_i) \cdot (1 - \varepsilon_i(t)) \cdot G_i(t - 1)$$
, for photosynthetically dormant season, (4.1b)

$$R_{i}(t) = fr_{i}(t) \cdot \{ [1 - m_{R,i} \cdot (1 + \varepsilon_{i}(t))] \cdot R_{i}(t - 1) + w_{R,i} \cdot G_{i}(t) \},$$
(4.2)

where the index *i* denotes the reference to a species, $w_{G,i}(t)$ is the conversion rate from reserve into green biomass, $w_{R,i}$ the conversion rate from green into reserve biomass, $m_{R,i}$ is the mortality of the reserve biomass, $\varepsilon_i(t)$ is the unitless water stress and $fr_i(t)$ is the unitless flood resistance. The three parameters conversion rate $w_{G,i}(t)$, water stress $\varepsilon_i(t)$, and flood resistance $fr_i(t)$ are characteristics of the tree species that are dynamically linked to the hydrosystem along the Kuiseb River and described in more detail in Chapter 2.

The stochastic flood volume $V_{Flood}(t)$ was generated by a fractional autoregressive moving average model (FARIMA(p,d,q), $p,q \in N$) (Kokoszka and Taqqu, 1995; Stoev and Taqqu, 2004) to generate time series with both short- and long-term dependence structures that are present in many hydrologic processes (Montanari et al., 1997; Hurst, 1951). The short term dependence structure is determined by the real polynomials X_p and Ψ_q of degree p and q. The autoregressive part of FARIMA is represented by the coefficients of X_p ,

$$X_{p}(\lambda) = 1 - \chi_{1}\lambda - \chi_{2}\lambda^{2} - \dots - \chi_{p}\lambda^{p}, \qquad (4.3)$$

where $X_1(\lambda) = 1 - 0.192\lambda$ and λ is a random number drawn from a normal distribution with mean 0 and standard deviation 1. The moving average part is represented by the coefficients of Ψ_q :

$$\Psi_q(\lambda) = 1 - \psi_1 \lambda - \psi_2 \lambda^2 - \dots - \psi_q \lambda^q , \qquad (4.4)$$

with $\Psi_1(\lambda) = 1 - 0.8969\lambda$. The long term behaviour is governed by *d* that is an arbitrary fractional real number:

$$0 < d < 1 - 1/\omega$$
, and $1 < \omega < 2$. (4.5)

The relationship between *d* and the Hurst-Exponent *H* is as follows:

$$H = d + 1/\omega \,. \tag{4.6}$$

We assumed *H* to be 0.75 (with $\omega = 1.99$ and d = 0.25), and p = q = 1. The time series were generated with FARIMA(p=1,d=0.25,q=1) and adjusted to the observed mean annual flood volume $\mu_{Flood} = 3,269,000 \text{ m}^3$, and thus yielding

$$V_{Flood}(t) = e^{(FARIMA(1,0.25,1) + \log(\mu_{Flood}))}.$$
(4.7)

The applied model version is characterised by a high sensitivity to changes in the duration of disturbance events such as dry periods and disruptive floods. Further, for many possible ecosystems, fluctuations in hydrological variables are elevated, such as transpiration and depth to ground water.

4.2.4 Performance and requirements

In this study the performance measures included two attributes because we assessed the management performance with regard to performance of ecology (biodiversity) and secured water supply for humans.

In Chapter 2 the health of an ecosystem with parameterisation Ω_e was given by $P_{3,e} = f(\Omega_e)$, which shows the ability of the parameter combination Ω_e to model three species coexistence. If $P_{3,e}$ is small, Ω_e only led to the observed biodiversity under very specific flood conditions, while a $P_{3,e}$ near 1 indicates that the parameter combination led to three species coexistence in almost all flood realisations with the same stochastic properties. In this study we assessed all parameter sets with $P_{3,e} \ge 0.03$ evaluated in Chapter 2 and express ecological performance as relative number of parameter sets with $P_{3,e} \ge 0.1$:

$$N_{0.1} = \frac{\#B(P_{3,e} \ge 0.1)}{\#B(P_{3,e} \ge 0.03)},$$
(4.8)

where #B is the total number of parameter sets.

The ecosystem along the Kuiseb River is forced by the hydrology, in particular it is the stochasticity of the flood regime that forces the ecosystem most of all by influencing the growth and mortality rates of the species (Arnold et al., 2009). This stochasticity can be either adverse or favourable with regard to the biodiversity of the ecosystem. Therefore, we evaluated $N_{0,1}$ for the worst and the best case in the unmanaged system to estimate the critical and the windfall reward for the ecology in a managed system:

$$r_c^{eco} = N_{01}^c = 19.3\%$$
, and (4.9a)

$$r_w^{eco} = N_{0.1}^w = 72.4\%, \tag{4.9b}$$

That is, when measuring the robustness of a decision, we require the minimum acceptable ecological performance to be no less than the worst case under unmanaged conditions (Eq. 4.9a). On the other hand, when measuring the opportuneness of a decision, we require the ecological performance to be larger than the best case under unmanaged conditions (Eq. 4.9b).

For assessing the ecohydrological management performance in terms of human utility, we assumed that humans desire a reliable water supply from the ground water storage. The secured water supply is given as long as the ground water table does not fall below a certain threshold. Otherwise the salinity of the lifted water would be too elevated and ground water pumping must be stopped. Therefore, we counted the number of time steps where ground water pumping was secured, i.e. the ground water table did not fall below the given threshold (section 4.2.9). We express secured water supply for humans as:

$$P_{\rm sec}^{0.25} = \frac{\min \sum p_{\rm sec}(\Omega_e, \Omega_h)}{\tau},\tag{4.10}$$

where p_{sec} is the number of time steps with secured water supply for each ecological parameter set $\Omega_{\rm e}$ and each hydrological parameter set $\Omega_{\rm h}$, τ is the total number of time steps, and $P_{\rm sec}^{0.25}$ denotes the 0.25 percentile of time steps with secured water supply for all parameter sets $\Omega_{\rm e}$ and $\Omega_{\rm h}$. (The variety of hydrological parameter sets is a consequence of the uncertainty model. Their sampling procedure is described in section 4.2.8.)

We set the critical reward for the secured water supply for humans at

$$r_c^{wat} = P_{\rm sec}^{0.25,c} = 0.95 \,, \tag{4.11}$$

that is, when measuring the robustness of a decision, we require the minimum acceptable ground water supply to be given in no less than 95% of the seasons. Since r_w is usually much greater than r_c (Ben-Haim, 2006) we did not measure the opportuneness for human utility because r_c^{wat} is already a highly demanded performance criterion.

4.2.5 Uncertainty model

We know that the stochastic properties of the flood regime (Eq. 4.7) are uncertain, and that there are a range of possible values of χ_1 , ψ_1 , d and μ_{Flood} that will lead to different time series of the flood regime.

We assume that uncertainty in the flood regime parameters may be represented by intervals of unknown size around each parameter (envelope-bound info-gap model (Ben-Haim, 2006)). Hence, the uncertainty model can be expressed as:

$$U(\alpha) =$$

$$\{\chi_{1},\psi_{1},d,\mu_{Flood}: \left|\frac{\chi_{1}-\widetilde{\chi}_{1}}{\widetilde{\chi}_{1}}\right| + \left|\frac{\psi_{1}-\widetilde{\psi}_{1}}{\widetilde{\psi}_{1}}\right| + \left|\frac{d-\widetilde{d}}{\widetilde{d}}\right| + \left|\frac{\mu_{Flood}-\widetilde{\mu}_{Flood}}{\widetilde{\mu}_{Flood}}\right| \le \alpha\}, \alpha \ge 0,$$

$$(4.12)$$

where α is the horizon of uncertainty. The larger the value of α , the greater the range of unknown variation of the actual values χ_1 , ψ_1 , d and μ_{Flood} around the nominal values $\tilde{\chi}_1$, $\tilde{\psi}_1$, \tilde{d} and $\tilde{\mu}_{Flood}$ (Table 4.1). Since the value of α is not known $U(\alpha)$ is an unbounded family of nested sets of values whose deviation from the nominal values is nowhere greater than α . The envelope-bound model enables us to vary the actual values at different rates around the centre of the 4d-hypersphere given by the nominal values. If $\alpha = 0$, then $\tilde{\chi}_1$, $\tilde{\psi}_1$, \tilde{d} and $\tilde{\mu}_{Flood}$ are the only possible values in absence of uncertainty and $U(0) = \{\tilde{\chi}, \tilde{\psi}_1, \tilde{d}, \tilde{\mu}_{Flood}\}$, i.e. the nominal model is the actual model. The parameter sampling procedure of the actual values around the 4d-hypersphere is described in section 4.2.8.

4.2.6 Robustness and opportuneness function

A risk averse decision maker will tend to concentrate on the robustness function. That is, the decision maker desires immunity to uncertainty with regard to failure. The robustness function $\hat{\alpha}$ of a management decision m_i expresses the greatest level of uncertainty α that still meets the pre-determined critical reward, i.e. a large value of $\hat{\alpha}$ is desirable. Here, the critical

reward was given by $N_{0.1}^c = 19.3\%$ for ecological performance and $P_{sec}^{0.25,c} = 0.95$ for secured ground water supply. The robustness functions for these two attributes were formulated as:

$$\hat{\alpha}(m_i, N_{0,1}^c) = \max\{\alpha : \min N_{0,1}^{man}[m_i] \ge N_{0,1}^c\}, \text{ and}$$
(4.13a)

$$\hat{\alpha}(m_i, P_{\text{sec}}^{0.25,c}) = \max\{\alpha : \min P_{\text{sec}}^{0.25}[m_i] \ge P_{\text{sec}}^{0.25,c}\}.$$
(4.13b)

A risk loving decision maker will tend to prefer the opportuneness function, since the decision maker hopes that the uncertainty will grant an unexpected reward. The opportuneness function $\hat{\beta}$ expresses the least level of uncertainty which entails the possibility of sweeping success, i.e. a small value of $\hat{\beta}$ is desirable because it reflects the opportunity that a good performance is possible even in the presence of little parameter uncertainty. The opportuneness function for ecological performance was formulated as:

$$\hat{\beta}(m_i, N_{0,1}^w) = \min\{\alpha : \max N_{0,1}^{man}[m_i] \ge N_{0,1}^w\}.$$
(4.14)

4.2.7 Parameterisation and implementation

.

The sampling of the ecological parameter sets Ω_e was already done in Chapter 2 to investigate uncertainty in the ecological model with regard to the model output. These parameter sets can be considered as potential ecosystems that could have been existed under the past flood regime. In this study we used the ecological parameter sets to investigate the uncertainty in future flood regimes with regard to the performance of management decisions.

We sampled the hydrological parameter sets Ω_h from the surface of a 4d-hypersphere whose centre is given by the nominal values $\tilde{\chi}_1$, $\tilde{\psi}_1$, \tilde{d} and $\tilde{\mu}_{Flood}$, estimated in Chapter 2 (Table 4.1). Depending on the horizon of uncertainty α we sampled the actual values χ_1 , ψ_1 , d, μ_{Flood} as follows:

$$\chi_1 = \tilde{\chi}_1 + \tilde{\chi}_1 \cdot \alpha \cdot \cos \rho \cdot \sin \nu_1 \cdot \sin \nu_2, \qquad (4.15a)$$

$$\psi_1 = \widetilde{\psi}_1 + \widetilde{\psi}_1 \cdot \alpha \cdot \sin \rho \cdot \sin \nu_1 \cdot \sin \nu_2, \qquad (4.15b)$$

$$d = \tilde{d} + \tilde{d} \cdot \alpha \cdot \cos \upsilon_1 \cdot \sin \upsilon_2 \text{, and}$$
(4.15c)

$$\mu_{Flood} = \widetilde{\mu}_{Flood} + \widetilde{\mu}_{Flood} \cdot \alpha \cdot \cos \upsilon_2, \qquad (4.15d)$$

where $\rho \in (0,2\pi)$ and $\upsilon_1, \upsilon_2 \in (0,\pi)$ are random numbers drawn from a uniform distribution.

We used Model C as presented in Chapter 2: For each ecological parameter set Ω_e with $P_{3,e} \ge 0.03$ evaluated in we run the model with 100 realizations of stochastic identical flood regimes given by the parameter set Ω_h . The parameter set Ω_h was sampled by (Eq. 4.15a-d) and depended on the uncertainty horizon α . After each run we checked the simulation for three species coexistence, i.e. the average reserve biomass during the last 1000 years (2000 time steps) must exceed the reserve biomass necessary to maintain 10 adult individuals of average size of each species. If three species coexistence was given we continued the simulation for another 500 years (1000 time steps) but now with a given management strategy (Table 4.2 and 4.3).

To evaluate the performance of the management decision with regard to the ecological requirement we checked the simulation again for three species coexistence during the last 500 years and evaluated the minimum (for robustness) or maximum (for opportuneness) value of $P_{3,e}$ of all parameter sets Ω_h . A management decision was robust at uncertainty level α if the relative number of parameter sets with $P_{3,e} \ge 0.1$ in a managed system ($N_{0,1}^{man}$) was no less than the critical threshold ($N_{0,1}^e = 19.3\%$). On the other hand a decision was opportune at the least level of uncertainty which facilitated the exceeding of the windfall reward ($N_{0,1}^w = 72.4\%$).

To evaluate the performance of the management decision with regard to the human requirement we recorded the minimum number of time steps where ground water pumping was secured (p_{sec}), i.e. the depth to ground water did not exceed 12 m, of all parameter sets $\Omega_{\rm h}$. A decision was robust at uncertainty level α if the 0.25 percentile of all p_{sec} was no less than 950 per 1000 time steps, i.e. $P_{sec}^{0.25,c} \ge P_{sec}^{0.25,c}$ with $P_{sec}^{0.25,c} = 0.95$.

4.2.8 Management scenarios

The management strategies applied in this study are summarised in Table 4.2 and 4.3. They were all based on a maximum ground water depth of 12 m and a ground water extraction rate of 25 m³/ha·season. For strategies m_1 , m_2 and m_3 the ecosystem was not regulated, but plant water stress led to a pumping stop for Strategy m_2 and additionally to artificial irrigation of the upper soil layer for Strategy m_3 . These three strategies only consider the regulation of the hydrosystem but not that of the ecosystem. For the other strategies additional ecosystem regulation was integrated - they were applied once a year (denoted by index *a*) or every ten

years (denoted by index *b*). Those ecohydrological management strategies were either flexible by regulating the most dominant species ($m_{4a,b}$) or inflexible by working with a fixed regulation rate for a specific plant species (m_{5a} - m_{7b}).

Table 4.2. Management strategies applied in this study including only hydrological management. We restricted the maximum depth to ground water to 12 m for each scenario. The ground water extraction was $25 \text{ m}^3/\text{ha}$ ·season.

Strategy m_i	Hydrological management
1	Standard (Maximum ground water depth 12 m, extraction rate 25 m ³ /ha ⁻ season)
2	Pumping stop when at least one species suffers from water stress (Stromberg et al., 1993)
3	Artificial irrigation (25 m ³ /ha·season) when at least one species suffers from water stress

Table 4.3. Management strategies applied in this study including ecological management. We restricted the maximum depth to ground water to 12 m for each scenario. The ground water extraction was 25 m³/ha·season.

Strategy <i>m_i</i>	Ecological management
4a	Reduction of largest biomass to 2 nd largest (annually)
4b	Reduction of largest biomass to 2 nd largest (every 10 years)
5a	Reduction of Wild Tamarix by 10% (annually)
5b	Reduction of Wild Tamarix by 10% (every 10 years)
6a	Reduction of Camel Thorn by 10% (annually)
6b	Reduction of Camel Thorn by 10% (every 10 years)
7a	Reduction of Ana Tree by 10% (annually)
7b	Reduction of Ana Tree by 10% (every 10 years)

4.3 Results

In Fig. 4.1 we plotted the robustness performance curves for the ecology (Fig. 4.1a) and the water supply (Fig. 4.1b). These curves give an impression about the immunity of each decision to failure. By applying the robustness functions $\hat{\alpha}(m_i, N_{0.1}^c)$ (Eq. 4.13a) and $\hat{\alpha}(m_i, P_{sec}^{0.25,c})$ (Eq. 4.13b) the greatest level of uncertainty α that still meets the pre-determined

critical rewards $N_{0.1}^c$ and $P_{\text{sec}}^{0.25,c}$ of a management decision m_i can be evaluated. For a risk averse decision maker, of course, a large value of $\hat{\alpha}$ is desirable. In terms of ecological performance and with the given ecological performance requirement $N_{0.1}^c = 19.3\%$ only three strategies resulted in a robustness of $\hat{\alpha}(m_i, N_{0.1}^c) > 0\%$ (Table 4.4). The most robust strategy was m_{4a} with $\hat{\alpha}(m_{4a}, N_{0.1}^c) = 28\%$. In terms of secured water supply and with the given performance requirement $P_{\text{sec}}^{0.25,c} = 0.95$ the management strategies were more robust, often reaching a robustness of $\hat{\alpha}(m_i, P_{\text{sec}}^{0.25,c}) > 100\%$, except for strategies m_{4a} and m_{6a} , resulting in low robustness of $\hat{\alpha}(m_{4a}, P_{\text{sec}}^{0.25,c}) = 11\%$ and $\hat{\alpha}(m_{6a}, P_{\text{sec}}^{0.25,c}) = 14\%$.

Table 4.4. Results for ecological (Eq. 4.13a) and human (Eq. 4.13b) robustness $(\hat{\alpha}(m_i, N_{0.1}^c = 19.3\%)$ and $\hat{\alpha}(m_i, P_{sec}^{0.25,c} = 0.95)$) and ecological opportuneness (Eq. 4.14) $(\hat{\beta}(m_i, N_{0.1}^w = 72.4\%))$. Large values are desirable for robustness and small values for opportuneness.

Strategy <i>m_i</i>	$\hat{\alpha}(m_i, N_{0.1}^c)$	$\hat{\alpha}(m_i, P_{\text{sec}}^{0.25, c})$	$\hat{\beta}(m_i, N_{0.1}^w)$
1	0%	> 100%	0%
2	0%	0%	2%
3	0%	0%	1%
4a	28%	11%	0%
4b	20%	48%	0%
5a	5%	> 100%	0%
5b	0%	> 100%	0%
6a	0%	14%	> 100%
6b	0%	> 100%	8%
7a	0%	> 100%	> 100%
7b	0%	> 100%	10%

Further, in Fig. 4.2 we plotted the opportuneness performance curves for the ecology. These curves allow for assessing the strategies with regard to the opportunity for unexpected but potentially favourable ecological performance. By applying the opportuneness function $\hat{\beta}(m_i, N_{0,1}^w)$ (Eq. 4.14) the least level of uncertainty can be evaluated which entails the

possibility of sweeping success, i.e. a small value of $\hat{\beta}$ is desirable. With the given ecological performance requirement $N_{0.1}^w = 72.4\%$ all strategies resulted in extremely low values around $\hat{\beta}(m_i, N_{0.1}^w) = 0\%$, except Strategy m_{6a} reaching an opportuneness of $\hat{\beta}(m_i, N_{0.1}^w) > 100\%$, indicating a very low possibility of unexpected ecological performance in the face of severe flood regime uncertainty.

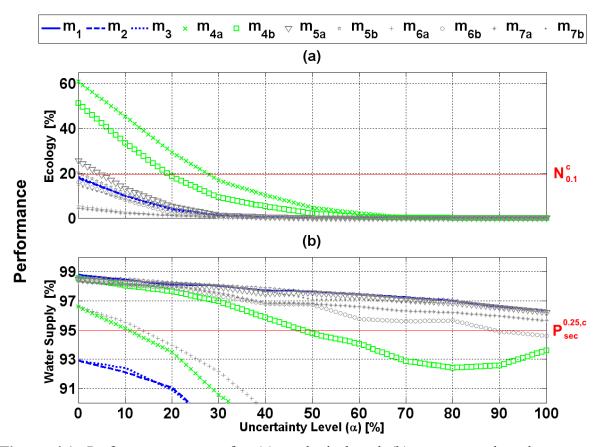


Figure 4.1. Performance curves for (a) ecological and (b) water supply robustness of management decision m_i . The red lines denote the ecological $(N_{0.1}^c)$ and water supply $(P_{sec}^{0.25,c})$ performance requirements (section 4.2.4) below which the performance of a decision is unacceptable. Blue are the purely hydrological, green the flexible ecohydrological and grey the inflexible ecohydrological strategies (Section 4.2.8 and Table 4.2 and 4.3).

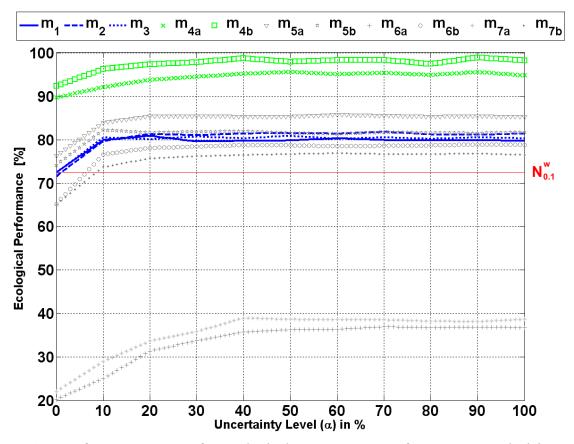


Figure 4.2. Performance curves for ecological opportuneness of management decision m_i . The red lines denote the ecological performance requirement $N_{0.1}^w$ (section 4.2.4) which is desired to be exceeded, otherwise the decision is not opportune to sweeping success. Blue are the purely hydrological, green the flexible ecohydrological and grey the inflexible ecohydrological strategies (Section 4.2.8 and Table 4.2 and 4.3)

In order to show which management strategies comply with both ecological and water supply requirements we plotted the ecological versus water supply performance plane (Fig. 4.3) for the robustness functions. The plane is divided into four segments representing the areas where (1) only secured water supply for humans, (2) both secured water supply and ecological performance, (3) only ecological performance, or (4) neither the one nor the other performance fulfil the respective requirements (critical rewards). The plane illustrates that, with the given critical rewards, only three strategies (m_{4a} , m_{4b} , m_{5a}) were appropriate to fulfil both water supply and ecological performance requirements at the same level of uncertainty. Further, Strategy m_{4b} was the strategy with the greatest part located in the second segment.

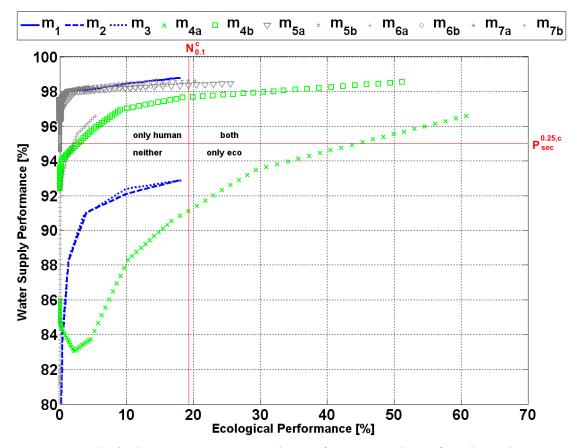


Figure 4.3. Ecological versus water supply performance plane for the robustness of management decision m_i . The red cross lines denote the ecological $(N_{0.1}^c)$ and water supply $(P_{sec}^{0.25,c})$ performance requirements (section 4.2.4) below which the performance of a decision is unacceptable. Consequently, the plane is devided into four segments representing the areas where only human utility, both human and ecological utilities, only ecological utility, or neither the one nor the other utility fulfil the respective performance requirements. Blue are the purely hydrological, green the flexible ecohydrological and grey the inflexible ecohydrological strategies (Section 4.2.8 and Table 4.2 and 4.3).

In the next step we plotted the performance of management strategies applied on shorter (annually, denoted by index *a*) and larger time scale (every ten years, denoted by index *b*). Fig. 4.4 depicts the performance curves for ecological and water supply robustness of management strategy m_i , whereas Fig. 4.5 depicts the performance curves for ecological opportuneness. Considering only the robustness of a decision in terms of ecological performance results in better performance for strategies applied on shorter time scale (Fig. 4.4a). However, when taking into account the robustness in terms of secured water supply and the opportuneness of a decision in terms of ecological performance the strategies applied on larger time scale result in elevated values for both robustness and opportuneness (Fig. 4.4b and Fig. 4.5).

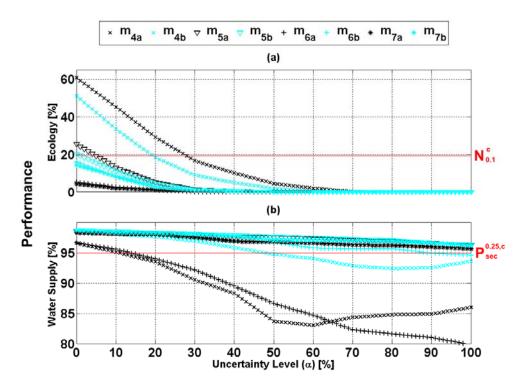


Figure 4.4. Performance curves for (a) ecological and (b) water supply robustness of management decision m_i , divided into decisions that take action every year (black markers) and every ten years (blue markers).

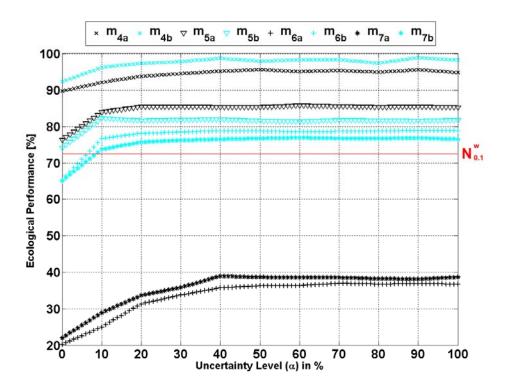


Figure 4.5. Performance curves for ecological opportuneness of management decision m_i , divided into decisions that take action every year (black markers) and every ten years (blue markers).

In order to show how the biomass changed when the flexible integrated management strategies m_{4a} and m_{4b} were applied we plotted the histograms of the average reserve biomass per parameter combination (artificial ecosystem) for each species (Fig. 4.6). The histograms illustrate that for each species the average reserve biomass was much larger than the coexistence criterion of ten equivalent adult individuals. Compared to the natural (unmanaged) ecosystems the larger values of reserve biomass under managed conditions were replaced by smaller values, particularly when being applied on a smaller time scale.

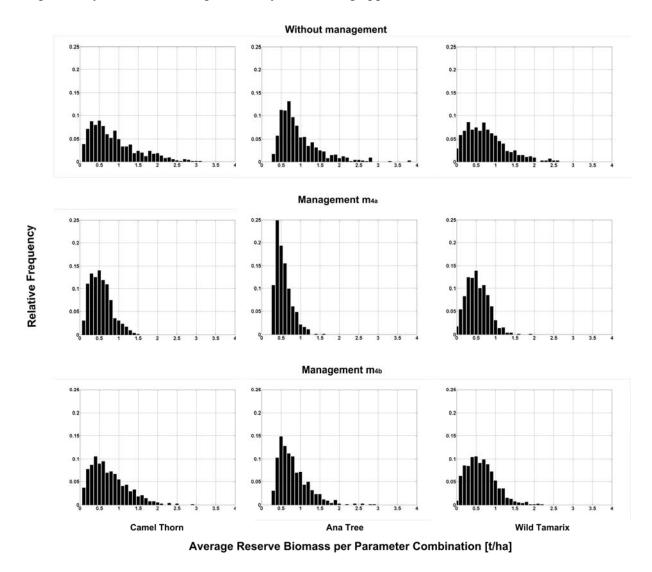


Figure 4.6. Histograms of the average reserve biomass per parameter combination without management (upper row), with management strategie m_{4a} (yearly, middle row) and with management strategies m_{4b} (every ten years, lower row) for Camel Thorn (left), Ana Tree (middle) and Wild Tamarix (right). The criterions for coexistence were based on the reserve biomass of ten adult individuals of average size of each species, which correspond to 0.051 metric ton /ha (Camel Thorn), 0.271 metric ton/ha (Ana Tree), and 0.003 metric ton /ha (Wild Tamarix).

The results of this paper are based on the assumption that the extraction of ground water is stopped if the threshold of the maximum depth to ground water (here: 12 m) is exceeded. Further, the rate of ground water extraction was restricted to 25 m³/ha season. It can be supposed that both the ground water threshold and the extraction rate restriction are determinants for the performance of the considered management strategies as they influence both the periods where pumping is allowed (effects on water supply for the humans) and the risk of causing water stress for the tree species (effects on competition strength and species coexistence). However, further studies on this issue revealed that this is not the case – the qualitative propositions are still the same.

Table 4.5. Best performance results for management strategies (Table 4.3) applied once a year (bright tags) or every ten years (dark tags) for Model C with regard to ecological (*eco*) and water supply (*wat*) performance.

	Best performance			
Strategy m_i	есо	wat		
4a,b	а	b		
5a,b	а	b		
6a,b	b	b		
7a,b	b	b		

When applying the ecohydrological management strategies one can regulate the vegetation at different time scales - once a year (bright tags in Table 4.5) or every ten years (dark tags in Table 4.5). For the majority of strategies the applications on a longer time scale performed better than those applied on the annual time scale. The only exception of this tendency was found for the flexible strategies $m_{4a,b}$ and the strategies $m_{5a,b}$, which regulate the Wild Tamarix by 10%.

4.4 Discussion

The info-gap-theoretical approach taken in this paper enables covering two sources of uncertainty: (a) uncertainty in the future flood parameters, and (b) uncertainty in the type of plant community represented by the different ecological parameter sets considered. To see the latter, note that the measures for human and ecological performance of a management strategy

used count the number of parameter combinations (and so potential plant communities) that allow meeting the demands on water supply and species coexistence with a certain minimum probability (minimum percentage of runs). The larger this number, the larger the range of plant communities to which the management strategy can be applied by meeting all demands.

In the present paper, a management strategy is said to be robust or opportune if its performance exceeds a certain threshold value. Although being normatively set, this threshold value also accounts for the limitations set by the internal dynamics of the ecohydrological system. This is done by using the performance of the un-managed system as basis for the threshold value desired.

4.4.1 Comparison of management strategies

The performance curves for robustness and opportuneness give an impression about the immunity to failure (Fig. 4.1) and the least level of uncertainty which entails the possibility of unexpected ecological performance (Fig. 4.2). Both functions enable a decision maker to formulate preferences on the options in the light of the uncertainties, here the uncertainty about the stochasticity of future flood regimes. But how would a risk-averse or risk-loving decision maker decide? In general, a risk-averse decision maker concentrates more on robustness than on opportuneness. However, robustness must be balanced against agility, otherwise, decision making can be lethargic and opportuneness can be lossed (Ben-Haim, 2006). Further, when management performance is assessed in terms of several attributes, here ecology and water supply, the management decision can be balanced to fulfil all requirements accordingly. The ecological versus water supply performance plane of robustness (Fig. 4.3) assists to find a decision that prefers both the ecological and secured water supply performance under particular critical rewards.

Considering the robustness curves with regard to ecological performance (Fig. 4.1a), the most robust strategy is m_{4a} , which intends to regulate the tree species that is actually dominant at the time of control on annual time scale. This holds not only for the given ecological performance requirement in this study but also for a wide range of possible critical reward values $N_{0.1}^c$. However, when considering the robustness curves with regard to water supply performance (Fig. 4.1b), m_{4a} only results in low robustness for the given water supply performance requirement in this study and also for a wide range of possible critical values $P_{sc}^{0.25,c}$. In this case a purely risk-averse decision maker would come into conflict because

considering only the robustness functions from ecological and human points does not deliver a clear preference on a certain decision. Hence, other tools have to be considered adequately, e.g. the ecological versus water supply performance plane of the ecological and water supply robustness (Fig. 4.3), which gives an overview in what extend each strategy contributes to both ecological and water supply performance. Note, that the cross lines (red), defined by the ecological and water supply performance requirements, are in fact flexible and can be changed by the decision maker, depending on his/her aversion to risk. In this study m_{4b} is the most preferred decision because it contributes with the largest part to segment two (ecological and water supply performance). Considering additionally the ecological opportuneness curves in Fig. 4.2 reveals once again m_{4b} as the best strategy because it shows the least level of uncertainty which entails the possibility unexpected ecological performance for a wide range of possible performance requirements ($N_{0,1}^{w}$).

These results illustrate the need for adequately used objective criterions to evaluate management strategies in strongly coupled eco-hydrological systems that are impacted by human activity (ground water extraction). The criterions must ponder thoroughly between the robustness and opportuneness of each strategy with regard to both the ecological and water supply performance.

The ranking orders among the different management strategies are insensitive to increasing uncertainty in the flood parameters. This is true for both the water supply and the ecological performance in terms of robustness and opportuneness. All the strategies exclusively accounting for the hydrological conditions (m_1, m_2, m_3) evidently reach too short as they endanger the coexistence of the three tree species (Fig. 4.1a) and partly even fail the demands on the water supply $(m_2, m_3, \text{ in Fig. 4.1b})$. This also indicates that the suggestion of supporting the ecosystem by stopping pumping (Stromberg et al., 1993) or artificially irrigating when recognizing symptoms of water stress at any tree species is not effective. The reason is the altered relative abundance of the three species caused by the pumping (note that the species differ in their sensitivity to water availability) that is too inert to respond to and benefit from an abrupt stop of pumping or start of artificial irrigation. With other words, pumping has long-lasting effects on the species composition that cannot be counteracted by mere abrupt attempts to improve the hydrological situation. This shows the necessity of a fully integrated management combining water extraction with direct regulation of the vegetation structure. Our model results indicate that regulating a particular tree species can be

beneficial for the water supply but counterproductive for the species coexistence under increasing uncertainty in future flood parameters. This is understandable as, in principle, all species can suffer from increasing uncertainty, depending on their ecological traits (e.g. sensitivity to water stress or flood events) and the varied flood parameters (e.g. volume, short/long term memory). Additional regulation in time of pressure can drive species to extinction. This risk is missing under the Strategy $m_{4a,b}$ where the tree species is regulated that is actually dominant at the time of control. This strategy keeps the vegetation structure (species composition and relative abundance) in balance. Doing so, it effectively counteracts any imbalance in the plant community caused by water extraction without markedly reducing the water supply for the humans.

To preserve the structure of the ecohydrological system seems to be crucial for sustainability. Strategy $m_{4a,b}$ is highly flexible and based on information (species abundance) attainable through monitoring. It also belongs to the strategies with the most elevated robustness (Fig. 4.1 and 4.3) and opportuneness (Fig. 4.2) against uncertainty in future flood regime parameters. However, large values for the reserve biomass of each species are less likely under the managed conditions (Fig. 4.6). This introduces a trade-off between the conservation of the vegetation structure (biodiversity/coexistence) and the total biomass (productivity) of a system. Defining clear management objectives for the vegetation system is therefore essential to ensure the application of the best performing management strategy. Further, within the model framework applied in this paper, it is not possible to conclude how the reduction of biomass has to be realised in detail, e.g. if the biomass regulation depends on the age structure. Both the normative management objectives and the detailed implementation of the biomass regulation are important tasks, but beyond the scope of this paper and subject of further research.

4.4.2 Performance under increasing uncertainty

Increasing uncertainty in the flood parameters reduces the performance of robustness of all the management strategies considered in this paper (Fig. 4.1). Shape and strength of the decline, however, differ for water supply and ecological performance. In case of *water supply* performance, there is a critical threshold (20%) above which uncertainty has a noticeable effect and the management strategies differ in terms of their performance. The only exception are those strategies where pumping is stopped if there are signs of water stress for the tree species (m_2 , m_3) or where Camel Thorn is regulated each year (m_{6a}) or where the most dominant species is regulated each year (m_{4a}). In case of these strategies, the water supply performance is significantly reduced and immediately responding to increasing uncertainty in the flood parameters. These findings are all reflection of two facts: First, water supply is only adversely affected if the uncertainty in the flood parameters is such strong that the water volume increasingly falls below the threshold where pumping is stopped. Second, water supply is only affected by dry periods in the flood time series resulting from a change in future flood stochasticity (short/long term memory) and amplifying water scarcity. In case of *ecological* performance (coexistence of three tree species), the picture is different. Here, increasing uncertainty immediately reduces the ecological performance indicating a loss of species for most of the ecosystems. The strength of this decline depends on the chosen management strategy. The reason for this finding is that any change in short/long term memory of the flood – regardless of upward or downward – can alter the demographic processes (plant growth, mortality) but also the competition strengths between the tree species. This influences the conditions of coexistence with implications for the composition of the plant community.

This illustrates that the ecological performance is much more sensitive to increasing uncertainty in the flood parameters than the water supply performance. Hence, when exclusively focusing on the water supply, critical hydrological changes can be overseen. However, the more sensitive vegetation structure (species composition) can be used as more sensitive indicator and pre-warning system.

The performance of ecological opportuneness of all management strategies increases with increasing uncertainty in the flood parameters (Fig. 4.2). Again the strategies which keep the vegetation structure in balance ($m_{4a,b}$) by regulating the species that is actually dominant at the time of control reveal the best ecological performance, i.e. they are most opportune to gain an unexpected performance under the future flood regime uncertainty.

4.4.3 Role of the system model

The insensitivity of the ranking orders among the strategies to uncertainty in the flood parameters can be a result of the specific coupling between the hydrological and ecological system assumed in this paper. The floods were assumed to occur in the middle of the vegetation period (Eq. 4.1 - 4.2). In reality, however, there is certain variability in the time of flood occurrence. This means, that, with a certain chance, floods can also occur before the sprouting of the green biomass in the respective year. In this case, also the remaining green

biomass from the preceding year is affected by the flood. This would result in modified vegetation dynamical equations. To assess the robustness of the presented findings on the eco-hydrological system dynamics and the resource management strategies against these modifications is an important task but is beyond the scope of this paper and subject of further research.

All findings on the performance of the considered management strategies could be explained by referring to the functioning of the ecohydrological ephemeral system and the feedback loops between water resources and plant community. This underpins the necessity of working with a fully coupled ecohydrological model. Species competition was found to be an important mechanism interlinking water resources and plant community and has therefore to be adequately considered. Hence, both the structure of the plant community (species composition, relative abundance, the species' ecological traits) and the mechanisms of plant competition have to be explicitly incorporated in ecohydrological models.

4.5 Conclusions

This study emphasises the need of working with fully coupled ecohydrological models when investigating management scenarios for water limited environments such as ephemeral rivers. These models have to consider explicitly the linkage between the dynamic of water resources and the structure of the plant community including the species composition, mechanisms of plant competition, and species specific traits, because preserving the structure of a vegetation system seems to be crucial for the sustainable use of ground water along ephemeral rivers. Given that the ecological performance is more sensitive to increasing uncertainty in the flood parameters than the water supply performance, we suggest that the vegetation structure can be used as sensitive indicator and pre-warning system for changing environmental conditions.

In this study, the integrated strategy which regulates the most dominant species on larger time scale performs best in terms of the robustness of ecological and water supply performance, and the possibility of unexpected but favourable ecological performance. With the integrated strategy it is most likely to sustainably use the ground water while preserving the natural vegetation structure, however, with the effect of reducing the probability of a large total system biomass.

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Chapter 5

Sustainable water extraction along ephemeral rivers: On the role of ecohydrological feedbacks and uncertainty

5.1 Introduction

Ephemeral rivers are located throughout the world's arid regions (WRC, 2005) and denote linear oases in otherwise dry areas (Jacobson et al., 1995). Their water limited ecosystems are driven by ecohydrological feedbacks comprising the temporary floods, the subsurface water storage and the ecosystem dynamics. Often both the water and the ecosystem are diversely used by humans, e.g. water supply for drinking, farming and mining, or tourism (Dahan et al., 2008). The sustainable extraction of ground water is essential to preserve the natural ecosystem. This requires a well developed understanding of the ecohydrological feedbacks. Models can help to increase the mechanistic understanding of coupled processes along ephemeral rivers. However, the development of these models is associated with severe uncertainty in the model structure, the parameterisation and, eventually, the future stochastic flood regimes. While the uncertainty in the model structure and parameterisation can be dealt with by considering several model versions and parameter combinations (see Chapter 2 and 3), the uncertainty in the future flood regime is much more critical. There is an information gap between what is known about the actual and what needs to be known about the future flood regime parameters to make competent management decisions. One powerful approach to master this challenge is the information-gap (info-gap) decision theory that can quantify this uncertainty and, moreover, facilitates the estimation of the robustness of management decisions under uncertainty (Ben-Haim, 2006).

In this study, we apply the info-gap decision theory and use several model versions and parameterisations developed within an ecohydrological modelling framework (Chapter 2 and 3). The objective is to assess consequences for the design of management strategies for sustainable water extraction meeting given minimum requirements on the water supply (water

performance) and preserving the species composition of the vegetation (ecological performance). Further, we clarify the relative importance of ecohydrological feedbacks and uncertainty for the design of sustainable strategies for water extraction in ecosystems along ephemeral rivers. To assess the role of the ecohydrological feedbacks, three models (A, C, D, see Chapter 2 and 3) were considered that differ in the assumptions on ecological traits of the plant species (phenology, sensitivity to floods) determining the plants' response to the water resources. Further, the models differed in the sensitivity to a change in flood stochasticity and fluctuations of hydrological variables such as transpiration and depth to ground water (Chapter 3). All models comply with an observed ecological pattern along the Kuiseb River in Namibia – the coexistence of three tree species. However, only one of the models (Model C) complies with two ecohydrological patterns - the species specific access to the subsurface water storage and the species specific vulnerability to the magnitude of flood events.

5.2 Methods and materials

For this study the info-gap model requires the following elements (Ben-Haim, 2006): (1) Three distinct system models that deliver a measure of performance as a result of each management strategy. (2) Performance requirements for the evaluation of management robustness (possibility to failure). (3) A model describing the uncertainty of future flood regime stochasticity.

5.2.1 System models

The applied system models result from previous studies and are subversions of an ecohydrological model framework (Chapter 2 and Chapter 3). For each model the flood resistance and time of leaf shedding (phenology) is implemented as (i) same or (ii) different between species (Table 5.1). As a consequence the driving system mechanisms are different: In Model A, structurally the simplest model, the coexistence is mainly driven by niche partitioning, whereas in Model C, structurally the most complex model, the species specific vulnerability to flood disturbance drives the coexistence. Eventually, both successful mechanisms are combined in Model D. For all models, there are many parameter combinations available leading to three species coexistence. These parameter of parameter combinations leading to three species coexistence was used to evaluate the ecological

performance under each management strategy. For more details regarding the parameterisation and implementation of the model framework please refer to Chapter 2 and Chapter 3.

Table 5.1. System models applied in this study. The denotation, implementation of system processes and model properties referred to the hydrosystem result from previous studies (Chapter 2 and Chapter 3).

System mo	del A	С	D	
Processes/Property				
Input				
Number of parameters	23	29	27	
Flood resistance	same for all	species specific	species specific	
Phenology	same for all	species specific	same for all	
Modelled Output				
Sensitivity to changes in flood cyclic	ity low	high	high	
Fluctuations in hydrological variables	s low	high	elevated	

The output properties of each model are also different (Table 5.1): For Model C and D the parameter combinations leading to three species coexistence are very sensitive to changes in flood cyclicity, whereas for Model A they are insensitive (Chapter 3, Fig. 3.5). Further, fluctuations in hydrological variables such as transpiration and depth to ground water are highest for Model C and lower for Model A and D (Chapter 3, Fig. 3.4).

5.2.2 Performance requirements

In this study the performance measures included two attributes because we assessed the management performance with regard to performance of ecology (biodiversity) and secured water supply for humans.

The success of a parameter combination Ω , i.e. the ability to model three species coexistence, depends on the applied flood time series. Since the flood regime is stochastic several runs with several flood realisations are necessary to assess whether coexistence is very likely or not (for a certain parameter combination). Therefore, we introduced the variable $P_3(\Omega)$, which is the probability of coexistence for Ω :

$$P_3(\Omega) = \frac{\#B(n=3)}{100},\tag{5.1}$$

where #B(n=3) is the number of flood realisations that led to coexistence of all three species. A small P_3 indicates low probability of coexistence, whereas a P_3 near 1 indicates that the parameter combination led to three species coexistence in almost all flood realisations with the same stochastic properties. We expressed ecological performance as relative number of parameter combinations with $P_3 \ge 0.1$:

$$N_{0.1}^{man} = \frac{\#B(P_3 \ge 0.1)}{\#B(P_3 \ge 0.03)},$$
(5.2)

where #B(P3) is the total number of parameter sets that led to the denoted probability of coexistence. Since the stochasticity in flood regime can be adverse we evaluated the critical ecological reward r_c^{eco} for the worst case under "natural" (unmanaged) conditions (Table 5.2). That is, when measuring the robustness of a decision, we require the minimum acceptable ecological performance to be no less than the worst case under "natural conditions (r_c^{eco}). For the secured water supply for humans we fixed the critical water supply reward r_c^{wat} to 95% for each system model (Table 5.2). That is, we require the minimum acceptable ground water supply to be given in no less than 95% of the time. We expressed secured water supply performance as:

$$P_{\rm sec}^{0.25} = \frac{\min \sum p_{\rm sec}(\Omega_e, \Omega_h)}{\tau},$$
(5.3)

where p_{sec} is the number of time steps with secured water supply for each ecological parameter set $\Omega_{\rm e}$ and each hydrological parameter set $\Omega_{\rm h}$, τ is the total number of time steps, and $P_{\rm sec}^{0.25}$ denotes the 0.25 percentile of time steps with secured water supply for all parameter sets $\Omega_{\rm e}$ and $\Omega_{\rm h}$.

5.2.3 Stochastic flood regime

The dynamic of the biomass and water resource for each model is driven by a stochastic flood regime, which was generated by a fractional autoregressive moving average model (FARIMA(p,d,q), $p,q \in N$) (Kokoszka and Taqqu, 1995; Stoev and Taqqu, 2004). This flood regime generator generates time series with both short- and long-term dependence structures. The short term dependence structure is determined by the real polynomials X_p and Ψ_q of degree p and q. The autoregressive part of FARIMA is represented by the coefficients of X_p ,

$$\mathbf{X}_{p}(\boldsymbol{\lambda}) = 1 - \chi_{1}\boldsymbol{\lambda} - \chi_{2}\boldsymbol{\lambda}^{2} - \dots - \chi_{p}\boldsymbol{\lambda}^{p}, \qquad (5.4)$$

where $X_1(\lambda) = 1 - 0.192\lambda$ and λ is a random number drawn from a normal distribution with mean 0 and standard deviation 1. The moving average part is represented by the coefficients of Ψ_q :

$$\Psi_q(\lambda) = 1 - \psi_1 \lambda - \psi_2 \lambda^2 - \dots - \psi_q \lambda^q , \qquad (5.5)$$

with $\Psi_1(\lambda) = 1 - 0.8969\lambda$. The long term behaviour is governed by *d*, which is a real number:

$$0 < d < 1 - 1/\omega$$
, and $1 < \omega < 2$. (5.6)

The relationship between *d* and the Hurst-Exponent *H* is as follows:

$$H = d + 1/\omega \,. \tag{5.7}$$

We assumed *H* to be 0.75 (with $\omega = 1.99$ and d = 0.25), and p = q = 1. The time series were generated with FARIMA(p=1,d=0.25,q=1) and adjusted to the observed mean annual flood volume $\mu_{Flood} = 3,269,000 \text{ m}^3$ (Chapter 2), and thus yielding

$$V_{Flood}(t) = e^{(FARIMA(1,0.25,1) + \log(\mu_{Flood}))}.$$
(5.8)

5.2.4 Uncertainty model

We know that the stochastic properties of the flood regime (Eq. 5.8) are uncertain, and that there are a range of possible values of χ_1 , ψ_1 , d and μ_{Flood} that will lead to different time series of the flood regime.

We assume that uncertainty in the flood regime parameters may be represented by intervals of unknown size around each parameter (envelope-bound info-gap model (Ben-Haim, 2006)). Hence, the uncertainty model can be expressed as:

$$U(\alpha) =$$

$$\{\chi_{1},\psi_{1},d,\mu_{Flood}: \left|\frac{\chi_{1}-\widetilde{\chi}_{1}}{\widetilde{\chi}_{1}}\right| + \left|\frac{\psi_{1}-\widetilde{\psi}_{1}}{\widetilde{\psi}_{1}}\right| + \left|\frac{d-\widetilde{d}}{\widetilde{d}}\right| + \left|\frac{\mu_{Flood}-\widetilde{\mu}_{Flood}}{\widetilde{\mu}_{Flood}}\right| \le \alpha\}, \alpha \ge 0,$$
(5.9)

where α is the horizon of uncertainty. The larger the value of α , the greater the range of unknown variation of the actual values χ_1 , ψ_1 , d and μ_{Flood} around the nominal values $\tilde{\chi}_1$, $\tilde{\psi}_1$, \tilde{d} and $\tilde{\mu}_{Flood}$ (Chapter 4, Table 4.1). Since the value of α is not known $U(\alpha)$ is an unbounded family of nested sets of values whose deviation from the nominal values is nowhere greater than α . The envelope-bound model enables us to vary the actual values at different rates around the centre of the 4d-hypersphere given by the nominal values. If $\alpha = 0$, then $\tilde{\chi}_1$, $\tilde{\psi}_1$, \tilde{d} and $\tilde{\mu}_{Flood}$ are the only possible values in absence of uncertainty and $U(0) = \{\tilde{\chi}, \tilde{\psi}_1, \tilde{d}, \tilde{\mu}_{Flood}\}$, i.e. the nominal model is the actual model. The parameter sampling procedure of the actual values around the 4d-hypersphere is described in the next section.

5.2.5 Flood parameter sampling

We sampled the flood regime parameters (Ω_h) from the surface of a 4d-hypersphere whose centre is given by the nominal values $\tilde{\chi}_1$, $\tilde{\psi}_1$, \tilde{d} and $\tilde{\mu}_{Flood}$ (Chapter 4, Table 4.1). Depending on the horizon of uncertainty α we sampled the actual values χ_1 , ψ_1 , d, μ_{Flood} as follows:

$$\chi_1 = \tilde{\chi}_1 + \tilde{\chi}_1 \cdot \alpha \cdot \cos \rho \cdot \sin \nu_1 \cdot \sin \nu_2, \qquad (5.10a)$$

$$\psi_1 = \widetilde{\psi}_1 + \widetilde{\psi}_1 \cdot \alpha \cdot \sin \rho \cdot \sin \nu_1 \cdot \sin \nu_2, \qquad (5.10b)$$

$$d = \tilde{d} + \tilde{d} \cdot \alpha \cdot \cos \upsilon_1 \cdot \sin \upsilon_2, \text{ and}$$
(5.10c)

$$\mu_{Flood} = \widetilde{\mu}_{Flood} + \widetilde{\mu}_{Flood} \cdot \alpha \cdot \cos \upsilon_2, \qquad (5.10d)$$

where $\rho \in (0,2\pi)$ and $\upsilon_1, \upsilon_2 \in (0,\pi)$ are random numbers drawn from a uniform distribution.

5.2.6 Robustness function

When parameter uncertainty is adverse it entails the possibility of failure. We quantified this aspects of uncertainty by evaluating the robustness function $\hat{\alpha}$ of management strategies:

$$\hat{\alpha}(m_i, r_c^{eco}) = \max\{\alpha : \min N_{0,1}^{man}[m_i] \ge r_c^{eco}\}, \text{ and}$$
 (5.11a)

$$\hat{\alpha}(m_i, r_c^{wat}) = \max\{\alpha : \min P_{\text{sec}}^{0.25}[m_i] \ge r_c^{wat}\},$$
(5.11b)

which expresses the greatest level of uncertainty α that still meets the pre-determined critical reward, i.e. a large value of $\hat{\alpha}$ is desirable.

5.2.7 Management scenarios

The management strategies applied in this study were the same as in Chapter 4 (Table 4.2 and 4.3). They were all based on a maximum ground water depth of 12 m and a ground water extraction rate of 25 m³/ha·season. For strategies m_1 , m_2 and m_3 the ecosystem was not regulated, but plant water stress led to a pumping stop for Strategy m_2 and additional to artificial irrigation of the upper soil layer for Strategy m_3 . These three strategies only consider the regulation of the hydrosystem but not that of the ecosystem. For the other strategies additional ecosystem regulation was integrated - they were applied once a year (denoted by index *a*) or every ten years (denoted by index *b*). Those ecohydrological management strategies were either flexible by regulating the most dominant species at a flexible rate ($m_{4a,b}$) or inflexible by working with a fixed regulation rate for a specific plant species ($m_{5a}-m_{7b}$).

5.3 Results

Table 5.2 shows that with increasing structural complexity of the system model the ecological performance requirement decreased. Hence, for Model A the calculated ecological performance requirement was most elevated ($r_c^{eco} = 62.6\%$) and for Model C it reached the lowest value ($r_c^{eco} = 19.3\%$).

Table 5.2. Ecological and water supply performance requirements for the investigation of the robustness (r_c) of management strategies. The smallest number of parameters was implemented for Model A, whereas Model C was the most complex model.

	Critical Reward r_c [%]				
System Model	Ecosystem (r_c^{eco})	Water Supply (r_c^{wat})			
А	62.6	95			
С	19.3	95			
D	49.7	95			

Figures 5.1-5.3 show the performance curves of the applied management strategies (Table 4.2 and 4.3) for (a) the ecological and (b) the water supply performance. These curves give an impression about the immunity of each strategy to failure. In other words, they illustrate the greatest level of uncertainty in the flood regime parameters that still meets the pre-determined

critical rewards for ecology (r_c^{eco}) and water supply (r_c^{wat}). For Model A and D, none of the applied management strategies met the pre-determined ecological performance requirement (Fig. 5.1a and 5.3a). On the other hand, for Model C, three strategies met the ecological performance requirement: Strategy m_{4a} was robust up to an uncertainty level of 28%, Strategy m_{4b} up to 20%, and Strategy m_{5a} up to 5% (Fig. 5.2a). Two of these strategies (m_{4a} , m_{4b}) belonged to the management category, which is flexible in terms of ecosystem regulation. The third strategy (m_{5a}) only regulated the Wild Tamarix by a fixed rate of 10% per year (Chapter 4, Table 4.3). The performance of the management strategies in terms of secured water supply depicted a different picture. For Model A, again none of the strategies could meet the performance requirements (Fig. 5.1b), whereas for Model D, all strategies were robust up to an uncertainty level of >100% except m_2 and m_3 (Fig. 5.3b). For both strategies the water supply performance reached only less than 46% at an uncertainty level of 0%. Also for Model C the strategies m_2 and m_3 could not meet the defined performance requirement for secured water supply. The flexible ecohydrological strategies m_{4a} and m_{4b} were robust up to an uncertainty level of 11% and 48% (Fig. 5.2b).

The performance requirement for the secured water supply was a normative threshold that can be adapted to subjective needs. However, the ecological performance requirement is a rather descriptive threshold (Eq. 5.2), which is determined by the system model and its structural complexity. It represents the system under un-managed conditions. Applying it enhances the failing of qualitative assessment of the management strategies. Therefore, another option to assess them is to compare only their relative performance by evaluating the ranking order for both the ecological and the water supply performance. In Table 5.3 the blue tags denote management strategies that only regulate the hydrosystem (m_1 , m_2 , m_3) and the green tags denote those strategies, which regulate both the eco- and the hydrosystem by regulating the most dominant species (flexible strategies $m_{4a,b}$). The strategies that only regulate the hydrosystem performed best for both Model A and Model D. Whereas for Model C, particularly in terms of the ecological strategies.

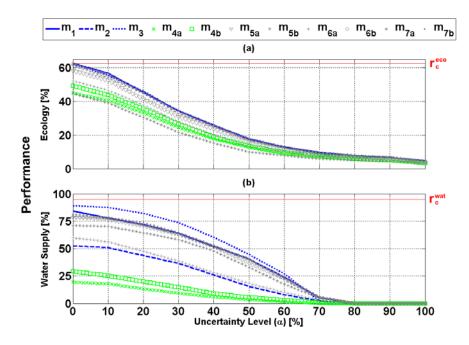


Figure 5.1. Model A (Table 5.1). Performance curves for (a) ecological and (b) water supply robustness of management strategy m_i . The red lines denote the ecological (r_c^{eco}) and water supply (r_c^{wat}) performance requirements (Section 5.2.2 and Table 5.2) below which the performance of a decision is unacceptable. Blue are the purely hydrological, green the flexible ecohydrological and grey the inflexible ecohydrological strategies (Section 5.2.7 and Table 4.2 and 4.3).

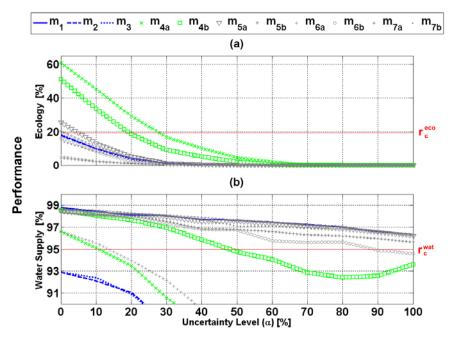


Figure 5.2. Model C (Table 5.1). Performance curves for (a) ecological and (b) water supply robustness of management strategy m_i . The red lines denote the ecological (r_c^{eco}) and water supply (r_c^{wat}) performance requirements (Section 5.2.2 and Table 5.2) below which the performance of a decision is unacceptable. Blue are the purely hydrological, green the flexible ecohydrological and grey the inflexible ecohydrological strategies (Section 5.2.7 and Table 4.2 and 4.3).

5.4 Discussion

Ecohydrological feedbacks and uncertainty are immanent in ecosystems along ephemeral rivers. Feedbacks result from complex interactions between water resources and vegetation and uncertainty is present in three respects: (a) unpredictability in the occurrence, length und strength of floods, (b) uncertainty in the parameters of the stochastic flood regimes due to a lack of information or environmental change, and (c) uncertainty in the parameters of the vegetation model due to the same reasons. All these factors can alter the system dynamics. The present study aimed to assess consequences for the design of management strategies for sustainable water extraction meeting given minimum requirements on the water supply (water performance) and preserving the species composition of the vegetation (ecological performance). To assess the role of the ecohydrological feedbacks, three models (A, C, D) were considered that differ in the assumptions on ecological traits of the plant species (phenology, sensitivity to floods) determining the plants' response to the water resources and flood regime.

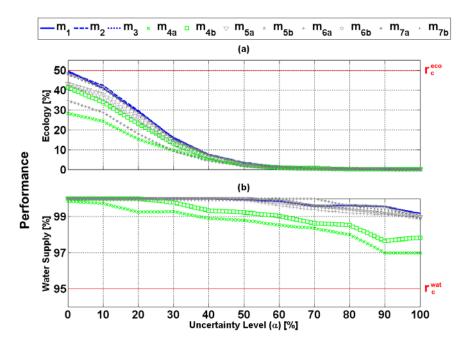


Figure 5.3. Model D (Table 5.1). Performance curves for (a) ecological and (b) water supply robustness of management strategy m_i . The red lines denote the ecological (r_c^{eco}) and water supply (r_c^{wat}) performance requirements (Section 5.2.2 and Table 5.2) below which the performance of a decision is unacceptable. Blue are the purely hydrological, green the flexible ecohydrological and grey the inflexible ecohydrological strategies (Section 5.2.7 and Table 4.2 and 4.3). The strategies m_2 and m_3 are not illustrated due to the very low performance (for both the water supply performance was <46% at an uncertainty level of 0%).

5.4.1 Ranking orders of management strategies

A broad range of management strategies for water extraction was assessed and compared regarding (water and ecological) performance (Table 5.3). Regarding the parameter of the stochastic flood regime, for all models the resulting ranking orders were found to be robust against increasing uncertainty. From the point of view of water supply, the strategy (m_1) that ignores water stress and structure of the vegetation was found to be best. This is not surprising as the only restriction for the ground water extraction is the maximum depth to ground water (here: 12 m) that must not be exceeded. Consequently, of all strategies, m_1 is the least restricted one and water supply is secured for most of the time.

When considering the ecological performance (preservation of species coexistence), however, the ranking orders and so the optimal strategy were found to be different for different models. For Models A and D, the purely hydrological strategies perform best, whereas for Model C the integrated strategy that regulates the most dominant species every ten years performs best. The reason for the model-dependent ranking orders lies in the coexistence mechanisms underlying the different models. For Model A and D, all species are assumed to be homogeneous in one ecological trait - the phenology, i.e. all species are evergreen. As a result, all species permanently compete with each other for water. In this case, species coexistence requires a balance between growth rate (water use efficiency) and water stress (water driven mortality). Hence, high/low mortality is always combined with high/low growth rate. As a result, losses of plants due to water extraction primarily occurring among species with high water stress will be compensated by the same species during the next flood because of its water use efficiency that is higher than for the other less vulnerable, but also less effective species. Therefore, water extraction does not alter the species composition of the vegetation. In Model C, the situation is different. Here, the species differ in their phenology (time of leaf shedding). In this case, coexistence requires niche differentiation in the sense that the species utilise different water resources (shallow, unsaturated zone, groundwater). These water resources, however, differ in their vulnerability to water extraction and so do the affiliated species. Consequently, water extraction shifts the species composition towards the species with ground water access. Here, a regulation of the most dominant species is necessary to preserve the species composition. This shows that the three models differ in the sensitivity of the species composition of the vegetation to water extraction and so in the need to regulate the vegetation for preserving species coexistence.

Our results imply that integrated management strategies that combine ground water extraction with the regulation of the most dominant species to preserve the vegetation structure is not generally the best solution. However, our results allow characterising the range of application: Such an integrated management strategy is appropriate if the vegetation along the ephemeral river consists of plant species that use different water resources (niche differentiation) and differ in their sensitivity to floods. Such heterogeneity in the ecological traits of the species is common in vegetation systems, while the homogeneity assumed in Models A and D is rather hypothetical. This shows the relevance of the integrated strategy.

Table 5.3. Ranking orders of management strategies m_i (Chapter 4, Table 4.2 and 4.3) for models A, C and D with regard to ecological (*eco*) and water supply (*wat*) performance. The tags denote management strategies that only regulate the hydrosystem (m_1 - m_3 , blue tags) or both the eco- and the hydrosystem by flexible regulating the biomass of the most dominant speices (m_{4a} , m_{4b} , green tags). White are the inflexible ecohydrological strategies that regulate the ecosystem with fixed rates (m_{5a} - m_{7b}).

	Model A		Model C			Model D	
Rank	есо	wat	есо	wat		есо	wat
1	1,2	3	4a	1		1	1,5a,7a,7b
2	-	1	4b	7b		3	-
3	5b	7b	5a	5b		2	-
4	3	5b	5b	4b		5b	-
5	6b	6b	3	5a		6b	5b,6b
6	7b	5a	1	6b		7b	-
7	5a	7a	2	7a		5a	6a
8	6a	6a	6b	4a,6a		6a	4b
9	4b	2	7b	-		4b	4a
10	4a	4b	6a	2,3		7a	3
11	7a	4a	7a	-		4a	2

5.4.2 Ecohydrological feedbacks or uncertainty?

One major aim of this study was to clarify the relative importance of ecohydrological feedbacks and uncertainty for the design of sustainable strategies for water extraction in ecosystems along ephemeral rivers. Our results indicate that the best strategy is robust against uncertainty in the parameters of the flood regime, but strongly dependent on the assumptions on the plants' species-specific response to the water resources (access to water storages,

sensitivity to flood events) and so on the structure of the ecohydrological feedbacks between water and vegetation. Whether the purely hydrological or the fully integrated ecohydrological strategy is more favourable depends on whether the plant species coincide or differ in their responses. This shows that a lack of information on the ecohydrological feedbacks is more critical for strategy planning than uncertainty in some parameters. This also underpins the necessity of using models that are explicit in the ecohydrological feedbacks and account for the differentiation in the responses of the species in a plant community. Otherwise there is a high risk of oversimplification and counterproductive management conclusions.

5.4.3 Relationship between model complexity and strategy performance

When assessing the performance of management strategies it can be useful to define minimum requirements on the performance. These minimum requirements can be calculated by rules that characterise the system under study (rather descriptive) or that are subjectively fixed (rather normative). In this study we used both methods by calculating the minimum requirement on the ecological performance and by fixing the value for reliable water supply from the ground water. The required minimum ecological performance is a relative value resulting from the number of parameter combinations ensuring species coexistence relative to the total number of parameter combinations under un-managed conditions (Eq. 5.2). This relative value decreases with increasing structural complexity of the model used. Table 5.2 highlights that the number of parameter combinations ensuring species coexistence is higher for the simplest model (Model A) than for the more complex models (Model D and C). This is not surprising as this is a reflection of the well-known finding (Baumgartner et al., 2008) that models with low complexity are applicable to a broader range of situations (each represented by a certain parameter combination) than models with higher complexity.

5.5 Conclusions

The system model plays a critical role when assessing consequences for the design of management strategies for sustainable water extraction while preserving the species composition of the vegetation. Only for one of three system models the strategy that combines ground water extraction with the regulation of the most dominant species was best. This illustrates that fully integrated management strategies are not generally the best solution. However, the range of application can be constrained to ecohydrological systems along

ephemeral rivers that consist of plant species using different water resources and differing in their sensitivity to floods. Such heterogeneity in ecological traits of species is common in vegetation systems, highlighting the relevance of integrated management strategies. Given that the descriptive (ecological) performance requirement, applied in this study, depends on the structural complexity of the system model, reflects the well-known findings that models with low complexity are applicable to a broader range of situations than models with higher complexity.

The best strategy, investigated in this study, is robust against uncertainty in the parameters of the flood regime, but strongly depends on the structure of the ecohydrological feedbacks between water and vegetation. This shows that a lack of information on the ecohydrological feedbacks is more critical for strategy planning than uncertainty in some parameters and underpins the necessity of using models that are explicit in the ecohydrological feedbacks and account for the differentiation in the responses of the species in a plant community. Further, it indicates that, if a model gives satisfactory results (here the coexistence pattern), but for the wrong reasons, essential effects such as the ecohydrological feedbacks may be neglected and eventually lead to counterproductive management conclusions.

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Chapter 6

Synthesis

Ephemeral rivers are located throughout the world's arid regions. They are characterised by temporary surface flow that strongly varies between seasons and years. Along the river course often a coupled eco-hydrological vegetation-groundwater system has established, which is referred to as linear oasis, reflecting the ecological and socio-economic importance of ephemeral rivers in otherwise dry areas.

The Kuiseb River in Namibia denotes such a linear oasis with eco-hydrological feedbacks between the vegetation and the ground water resource. Temporary floods infiltrate into sediments, which are accumulated in geological pools of impermeable bedrocks. This enables the formation of shallow ground water. The low depth to ground water allows root water uptake by plants and the establishment of a thriving ecosystem. Besides, the river and its environment is diversely used by humans, e.g. by exploiting the ground water for drinking, farming, and mining. Further, it is essential for the survival of the rural Topnaar community and economical important due to its touristic attraction. Therefore, a sustainable resource management is needed, which clearly requires a well developed understanding of the ecohydrologcial processes along ephemeral rivers.

The objective of this research was to develop a model framework based on the Kuiseb River that integrates both ecological and hydrological system dynamics. Such a framework helps to increase the mechanistic understanding of driving ecohydrological processes along ephemeral rivers by testing assumptions and generating hypotheses. Further, it can be applied to investigate management strategies in terms of their ability to sustainably exploit the ground water resource while preserving the natural vegetation structure.

Uncertainty played a critical role throughout this research due to the scarce information available for both the eco- and the hydrosystem. In particular, the research focused on three types of uncertainty: (1) The parameterisation of the population model, which was challenging as this requires long-term observation of species abundance that is not available. This parameterisation problem was addressed by using pattern-oriented model calibration, in that the species parameters were adjusted such that the resulting parameterisation reproduces the observed three species coexistence pattern along the river course under study. (2) The inherent uncertainty in the occurrence of flood events, which is driven by unpredictable rainfall events. Throughout this study the unpredictability was described with a stochastic process characterised by parameters such as frequency, duration and short/long term memory of flood events. In order to address the parameterisation problem to this type of uncertainty, for each parameter combination the model run 100 times with stochastic identical flood realisations, eventually leading to a quantification of the uncertainty in parameterisation. (3) The uncertainty in parameters describing the (stochastic) flood regimes. This uncertainty arises due to the scarce information about the runoff data along ephemeral rivers because often monitoring systems are rare and the temporary character of the flood events hinders the measurement of large time series. The influence of this particular type of uncertainty on the robustness and significance of integrated management strategies was investigated without neglecting the preceding types of uncertainty.

6.1 Summary

In Chapter 2, the integrated ecohydrological model framework was developed based on available information for the environment along the middle section of the ephemeral Kuiseb River. The conceptual model integrates ecological and hydrological dynamics on seasonal time scale based on an ecological population model and a hydrological storage model. In order to address important processes of the plant community dynamics and their response to the hydrological system in an adequate way, the plant biomass was differentiated into green and reserve biomass. The green biomass describes all the parts of a plant that perform photosynthesis, while the reserve biomass covers all parts of the plant that are photosynthetically inactive. Water is available for plants from both the unsaturated and the ground water storage, which are driven by stochastic flood events. The flood volume was generated by a fractional autoregressive moving average model (FARIMA), which generates time series with both short- and long term dependence structures that are present in many hydrologic processes. The population model and the hydrological storage model are linked via growth, mortality and transpiration. Both the growth and mortality of biomass depend on the water availability, which is driven by the flood regime (duration, intensity, frequency) and the competition with other species. On the other hand, the water volumes in the unsaturated and ground water layer are influenced by the transpiration rate of the vegetation system, which is itself driven by the biomass dynamics.

As mentioned before, the parameterisation problem concerning the population model was addressed by using pattern-oriented model calibration. The population parameters were found by Latin hypercube sampling of the parameter space, which was qualitatively constrained by plausibility checks and available information such as root depths, growing rates and transpiration rates. The pattern-oriented model calibration was a powerful method to constrain the number of possible parameter combinations (artificial ecosystems). However, there were still many parameterisations that correspond with the observed coexistence pattern. This uncertainty in parameterisation was explicitly considered for further investigations throughout this study by applying the ensemble statistics of all parameter combinations that lead to the observed pattern. Further, in order to address structural uncertainty in the strength of linkage between eco- and hydrosystem, four model versions were selected with increasing degree of complexity of the population model. In particular, processes that enable coexistence mechanisms such as trade-offs or niche partitioning were integrated differently: Time of leaf shedding (phenology) and vulnerability to flood disturbance (flood resistance) were implemented as (i) same or (ii) different between species. Chapter 3 illustrated that only three of the four model versions were appropriate to model the observed coexistence pattern. Further, only one of them (Model C) complied with two other observed patterns that arise from eco-hydrological feedbacks – the species specific source of water from the subsurface and the species specific vulnerability to the magnitude of flood events. The results illustrated that specific model structures are necessary to model the coexistence pattern.

In Chapter 3, the small structural variations between the model versions were used to investigate the influence of coexistence mechanisms on the fluctuations of hydrological variables such as transpiration and depth to ground water. The results suggest that the species specific response to the flood disturbance enhances elevated fluctuations of hydrological variables, which is, however, amplified by integrating the observed species specific phenology. The time of leaf shedding causes temporal variations in plant water uptake and, hence, elevated fluctuations in transpiration and depth to ground water.

In Chapter 4, a variety of management strategies were assessed, in terms of ground water extraction, regarding their performance under different (artificial) eco-hydrological systems and under uncertainty in the future (stochastic) flood regimes. The management strategies were investigated in terms of their ability to sustainably exploit the ground water resource

while preserving the vegetation structure (coexistence of three tree species). For this, the information gap decision theory was applied. Model C (from Chapter 2 and Chapter 3) was the most reliable model version and was applied as system model, because it complied with three qualitative patterns observed along the Kuiseb River (coexistence, plant water source, vulnerability to flood events). Since the management performance was investigated for two attributes, two performance requirements were needed for the ecological and the water supply performance. The required minimum ecological performance was a descriptive value reflecting the "natural" (un-managed) ecosystem conditions. On the other hand, the water supply performance requirement was a normative value reflecting a maximum failure rate of ground water extraction of 5% per year. Eventually, an uncertainty model was applied that describes the horizon of uncertainty around the flood parameters estimated in Chapter 2 by varying from 0% (no uncertainty) to 100%.

Parameter uncertainty can lead to worse (adverse) or better than expected (favourable) management performance. The first refers to the greatest level of uncertainty that still meets the pre-determined performance requirements, whereas the second refers to the least level of uncertainty, which entails the possibility of unexpected but potentially favourable performance. Both aspects were considered when investigating the performance of management strategies applied in this research, which were the same for Chapter 4 and Chapter 5. They were all based on a fixed extraction rate from ground water and constrained to maintain at least a certain ground water level. In order to investigate the importance and necessity of integrated eco-hydrological management, the strategies differed between purely hydrological and (in)flexible ecohydrological regulations. Further, the latter were applied on smaller and longer time scale. For the purely hydrological strategies the ecosystem was not regulated but plant water stress was used as an indicator to stop extraction or to additional artificial irrigation of the upper soil layer. The ecohydrological strategies removed parts of a selected species with a fixed rate (inflexible) or they removed parts of only the most dominant species by a flexible rate (flexible).

In Chapter 5, the consequences for the design of management strategies were assessed, when applying several system models (from Chapter 2 and 3) that arise from the same conceptual model framework, but differ in the assumptions on ecological traits of the plant species regarding the plants' response to the water regime. Further, the relative importance of ecohydrological feedbacks and parameter uncertainty for the design of sustainable strategies for water extraction along ephemeral rivers was clarified.

6.2 Conclusions

The modelling of three species coexistence in a water limited environment is challenging because feedbacks between ecology and hydrology have to be implemented in an appropriate way. Therefore, a fully integrated ecohydrological model framework, such as developed in this research, is appropriate to investigate system processes and to conclude management strategies that sustainably exploit the ground water resource while preserving the natural vegetation structure. The subsequent process of changing the model structure and comparing the outcomes with observed ecological and ecohydrological patterns proved to be appropriate to identify a reliable model structure with corresponding parameter combinations.

The different model versions, applied in this research, underlie different ecohydrological structures, illustrating that, in a model, the driving coexistence mechanism is defined by the model structure, whereas its robustness is controlled by the combination of the population parameters. Further, flood events can act as water resource or environmental disturbance or a combination of both. When acting as environmental disturbance the long term cycles of the flood regime strongly affect the robustness of the parameter combinations. This highlights the relevance of the long term memory of hydrological processes in water limited ecosystems such as those along ephemeral rivers.

The hydrological storage model was the same for all model versions. The distributions of average transpiration and depth to ground water were similar throughout the applied model versions, whereas their distributions of fluctuations were different. This suggests that the average values of hydrologic variables are probably influenced by the applied hydrological model, whereas the fluctuations of both are probably controlled by the applied ecological model.

The benefit of ecohydrological models appears, when assessing the consequences for the design of management strategies that aim to regulate both the water resource and the vegetation. This research underpins the necessity of using models that are explicit in the ecohydrological feedbacks and account for the differentiation in the responses of the species in a plant community. It illustrates that the range of application of integrated management strategies can be constrained to ecohydrological systems along ephemeral rivers that consist of plant species using different water resources and differing in their sensitivity to floods. Such heterogeneity in ecological traits of species is common in vegetation systems, highlighting the relevance of integrated management strategies.

Given that the best strategy, investigated in this research, is robust against uncertainty in the parameters of the flood regime, but strongly depends on the structure of the ecohydrological feedbacks between water and vegetation illustrates that a lack of information on the ecohydrological feedbacks is more critical for strategy planning than uncertainty in some parameters. Further, it indicates that, if a model gives satisfactory results (here the coexistence pattern), but for the wrong reasons, essential effects such as the ecohydrological feedbacks may be neglected and eventually lead to counterproductive management conclusions.

6.3 Outlook

This research illustrates that qualitative patterns can be considered and applied as integrated response of ecohydrological systems on time scales reaching from months to decades. While hydrological research often investigates processes on smaller time scale by using integrated system responses such as runoff or soil moisture, ecohydrological research promises to be a powerful tool, which uses "soft" information such as vegetation structure, to investigate processes leading to equilibrium patterns on a large time scale.

Future research in terms of ecohydrological feedbacks along ephemeral rivers should focus on both the generic, rather theoretical aspects, and the site specific, rather practical model modification. With regard to the generic aspects it can be hypothesised that the geological pool and riffle structure influences the composition of the plant community. In general the ground water flow is several orders of magnitude slower than the surface runoff. Therefore the sequences of ground water pools respond with a time lag and, hence, play a critical role as buffer mechanism. Further, it is not unusual that several small flood events occur successively. The species specific respond to this particular environmental disturbance probably enhances further coexistence mechanisms. However, to investigate this, the time scale needs to be decreased to weeks or days.

The adaption of the model to site specific requirements aims at the improved understanding of the influence of local ecohydrological feedbacks on the ecosystem structure. It can be hypothesised that ecological processes such as seed dispersal, plant recruitment and competition for water in the unsaturated soil layer are driven by hydrological processes such as frequency and intensity of overbank inundations, which eventually facilitates a site specific spatiotemporal species composition and age structure. On the other hand, these local ecosystem dynamics probably affect the statistics of total ecosystem transpiration, which is, however, comparatively little discussed and should, therefore, be also focused in future research.

Appendix of Chapter 2

Number of individuals

The number of adult individuals in population i ($N_{\text{Ind},i}$) was calculated to define the coexistence criterion for the parameter sampling (section 2.2.6):

$$N_{Ind,i} = \frac{R_i * A_{seq}}{R_{1,i}},$$
 (A1)

where $R_{1,i}$ denotes the reserve biomass of one adult individual of population *i*. We simplified the shape of an individual (reserve biomass above and below subsurface) to be a right circular cylinder with maximal trunk radius r_i , maximal height h_{max} and wood density ρ_i :

$$R_{1,i} = \pi * r_i^2 * h_{\max} * \rho_i \,. \tag{A2}$$

Appendix of Chapter 3

Conversion rate from reserve to green biomass

The conversion rate from reserve to green biomass, $w_{G,i}(t)$, is described by a sigmoid function that depends on the water volume in the alluvium that can be reached by the plant roots $(V_{WS,i}(t))$ and the total reserve biomass of the ecosystem in the previous time step

$$(R_{total}(t-1) = \sum_{i=1}^{n} R_i(t-1)):$$
(P1)

$$w_{G,i}(t) = \frac{u_i}{1 + e^{b_i(c_i - \frac{V_{WS,i}(t)}{R_{total}(t-1)})}},$$
(B1)

where a_i , b_i and c_i are the shape parameters of the sigmoid function, and *i* denotes the reference to a species.

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Selbständigkeitserklärung

Ich erkläre, dass ich die vorliegende Arbeit selbständig und unter Verwendung der angegebenen Hilfsmittel, persönlichen Mitteilungen und Quellen angefertigt habe.

Leipzig, 23. Dezember 2009

Sven Arnold

Lebenslauf

Sven Arnold wurde am 5. September 1980 in Karl-Marx-Stadt (jetzt Chemnitz), Deutschland geboren. Er besuchte das Johannes-Kepler-Gymnasium in Chemnitz bis 1999. Im Oktober 2000 nahm er das Studium der Geoökologie an der TU Bergakademie Freiberg auf. Bis zu seinem Abschluss als Dipl.-Geoökologe 2006 sammelte er praktische Erfahrungen bei seinen Auslandsaufenthalten in Brasilien (SINAENCO, Recife) und Australien (Centre for Mined Land Rehabilitation, Brisbane). Ab Ende 2006 war er als Doktorand am Helmholtz Zentrum für Umweltforschung GmbH in Leipzig angestellt. In dieser Zeit fertigte Sven Arnold an den Departments Hydrosystemmodellierung und Ökosystemanalyse unter der Betreuung von Prof. Dr. Sabine Attinger, PD Dr. habil. Karin Frank und Dr. Anke Hildebrandt die hier vorliegende Doktorarbeit an. Die Dissertation wurde im Dezember 2009 zur Erlangung des akademischen Grades doctor rerum naturalium an der Chemisch-Geowissenschaftlichen Fakultät der Friedrich-Schiller-Universität Jena eingereicht.

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