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Regeneration and utilization of *Faidherbia albida* and
Acacia erioloba along ephemeral rivers of Namibia

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To my parents

Regeneration and utilization of *Faidherbia albida* and *Acacia erioloba* along ephemeral rivers of Namibia

ABSTRACT

Faidherbia albida and *Acacia erioloba* are important fodder trees for the livestock of local farmers and wildlife along ephemeral rivers of the Namib Desert. In this study, the regeneration processes of the two tree species and their utilization by local resource users was studied in the ephemeral rivers Kuiseb, Omaruru and Ugab.

Total germination of *F. albida* seeds was highest after seeds were ingested and voided by goats (42.3 %) and oryx (40.5 %). *Acacia erioloba* seeds germinated highest (72.8 %) when ingested by oryx while goat-ingested *A. erioloba* seeds showed an early germination start but only 51.7 % germinated in total. Cattle ingestion did not increase overall seed germination or germination speed. With a seed burial experiment it was shown that seedling emergence of *F. albida* (55.2 %) and *A. erioloba* (92.8 %) was most successful at 5 cm burial depth compared to 10 and 15 cm.

Successfully emerged seedlings in the field exhibited accelerated root growth with age. *Faidherbia albida* roots had an average daily root growth of 0.9 cm and *A. erioloba* of 1.2 cm after 31 growth days, compared to 1.3 cm and respectively 1.5 cm after 63 days. A significant difference in the root/shoot ratios of both study species demonstrates a stronger root growth of both species in pure sand (*F. albida* 1.09, *A. erioloba* 0.47) compared to seedlings growing in sand with silt and/or clay (*F. albida* 0.43, *A. erioloba* 0.31).

The fitness and annual growth of juveniles indicate regeneration problems in areas with high livestock numbers. *Faidherbia albida* as well as the overall slower growing *A. erioloba* juveniles exhibited poor fitness and a low average annual height increase of 15.7 cm and 5.9 cm respectively at locations with high livestock density. In comparison juveniles of both species showed good fitness and an average annual height increase of up to 55.0 cm (*F. albida*) and 17.3 cm (*A. erioloba*) in areas with low livestock density. The damaging effect of livestock was further underlined by the large numbers of unprotected *F. albida* and *A. erioloba* seedlings (83-93 %) that were eaten in the field.

For both species, the active river channel does not present a safe environment for seedling establishment. In the active channel 83 % (*F. albida*) and 96 % (*A. erioloba*) of the 8-month old seedlings were eliminated during a subsequent flood event while successful establishment has occurred in the past at locations on the flood plains. *Faidherbia albida* prefers places close to the active channel: up to 85 % of the adult and juvenile trees were growing within 20 m of a clearly defined active watercourse. In contrast, *A. erioloba* successfully establishes at locations at >20 m distance from the channel (94 to 100 %).

An examination of the utilization of the two study species by the local resource users shows that particularly goat kids depend on *F. albida* and *A. erioloba* pods for fodder. Large *F. albida* trees produce ~ 175 kg of pods per year, while *A. erioloba* yields ~200 kg. This is equivalent to a market value of ~ 600 N\$ from pod sales or goat production for *F. albida* and ~200 N\$ from pod and ~700 N\$ from goat production for *A. erioloba*.

This study shows that the successful regeneration of *F. albida* and *A. erioloba* in the ephemeral rivers of Namibia is threatened by increasing land-use intensity. The growing threat to the tree population through reduced tree regeneration will limit the livelihoods of the local farmers in the future.

Regeneration und Nutzung von *Faidherbia albida* und *Acacia erioloba* entlang ephemerer Flüsse in Namibia

KURZFASSUNG

Faidherbia albida und *Acacia erioloba* sind wichtige Futterbäume für das Nutzvieh von Kleinbauern entlang ephemerer Flüsse in der Namib Wüste. Die vorliegende Arbeit untersucht Regenerationsprozesse von *F. albida* und *A. erioloba* und deren Nutzung in den ephemeren Flüssen Kuiseb, Omaruru und Ugab.

Die höchste Keimrate von *F. albida* Samen wurde von Samen erreicht die von Ziegen (42,3 %) und Oryxantilopen (40,5 %) gefressen und wieder ausgeschieden wurden. Auch *A. erioloba* Samen die von Oryxantilopen verzehrt wurden zeigten guten Keimungserfolg (72,8 %), wohingegen nach Ziegenverzehr nur 51,7 % keimten, jedoch ein früher Keimungsbeginn zu verzeichnen war. Samen die mit einer 10 cm dicken Substratschicht bedeckt waren, zeigten einen geringen Keimungserfolg (*F. albida* 2,4 %, *A. erioloba* 4,8 %) gegenüber einer 5 cm starken Bedeckung (*F. albida* 55,2 %, *A. erioloba* 92,8 %).

Das Wurzelwachstum von *F. albida* und *A. erioloba* Keimlingen beschleunigte sich mit steigendem Alter der Pflanzen. Im Alter von 31 Tagen nahm die Wurzellänge von *F. albida* Keimlingen um durchschnittlich 0,9 cm und nach 63 Tagen um 1,3 cm pro Tag zu. Die Wurzeln von *A. erioloba* Keimlingen wuchsen im Durchschnitt täglich 1,2 cm (31 Tage) im Vergleich zu 1,5 cm (63 Tage). Ein signifikanter Unterschied im Wurzel/Spross Verhältnis der Keimlinge belegt ein stärkeres Wurzelwachstum beider Arten in reinem Sand (*F. albida* 1,09, *A. erioloba* 0,47) gegenüber Sand mit Schluff und/oder Ton (*F. albida* 0,43, *A. erioloba* 0,31).

Der Gesundheitszustand (Fitness) und der jährliche Zuwachs von Jungpflanzen der beiden Baumarten belegen Regenerationsprobleme in Gebieten mit hohem Viehbesatz. *Faidherbia albida* als auch die langsamer wachsenden *A. erioloba* Jungpflanzen waren in schlechtem Zustand und hatten einen niedrigen durchschnittlichen jährlichen Höhenzuwachs von 15,7 cm bzw. 5,9 cm bei hoher Viehdichte. Im Vergleich dazu waren Jungpflanzen beider Arten in gutem Zustand mit einem Jahreszuwachs von 55,0 cm (*F. albida*) und 17,3 cm (*A. erioloba*) bei geringer Viehdichte. Der schädigende Einfluss des Viehs wird zudem durch die hohe Anzahl an gefressenen ungeschützten Keimlingen beider Baumarten (83-93 %) belegt.

Das eingeschnittene Flussbett ist im Vergleich zu den höherliegenden Ebenen ein ungünstiger Standort für die Etablierung der beiden Baumarten. Eine Folgeflut eliminierte 83 % (*F. albida*) bzw. 96 % (*A. erioloba*) der acht Monate alten, im Flussbett wachsenden Keimlinge. Auf den an das Flussbett angrenzenden Ebenen dagegen konnten sich die beiden Baumarten in der Vergangenheit etablieren. Dabei bevorzugt *F. albida* die näher am Flussbett liegenden Standorte: bis zu 85 % der Alt- und Jungpflanzen wuchsen im Abstand von bis zu 20 m vom Flussbett. *Acacia erioloba* Bestände (94 bis 100 %) finden sich dagegen hauptsächlich im Abstand von mehr als 20 m vom Flussbett.

Untersuchungen zur Nutzung von *F. albida* und *A. erioloba* ergaben, dass vor allem Ziegenlämmer auf die Früchte dieser Baumarten angewiesen sind. Große Bäume produzieren etwa 175 kg (*F. albida*) bzw. 200 kg (*A. erioloba*) Früchte pro Jahr. Dies entspricht einem derzeitigen Marktwert von ~600 N\$ (durch Ziegenproduktion sowie Fruchteverkauf) bei *F. albida* bzw. ~700 N\$ (Ziegenproduktion) und ~200 N\$ (Fruchteverkauf) bei *A. erioloba*.

Die vorliegende Arbeit zeigt, dass eine erfolgreiche Regeneration von *F. albida* und *A. erioloba* in den ephemeren Flüssen Namibias durch steigende Landnutzungsintensität gefährdet ist. Hohe Viehdichten bedrohen die Baumbestände und dadurch die Lebensgrundlage der lokalen Kleinbauern.

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ABBREVIATIONS

A	Area of river cross section (with minimal overbank height as lowest point)
ADMP	Annual dry matter production
Ae	<i>Acacia erioloba</i>
al	Adult livestock
AP	Annual pod production
AWB	Average dry weight per m ³ browse
AWP	Average dry weight of single pod
BW	Body weight
c	Cone
Cb	Crown base
D	Cross section distance
DDM	Daily dry matter
DWA	Department of Water Affairs
Fa	<i>Faidherbia albida</i>
GPS	Global Positioning System
HL	High livestock numbers
hs	Hemisphere
L	Lower riverine woodland of Kuiseb
LL	Low livestock numbers
LMV	Local market value
M	Middle riverine woodland of Kuiseb
m	Mannings' roughness coefficient
MAWF	Ministry of Agriculture, Water and Forestry
MBH	Maximum browse height
MV	Monetary value
n	Number of annual offspring of livestock
NBRI	National Botanical Research Institute
NP	Number of pods per m ³
osl	Annual offspring of livestock
P	Water production from bulk water abstraction
PB	Potential browse
PF	Productivity factor
Q	Discharge in m ³ /s
r	Crown radius, calculated from average crown diameter
SADC	South African Development Community
SE	Standard Error
S _o	Slope
U1	Upper 1 riverine woodland of Kuiseb
U2	Upper 2 riverine woodland of Kuiseb
UNCBD	United Nations Convention on Biological Diversity
UNCCD	United Nations Convention to Combat Desertification
UNFCCC	United Nations Framework Convention on Climate Change
V	Volume
V _c	Crown volume

1. INTRODUCTION

1.1 General introduction

Namibia is the driest country south of the Sahara. Its climate is arid to semi-arid and is characterized by highly unpredictable rainfall in space, time and amount. Within the borders of Namibia, terrestrial water sources are scarce. All interior rivers are ephemeral, while the perennial rivers are located along the southern and northern border of Namibia.

According to Jacobson (1997) and the WRC (2005), ephemeral rivers are predominant on a global scale, but are nevertheless the least understood. Ephemeral rivers occur mainly in the drylands of the world, where poverty and underdevelopment are often major challenging factors (Seely et al., 2003). In ephemeral rivers, water flow only occurs for hours up to a few days in the usually dry river bed before the channel dries up again. Sometimes no surface floods occur for several years (Jacobson et al., 1995; Seely et al., 2003).

Only 10 % of the inhabitants of Namibia use perennial rivers where water is available throughout the year, for their livelihoods. The other 90 % depend on ephemeral systems, including the 12 westward flowing ephemeral rivers of the Namib Desert (20 %) (Jacobson et al., 1995; NWRMR, 2000). Population growth, sedentarization as well as drought events are putting increasing pressure on the ephemeral rivers of Namibia (Jacobson et al., 1995; Seely et al., 1995; Seely et al., 2003). Although evidence is limited to date, it is foreseen that changes in the hydrologic regime, the driving force behind biological patterns and processes, will result in changes in the structure and functioning of the ephemeral river ecosystems (Jacobson, 1997). These changes, in addition to climate change, are expected to have huge impacts such as land degradation and desertification (Seely et al., 2003).

Namibia is signatory to the UN Convention on Biological Diversity (UNCBD), the Convention to Combat Desertification (UNCCD) and the Framework Convention of Climate Change (UNFCCC). With reference to the dry and sub-humid lands program of the UNCBD, 'Namibia's ten-year strategic plan of action for sustainable development through biodiversity conservation' addresses the need to understand the dynamics behind the ecological, physical and social processes of the dry

and sub-humid environments and to assess the consequences of their loss and change (UNCBD, 2000; Barnard et al., 2002). Objective 5 of this plan makes specific reference to Namibia's wetlands. It calls to adopt "measures improving the protection of wetland ecosystems, biological diversity and essential ecological processes, as well as improving the sustainability of wetland resource use and preventing wetland loss and degradation" (Barnard et al., 2002). The necessity for the sustainable development of Namibia's water bodies has also been realized by the Namibian Water Resource Management Review (NWRMR, 2000). In the frame of the new Water Resource Management Act (GRN, 2004), two ephemeral rivers have been selected to establish pilot basin management committees. The main objective is to bring all stakeholders together and develop a common vision and integrated approach for the water basin resource management. One of these committees was already successfully established in the Kuiseb River basin, the main research area in this study.

With regard to the high population growth and limited natural resources of Namibia, awareness raising of decision makers and resource users with regard to ephemeral river ecosystems is very important (Jacobson and Jacobson, 1995). So far, ephemeral rivers have been mostly ignored by governments and water authorities due to their limited surface flow despite their importance for people, livestock and wildlife and the nation as a whole (Seely et al., 2003). Nevertheless, efforts are made by many countries of the South African Development Community (SADC) to revise this. This is of especial importance as the situation in southern Africa could drastically change through increased aridity due to climate change. At present, policy guidelines and information to guide management and decision makers are missing or incomplete (Seely et al., 2003). The authors underline that the "major challenge... is to balance rights, expectations, responsibilities and opportunities of local people,....., with requirements of the ecosystem to maintain these desired services and with expectations and aspirations of the global community" (Seely et al., 2003). Over the past years, interest in understanding ephemeral river systems has increased, and a variety of activities as well as research has been carried out in ephemeral rivers in southern Africa.

Twelve of Namibia's ephemeral rivers cross the hyper-arid desert in an east-west direction and are often referred to as 'lifelines' (Jacobson and Jacobson, 1995; Jacobson et al., 1995; Kok and Nel, 1996; Jacobson, 1997). They present a vital habitat

for humans, livestock and wildlife in the otherwise harsh desert environment (Hamilton et al., 1977; Seely et al., 1980; Hamilton III, 1985; Jacobson et al., 1995; Jacobson, 1997). The rural communities living in the river catchments depend on the vegetation of catchment and river for their agricultural, both commercial and communal, and tourism activities. Large-scale mines, the coastal towns Walvis Bay and Swakopmund as well as the capital Windhoek depend on the ephemeral rivers for their water supply (Jacobson et al., 1995). As a consequence, the hydrological system of several ephemeral rivers has been altered through dam construction and water abstraction (Jacobson et al., 1995). At present, information concerning ephemeral rivers is still limited, making the development of management strategies and determination of sustainable abstraction rates difficult.

On a smaller scale, overuse and elimination of the vegetation of the ephemeral rivers is expected to have significant effects on the ephemeral river ecosystem and the livelihoods of the people living in these areas. A lack of recruitment of trees and shrubs in the ephemeral rivers has already been observed. A loss of the tree species *Faidherbia albida* and *Acacia erioloba*, two key resources of the ephemeral river ecosystem, would limit the capacity to support wild and domestic animals and the human population (Jacobson et al., 1995). Similar to acacia trees in the Middle East (Rohner and Ward, 1999), a biodiversity decline would also be expected. *Faidherbia albida* and *A. erioloba* have been acknowledged as valuable fodder species in many parts of Africa (Le Houérou, 1980; Walker, 1980; Baumer, 1983; CTFT, 1989; Dicko and Sikena, 1992; Barnes et al., 1997). However, the understanding of the basic life history and ecology of most organisms in the ephemeral river catchments is still too limited to ensure their sustainable use (Jacobson et al., 1995). The ecological, social and economic characteristics of ephemeral rivers need to be studied and understood for both conservation and development reasons (Seely et al., 2003). Knowledge of population dynamics, e.g., recruitment and survival of vegetation, is still missing (Jacobson et al., 1995). In addition to biophysical research, participatory research methods are strongly recommended to integrate local resource users.

This study investigates the key processes leading to successful regeneration and recruitment of *F. albida* and *A. erioloba* in ephemeral rivers, with specific focus on the Kuiseb River. Emphasis is given to the role of large herbivores, especially livestock,

and to flood related processes. Furthermore, the socio-economic contribution of the two tree species is assessed.

1.2 Research objectives and key questions

The ephemeral rivers of arid to semi-arid western Namibia are experiencing increasing pressure through unsustainable utilization of their natural resources. *Faidherbia albida* and *A. erioloba* are key resources for farmers, livestock and wildlife along these ephemeral rivers. Increasing livestock densities can have a negative influence on the vulnerable recruitment processes of these tree species and on peoples' livelihoods.

This research aims to contribute to the understanding and sustainable management of ephemeral river ecosystems of Namibia. Its purpose is to assess the influence of land use on the regeneration of *F. albida* and *A. erioloba* in the Kuiseb ephemeral river, with further reference to other ephemeral rivers. This is achieved by examining biophysical factors (vegetation, floods, soil) and relating them to the socio-economic situation of the communal farmers in selected areas. Figure 1.1 presents the linkages between the various factors.

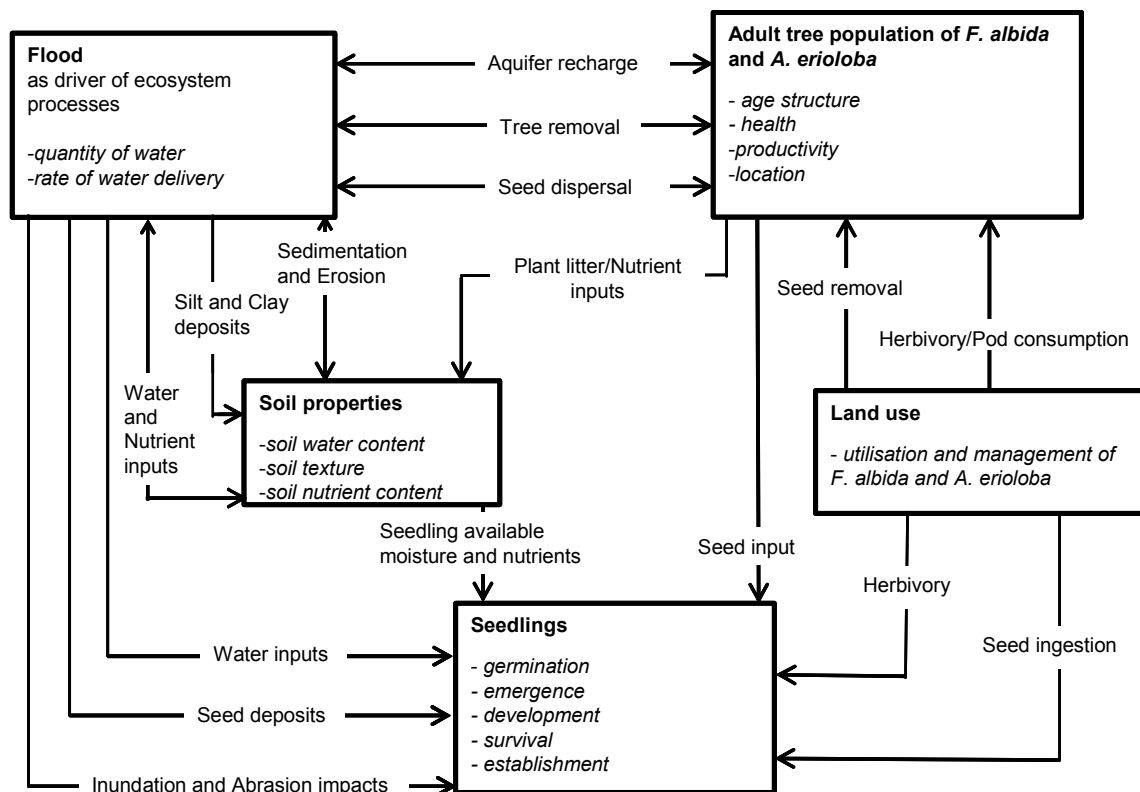


Figure 1.1: Linkages that determine tree regeneration in ephemeral rivers - a conceptual framework.

The following objectives are addressed in this study.

Objective 1

To determine abiotic and biotic factors relevant for *F. albida* and *A. erioloba* regeneration.

Key questions

1. Does seed ingestion have an influence on germination rate and success?
2. How deep can seeds be buried and still manage to germinate and emerge?
3. Is water a determining factor for seed germination and seedling growth?
4. Do soil characteristics (soil texture) influence seedling root and shoot growth?
5. Do seedlings utilize nitrogen from the air?

Objective 2

To determine influence of land use on regeneration of *F. albida* and *A. erioloba*.

Key questions

1. Is regeneration failing to take place?
 - a. Does size class distribution reflect disturbance of the population?
 - b. Do juvenile and adult densities differ?
2. How does livestock influence the survival of seedlings and juvenile growth?
3. Is the plant fitness of juvenile *F. albida* and *A. erioloba* influenced by land use?

Objective 3

To determine safe sites for *F. albida* and *A. erioloba* regeneration.

Key questions

1. What is the survival rate of seedlings after reflooding?
2. What discharge is needed to allow regeneration at elevated floodplains (safe sites) along the Kuiseb River?
3. Where is successful regeneration taking place across a river cross-section profile?

Objective 4

To describe the value of *F. albida* and *A. erioloba* for the communal farmers.

Key questions

1. How are the study species used by the communal farming population of three selected ephemeral rivers?
2. Do the local users apply any management strategies to sustainably use the resource?
3. What is the monetary value of the two study species?

1.3 Literature Review

1.3.1 Ephemeral rivers

Floods of ephemeral rivers are "characterized by their magnitude, duration, total flow volume and number and magnitude of discharge peaks during the flood" (Jacobson, 1997). Ephemeral rivers have an unpredictable and erratic flow regime triggered by highly variable rainfall in the river catchment. Surface flow lasts from days to weeks and occurs during the rainy season, but years can be floodless if rains are not sufficient (Jacobson, 1997; Seely et al., 2003). In ephemeral rivers, water level and discharge increase until rainfall ceases after which evaporation and infiltration lead to a decrease in the flood volume until the surface water disappears (WRC, 2005). Characteristic of the ephemeral river floods are a fast expansion downriver and a downstream decrease in water availability and stream power (hydrologic decay). This differs from perennial systems, where water is available throughout the year and lateral inundation typical after a slow rise in stage (Jacobson, 1997) (Figure 1.2). In perennial rivers, lateral inundation of the riparian habitat occurs seasonally after heavy rainfall or snow-melts in the mountains (Mertes, 2005). Along ephemeral rivers, inundations are less predictable and might only occur once within several years (Jacobson, 1997). The discharge in perennial rivers is also less variable, while in ephemeral systems it decreases downstream due to infiltration and evaporation (Jacobson et al., 1995).

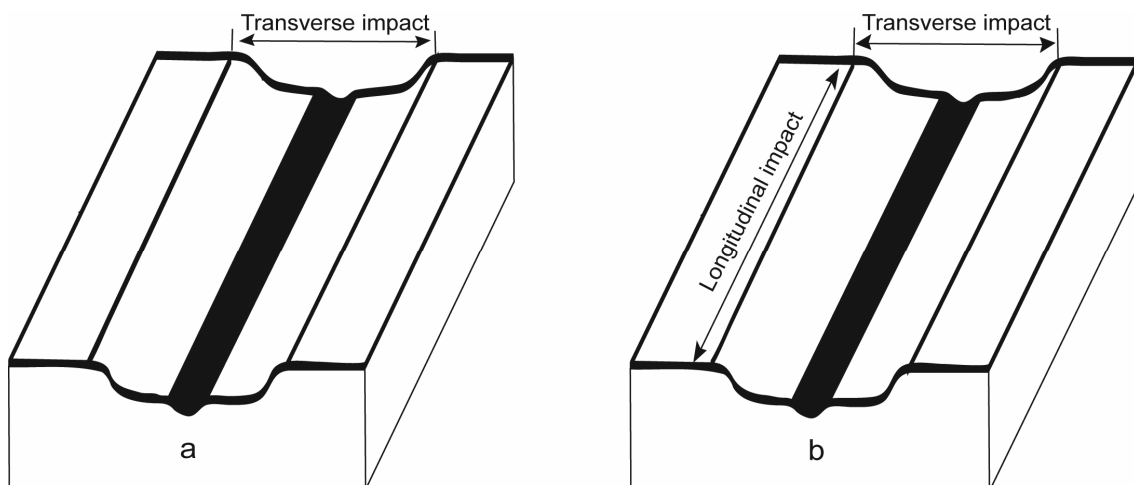


Figure 1.2: Direction of the major influence of surface floods in (a) perennial (transverse) and (b) ephemeral rivers (longitudinal and transverse) (adapted from Bendix, 1994b).

Surface and subsurface water provided by ephemeral rivers is important for the natural biodiversity in drylands, e.g., for vegetation and other biota (Seely et al., 2003). The rare surface flows contribute to many biotic and abiotic patterns and processes: Sediments are eroded or deposited, organic material is transported and retained, habitats are created or destroyed, food sources for fauna are created, enhanced or even diminished (Jacobson, 1997; Jacobson et al., 1999; Friedman and Lee, 2002). The surface floods are crucial for the groundwater recharge of the underlying ephemeral river aquifer, which can store large volumes of water (Jacobson et al., 1995; Seely et al., 2003). It is very difficult to measure this recharge due to site-specific features such as rainfall intensity, soil condition and moisture, surface topography, vegetation cover, land use as well as water table and aquifer characteristics (Christelis and Struckmeier, 2001). This makes it difficult to compute sustainable groundwater use (Seely et al., 2003). The groundwater aquifers provide comparatively secure access to water through boreholes and pumps, which allows permanent settlements, sedentary livestock farming, irrigation and industrial activities (Jacobson et al., 1995; Seely et al., 2003). Nevertheless, these activities are in constant competition for water with the environment, flora and fauna (Seely et al., 1980; Ward and Breen, 1983; Seely et al., 2003). Seely et al. (2003) emphasize that "water consumption should be carefully weighed against the value of the riparian vegetation". Altering the flow patterns through water impoundments in the upper reaches can have long-term impacts on the complex ephemeral system. The effects are various, e.g., reduced inflow of nutrient material and generally reduced productivity of the system (Agnew and Anderson, 1992; Seely et al., 2003). Impacts on aquifer recharge, channel morphology and vegetation structure and distribution can also be expected (Friedman and Lee, 2002; Seely et al., 2003). Limited data concerning historic flood events coupled with high variability make it difficult to understand and sustainably manage ephemeral rivers (WRC, 2005).

Classification of non-perennial rivers has been attempted by many authors. In the work of Uys and O'Keefe (1997), rivers are classified along a continuum gradient from intermittent, seasonal to episodic stream. The continuum is related to flow variability, which increases towards the episodic state, while flow predictability decreases. In ephemeral rivers, floods are related to unpredictable rainfall events, dry periods last longer than floods, and within five years floods occur in most years. This

differs from episodic rivers, which might not flow within a five-year period, and floods occur only after extreme precipitation high in the catchment. Jacobson (1997) defined ephemeral rivers as watercourses with a measurable discharge of less than 10 % per year. Boulton et al. (2000) distinguished between ephemeral, intermittent or temporary and semi-permanent streams. In South Africa non-perennial rivers were classified as semi-permanent (no surface flow for 1-25 % of time), ephemeral (no surface flow for 26-75 % of time) and episodic (no surface flow for at least 76 % of time) although there is still dispute under the experts and only limited scientific proof. Under the South African classification many rivers in Namibia would be considered episodic instead of ephemeral, e.g. Kuiseb River (WRC, 2005). Until a unified classification system is established, the term ephemeral will be applied in this work, but the South African classification will be kept in mind.

1.3.2 Riparian habitats

According to Naiman et al. (1993), "natural riparian corridors are the most diverse, dynamic and complex biophysical habitats on the terrestrial portion of the earth". Riparian habitats are highly acknowledged for their contribution to biodiversity (Risser, 1990; Naiman et al., 1993) and structural diversity of habitats (Smith et al. 1993). They are further important for humans, wildlife and other biota (Jacobson et al., 1995; Seely et al., 2003).

The vegetation growing along perennial and ephemeral river systems is supported by the available surface and groundwater. According to Baker (2005) ephemeral streams do not have the hydrologic conditions to support true riparian vegetation compared to perennial ones. The author underlines that along ephemeral rivers the vegetation does not require the high soil moisture and water availability as in perennial systems and can therefore not be considered as truly riparian. This study follows the definition of CDOW (2004) who consider plant communities affected by and growing adjacent to perennial or ephemeral water bodies, such as rivers, as riparian. Furthermore, riparian vegetation is characterized as distinctly different to the neighboring upland vegetation. Although the habitats along perennial rivers differ from ephemeral ones and support different riparian vegetation as well as an aquatic

ecosystem (Figure 1.3), the riparian habitats have both similar characteristics and functions.

Riparian landscapes are formed through combined hydrological, geomorphologic and ecological processes (Malanson, 1993; Naiman et al., 1993) and display steep environmental gradients (Naiman et al., 1993). The dynamics and ecological characteristics of the riparian zones are closely interlinked with and regulated by streamflow, sedimentation and woody debris (Naiman et al., 1993). The authors describe riparian corridors as zones that stretch over the entire stream channel uplands as far as elevated water tables or floods might reach and where soils are able to hold water. Riparian corridors provide very diverse habitats, landforms and communities as well as ecosystem services (Naiman and Décamps, 1990; Naiman et al., 1993). They present important pathways for plants and animals, especially in ephemeral rivers (Hamilton et al., 1977; Seely et al., 1980; Hamilton III, 1985).

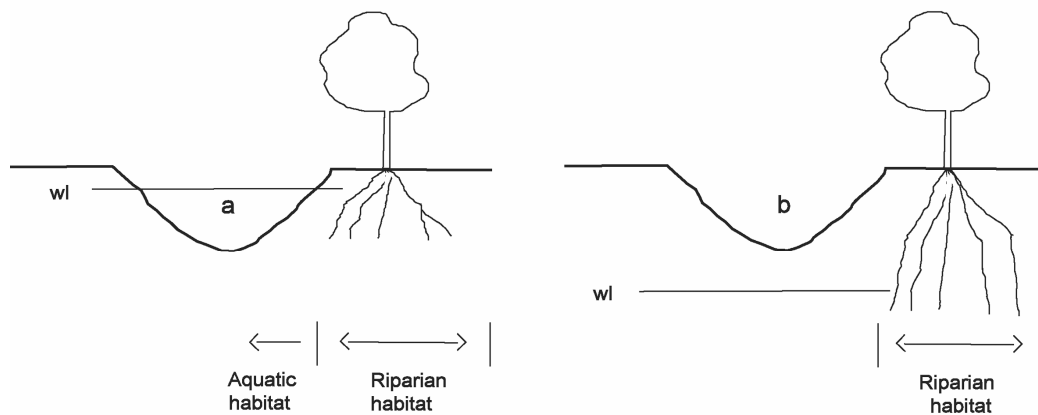


Figure 1.3: Schematic diagram of a perennial (a) and ephemeral (b) riparian habitat, wl illustrates the surface and subsurface water level (adapted from Baker, 2005).

According to Asplund and Gooch (1988), the concept of biological succession is difficult to apply to riparian zones (with special reference to riparian zones in Southwest America). The authors argue that habitat disturbance and instability is not a criterion for biological succession, which they define as habitat/species change through biological activity of a sequence of species. No real biological succession with species replacement takes place in riparian zones. The riparian tree community is in a perpetual succession due to persistent and predictable disturbance events. The situation in riparian

zones can be described as a non-equilibrium situation where periodic population reductions and environmental fluctuations prevent the process of competitive equilibrium (Huston, 1979). In general, equilibrium is difficult to achieve in a landscape where disturbance events affect large parts of it (Sprugel, 1991).

The main driving and influencing factor of the riparian corridors and the distribution of vegetation is the streamflow (Franz and Bazzaz, 1977; Friedman and Lee, 2002). Floods are not only responsible for the destruction of old vegetation patches but also for the creation of new ones (Naiman et al., 1993; Friedman and Lee, 2002; WRC, 2005). In the South African ephemeral Nyl River, spatial distribution of specific plant species and communities is influenced by the variation in flood events (Higgins et al., 1996). Woody debris influences the water flow of the stream and thereby nutrient inflow, sedimentation and channel morphology (Jacobson et al., 1999). Strong vertical and lateral gradients are visible in the riparian vegetation, triggered by floods events variable in time and scale (Franz and Bazzaz, 1977). Annually, sediments are redistributed and sorted, and channel morphology is changed through floods (Friedman and Lee, 2002). In non-perennial, ephemeral and episodic rivers the dynamics of the lateral zones of flood banks depend on the frequency of inundation (WRC, 2005). In perennial river systems, these dynamics are the main factors influencing the riparian vegetation, but compared to ephemeral rivers these effects are probably of a smaller scale.

Surface floods bring water and nutrients into the system, replenish the groundwater (Jacobson et al., 1995) and rejuvenate ephemeral watercourses and the associated drylands (Friedman and Lee, 2002). These surface flows are unpredictable in space and time and are crucial for germination and establishment of riparian vegetation (Jacobson et al., 1995). In order to survive, riparian vegetation needs to have access to a constant groundwater source. Structure, productivity as well as spatial and temporal distribution of vegetation along lateral and longitudinal gradients depend on magnitude, frequency, duration and total volume of these floods (Jacobson, 1997; Seely et al., 2003).

Especially in arid countries, the riparian corridors have always attracted people and wildlife (Naiman et al., 1993; Seely et al., 2003) and increasingly do so (Seely et al., 2003). Within one kilometer of these riparian oases, often more than half of the

population of a country derives its livelihoods from the available natural resources (Naiman et al., 1993). Riparian habitats also present an attraction for tourism and tourism activities due to their scenic environment and biodiversity value (Seely et al., 2003).

Much of the riparian vegetation in more developed areas of the world has been destroyed in the process of development activities, industrialization and economic growth. Alteration to the landscape and to the hydrologic regimes has affected the dynamics of fundamental processes maintaining the riparian corridors (Naiman et al., 1993). Today, the consequences are apparent, and costly efforts are undertaken to restore these habitats to their natural condition. In South Africa, the increase in ephemeral rivers systems due to climate conditions, geomorphology and human influence (WRC, 2005) puts increasing stress on the riparian vegetation. For ephemeral river ecosystems it can be expected that alterations to the flow regimes will lead to reduced productivity and desertification (Seely et al., 2003). The large variability of flood events in space and time together with the lack of long-term flood data makes it increasingly difficult, as pressure on them increases, to understand and manage the resources of ephemeral rivers (Seely et al., 2003). It is therefore crucial for science and politics to recognize the importance of riparian landscapes for ecosystem processes as well as for regional biodiversity (Naiman et al., 1993).

1.3.3 Plant regeneration

Regeneration is a crucial process in plant community dynamics (Grime and Hillier, 1992). Factors such as pollination, flower production, seed production and dispersal as well as favorable climate conditions are important preconditions for regeneration. Grime and Hillier (1992) therefore suggest including regeneration processes in descriptive models at the landscape scale. To date, most research on the dynamics of riparian vegetation has been carried out on perennial rivers. Even though many of these findings can be applied to ephemeral rivers, the unique characteristics of these rivers need to be taken into consideration (Figure 1.4). In ephemeral rivers, suitable climate conditions for successful regeneration are rare and might only exist once in a lifetime of a plant. Seedlings need to display both vigorous above- and below-ground growth. The developing root systems need to use the available soil moisture to reach permanently

wet horizons (e.g., groundwater), and the shoots of the plant need to be well developed to survive subsequent flooding (Jacobson et al., 1995).

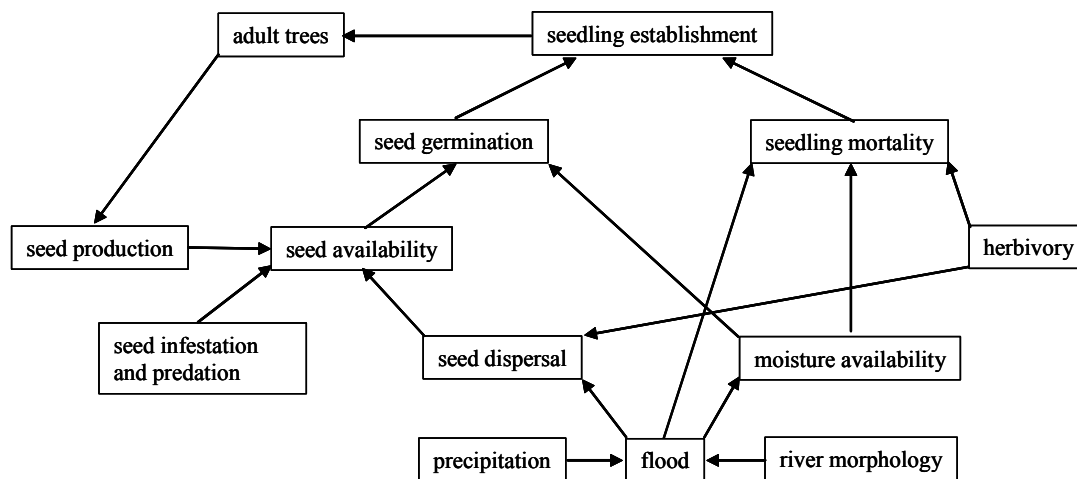


Figure 1.4: Schematic diagram of the processes leading to seedling establishment in an ephemeral river (adapted from Wiegand et al., 1999). The direction of the effects is indicated by arrows.

Asplund and Gooch (1988) describe riparian habitats as both "resilient and delicate". In fluvial systems, perennial and ephemeral, environments for riparian vegetation are continuously both created and destroyed. Through fluvial geomorphic processes, sediments are either accumulated or eroded, thereby creating or destroying sites for potential seedling establishment (McBride and Strahan, 1984; Barsoum, 2002).

Water plays a major role in the distribution, establishment and survival of riparian vegetation (McBride and Strahan, 1984). The flood water disperses and deposits seeds downstream (hydrochory). Depending on the timing and magnitude of the flood and the buoyancy of the seeds or pods, these may be deposited laterally on elevated landforms, where conditions for germination and establishment are more favorable (Schneider and Sharitz, 1988; Pettit and Froend, 2001; Barsoum, 2002). This is especially important for areas where frequent and destructive floods remove riparian vegetation and soil (Pettit and Froend, 2001). Inundation and battering of established seedlings by flood sediments (McBride and Strahan, 1984), erosion and abrasion of sediments where seedlings have established are some of the factors that influence survival of seedlings in riparian habitats. Seedlings established at low elevation on the floodplain are especially vulnerable (Barsoum, 2002). For riparian vegetation, seed fall is the primary dispersal mechanism, enhanced through secondary dispersal by water

(Pettit and Froend, 2001). Downstream and up-slope dispersal is, according to Pettit and Froend (2001), crucial in finding 'safe sites' for germination and establishment and presents an important recruitment mechanism. Large floods not only destroy but also can create potential 'safe sites' for germination and establishment through removal of competing riparian vegetation (Pettit and Froend, 2001; Barsoum, 2002).

In other habitats, germination usually occurs at sites and times that are advantageous for the establishment and future maturation of seedlings (Asplund and Gooch, 1988). With regard to riparian habitats, the authors found that this elementary principle of reproduction does not apply. A moist substrate which is suitable for germination is mainly found close to the watercourse, yet these sites are also the ones that are affected by flash flooding, which limits the continuous survival of the seedlings. Seedlings that managed to establish further away from the main channel have a chance to survive due to reduced influence of scouring and abrasion (Asplund and Gooch, 1988). In general, after establishment, seedling survival is dependent on an environment without extremes, which means neither high nor low water flow (Barsoum, 2002).

1.3.4 Flood pulse concept and disturbance ecology

The flood pulse concept (periodic inundation and drought) has been mainly used to describe the dynamics of perennial systems. Floods are the main driving force behind river ecosystem processes and responsible for the provision of organic matter and nutrients (Naiman et al., 1993) to river and floodplain (Walker et al., 1995). Walker et al. (1995) argue that the flood pulse concept alone does not best describe a perennial river. Two concepts need to be incorporated: The river continuum concept describes longitudinal linkages (upstream-downstream) in the upper reaches of a large river, while lateral linkages (river-floodplain) dominate the system in the lower reaches (flood pulse concept).

With regard to dryland rivers, there are two contradicting opinions concerning the relevance of the flood pulse concept. Junk et al. (1989) argue that the flood pulse concept is difficult to apply to dryland rivers due to the variability of the flood pulse itself. The adaptation of organisms in systems with variable and unpredictable pulses is reduced or prevented. Walker et al. (1995), on the other hand, point out that many biota in dryland river systems display life-history strategies such as opportunism and

flexibility, which the authors regard as adaptation strategies to unpredictable pulses. This view is supported by Jacobson (1997), who worked in the ephemeral river systems of Namibia. Naiman et al. (1993) also point out that the ecological and evolutionary significance of flood pulse does not depend on their regularity. Walker et al. (1995) and Jacobson (1997) agree that floods are of great significance for all processes in the riparian system, disregarding their variability in space and time.

Surface floods within ephemeral river ecosystems can be considered as "key ecological organizers responsible for the existence, productivity, and interactions of the main biotic elements" (Jacobson, 1997). When applying the flood pulse concept to ephemeral rivers, longitudinal linkages might be of even greater importance than lateral ones (Jacobson, 1997), and hydrological regulations are suggested to have significant influence on flood pulses (Walker et al., 1995; Middleton, 2002).

Disturbance ecologists regard fire, storm, floods, etc., as natural disturbance events variable in space and time that are important for community structure, dynamics and species diversity (Sousa, 1984; Pickett and White, 1985; Sprugel, 1991; Begon et al., 1996;). The intermediate disturbance hypothesis by Connell (1978) states that species diversity is highest under intermediate levels of disturbance. A high level of disturbance frequency will limit diversity to stress-tolerant species and created gaps will remain at a pioneer stage. The same diversity limiting effect has a low frequency, which leads to species exclusion through competition (Begon et al., 1996). Similarly, it has been found that low and high disturbance intensity will lead to reduced diversity. A burning experiment in South Africa regarding the effect of scale upon species diversity found that the scale of disturbance correlates with diversity but that it does not follow the intermediate disturbance hypothesis of Connell. The highest diversity was found at a large scale of disturbance but with a low frequency, (Schwilk et al., 1997). According to Reynolds et al. (1993), the difficulty in recognizing and measuring disturbance makes the intermediate disturbance hypothesis a difficult concept. Ward and Stanford (1983) support the intermediate disturbance hypothesis and found that in a stream habitat species diversity is suppressed if disturbance events are severe. For ephemeral rivers, Jacobson (1997) suggests not viewing flood pulses as disturbance. The author supports the view of Junk et al. (1989), who consider rather the absence of flood pulse as a disturbance of a floodplain-river ecosystem.

2. STUDY AREAS AND SPECIES

2.1 Ecology of the ephemeral river catchments in western Namibia

Twelve of Namibia's ephemeral rivers are situated in the arid west, crossing the hyper-arid Namib Desert in an east to west direction. They all exhibit a tremendous environmental gradient (topography and climate) from their inland headwaters to their river deltas. The extreme hydrology of these ephemeral rivers makes them according to Jacobson (1997) "the driest and most variable rivers yet described". Average annual rainfall, catchment size (between 2000 and 30,000 km²) and upstream dams influence the frequency of flooding (Jacobson et al., 1995). All ephemeral rivers in western Namibia have their headwaters in better watered highland areas further inland and end in the Atlantic Ocean or in the Central Namib Sand Sea (Stengel, 1964; Stengel, 1966; Jacobson et al., 1995). The precipitation falling in the upper catchment up to the western escarpment (see Figure 2.5) is the main water source of floods in the ephemeral rivers. Only on rare occasions is there enough rainfall in the lower reaches of the catchments to contribute to surface floods (Stengel, 1964; Stengel, 1966; Jacobson et al., 1995; Jacobson, 1997).

Average annual rainfall in the headwaters of the ephemeral rivers ranges from 100 to 400 mm and declines to 0-50 mm towards the coast (Stengel, 1964; Stengel, 1966). The rainy season lasts from October to May, with peak rainfall usually occurring from January to March, which are the hot summer months of Namibia (Schulze, 1969; Jacobson, 1997). Water-saturated clouds move in from the Indian Ocean and release their moisture in the form of strong convective rainfall events (Logan, 1960; Tyson, 1986). On their way, the clouds lose most of their moisture, which decreases even further towards the west. Due to the steep drop from the escarpment zone to the desert plains (approx. 1000 m), the remaining relative humidity is further lost through adiabatic heating. This results in a steep climatic gradient with increased variability of rainfall events in an east to west direction. Closer to the coast, this effect is emphasized through inversion. Air low in moisture warms and rises up, allowing cool and dry air from the cold Benguela current to flow east. This results in cool, dry air close to the ground and moist, warm air above. This situation is relatively stable and is only reversed when rare climatic conditions, mainly at the beginning and end of the summer,

result in a breakdown of the inversion (Logan, 1960). In addition to the summer rains, the three southern-most ephemeral rivers can also experience winter rainfall (Kuisseb, Tsondab, Tsauchab) (Jacobson et al., 1995).

Even though each ephemeral river is unique with its own typical climatic, biological, geographic (Jacobson et al., 1995), geological, geomorphological, hydrological characteristics and variation, they all have underlying similarities. All these rivers have surface bedrocks, small streams and springs associated with geological formations (Jacobson et al., 1995), sparse vegetation, and thin and poor soils throughout their catchments (Jacobson, 1997). Typically, in the upper reaches of the ephemeral rivers, the channel is narrower and subject to more frequent flooding compared to the lower reaches, which broaden considerably. This influences the distribution of riparian vegetation, which occurs in denser stands in the lower reaches due to reduced disturbance and uprooting by flooding events (Jacobson et al., 1995).

The Damara Sequence, a group of rocks approximately 500 to 850 million years old, is underlying most of the western catchments. After tectonical activities such as folding, faulting and erosion, these rocks were covered by sediments. This period of sedimentation was followed by extended erosion activities. The northern ephemeral rivers are characterized by mountains and folds (Damara Orogen), which have originated from the collision of the Congo Craton and the South American continent (Swart, 1992). The characteristic canyons of the southern ephemeral rivers (e.g., Kuisseb, Swakop) were created approximately 2 to 4 million years ago, initiated by epeirogenic uplift and erosion activities (Ward, 1987).

Despite geological differences in the various catchments, the soils of the ephemeral river floodplains are alluvial in the Fluvent suborder, and their composition depends upon the magnitude of flood events as well as on the source material transported and deposited (Jacobson et al., 1995; Jacobson et al., 2000a). Sands, silts and clays are transported with the floods and deposited in the middle and lower reaches of the river (Jacobson et al., 2000a). These soils are mostly sands or loamy sands with organic matter-rich silts (10-20 %) and alternating layers of fluvial and aeolian sand as well as gravels (Jacobson et al., 1995; Jacobson et al., 2000a). These silt and clay layers can sometimes limit infiltration and therefore act as a "hydraulic barrier" in the otherwise well-drained substrate (Jacobson et al., 2000a). Furthermore, organic material

and nutrients are transported by the floods (Jacobson et al., 2000b). Large elements such as logs are deposited first, while finer organic material is left in the middle and lower reaches due to reduced stream power and decreased flood volume downstream (hydrologic decay) (Jacobson et al., 1995; Jacobson et al., 1999; Jacobson et al., 2000b). It is expected that the deposition patterns of sediments, organic material and nutrients create longitudinal as well as lateral patterns, which are reflected in the riparian communities, their composition and productivity (Jacobson et al., 2000a).

For the ephemeral rivers in western Namibia, data concerning floods, flood discharge and flood volume is available for the time since 1970, with some gauging stations being established as early as the mid 1960's. These stations are maintained and the data are managed by the Department of Water Affairs (Ministry of Agriculture, Water and Forestry). Typical for the ephemeral rivers is a distinct curvilinear relationship "between many flow characteristics and distance downstream" that has been established by Jacobson (1997). He further describes this trend as "the most distinctive hydrologic feature" of the ephemeral rivers of Namibia. From the rivers headwater until the western escarpment, flow volume increases, while it decreases in the Namib Desert plains. Increasing aridity together with hydrologic decay is responsible for increasing flood variability downstream. A corresponding curvilinear relationship of distance and hydrologic characteristics was observed for mean discharge, individual flood duration and total annual flow days (Jacobson, 1997).

Water users along these ephemeral rivers often manage their water in different ways, thus causing different impacts. Dams and groundwater abstraction from the aquifer are used for industry, agriculture and water supplies for urban communities (Seely et al., 2003). In contrast, small-scale farmers mainly depend on local boreholes to access the hardrock aquifer groundwater for their daily consumption and farming activities. The impoundments in the upper reaches of several ephemeral rivers can reduce or eliminate downstream flow, reduce flood volume and peak discharges as well as aquifer recharge (Jacobson et al., 1995). Groundwater depth in these ephemeral rivers can vary from near surface to a depth of more than 10 m (Jacobson et al., 1995). Changes in the groundwater recharge due to climate change, river impoundments in the upper reaches or water abstraction (see Figure 2.2) may have a negative influence on the riparian vegetation, possibly causing die-off of trees (Seely et al., 1980; Ward and

Breen, 1983). Typical woody riparian vegetation of the ephemeral rivers of western Namibia includes indigenous plants such as *Acacia erioloba*, *Euclea pseudobenus*, *Faidherbia albida*, *Ficus spp.*, *Salvadora persica*, *Tamarix usneoides*, *Combretum imberbe*, *Colophospermum mopane* and *Hyphaene petersiana* but also invasive species (e.g., *Prosopis glandulosa*) (Giess, 1962; Giess, 1971; Jacobson et al., 1995).

2.2 Land use and land-use history of the ephemeral river catchments

Historically, there is evidence of people living as nomadic hunter-gatherers in the western catchments dating back to the Pleistocene (Shackley, 1983). Nomadic hunting and gathering was essential to cope with the high climate variability of the western catchments in search of food and water (Kinahan, 1990). Archaeological sites were found near inselbergs and for example along the three most southern ephemeral rivers of the Namib Desert (Kuisseb, Tsondab and Tsauchab). It is expected that throughout most of the Pleistocene, people and wildlife migrated along these rivers as water and food availability demanded (Shackley, 1983; Sandelowsky, 1974). These nomadic patterns have only changed in the past four thousand years with the introduction of livestock from northern parts of Africa, which initiated agricultural development and a change from nomadic hunter-gatherers to nomadic pastoralists and finally to sedentary subsistence farming (Sandelowsky et al., 1979; Kinahan, 1990; Kinahan, 1991). The beginning of colonization in 1884 marked the disappearance of nomadic pastoralism. In 1915, Germany handed over the colony to South Africa, which governed the country on behalf of the League of the Nations from 1920 onwards. This started the South African segregation policy in Namibia, which was carried out under the Union Land Settlement Act of 1912 and South Africa's Native Land Act of 1913. Black people were resettled into reserves/homelands (Lau and Rainer, 1993) and were only allowed to live and farm in areas allocated to them. The reserve areas were mainly located in areas where conditions were less favorable for farming (Adams et al., 1990). In contrast, white farmers were encouraged to establish commercial farms in favorable areas previously occupied by black farmers and were supported in their activities by a variety of subsidies (Adams et al., 1990; Lau and Rainer, 1993; Rohde, 1993). These areas were mostly situated in the upper reaches of the catchments, where higher precipitation rates allowed sedentary European farming systems. In 1964, the South African authorities

introduced the Odendaal Plan to combine and enlarge established ethnic homelands. This further weakened the economic independence of Namibia's communities (Jacobson et al., 1995). After a long struggle, Namibia finally gained independence on March 21, 1990.

Today, the land tenure situation in the catchments still reflects the more than 70-year-long process of colonization, segregation and resettlement. Within the catchments, three main land-tenure systems prevail: privately owned farmlands mainly in the upper eastern reaches, communally owned farmland in the middle and lower reaches and conservation or tourism areas in the most western areas. Eight out of the 12 ephemeral rivers have their headwaters in private farmland, 10 rivers pass through communal land and all of them have their river deltas in conservation or tourism areas (Jacobson et al., 1995).

Commercial farmers derive their livelihoods from livestock farming in fenced pastures on farms large enough to allow for seasonal stock rotation. In communal farming areas, livestock roams freely, either herded or unherded, and contributes to household food security and plays an important role as a symbol for status and wealth (Næraa et al., 1993). The process of resettlement of the black population in low-productive areas also affects farming practices. Access to areas with higher rainfall further inland was prohibited by boundaries and made nomadic pastoralism in a west to east direction impossible. Furthermore, the establishment of boreholes as reliable and permanent water sources for humans and livestock permitted a more sedentary farming system, with water not being a limiting factor. This resulted in increasing pressure on the limited fodder sources within the catchments. The functioning of the catchments as ecological units was thereby interrupted (Jacobson et al., 1995). This was further aggravated by the establishment of ground dams and river impoundments in the upper reaches, supported by subsidies during the apartheid era (Lau and Rainer, 1993).

2.3 Study site selection and study areas

The Kuiseb, Omaruru and Ugab rivers were selected as study sites out of the 12 ephemeral rivers in western Namibia. The Kuiseb River was chosen as the main study area due to a database of 40 years of research, making this river one of the best researched ephemeral rivers. The Omaruru and Ugab rivers are the nearest suitable neighbors to the Kuiseb River.

2.3.1 The Kuiseb ephemeral river

The Kuiseb ephemeral river (Table 2.2) is one of the major westward flowing ephemeral rivers of Namibia. Presently it is monitored along 6 gauging stations, 4 of them located in the main stem Kuiseb River. The other 2 operational stations are located in the tributaries and monitor water flow into the middle Kuiseb River. Most stations were established in 1977/1978 (Jacobson, 1997); however, historic flood events have been observed and described since 1837 (Stengel, 1964). Between 1837 and 1963, the Kuiseb reached the Atlantic Ocean 15 times (Stengel, 1964) and then once more in 2000 (personal observation). Floods usually occur between December and April and can last for several days before receding (Table 2.1). In November 2004, the earliest-ever recorded flood event took place (Henschel, personal communication).

Table 2.1: Flood recordings at Gobabeb from 1962-2005. Total number of days with flowing surface water recorded per flood season (October-April) (Source: Gobabeb Training and Research Centre)

Season	Total days of flood	Season	Total days of flood	Season	Total days of flood
1962-63	68	1977-78	7	1992-93	23
1963-64	0	1978-79	8	1993-94	6
1964-65	26	1979-1980	0	1994-95	17
1965-66	18	1980-81	0	1995-96	3
1966-67	22	1981-82	0	1996-97	33
1967-68	11	1982-83	0	1997-98	4
1968-69	18	1983-84	0	1998-99	7
1969-1970	1	1984-85	0	1999-2000	23
1970-71	34	1985-86	18	2000-01	4
1971-72	43	1986-87	9	2001-02	8
1972-73	15	1987-88	20	2002-03	4
1973-74	102	1988-89	9	2003-04	6
1974-75	10	1989-1990	25	2004-05	15
1975-76	61	1990-91	6		
1976-77	8	1991-92	4		

The number of floods per year and the total recorded floods decrease downstream while transmission losses increase considerably. At the upper-most gauging station (Friedenau), a total of 118 floods and an average of 7.9 floods per year were recorded. At the Rooibank gauging station, the last one before the Delta, this declines to a total of 13 floods and an average of 0.9 annual flood events. This longitudinal trend is not reflected in the average flood days, which is 3.7 d at Friedenau, 11.1 d at Schlesien and 2.2 d at Rooibank (58 km, 304 km and 530 km from headwaters) (Jacobson et al., 1999). Between Gobabeb (479 km from headwaters) and the Rooibank Weir, the authors calculated transmission losses of an average 86 %.

Table 2.2: Kuiseb ephemeral river characteristics (Jacobson et al., 1995)

Characteristic	Data
Catchment area	15 500 km ²
River length	~560 km
Elevation range	0-2081 m
Precipitation range	0-335 mm
Gauging points on river	14 (6 operational)
Common riparian vegetation	<i>Acacia erioloba</i> , <i>Acanthosicyos horridus</i> , <i>Euclea pseudobenus</i> , <i>Faidherbia albida</i> , <i>Ficus spp.</i> , <i>Salvadora persica</i> , <i>Tamarix usneoides</i>
Total population	24,935
Land tenure	private 63 % (109 private farms), communal 0 %, park 37 % (inhabited by the rural Topnaar community)
Political regions	Erongo, Khomas

The Kuiseb River has its headwaters in the Khomas Hochland at an elevation of around 2000 m (Stengel, 1964; Jacobson et al., 1995). It forms a natural border between the southern Sand Sea desert and the northern Gravel Plain desert. Regular floods carry away the dune sand blown into the river by wind and maintain the river course (Seely et al., 1980). The Khomas Hochland receives an average of 100-400 mm, the escarpment zone 50-100 mm (Stengel, 1964) and all other areas between 15-75 mm annual rainfall (Seely et al., 1980). Precipitation in the Khomas Hochland and the escarpment zone is the main contribution to the river flow of the Kuiseb, while rainfall in the other areas is usually too low to be of significance (Seely et al., 1980). From the

Khomas Hochland to the Kuiseb Canyon, the river has cut its present bed more than 200 m into schist and quartzite (Late Precambrian metasediments) (Marker, 1977; Ward, 1987) and often flows over exposed bedrock at an average channel slope of 0.0034 m/m over 280 river kilometers (Jacobson, 1997). Approximately 150 km from the coast, the canyon features become less distinct, and a sandy channel with flood plains begins to form with only few bedrock outcrops crossing the channel (Theron et al., 1980; Huntley, 1985; Ward, 1987). At the Gobabeb Weir, the channel broadens into a wide and shallow valley before it reaches the delta, which is dominated by many small indistinct channels and low dunes (Theron et al., 1980; Huntley, 1985; Jacobson, 1997). Within the canyon, the river channel is less than 100 m wide and starts to broaden approximately 45 km east of Gobabeb. A maximum river width of more than 3 km was measured by Seely et al. (1980). Theron et al. (1980) and Huntley (1985) defined several subsections of the Kuiseb River according to climatic, geological and hydrologic characteristics (Figure 2.1):

- Khomas Hochland and escarpment zone (~ 230 km)
- Kuiseb Canyon (~ 130 km)
- Upper riverine woodland (Harubes to Gobabeb gauging weir) (~ 50 km)
- Middle riverine woodland (Gobabeb gauging weir to Swartbank) (~ 30 km)
- Lower riverine woodland (Swartbank to Rooibank) (~ 40 km))
- Kuiseb Delta (~ 30 km)

In this study, the upper riverine woodland was further divided into two riverine woodlands (Harubes to Homeb and Homeb to Gobabeb Weir) (U1, U2) (Figure 2.1). This distinction was made following Seely et al. (1980), who reported an increasing patchiness of the vegetation from Homeb in an upriver direction. Furthermore, the four sections differ in their hydrological characteristics:

In the upper riverine woodland U1, floods are strong and frequent and the groundwater table is relatively high. The active channel is deeply incised with narrow flood plains high above the channel. A similar flood frequency is found in the upper riverine woodland U2 (Jacobson, 1997), with groundwater depth around 4-6 m (Henschel, personal communication). In this section the active river channel widens and the floodplains are broader and less elevated above the channel. In the middle riverine

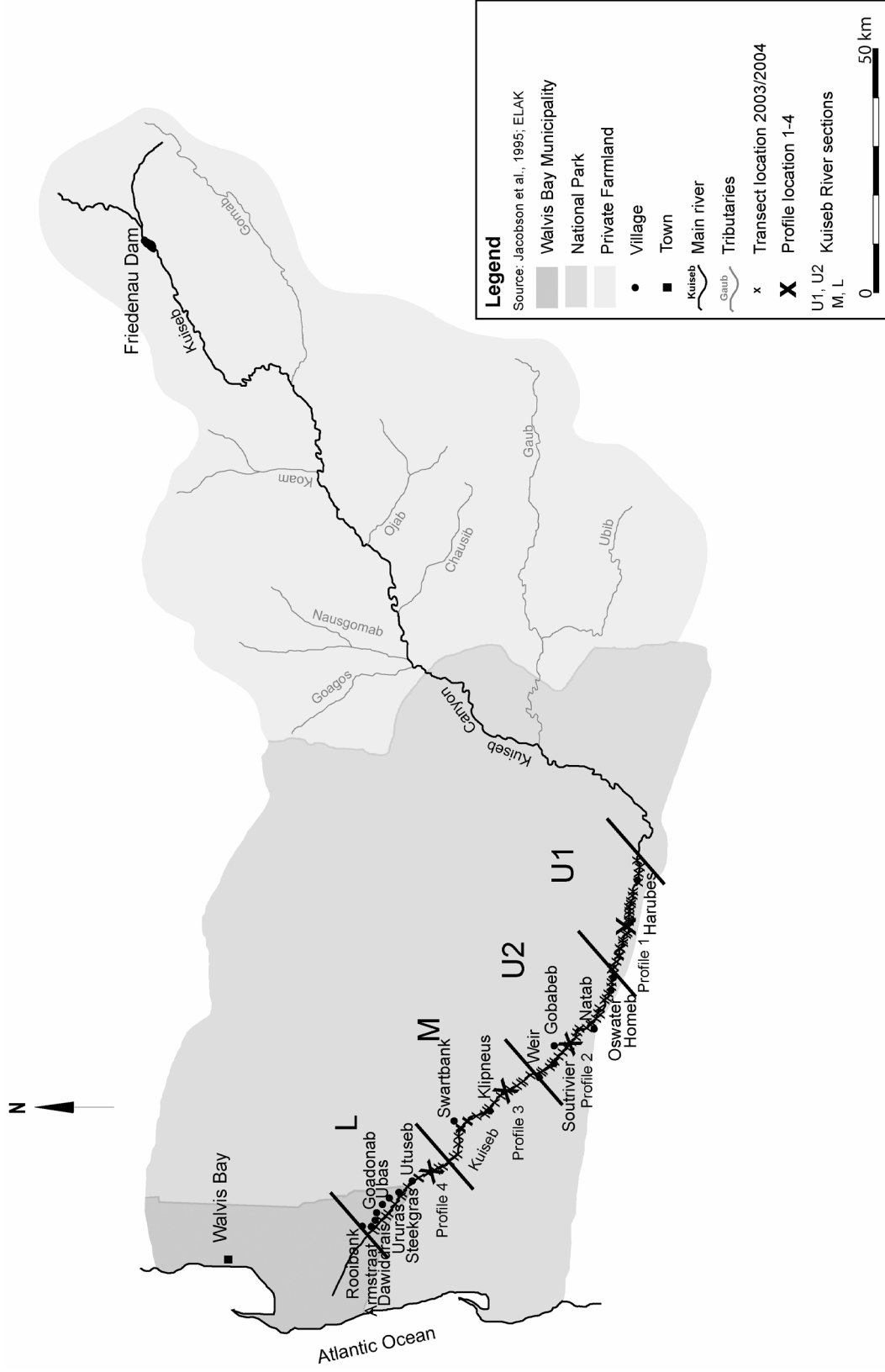


Figure 2.1: Kuseib River catchment with main river stem and tributaries. Villages and four river sections differing in livestock densities (U1, U2, M, L) are demarcated and locations of the study sites marked with x.

woodland M, deeper water tables and fewer and smaller surface floods are characteristic for this section (Lenz et al., 1995; Jacobson, 1997) as well as wide, expanding floodplains. A drop of the water table was recorded between 1972 and 1992/93 (Lenz et al., 1995). This decline could be the result of reduced floods that were not strong enough to recharge the aquifer. It could be expected that exceptional surface floods such as in 2000 are needed to recharge the aquifer sufficiently. During drought years, a groundwater drop would gradually occur caused by local water abstraction and transpiration of the vegetation (Bate and Walker, 1993). Characteristic for the lower riverine woodland L is the bulkwater abstraction scheme, which has led to a continuous drop in groundwater table from 7 to 15 m over the past decades (Figure 2.2). In this section, the main active channel splits up in several smaller channel-like structures intersecting the broad floodplains.

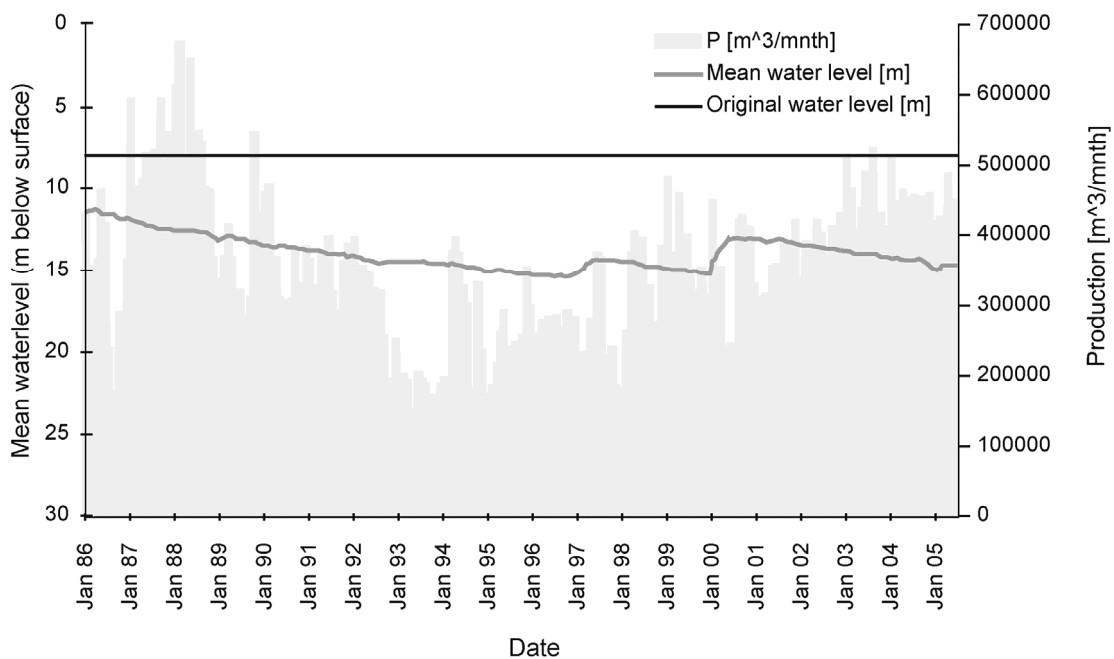


Figure 2.2: Water production (P) [$\text{m}^3\text{mnth}^{-1}$] and water level changes [m] from 1986-2005 at NamWater abstraction sites Swartbank/Rooibank A, Kuiseb River, (van Wyk, NamWater). The original water level before water abstraction started is indicated by a black line.

Vegetation

The riverine woodlands of the Kuiseb are mainly formed by *Acacia erioloba*, *Acanthosicyos horridus*, *Euclea pseudobenus*, *Faidherbia albida*, *Ficus spp.*, *Salvadora persica* and *Tamarix usneoides* (Jacobson et al., 1995). Even though these trees are all indigenous to southern Africa, none of them is a true desert species (Seely et al., 1980). Access to groundwater allows them to flourish in an otherwise desert environment. Theron et al. (1980) described 14 plant communities and 40 variations of the riparian vegetation of the Kuiseb. The authors determined a well developed *F. albida* community in the upper and middle riparian woodlands. *Faidherbia albida* grow close to the main river channel or occur as individuals in the main channel (Seely et al., 1980; Theron et al., 1980; Theron et al., 1985; Jacobson et al., 1995; Jacobson, 1997). In the lower riparian woodland, *F. albida* is found as a solitary tree. *Acacia erioloba* communities dominate the broader floodplains of the middle and lower woodlands but also occur as individuals on the narrower floodplains of the upper riparian woodlands.

In the river sections where the channel broadens and the floods are slower, non-woody perennial vegetation often dominates. Downriver from Gobabeb, *Cladoraphis spinosa* covers extensive parts of the river channel (Seely et al., 1980; Theron et al., 1980; Theron et al., 1985; Jacobson, 1997). The shrub *Pechuel-loeschea leubnitziae* occurs in the channel and on the floodplain (Jacobson, 1997) together with alien herbaceous species such as *Datura innoxia*, *Datura stramonium*, *Nicotiana glauca* and *Ricinus communis*. The lack of strong floods in the middle and lower riverine woodland areas allows small sand dunes to develop, which support dune species such as *Stipagrostis sabulicola* and *Acanthosicyos horridus* (Seely et al., 1980).

People and livestock

The catchments of the ephemeral rivers of the Namib Desert are home to approximately 20 % of the Namibian population, who live and depend directly or indirectly on these rivers for their livelihoods (Jacobson et al., 1995). The resources of the Kuiseb River are shared by commercial farmers in the upper catchment, communal farmers in the middle catchment and residents and industries of Walvis Bay in the lower catchment (Jacobson et al., 1995; WRC, 2005). The Topnaar community along the middle reaches of the river makes a living from subsistence farming. They are often referred to as the rural Topnaar

or !Khuseb ≠Aonin (Henschel et al., 2004). The vegetation of the Kuiseb River is essential for their survival.

Table 2.3: Population development of the Topnaar community along the Kuiseb River from 1957-2001 (Jenkins and Brain, 1967; Köhler, 1969; Dentlinger, 1983; CSO, 1994; Botelle and Kowalski, 1995; CO, 2002)

Year	1957	1966	1978	1991	1994	2001
Total number	197	133	213	332	384	262

The Topnaar (Table 2.3) are a Nama tribe of Khoekhoen origin and one of the oldest ethnic groups of Namibia. For 400 years, they live in the Namib Desert as hunter-gatherers and pastoralists. Traditionally, they used to live a semi-nomadic lifestyle, which changed to a more sedentary life with the establishment of boreholes (Botelle and Kowalski, 1995).

Table 2.4: Numbers of animals of different livestock types along the Kuiseb River (Jenkins and Brain, 1967; Köhler, 1969; Dentlinger, 1983; DVS, 1983-1993/1995-1996; Kooitje, personal communication)

Year	Goats	Sheep	Cattle	Donkey
1957	2008	-	58	235
1966	1754	-	-	-
1978	1435	73	29	-
1983	1814	19	117	112
1984	1849	19	117	-
1985	983	2	81	90
1986	1199	5	90	86
1987	879	3	83	67
1988	1444	2	82	63
1989	1,615	2	105	64
1990	2165	2	128	90
1991	2310	20	154	110
1992	2351	29	169	125
1993	2374	30	163	120
1995	1575	12	334	150
1996	1326	10	316	150
2002	3023	110	156	270
2003	3455	172	213	210
2004	3268	147	134	283

Conflicts arise from bulk water abstractions between Swartbank and Rooibank for urban and industrial use (Henschel et al., 2004), which have resulted in lowered water tables (see Figure 2.2). Today, half of the traditional areas of the Topnaar are situated in the Namib Naukluft Park (Botelle and Kowalski, 1995). This is a unique situation, but also restricts rural development activities due to park regulations (Botelle and Kowalski 1995; Henschel et al., 2004). The livelihood of the rural Topnaar largely depends on subsistence farming with goats and cattle (Table 2.4) and traditional harvesting and processing of the !nara fruit (*Acanthosicyos horridus*) (Dentlinger, 1983; Moser and Henschel, 2004).

2.3.2 The Omaruru ephemeral river

Water from the Omaruru River (Figure 2.3) is abstracted to supply Rössing Uranium Mine and Hentjes Bay as well as Swakopmund (Jacobson et al. 1995). The characteristics of the Omaruru catchment are presented in Table 2.6.

Table 2.5: Omaruru ephemeral river characteristics (Jacobson et al. 1995)

Characteristic	Data
Catchment area	13 100 km ²
River length	330 km
Elevation range	0-2082 m
Precipitation range	0-375 mm
Gauging points on river	5
Common riparian vegetation	<i>Acacia erioloba</i> , <i>Euclea pseudobenus</i> , <i>Faidherbia albida</i> , <i>Salvadora persica</i> , <i>Tamarix usneoides</i> , <i>Ficus spp.</i> , <i>Combretum imberbe</i>
Total population	11,990
Land tenure	private 46 % (private farms 102), communal 52 %, park 2 %
Political regions	Otjozondjupa, Erongo

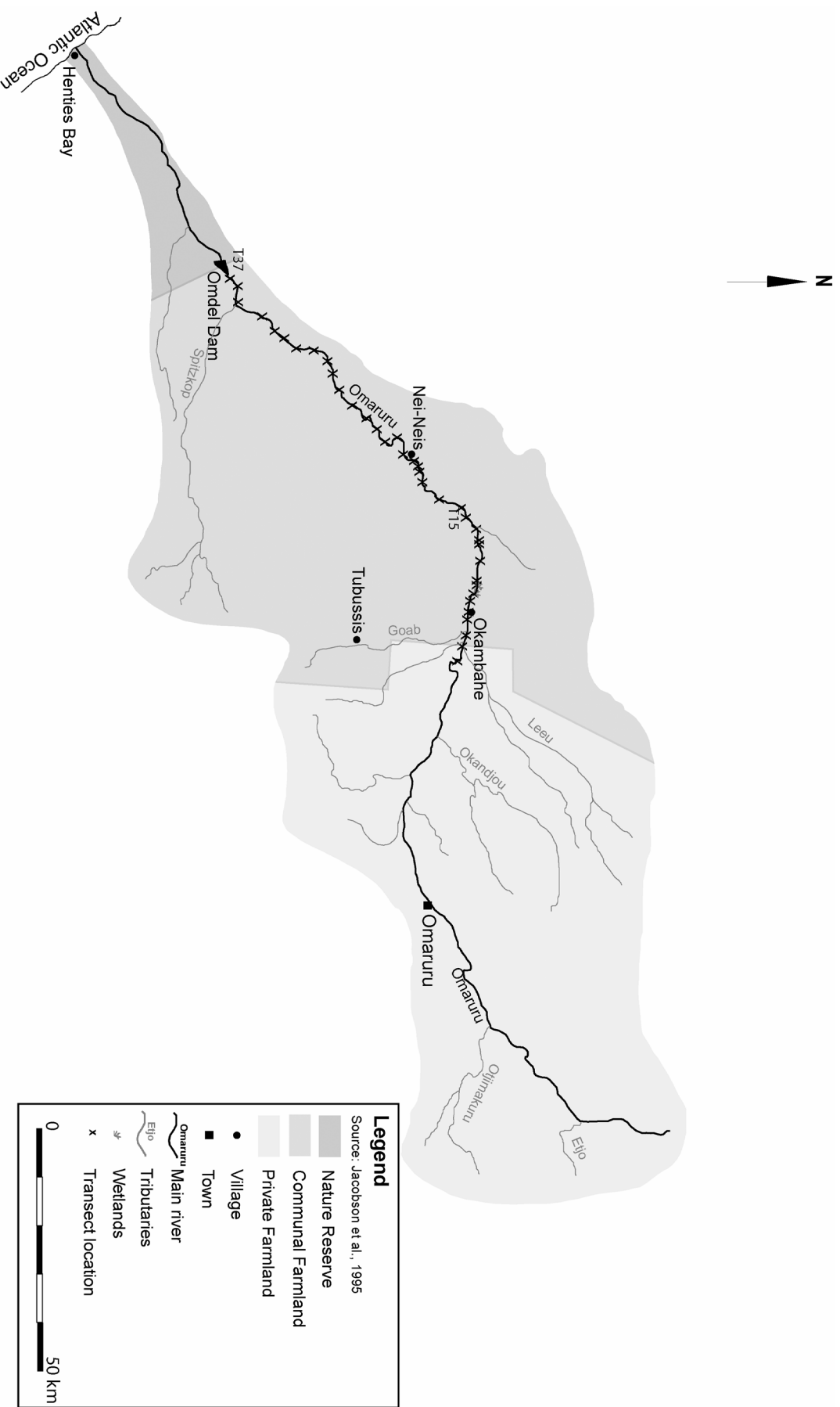


Figure 2.3: Omaruru river catchment with main river stem and tributaries. Locations of the study sites are marked with x.

2.3.3 The Ugab ephemeral river

Agriculture and tourism are two of the major activities in the Ugab ephemeral river catchment. Special features of the Ugab (Figure 2.4) are its scenic environment in the lower reaches and the presence of rhinoceros and desert elephants. Characteristics of the Ugab River are presented in Table 2.6.

Table 2.6: Ugab ephemeral river characteristics (Jacobson et al. 1995)

Characteristic	Data
Catchment area	28 400 km ²
River length	450 km
Elevation range	0-1865 m
Precipitation range	0-535 mm
Gauging points on river	7
Common riparian vegetation	<i>Acacia erioloba</i> , <i>Euclea pseudobenus</i> , <i>Faidherbia albida</i> , <i>Salvadora persica</i> , <i>Tamarix usneoides</i> , <i>Combretum imberbe</i> , <i>Colospermum mopane</i>
Total population	34,460
Land tenure	private 60 % (private farms 292) communal 38 %, Park 2 %
Political regions	Otjozondjupa, Erongo, Kunene

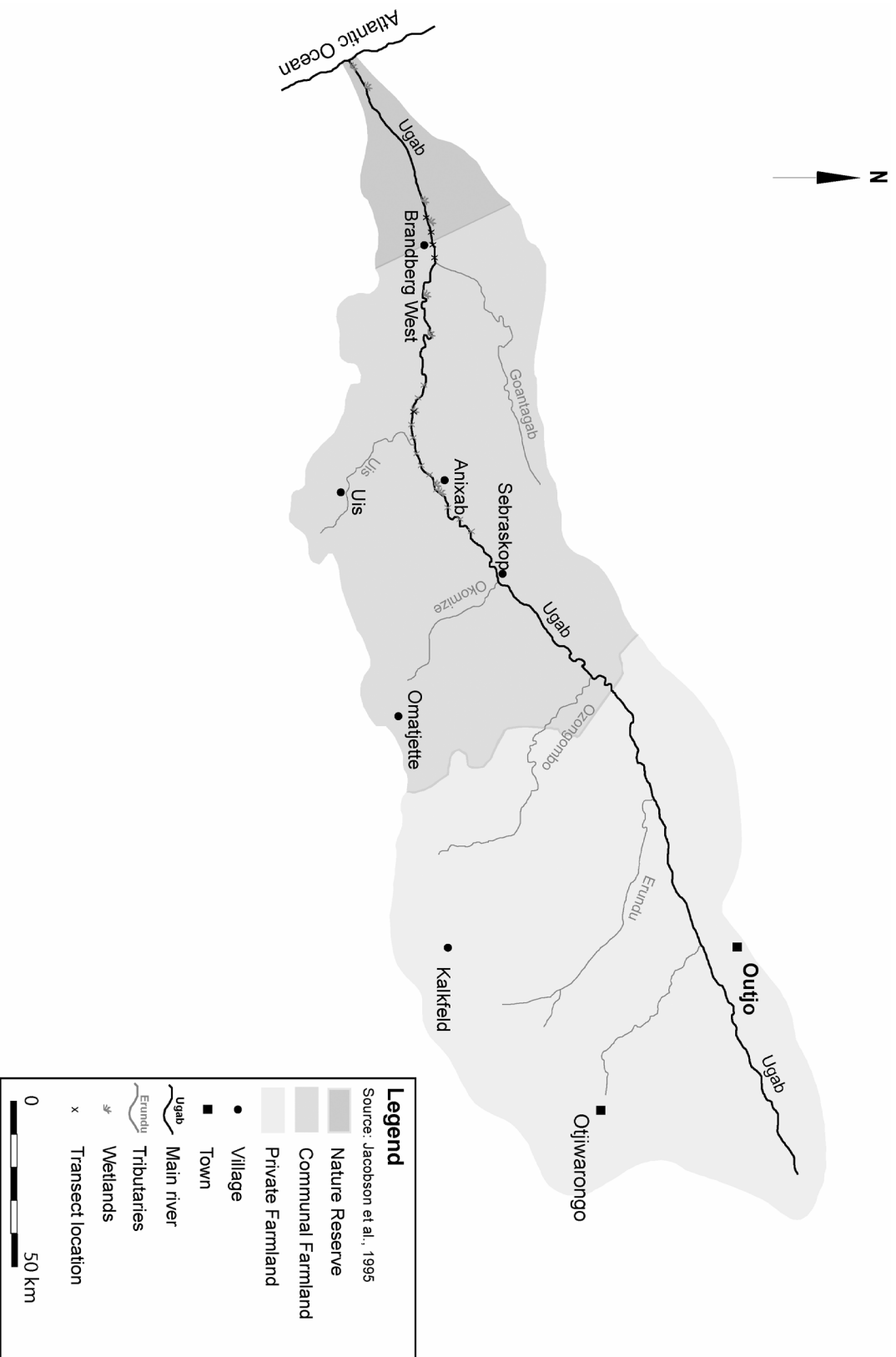


Figure 2.4: Ugab river catchment with main river stem and tributaries. Locations of the study sites are marked with x.

2.4 Study species

Faidherbia albida and *Acacia erioloba* are two of the dominating tree species of the ephemeral river ecosystem in west Namibia and of great economic and ecological importance (Leggett, 1992; Leggett, 1993; Jacobson et al., 1995; Leggett et al., 2001). Both species are found throughout Africa and provide browse and pods as fodder for livestock and wild animals, as well as building material, medicinal products and shade. The distribution of the two species in Namibia is illustrated in Figure 2.5.

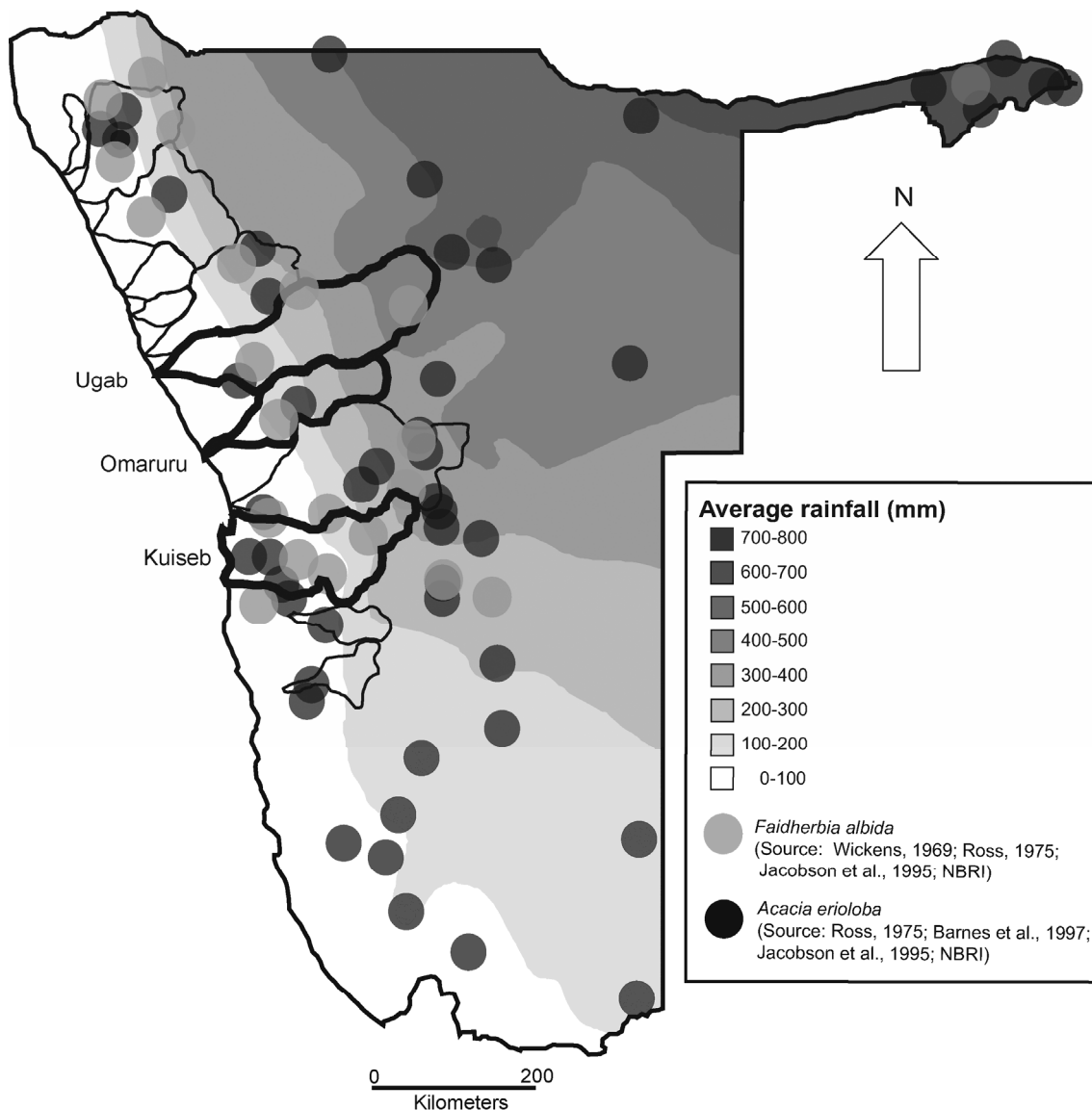


Figure 2.5: Distribution of *Faidherbia albida* and *Acacia erioloba* trees in Namibia and outlines of the catchment areas of the ephemeral rivers of the Namib Desert (the Kuiseb, Omaruru and Ugab ephemeral river catchments are marked with bold outlines). The map also shows the average annual rainfall in Namibia.

2.4.1 *Faidherbia albida* (Del.) A. Chev. (Family Leguminosae, subfamily Mimosoideae)

Faidherbia albida, a pioneer tree on low-lying sandbanks (Dunham, 1989), is often considered a critical species for conservation practices in arid and semi-arid regions (CTFT, 1989). Throughout its distribution range in Africa, *F. albida* prefers sites that are associated with water, e.g., along rivers, at the edges of lakes and ponds with alluvial deep sandy soils such as the alluvial soils of floodplains (Feely, 1965; CTFT, 1989; Coates-Palgrave, 2002). Especially in its southern and eastern habitats, *F. albida* is part of well defined riverine habitats, while in its western distribution it also grows away from the river banks (Wickens, 1969). The origin of *F. albida* is still disputed. Wickens (1969) supports the theory that *F. albida* originates from riparian environments in eastern and southern Africa and not from northern Africa.

In Namibia, *F. albida* is commonly found as solitary trees or in dense stands along ephemeral watercourses (Wickens, 1969; Theron et al., 1980; Theron et al., 1985). It is known under the following names: winterthorn, white thorn, apple-ring acacia, anaboom (Afrikaans) and anahais (Nama) (CTFT, 1989; Eiseb et al., 1991; Timberlake et al., 1999).

Faidherbia albida (Figure 2.6) is a fast growing large tree and can reach a size of over 20 m height with a crown of approximately the same size (Ross, 1975; Carr, 1976; CTFT, 1989; Leggett et al., 2001; Coates-Palgrave, 2002). Van den Eynden et al. (1992) reported trees even higher than 30 m and stem diameters at breast height can exceed 1-2 m (Wickens, 1969; Ross, 1975; Carr, 1976; Leggett et al., 2001). The bark of young individuals is smooth and whitish grey in color and becomes brown to whitish grey and more cork-like with time (Ross, 1975; Carr, 1976; CTFT, 1989; Coates-Palgrave, 2002). The tree can live to an age of 70 to 90 years with individuals being reported as old as 150 years (Wickens, 1969; CTFT, 1989). *Faidherbia albida* has long cream-white to yellow flowers (3.5-16 cm long), which produce orange-reddish/brown pods (see Figure 2.6). The indehiscent pods are spiral shaped and contain dark brown seeds. The seeds are 10 mm x 6 mm in size and can remain viable for many years. Three months after flowering, the pods are shed. The blue or grey-green bipinnate leaves are between 3 and 7.5 cm long (rachis) and 2-8 cm wide and consist of 2-12 pairs of pinnae, each between 2.5 and 5.5 cm long with 6 to 23 pairs of leaflets. Thorns can be up to

3 cm long, are thickened at their base and develop in pairs at the base of the leaves (Wickens, 1969; Ross, 1975; Carr, 1976; CTFT, 1989; Coates-Palgrave, 2002).



Figure 2.6: Mature *Faidherbia albida* tree (a), flowers (b) and pods (c).

In ephemeral rivers, *F. albida* does not shed its foliage completely at the end of the dry season/start of the rainy season as it does in other regions (Wickens, 1969; van Wyk et al., 1985; CTFT, 1989). Van Wyk et al. (1985) observed foliage on trees along the Kuiseb throughout the year, although *F. albida* partly sheds its leaves during the wet season (October-March). Leaves and flowers grow mainly during the dry season

(from April to October); the main flowering season is from June to August. Pod fall has been observed to peak between November and January, but can occur more or less the entire year (Table 2.7) (Seely et al., 1980; van Wyk et al., 1985).

The tree has strong and fast growing tap roots to secure permanent water availability (Bate and Walker, 1980). Even though its ecological optimum is in areas with annual rainfall of 500 to 800 mm (CTFT, 1989), in the ephemeral rivers of Namibia the tree grows in areas with less than 20 mm annual rainfall, depending entirely on surface floods and groundwater (Seely et al., 1980; Jacobson et al., 1995).

Table 2.7: Annual phenology change of *Faidherbia albida* along the Kuiseb River, degree of shading indicates phenology presence and intensity (white=not present; light grey=present but low intensity, dark grey=present and high intensity) (van Wyk et al., 1985)

Phenology	J	F	M	A	M	J	J	A	S	O	N	D
Inflorescence	Light grey	Light grey	White	White	White	Dark grey	Dark grey	Dark grey	Light grey	Light grey	Light grey	Light grey
Green pods	Light grey	Light grey	Light grey	White	White	White	White	Light grey	Dark grey	Dark grey	Light grey	Light grey
Pod fall	Dark grey	Light grey	Light grey	Light grey	Light grey	Light grey	Light grey	White	White	White	Dark grey	Dark grey

An important ecological aspect is the species' influence on wood retention in the ephemeral river channels and that it is a source of coarse particulate organic matter (Jacobson et al., 1999). In contrast to other areas (CTFT, 1989), no nutrient accumulation under *F. albida* trees could be observed in the floodplain of the Kuiseb River (Abrams et al., 1997). The authors write that flood events probably homogenize the nutrient content under the trees through deposition and erosion of organic and inorganic matter. Furthermore, *F. albida* is a fodder plant for both domestic and wild animals (Feely, 1965; Jenkins and Brain, 1967; Ross, 1975; Hamilton et al., 1977; Seely et al., 1980; Hamilton III, 1985; Huntley, 1985; CTFT, 1989; Jacobson et al., 1995; Jacobson, 1997; Fennessy et al., 2001; Coates-Palgrave, 2002), especially during the dry season when other fodder sources such as grass are scarce (CTFT, 1989; Leggett et al., 2001; Coates-Palgrave, 2002). A pod output of up to 7623 kg per hectare has been calculated in well developed *F. albida* stands along the Kuiseb River (van Wyk et al., 1985) with an average of 180-200 kg of pods per large tree (Seely et al., 1980; Jacobson et al., 1995; Jacobson 1997). Further research showed that *F. albida* pods and leaves

provide twice the net energy and larger amounts of protein than dry grass (CTFT, 1989), and farmers collect the pods to feed their livestock (Jacobson et al., 1995). In times of famine, the *F. albida* seeds were also used for human consumption (Dentlinger, 1983; CTFT, 1989; van den Eynden et al., 1992).

Other uses include medicinal and building purposes. In East and West Africa, the bark and roots of *F. albida* have been reportedly used against respiration infections, colds and influenza, digestion problems, kidney and bladder illnesses, malaria and other fevers. The wood is used for building houses or for the production of mortars, canoes, furniture or drums (CTFT, 1989). Many of the constructions along the Kuiseb River, e.g., kraals and houses, are made from *F. albida* wood (Jacobson et al., 1995).

2.4.2 *Acacia erioloba* E. Mey. (Family Leguminosae, subfamily Mimosoideae)

The Namibian common names of *Acacia erioloba* are camel thorn or giraffe thorn (English), kameeldoring (Afrikaans), omumbonde (Herero), omuande (Kwanyama), //ganab (Nama) or munto ghutu (Kavango) (Eiseb et al., 1991; Barnes et al., 1997; Coates-Palgrave, 2002).

Acacia erioloba (Figure 2.7) is a pioneer acacia and considered to be a key species for the restoration and increase in productivity of non-arable lands in the arid and semi-arid parts of Africa. Its natural distribution is closely related to the presence of the deep Kalahari sand formations, which are transported by the major rivers of the Namib Desert, e.g., Kuiseb (Barnes et al., 1997). *Acacia erioloba* develops best on deep alluvial soils deposited along drainage lines, river beds and in valleys (Leistner, 1967; Milton, 1991; Roodt, 1998), and its distribution is expected to be limited by soil and not by frost. Its ecological amplitude ranges from rainfall areas of >1000 mm to 10 mm annual precipitation (Leistner, 1961; Barnes et al., 1997). The trees often grow as individuals but can also be part of a plant community as for example along the Kuiseb and other ephemeral rivers (Giess, 1962; Jenkins and Brain, 1967; Giess, 1971; Seely et al., 1980; Theron et al., 1980; Leggett, 1992; Leggett, 1993; Jacobson et al., 1995).

Acacia erioloba can grow to a height of up to 15 m, with a flattened crown reported to reach as much as 22 m in diameter and a stem diameter of 1 m (Ross, 1975; Carr, 1976; Coates-Palgrave, 2002). Depending on rainfall and water availability in the ground, *A. erioloba* can either exist as a shrub or as a tree (Ross, 1975; Barnes et al.,

1997). In Namibia, *A. erioloba* is one of the main tree species found along the ephemeral rivers (Jacobson et al., 1995; Leggett et al., 2001). It is a slow growing tree with a taproot system to access deep water sources (Bate and Walker, 1980; Barnes et al., 1997; Coates-Palgrave, 2002). The rough and fissured bark of the tree is dark-greyish brown to blackish. Branches have a grey or reddish-brown to purple color (Ross, 1975; Carr, 1976). The thorns of *A. erioloba* occur in pairs and can be up to 10 cm long. They are thickened at the base where they are merged together (Barnes et al., 1997). The leaves have 2-5 pinnae and the rachis is 1.5-5.0 cm long with each pinnae having 8-18 pairs of leaflets. The flowers (see Figure 2.7) are bright yellow (Ross, 1971; Ross, 1975; Carr, 1976), and the peak flowering period along the Kuiseb has been observed from November to January, although flower production can occur most of the year (van Wyk et al., 1985). The tree starts to develop flowers at the age of 10 years and produces large amounts of pods from 20 years onwards (Barnes et al., 1997). The indehiscent pods are half-moon shaped and have a light grey color (Ross, 1975; Carr, 1976). Pod fall varies, but the main pod fall along the Kuiseb River has been observed between March and August (van Wyk et al., 1985) (Table 2.8). The epileptically shaped pods have dark brown seeds of 8-14 mm x 7-10 mm in size (Ross, 1971; Ross, 1975; Carr, 1976). Morphological and chemical dissimilarity within *A. erioloba* is large and can probably be attributed to the genetic variation if site and age of the tree are uniform (Barnes et al., 1997).

Table 2.8: Annual phenology change of *Acacia erioloba* along the Kuiseb River, degree of shading indicates phenology presence and intensity (white=not present; light grey=present but low intensity, dark grey=present and high intensity) (van Wyk et al., 1985)

Phenology	J	F	M	A	M	J	J	A	S	O	N	D
Inflorescence	Dark grey	Light grey	Light grey	Light grey	White	White	Light grey	Light grey	Light grey	Light grey	Dark grey	Dark grey
Green pods	Dark grey	Dark grey	Dark grey	Dark grey	Light grey	Light grey	Light grey	Light grey	Light grey	Light grey	Light grey	Light grey
Pod fall	Light grey	Light grey	Dark grey	Dark grey	Dark grey	Dark grey	Dark grey	Dark grey	White	Light grey	Light grey	Light grey

Acacia erioloba pods are known for their nutritious value. Pods, young shoots, flowers and leaves provide valuable fodder for livestock and wild animals during the dry winter season, when other food sources are scarce (van Wyk et al., 1985; Barnes et

al., 1997). At the Kuiseb River, an *A. erioloba* pod production of 15.6 kg per tree was calculated by Seely et al. (1980).

Acacia erioloba is also used for shade, firewood, charcoal production, building and fencing (Carr, 1976; van den Eynden et al., 1992; Coates-Palgrave, 2002). The gum of *A. erioloba* can be eaten, and dissolved in hot water it is useful against coughs and colds (van den Eynden et al., 1992). The pod pulp is also known to be used as a food supplement of the Topnaar community of the Kuiseb River (Dentlinger, 1983; van den Eynden et al., 1992), while the seeds are used as a coffee substitute (van den Eynden et al., 1992).



Figure 2.7: Mature *Acacia erioloba* tree (a), flowers (b) and pods (c).

3. GERMINATION AND EARLY SEEDLING DEVELOPMENT OF *FAIDHERBIA ALBIDA* AND *ACACIA ERIOLOBA*

3.1 Introduction

Conditions favorable for germination, seedling growth and establishment of *Faidherbia albida* and *Acacia erioloba* are very variable in the ephemeral rivers of the Namib Desert and might only occur once within the life expectancy of an individual (Jacobson et al., 1995).

Seed germination is crucial for successful seedling regeneration and one of the most vulnerable stages in the life-cycle of a plant. The highest mortality risk for a plant occurs between seed dispersal and seedling emergence (Fenner, 1987). *Faidherbia albida* and *A. erioloba* pods with seeds that have fallen onto the ground or seeds voided after herbivore consumption are transported with flood water away from the seed source. After the flood water recedes, the seeds are deposited with sediments, which have to provide enough moisture for successful germination. Initial seed germination can be frequently inhibited by dormancy to delay germination until favorable conditions are present. Through extended water exposure or stratification of the seed coat this dormancy can be overcome (Evans and Blazich, 1999). Stratification in the digestive tract of eland, elephant and other ungulates has been found to enhance *A. erioloba* seed germination (Leistner, 1961; Hoffmann et al., 1989; Miller, 1995). *Faidherbia albida* seeds germinated to a higher percentage after cattle and goat ingestion (Wickens, 1969; Shayo and Udén, 1998).

In the ephemeral rivers, animals only play a minor role in seed dispersal. They move the seeds away from the seed source, but flood water is the main long-distance transport path. Seeds in dung and seed pods are transported with floods and deposited in or on top of sediments along shorelines and retention objects. This can be up to 50 km from the source as found for *F. albida* seed pods (Jacobson, 1997). Once seeds have successfully germinated and emerged, seedlings risk death if the root growth cannot keep pace with the declining water table (McBride et al., 1989). Johnson (1994) points out that plant characteristics such as rapid root and height growth are necessary mechanisms for coping with flooding, drought and sedimentation. These traits in

addition to tolerance to low soil fertility and soil submergence are important for plant survival in river systems.

In the ephemeral rivers of the Namib Desert, land-use intensification and alterations to the water regime will affect the conditions for regeneration of *F. albida* and *A. erioloba*. To understand the influence of this change, this study aims to determine how seed germination as well as seedling emergence and development are influenced by water availability, herbivores and soil properties. For this, seed exposure to water and seed ingestion by livestock prior to germination, was studied. Seedling emergence from seeds buried at various depths and the influence of additional water supply on seedling performance were determined. Root and shoot parameters of seedlings were measured to establish the influence of soil texture on seedling performance.

3.2 Material and methods

3.2.1 Germination

The germinability of seeds after water exposure for different periods of time and/or ingestion by large herbivores was determined for *F. albida* and *A. erioloba*. A germination experiment was carried out ex-situ from December 2004 to January 2005, a period within the main flood season when flood events would allow germination. The seeds were germinated under natural day length conditions and were exposed to the temperature fluctuations occurring during this period, although the amplitude of the fluctuations was smaller indoors than outside. This setup allowed testing the influence of water and seed ingestion on seed germinability, even though a variety of other factors, such as temperature, also play a role in germination processes. However a major change in the natural germination conditions is expected to occur based on water availability and livestock numbers.

Pods of *F. albida* and *A. erioloba* were gathered in May 2004 from 10 trees per species. Per tree, a maximum of 50 pods was collected. Goat and cattle faeces were collected in June and July 2004 between Gobabeb and Soutrivier and oryx faeces approximately 25 km upriver from Homeb (see Figure 2.1). In addition, pods collected in January 2003 were used to determine the influence of seed age on germination success. Pods and faeces were stored in a dry place in boxes or paper bags until October

2004. In October/November 2004, the *F. albida* and *A. erioloba* seeds were removed from faeces and pods. Tree seeds in faeces were identified and all seeds were distinguished between intact and damaged (compare Wickens, 1969; Miller, 1995; Hoffmann et al., 1989). In December (04.12.04), undamaged seeds (n=20 or less if not enough available) were placed on sand in Petri dishes with 8 replicates per treatment. For sterilization, the seeds were soaked for 5 minutes in 1 % sodium hydrochloride and rinsed three times with tap water before they were placed on moist sand in lines and facing the same direction. Each Petri dish was filled with 40 g of dry river sand from the Kuiseb River that was sieved to 2 mm and sterilized for 24 h at 200° C. Prior to sowing, the sand was moistened with 10 ml of tap water. During the experiment, the Petri dish was covered with another Petri dish and the sand was kept continuously moist. Treatments (24 h and 72 h of seed soaking in water) were carried out prior to sowing. The seed treatments are presented in Table 3.1. Not all germination tests could be carried out for seeds of both species due to a lack of seeds. Germination was considered successful when the radicle extended 2 mm beyond the testa. Germinated seeds and seeds infested with fungi were removed from the Petri dish. Recordings were made daily for 43 days and a last recording was done at day 46. Accumulated germination was calculated. The difference in total germination between treatments was tested per species with One-way ANOVA (Zar, 1999).

Table 3.1: Different treatments of *Faidherbia albida* and *Acacia erioloba* seeds in an ex-situ germination experiment from December 2004 to January 2005 prior to sowing

	<i>Faidherbia albida</i>	<i>Acacia erioloba</i>
Treatment	Seeds per dish	Seeds per dish
New seeds	20	20
Old seeds	20	15
Goat	20	20
Oryx	20	16
Cattle	20	20
New seeds, 24 h watered	20	20
New seeds, 72 h watered	20	20
Goat, 24 h watered	20	
Oryx, 24 h watered	20	
Cattle, 24 h watered	20	

3.2.2 Seed burial

An ex-situ seed burial experiment was established on 02.12.04 to determine the influence of burial depth on the ability of seedlings to emerge. Pods were collected in May 2004 and stored in a dry place until October 2004 (see 3.2.1). Seeds were removed from the pods and only undamaged seeds used for the experiment. They were soaked in water for 24 h before they were sown at three different depths in black plastic containers: i.e., 5 cm, 10 cm and 15 cm below the surface. The containers were filled with river sand sieved to ≤ 2 mm and watered with tap water to full saturation on the day prior to sowing. Seeds at 5 cm and 10 cm were sown in 50 l container and seeds at 15 cm in 70 l ones. Seeds of each species were sown in 5 rows with 25 seeds in each row. Throughout the experiment the sand was kept moist. Seedling emergence was recorded and emerging seedlings removed daily until 21.01.05 (50 days) and every second day from 25.01. until 02.03.05 (36 days). No recordings were carried out between 22.01. and 24.01.05. Seedlings were considered emerged when the cotyledons were fully above ground. The difference in total emergence between treatments was tested per species with the Unpaired t test (Zar, 1999).

3.2.3 Additional seedling watering

Water is often a limiting factor in seedling establishment. To test the influence of water availability on seedling survival and growth, a watering experiment was established immediately after the January 2004 flood. A plot with a high density of newly emerged seedlings was selected near Gobabeb. A high fence was built around the seedlings to protect them from cattle and donkey trampling. On 24.01. and 26.01.04, healthy, not damaged, and not withered *F. albida* (n=60) and *A. erioloba* (n=40) seedlings were selected, marked and protected individually with a mesh fence. Distance between seedlings was >20 cm. On 10.02.04, half of the seedlings of each species (*F. albida* n=30 and *A. erioloba* n=20) were equipped with a watering device. A 15-cm black pipe with a diameter of 3.4 cm was inserted into the ground 10 cm from each seedling. Watering was carried out with a 1-l plastic bottle inserted into the black tube to avoid evaporation. At each not-watered seedling, the pipe was inserted once into the ground and then removed. The distance between watered and not-watered seedlings was 2 m to reduce the influence of the watering. All remaining and newly emerging seedlings were

removed from the plot to reduce competition. From 14.02 to 06.08.04, the seedlings were watered and survival monitored as presented in Table 3.2. Stem diameter was measured at the stem collar in week 28 after selection with a caliper. The differences in seedling survival between treatments were tested for each species with Fisher's exact test. Differences in stem diameter in week 28 were tested with the Unpaired t test with Welch correction (Zar, 1999).

Table 3.2: Schedules of watering and monitoring of *Faidherbia albida* and *Acacia erioloba* seedlings in in-situ watering experiment, Gobabeb, Kuiseb River, 2004

Period	Watering	Monitoring
14.02.-20.03.04	weekly	weekly
20.03.-28.05.04	two weekly	twice
28.05.-06.08.04	21.06.04	twice

3.2.4 Seedling performance

To analyze the performance of the newly germinated seedlings, an excavation method was applied in the Kuiseb River near Gobabeb. Seedlings were excavated after 31 days and after an average of 63 days since emergence of the first seedlings. The primary root was excavated to its maximum extension. No secondary root system was followed.

In February 2004, *F. albida* (n=17) and *A. erioloba* (n=15) seedlings were selected systematically across the entire flooded area of the river bed and excavated. Selection criteria were good plant development and withered or missing cotyledons. For calculation of growth rate, the time since first observed seedling was used.

For the second excavation (March/April 2004), seedlings were selected out of a pool of 251 seedlings. Seedlings from this group were the first seedlings that had appeared after the flood had receded, across the entire flood channel over a distance of approximately 1.25 km at Gobabeb. These seedlings were selected between 24.01. and 30.01.04 and protected for a survival study (see 4.2.2). To select seedlings from this pool, a stratified-random selection was applied. Seedlings were classified as big and small (stem circumference at stem collar ≤ 0.3 cm=small, >0.3 cm=big). The riverbed was divided in two areas: high (>30 cm) and low (≤ 30 cm) sediment banks. Seedlings were sorted into four groups (small-high, big-high, small-low, big-low) and selected randomly. No small *F. albida* were available at high banks. The seedlings (*F. albida* n=17, *A. erioloba* n=19) were excavated by digging a hole close to the seedling. If other

suitable seedlings were growing close to a selected seedling, these were also excavated and used. Securing the seedling shoot, the main root was carefully excavated, washed and stored in a paper bag. Seedling height, stem diameter at collar and presence or absence of nodules were recorded. Shoots were also stored in a paper bag. Shoots and roots were oven dried for three days at 60° C and dry weight was determined with a Mettler AE 100 analytical balance (accuracy 0.0001 g). Different soil layers were identified and soil texture determined with the finger test (AG Boden, 1996) up to 100 cm depth. In each layer, the soil moisture was measured with a ThetaProbe M12x. If no different soil layers could be identified, soil moisture was measured in the dry top layer, start of the moisture zone up to 30 cm, 30-60 cm and 60-100 cm depth. In each layer, the ThetaProbe was inserted randomly 10 times and measurements taken. From the collected data, the following analyses were done.

Root growth: Daily root growth rate was calculated for both excavations surveys. The number of days of root growth was counted from 24.01.04 onwards, i.e., the day when the first emerged seedlings were observed. The Unpaired t test was applied to test root growth differences between the two excavation dates per species (Zar, 1999).

Root/shoot ratio: The root/shoot ratio was calculated for both species. The relationship between soil texture and root/shoot ratio was tested with the Unpaired t test (Zar, 1999).

Nitrogen fixation (¹⁵N): Seedlings with root nodules (*F. albida* n=6, *A. erioloba* n=7) and seedlings without (*F. albida* n=9, *A. erioloba* n=10) were used for ¹⁵N analyses. Leaves were oven dried for three days at 60° C and finely ground material (0.2 mm) analyzed with a mass spectrometer for ¹⁵N (SERCON Ltd., Cheshire, UK) at the laboratory of the Institute of Plant Nutrition, University of Bonn. Differences in ¹⁵N between seedlings with and without nodules were tested with the Unpaired t test (Zar, 1999).

3.2.5 Data analyses

GraphPad InsStat 3.05 and Statistica 6.0 were used for the statistic tests. All data were tested for normal distribution with the Kolmogorov-Smirnov test prior to further analyses. A significance level of 5 % was applied to all statistic tests (Zar, 1999). The detailed results of the tests are presented in Appendix I.

3.3 Results

3.3.1 Germination

Maximum percentage of *F. albida* germination at day 46 was less than 50 % in all treatments (Figure 3.1). The *F. albida* seed treatment goat ingestion/24 h watered displayed high germination in the first 10 days while all others were later. Both goat and oryx ingested *F. albida* seeds (watered and not-watered) reached the highest total germination percentages.

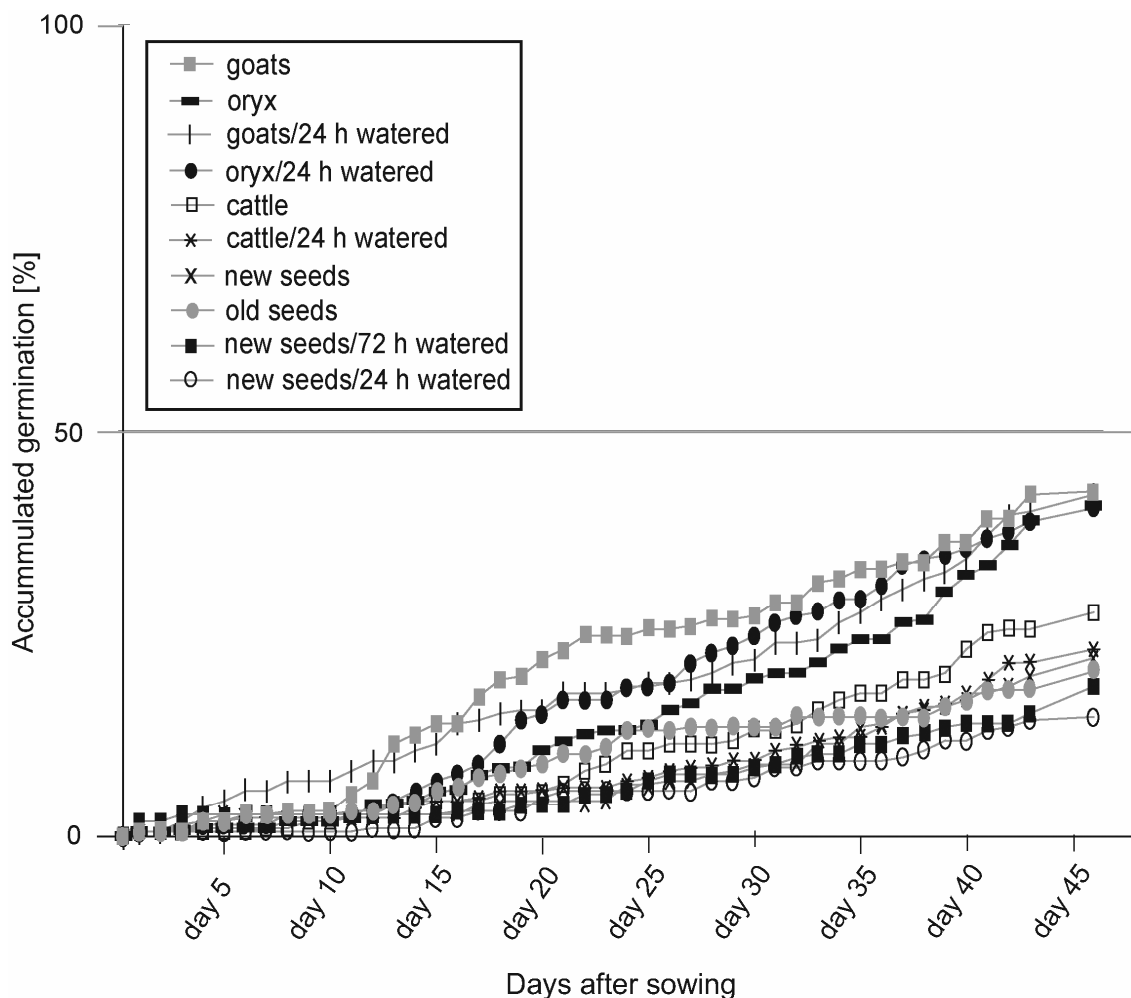


Figure 3.1: Accumulated germination percentage of *Faidherbia albida* seeds having received different treatments prior to sowing (means of 8 replicates), December 2004-January 2005. New seeds were from the previous season and exposed to water for 24 or 72 h. The seeds ingested by goats, cattle or oryx were germinated with and without water exposure for 24 h. Untreated new seeds and old seeds (collected two previous seasons ago) were used as control.

Apart from *A. erioloba* seeds ingested by cattle, new seeds watered for 24 h and 72 h as well as old seeds, all *A. erioloba* seeds reached more than 50 % of total germination (Figure 3.2). The oryx- and goat-ingested *A. erioloba* seeds showed a high germination percentage in the first 10 days. New seeds reached similar final values to those of oryx-ingested seeds but with a lower germination percentage at the onset.

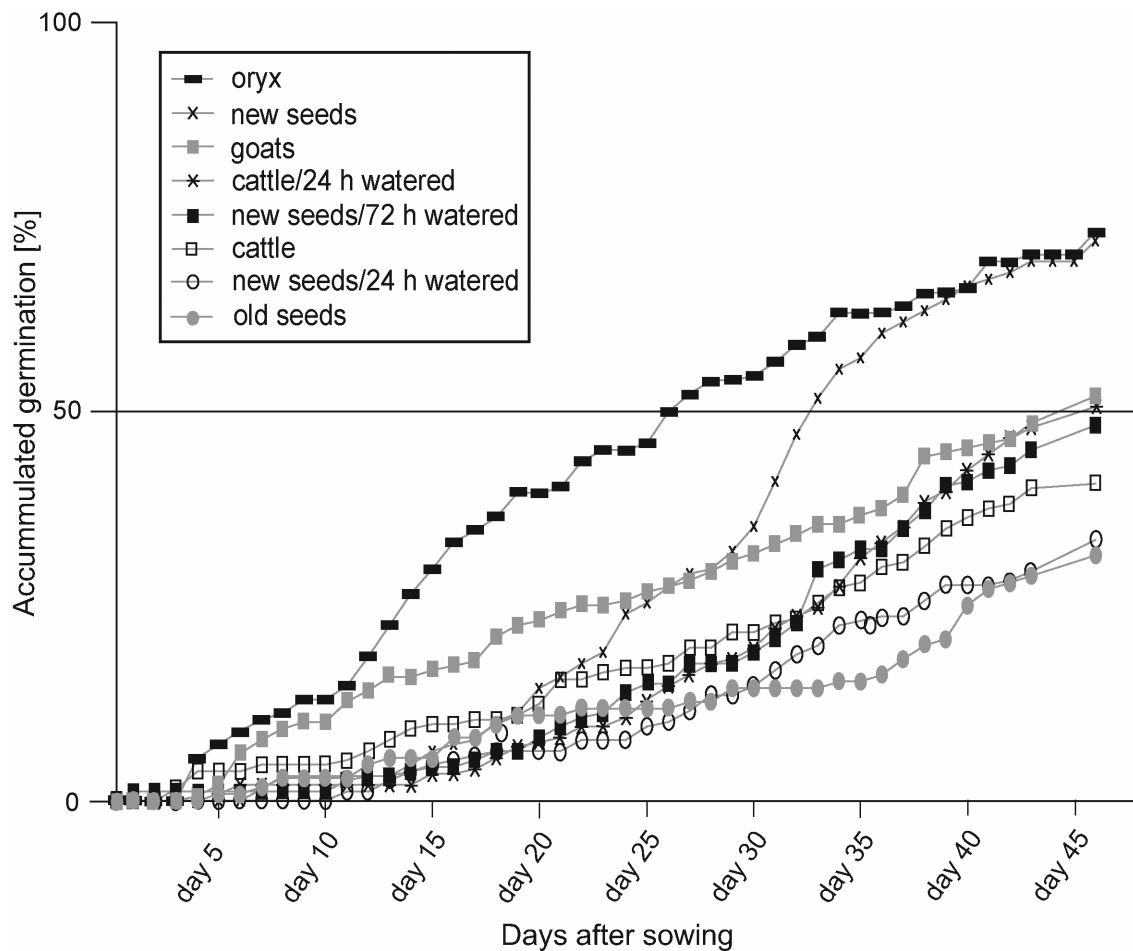


Figure 3.2: Accumulated germination percentage *Acacia erioloba* seeds having received different treatments prior to sowing (means of 8 replicates), December 2004-January 2005. For procedures and conventions see Figure 3.1.

Faidherbia albida seeds ingested by oryx and watered or not-watered for 24 h were found to be significantly different to all treatments except for goat- and cattle-ingested watered and not-watered seeds (Table 3.3). Cattle-ingested seeds were not significantly different to the other treatments, while watered cattle-ingested seeds (24 h) differed to watered or unwatered goat-ingested seeds. Goat-ingested seeds (watered or

not-watered) were also significantly different from old seeds and watered new seeds (24 h and 72 h) ($p < 0.05$, Tukey-Kramer Multiple Comparisons test).

Oryx-ingested *A. erioloba* seeds were significantly different from old seeds, cattle-ingested seeds and watered new seeds (24 h and 72 h) but not from new seeds, goat-ingested seeds and cattle-ingested 24 h watered seeds (Table 3.3). Cattle-ingested *A. erioloba* seeds were found to be significantly different from new seeds and oryx-ingested seeds. Watered cattle-ingested seeds did not differ significantly from any treatment ($p < 0.05$, Tukey-Kramer Multiple Comparisons test).

Table 3.3: Mean (\pm SE, 8 replicates) accumulated germination percentage at day 46 after sowing of *Faidherbia albida* and *Acacia erioloba* seeds, December 2004-January 2005. New seeds were from the previous season and exposed to water for 24 or 72 h. The seeds ingested by goats, cattle or oryx were germinated with and without water exposure for 24 h. Untreated new seeds and old seeds (collected two previous seasons ago) were used as control. Values followed by different letters are significantly different at $p < 0.05$ (One-way ANOVA with Tukey-Kramer Multiple Comparison post test)

Treatment	<i>Faidherbia albida</i> germination [%]		<i>Acacia erioloba</i> germination [%]	
New seeds	21.8 \pm 3.8	a	71.5 \pm 4.9	bc
New seeds, 24 h watered	14.4 \pm 2.0	a	33.2 \pm 3.2	a
New seeds, 72 h watered	17.9 \pm 3.3	a	47.9 \pm 6.5	a
Old seeds	20.2 \pm 4.6	a	31.5 \pm 5.9	a
Cattle	27.0 \pm 3.1	ab	40.6 \pm 4.8	a
Goats	42.3 \pm 5.3	b	51.7 \pm 4.9	ab
Oryx	40.5 \pm 4.2	bc	72.8 \pm 5.1	bc
Cattle, 24 h watered	22.7 \pm 4.0	ac	50.3 \pm 5.2	ab
Goats, 24 h watered	41.7 \pm 3.0	b		
Oryx, 24 h watered	40.3 \pm 5.2	bc		

3.3.2 Seed burial

No seedlings emerged from a burial depth of 15 cm. Less than 5 % seedlings of both species emerged from 10 cm burial depth (Table 3.4). From 5 cm depth, 92.8 \pm 7.7 % *A. erioloba* and 55.2 \pm 10.0 % of *F. albida* seedlings emerged successfully. Significantly more seedlings emerged in total from 5 cm depth than from 10 cm of both study species ($p < 0.0001$, Unpaired t test). Most seeds excavated from 10 and 15 cm depth showed signs of germination (radicle development).

Table 3.4: Accumulated emergence of *Faidherbia albida* and *Acacia erioloba* seedlings after 86 days after sowing (mean \pm SE of 5 replicates). Seeds were buried ex-situ at 5, 10 and 15 cm depth in black plastic containers, December 2004-January 2005

Species	5 cm burial depth [%]	10 cm burial depth [%]	15 cm burial depth [%]
<i>Faidherbia albida</i>	55.2 \pm 4.5	2.4 \pm 1.6	0.0 \pm 0.0
<i>Acacia erioloba</i>	92.8 \pm 3.4	4.8 \pm 3.9	0.0 \pm 0.0

3.3.3 Additional seedling watering

Faidherbia albida and *A. erioloba* seedlings showed no significant difference in survival between not-watered and watered seedlings ($p > 0.05$, Fisher's exact test). Although not significant, more seedlings of both species withered in the watered treatment (Table 3.5). No significant difference in stem diameter (Table 3.6) was found between watered and not-watered seedlings for both species ($p > 0.05$, Unpaired t test with Welch correction).

Table 3.5: Relative number of withered watered or not-watered *Faidherbia albida* and *Acacia erioloba* seedlings in a watering experiment, week 28, Gobabeb, Kuiseb River, 2004 (n=number of seedlings)

Species	Watered [%]	Not-watered [%]	
<i>Faidherbia albida</i>	26.7 (n=30)	10.0 (n=30)	ns
<i>Acacia erioloba</i>	35.3 (n=17)	10.0 (n=20)	ns

ns means not significant

Table 3.6: Mean (\pm SE) stem diameter of watered or not-watered *Faidherbia albida* and *Acacia erioloba* seedlings in week 28, Gobabeb, Kuiseb River, 2004 (n=number of seedlings)

Species	Stem diameter watered [mm]	Stem diameter not-watered [mm]	
<i>Faidherbia albida</i>	3.6 \pm 0.2 (n=22)	4.1 \pm 0.3 (n=26)	ns
<i>Acacia erioloba</i>	5.0 \pm 0.3 (n=13)	4.6 \pm 0.2 (n=17)	ns

ns means not significant

3.3.4 Seedling performance

Root growth rate

The daily root growth rate of *F. albida* roots (Table 3.7) was significantly higher after 63 days compared to 31 days ($p < 0.05$, Unpaired t test). Although the growth rate of *A. erioloba* roots (Table 3.7) after 63 days was higher than after 31 days, no significant

difference was found between the two surveys. Soil moisture in sand layers was 4.4 ± 1.7 Vol % (n=142) and 13.4 ± 8.9 Vol % in silt/clay layers (n=23).

Table 3.7: Root length (mean \pm SE) and daily root growth rate (mean \pm SE) of *Faidherbia albida* and *Acacia erioloba* seedlings 31 and 63 days after emergence, Gobabeb, Kuiseb River, 2004 (n=number of seedlings)

Species	31 d root length [cm]	63 d root length [cm]	31 d growth rate	63 d growth rate	
<i>Faidherbia albida</i>	28.7 \pm 2.4 (n=17)	79.8 \pm 6.5 (n=17)	0.9 \pm 0.1 (n=17)	1.3 \pm 0.1 (n=17)	*
<i>Acacia erioloba</i>	38.7 \pm 3.6 (n=15)	97.5 \pm 7.8 (n=19)	1.2 \pm 0.1 (n=15)	1.5 \pm 0.1 (n=19)	ns

* indicates significance level of $p < 0.05$

ns means not significant

Root/shoot ratio, soil texture and soil moisture

The root/shoot ratios of *F. albida* and *A. erioloba* were both wider in moist soil with pure sand than in sand with silt and clay layers (Table 3.8). Root/shoot ratios in sand were found to be significantly wider than in clay/silt for both species ($p < 0.05$, Unpaired t test).

Table 3.8: Mean (\pm SE) root/shoot ratios of *Faidherbia albida* and *Acacia erioloba* seedlings, 63 days after emergence in two different substrates (sand and sand with silt/clay layers), Gobabeb, Kuiseb River, 2004 (n=number of seedlings)

Species	Root/shoot ratio sand	Root/shoot ratio silt/clay	
<i>Faidherbia albida</i>	1.09 \pm 0.16 (n=9)	0.43 \pm 0.08 (n=8)	*
<i>Acacia erioloba</i>	0.47 \pm 0.05 (n=11)	0.31 \pm 0.05 (n=8)	*

* indicates significance level of $p < 0.05$

Nitrogen fixation (% ^{15}N)

The percent of ^{15}N in *F. albida* and *A. erioloba* shoots with nodulated roots was similar to that in unnodulated roots (Table 3.9). No significantly different ^{15}N % between roots with and without nodules was found in shoots of either species ($p > 0.05$, Unpaired t test).

Table 3.9: Mean (\pm SE) percent of atomic ^{15}N in *Faidherbia albida* and *Acacia erioloba* seedling shoots with nodulated and unnodulated roots 63 days after emergence, Gobabeb, Kuiseb River, 2004 (n=number of seedlings)

Species	^{15}N % with nodules [%]	^{15}N % without nodules [%]	
<i>Faidherbia albida</i>	0.3676 \pm 0.0002 (n=6)	0.3678 \pm 0.0002 (n=9)	ns
<i>Acacia erioloba</i>	0.3678 \pm 0.0002 (n=7)	0.3679 \pm 0.0001 (n=10)	ns

ns means not significant

3.4 Discussion

Both study species showed low germination rates in seeds of more than two years old, but not-watered and watered new seeds did not perform better either. The better performance of not-watered new *A. erioloba* seeds is an exception. It seems that age reduces the overall germinability of *A. erioloba* seeds, while *F. albida* appears to be less affected. At the time of the experiment, the collected *F. albida* seeds were nearly one year old. Therefore, new seeds produced immediately before the flood season (October-March) would have probably shown a similar difference between old and new seeds. *Faidherbia albida* as well as *A. erioloba* seed pods usually lie on top of the soil surface until removed by animals or floods. This means that seed production has to be sufficient every year if seed material is to be available when hydrologic conditions are favorable. If seeds are not reached by a flood in the year of their production, their contribution to regeneration will diminish with time since seed exposure to sunlight, heat and temperature changes reduces the germinability of the seeds.

According to Miller (1995) the number of *Acacia* seeds surviving the passage through the gut increases with increasing body size of the herbivores. This has been confirmed for *F. albida* by Shayo (1998). Cattle, similar to oryx, are thus expected to void large proportions of the ingested seeds undamaged and thus contribute more to germination than sheep and goats. This can be confirmed for oryx considering the high germination rate of oryx-ingested seeds, but not for cattle. *Faidherbia albida* displayed overall low germination, but the consumption of seeds by goats and oryx as well as their exposure to water for an extended period increased germination. Germination of *A. erioloba* seeds was also improved by oryx consumption, although new seeds reached a similar total germination percentage. The digestion of seeds by goats and oryx seems to enhance water permeability of the seed coat. Exposed to floodwater, these seeds will be able to take up water during transportation. Especially goat-ingested seeds had an early germination begin, while water exposure for various periods of time alone did not suffice to enhance seed-coat water permeability. The results for cattle-ingested and new *A. erioloba* seeds are opposite to the findings of Hoffmann et al. (1989) but similar to those of Barnes (2001) for small *A. erioloba* seeds. Also in *F. albida* germination experiments by Wickens (1969) and Masamba (1994) higher overall germination

percentage than in this study were scored. A different seed origin and experimental setup might be responsible and make comparisons difficult.

In an ephemeral river environment, germination speed is decisive for seedling survival. The moisture in the soil after the floods recede is the only water available to the seedling for reaching a permanent water supply for growth and establishment. In the hot desert environment, evaporation is high and soil water diminishes fast. Seedlings from seeds that germinated early are able to take full advantage of the available water, while seeds that take longer have either less water available for seedling growth or will not be able to germinate at all in the drying substrate. By increasing early germination, herbivores are able to contribute to overall seed germination success. Although these data show that seed germination benefits from herbivore consumption, depending on the animal type, only a proportion of the consumed seeds are voided undamaged thus reducing the total amount of seeds available for germination. At the same time, damage by bruchid beetles is possibly reduced through pod/seed consumption by large herbivores (Coe and Coe, 1987; Barnes, 2001), which would be again beneficial for the two study species. However, no germination is possible to occur without sufficient water availability, leaving water as the primary factor for seed germination and regeneration.

Not only are seeds transported in a flood but also sediments, which are deposited with the seed material. In order to germinate, it is favorable for the seeds to be embedded in the moist sediments and thus protected from drying and direct sun exposure. Seeds embedded in a moist substrate are able to take up water through a larger seed surface than seeds lying on top of the substrate. If seeds are on top or too close to the surface, the substrate can dry out before the radicle can extend and roots develop for water uptake from deeper layers. If the sediment layer above the seed is too thick, *F. albida* as well as *A. erioloba* seedlings are not able to break through the soil in order to bring their cotyledons to the surface for photosynthesis and seedling growth. Germination took place in the sediments independent of the burial depth (personal observation), similar to observations of other *Acacia* species (Marchante et al., 2004), but seedling emergence was not always possible. In the experiment, seeds deposited at 5 cm depth managed to emerge well, while a 10 and 15 cm sediment cover was too thick for successful seedling emergence. These findings correspond with those for

Phalaris paradoxa seeds in undisturbed soil in Australia (Taylor et al., 2005) and two tropical weed species (*Bidens pilosa* L., *Achyranthes aspera* L.) (Fenner, 1985). *Acacia suaveolens* seeds deeply buried in ant nests also could not germinate and emerge (Auld, 1986). This means that these seeds are lost for regeneration. Burial depth is therefore a crucial factor in the life cycle of a plant in a dynamic river environment.

Faidherbia albida and *A. erioloba* seedlings that germinate successfully and escaped browsing and other herbivory influence have to establish a sufficient root system for water and nutrient supply. Although nodules at some of the roots of both study species indicated nitrogen fixing activity, which is common for Mimosoideae (Barnes et al., 1996), no such activity was found for both study species. This differs to the findings of Barnes et al. (1996) who found nitrogen fixation, although this was low for *A. erioloba* and *F. albida*, the latter with slightly higher rates than *A. erioloba*. The effectiveness of nitrogen fixing bacteria might be limited in the river substrate due to frequent disturbance and flooding. *Faidherbia albida* and *A. erioloba* therefore are dependent on the groundwater and substrate for their nitrogen supply at the seedling stage, but might start nitrogen fixation after establishment.

The soil water available for root and shoot growth after a flood is related to flood magnitude as well as soil texture. The fast and good development of the root system for accessing permanent water sources is an important trait for plant survival (Witkowski, 1991; Wilson and Witkowski, 1998). This fast development is especially important in desert environments where surface water is scarce and roots need to reach permanent moisture if the plant is to survive. Overall root growth rate of *F. albida* was slower than that of *A. erioloba* but faster than measured by Gupta et al. (1973). This underlines that *F. albida* is dependent on readily available soil water (CTFT, 1989) close to the surface, while *A. erioloba* is able to reach deeper moisture zones. Root growth rate also increased with time in both species. This is probably related to increasing photosynthesis activity of the growing shoot parts, providing the roots with the necessary photosynthates for growth. For seedling establishment, this acceleration is an advantage and is decisive for regeneration success.

Surface watering to enhance seedling performance did not have any positive effect on the seedlings. The provided surface water might not have infiltrated deep

enough into the substrate to reach the growing roots. Water logging, similar to reflooding, might have occurred close to the surface and contributed to seedling death.

The root/shoot ratio of both study species was larger in pure sand than in the substrate with silt/clay layers. Compared to the above-ground biomass, more energy is allocated to root growth in sand to reach deeper substrate layers with permanent water availability. In substrate layers with high silt or clay content, strong secondary root development has been observed. Similar observations have been made of wheat (Begon et al., 1996). In West Africa, *F. albida* grows preferably on silty soils (CTFT, 1989) and Jacobson et al. (2000a) found high silt contents along the active river course where *F. albida* mostly grows. Plants were probably using these layers for moisture and nutrient supply (Jacobson et al., 2000a) through secondary roots, while the primary root was growing towards the permanent moisture zone. These plants can afford to invest in shoot development rather than in fast root penetration, resulting in a smaller root/shoot ratio than plants with fast primary root growth. This is confirmed by Gupta et al. (1973), who found that shoot development only started after the seedling was able to provide a reliable water supply to the plant. The authors further pointed out that this can vary considerably depending on soil texture and available water.

3.5 Conclusion

Water availability and the type and amount of deposited sediments are crucial for the germination and seedling establishment processes. If the seeds are embedded too deeply in the sediments, seedlings will not be able to emerge, independent of seed germinability. The growth substrate deposited with a flood determines how much energy can be allocated to root and shoot growth. Silt and clay transport into the river system is needed to support fast seedling growth and their presence is crucial for seedling establishment.

For successful regeneration, it is necessary for *F. albida* and *A. erioloba* to have a high annual seed output. The consumption of some of the seeds by large herbivores will not reduce regeneration success as long as a sufficient proportion of new seed material remains in the river. Seeds voided undamaged by some herbivores (goats and oryx) even demonstrate enhanced germination success.

4. INFLUENCE OF LIVESTOCK ON *FAIDHERBIA ALBIDA* AND *ACACIA ERIOLOBA* REGENERATION

4.1 Introduction

Recruitment, establishment and survival of trees are closely linked to the influence of mammalian herbivores (Reichenbacher, 1984; Auble and Scott, 1998; Robertson and Rowling, 2000; Pettit and Froend, 2001). Studies of dryland river systems in Australia showed that livestock grazing, in addition to river regulation, was responsible for the degradation of riparian zones (Pettit and Froend, 2001). Robertson and Rowling (2000) found that livestock has a major negative effect on the vegetation along rivers and seedlings as well as juveniles were severely reduced in areas with stock access. The carrying capacity of an ecosystem is often threatened by an increase in domestic animals, a side effect of human population increase (Coe et al., 1976). Goats, the main domestic animal found along the ephemeral rivers of west Namibia (Ward et al., 1998), have often been identified as “razor(s) of forests” responsible for damage and degradation of established plants as well as destruction of regeneration (von Maydell, 1980). Therefore, the impact of livestock on the riparian vegetation has to be taken into consideration for the sustainable management of river ecosystems (Elmore and Beschta, 1987; Robertson and Rowling, 2000).

The ephemeral rivers are an important source for water and food in a resource-poor environment. Population increase in Namibia and along the lower ephemeral rivers is putting increasing pressure on the scarce resources water and land. To sustainably manage the ephemeral river ecosystems of Namibia and in order to predict changes in the vegetation in relation to land use, it is important to quantify regeneration success in response to altered disturbance and stress regimes. Based on seedling monitoring and vegetation surveys, this study investigates how livestock influences the regeneration of two fodder tree species in ephemeral rivers of the Namib Desert.

4.2 Material and methods

4.2.1 Variation of livestock density

The Kuiseb River was subdivided into four sections, differing in their hydrological characteristic as well as in land use (see 2.3.1). The upper woodlands U1 and U2 are well watered with low and high livestock presence, respectively, while the middle and lower woodlands M and L experience low water availability in combination with medium livestock utilization. A bulk water abstraction scheme is located in lower woodland L.

The area of the four Kuiseb River sections was estimated with the GIS software Touratech QV 3.0 from data provided by the Environmental Learning and Action in the Kuiseb Project. Total livestock density (goats, sheep, cattle and donkeys) was calculated in kilogram per km² in each Kuiseb River section (U1, U2, M, L) from the average of three livestock surveys (2002, 2003, 2004) carried out by the Agricultural Extension Officer (see 2.3.1). For this calculation, the following weights were used as recommended by the Ministry of Agriculture, Water and Forestry (MAWF): goats=40 kg, sheep=60 kg, donkeys=250 kg and cattle=360 kg. Although no settlements are present in river section U1, two villages with livestock are located nearby. Since livestock moves as far as several kilometers away from the farm, 50 % of the livestock numbers from the closest village (Homeb) were used to calculate livestock densities for this section.

To assess the spatial browsing pressure by goats/sheep, dung deposits were recorded along transects in the Kuiseb River survey 2004. Goat and sheep faeces were difficult to distinguish and therefore combined to one group. In each transect along river sections with a clearly defined active main channel (U1, n=11; U2, n=12) a 0.25 m² quadrat was placed randomly every 100 m and in addition 50 m from the channel. Faeces pellets within the quadrat were counted. The average density of goat/sheep pellets per 0.25 m² was calculated and differences in density at 50 m and >50 m distance from the main channel in the river sections U1 and U2 was tested with the Mann-Whitney test (Zar, 1999).

4.2.2 Seedling survival

Tree seedlings at an early age are very vulnerable to herbivory. To test the influence of livestock on seedling survival, the fate of protected and unprotected seedlings was monitored after two flood seasons (16.04.-20.04.03, 18.01.-21.01.04 and 26.01.-27.01.04). In 2003 and 2004, the mortality of seedlings was tested at sites differing in livestock numbers. In 2003, seedlings were selected in areas with high livestock numbers at Soutrivier (19.05. and 20.05.03) and Gobabeb (15.05. and 16.05.03.) as well as at a location with low livestock numbers approximately 25 km upriver from Homeb (22.05., 25.05. and 26.05.03) (see Figure 2.1). Seedlings were selected systematically over a distance of 1 to 2 km after the flood had receded. All healthy seedlings were selected. Seedlings from the same species growing close by were selected as a pair. By throwing a coin, it was determined which one of the two seedlings was to be protected by a mesh fence. If no seedling from the same species was growing nearby, the next encountered seedling of the same species was used for the pair. Location and sample size in this experiment are presented in Table 4.1.

Table 4.1: Sample design for 2003 and 2004 seedling survival experiment. Monitoring of *Faidherbia albida* and *Acacia erioloba* seedling fate at locations with low and high livestock numbers for 29 weeks (n=number of seedlings)

2003			
Location	Livestock numbers	Species	Monitoring weeks after establishment
25 km upriver from Homeb	low	<i>F. albida</i> (n=199)	1-26, 28, 29
Gobabeb	high	<i>F. albida</i> (n=115) <i>A. erioloba</i> (n=84)	1-27, 29
Soutrivier	high	<i>F. albida</i> (n=150) <i>A. erioloba</i> (n=50)	1-26, 28, 29, 30, 32, 34
2004			
Location	Livestock numbers	Species	Monitoring weeks after establishment
10 km upriver from Homeb	low	<i>F. albida</i> (n=60)	1-5, 8, 14, 16, 24, 28
Oswater	high	<i>F. albida</i> (n=50) <i>A. erioloba</i> (n=10)	1-6, 9, 15, 17, 25, 29
Gobabeb	high	<i>F. albida</i> (n=60) <i>A. erioloba</i> (n=60)	2-6, 9, 13, 17, 29
Soutrivier	high	<i>F. albida</i> (n=60) <i>A. erioloba</i> (n=60)	1-5, 9, 17, 21, 29
7 km downriver from Gobabeb Weir	low	<i>F. albida</i> (n=43) <i>A. erioloba</i> (n=17)	1-5, 9, 13, 17, 25, 29

Seedling fate (alive, dry, eaten, unknown) was monitored weekly until week 29 from date of experiment establishment. No recordings were taken in week 27 for the Soutrivier and Upriver sites and week 28 for the Gobabeb site. To accommodate the growth of the seedling, fence size was increased depending on the size of the plant. At the Soutrivier site, all alive protected seedlings were measured in week 30 (height above ground, stem diameter at stem collar) with a caliper and fences were removed. The fate of these seedlings was monitored in week 32 and 34.

In 2004, five monitoring sites were established: 10 km upriver from Homeb (16.02.04), Oswater (09.02.04), Gobabeb (24.01., 26.01., 27.01., 29.01. and 30.01.04), Soutrivier (26.01., 03.02. and 04.02.04) and 7 km downriver from the Gobabeb Weir (13.02.04) (Table 4.1). The first seedlings emerging after the flood had receded were selected across the entire inundated flood channel. Selection criteria were: healthy and not damaged seedling with fresh cotyledons. When a seedling was found, the closest seedling in a comparative development stage was also selected. By throwing a coin, it was determined which seedling of the pair was to be protected and which would remain unprotected. If there was more than one suitable *F. albida* seedling close by, a maximum of two seedling pairs was selected at one location. Due to a lack of *A. erioloba* seedlings, more than two seedling pairs were chosen if present, but fewer *A. erioloba* than *F. albida* seedlings were monitored overall. At Gobabeb, more seedlings than needed were marked, and seedlings were selected randomly.

For analyses, data from sites with high as well as low livestock numbers were combined. The fate of protected and unprotected *F. albida* and *A. erioloba* seedlings after 29 weeks from experiment establishment was calculated in percent and compared per species with chi-square (Zar, 1999). Protected seedlings eaten by livestock due to fence removal were excluded from the analyses. The fate of unprotected seedlings after 30 weeks of protection at Soutrivier was established in percent, and average height above ground as well as stem diameter were determined.

4.2.3 Vegetation transects

According to Gregory et al. (1991), the variability of vegetation in a riparian system occurs across strong vertical, lateral and longitudinal gradients. Similar to studies by van Coller et al. (1997), belt transects perpendicular to the river in a downriver direction were used in this study.

Faidherbia albida and *A. erioloba* trees were surveyed along belt transects in the Kuiseb, Omaruru and Ugab rivers. Distances between transects were measured with a car odometer. If the transect was located in an area without vegetation or where access was hindered, the transect point was moved to the nearest suitable location. The maximum extension of transects was determined by natural borders, e.g. dunes, rocks or high flood marks (silt layers, flood debris) and geographical coordinates of the transect determined with a GPS (Garmin 72).

From October to December 2003, belt transects were surveyed in the upper, middle and lower woodlands of the Kuiseb River (n=58) (see 2.3.1). The transects were 20 m wide and placed perpendicular to the river course at 2.5 km intervals. In August 2004, additional transects were surveyed in the Kuiseb and in October 2004 in the Omaruru and Ugab rivers. In the Kuiseb River (n=32), the transects were 4 m wide and placed at 5 km intervals in the river sections L and M and at 2.5 km in sections U1 and U2. The transects along the Omaruru River were 4 m (n=14) and 20 m (n=23) wide. Transects 1-14 (Figure 2.3) were 4 m wide and placed at approximately 2.5 km intervals. The location of these transects approximately corresponded with the location of settlements along the river. From Transect 15 to Transect 37, fewer settlements were present, the river became wider and the vegetation more sparse. The transects were placed at 5 km intervals and had a width of 20 m. Due to wetlands and presence of elephants in the Ugab River, 10 m wide transects were located at approximately 5 km intervals if access permitted.

In this study, juveniles are, similar to Plieninger et al. (2004), considered as a sign of recent recruitment. Juveniles are still vulnerable to herbivory (Grubb, 1977), competition or desiccation and their presence does not guarantee successful regeneration of a population. *Faidherbia albida* and *A. erioloba* juveniles have an upright, often shrub-like habitus without clear stem and crown development and no flowers or pods on or under the plant. Most juveniles in the Kuiseb and Omaruru rivers

are expected to have established after the 2000 flood. For the Ugab, no establishment date could be estimated. Estimates of stem height were carried out with a 4 m long measuring pole for generative juveniles in the Kuiseb River survey 2003 and for generative and vegetative juveniles in all other surveys. Vegetative juveniles are plants that sprout from submerged plant parts or roots (Everitt, 1968; Legionnet et al., 1997; Barsoum, 2002). Adult trees were counted in all surveys, and in 2004 crown diameters (maximum diameter and diameter in 90°) of adult trees were estimated. Fitness assessment (good, poor) was done for juveniles in both surveys. Growth vigor and percentages of browsed/dry branch tips and dead branches were used to evaluate the juveniles. Juveniles were considered to be in a good fitness if more than 50 % of the branches had growth signs and not more than 30 % of the branches were dry. Good fitness was also recorded if up to 50 % of the branches were dry but strong leaf and branch growth was visible. If 50 % or more branches were dead, the plant was rated as poor.

To record the browsing influence of livestock on juvenile growth, generative juveniles from vegetation survey 2003 along the Kuiseb River were re-measured in September/October 2004, about one year after the first survey. All transects where juveniles were recorded in 2003 were revisited and the juveniles (*F. albida* n=57, *A. erioloba* n=469) identified according to their GPS readings. Only juveniles between 0-150 cm height at the first survey were re-measured. If no clear identification of the juvenile was possible, no measurement was carried out.

The following analyses were made from the survey data. Tests to determine differences between study sites were only carried out for the Kuiseb sections. For Omaruru and Ugab, only differences within the rivers were tested.

Size-class distribution: The surveyed adult trees of the three rivers were classified into five size classes according to the averaged crown diameter. Juveniles, as an expression of the most recent recruitment event, were included as a sixth size class. A difference in size-class distribution between study sites was tested for each study species with chi-square (Zar, 1999). The following size classes were used:

Size class 1: juveniles; size class 2: 1 m -<5 m; size class 3: 5 m -<10 m; size class 4: 10 m -<15 m; size class 5: 15 m -<20 m; size class 6: \geq 20 m.

Juvenile height increase: The height increase of juveniles ≤ 150 cm of both study species was compared between the Kuiseb River sections with the Kruskal-Wallis test followed by Dunn's Multiple Comparison test (Zar, 1999).

Tree density: The mean number of trees per hectare (density) was calculated for adults and juveniles of both study species. Transect lengths were estimated from GPS data. In the Kuiseb River section L, the length of four transects was measured only to the start of high dunes on the northern riverside, where no or only little river influence was visible. Density data were calculated up to the dunes. The Mann-Whitney test was applied to determine density differences of juvenile and adults within the study sites (Zar, 1999).

Plant fitness: Oba and Post (1999) reported browse being removed from ground level to 150 cm above ground by goats in Kenya. This height in addition to own browse height measurements (see 6.3.2) was used to determine two juvenile size groups: juvenile height \leq and > 150 cm. The fitness (good, poor) of juveniles in both size groups from the surveys 2003 and 2004 for the Kuiseb and 2004 for Omaruru and Ugab rivers was calculated in percent of the total number of surveyed juveniles. In the Kuiseb River, in 2003 only the height of generative juveniles was measured, therefore in the upper woodlands U1 and U2 no fitness analyses of vegetative *F. albida* juveniles could be calculated. Nevertheless, results from this fitness assessment were included into the total fitness analyses to increase the overall sample size. Differences in juvenile size group fitness between the study sites were tested with chi-square. Fisher's exact test was used to determine differences between juvenile size group fitness within the study sites (Zar, 1999).

4.2.4 Data analyses

Touratech QV 3.0 software was used to calculate the area covered by the river sections (see 4.2.1). The statistical packages GraphPad InsStat 3.05 and Statistica 6.0 were used for all statistical analyses. All data were tested for normality with the Kolmogorov-Smirnov test. A significance level of 5 % was used throughout all statistical analyses (Zar, 1999). Detailed test results are presented in Appendix II.

4.3 Results

4.3.1 Variation of livestock density

Along the Kuiseb River, livestock density varied between the river sections (Table 4.2). Total livestock density per square kilometer was highest in section U2 and lowest in section L.

Table 4.2: Total livestock density calculated from added weight of goats, sheep, donkeys and cattle, multiplied with average livestock numbers in four Kuiseb River sections (U1, U2, M, L; see Figure 2.1)

River section (area)	Livestock density ^a [kg km ⁻²]
U1 (8.2 km ²) ^b	2148
U2 (13.4 km ²) ^b	8543
M (27.2 km ²) ^b	2719
L (44.7 km ²) ^b	1657

^aaverage from 2002, 2003, 2004 livestock survey data (Kooitje, personal communication)

^briver section size estimated in GPS software Touratech with data from Environmental Learning and Action at the Kuiseb Project

In the upper river sections U1 and U2, goat/sheep faeces counts were significantly higher within 50 m from the channel than at distances >50 m ($p < 0.05$, Mann-Whitney). At distances of 0-50 m, the mean (\pm SE) count was 3.0 (± 0.5 , $n=17$) and at >50 m an average (\pm SE) of 1.5 (± 0.3 , $n=36$) goat/sheep pellets was found per 0.25 m².

4.3.2 Seedling survival

No or very few unprotected *F. albida* and *A. erioloba* seedlings survived in both years in locations with high livestock numbers (Figures 4.1 and 4.2), while at locations with low livestock numbers, seedlings were able to survive for 29 weeks. In 2003, causes of death of protected seedlings included drying after an attack by caterpillars (African Army Worm) of the moth *Spodoptera exempta* and other insect herbivory. Desiccation was a major reason for *F. albida* seedling death in both years with both high and low livestock numbers, except for unprotected seedlings in areas with high livestock numbers. The seedling fate of *F. albida* and *A. erioloba* in 2003 differs significantly between unprotected and protected sites in locations with high livestock numbers (HL)

($p < 0.0001$, chi-square). The fate of unprotected and protected *F. albida* seedlings was not to be found significantly different in areas with low livestock numbers (LL). The fate of unprotected *F. albida* seedlings differs significantly between sites with high and low livestock numbers ($p < 0.0001$, chi-square).

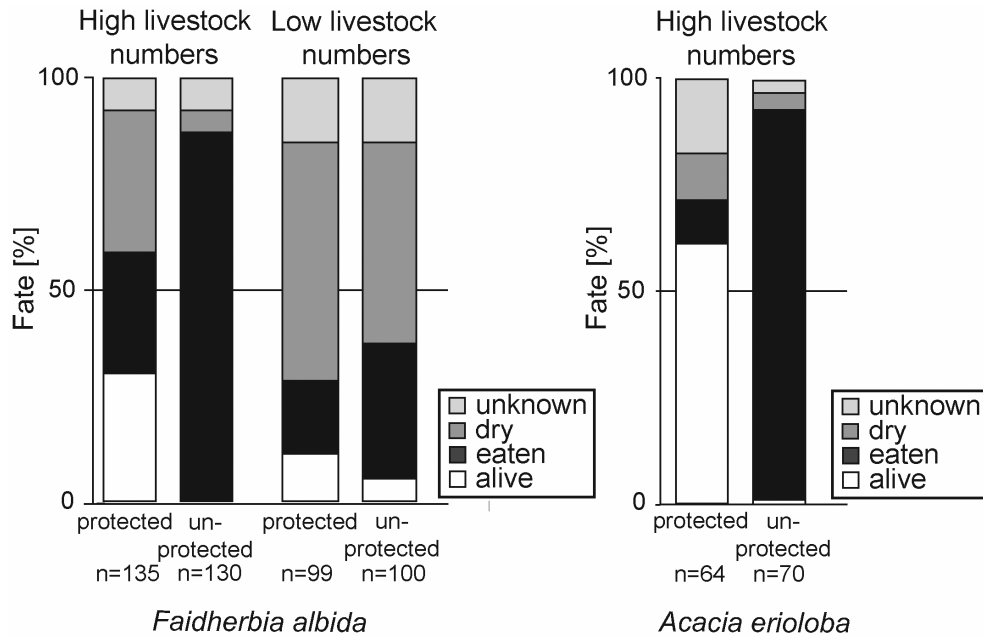


Figure 4.1: Fate (alive, eaten, dry, unknown) of protected and unprotected *Faidherbia albida* and *Acacia erioloba* seedlings [%] after 29 weeks at locations with high and low livestock numbers in the Kuiseb River, 2003 (n=number of seedlings).

In 2004, the fate of unprotected *F. albida* and *A. erioloba* seedlings is significantly different to that of protected seedlings in areas with high livestock numbers and for *F. albida* in areas with low livestock numbers ($p < 0.05$, chi-square). For *A. erioloba*, no significant difference between protected and unprotected seedlings was found in low livestock areas. A significant difference was found between locations with high and low livestock numbers for both unprotected *F. albida* and *A. erioloba* seedlings ($p < 0.0001$, chi-square).

Within the first two weeks after removing protective fences, 60.0 % of the then unprotected seedlings were eaten (n=40). In total 80.0 % of the unprotected seedlings were eaten within four weeks after fence removal. The average height (\pm SE) above ground at day of fence removal was 20.5 cm (\pm 2.5 cm) for *F. albida* (n=23) and 8.1 cm (\pm 1.2 cm) for *A. erioloba* (n=17). Average stem diameter (\pm SE) measured 3.6 mm (\pm 0.6 mm) for *F. albida* (n=23) and 2.8 mm (\pm 0.3 mm) for *A. erioloba* (n=17).

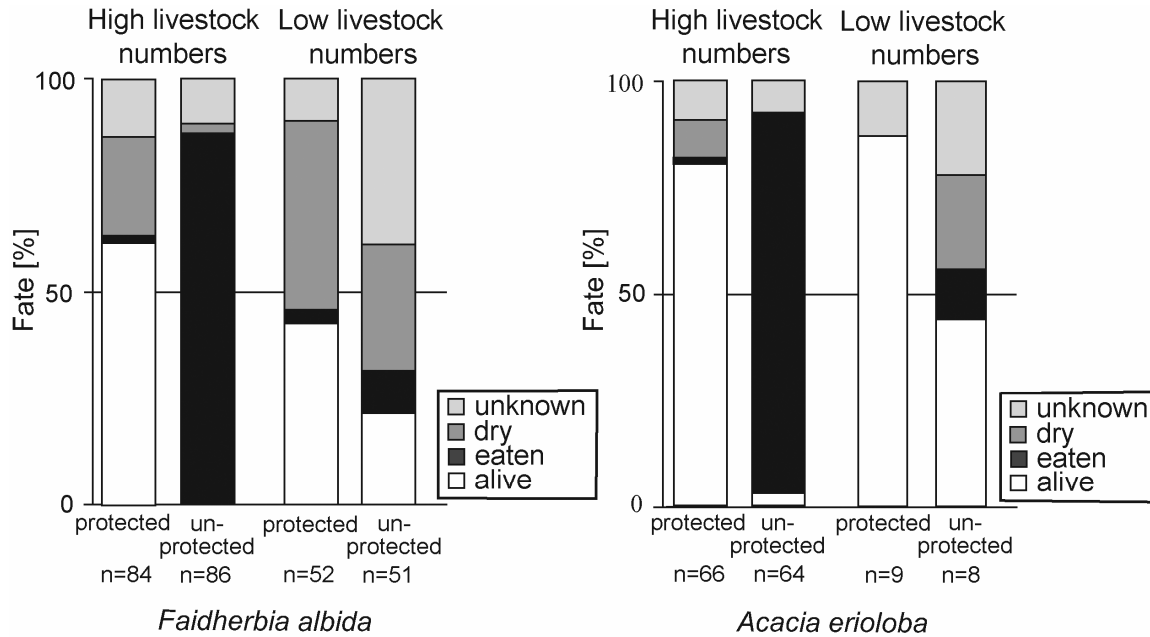


Figure 4.2: Fate (alive, eaten, dry, unknown) of protected and unprotected *Faidherbia albida* and *Acacia erioloba* seedlings [%] after 29 weeks at locations with high and low livestock numbers in the Kuiseb River, 2004 (n=number of seedlings).

4.3.3 Juvenile height increase

The height increase of *F. albida* juveniles was highest in river section U1 and decreased towards the sections M and L (Table 4.3). *Acacia erioloba* height increase was lowest in section U2 and highest in section M. Height increases differed significantly between sections for *F. albida* and *A. erioloba* ($p < 0.05$, Kruskal Wallis). *Acacia erioloba* height increase in river sections U2 and M was significantly different ($p < 0.05$, Dunn's Multiple Comparison Test), while for the other sections and for *F. albida* no difference could be found between any two sections.

Table 4.3: Average annual height increase (mean \pm SE) of *Faidherbia albida* and *Acacia erioloba* juveniles in four Kuiseb River sections (U1, U2, M, L; see Figure 2.1), 2003-2004 (n=number of juveniles)

River section	<i>Faidherbia albida</i> [cm a ⁻¹]	<i>Acacia erioloba</i> [cm a ⁻¹]
U1	55.0 \pm 17.4 (n=10)	17.3 \pm 5.6 (n=28)
U2	15.7 \pm 9.4 (n=21)	5.9 \pm 1.8 (n=80)
M	0.3 \pm 9.5 (n=17)	19.1 \pm 2.2 (n=162)
L	1.1 \pm 4.6 (n=9)	11.2 \pm 1.6 (n=199)

4.3.4 Size-class distribution

A relatively large number of juveniles of both study species are present at all study sites (Figures 4.3, 4.4 and 4.5). In all Kuiseb River sections, *F. albida* juveniles are less than 50 % of all trees, while *A. erioloba* juveniles provide >50 % of the sampled trees in the river sections U1 and M. Size class 5 m -<10 m and size class 10 m -<15 m form the largest proportions at all locations for both study species. In the Omaruru and Ugab rivers, less than 50 % of *F. albida* are juveniles and few trees are present in size class 1 m -<5 m. *Acacia erioloba* in the Ugab has more than 50 % of the trees in the juvenile class and size class ≥ 20 m is completely absent. A significant difference in *A. erioloba* size-class distribution was found among the Kuiseb River sections ($p < 0.0001$, chi-square). *Faidherbia albida* size classes do not differ significantly between river sections.

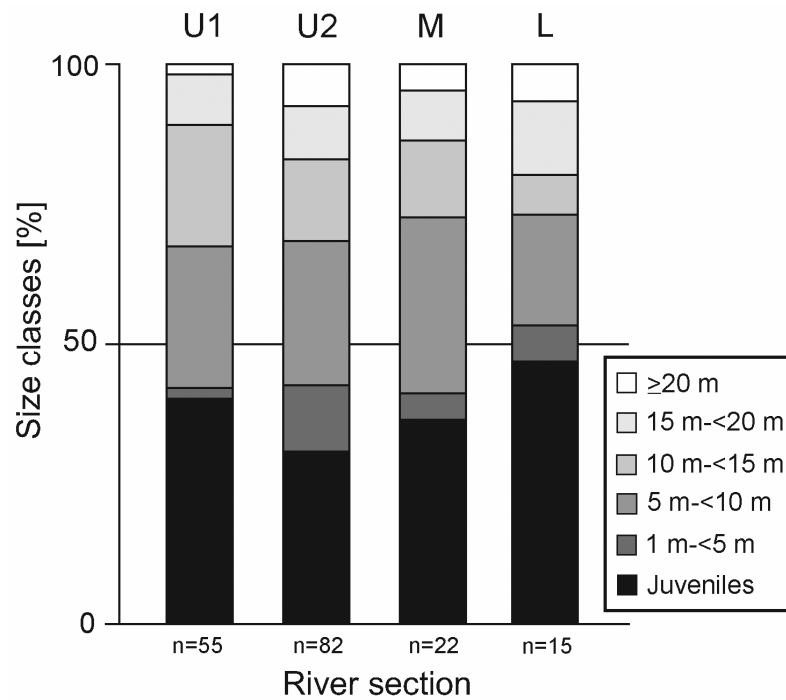


Figure 4.3: Relative number [%] of *Faidherbia albida* trees in six size classes in four Kuiseb River sections (U1, U2, M, L; see Figure 2.1), 2004 (n=number of trees). Juveniles are trees without clear stem and crown development and no flower or pod production. They form one size class while adult trees are grouped in five size classes according to their crown diameter.

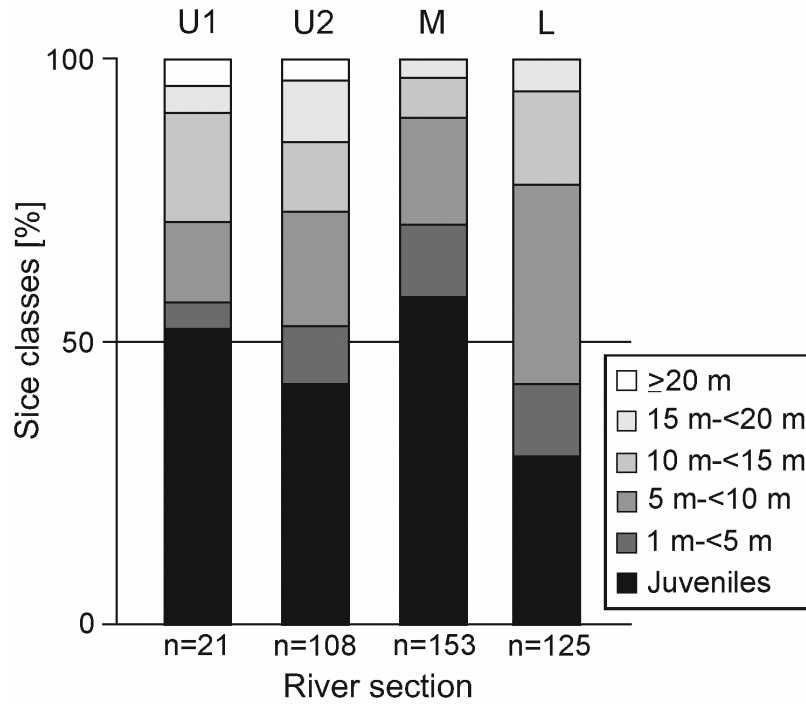


Figure 4.4: Relative number [%] of *Acacia erioloba* trees in six size classes in four Kuiseb River sections (U1, U2, M, L; see Figure 2.1), 2004 (n=number of trees). For procedures and conventions see Figure 4.3.

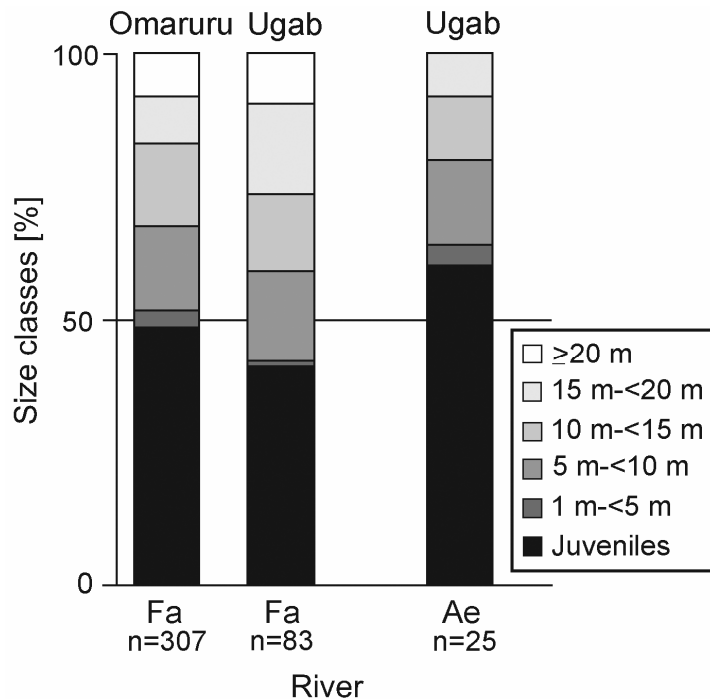


Figure 4.5: Relative number [%] of *Faidherbia albida* (Fa) trees in six size classes in Omaruru and Ugab rivers and *Acacia erioloba* (Ae) trees in the Ugab River, 2004 (n=number of trees). For procedures and conventions see Figure 4.3.

4.3.5 Tree density

Within the river sections of the Kuiseb, a decline in density of *F. albida* adults is visible from river section U1 to L (Table 4.4). *Faidherbia albida* juveniles show a similar trend, but display a density drop in section U2. Densities of *A. erioloba* juveniles increase from U1 to M and display a sudden decrease in L. Adult densities increase between U1 and U2 but remain relatively constant in the other sections. Densities of *F. albida* juveniles are significantly different to adult densities in sections U2 and L and juvenile and adult densities of *A. erioloba* differ significantly in section L ($p < 0.05$, Mann-Whitney). Juvenile densities in Omaruru and Ugab (Table 4.5) were not found to be significantly different to adult densities ($p > 0.05$, Mann-Whitney).

Table 4.4: Mean (\pm SE) density of *Faidherbia albida* and *Acacia erioloba* juvenile and adult trees in four Kuiseb River sections (U1, U2, M, L; see Figure 2.1), 2003/2004 (n=number of transects)

River section	<i>Faidherbia albida</i> [trees ha ⁻¹]			<i>Acacia erioloba</i> [trees ha ⁻¹]		
	juvenile	adult		juvenile	adult	
U1 (n=27)	22.4 \pm 4.8	26.3 \pm 4.0	ns	8.4 \pm 2.2	6.6 \pm 1.8	ns
U2 (n=25)	4.0 \pm 1.1	16.1 \pm 4.1	*	19.3 \pm 5.6	20.2 \pm 5.5	ns
M (n=22)	5.6 \pm 1.8	4.6 \pm 0.9	ns	32.8 \pm 9.7	18.8 \pm 2.6	ns
L (n=16)	1.1 \pm 0.4	1.7 \pm 0.3	*	9.7 \pm 1.2	18.4 \pm 1.8	*

* indicates significance level of $p < 0.05$
ns means not significant

Table 4.5: Mean (\pm SE) density of *Faidherbia albida* and *Acacia erioloba* juvenile and adult trees in Omaruru and Ugab rivers, 2004 (n=number of transects)

River	<i>Faidherbia albida</i> [trees ha ⁻¹]			<i>Acacia erioloba</i> [trees ha ⁻¹]		
	juvenile	adult		juvenile	adult	
Omaruru (n=37)	20.6 \pm 5.0	16.9 \pm 2.4	ns	-		
Ugab (n=16)	11.0 \pm 4.2	11.3 \pm 2.5	ns	2.3 \pm 1.2	2.1 \pm 0.7	ns

ns means not significant

4.3.6 Juvenile fitness in two size groups

All *F. albida* juveniles and *A. erioloba* juveniles >150 cm display a decrease in fitness from U1 to L, while for *A. erioloba* juveniles ≤150 cm poor fitness is relatively high but constant in all sections (Figures 4.6 and 4.7). The fitness of the two juvenile size groups of both study species differs significantly between the river sections ($p < 0.05$, chi-square). *Acacia erioloba* juveniles ≤150 cm are significantly different from juveniles >150 cm in all sections ($p < 0.0001$, Fisher's exact test). For *F. albida*, no significant fitness difference was found between size groups in the sections ($p > 0.05$, Fisher's exact test).

In the Omaruru River, the majority of *F. albida* juveniles ≤150 cm are of poor fitness while *F. albida* juveniles >150 cm and both juvenile size groups in the Ugab River demonstrate good fitness (Figure 4.8). *Acacia erioloba* in the Ugab performed poorly in the ≤150 cm group. A significant difference in fitness between size groups was found for *F. albida* in the Omaruru and Ugab rivers ($p < 0.001$, Fisher's exact test). No statistic test was carried out for *A. erioloba* due to the small sample size.

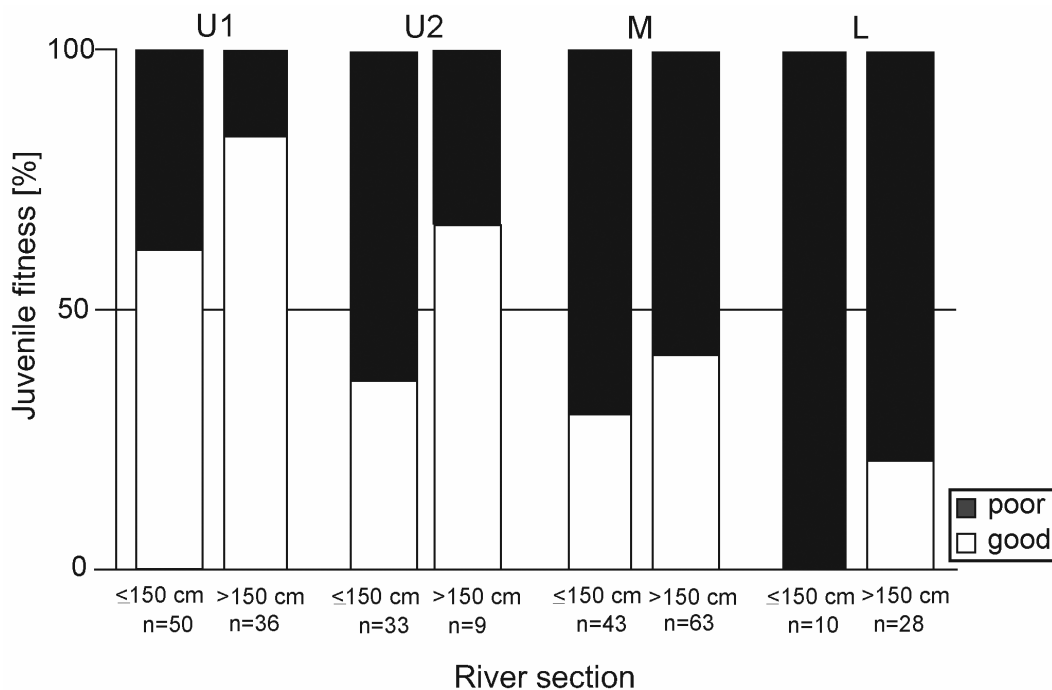


Figure 4.6: Relative number [%] of *Faidherbia albida* juveniles with good/poor fitness in two size groups (≤ and >150 cm) in four Kuiseb River sections (U1, U2, M, L; see Figure 2.1), 2003/2004 (n=number of juveniles). Fitness assessment was based on growth vigor and percentage of browsed/dry branch tips as well as dead branches.

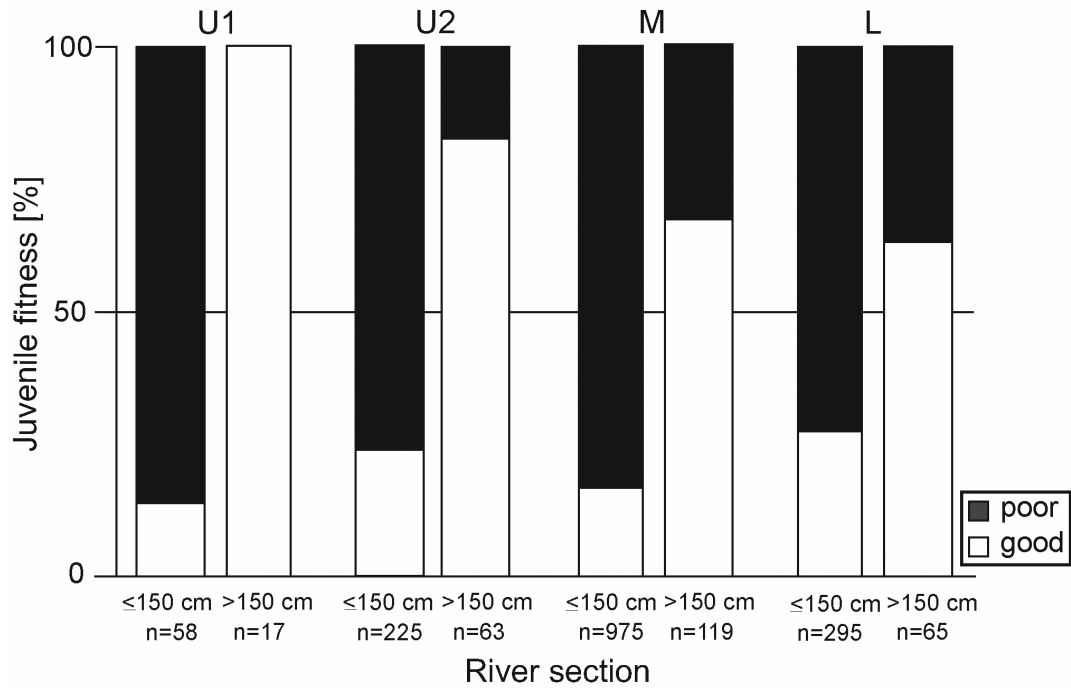


Figure 4.7: Relative number [%] of *Acacia erioloba* juveniles with good/poor fitness in two size groups (\leq and >150 cm) in four Kuiseb River sections (U1, U2, M, L; see Figure 2.1) 2003/2004 (n=number of juveniles). For procedures and conventions see Figure 4.6.

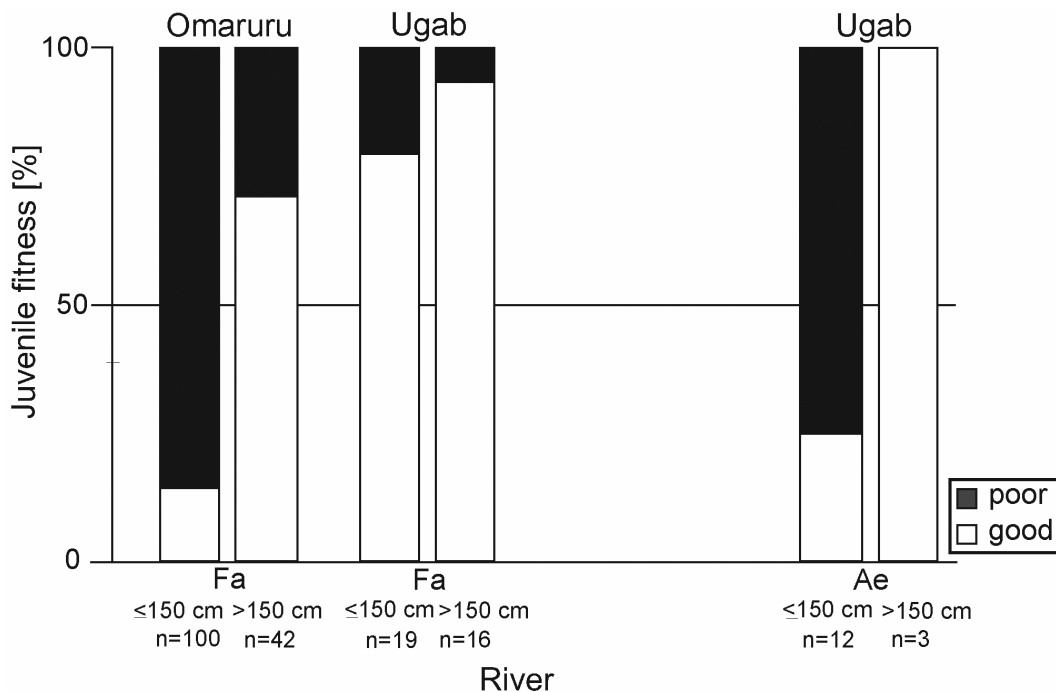


Figure 4.8: Relative number [%] of *Faidherbia albida* (Fa) juveniles with good/poor fitness in two size groups (\leq and >150 cm) in Omaruru and Ugab rivers and percentage of *Acacia erioloba* (Ae) juveniles with good/poor fitness in two size groups in the Ugab River (\leq and >150 cm), 2004 (n=number of juveniles). For procedures and conventions see Figure 4.6.

4.4 Discussion

Results of this first regeneration survey show that regeneration of *F. albida* and *A. erioloba* is very patchy and varies considerably in the Kuiseb River sections and in the Omaruru and Ugab rivers. Juveniles of *F. albida* and *A. erioloba* were present in all study sites irrespective of livestock densities, but regeneration failure was detected for some areas. At locations with high juvenile numbers, the maturation of a juvenile is not ensured, since juveniles are still vulnerable to desiccation (Johnson, 1994) and herbivores (Grubb, 1977).

In the size-class distribution, a reflection of regeneration events in the past (Pettit and Froend, 2001), no trend in size class distribution is visible for either species in all rivers. This is different to the results of Theron et al. (1985) for the Kuiseb River and of Viljoen and Bothma (1990) for *F. albida* in the Hoanib River, who found a continuous decrease in numbers with increasing size. The tree population along ephemeral rivers can experience severe disturbance by large floods, and at any flood event trees in any size class can be removed. At the same time, continuous regeneration is unlikely to occur due to limited precipitation and the unpredictable flow regime of ephemeral rivers. This results in episodic and patchy localized regeneration or die back that is not uniform within a river system and also not between river systems. This means that after a flood event trees will be removed from a site, but no regeneration occurs there. As a consequence, if regeneration takes place, a large number of juveniles need to survive and mature to ensure rejuvenation of the population. This fine balance is affected if juveniles are weakened, removed or die, e.g., through herbivore influence. Similar juvenile and adult or higher juvenile than adult densities point towards the functioning of this balance, while a lower juvenile density than that of adults indicates a lack of regeneration events or the result of regeneration disturbance at the seedling or juvenile stage.

Domestic herbivore influence occurs mostly close to farm settlements depending on the roaming range of the domestic animals. Goats and sheep walk approximately 5 km and cattle up to 15 km from their home kraal, but can move further away in times of fodder shortage. Donkeys are semi-wild and stay in the field unless they are needed at the farms for transport (Kooitje, personal communication). The presence and range of livestock is decisive for the regeneration success of the riparian

vegetation and affects the regeneration potential of *F. albida* and *A. erioloba*. High livestock numbers result in elimination of seedlings at an early stage and reduced juvenile growth. This means that after successful germination and seedling emergence (see Chapter 3) no or only few seedlings are able to establish, and even then will not be able to mature. This leads to little to no rejuvenation of the *F. albida* and *A. erioloba* tree population in areas with high livestock densities. Also in areas with few livestock, low vegetation density can result in a disproportionately higher livestock impact on the vegetation than expected from the number of animals.

After successful germination, the survival of the emerging seedlings depends on various other factors such as herbivory and desiccation (Solbrig, 1980). In the Kuiseb River, livestock completely remove young seedlings. Both study species are exposed to the threat of herbivore consumption, and almost all unprotected seedlings in areas with livestock access are eaten within the first weeks after emergence. In an herbivore exclusion experiment, Christensen and Muller (1975) found similar effects on unprotected seedlings through grazing. Protected and unprotected seedlings in areas with fewer livestock have a chance to survive, but other influences such as insect attacks, lack of water or covering with sand (personal observation) can lead to death over time. Causes and extent of seedling death can vary considerably from year to year (Fenner, 1987; Stromberg and Patten, 1990). *Faidherbia albida* seems to be more vulnerable to desiccation than *A. erioloba*, although it is difficult to assess the cause of death from the dry remains of a seedling. Drying can be the result of lack of water, grazed roots, disease or genetic defect (Fenner, 1987). In 2003, an insect attack contributed to the death of a large proportion of both protected and unprotected seedlings in areas with low livestock impact, reducing the overall survival rate. In 2004, there was no such influence and a larger proportion of seedlings survived, except in areas with high livestock density. The presence of livestock overrides the natural fluctuation, leaving almost no seedlings alive for establishment and growth.

The vulnerability of *F. albida* and *A. erioloba* remains beyond the early seedling age. After 30 weeks of protected growth and the development of considerable above-ground biomass, a majority of seedlings was eaten as soon as the protection was removed. According to Oba and Post (1999), plants need to be 150 cm high to escape the browsing impact of goats. These findings are further underlined in the present study

by the different height increase of *F. albida* and *A. erioloba* juveniles in areas with low and high livestock densities. Both species hardly grew in river section U2 with high livestock numbers but showed a good height increase in section U1, where few livestock roam despite the calculated livestock density. Herbivore influence in section U2 was further indicated by poor juvenile (≤ 150 cm) performance. The growth and juvenile fitness data show that livestock influence in river section U1 as a whole was small and is likely limited to the close vicinity of the settlement. This situation was observed for *F. albida* in the Kuiseb the river sections U2, M and L and in the Omaruru River. The further reduction in height increase of *F. albida* in river sections M and L, underlined by the poor performance of the smaller and larger juveniles, is probably related to livestock impact and reduced water availability due to fewer surface floods (Jacobson et al., 1997) and lowered water tables (Lenz et al., 1995). In contrast, good fitness of *F. albida* juveniles >150 cm in the upper woodlands U1 and U2 and in the Ugab and Omaruru rivers shows that at these locations growth conditions are suitable for *F. albida* (see Chapter 5). This means that there is enough water available for these juveniles, and they thus have a good chance to develop into mature trees. Although water availability at the onset of regeneration was sufficient for germination and seedling emergence at all locations, herbivory and probably lack of accessible water at a later stage will make it difficult for a large proportion of *F. albida* juveniles to mature and thereby reduce the regeneration potential of this species.

For *A. erioloba*, the poor fitness of the small juveniles in the river sections U2, M and L and the good fitness of larger juveniles indicate that livestock limits regeneration. This is confirmed by low juvenile growth in river section U2, but is contradicted by the good height increase in sections M and L. Here, the recorded height increase indicates suitable growth conditions for this species and little disturbance by herbivores. Lowered water tables in these sections do not seem to affect *A. erioloba* juveniles, since these are probably able to reach the deeper water sources through their strong root growth (see Chapter 3). In the river sections M and L, juveniles were found in large clusters close or under adult trees. Due to the difficulty in identifying individual juveniles in clusters, only solitary juveniles or those growing in small groups were used for the growth measurements. These juveniles will be probably visited by livestock less frequently than those close or under trees, where livestock often rests or feeds in the

shade. Therefore, mainly the growth of the juveniles with reduced livestock impact was recorded, which can have resulted in these contradictory findings. Poor performance of *A. erioloba* juveniles ≤ 150 cm in upper woodland U1 of the Kuiseb River and the Ugab River is probably the result of frequent inundation and water logging. Here, the flood plains are small and flood events more frequent than in the other areas. Since no herbivory influence was found for *F. albida* in these sections, *A. erioloba* is probably not negatively affected by herbivores either. It can be expected that larger *A. erioloba* juveniles had managed to germinate at suitable sites not reached by subsequent floods, and that all other factors were favorable for establishment and growth.

Along the ephemeral rivers, a large distance to the active water channel is advantageous for survival, as inundation and scouring and also herbivory is reduced. It seems that within a river cross section, herbivory is heavier close to the main watercourse. During their search for fodder, the livestock, especially goats and sheep, moves close to the watercourse, where adult *F. albida*, their preferred fodder source (see Chapter 6), grow in dense stands. As a consequence, this area can experience a higher browsing impact than locations further from the channel. *Acacia erioloba* juveniles grow at a greater distance from channels and thus also from mature *F. albida* in the river sections U1 and U2 of the Kuiseb River (see Chapter 5), which likely reduces the frequency of damage to *A. erioloba* seedlings and juveniles by livestock thus increasing their chance to survive. Seedlings of *A. erioloba* can develop into a size (>150 cm) where herbivore browsing does not limit their growth, yet their slow growth performance in the early years (Barnes et al., 1997) makes it difficult for the juveniles to reach a sufficient size within a short period of time. Goats and other livestock damage *A. erioloba* seedlings and juveniles during occasional browsing. On floodplains without clear water channel structures and scattered *F. albida* and *A. erioloba* tree distribution, such as river section L and to some extent also section M, browsing pressure is expected to be less focused than in *F. albida* stands along river channels. Nevertheless, a destructive effect on seedlings and juveniles growing nearby adult trees was observed. Livestock often passes by adult trees in search for fodder or to rest under them. Cattle have been observed to kill seedlings by trampling and feeding when standing under trees. Although seedlings and juveniles will not be completely eliminated by livestock,

their recruitment into the adult population is restricted, making locations close to adult trees unsuitable for regeneration.

4.5 Conclusion

The size-class distribution of the two study species shows that regeneration events are episodic in space and time and do not occur uniformly across a river profile. Due to the variability within an ephemeral river environment, disturbance in the population dynamics were difficult to detect from the size-class distribution, but were identified in the density analyses. Livestock negatively influences the regeneration and population developments of *F. albida* and *A. erioloba* along the ephemeral rivers of the Namib Desert. It is expected that if hydrological conditions are suitable for *F. albida* and *A. erioloba*, regeneration will be mainly controlled by livestock densities. If the regeneration potential of *F. albida* and *A. erioloba* is reduced through increased livestock densities, fewer trees will be available for fodder production in the future and livestock husbandry in the ephemeral rivers will be limited. In addition the ecosystem functioning of the rivers will be disturbed if the tree population were to become diminished.

5. SAFE SITES FOR *FAIDHERBIA ALBIDA* AND *ACACIA ERIOLOBA* SEEDLING ESTABLISHMENT

5.1 Introduction

One of the major factors influencing the functioning and structure of the riparian zone is the hydrologic regime (Everitt, 1968; Franz and Bazzaz, 1977; Barnes, 1985; Bradley and Smith, 1986; Salo et al., 1986; Baker, 1990; Stromberg et al., 1991; Johnson, 1994; Scott et al., 1997; Cooper et al., 1999; Jacobson et al., 2000a; Bendix and Hupp, 2000; Pettit and Froend, 2001; Pettit et al., 2001; Shafroth et al., 2002). The distribution of riparian vegetation in relation to hydrological conditions has been studied extensively for perennial systems (McBride and Strahan, 1984; Hupp and Osterkamp, 1985; Bradley and Smith, 1986; Baker, 1988; Bendix, 1994a,b; Baker and Walford, 1995; Parker and Bendix, 1996). Mechanical forces exercised by floods that transport propagules and sediments, as well as anaerobic conditions during flooding, are some of the factors relevant for the survival and distribution of riparian vegetation (Bendix, 1999). Floodplain elevation, topography, sediment size and groundwater depth as well as floodplain age and frequency of floodplain flooding further affect species distribution (Kalliola and Puhakka, 1988). Flow regulations, such as river dams, are found to influence the riparian vegetation in perennial systems (Johnson, 1994; Friedman and Auble, 1999; Fenner et al., 1984; Bradley and Smith, 1986; Rood and Heinze-Milne, 1989). However, little work has been carried out on this relationship in ephemeral rivers (Shafroth et al., 2002).

Infrequent large-magnitude floods are necessary to transport seeds onto the floodplains above the active channel where seedlings are able to emerge in moist and sites potentially safe from subsequent flooding and scouring (Scott et al., 1997; Auble and Scott, 1998; Cooper et al., 1999; Pettit and Froend, 2001; Pettit et al., 2001). Similar to findings in other dryland rivers, the vegetation in the ephemeral rivers of Namibia is expected to be driven by physical and not successional processes (Pettit and Froend, 2001; Baker and Walford, 1995). The demand for water in Namibia has led to plans for further water exploitation of the ephemeral rivers. Already two decades ago, first effects of hydrological change on the riparian vegetation were observed in some of the ephemeral rivers (Seely et al., 1980; Ward and Breen, 1983). Analyses of the

ecological impacts of changes in a river ecosystem are difficult due to the lack of assessments prior to these changes (Rood and Heinze-Milne, 1989).

The objective of this study is to understand the spatial distribution of the fodder trees *Faidherbia albida* and *Acacia erioloba* along three ephemeral rivers (Kuisseb, Omaruru, Ugab) and to characterize safe regeneration sites. Seedling survival after reflooding was determined and the flood volume needed for overbank flooding estimated. The distribution of *F. albida* and *A. erioloba* in relation to the active water channel was studied.

5.2 Material and methods

5.2.1 Seedling survival after flooding

To determine the influence of reflooding on established seedlings, all *F. albida* (n=15) and *A. erioloba* (n=42) seedlings remaining from the seedling survey experiment 2003 at Gobabeb (Chapter 4) were selected in December 2003. The seedlings were marked with a round metal bar, diameter 10 mm and length 1.5 m, in order to find the plant location after a flood. The bar was inserted 1.25 m into the ground in flow direction 25 cm south and 25 cm downriver of the plant to reduce bar influence during flooding on the seedling. Protection fences were removed from the seedlings the day before the flood event. The fate of the plants was determined immediately after the flood had receded completely and one month thereafter (26.02.04) in case seedlings had managed to resprout from submerged roots or plant parts. Percentage of dead seedlings was calculated per species.

5.2.2 Characteristics of overbank floods

Only sites that are protected from subsequent flooding provide the “safety” for seedling establishment and survival. To determine how the middle Kuisseb River varies in terms of overbank flood frequency and to see how often requirements for overbank floods were met in the past, cross-section profiles of the active river channel were measured at 5 km intervals on 02.08., 05.08., 09.08. and 10.08.04 (n=21). Additional profiles (n=8) were recorded on 15.03.05 to increase the sample size. A simplified cross-section profile was established with a theodolite (Pentax AL 200). Recordings were taken in the middle of the main channel, at the base of the riverbank and at the highest point of the

riverbank on each side. Distances between recording points were measured with a tape measure. The slope-area method with the Manning equation (Rantz, 1982) was applied to calculate the flood volume needed to reach the overbank at the lowest side of the cross-section profile. The roughness coefficient (n) was estimated as 0.035 (van Langenhove, personal communication). The slope of the riverbed (S_o) was calculated from 1:50000 topographic maps. The distance of each cross-section profile to the Gobabeb Weir was measured with the GIS software Touratech. Considering the simplified survey methods, the results can only be seen as an approximation. For the calculations, Manning's equation was rewritten as follows to calculate discharge (Q [m^3]) (5.1). It was assumed that flow conditions were uniform:

$$Q = S_o^{1/2} / n A^{5/3} / D^{2/3} \quad (5.1)$$

Cross-section distance (D [m]) was measured and height measurements of the lowest overbank used to calculate the cross section area (A [m^2]). Flood recordings from the Department of Water Affairs (DWA) were used to analyze recurrence of floods reaching the overbank since the flood season 1978/79. Transmission loss calculations from Jacobson (1997) were used to determine the theoretically recorded flood volume at the Gobabeb Weir for each cross-section overbank volume.

5.2.3 Vegetation transects

Vegetation surveys along the Kuiseb, Omaruru and Ugab rivers were carried out along belt transects in the Kuiseb River from October to December 2003 ($n=58$) and August 2004 ($n=32$) and in October 2004 in the Omaruru ($n=37$) and Ugab ($n=16$) rivers. Transects were placed perpendicular to the river and surveyed over the entire length. Transect width and intervals between transects were dependent on the density of the vegetation and the width of the river channel and adjacent flood plains. The vegetation cover type of each transect (open, open with individual trees, open woodland, woodland) was determined and the coordinates of start and endpoint of each cover type were recorded with a GPS. Open covers did not support any adult woody vegetation, but grass and herbaceous species were sometimes present. Covers that were largely open but had occasional adult woody vegetation were determined as open with individual

trees. Similar openness but with more adult trees was identified as open woodland. Woodlands are areas where adult trees dominate and no large open area is present. Channels were defined as components with an incised river bed and adjacent flood plains, and channel coordinates were determined with a GPS. The study species were identified as adults and juveniles. Juvenile plants had no flowers or seed pods and often a shrub-like habitus, especially *A. erioloba*. In the Kuiseb River survey 2003, only juveniles and in 2004 both adults and juvenile plants were surveyed. The coordinates of the location of each study species were determined with a GPS. Analyses were carried out as followed:

Spatial distribution of juvenile and adult plants: The proportion of juveniles and adults growing in the main channel and within 20 m of the channel was calculated as a percent of the total juvenile and adult population per river section or river. In the Kuiseb River distances from the main channel were only calculated for the river sections U1, U2 and river sections M, since in the river section L several small channels had developed. GPS recordings of tree location and the demarcation of the main channel were used to estimate distances. Differences in juvenile and adult locations were tested between river sections with chi-square and within rivers sections and rivers with Fisher's exact test (Zar, 1999).

Vegetation cover: The expanse of the four main cover types (open, open with individual trees, open woodland and woodland) was calculated from GPS data of all surveyed transects. The number of juveniles in each vegetation cover type was counted (observed frequency). The expected frequency of juveniles was calculated according to the proportion of the four main vegetation covers under the assumption that juveniles are distributed equally in each cover type. Chi-square analyses were carried out to determine the association of juveniles with vegetation cover types (Zar, 1999).

5.2.4 Vegetation and topographic profiles in the Kuiseb River

Four detailed profiles of the river cross section were established in June 2004 (see Figure 2.1) in the Kuiseb River. In each river section (U1, U2, M and L; see Figure 2.1), a line transect was surveyed perpendicular to the river. At 10 m intervals along the transect, all plants touching or overhanging the line were identified and recorded. Development stage of the woody vegetation (adult, juvenile, seedling) was noted. A 4-

m long measuring pole was used to determine the height of the plants. If the tree was higher than 4 m, the pole was placed next to the tree and the height estimated visually. For *Acanthosicyos horridus* and *Salvadora persica*, width, length and height were also determined with the 4 m pole. All other plants (grasses, herbaceous species) were sorted into size groups ranging from small, medium to big. A topographic profile of the entire transect was established with a theodolite (Pentax AL 200).

5.2.5 Data analyses

For data analyses and presentation, Microsoft Excel, GPS Trackmaker 11.8, Ozi Explorer 3.9, Touratech QV 3.0 and Adobe Illustrator 10.0 software were used. Statistic tests were carried out with GraphPad InsStat 3.05 and Statistica 6.0. In all statistical analyses, a significance level of 5 % was applied (Zar, 1999). All test results are presented in detail in Appendix III.

5.3 Results

5.3.1 Seedling survival and overbank floods

After a flood in 2004 (overbank was not reached) 8-month-old seedlings (germinated in April 2003) growing in the active river channel were inundated between 12 h and 72 h. After the flood water had receded completely, 83.3 % of *F. albida* (n=15) and 95.5 % of *A. erioloba* (n=42) were found dead from scouring or sediment covering.

Table 5.1: Median, minimum and maximum flood water discharge needed for overbank floods along the middle Kuiseb River (sections U1, U2, M; see Figure 2.1), 2004/2005

River section	Median [m ³ s ⁻¹]	Minimum [m ³ s ⁻¹]	Maximum [m ³ s ⁻¹]
All (n=29)	59	4	290
U1 (n=10)	58	23	290
U2 (n=10)	93	16	173
M (n=9)	31	4	85

The analyses of the Kuiseb River cross sections (n=29) show that a peak flood discharge of 289.6 m³s⁻¹ needs to be recorded at the Gobabeb Weir in order for the entire middle Kuiseb River (upper woodlands U1, U2 and middle woodland M) to experience overbank floods (Table 5.1). To overflow 50 % of the river's floodbanks, a flood discharge of 58.9 m³s⁻¹ is necessary. Section U2 needs the highest median flood peak discharge in order to reach 50 % of the flood plains and has recorded the fewest median floods in the past 19 flood events (Table 5.2). Flood events in section M met the median, minimum and maximum requirements most frequently.

Table 5.2: Number of floods that have reached median, minimum and maximum discharge causing overbank floods in three Kuiseb River sections (U1, U2, M; see Figure 2.1) since season 1978/79 (n=19)

River section	Median	Minimum	Maximum
All	8	18	1
U1	8	15	1
U2	3	16	1
M	11	18	4

5.3.2 *Faidherbia albida* and *Acacia erioloba* juvenile and adult growth locations in relation to active channel

Within the four river sections of the Kuiseb (Table 5.3), nearly all adult and juvenile *A. erioloba* grew outside of the main channel. Juvenile *F. albida* were found in the active channel but showed a decreased channel relation from river sections U1 to L. Adult *F. albida* were found in channel-like structures in the river sections U1, U2 and the river section L. A significant difference in *F. albida* juvenile channel relation was tested between the sections ($p < 0.0001$, chi-square). The number of *F. albida* juveniles outside of the main channel are significantly higher than adults in section U1 ($p < 0.0001$, Fisher's exact test). For river sections U2, M and L no significant difference was found. No statistic test was carried out for *A. erioloba* due to low values.

Table 5.3: Relative number of juvenile and adult *Faidherbia albida* and *Acacia erioloba* trees growing in channel structures in four Kuiseb River sections (U1, U2, M, L; see Figure 2.1), 2003/2004 (n=number of trees)

River section	<i>Faidherbia albida</i> [%]			<i>Acacia erioloba</i> [%]	
	juvenile	adult		juvenile	adult
U1	27.8 (n=133)	2.0 (n=50)	*	0 (n=76)	0 (n=17)
U2	8.1 (n=62)	5.1 (n=39)	ns	0 (n=296)	0 (n=53)
M	1.5 (n=131)	0 (n=14)	ns	0.1 (n=1044)	0 (n=64)
L	0 (n=38)	12.5 (n=8)	ns	0.3 (n=315)	0 (n=88)

* indicates significance level of $p < 0.05$
ns means not significant

In the Omaruru River, a similar number of juveniles and adult *F. albida* trees were observed in the main flood channel, while fewer adults than juveniles were found in channel structures in the Ugab River (Table 5.4). The number of juvenile and adult *F. albida* found growing in channel structures in the Omaruru and Ugab rivers, was not significantly different.

Table 5.4: Relative number of juvenile and adult *Faidherbia albida* and *Acacia erioloba* trees growing in channel structures in the Omaruru and Ugab rivers, 2004 (n=number of trees)

River	<i>Faidherbia albida</i> [%]			<i>Acacia erioloba</i> [%]	
	juvenile	adult		juvenile	adult
Omaruru	41.8 (n=134)	37.5 (n=136)	ns	-	-
Ugab	28.6 (n=35)	18.4 (n=49)	ns	0 (n=15)	0 (n=10)

Acacia erioloba adults and juveniles in the river sections U1, U2 and M were not growing close to the main channel (Table 5.5). The main channel attracted adult *F. albida* in U1 and U2 but had no influence in section M. Juvenile *F. albida* displayed a decreasing channel relation from river sections U1 to M. Channel relation of juvenile and of adult *F. albida* differs significantly between the river sections ($p < 0.001$, chi-square). A significant difference between juvenile and adult distribution in the river sections along the channel was found for *F. albida* in section U2 and M ($p < 0.05$, Fisher's exact test). No analyses were made in the river section L because the main channel split into several small channels and for *A. erioloba* due to low values.

Table 5.5: Relative number of juvenile and adult *Faidherbia albida* and *Acacia erioloba* trees growing 0-20 m from the main channel in four Kuiseb River sections (U1, U2, M, L; see Figure 2.1), 2003/2004 (n=number of trees)

River section	<i>Faidherbia albida</i> [%]			<i>Acacia erioloba</i> [%]	
	juvenile	adult		juvenile	adult
U1	49.5 (n=99)	46.9 (n=49)	ns	0 (n=78)	0 (n=19)
U2	29.8 (n=57)	73.0 (n=37)	*	2.0 (n=296)	5.7 (n=53)
M	26.2 (n=130)	0 (n=14)	*	1.2 (n=1040)	0 (n=64)
L ^a	-	-		-	-

* indicates significance level of $p < 0.05$

ns means not significant

^ain section L several small channel like structures

In the Ugab River more than half of *F. albida* juveniles were found close to the active watercourse. Few adult and no juvenile *A. erioloba* were growing 0-20 m from the channel (Table 5.6). More than 80 % of the *F. albida* juveniles in the Omaruru River occurred 0-20 m from the channel. Significantly more *F. albida* juveniles than adults grew within 20 m of the channel in the Omaruru River ($p < 0.0001$, Fisher's exact test). No significant difference was found between juvenile and adult *F. albida* distribution for the Ugab.

Table 5.6: Relative number of juvenile and adult *Faidherbia albida* and *Acacia erioloba* trees growing 0-20 m from the main channel in the Omaruru and Ugab rivers, 2004 (n=number of trees)

River	<i>Faidherbia albida</i> [%]			<i>Acacia erioloba</i> [%]	
	juvenile	adult		juvenile	adult
Omaruru	84.6 (n=78)	45.4 (n=86)	*	too few values	
Ugab	52.0 (n=25)	46.2 (n=39)	ns	0 (n=15)	10.0 (n=10)

* indicates significance level of $p < 0.05$

ns means not significant

5.3.3 Vegetation cover types

Along the Kuiseb River sections U2 and M (Table 5.7), juvenile *F. albida* are not associated with any specific cover type. Juveniles of *F. albida* in sections U1 and L and of *A. erioloba* in all other sections display preferences but no clear trend is visible.

Table 5.7: Association of *Faidherbia albida* and *Acacia erioloba* juveniles with open, open plus individual trees, open woodland and woodland vegetation cover in four Kuiseb River sections (U1, U2, M, L; see Figure 2.1) determined by χ^2 statistics

		<i>Faidherbia albida</i>				
River section		Open	Open plus individual trees	Open woodland	Wood-land	p
U1	observed	3	12	27	54	<0.0001
	expected	1	36	35	24	
U2	observed	0	15	21	21	<0.4201
	expected	0	11	27	19	
M	observed	6	32	66	25	<0.7415
	expected	7	36	65	21	
L	observed	1	5	31	1	<0.0023
	expected	1	15	19	2	

		<i>Acacia erioloba</i>				
River section		Open	Open plus individual trees	Open woodland	Wood-land	p
U1	observed	0	31	16	31	<0.0026
	expected	1	29	29	29	
U2	observed	0	16	162	118	<0.0001
	expected	0	58	140	98	
M	observed	21	104	496	422	<0.0001
	expected	56	291	523	173	
L	observed	4	79	206	25	<0.0001
	expected	11	124	160	19	

The analyses of the vegetation-cover association of juveniles in the Omaruru and Ugab rivers (Table 5.8) show that *F. albida* in the Omaruru grew mainly in open woodland or woodland structures ($p < 0.05$, chi-square). Along the Ugab, both study species were equally associated with all cover types.

Table 5.8: Association of *Faidherbia albida* and *Acacia erioloba* juveniles with open, open plus individual trees, open woodland and woodland vegetation cover in the Omaruru and Ugab rivers, determined by χ^2 statistics

<i>Faidherbia albida</i>						
River		Open	Open plus individual trees	Open woodland	Woodland	p
Omaruru	observed	0	0	65	6	<0.0014
	expected	0	9	48	14	
Ugab	observed	0	7	9	9	<0.8013
	expected	0	5	10	10	

<i>Acacia erioloba</i>						
River	Species	Open	Open plus individual trees	Open woodland	Woodland	p
Ugab	observed	0	5	9	1	<0.0614
	expected	0	3	6	6	

5.3.4 Vegetation and topographic profiles in the Kuiseb River

The cross-section profiles of the Kuiseb River sections (see Figure 2.1) illustrate section-typical channel and floodplain topography as well as preferred growth locations of *F. albida* and *A. erioloba* (Figure 5.1). Profile 1 (Figure 5.1a) is the shortest of all transects with a small and deep main river channel and small drainage lines on the floodplains and located in the river section U1. *Faidherbia albida* is located mainly along the channel and *A. erioloba* on the floodplains. Profile 2 is situated in section U2 (Figure 5.1b) where *F. albida* grow in small woodlands adjacent to the main channel and *A. erioloba* start to develop woodlands on a widening floodplain. In Profile 3 (Figure 5.1c) and Profile 4 (Figure 5.1d), the profiles of the middle and lower river sections, no relation of *F. albida* with channels can be observed and overall fewer individuals are found in these profiles. Here *A. erioloba* is the dominant woody species and forms small woodlands, while *F. albida* is scattered on the flood plain. In these two profiles, grasses and other herbaceous species are a major component of the vegetation.



Figure 5.1: Vegetation and topography of four Kuiseb River sections (U1, U2, M, L; see Figure 2.2) is presented along cross sections perpendicular to the river, 2004. The main woody vegetation (*F. albida*, *A. erioloba*, *T. usneoides*, *E. pseudobenus*, *A. horridus*, *S. persica*, *S. plumosa*) and grasses (*C. spinosa*, *Stipagrostis*) are displayed by specific symbols (see legend). All other species are displayed by a ∇ . Due to the small scale in Profile 3 and 4, not every recorded grass species and other vegetation is displayed. The topography of channels and floodplains are presented in scale [m]. The size of the vegetation is standardized and does not reflect the real size.

5.4 Discussion

A dynamic river environment, although at periods dry as in ephemeral rivers, allows successful seedling growth and establishment at sites with little disturbance. *Faidherbia albida* and *A. erioloba* seedlings growing in the active channel of ephemeral rivers have little chance to survive subsequent floods. Seedlings establishing in the active watercourse due to its good water supply will rarely be able to grow into mature trees. The main channel can experience several flooding events during one flood seasons or is flooded in following seasons, which can result in uprooting, breaking or bending of the plants (Bendix, 1998) or overlaying with river sediments. In the Kuiseb River, *F. albida* and *A. erioloba* seedlings were either removed or covered with sediments. Even if they resprout and grow vegetatively from submerged plant parts (Stromberg and Patten, 1990), continuous flood scouring will keep them small. The few *F. albida* juveniles and comparatively small number of *F. albida* adults as well as the complete absence of *A. erioloba* trees in the active channel in the Kuiseb River confirms that the physical forces exercised by floods in the active channel make this location unsuitable for regeneration. Similar patterns have been observed elsewhere where seedlings and saplings were not able to reach maturity because they were destroyed in floods (Cooper et al., 1999; Bendix and Hupp, 2000; Pettit and Froend, 2001; Shafroth et al., 2002). Mature trees were only able to exist at higher elevations, in protected river bends or at a greater distance from the river. If seedlings and juveniles are able to grow very fast (Johnson, 1994) and are tolerant to soil submergence and/or if there are low-magnitude or no floods for several seasons (see 2.3.1), establishment and maturation is possible. The presence of adult *F. albida*, a fast growing tree (CTFT, 1989), in the active channel of the Kuiseb River as observed by Jacobson et al. (1999) was related to several years without floods in the early 1980s, which led to the establishment of trees in the channel and the formation of tree islands. These tree islands are more common in the Omaruru and Ugab than in the Kuiseb River. In the Omaruru River, the establishment of large numbers of *F. albida* in the active channel is assumed to be the consequence of reduced surface floods in the studied sections of the river. The Ugab River on the other hand has regular surface water after good rains in the upper catchment. It is expected that these flood forces are too strong to allow plants to establish in the river bed, a situation similar to that observed in the Kuiseb River.

Seedlings and juveniles are not affected by scouring or inundation in locations on the flood plains above the active channel. In the Kuiseb River, not all flood events in the past had the magnitude to reach overbank and if they did, they only inundated some locations. At these locations, seedlings have a good chance to survive. For the seeds to reach overbank sites, not the total discharge but the peak discharge at any flood event is important. Dam constructions upriver might not reduce the total amount of water flowing into the lower parts but influence the maximum flood peaks (McBride and Strahan, 1984; Friedman and Auble, 1999). This limits the number of overbank floods and thus the regeneration success of the two study species and other riparian vegetation.

Not all overbank locations, although safe from scouring, inundation and covering with sediments, are equally suitable for regeneration and establishment of *F. albida* and *A. erioloba*. Even though no clear vegetation cover type preference of the juveniles could be shown, open areas seem to be the least suitable for regeneration. In these locations, low seed provision and limited seed retention can be expected. Retention mechanisms will probably work better in open woodland and woodland on flood plains where flood speed and strength are reduced by the density of the riparian vegetation (Bendix and Hupp, 2000; Shafroth et al., 2002) and sedimentation is increased (Shafroth et al., 2002). This means that the flood force in these locations is expected to be lower, thus reducing the disturbance and mortality of seedlings and juveniles and thereby increasing regeneration success.

Stromberg et al. (1991) argue that different tolerance of moisture saturated soils or drought may contribute to niche partitioning between two species. *Faidherbia albida* depends on reachable water sources and regenerates successfully at locations close to a clearly developed active channel in the Kuiseb river sections U1 and U2, and in the Omaruru and Ugab rivers. This confirms the findings for the Kuiseb River by Seely et al. (1980), Theron et al. (1980), Theron et al. (1985) and Bate and Walker (1993) and for the Omaruru and Ugab rivers by Leggett (1992, 1993) as well as along the Zambezi River, where *F. albida* established on sandbanks while its abundance dropped on higher terraces (Dunham, 1989). Two reasons seem to be important for the near watercourse growth of *F. albida*. Accessible groundwater and silt deposits are crucial for *F. albida* growth and decline with distance from the active channel and downriver (Lenz et al., 1995; Jacobson et al., 2000a). For *A. erioloba*, a greater distance

from the watercourse appears to be necessary for development and survival as seen in sections U1 and U2. Although slow growing in the beginning, *A. erioloba* is known for a fast growing root system (see Chapter 3) and the ability to reach water tables up to 40 m deep (Barnes et al., 1997). This makes *A. erioloba* well adapted to the Kuiseb sections M and L with their wide floodplains, small active water channels and low water tables. Similar to other *Acacia* species (Petitt et al., 2001), *A. erioloba* seems to be less tolerant to water logging by long lasting floods, frequent flooding or unstable sediments. Reichenbacher (1984) recorded *Acacia greggii* only at a great distance from the active channel on floodplains with dropping water tables.

5.5 Conclusion

In an ephemeral river environment differing in flood frequency, flood magnitude, flood bank width and water availability, *F. albida* and *A. erioloba* exist next to each other in specific ecological niches without interspecific competition for natural resources. While the ecological requirements for *F. albida* regeneration are best met close to active water channels, *A. erioloba* seems to be better suited for positions further away with lower water availability. Locations with good surface and subsurface water supply such as the main river channel are not safe locations for seedling establishment and survival. Although *F. albida* and *A. erioloba* are dependent on flood water for seedling regeneration, seedling and juvenile survival of both species is hampered by flood scouring. A reduction of large overbank floods through reduced peak discharge will threaten both *A. erioloba* and *F. albida* seedling establishment processes. Should water availability be reduced through climate or human change, particularly *F. albida* establishment and survival will be threatened and the disappearance of this species from the ephemeral river environment can be expected. An encroachment of *A. erioloba* or other species to locations previously occupied by *F. albida* can be one effect.

6. CONTRIBUTION OF *FAIDHERBIA ALBIDA* AND *ACACIA ERIOLOBA* TO THE LIVELIHOODS OF COMMUNAL FARMERS

6.1 Introduction

In subsistence land-use systems, livestock keeping has high priority and domestic animals are used for transport, own consumption, income generation and serve as an insurance (Amir, 1992). Forage trees play a crucial role as a supplement to livestock fodder sources in many parts of semi-arid to arid Africa (Baumer, 1992; Shayo, 1998). In areas where rainfall is too low to produce sufficient grazing land, indigenous trees and shrubs are essential for livestock and wildlife (Shayo, 1998) and due to their year-round provision of feed they are of great economic importance (Amir, 1992). Along the middle and lower reaches of the ephemeral rivers of west Namibia, the majority of people derive their livelihoods from small-scale farming in communal farming areas (Jacobson et al., 1995). Cash income of the communal farmers is mainly derived from state pensions of the elderly, income from employed family members and to some extent from livestock marketing. Occasional sale of livestock and alternative income generating activities help to pay for school fees, medication and other needed items. Money to buy fodder for livestock is limited, making the farmers more or less entirely dependent on the natural resources of the surrounding river environment. Due to the aridity of the western parts of Namibia, the lush riparian vegetation is the only reliable fodder source. Especially the tree *Faidherbia albida*, but also *Acacia erioloba*, provides fodder for the livestock of communal small stock farmers (Seely et al., 1980; Jacobson et al., 1995). In addition, the sale of their pods contributes to income generation and household security (Jacobson et al., 1995).

Faidherbia albida and *A. erioloba* are threatened by changes to the hydrologic regime (Seely et al., 1980; Ward and Breen, 1983; Jacobson et al., 1995) and increasing livestock densities (Chapters 3, 4, 5). To advise decision makers and to implement sound management strategies for the ephemeral rivers, the socio-economic consequences of changes in the ephemeral river vegetation need to be understood. This chapter investigates utilization and management practices of *F. albida* and *A. erioloba* by communal farmers along three ephemeral rivers and the monetary value of the two species. For this, farmers were interviewed using a questionnaire. Annual pod

production and livestock-accessible biomass stock of the two tree crops was assessed. The monetary value of the trees was related to pod market value and livestock production.

6.2 Material and methods

6.2.1 Questionnaire

Structured interviews (n=106) were carried out in the communal farming areas of three ephemeral rivers: Kuiseb (May, June 2004), Omaruru (October 2004) and Ugab (October 2004). The questionnaires used for the Omaruru and Ugab rivers were a slightly modified version of that for the Kuiseb questionnaire (Appendix IV). Households involved in small-stock farming activities were visited in 46 villages (Kuiseb=13, Omaruru=17, Ugab=16).

Interviews were undertaken with a translator and with transcribers in Afrikaans or Damara-Nama. The interview partners were selected systematically on a household basis. In Okambahe, a small town along the Omaruru River, 10 households were selected with the help of the local agricultural extension officer. The household head was interviewed or the herder/caretaker of the animals if the household head was absent (Kuiseb=33, ♀=9, ♂=24, Omaruru=41: ♀=23, ♂=18, Ugab=32: ♀=16, ♂=16).

6.2.2 Pod production

In the Kuiseb River, near Gobabeb (see Figure 2.1), adult *F. albida* (n=39) and *A. erioloba* (n=40) trees were selected. The trees had to be in good health and the crown not shaded more than 25 % by other trees. The first adult tree of each study species complying with these criteria was chosen at a minimum distance of 50 m up- and downriver from the abstraction borehole of Gobabeb. This distance was selected to avoid drawdown effects from the borehole that might influence tree fitness. From this tree, the nearest neighbor was included in the sample. If the nearest tree did not comply with the selection criteria, the closest suitable tree was used. The selected trees were permanently marked and their coordinates determined with a GPS (Garmin 72). The height above the ground of the lowest branches (crown base) and tree height were estimated by placing a 4-m long pole next to the tree and crown height (h [m]) calculated. Crown diameters (maximum crown diameter and at diameter in 90° to this)

were estimated to determine the crown radius (r [m]). To estimate crown volume, each tree was characterized by a geometrical form describing the general shape of the crown (cone, hemisphere). For hemisphere calculations, all measurements were averaged (height and diameters) and for the cone only the estimated crown diameters. The equations 6.1 and 6.2 were used to calculate the crown volume (V_c [m^3]):

$$\text{Cone}(c): V_{c_c} = 1/3 r^2 \pi h \quad (6.1)$$

$$\text{Hemisphere}(hs): V_{c_{hs}} = 2/3 r^3 \pi \quad (6.2)$$

To determine annual pod production, the selected trees were surveyed monthly from September 2003 to January 2004 and every two months from January to August 2004. At each survey, a representative crown volume of $1 m^3$ was selected and the number of ripe pods ($NP m^{-3}$) counted. To simplify calculations, it was assumed that each tree had only one fruiting period and pod fall between surveys was not considered. The highest number of ripe pods at any one survey was used to calculate annual pod production. To accommodate unproductive crown volume such as dry branches and gaps in the tree crown, each tree was assigned a productivity factor (PF) of 1, 0.75, 0.5 or 0.25 corresponding to 100 %, 75 %, 50 % or 25 % crown productivity, respectively.

To calculate pod production, the average dry weight of a single pod was determined from randomly collected pods. Pods from each study species were collected from the ground at peak pod fall periods (*F. albida*: December 2003, *A. erioloba*: March 2004). Trees (*F. albida* $n=26$, *A. erioloba* $n=15$) were selected at 2 km intervals in an upriver direction starting 2 km west of Soutrivier (see Figure 2.1). One additional *F. albida* tree was sampled approximately 60 river kilometers downriver from Soutrivier. Distances between trees were measured with a car odometer. If possible, both species were collected at the same location. Thirty pods were collected randomly from the ground by throwing a $1 m^2$ quadrat and collecting all the pods within the quadrat. This procedure was repeated until a minimum of 30 pods was collected. If less than 30 pods were available in total, all were collected. *Faidherbia albida* pods still clustered after pod fall were regarded as one pod, since no differentiation between single pods and pod clusters was made in the pod count surveys. The pods were stored in a dry place at room temperature until April/May 2004 and then oven dried at $60^\circ C$

for three days. Dry weight of pods (*F. albida* n=767, *A. erioloba* n=308) was determined with a Mettler AE 100 analytical balance (balance accuracy to 0.001 g) and average dry weight of one pod (AWP [g]) calculated. Equation 6.3 was used to calculate annual pod production (AP [g]) per tree incorporating the results for V_c [m³] from equation (6.1) or (6.2) depending on the crown shape:

$$AP = V_c \times PF \times NP \times AWP \quad (6.3)$$

The trees from the pod production study were sorted into three tree classes using the average crown diameter. Average pod production was calculated for each tree class of each species.

Faidherbia albida: tree class 1: < 8.5 m; tree class 2: 8.5 m-<17 m; tree class 3: ≥17 m

Acacia erioloba: tree class 1: <7.5 m; tree class 2: 7.5 m-<15 m; tree class 3: ≥15 m

6.2.3 Browsable biomass stock

Annual biomass stock produced by *F. albida* and *A. erioloba* trees and accessible for livestock was estimated in June 2004. In the Kuiseb River, 10 trees per species were selected based on the following criteria: The selected trees had to be mature without a visible browse line and the lowest branches had to be less than 2 m above the ground. Under each tree (*F. albida* n=10, *A. erioloba* n=10) a 1 m² quadrat was randomly placed three times. Within the borders of the quadrat, leaves and palatable (soft) branches of the crown were harvested 30 cm in a vertical direction (0.3 m³). The harvested biomass was oven dried for three days at 60° C. Dry weight was determined with a Mettler AE 100 analytical balance (balance accuracy to 0.001 g) and average dry biomass per m³ (AWB [g m⁻³]) calculated. Potential regrowth of leaves and branches was not taken into consideration in these calculations.

The trees from the vegetation surveys 2004 in the Kuiseb, Omaruru and Ugab rivers were sorted into three tree classes to calculate average biomass stock per tree class. Productivity factor (PF), height of browse line and height of lowest branches (crown base) had been recorded for adult individuals in the vegetation surveys of 2004 (see Chapter 4 and 5). Trees with a distinct browse line usually did not have any branches below this line and were thus only used for browse line calculations. If there

was no browse line or the browse line was visible but not distinct, then lower branches were present and these were used for calculation of average branch height above ground (crown base). Maximum browse height and average branch height above ground were determined from these data and used for browse production calculations. Trees with a crown base (C_b [m]) \geq Max browse height (MBH [m]) were treated as 0 potential browse (PB) in the calculations. The potential browse (PB [g]) per tree was calculated as with r [m] being the radius of the crown calculated from the crown diameters(6.4).

$$PB = (MBH - C_b) \times r^2 \pi \times PF \times AWB \quad (6.4)$$

6.2.4 Monetary value of trees

Information from the questionnaire survey based on the market prize (average) of a large Hessian bag (empty 50-kg flour bag) filled with pods was used to calculate the monetary value per species and tree class. The weight of a Hessian bag filled with *F. albida* or *A. erioloba* pods was determined with a 10 kg and 20 kg spring balance: 1 bag=6 kg *F. albida* pods and 15 kg *A. erioloba* pods. The market value of the amount of pods produced per species and tree class was calculate in Namibian Dollars (N\$).

The biomass concept to determine the carrying capacity of Namibian rangelands (Bester, 1995) was used to compute dry matter output versus dry matter demand of ruminants (Oba and Post, 1999). The daily dry matter (DDM [kg a⁻¹]) demand of ruminants was calculated for adult goats and sheep as 2 % of body weight (BW [kg]) (Holecheck et al., 1995) and for cattle as 2.5 % body weight (Jahnke, 1982). Body weights recommended by the Ministry of Agriculture, Water and Forestry were applied in the calculations: goats=40 kg, sheep=60 kg and cattle=360 kg. To simplify calculations, no differentiation was made between age and development stages of the animals. In addition, the market value of potential offspring was taken added. For the calculations of the monetary value of *F. albida* and *A. erioloba* trees in three tree classes, the annual dry matter provision (ADMP [kg a⁻¹]) per tree (pods+browse) was divided by the annual dry matter demand of each animal type (BW(al) x Y^a x 365 [kg a⁻¹]) to determine how many animals could be supplied with dry matter. The monetary value (MV [N\$]) per tree species and tree class was calculated in Namibian Dollars (1 N\$=0.13 €) from the local market value (LMV [N\$]) of adult livestock (al): goats

(450 N\$), sheep (450 N\$), cattle (3500 N\$) plus annual offspring (osl): goats 3-6 months (250 N\$), sheep 3-6 months (250 N\$) and cattle 4-6 months (950 N\$) (Khurisab, personal communication). Due to the dominance of female adults in each livestock type, only females and their offspring were used for the calculations. The market value of donkeys was not considered. The monetary value was calculated with equation 6.5:

$$MV = \left[\frac{ADMP}{(BW_{al} \times Y^a \times 365)} \right] \times LMV_{al} + \left[\frac{ADMP}{BW_{al} \times Y^a \times 365} \right] \times n_{osl}^b \times LMV_{osl} \quad (6.5)$$

$Y^a=0.02$ for goat/sheep, 0.025 for cattle

n^b =number of annual offspring from livestock (goats=2osl, sheep=2osl, cattle=1osl)

6.2.5 Data analyses

Statistical analyses were carried out with GraphPad InStat 3.05 and Statistica 6.0. All data were tested for normality prior to further statistical analyses (Kolmogorov-Smirnov). A significance level of 5 % was applied in all tests (Zar, 1999). Detailed test results are presented in Appendix IV.

6.3 Results

6.3.1 Tree utilization by natural resource users

Farming with goats was done by every farmer while farming with sheep and cattle was less common (Table 6.1). More than 50 % of the farmers interviewed owned one or more donkey.

Table 6.1: Relative number of farmers (n=106) owning goats, sheep, cattle or donkeys along the Kuiseb, Omaruru and Ugab rivers, 2004

Livestock type [%]			
Goats	Sheep	Cattle	Donkeys
100.0	18.9	22.6	67.0

For goats, sheep and cattle, *F. albida* was ranked the most important fodder source, while *A. erioloba* was ranked highest for donkeys (Table 6.2). *Salvadora persica* and *Euclea pseudobenus* were reported to be consumed by some animals but were less favored. *Tamarix usneoides* was not consumed at all.

Table 6.2: Ranking of woody plants by farmers according to livestock fodder preference along the Kuiseb, Omaruru and Ugab rivers, 2004; rank 1 indicates the highest and rank 4 the lowest preference (n=number of farmers responding to this question)

Species	Goats (n=104)	Sheep (n=20)	Cattle (n=22)	Donkeys (n=69)
<i>Acacia erioloba</i>	2	3	2	1
<i>Euclea pseudobenus</i>	4	x	x	x
<i>Faidherbia albida</i>	1	1	1	2
<i>Salvadora persica</i>	3	2	x	3
<i>Tamarix usneoides</i>	x	x	x	x

Only data from the Kuiseb interviews were available for the main collection times for *F. albida* and *A. erioloba* pods (Figure 6.1). Pods of both species were collected throughout the year. The peak collection period for *F. albida* pods was from December to March and for *A. erioloba* from June to August. There is no overlap in peak collection periods. *Faidherbia albida* pods were collected by 83.0 % and *A. erioloba* pods by 61.3 % of the farmers interviewed (n=106). The collected pods were stored by 83.7 % (n=92) and fed directly to the animals by 16.3 %.

Contribution of *Faidherbia albida* and *Acacia erioloba* to the livelihoods of communal farmers

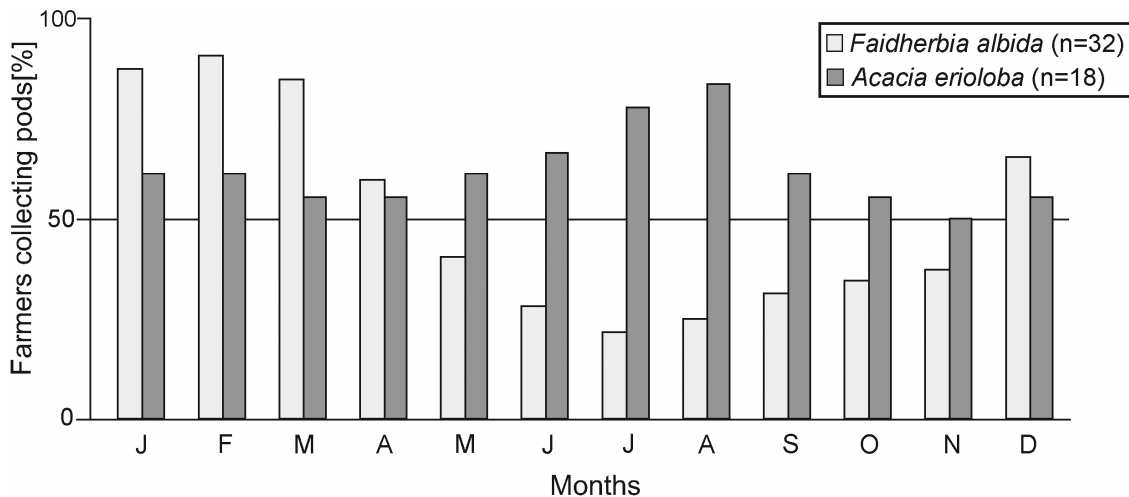


Figure 6.1: Relative number [%] of farmers collecting *Faidherbia albida* and *Acacia erioloba* pods along the Kuiseb River throughout a year, 2004 (n=number of farmers responding to this question).

Farmers travel on foot and with donkey carts to collect pods. The distance traveled by farmers of the Kuiseb (n=29) ranged between 1.0 km (minimum) and 23.0 km (maximum) and was on average 8.6 ± 1.3 km (mean \pm SE). Pods were collected from the ground after pod fall, but also from the tree if pods were sparse on the ground.

Table 6.3: Relative number of farmers (n=92) feeding different livestock types with collected *Faidherbia albida* and *Acacia erioloba* pods along the Kuiseb, Omaruru and Ugab rivers, 2004

Livestock type [%]					
Goat kids	Pregnant goats	Other adult goats (sick, old)	Lambs	Calves	Donkeys
100.0	75.0	63.0	5.4	14.1	4.4

Goat kids were fed with the collected pods by all farmers (Table 6.3). Pregnant, sick and old goats were fed with pods by most farmers interviewed in contrast to calves, donkeys and lambs. The goat kids were fed with the pods for a period of 4.0 ± 0.3 months (mean \pm SE). These farmers (n=70) started feeding pods at the age of 2.8 ± 0.1 months (mean \pm SE) until the animals were 6.7 ± 0.4 months (mean \pm SE) old.

Leaves are another product of the study species that was collected to feed animals. Goat kids receive them before they are able to eat pods, but leaves were also fed to adult goats and other animals (Table 6.4). Of the interviewed farmers (n=97), 29.9 % collected *F. albida* and 9.5 % *A. erioloba* leaves.

Contribution of *Faidherbia albida* and *Acacia erioloba* to the livelihoods of communal farmers

Table 6.4: Relative number of farmers (n=92) feeding different livestock types with collected *Faidherbia albida* or *Acacia erioloba* leaves along the Kuiseb, Omaruru and Ugab rivers, 2004

	Livestock type [%]					
	Goat kids	Pregnant goats	Other adult goats (sick, old)	Lambs	Calves	Donkeys
	84.6	30.8	42.3	15.4	7.7	7.7

Only few farmers sold collect pods (Table 6.5). Farmers buy more *F. albida* than *A. erioloba* pods. The market value of one Hessian bag filled with *F. albida* pods (10-30 N\$) is slightly higher than that of *A. erioloba* pods (10-20 N\$) (n=3).

Table 6.5: Relative number of farmers marketing (selling and buying) *Faidherbia albida* or *Acacia erioloba* pods along the Kuiseb, Omaruru and Ugab rivers, 2004 (n=number of farmers responding to this question)

Marketing activity	<i>Faidherbia albida</i> [%]	<i>Acacia erioloba</i> [%]
Selling	Yes=4.8	Yes=2.1
	No=95.2 (n=104)	No=97.9 (n=94)
Buying	Yes=23.5	Yes=2.7
	No=76.5 (n=51)	No=97.3 (n=74)

The amount of *F. albida* trees in the immediate surroundings was reported to be sufficient by 70.5 % of the farmers (n=105). Most of the 29.5 % farmers with the opinion that too few *F. albida* trees were available live along the Omaruru River (71.0 %). With regard to *A. erioloba*, 54.4 % (n=103) consider the quantity of trees as sufficient. A total of 91.5 % of the farmers not satisfied with the number of available trees live along the Omaruru and Ugab rivers.

Planting of trees was carried out by 2.9 % of the farmers (n=105) for *F. albida* and 1.9 % for *A. erioloba*. *Faidherbia albida* or *A. erioloba* adult trees were cut by 2.0 % (n=99) of the farmers. Along the Kuiseb River, 6.5 % of the farmers reported that they protect *F. albida* or *A. erioloba* (n=31) seedlings.

6.3.2 Production of pods and browsable biomass stock

Mean pod weight (\pm SE) of *F. albida* (9.8 g \pm 0.3, n=767) and *A. erioloba* (11.5 g \pm 0.3, n=308) was used for calculation of annual pod production (Table 6.6).

Table 6.6: Mean (\pm SE) annual pod production of *Faidherbia albida* and *Acacia erioloba* trees in three tree classes at Gobabeb, Kuiseb River, 2003-2004 (n=number of trees)

Species	Tree class 1 [kg year ⁻¹]	Tree class 2 [kg year ⁻¹]	Tree class 3 [kg year ⁻¹]
	< 8.5 m	8.5 m -<17 m	\geq 17 m
<i>Faidherbia albida</i>	4.4 \pm 3.3 (n=6)	46.6 \pm 10.7 (n=27)	175.3 \pm 52.2 (n=6)
	<7.5 m	7.5 m -<15 m	\geq 15 m
<i>Acacia erioloba</i>	6.7 \pm 2.0 (n=10)	35.7 \pm 5.6 (n=25)	212.4 \pm 96.1 (n=5)

Average browse height of *F. albida* and *A. erioloba* trees was 1.5 m for both species (Table 6.7). Browse weight and browse line height (Table 6.7) were used for calculation of browsable biomass stock (Table 6.8).

Table 6.7: Mean (\pm SE) browse weight and mean (\pm SE, Min/Max) browse line height of *Faidherbia albida* and *Acacia erioloba* trees in the Kuiseb River, 2004 (n=number of samples)

Species	Browse weight [g m ⁻³] (mean \pm SE)	Browse line height [m] (mean \pm SE; Min/Max)
<i>Faidherbia albida</i>	79.60 \pm 5.81 (n=29)	1.51 \pm 0.03 (1.00/2.00) (n=74)
<i>Acacia erioloba</i>	87.49 \pm 10.17 (n=30)	1.46 \pm 0.02 (1.00/2.00) (n=100)

Table 6.8: Mean (\pm SE) annual production of browsable biomass stock of *Faidherbia albida* and *Acacia erioloba* trees in three tree classes in the Kuiseb River, 2004 (n=number of trees)

Species	Tree class 1 [kg year ⁻¹]	Tree class 2 [kg year ⁻¹]	Tree class 3 [kg year ⁻¹]
	< 8.5 m	8.5 m -<17 m	\geq 17 m
<i>Faidherbia albida</i>	0.9 \pm 0.2 (n=93)	3.0 \pm 0.4 (n=155)	8.8 \pm 1.6 (n=68)
	<7.5 m	7.5 m -<15 m	\geq 15 m
<i>Acacia erioloba</i>	1.5 \pm 0.1 (n=96)	4.6 \pm 0.5 (n=101)	6.4 \pm 1.4 (n=36)

6.3.3 Monetary value of trees

In all tree classes, the annual monetary value of *F. albida* trees from pod sales (Table 6.9) is similar to that of goat production (Table 6.10). The monetary value of both sheep and cattle production are lower than those that can be obtained from goat production. The income derived from cattle production is the lowest overall and less than half of the income from pod sales or goat production. The *A. erioloba* market value from goat, sheep or cattle production is higher than from pod marketing (Tables 6.9 and 6.10). The monetary value of a tree from goat production in anyone tree class is highest compared to sheep and cattle production. Goat production scores more than three times the amount obtained from direct pod sales.

Table 6.9: Mean (\pm SE) annual monetary value of *Faidherbia albida* and *Acacia erioloba* trees in three tree classes calculated from market value of annual pod production in Kuiseb, Omaruru and Ugab rivers, 2004 (n=number of trees)

Species	Tree class 1 [N\$]	Tree class 2 [N\$]	Tree class 3 [N\$]
	< 8.5 m	8.5 m -<17 m	\geq 17 m
<i>Faidherbia albida</i> ^a	14.7 \pm 10.9 (n=6)	155.5 \pm 35.7 (n=27)	584.4 \pm 174.1 (n=6)
	<7.5 m	7.5 m -<15 m	\geq 15 m
<i>Acacia erioloba</i> ^b	6.7 \pm 2.0 (n=10)	35.7 \pm 5.6 (n=25)	212.5 \pm 96.1 (n=5)

^a*F. albida* 1 kg=3.3 N\$, ^b*A. erioloba*: 1 kg=1.0 N\$

Table 6.10: Mean (\pm SE) annual monetary value of *Faidherbia albida* and *Acacia erioloba* trees in three tree classes from market value of goats, sheep and cattle. Value is calculated from the market value of female animals provided with necessary dry matter by the trees (pods+leaves) plus the market value of potential annual offspring

Livestock type	<i>Faidherbia albida</i>			<i>Acacia erioloba</i>		
	Tree class 1 [N\$]	Tree class 2 [N\$]	Tree class 3 [N\$]	Tree class 1 [N\$]	Tree class 2 [N\$]	Tree class 3 [N\$]
Goats (female plus 2 offspring ^a)	17.3 \pm 11.1	161.6 \pm 36.3	599.0 \pm 175.0	26.5 \pm 6.5	130.9 \pm 18.2	711.8 \pm 312.5
Sheep (female plus 2 offspring ^a)	11.6 \pm 7.4	107.7 \pm 23.2	399.4 \pm 116.7	17.6 \pm 4.3	87.3 \pm 12.2	474.5 \pm 208.3
Cattle (female plus 1 offspring ^a)	7.2 \pm 4.6	67.3 \pm 15.1	249.4 \pm 72.9	11.0 \pm 2.7	54.5 \pm 7.6	296.4 \pm 130.1

^aKhurisab and Makembe, personal communication

6.4 Discussion

Although the farmers along the ephemeral rivers farm with a variety of animals, goats are present in the largest numbers. Due to their dominant role in the livelihoods of the population, the data are discussed mainly in relation to goat farming.

This study shows that the local farmers take great care of their animals. They spend time and effort to collect fodder, especially *F. albida* but also *A. erioloba* pods and leaves, for goat kids and pregnant goats as well as old and sick animals. The collection habits of the farmers and the fodder preference of the livestock demonstrate that *F. albida* plays the most important role as a fodder source among the common woody vegetation in the ephemeral rivers of western Namibia followed by *A. erioloba*. *Faidherbia albida* pod shells are softer than those of *A. erioloba*, which is one of the reasons for the overall preference by the animals. Donkeys have strong grinding back teeth and are able to grind the thicker *A. erioloba* pods better. This implies that a loss of *F. albida* will force the livestock to use other less preferred plants and probably limit livestock production as a whole.

The extent to which farmers value the two study species is also reflected in the long distances they travel to collect pods. This investment is rewarded by the access to areas where livestock does not roam frequently and pods are thus readily available. Conflicts between livestock needs for pods in the field and pods needed to feed animals in the kraal are thus reduced. The farmers are well aware of the seasonal availability of the valuable resource, and pods are collected intensively when available during the species' typical peak pod fall of the species (van Wyk et al., 1985). Thus a reliable fodder supply is provided by both species throughout the year. These pods are important as a fodder supply for livestock kept at the house and for livestock in the field. Pods collected during these periods are usually stored but also used for direct feeding. Goat kids are born in May/June and again in December/January (Kooitjie, personal communication). Each goat kid will be fed for nearly four months with pods, starting when the animal is three months old. This means that the main need for pods for goat kids is from March/April to July/August and again from August/September to November/December. There is also a high demand for pods during the main pregnancy periods of the goats. This demand can only be met if enough *F. albida* pods are stored or farmers also feed *A. erioloba*. Since only few farmers use *A. erioloba* for feeding,

they have to find other ways to provide fodder for their animals. Throughout most of the year, some *F. albida* pods remain in the tree. Daily fodder demands can be partly met by collecting pods from the trees. Entangled pods are shaken loose and fall to the ground. In the off-season period, it is a laborious job to fill one bag. The large quantities of *A. erioloba* pods during the times of *F. albida* pod scarcity could balance the need for fodder, but only few farmers make use of these pods and claim that they are not favored by the animals and if fed result in colic. The leaves collected by some farmers to feed those goat kids too small to feed on pods can be used to provide additional nutrients during times with fewer *F. albida* pods. During these periods, leaves are a reliable fodder source for adult goats but also sheep, cattle and donkeys. This means that during the time of *F. albida* pod scarcity, farmers use other parts of the tree for fodder. *Faidherbia albida* and to some extent also *A. erioloba* play a central role in livestock husbandry, and without the two species livestock production in the ephemeral rivers will be severely limited.

The majority of farmers perceived the presence and availability of *F. albida* trees for fodder as sufficient in their immediate environment but not of *A. erioloba*. The main reason for the reported insufficiency of *A. erioloba* is probably related to the absence of *A. erioloba* along the main river channel. Most unsatisfied farmers lived along the Omaruru and Ugab rivers, where naturally fewer *A. erioloba* trees are present (Chapter 3). Here most *A. erioloba* trees grow scattered in the side channels and tributaries. Farmers who were not satisfied with the availability of *F. albida* trees were mostly situated at locations where water availability was reduced due to lowered water tables or limited surface floods. These farmers often pointed out that absence or reduced productivity of the trees was related to lack of water. Water availability has an impact on the fitness and survival of adult *F. albida* trees and also on their productivity (personal observation). No efforts are undertaken by the farmers to plant trees or protect small trees from their livestock and no long-term problems with regeneration were envisaged. This illustrates the perception of the farmers that nature is responsible for the trees. The farmers regard themselves as the natural users of the available resources, but do not feel that they are also responsible for them. As soon as resources get scarce, the blame is placed elsewhere.

The trees of the two study species and particularly the larger ones contribute considerably to the fodder provision of livestock in the study region. Average pod production estimates of the trees in tree class 3 correspond with findings from Seely et al. (1980) and Jacobson et al. (1995) for *F. albida* (180-200 kg per large tree). The low pod output estimate for *A. erioloba* by Seely et al. (1980) is probably linked to the size of the study trees but could also be related to annual variations in pod production (Seely et al., 1980). Compared to pods, the contribution of browse to the fodder requirements of livestock and wildlife remains relatively small. The inaccessibility of the majority of leaves and fresh shoots for the animals limits the proportion of browse and thus the nutrient intake from this source. Nevertheless, browse is available throughout the year, presenting a more continuous and reliable fodder source than the seasonal pods.

During periods with low or no river floods due to drought in the catchment, collection and storage of pods of the two study species can be critical for the survival of livestock. Short drought spells would be expected not to influence the productivity of the riparian vegetation, since the trees mainly rely on groundwater. Only longer drought periods in the upper catchment, which can result in reduced or no surface floods and as a consequence reduced groundwater recharge, could possibly influence tree fitness and thus productivity. This was observed in sections of the Kuiseb River where water tables were lowered through abstraction schemes (Chapter 4).

The value of the two study species as a fodder source is underlined by their market value. The market price per kilogram of *F. albida* and *A. erioloba* pods is higher than valued fodder resources elsewhere such as the hay of the legume *Vigna unguiculata* (cowpea) or the leaves of the legume tree *Pterocarpus lucens* (Dicko and Sikená, 1992). Compared to the cash income of a household from a state pension (250 N\$ per month) (Gaomab II, 2005), the calculated monetary value of the study species from pod or from animal value is considerable. The loss of one large *F. albida* tree would be comparable to the loss of up to two monthly pension payments or three for *A. erioloba* depending on the animal type. Considering the life-time pod and browse production of a tree, the total loss would be even higher.

6.5 Conclusion

Faidherbia albida is the most important fodder tree growing along the ephemeral rivers in western Namibia and is highly valued by the local resource users. *Acacia erioloba* is reported as useful but does not play the same role as *F. albida* for the farmers. This perception of the farmer is reflected by the local market value from pod production. The high monetary value of *A. erioloba* from livestock production is countered by the reluctance of farmers to feed *A. erioloba* pods.

At present, the natural resource users do not apply any management strategies with regard to the two fodder trees but recognize changes in their abundance and productivity. A loss or reduction in the study species, particularly *F. albida*, means that the local farmers will not be able to derive their livelihoods from small-scale farming along the ephemeral rivers. They would be increasingly dependent on cash income from state pensions or on employed family members. A migration of the rural population to the cities might also occur, especially of the younger generation, with the threat of poverty and unemployment. The development potential of the rural communities would be thereby severely hampered. A change towards more responsibility for their own resources can lead to a better awareness and a more sustainable utilization of the scarce and vulnerable resources.

7. PERSPECTIVES

It is difficult to predict where and when successful regeneration of *F. albida* and *A. erioloba* is going to take place in an ever changing and dynamic river environment. Considering the linkages determining tree regeneration in an ephemeral river system as presented in Figure 1.1, it becomes clear that processes needed for successful regeneration have changed. The following conclusions can be summarized from this study:

- Silt deposits, surface water and groundwater availability are crucial for early regeneration processes and seedling establishment.
- The regeneration potential of *F. albida* and *A. erioloba* in the ephemeral rivers is limited through high livestock densities and the positive influence of livestock on seed germination is countered by their destructive effect on seedlings and juveniles.
- Regeneration at safe sites is rare and unpredictable and requirements differ between *F. albida* and *A. erioloba* .Successful regeneration occurs mainly on elevated sites above the active river channel.
- The loss of *F. albida* and to a smaller extend also *A. erioloba* will lead to the reduction of the carrying capacity of the ephemeral rivers for livestock production in western Namibia.

Regionally, awareness raising of farmers and decision makers is necessary in order to implement sustainable livestock management strategies along the ephemeral rivers of western Namibia. To reduce total livestock numbers and to allow farmers to react to reduced fodder availability in time, local marketing facilities need to be established. To ensure seedling and juvenile survival until the trees have reached a sufficient size, protection mechanisms have to be implemented in areas with high livestock densities. Projects involving the monitoring of vegetation by local resource users need to be put into practice to increase their awareness and help to protect the environment. Information on nutritional values and browse production of all utilized vegetation is needed.

In order to manage and utilize the ephemeral rivers of Namibia in a sustainable way on a national scale the response of the dynamics of the major plant species

populations to land-use and hydrologic changes and the dynamics of plant communities need to be studied. The determination of the vulnerability of the vegetation to increased livestock densities and reduced water availability as well as ecosystem models are necessary to predict changes in the ephemeral river system. It will be important to determine the water requirements (environmental flow) of ephemeral rivers to ensure the future functioning of the river ecosystem processes. This includes the determination of the necessary flood water volume, the required water velocity in the channel, the need for pulses of high flows, and the natural and human-induced changes to the natural flow regime. For this, water needs for plant regeneration and growth have to be assessed. Groundwater availability and dynamics across lateral and longitudinal river cross sections need to be studied to understand spatial and temporal water availability for the vegetation. Further experiments are necessary to quantify the combined effects of water availability and livestock on plant regeneration.

Plans for large dam constructions upriver from the communal farming areas as well as new or increased water abstraction from the groundwater aquifer of the ephemeral rivers have to be weighed against the potential threat to the riparian vegetation.

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9. APPENDICES

Appendix I: Germination, seed burial and seedling development

Appendix I.i: Difference in accumulated germination percentage of *Faidherbia albida* and *Acacia erioloba* seeds between different treatments at day 46, determined with One-way ANOVA statistics

Species	Test component	Test	p
<i>Faidherbia albida</i>	new seeds - old seeds ns	One-way ANOVA, Tukey post test	<0.0001
	new seeds - goat *		
	new seeds - oryx *		
	new seeds - cattle ns		
	new seeds - new seeds 24h ns		
	new seeds - new seeds 72h ns		
	new seeds - goat *		
	new seeds - oryx 24h *		
	new seeds - cattle 24h ns		
	old seeds - goat **		
	old seeds - oryx *		
	old seeds - cattle ns		
	old seeds - new seeds 24h ns		
	old seeds - new seeds 72h ns		
	old seeds - goat 24h **		
	old seeds - oryx 24h *		
	old seeds - cattle 24h ns		
	goat - oryx ns		
	goat - cattle ns		
	goat - new seeds 24h ***		
	goat - new seeds 72h **		
	goat - goat 24h ns		
	goat - oryx 24h ns		
	goat - cattle 24h *		
	oryx - cattle ns		
	oryx - new seeds 24h ***		
	oryx - new seeds 72h **		
	oryx - goat 24h ns		
	oryx - oryx 24h ns		
	oryx - cattle 24h ns		
	cattle - new seeds 24h ns		
	cattle - new seeds 72h ns		
	cattle - goat 24h ns		
	cattle - oryx 24h ns		
	cattle - cattle 24h ns		
	new seeds 24h - new seeds 72h ns		
	new seeds 24h - goat 24h ***		
	new seeds 24h - oryx 24h ***		
	new seeds 24h - cattle 24h ns		
	new seeds 72h - goat 24h **		
	new seeds 72h - oryx 24h **		
	new seeds 72h - cattle 24h ns		
goat 24h - oryx 24h ns			
goat 24h - cattle 24h *			
oryx 24h - cattle 24h ns			

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Species	Test component	Test	p
<i>Acacia erioloba</i>	new seeds - old seeds *** P<0.001	One-way ANOVA, Tukey post test	<0.0001
	new seeds - goat ns P>0.05		
	new seeds - oryx ns P>0.05		
	new seeds - cattle ** P<0.01		
	new seeds - new seeds 24h *** P<0.001		
	new seeds -new seeds 72h * P<0.05		
	new seeds - cattle 24h ns P>0.05		
	old seeds - goat ns P>0.05		
	old seeds - oryx *** P<0.001		
	old seeds - cattle ns P>0.05		
	old seeds - new seeds 24h ns P>0.05		
	old seeds - new seeds 72h ns P>0.05		
	old seeds - cattle 24h ns P>0.05		
	goat - oryx ns P>0.05		
	goat - cattle ns P>0.05		
	goat - new seeds 24h ns P>0.05		
	goat - new seeds 72h ns P>0.05		
	goat - cattle 24 h ns P>0.05		
	oryx - cattle ** P<0.01		
	oryx -new seeds 24h *** P<0.001		
	oryx - new seeds 72h * P<0.05		
	oryx - cattle 24h ns P>0.05		
	cattle - new seeds 24h ns P>0.05		
	cattle - new seeds 72h ns P>0.05		
	cattle - cattle 24h ns P>0.05		
	new seeds 24h - new seeds 72h ns P>0.05		
new seeds 24h - cattle 24h ns P>0.05			
new seeds 72h - cattle 24h ns P>0.05			

Appendix I.ii: Difference in seedling emergence success after burial of *Faidherbia albida* and *Acacia erioloba* seeds at 5 and 10 cm depth, determined with Unpaired t test statistics

Species	Test component	Test	p
<i>Faidherbia albida</i>	<i>F. albida</i> 5 cm-10 cm	Unpaired t test	<0.0001
<i>Acacia erioloba</i>	<i>A. erioloba</i> 5 cm-10 cm	Unpaired t test	<0.0001

Appendix I.iii: Difference in seedling fate (alive/dead) between watered and not-watered *Faidherbia albida* and *Acacia erioloba* seedlings in watering experiment in the Kuiseb River, Gobabeb, determined with Fisher's exact test statistics

Species	Test component	Test	p
<i>Faidherbia albida</i>	alive/dead - watered/not-watered	Fisher's exact test	0.1806
<i>Acacia erioloba</i>	alive/dead - watered/not-watered	Fisher's exact test	0.1090

Appendix I.iv: Difference in stem collar size between watered and not-watered *Faidherbia albida* and *Acacia erioloba* seedlings in the Kuiseb River, Gobabeb, determined with Unpaired t test with Welch correction statistics

Species	Test component	Test	p
<i>Faidherbia albida</i>	stem collar week 28	Unpaired t test with Welch correction	0.1333
<i>Acacia erioloba</i>	stem collar week 28	Unpaired t test with Welch correction	0.2645

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Appendix I.v: Difference in daily root growth of *Faidherbia albida* and *Acacia erioloba* seedlings in the Kuiseb River between 31 and 63 days, Gobabeb, determined with Unpaired t test statistics

Species	Test component	Test	p
<i>Faidherbia albida</i>	Growth rate 31 d vs 63 d	Unpaired t test	0.0169
<i>Acacia erioloba</i>	Growth rate 31 d vs 63 d	Unpaired t test	0.1162

Appendix I.vi: Difference in root/shoot ratio of *Faidherbia albida* and *Acacia erioloba* seedlings growing in sand and sand plus silt/clay layers in the Kuiseb River, Gobabeb, determined with Unpaired t test statistics

Species	Test component	Test	p
<i>Faidherbia albida</i>	Root/shoot ratio in sand/sand with silt/clay	Unpaired t test	0.0026
<i>Acacia erioloba</i>	Root/shoot ratio in sand/sand with silt/clay	Unpaired t test	0.0373

Appendix I.vii: Difference in ¹⁵N % in shoots of *Faidherbia albida* and *Acacia erioloba* seedlings with nodulated and unnodulated roots in the Kuiseb River, Gobabeb, determined with Unpaired t test statistics

Species	Test component	Test	p
<i>Faidherbia albida</i>	¹⁵ N in shoots with roots with and without nodules	Unpaired t test	0.4060
<i>Acacia erioloba</i>	¹⁵ N in shoots with roots with and without nodules	Unpaired t test	0.6196

Appendix II: Effect of livestock on regeneration

Appendix II.i: Difference between goat faeces counts at ≤ and >50 m distance to active river channel in Kuiseb sections U1 and U2 (see Figure 2.1), determined with Mann-Whitney statistics

River section	Test components	Test	p
U1, U2	Goat faeces in ≤ and >50 m distance, goat	Mann-Whitney	0.0057

Appendix II.ii: Difference in fate between protected and unprotected *Faidherbia albida* and *Acacia erioloba* seedlings in areas with high (HL) and low (LL) livestock numbers, Kuiseb River, 2003, determined with χ^2 statistics

Species	Test component	Test	df	χ^2	p
<i>Faidherbia albida</i>	Protected-unprotected HL	chi-square	3	106.89	<0.0001
	Protected-unprotected LL	chi-square	3	7.45	0.0588
	Unprotected HL-LL	chi-square	3	79.25	<0.0001
<i>Acacia erioloba</i>	Protected-unprotected HL	chi-square	3	89.60	<0.0001

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Appendix II.iii: Difference in fate between protected and unprotected *Faidherbia albida* and *Acacia erioloba* seedlings in areas with high (HL) and low (LL) livestock numbers, Kuiseb River, 2004, determined with χ^2 statistics

Species	Test component	Test	df	χ^2	p
<i>Faidherbia albida</i>	Protected-unprotected HL	chi-square	3	138.98	<0.0001
	Protected-unprotected LL	chi-square	3	15.63	0.0014
	Unprotected HL-LL	chi-square	3	82.83	<0.0001
<i>Acacia erioloba</i>	Protected-unprotected HL	chi-square	3	107.45	<0.0001
	Protected-unprotected LL	chi-square	3	4.11	0.2501
	Unprotected HL-LL	chi-square	3	38.36	<0.0001

Appendix II.iv: Difference in annual height increase of *Faidherbia albida* and *Acacia erioloba* juveniles in two size groups in four Kuiseb River sections (U1, U2, M, L; see Figure 2.1), determined with Kruskal-Wallis statistics

Species	Test components	Test	p
<i>Faidherbia albida</i>	0-150 U1 vs. 0-150 U2 ns P>0.05	Kruskal-	0.0437
	0-150 U1 vs. 0-150 M ns P>0.05	Wallis,	
	0-150 U1 vs. 0-150 L ns P>0.05	Dunn's	
	0-150 U2 vs. 0-150 M ns P>0.05	Multiple	
	0-150 U2 vs. 0-150 L ns P>0.05	Comparison	
	0-150 M vs. 0-150 L ns P>0.05	Test	
<i>Acacia erioloba</i>	0-150 U1 vs. 0-150 U2 n P>0.05	Kruskal-	0.0017
	0-150 U1 vs. 0-150 M ns P>0.05	Wallis,	
	0-150 U1 vs. 0-150 L ns P>0.05	Dunn's	
	0-150 U2 vs. 0-150 M *** P<0.001	Multiple	
	0-150 U2 vs. 0-150 L ns P>0.05	Comparison	
	0-150 M vs. 0-150 L ns P>0.05	Test	

Appendix II.v: Difference in size-class distribution of *Faidherbia albida* and *Acacia erioloba* between four Kuiseb River sections (U1, U2, M, L; see Figure 2.1), determined with χ^2 statistics

River section	Test component	Test	df	χ^2	p
U1, U2, M, L	<i>F. albida</i> size classes	chi-square	15	11.371	0.7259
U1, U2, M, L	<i>A. erioloba</i> size classes	chi-square	15	47.371	<0.0001

Appendix II.vi: Difference in densities between juvenile and adult *Faidherbia albida* and *Acacia erioloba* trees within the Kuiseb River sections (U1, U2, M, L; see Figure 2.1), determined with Mann-Whitney statistics

River section	Test components	Test	p
U1	Density juveniles vs density adults (<i>F. albida</i>)	Mann-	0.2645
	Density juveniles vs density adults (<i>A. erioloba</i>)	Whitney	
U2	Density juveniles vs density adults (<i>F. albida</i>)	Mann-	0.003
	Density juveniles vs density adults (<i>A. erioloba</i>)	Whitney	
M	Density juveniles vs density adults (<i>F. albida</i>)	Mann-	0.3661
	Density juveniles vs density adults (<i>A. erioloba</i>)	Whitney	
L	Density juveniles vs density adults (<i>F. albida</i>)	Mann-	0.0288
	Density juveniles vs density adults (<i>A. erioloba</i>)	Whitney	

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Appendix II.vii: Difference in densities between juvenile and adults *Faidherbia albida* and *Acacia erioloba* trees within the Omaruru and Ugab rivers, determined with Mann-Whitney statistics

River	Test components	Test	p
Omaruru	Density juveniles vs density adults (<i>F. albida</i>)	Mann-Whitney	0.2079
Ugab	Density juveniles vs density adults (<i>F. albida</i>)	Mann-Whitney	0.1997
	Density juveniles vs density adults (<i>A. erioloba</i>)		0.6183

Appendix II.viii: Difference in fitness of *Faidherbia albida* and *Acacia erioloba* juveniles in two size groups between four Kuiseb River sections (U1, U2, M, L; see Figure 2.1) determined with χ^2 statistics and differences and difference in juvenile fitness between size groups within the Kuiseb River sections, determined with Fisher's exact test statistics

River section	Test component	Test	df	χ^2	p
U1, U2, M, L	<i>F. albida</i> juveniles good vs poor 0-150 cm	chi-square	3	18.393	0.0004
U1, U2, M, L	<i>A. erioloba</i> juveniles good vs poor 0-150 cm	chi-square	3	21.970	<0.0001
U1, U2, M, L	<i>F. albida</i> juveniles good vs poor >150 cm	chi-square	3	28.063	<0.0001
U1, U2, M, L	<i>A. erioloba</i> juveniles good vs poor >150 cm	chi-square	3	11.237	0.0105
U1	<i>F. albida</i> juveniles 0-150 vs > 150	Fisher's exact test			0.0529
U2	<i>F. albida</i> juveniles 0-150 vs > 150	Fisher's exact test			0.1391
M	<i>F. albida</i> juveniles 0-150 vs 150	Fisher's exact test			0.3067
L	<i>F. albida</i> juveniles 0-150 vs 150	Fisher's exact test			0.1679
U1	<i>A. erioloba</i> juveniles 0-150 vs 150	Fisher's exact test			<0.0001
U2	<i>A. erioloba</i> juveniles 0-150 vs 150	Fisher's exact test			<0.0001
M	<i>A. erioloba</i> juveniles 0-150 vs 150	Fisher's exact test			<0.0001
L	<i>A. erioloba</i> juveniles 0-150 vs 150	Fisher's exact test			<0.0001

Appendix II.ix: Difference in fitness of *Faidherbia albida* juveniles in two size groups within the Omaruru and Ugab rivers, determined with Fisher's exact test statistics

River	Test component	Test	p
Omaruru	<i>F. albida</i> juveniles good vs poor 0-150 vs > 150	Fisher's exact test	<0.0001
Ugab	<i>F. albida</i> juveniles good vs poor 0-150 vs 150	Fisher's exact test	0.0004

Appendix III: Safe sites for *Faidherbia albida* and *Acacia erioloba* regeneration

Appendix III.i: Difference in number of *Faidherbia albida* juveniles and adults growing in and outside the active channel in the Kuiseb River sections (U1, U2, M, L; see Figure 2.1), determined with χ^2 statistics and difference between juveniles and adults within the river sections, determined with Fisher's exact test statistics

River section	Test component	Test	df	χ^2	p
U1, U2, M, L	<i>F. albida</i> juveniles in and out channel	chi-square	3	50.893	<0.0001
U1, U2, M, L	<i>F. albida</i> adults between river in and out channel	chi-square	3	2.977	0.3952
U1	<i>F. albida</i> juveniles vs adults in and out channel	Fisher's exact test			<0.0001
U2	<i>F. albida</i> juveniles vs adults in and out channel	Fisher's exact test			0.7036
M	<i>F. albida</i> juveniles vs adults in and out channel	Fisher's exact test			1.0000
L	<i>F. albida</i> juveniles vs adults in and out channel	Fisher's exact test			0.1739

Appendix III.ii: Difference between juvenile and adult *Faidherbia albida* growing in and outside of the active channel within the Omaruru and Ugab rivers, determined with Fisher's exact test

River	Test component	Test	p
Omaruru	<i>F. albida</i> juveniles vs adults in and out channel	Fisher's exact test	0.2905
Ugab	<i>F. albida</i> juveniles vs adults in and out channel	Fisher's exact test	0.5341

Appendix III.iii: Difference between *Faidherbia albida* juveniles and adults growing at \leq or >20 m distance from active channel in four Kuiseb River sections (U1, U2, M, L; see Figure 2.1), determined with χ^2 statistics and difference between juveniles and adults within river sections, determined with Fisher's exact test statistics

River section	Test component	Test	df	χ^2	p
U1, U2, M	<i>F. albida</i> juveniles in \leq or >20 m from channel	chi-square	2	14.292	0.0008
U1, U2, M	<i>F. albida</i> adults in \leq or >20 m from channel	chi-square	2	21.994	<0.0001
U1	<i>F. albida</i> juveniles vs adults in \leq or >20 m from channel	Fisher's exact test			0.8616
U2	<i>F. albida</i> juveniles vs adults in \leq or >20 m from channel	Fisher's exact test			<0.0001
M	<i>F. albida</i> juveniles vs adults in \leq or >20 m from channel	Fisher's exact test			0.0407

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Appendix III.iv: Difference between juvenile and adult *Faidherbia albida* growing in \leq or >20 m distance from the active channel in the Omaruru and Ugab rivers, determined with Fisher's exact test statistics

River	Test component	Test	p
Omaruru	<i>F. albida</i> juveniles vs adults in \leq or >20 m from channel	Fisher's exact test	<0.0001
Ugab	<i>F. albida</i> juveniles vs adults in \leq or >20 m from channel	Fisher's exact test	0.8413

Appendix III.v: Association of *Faidherbia albida* and *Acacia erioloba* juveniles with open, open plus individual trees, open woodland and woodland vegetation cover in four Kuiseb River sections (U1, U2, M, L; see Figure 2.1) determined by χ^2 statistics

		<i>Faidherbia albida</i>						
River section		Open	Open plus individual trees	Open woodland	Woodland	df	χ^2	p
U1	observed	3	12	27	54	3	59.09	<0.0001
	expected	1	36	35	24			
U2	observed	0	15	21	21	3	2.82	<0.4201
	expected	0	11	27	19			
M	observed	6	32	66	25	3	1.25	<0.7415
	expected	7	36	65	21			
L	observed	1	5	31	1	3	14.54	<0.0023
	expected	1	15	19	2			

		<i>Acacia erioloba</i>						
River section		Open	Open plus individual trees	Open woodland	Woodland	df	χ^2	p
U1	observed	0	31	16	31	3	14.24	<0.0026
	expected	1	29	29	29			
U2	observed	0	16	162	118	3	38.21	<0.0001
	expected	0	58	140	98			
M	observed	21	104	496	422	3	504.95	<0.0001
	expected	56	291	523	173			
L	observed	4	79	206	25	3	36.58	<0.0001
	expected	11	124	160	19			

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Appendix III.vi: Association of *Faidherbia albida* and *Acacia erioloba* juveniles with open, open plus individual trees, open woodland and woodland vegetation cover in the Omaruru and Ugab rivers, determined by χ^2 statistics

Faidherbia albida

River		Open	Open plus individual trees	Open woodland	Woodland	df	χ^2	p
Omaruru	observed	0	0	65	6	3	20.38	<0.0014
	expected	0	9	48	14			
Ugab	observed	0	7	9	9	3	1.00	<0.8013
	expected	0	5	10	10			

Acacia erioloba

River	Species	Open	Open plus individual trees	Open woodland	Woodland	df	χ^2	p
Ugab	observed	0	5	9	1	3	7.35	<0.0614
	expected	0	3	6	6			

Appendix IV: Socio-economic importance of *Faidherbia albida* and *Acacia erioloba*

Appendix IV.i: Questionnaire -Kuisseb River survey

Date:

Interviewers:

1. Name
2. Village
3. Sex
4. Do you own livestock? Yes/No
5. What kind of animals do you have/what kind of animals you take care of?
6. What do your animals like to eat most?

Goats

Sheep

Donkey

Cattle

Rank	Species	Rank	Species	Rank	Species	Rank	Species
	Camelthorn		Camelthorn		Camelthorn		Camelthorn
	Anatree		Anatree		Anatree		Anatree
	Euclea		Euclea		Euclea		Euclea
	Salvadora		Salvadora		Salvadora		Salvadora
	Tamarix		Tamarix		Tamarix		Tamarix

7. Do you collect Anatree (Yes/No) and Camelthorn (Yes/No) pods?
8. Do you store the pods? Yes/No
9. How far do you go to collect pods?
10. Which animals do you feed with these pods?
11. How old are your animals when you start giving them pods?
12. How old are your animals when you stop giving them pods?
13. When do you collect Anatree pods?
14. Do you sell/buy Anatree pods? Yes/No
15. What is the price for one bag?
16. When do you collect Camelthorn pods?
17. Do you sell/buy Camelthorn pods? Yes/No

18. What is the price for one bag?
19. Are there enough Anatreas and Camelthorn trees for your livestock? Yes/No? If no, why not?
20. Do you plant Anatreas Yes/No and Camelthorn trees? If yes how many?
21. Do you protect small Anatreas and Camelthorn trees Yes/No, If yes, how?
22. Do you cut living trees? Yes/No, If yes, what for? How many per month?
23. Do you collect leaves? Yes/No
24. From which trees do you collect leaves?
25. Which animals do you feed with these leaves?

Appendix IV.ii: Questionnaire -Omaruru/Ugab rivers survey

Date:

Interviewers:

1. Name
2. Village
3. Sex
4. Do you own livestock? Yes/No
5. What kind of animals do you have/what kind of animals you take care of?
6. What do your animals like to eat most?

Goats

Sheep

Donkey

Cattle

Rank	Species	Rank	Species	Rank	Species	Rank	Species
	Camelthorn		Camelthorn		Camelthorn		Camelthorn
	Anatree		Anatree		Anatree		Anatree
	Euclea		Euclea		Euclea		Euclea
	Salvadora		Salvadora		Salvadora		Salvadora
	Tamarix		Tamarix		Tamarix		Tamarix

7. Do you collect Anatree (Yes/No) and Camelthorn (Yes/No) pods?
8. Do you store the pods? Yes/No
9. Which animals do you feed with these pods?
10. How old are your animals when you start giving them pods?
11. How old are your animals when you stop giving them pods?
12. Do you sell/buy Anatree pods? Yes/No
13. What is the price for one bag?
14. Do you sell/buy Camelthorn pods? Yes/No
15. What is the price for one bag?
16. Are there enough Anatreas and Camelthorn trees for your livestock? Yes/No? If no, why not?
17. Do you plant Anatreas Yes/No and Camelthorn trees? If yes how many?
18. Do you protect small Anatreas and Camelthorn trees Yes/No, If yes, how?
19. Do you cut living trees? Yes/No, If yes, what for? How many per month?
20. Do you collect leaves? Yes/No
21. From which trees do you collect leaves?
22. Which animals do you feed with these leaves?

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