

Establishment and Development of phreatophytic Vegetation in the Foreland of River Oases at the southern Rim of the Taklamakan Desert

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Summary

Summary

In environments with extremely limited resource availability, the necessity to adapt to this resource limitation is the main constrain for high species diversity. The Taklamakan Desert in north western China with only 20 to 70 mm precipitation per year is such an extreme ecosystem. Furthermore, the substrate consists mainly of silt, which is easily moved with moderate winds, causing severe dust storms and leading to a highly dynamic landscape. In an ecosystem with such a low precipitation and highly dynamic landscape only a limited variation in life strategies can be expected. Vegetation does exist only along ephemeral rivers or around river oases, built along these rivers. The perennial plant species of the Taklamakan Desert are *Populus euphratica*, *Tamarix ramosissima*, *Alhagi sparsifolia*, *Karelinia caspia* and *Phragmites australis*, which form dominant or codominant stands. Establishment of these phreatophytes is only possible at rare flooding events, when the soil from surface to the groundwater is water saturated. When the flooding recedes the roots of the seedlings must grow extremely fast to follow the sinking water fringe down to get access to the permanent groundwater. After successful establishment the plants grow vertically with sand accumulation and horizontally through clonal growth.

The topic of this PhD thesis was to examine the groundwater depth of locations with different vegetation types in the foreland of a river oasis at the southern rim of the Taklamakan Desert and to assess whether differences in establishment success and root growth among species might explain this pattern. Furthermore, clone sizes of the species *Populus euphratica*, *Tamarix ramosissima* and *Alhagi sparsifolia* were determined and related to clonal and genetic diversity as well as to depth to the groundwater table.

The locations of the species differed in the distance to the groundwater table. Except for *T. ramosissima*, establishment success was very limited. Although *A. sparsifolia* and *K. caspia* differed in root growth, these differences did not explain the vegetation pattern and the differences in mean groundwater depth between stands of both species. Both species are capable to reach the permanent groundwater table within five to six months. Maximum clone size of *P. euphratica* and *A. sparsifolia* were 121 ha and 6.1 ha, respectively. Clone size increased with decreasing clonal diversity and increasing groundwater depth. *T. ramosissima* differed from the other species in much smaller clone sizes. Presumably, the extensive clonal growth is a compensation for the low establishment success of the other species.

In conclusion, the species of the oasis foreland show clear differences in the studied characteristics and thus exhibit differentiated life strategies. However, these differences seem to be irrelevant for the existence of the vegetation because old populations were found of all species in the oasis foreland. The existing vegetation and its regeneration is threatened by the growing human population and their intensified water use which causes the running dry of rivers and the decline of groundwater tables.

Zusammenfassung

In Ökosystemen, in denen Ressourcen nur begrenzt verfügbar sind, ist die Notwendigkeit der Anpassung an diese Ressourcenknappheit die größte Einschränkung für eine hohe Artendiversität. Die Taklamakan Wüste im Nordwesten Chinas mit nur 20 bis 70 mm Niederschlag im Jahr ist so ein extremes Ökosystem. Hinzu kommt, dass das sehr schluffhaltige Substrat schon durch leichten Wind in Bewegung gerät, was zu häufigen Staubstürmen führt und eine hohe Landschaftsdynamik zur Folge hat. Lediglich Arten, die an diesen geringen Niederschlag und an die hohe Landschaftsdynamik angepasst sind, können sich hier etablieren und entwickeln, was eine eingeschränkte Bandbreite an pflanzlichen Lebensstrategien erwarten lässt. Die Vegetation befindet sich nur entlang ephemerer Flussläufe oder im Vorland von Oasen, die an diesen Flüssen errichtet wurden. Die mehrjährigen Arten dieser Wüste sind *Populus euphratica*, *Tamarix ramosissima*, *Alhagi sparsifolia*, *Karelinia caspia* und *Phragmites australis*, die dominante oder co-dominante Bestände ausbilden. Eine Etablierung dieser Phreatophyten ist nur bei seltenen Überschwemmungsereignissen möglich, wenn der Oberboden bis zum Grundwasser wassergesättigt ist. Beim Rückgang der Überflutung müssen die Keimlinge mit extrem schnellem Wurzelwachstum dem sinkenden Wasserspiegel folgen um Anschluss zum Grundwasser zu finden. Nach erfolgreicher Etablierung wachsen die Pflanzen vertikal mit dem sich an ihnen akkumulierenden Schluff und horizontal durch klonales Wachstum.

Gegenstand der vorliegenden Doktorarbeit war es, die Grundwassertiefen von Standorten unterschiedlicher Vegetationstypen im Vorland einer Flussoase am Südrand der Taklamakan Wüste zu erfassen und zu untersuchen, ob diese unterschiedliche Etablierungserfolge nach einem Flutungsereignis und unterschiedliches Wurzelwachstum erklären können. Zudem wurde die Ausdehnung der Klone von *Populus euphratica*, *Tamarix ramosissima* und *Alhagi sparsifolia* untersucht und in Beziehung zur klonalen und genetischen Diversität sowie zur Grundwassertiefe gesetzt.

Die Standorte der Arten unterscheiden sich in der Grundwassertiefe. Abgesehen von *T. ramosissima* ist der Etablierungserfolg der Arten sehr gering. Das Wurzelwachstum unterschied sich zwischen den untersuchten Arten *A. sparsifolia* und *K. caspia*, diese Unterschiede ergaben aber keine Hinweise zur Erklärung des Vegetationsmusters und der Unterschiede der mittleren Grundwassertiefen beider Arten. Beide Arten sind in der Lage nach fünf bis sechs Monaten das Grundwasser im Flusstal zu erreichen. Die untersuchten Klone von *P. euphratica* und *A. sparsifolia* wiesen eine maximale Ausdehnung von 121 ha bzw. 6.1 ha auf. Die Klongröße nahm mit abnehmender klonaler Diversität und mit zunehmender Grundwassertiefe zu. *T. ramosissima* unterschied sich von den andern Arten durch geringere Klongrößen. Vermutlich stellt die ausgedehnte Klonalität der anderen Arten einen Kompensationsmechanismus für deren geringen Etablierungserfolg dar.

Zusammenfassend zeigt diese Arbeit, dass es unterschiedliche Kombinationen der untersuchten Pflanzenmerkmale und somit auch unterschiedliche Lebensstrategien der Arten im Oasenvorland gibt. Diese Unterschiede scheinen aber unbedeutend für die Existenz der Vegetation zu sein, da von allen Arten alte Bestände im Oasenvorland zu finden sind. Durch die wachsende Bevölkerung im Tarim Becken und deren steigenden Wasserverbrauch versiegen die Flüsse und sinkt der Grundwasserspiegel. Dadurch ist die existierende Vegetation und deren Verjüngung stark bedroht.

总言

总言

生态系统中在资源有限的情况下,物种适应这些稀有资源建立高物种多样化.中国西北的塔克拉玛干沙漠年平均降水量只有20-70毫米,这是一个极端的自然生态系统.此外,土壤已经被风化,这会导致频繁的沙尘暴,并具有高的景观动态特征.正如所料,降雨量低和高的景观动态特征使植被生存面临着巨大挑战.已经适应了极端环境条件的植被在这里已经建立起来.他们分布在短暂的河流沿岸,或盆地绿洲和沿江地带的绿洲.多年生长在沙漠的植被胡杨,怪柳,骆驼刺,花花藻和芦苇占主导或共同主导地位.当出现罕见的洪水,土壤达到饱和状态的时候,这种靠地下水生长的物种才有可能建立.当洪水退却时,幼苗的根系必须速度的深入沙漠之下,遵循下降的水位以找到地下水.植物经过成功的纵向生长,利用他们积累的流沙,通过克隆增长扩大.

本研究考察了在塔克拉玛干沙漠南部河流绿洲上的不同植被类型,以及是否可以解释在各自所生长的不同含水层的根系生长状况.此外,研究调查胡杨,怪柳和骆驼刺的克隆繁殖,以即与克隆关系,遗传多样性和含水层相互的联系.

物种分布在的不同的含水层.怪柳成功建立非常低.在考察的不同的物种骆驼刺和花花藻的根系生长时,发现没有证据说明与植被模式和含水层有关.两种植物的根系在河谷中经过5-6个月均达到的地下水.通过对克隆生长分布面积为121公顷和6.1公顷的胡杨和骆驼刺的调查.正如所料,含水层扩大和减少克隆多样性增加了克隆面积.怪柳不同于其他物种是他有一个小得多的克隆面积.对其他物种的大量克隆似乎给以描绘为是建立一个成功的补偿机制.

总而言之,这项工作表明,在绿洲试验的不同组合的物种,他们有着不同的生存策略.但是,这似乎对植被的存在是微不足道的,因为所有植被在山麓绿洲旧址都可以发现.在塔里木盆地人口增长导致高的水需求,致使河流干涸,地下水位下降,植被正面临着严重的威胁,他们的恢复困难重重.

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1 Introduction

Plant biodiversity at a global scale is highest in the tropics and decreases along the latitudinal gradient (Kreft and Jetz, 2007). Species richness has been found to be strongly dependent on resource availability; and thus, factors dependent on climate, such as water (in form of precipitation) and energy (potential evaporation and productivity) are the best predictors of species richness (Hawkins and Moran, 2003). As the abiotic conditions are sufficiently favourable, biotic factors such as competition and trophic interactions might be important drivers for adaptation to the tropical ecosystem and finally for speciation (Dobzhansky, 1950; Schemske, 2002). In contrast, in resource-limited areas such as cold or dry environments, abiotic factors such as frost and drought are the main constraints for plant richness (Schemske, 2002). The strong selective force of certain abiotic factors in extremely harsh environments becomes obvious when species from different families in different floristic realms are found to have evolved similar analogous adaptations. Desert environments are such ecosystems with only low species richness and a sparse vegetation cover. In this respect the Taklamakan Desert is a very extreme example, with annual precipitation well below 70 mm (Shmida, 1985), consisting of silt as a highly mobile substrate.

The Taklamakan Desert is one of the driest regions worldwide. The Taklamakan Desert is situated in the Xinjiang Uyghur Autonomous Region, China (Fig. 1.1). With a size of about 337000 km² it is the largest desert in China. The desert covers a large part of the Tarim

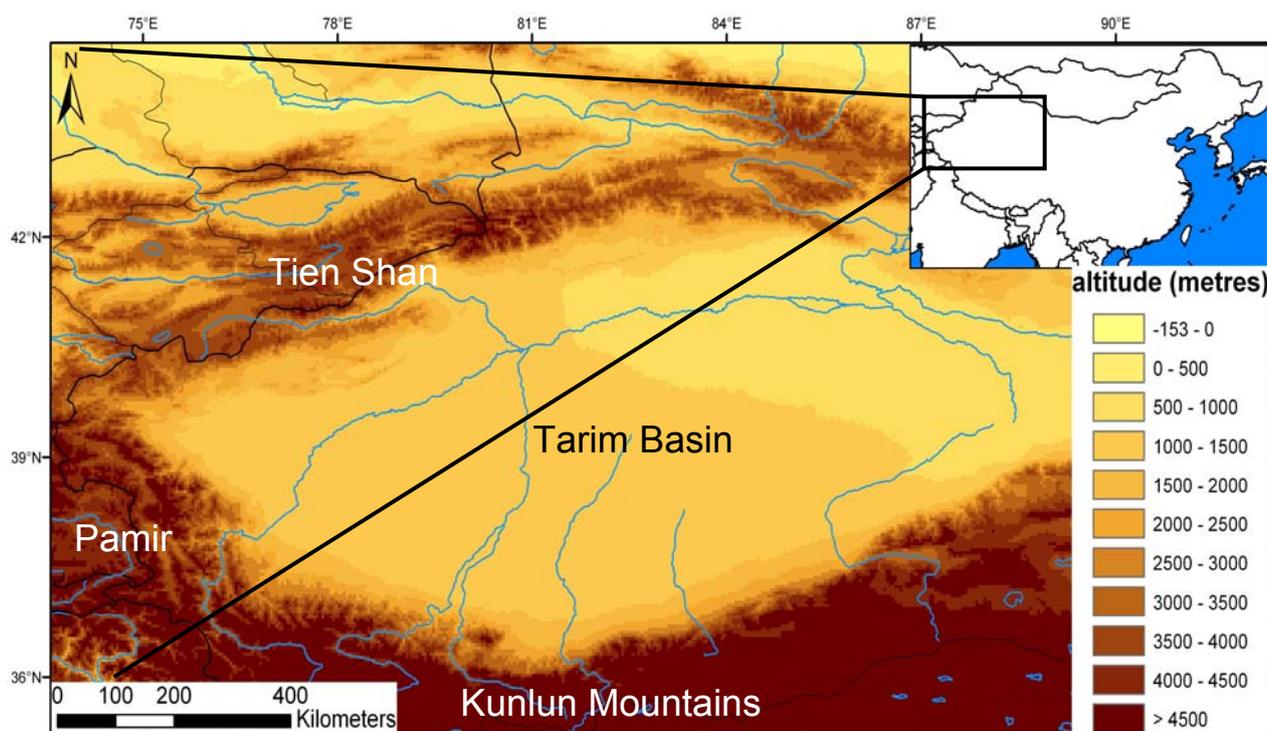


Fig. 1.1: Map of the study region (map by H. von Wehrden).

Basin, a high altitude basin without outflow. The land surface is inclined from 1400 m a.s.l. in the southwest to 800 m a.s.l. in the northeast. The basin is surrounded by high mountain ranges with the Tien Shan (of which the highest peak reaches 7450 m a.s.l.) to the north, the Pamir (8611 m a.s.l.) to the west and the Kun Lun Mountains (7712 m a.s.l.) to the south. This leads to the extremely arid conditions. Mean annual precipitation in the Tarim Basin ranges from 20 mm to 70 mm and potential evapotranspiration is between 2100 mm and 3400 mm (Zhou, 1993; Tian and Song, 1997). The climate is extremely continental, with hot summers and cold winters. Temperatures can reach 45 °C in summer and can be as low as -40 °C in the wintertime.



Fig. 1.2: *Populus euphratica* almost completely buried by a shifting sand dune.

The Taklamakan Desert came into existence in early Pleistocene when a great number of rivers fed by the melting snow deposited a thick and loose layer of silt and sand into the basin (Wu, 1981). Owing to prevailing northwestern winds on the western side of the Taklamakan Desert and northeastern winds on the eastern side, aeolic sediments have been and are still continuously accumulating at the southern margins of the Desert. The particle size of the sediment is rather small, ranging from silt to fine sand, which is easily moved with moderate wind speeds of $>2.6 \text{ m s}^{-1}$ (Li et al., 2008). At the southern fringe of the Taklamakan Desert winds blow with a velocity of $>6 \text{ m s}^{-1}$ on 90–110 days a year (Bruelheide et al., 2003), causing severe dust storms. The undulating topography of the Taklamakan Desert is the result of shifting dunes that reach heights of 100 m (Hedin, 1904) and even 120 m (Tsuchiya and Oguro, 2007). This results in a highly dynamic landscape (Fig. 1.2).

In summer, during snow and ice melt in the mountains, rivers carry an enormous amount of water into the desert and leave large floodplains. The large flooding results in extensive water erosion, where whole dunes are carried away (Fig. 1.3). Huge amount of sediments are relocated back into the desert with the floods, transport capacities can reach up to 193 kg m^{-3} (Gentelle, 1992). Some rivers carry a huge amount of water and reach far into the desert, such as e.g. the Hotan River, which cuts 400 km through the whole desert and feeds into the Tarim River. The whole river systems were continuously changing in the past due to shifting

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Fig. 1.3: Water erosion of a dune with *Populus euphratica*.

river beds and river diversions. For example, the lower reaches of the Hotan River were steadily shifting westward in the last 400 years (Zhou, 1993); whereas the lower reaches of the Keriya river were shifting eastward (Zhu and Lu, 1991). The water from the mountains recharges the groundwater which is only at a depth of 1 to 2 m in the deepest dune valleys (Hedin, 1899).

Human beings of the Taklamakan Desert have been depending on the rivers since prehistoric times. Settlements have been established at the fringe of the Desert, and along the rivers into the deserts. These are river oases with canal systems for irrigation and household water. Many of the ancient oases have been abandoned and are today buried by silt along the Southern Silk Road (Fig. 1.4). Causes for the abandonment were aeolic silt and sand encroachment in the cultivated areas, shifting river beds and a varying discharge of rivers due to changing amounts of glacial melt water (Coque et al., 1991; Gentelle, 1992).

Next to the natural processes of changing river flow, the inhabitants of the oases around the Taklamakan Desert also have had a great impact on the amounts of water in the rivers. In the last 50 years human populations were steadily increasing; for example, along the mainstream of the Tarim River, human population increased by a factor of four (Hao et al.,



Fig. 1.4: Distribution of recent and ancient oases in the Tarim Basin (after Zhou, 1993).

2009). In Qira Oasis, the human population in 2001 was 2.3 times greater than in 1949 (Zhang et al., 2004). In accordance with the growing population, anthropogenic activities increased, resulting in an expansion and intensification of irrigated farmland (Hao et al., 2009) and increased amount of water used for agricultural and industrial productivity and households (Cheng, 1997). To provide water for the increased water demand, more than 85000 dams and reservoirs have been constructed in the past five decades (Li et al., 2009). This resulted in a shortage of water flow into the desert, with the consequence of the lower reaches running dry. For example, in the middle reaches of the Tarim River major river branches of the inland delta fell dry (Thevs et al., 2008a; Li et al., 2009). The 321 km long lower section of the Tarim River was completely cut off with the two lakes Lop Nor and Lake Taitema running dry in 1970 and 1972, respectively (Hao et al., 2009).

Natural vegetation grows along ephemeral rivers (Thevs et al., 2008a and b) or in the foreland of river oases, as the oases were built along the rivers (Bruehlheide et al., 2003). The main natural constraints for the vegetation are the limited amount of precipitation water, accumulation of aeolic sediment and water erosion. The growing human population after 1958 also posed a major threat to the vegetation. Due to their expansion of agricultural and industrial areas, and in accordance with the intensified water use there was less water available for the vegetation (Hou et al., 2007). Along the lower reaches of the Tarim River, forests came into a severely degenerative state and some species even disappeared (Chen et al., 2006). For instance, Feng et al. (2001) found a decrease of forested area with *Populus euphratica* by two thirds between the years 1958 and 1978.

The function of such a natural vegetation belt around the river oases for the whole oasis system is manifold. The vegetation reduces wind velocity (Buckley, 1987; Zhao et al., 2008) and thus prevents or at least decreases desertification of the oases by soil erosion (Buckley, 1987; Barth, 1999). This is crucial as the oases at the southern rim of the Taklamakan Desert are steadily threatened by winds carrying silt and sand from the desert into the oases system. Thus, the natural vegetation belt is indispensable for the sustainability of the oases (Zhao et al., 2008). Furthermore, the vegetation belt is part of the oases agricultural system; it serves as a resource for fuel, firewood, construction material and as pasture for sheep, goats, donkeys and camels (Thomas et al., 2000).

The main perennial species growing naturally in the oases forelands are *Populus euphratica*, *Tamarix ramosissima*, *Alhagi sparsifolia*, *Karelinia caspia*, and *Phragmites australis* (Bruehlheide et al., 2003; see also chapter 2). Three of the species; *Populus euphratica*, *Tamarix ramosissima*, and *Alhagi sparsifolia*, and the introduced, non-native species *Calligonum caput-medusae* were the study species of an EC-funded project, which was conducted from 1998-2001. The focus of this project was the investigation of the physiological characteristics of the study species with the aim to use them to devise

sustainable management options of the foreland vegetation. The main results of this project which are also relevant to this PhD thesis are summarized below:

- Biomass production, determined with allometric regressions was found to be extremely high for desert vegetation. Gries et al. (2005) found a productivity of *P. euphratica* of 317–612 g m⁻² a⁻¹, with an upper limit that was higher than the lower limit of the range of biomass production in temperate forests of 600 g m⁻² a⁻¹ (Lieth, 1975). The productivity of *T. ramosissima* in homogeneous stands was between 310–715 g m⁻² a⁻¹, of *A. sparsifolia* 210–385 g m⁻² a⁻¹ and of *C. caput-medusae* 211–1130 g m⁻² a⁻¹. These productivity values were much higher than the value of 250 g m⁻² a⁻¹, which has been suggested as the upper limit of typical desert vegetation (Lieth, 1975).
- The plant species showed no indication of drought stress. Water potentials of the study species were extremely high, with midday water potentials (Ψ_{\min}) being greater or equal to -3.3 MPa, compared to typical desert plants with Ψ_{\min} of -6 MPa or even lower reported from plants in Baja California by Franco-Viszaino (1994), and from *Genista hirsuta*, *Thymus zygis* and *Juniperus oxycedrus* in the semiarid environment in Spain (Lansac et al., 1994) or the range of values between -5 to -8 MPa generally described for xerophytes by Larcher (2003).
- Water use efficiency of production (WUE_p) was low. The maximum value was encountered for *C. caput-medusae* with 1.8 g dry matter (DM) kg⁻¹ H₂O. This is even lower than the water use efficiency of production of broad-leaved trees of the temperate zone and herbaceous C₄ plants with 3–5 g DM kg⁻¹ H₂O and sclerophyllous shrubs with 3–6 g DM kg⁻¹ H₂O (Larcher, 2003).
- Artificial experimental flooding had no influence on the water potential (Thomas et al., 2006) and productivity of the plants (Gries et al., 2005). The irrigation water did reach down to a depth of 3.4 m. In contrast, Xu and Li (2006) found an increase of predawn water potential from -4.2 to -2.9 MPa in *Haloxylon ammodendron* and an increase from -4.9 to -2.9 MPa in *Reaumuria soongorica* after a rain pulse event, a reaction expected from desert plant species but not found in species in the oasis foreland.
- Expansion of agricultural activities and its intensified water use were also found in Qira Oasis. The agricultural area increased since 1956 and the desert moved closer at the northwestern outer foreland rim by a distance of 1 km. Both processes occurred at the expense of the natural vegetation belt which decreased in width by 1.5 km, and was on average 6 km in 2000 (Bruelheide et al., 2003).

These results indicate that the perennial species are not severely restricted by water shortage and are not dependent on surface water. This implies and was the main conclusion from the EC-funded project that all perennial species of the natural vegetation belt are phreatophytes (Arndt et al., 2004; Foetzki, 2003; Thomas et al., 2006, 2008; Gries et al., 2003, 2005; chapter 2).

Phreatophytes are plant species adapted to desert or arid environments with long and deep root systems for absorbing water from the permanent ground water supply. Roots can reach extraordinarily deep in the soil: *Boscia albitrunca* and *Acacia erioloba* can reach depths of 68 m and 60 m, respectively, in the central Kalahari, Botswana (Jennings, 1974 in Canadell et al., 1996), *Prosopis cineraria* was observed to reach rooting depths of 60 m in the Oman desert (Brown, 1992), and roots of *Prosopis juliflora* were found at a depth of 53 m (Phillips, 1963). Phreatophytes can be classified into obligate phreatophytes, which have only deep reaching roots to tap water from the groundwater, and facultative phreatophytes, which, in addition to the deep reaching roots, also have a wide spread shallow root system to catch moisture from sparse rainfall (Canadell and Zedler, 1995). Phreatophytes occur almost on all continents; in the southwest of Northern America (e.g. *Prosopis* spp., Phillips, 1963; Brunel, 2009), in the Namib desert (e.g. *Welwitschia mirabilis*, von Willert, 1994), in the Sahel zone (e.g. *Spartidium saharae*, Abdallah and Chaieb, 2007; *Acacia* spp., Stave et al., 2005), in central Asia (e.g. *Populus euphratica* and *Alhagi sparsifolia*, Arndt et al., 2004; Foetzki, 2003; Thomas et al., 2006, 2008; Gries et al., 2003, 2005), in the Mediterranean (e.g. *Genista* spp., Padilla and Pugnaire, 2007; *Retama sphaerocarpa*, Haase et al., 1996), and Australia (e.g. *Banksia* spp., Froend and Drake, 2006).

Successful establishment of phreatophytes is rare (Barnes, 2001; Acacio et al., 2007; Andersen and Krzywinski, 2007; Thevs et al., 2008b). In order to establish themselves, phreatophytes need water-saturated soils from the surface to the ground water for germination and establishment, which in desert or arid ecosystems can be found only shortly after or at sporadic flooding events. This explains why phreatophytes are mainly found along rivers or along former rivers (Thevs et al., 2008b). Establishment on an unstable substrate along rivers is rather difficult. On the one hand, the river banks need to be sufficiently moist for germination, but on the other hand, too strong current can wash the seeds away (Bradley and Smith, 1986; Gage and Cooper, 2004). This leaves only a small strip of suitable regeneration sites along the river beds and a small time window with favourable condition for establishment. As surface water recedes the phreatophytes must follow the sinking water fringe down with their roots to access the groundwater. To achieve this, the plants must have an extremely fast rooting depth (von Willert, 1994). Phreatophytes seem to adjust their root growth to the rate of decrease of the sinking water fringe. Von Willert (1994) and Padilla et al. (2007) found lower rates of rooting depth of irrigated plants compared to non irrigated plants,

therefore additional irrigation, or a flooding event of longer duration does not assure an increased establishment success.

Due to the unpredictable deposition of wind-driven sand in the Taklamakan desert, the chance of getting totally or partially buried by sand is very likely. Sand burial may change abiotic and biotic conditions of the plants, such as photosynthetically active radiation (Brown, 1997), moisture (Baldwin and Maun, 1983) and temperature (Baldwin and Maun, 1983) to which plants react with resource allocation from below-ground to the above-ground components (Brown, 1997) and stem elongation (Maun and Lapierre, 1984; Klimeš et al., 1993). Deep and prolonged sand burial might negatively restrain plant survival (Klimeš et al., 1993; Brown, 1997; Maun, 1997). Clonal integration enhances the chance of survival and plant performance (Yu et al., 2001; 2004) of buried ramets most likely due to the support with resources translocated from connected unburied ramets.

Furthermore, in extreme environments where establishment from seed is rare, as in the foreland of the river oases, clonality assures longtime persistence in the particular habitat (Honnay and Bossuyt, 2005). In clonal plant populations with very limited or only initial establishment, clones expand with time and might eliminate other genets through interclonal competition (Laberge et al., 2000; Barsoum, 2002; Travis and Hester, 2005), which in the worst scenario could end up in a monoclonal population. Without further establishment, clonal diversity, defined as the number and frequency of genets can only decline with time (Eriksson, 1993; Watkinson and Powell, 1993; Barsoum et al., 2004; Silvertown, 2008), whereas the genetic diversity, measured as heterozygosity, proportion of polymorphic loci and molecular variance can increase, in case the degree of heterozygosity plays as selective advantage in the elimination of genotypes. However, genetic diversity may also remain at the same level when the elimination of genotypes is random, or even decrease in case certain alleles are abolished which do not contribute to higher survival and competition capabilities in early life stages (Soane and Watkinson, 1979; Eriksson, 1993).

Objectives and outline of the study

In the EC-funded project researchers have found common characteristics among the perennial species which are rather untypical for desert vegetation and which might be the consequence of an analogous adaptation to the extreme environment of the Taklamakan Desert. Taking this into account the perennial species could have evolved similar strategies how to cope with the extreme drought and the highly dynamic substrate. However, as we find mainly dominant or codominant stands of the perennial species (see chapter 2), species must differ in some aspects of their life cycle. I concentrated on studying those characteristics of the plant species that can be considered relevant for the establishment and development of oasis foreland vegetation in the extreme arid and highly dynamic environment. In the four following chapters I present the different subprojects.

The first chapter assessed whether the perennial species form different vegetation types in the oasis foreland and whether these types differ in the distance to the groundwater table.

In the second chapter I concentrated on the establishment success of the different plant species. As the perennial species form mainly dominant and codominant stands I expected species differences in establishment rates and in the subsequent survival rates under natural conditions in the river plain.

As the species are all phreatophytes, I focused in the third chapter on root growth as one specific characteristic at the early stage of establishment. I assessed whether a species occurring at greater distance to the groundwater table has a faster rooting depth than a species growing closer to the groundwater table and whether drought initiates faster rooting depth.

As the study species grow vertically with sand accumulation and horizontally through clonal growth, I focused in the fourth chapter on clonality and the relation of clonality to the groundwater table. Taking clone size and groundwater depth as proxy variables of time since establishment, I expected (1) clonal and genetic diversity to decrease with clone size, (2) a decrease of clonal and genetic diversity with increasing depth of the groundwater table, (3) an increase of clone size with increasing depth of the groundwater table, and (4) that the species show the same pattern in these relationships.

Study area

The study was conducted in the vegetation belt in the western foreland of Qira Oasis (37°01' N, 080°48' E and 1365 m a.s.l.), a river oasis at the southern fringe of the Taklamakan Desert. It was selected because of its exposed location towards the open desert. I chose to study the vegetation in the northwest section of the vegetation belt, because this section is mainly facing the strong northwestern winds from the desert, blowing aeolic sediments into the oasis system. Qira River is the water source of Qira Oasis. In the 1980s the canal and road system of Qira Oasis was completely reconstructed and the farmland was newly arranged (Graefe et al., 2004). Simultaneously a reservoir was built upstream the Qira River, together with 40 km new canals and 153 sluice gates (Bruelheide et al., 2003). Most likely as an effect of the novel water management, extensive flooding of the river into the desert has been rare in the last 20 years (Zhang X., pers. communication).

Study species

Populus euphratica

Populus euphratica Oliv. (syn. *Populus diversifolia* Schrenk, Salicaceae, aspen or poplar) (Fig. 1.5) is indigenous to Central Asia (Wyckoff and Zasada, 2002). It is one of the main tree species of the Tugai riparian forests (Thevs et al., 2008a and b), but also occurs further away from present flood plains in ancient river plains (Thevs et al., 2008b).

P. euphratica is a dioecious tree species. Flowers are wind-pollinated and seeds are wind-dispersed, seeds weigh between 0.10–0.15 mg. Seeds lose their viability shortly after



Fig. 1.5: *Populus euphratica* forest, view from the top of a dune nearby.

maturity (pers. observation). *P. euphratica* is salt tolerant (Chen et al., 2002; Kang et al., 1996). Species of the poplar genus are well known for an extensive clonal growth, e.g. *P. tremuloides* has been reported to be the largest vascular plant species in the world (Mitton and Grant, 1996).

Tamarix ramosissima

Tamarix ramosissima Ledeb. (Tamaricaceae) (Fig. 1.6) belongs to the group of *T. chinensis* (with *T. parviflora* and *T. chinensis* s.str.). The genus *Tamarix* is indigenous to India, Central Asia, Northern Africa and Southern Europe (Baum, 1978) and has been introduced to many arid regions worldwide.



Fig. 1.6: *Tamarix ramosissima*.

Tamarix species spread vegetatively by resprouting from stems and roots (Brock, 1994) and are also capable to propagate by layering. *Tamarix* also reproduce sexually, they are pollinated by generalist insects as well as by wind (Di Tomaso, 1998) and seeds are dispersed by wind and water (Brock, 1994). Seeds are very small, weigh about 0.1 mg and lose their viability approximately after 4 weeks.

The shrubby growth form of *T. ramosissima* promotes sand accumulation. In this way, the species grows up on top of growing sand dunes forming nebkhas, typically encountered in old *Tamarix* stands. *T. ramosissima* is a halophyte; it excretes salt through glands in the leaves (Kleinkopf and Wallace, 1974) and by shedding twigs and leaves in fall. In consequence, the species accumulates salt underneath the shrubs.

Alhagi sparsifolia

Alhagi sparsifolia Shab. (Fabaceae, camelthorn) (Fig. 1.7), probably synonymous to *A. maurorum* Medik., *A. pseudoalhagi* (M. Bieb.) Desv., and *A. kirghisorum* Schrenk (Dickoré B., pers. communication to Foetzki, 2003) has its native range in salinized and arid regions of Northwestern China, Central Asia, India, Middle and Near East and is an invader in North America (Kurban et al., 1998).



Fig. 1.7: *Alhagi sparsifolia* stands.

Alhagi is a spiny, perennial shrub and is also considered a sand fixing plant. Shoots die over winter and resprout again in spring. *A. sparsifolia* flowers in June and July and seeds reach maturity by the end of September and in October. Seeds weigh between 4–5 mg and are dispersed by mammals. *Alhagi* as a legume is capable to fix atmospheric nitrogen in symbiosis with N₂-fixing bacteria (Arndt et al., 2004).

Karelinia caspia



Fig. 1.8: *Karelinia caspia* stands.

Karelinia caspia Less. (Asteraceae) (Fig. 1.8) grows in rock and sand deserts as well as in saline meadows in Central and Southwest Asia (Wu and Raven, 1994). It is a perennial shrubby species. Like *A. sparsifolia*, shoots of *K. caspia* die over winter and resprout again in spring. *K. caspia* spreads vegetatively and also reproduces sexually, the species flowers between July and September and sets fruits in September and October (pers. observation). The seeds are very small and weigh between 0.06–0.08 mg.

Phragmites australis

Phragmites australis (L.) Steud. (Poaceae) (Fig. 1.9) is a cosmopolitan species (Brix, 1999). Its wide distribution is accompanied by an enormous phenotypic diversity, wide range of euploidy levels and the occurrence of aneuploidy and physiological plasticity under diverse environmental conditions (Hansen et al., 2007). Known as a plant which is mainly growing in littoral zones of lakes, along rivers and canals, in shallow and freshwater swamps, it can also grow in arid zones along rivers where groundwater is available (Thevs et al., 2007).

P. australis is a perennial grass with extensive clonal growth (Amsberry et al., 2000). New establishment can be vegetatively by vegetative propagules or sexually from seeds. Seeds reach maturity



Fig. 1.9: *Phragmites australis* stands.

at the end of October and in November. They weigh between 0.06–0.16 mg (McKee and Richards, 1996) and are wind- or water-dispersed. Zhang X. (pers. communication) hardly found any mature seeds of *P. australis* and assumes that the species can hardly complete its life cycle in the oases forelands.

2 Life on the edge – To which degree does phreatic water sustain vegetation in the periphery of the Taklamakan Desert?

Helge Bruelheide; Beatrix Vonlanthen; Ute Jandt; Frank M. Thomas; Andrea Foetzki; Dirk Gries; Gang Wang; Ximing Zhang; Michael Runge

Applied Vegetation Science (2010) 13:56–71.

Abstract

Questions: Do the vegetation-specific patterns in the forelands of river oases of the Taklamakan Desert provide clues to the degree to which a vegetation type depends on unsaturated soil moisture, brought about by extensive floodings, or phreatic water?

Location: Foreland of the Qira Oasis on the southern rim of the Taklamakan Desert, Xinjiang Uygur Autonomous Region, China.

Methods: A vegetation map was prepared using a SPOT satellite image and ground truthing. Measurements of soil water contents were obtained from a flooding experiment carried and transformed into water potentials. Sum exceedance values were calculated as the percentage of days on which different thresholds of soil water potentials were transgressed. Groundwater depth was mapped by drilling 30 groundwater holes and extrapolating the distances to the whole study area.

Results: The vegetation was characterized by only six dominant or codominant species: *Alhagi sparsifolia*, *Karelinia caspia*, *Populus euphratica*, *Tamarix ramosissima*, *Calligonum caput-medusae* and *Phragmites australis*. The vegetation patterns encountered lacked any linear features typical for phreatophytes, thus not allowing direct conclusions on the type of the sustaining water sources. Soil water potentials never transgressed a threshold of pF 5 (-10 MPa) in horizons above the capillary fringe during periods without inundation, thus

representing water not accessible for plants. Depth to the groundwater ranged between 2.3 m and 17.5 m among plots and varied between 1.7 m and 8.0 m within a plot owing to dune relief. The seven main vegetation types showed distinct niches of groundwater depths, corresponding to the observed concentric arrangement of vegetation types around the oasis.

Conclusions: Inundation by flooding and unsaturated soil moisture are irrelevant for the foreland vegetation water supply. Although distances to the groundwater table can reach about 20 m, which is exceptionally large for phreatophytes, groundwater is the only water source for all vegetation types in the oasis foreland. In consequence, successful maintenance of oasis foreland vegetation will crucially depend on providing non-declining ground water tables.

Key words: China, Desert vegetation, Groundwater map, Oasis vegetation, Phreatophytes, Sum exceedance values, Soil matric potential, Soil texture, Soil water content, Soil water retention curves, Vegetation map, Xinjiang

Nomenclature: Flora Karakorumensis Database (Dickoré 1995; Dickoré B., pers. communication); Flora of China (<http://flora.huh.harvard.edu/china>)

3 Establishment and early survival of five phreatophytes of the Taklamakan Desert

Beatrix Vonlanthen; Ximing Zhang; Helge Bruelheide

Flora, in press.

Abstract

The establishment and survival of young individuals of five desert phreatophytes that form dominant or codominant stands round river oases at the southern rim of the Taklamakan Desert was studied to explain the patterns observed in the established vegetation. We hypothesized to find differences between species in the rates of establishment and survival as well as in the susceptibility to grazing. We expected species that grow at largest distances to the groundwater table to establish themselves more successfully and have higher survival rates. In addition, we expected the high grazing and browsing pressure in the oasis foreland to have a negative effect on seedling establishment, with less palatable species being less affected. Exclosure experiments were carried out along the banks of an ephemeral river. Seedlings and shoot or rhizome fragments were planted in either fenced or control plots. In addition, the naturally emerging seedlings after a flooding event were monitored for survival to the subsequent vegetation period. In contrast to expectations, the species did not differ in the survival of planted seedling and vegetative fragments. However, there were significant differences in the density of spontaneously emerging seedlings. *Tamarix ramosissima* had a much higher seedling density than the other species. Excluding livestock had a positive effect on the survival of planted seedlings and shoot or rhizome fragments. However, there were no species-specific exclosure effects, neither effects on the survival of spontaneously emerging seedling. The exclusion of grazers and browsers might generally enhance the vegetation coverage in the oases forelands, but it does not favour different species disproportionately. In conclusion, the species' regeneration niches explain only partly the patterns encountered in the established vegetation.

Key words: Regeneration, exclosure, grazing, *Populus euphratica*, *Tamarix ramosissima*, species composition

4 On the run for water – Root growth of two phreatophytes in the Taklamakan Desert

Beatrix Vonlanthen; Ximing Zhang; Helge Bruelheide

Journal of Arid Environment, resubmitted after major revision.

Abstract

Desert phreatophytes require extremely fast root growth for a successful establishment. We measured the speed of seedling root growth of two phreatophytic plant species, *Alhagi sparsifolia* and *Karelinia caspia*, which form dominant or co-dominant stands around river oases at the southern fringe of the Taklamakan desert. As *A. sparsifolia* occurs at sites with deeper groundwater, we expected the roots of this species to reach down more rapidly than those of *K. caspia*. After 16 weeks of growth in the field experiment, the roots of *K. caspia* and *A. sparsifolia* reached down 2.2 m and 1.7 m, respectively. After 12 weeks without irrigation in the glasshouse experiment, *A. sparsifolia* had a higher rooting depth (0.45 m) than with irrigation (0.30 m), while root depths of *K. caspia* showed the opposite pattern with 0.62 m and 0.72 m, respectively. Our results show clearly that both species are able to reach the groundwater table in the river valleys (6.5 m) within five to six months after germination. However, the encountered vegetation pattern is probably not caused by differences in the speed of rooting depth, but the result of a higher persistence of *A. sparsifolia*.

Key words: Relative growth rate, rooting depth, root: shoot ratio, irrigation, fertilization, groundwater depth

5 Clonal structure and genetic diversity of three desert phreatophytes

Beatrix Vonlanthen; Ximing Zhang; Helge Bruelheide

American Journal of Botany, (2010) 97:234–242.

Abstract

The objective of this paper was to assess clone sizes of three perennial desert plant species with AFLP markers and to relate them to clonal and genetic diversity and to hydro-ecology. The study was carried out at the southern rim of the Taklamakan Desert, where sexual regeneration is only possible at rare flooding events, resulting in rarely established cohorts with subsequent extensive vertical growth and horizontal clonal spread. In this environment repeated seedling establishment is excluded. We expected decreasing clonal and genetic diversity with increasing clone size and increasing distance to the groundwater table and a common response pattern among all study species. Maximum sizes of *Populus euphratica* and *Alhagi sparsifolia* clones were 121 ha and 6.1 ha, respectively, while *Tamarix ramosissima* clones reached a maximum size of only 38 m². In *P. euphratica* and *A. sparsifolia*, clonal diversity declined with increasing clone size and increasing distance to the groundwater table, while genetic diversity remained unaffected. *T. ramosissima* differed from the other species because of a much smaller clonality. Clone size and clonal diversity were found to be good proxy variables for clone age. Despite a considerable age of the clones, genetic diversity is maintained in the populations.

Key words: AFLP, *Alhagi sparsifolia*, clonal plants, genetic diversity, hyperarid environment, *Populus euphratica*, sand accumulation, *Tamarix ramosissima*

6 Synthesis

Novel insights

This PhD thesis significantly improved the level of understanding of the vegetation in the oases foreland. In the following the novel insights are summarized.

The perennial species form vegetation types that differed in distance to the groundwater table. The types with the lowest distance to the groundwater table were dominated by *Phragmites australis* and *Populus euphratica* and occurred at maximum groundwater distance of 9 m and 10 m, respectively. This distance has already been described for *P. euphratica* (Thevs et al., 2005; Zhang et al., 2005; Chen et al., 2006; Xu et al., 2007; Chen et al., 2008) and for *P. australis* (Chen et al., 2008). However, Thevs et al. (2007) and Zhang et al. (2005) found *P. australis* only at a maximum distance of 5.8 m to the groundwater table, which is much lower than the distance encountered in this PhD study. Similarly, Hou et al. (2007) described a lower threshold of groundwater depth of the two species, which was at a groundwater depth of 3.5 m and 4.5 m of *P. australis* and *P. euphratica*, respectively.

The groundwater table of vegetation types dominated by *Tamarix ramosissima* had an average depth of 8.7 m. This is lower than the reported ranges of about 10–12 m of other observations (Tang et al., 2003; Chen et al., 2006; Xu et al., 2007; Chen et al., 2008). However, our values are averages of the depth of the groundwater table. Especially the *Tamarix* species, which have the ability to fix and grow up with aeolic sediment and form nebkhas, have a high dune formation in the plots. Highest depth to the groundwater table of a *Tamarix* dune of our study was 14 m, but it can reach even 24 m (Gries et al., 2003) in the oasis foreland. *T. ramosissima* is a facultative phreatophyte (Di Tomaso, 1998) and might also take water up from upper soil layers. However, as the soil water potentials in the upper layers were always below -10 MPa, this source can be precluded.

Alhagi sparsifolia dominated vegetation types grow on sites with an average distance of 15 m to the groundwater table. The maximum groundwater depth at an *A. sparsifolia* site was even 19.9 m. This is higher than what was reported for *Alhagi maurorum* with a maximum distance of 15 m found in Israel (Shmueli, 1948) and for *A. sparsifolia* by Canadell et al. (1996), and also exceed the reported maximum distance for *A. sparsifolia* of 12 m (Chen et al., 2008).

In summary, the groundwater table found in our study seems rather deep. Despite this distance to the groundwater table, the species are phreatophytes because taking up water from upper soil layers is impossible. However, as described in the introduction, phreatophytes can reach even in more extreme depths, which can reach up to 68 m

(Jennings, 1974, cited after Canadell et al., 1996). These different groundwater niches observed for the study species resulted in the conclusion that the species should differ in one or more plant characteristics related to these differences.

Species differed in densities of spontaneous established seedlings. With 968 seedlings per 100 m² *T. ramosissima* had much higher seedling densities after a flooding event than *P. euphratica* with 9 seedlings, and *P. australis* and *A. sparsifolia* with each 1 seedling per 100 m². No newly established seedlings at all were found of *K. caspia*. Against my expectations, I did not find any differences in survival of seedlings between species. The survival to the next growing season was extremely low with less than one seedling per experimental unit. Such differences in the number of new established seedlings between *Tamarix* and *Populus* species are well known from studies in the USA. Sher et al. (2002) also found much higher seedling densities of *T. ramosissima* than of *Populus nigra*. As they encountered also higher survival rates than those observed in my study, they were able to observe the survival in subsequent years and found that either one of the species dominate on a river bank after 36 months of observation, what might indicate species-specific regeneration sites in the early years. Whether this phenomenon also occurs in the river valley around Qira Oasis might be subject for further studies.

The species-specific site conditions also played a role in our study. *A. sparsifolia* seemed to regenerate on river banks different from those preferred by the other species. Seeds of *A. sparsifolia* are rather large and dispersed by mammals, in contrast to the seeds of the other species which are small and wind dispersed. Those small seeds depend on retained soil moisture in the upper soil layers for germination and early growth to become protected from desiccation. This might not be so important for germination and survival of *A. sparsifolia* seedlings, of which the animal dropping that contains the seeds might offer additional protection from desiccation. Thus, *A. sparsifolia* seems to be capable to germinate and grow on different river banks than the other species. Additionally, I found sand accumulation mainly on sites dominated with *A. sparsifolia* seedlings. Differences in species distribution due to different capabilities to grow up with sand accumulation have been observed on coastal sand dunes (Maun, 1997; Wilson and Sykes, 1999). As *A. sparsifolia* is the species with the highest degree of sand accumulation and an occurrence at sites with deepest groundwater table this process might already start at the seedling stage.

As a conclusion, the vegetation pattern around the river oasis can be partly explained by species-specific regeneration sites. The different seed dispersal mode and the subsequent sand accumulation might be the reason for the dominant vegetation type of *A. sparsifolia* at sites with the highest degree of sand accumulation. *Tamarix* and *Populus* seem to establish at the same sites but probably have species-specific establishment success in the first years.

Within four months, roots of *A. sparsifolia* reached a depth of 1.7 m, whereas roots of *K. caspia* reached a depth of 2.2 m. These two species were faster in rooting depth than *Welwitschia mirabilis* which grew one meter within eight months (von Willert, 1994). However, Stave et al. (2005) found faster rooting depth of *Acacia tortilis* and *Faidherbia albida*, which reached 1.2 m and 0.8 m, respectively after 56 days. The species did differ in their rooting depth, however against the expectation; I found *A. sparsifolia*, the species growing at sites with deeper groundwater depth to grow more slowly in depth with their roots than *K. caspia*. In accordance with faster rooting depth, *K. caspia* had a higher water use. In contrast, *A. sparsifolia* used less water and might thus be able to survive and grow in drier soils, what might be important in the ability to grow up with sand burial.

The assumption that rooting depths increased with drought can be partly confirmed. Rooting characteristics were measured at two different developmental stages. At the first developmental stage, *A. sparsifolia* had deeper roots with drought, whereas at a later stage, *K. caspia* displayed a higher rooting depth with drought. These results are not as clear as the findings of von Willert (1994) and Stave et al. (2005); both studies found distinct deeper roots of plants left in drought than in irrigated plants.

In conclusion, both species showed extremely fast rooting depths. The extrapolation of the data revealed that both species are capable to reach the groundwater level within five to six months. However, the pattern of different vegetation types in the oasis foreland cannot be explained by different capabilities of fast rooting depth, but might be explained by the higher capability of *A. sparsifolia* to persist in drier soils and grow with sand burial than *K. caspia*.

Maximum clone sizes of *P. euphratica* and *A. sparsifolia* were 121 ha and 6.1 ha, respectively. These clone sizes are enormous as the largest clone of *P. euphratica* detected in this study is even larger than the largest higher organism known in the world today, which is a clone of *Populus tremuloides* covering an area of 81 ha in the USA (Barnes, 1966; Mitton and Grant, 1996). As expected, clonal diversity declined with increasing clone size and in case of *P. euphratica* with increasing distance to the groundwater table which I both assume to be related with time. These results of increasing clone size with declining clonal diversity are supported by the study of Travis and Hester (2005), who also found lower clonal diversity of *Spartina alterniflora* with marsh age and by the study of Barsoum et al. (2004) who found lower clonal richness in middle aged stands of *Salix alba* and *Populus nigra* than in young stands. Similarly, in a review of 20 studies Silvertown (2008) found a lower clonal diversity in old compared to young stands. Therefore, next to clone size, the two variables clonal diversity and distance to the groundwater table might be good proxy variables to estimate clone age.

Genetic diversity did not decrease with clone size, which indicates random elimination of genotypes with time. As seedling mortality of the study species was relatively high (see chapter 3), selection for homozygosity might have occurred before the genotypes reached adulthood. Against expectations, the species *A. sparsifolia* had decreasing clone size and increasing clonal diversity with increasing distance to the groundwater table, which might be due to the position of the populations of *A. sparsifolia*. This species occurred closer to the oasis where the distance to the groundwater was higher than at the border to the open desert (see chapter 2). The closer to the oasis, the more the locations are a sink for drifting sand, thus stands with the same clonal diversity might have a larger distance to the groundwater than stands farther away. Another distinct difference between species is the different growth form of *T. ramosissima* compared to the other two species. *T. ramosissima* propagated by layering, whereas *P. euphratica* and *A. sparsifolia* displayed a guerrilla type of clonal growth.

As a conclusion, *P. euphratica* and *A. sparsifolia* both showed extensive clonal growth, whereas *T. ramosissima* had a much smaller clonality. Clonal diversity and the distance to the groundwater table were found to be good proxy variables for clone size.

Species differences in their performance in the extreme environment

A summary of the studied plant characteristics of the study species is shown in Table 6.1. The species seem to differ in the way they cope with the harsh environment of the Taklamakan Desert. The analyses of different aspects of the same study species allowed to compare whether there are species-specific characteristics and to discuss whether there are species-specific combinations of these characteristics for the performance in this extreme environment.

Table 6.1: Summary of the study species and their performance in the studied plant characteristics.

| Species | Average depth to the groundwater table (chapter 2) | Number of spontaneous emerged seedlings per 100 m² (chapter 3) | Rooting depth after four months (chapter 4) | Maximum clone sizes (chapter 5) |
|-----------------------------|---|--|--|--|
| <i>Populus euphratica</i> | 7 m | 9 | | 121 ha |
| <i>Tamarix ramosissima</i> | 9 m | 968 | | 38 m ² |
| <i>Alhagi sparsifolia</i> | 15 m | 1 | 1.7 m | 6.1 ha |
| <i>Karelinia caspia</i> | 11 m | 0 | 2.2 m | |
| <i>Phragmites australis</i> | 6 m | 1 | | |

As the root growth experiment was done only with *K. caspia* and *A. sparsifolia*, root growth and establishment success can only be compared between these two species. In contrast to *A. sparsifolia*, no spontaneous seedling establishment was found at all of *K. caspia*. Even though the difference between the two species in rooting depth was very small, *K. caspia*, with the faster rooting depth, might be able to compensate for its very low rate of seedling recruitment with higher capabilities to keep pace with fast sinking water levels after establishment. This can be assumed to increase the survival in the early stage of establishment.

The establishment success and clonality were both assessed and thus can be compared among *A. sparsifolia*, *P. euphratica* and *T. ramosissima*. *A. sparsifolia* and *P. euphratica* both had extensive clonal growth, while only moderate numbers of newly established seedlings after a flooding event were encountered for these species. In contrast, *T. ramosissima* showed very high numbers of newly established seedlings but displayed a clonality limited to rooted subterranean stems. Thus *A. sparsifolia* and *P. euphratica* might compensate for limited seedling recruitment with clonal growth. In fact, I have found the same densities of ramets and individuals of *P. euphratica* (0.4 ramets m⁻²) and *T. ramosissima* (0.6 individuals m⁻²) stands under natural conditions in the oasis foreland (unpublished data).

It seems that *A. sparsifolia* as the species with intermediate clonal growth was also the species with intermediate performance in establishment and a less pronounced rooting depth. However, *A. sparsifolia* grew at sites with deepest groundwater table, which might indicate that this species has the highest capability in growing upwards with accumulating sand, and thus, might compensate for intermediate performance of other life cycle characteristics, in which *A. sparsifolia* ranks after the other species in the study region.

Conclusion

In conclusion, I found distinct differences between species in the studied aspects. *Alhagi sparsifolia* and *Karelinia caspia* both displayed a fast rooting depth at the seedling stage. However, both species are capable to reach the groundwater within five to six months at the site of establishment (see chapter 4), so that the differences in rooting depth between the species might be irrelevant for the existence in the extreme drought of the Taklamakan Desert. Thus, fast rooting depth seems to be a required adaptation to the arid environment, shared by different species, and thus is an analogous characteristic in the species' evolution.

Differences in clonal growth between the species were found to be more pronounced. Clonality is an adaptation to survive on the highly dynamic substrate and to persist in extreme environments, with rare seedling establishment. *P. euphratica* and *A. sparsifolia* (see chapter 5) and *K. caspia* (pers. observation) and *P. australis* (Amsberry et al., 2000) have extensive clonal growth, whereas the clonality of *T. ramosissima* is limited to propagation by layering. Therefore, clonality is not an analogous adaptation among all species. The extensive clonality of *P. euphratica*, *A. sparsifolia*, *K. caspia* and *P. australis* might compensate for the lower seedling establishment.

However, clonal integration might enhance the survival on dynamic soils when ramets are buried by silt and sand. As *T. ramosissima* has only limited clonal growth, this species might have higher capabilities to grow up with accumulating silt and sand, which explains the high dune formation in the *T. ramosissima* plots.

As a summary, the perennial species differ in their performance in the oases foreland and thus seem to have different strategies how to cope with the extreme drought. All strategies seem to work, as old populations of all species were encountered in the oasis foreland. However, the very limited sexual recruitment found in this study poses the question whether the species are capable to adapt to the ongoing decrease in water availability in the Tarim Basin. Zhang et al. (2003) consider the change in climate to be responsible for the beginning of desertification with the evolution of oases in the Tarim Basin in historic times, whereas the increased human activities with the intensified water use are responsible for the expansion of the desert and a reduction of the native vegetation belts around the oases in modern times. Thus, the shrinking of the natural vegetation coverage today is mainly caused by increased human activities. As the vegetation is of high importance for the sustainability of the oases, measures should be taken to conserve the remaining vegetation and promote new recruitment. A negative influence on the natural vegetation is mainly exerted by the following factors.

A sinking groundwater table is a consequence of the intensified water use, which negatively affects the natural growing vegetation (Hao et al., 2009). Chen et al. (2008) found a decreasing vegetation density, coverage and species number with increasing depth to the groundwater table. Therefore, the large vegetation degradation (Kong et al., 2009; Qi et al., 2007) and the increased desertified area (Tang et al., 2003) along the lower Tarim River are assumed to be due to the declining groundwater table. I found that vegetation is capable to grow up with sand burial, however, whether the vegetation is capable to follow the sinking water table remains an open question.

Drying of floodplains, another consequence of the intensified water use is also fatal for the long-term existence of the perennial species. Floodplain areas are needed for the sexual regeneration of the study species. In my study I found very low establishment success of the study species. A flood of such an extent as in 2005, in which new recruitment was possible at all, is very rare and happens only once every five to ten years in the foreland of Qira Oasis (Zhang X., pers. communication). With an intensified water use and further drying out of floodplain areas, successful regeneration especially of the species with very low establishment success, such as *K. caspia*, will occur even more rarely.

With increased human activities, the arable land expands at the expense of the natural indigenous vegetation belt (Bruelheide et al., 2003). My project was also affected by the expansion of agricultural land; as a sampling plot of *A. sparsifolia* was cut and reorganised for agricultural production.

Local governments and the local human population in the oases need to be sensitised for the importance of the existing vegetation. At the lower reaches of the Tarim River, the urgency to restore the destroyed habitat has been recognised and a large restoration project for 1.3 billion US\$ along the lower reaches of the Tarim River has been initiated. In the year 2000, water from nearby water lakes or dams were diverted into the lower reaches of the Tarim River (Li et al., 2009). Since the beginning of the restoration project an increase in vegetation cover (Kong et al., 2009; Li et al., 2009), increased biodiversity (Xu et al., 2007; Xu et al., 2009) and increased growth of the existing vegetation (Xu et al., 2007) has been found. Similarly, management plans are needed also for the oases' forelands, to conserve the existing vegetation and promote new establishment of the perennial plant species.

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Halle (Saale), 17. Februar 2010

8 Appendices

Publikationsliste***Veröffentlichungen***

Bruehlheide, H., B. Vonlanthen, and X. Zhang. Subterranean giants – The hidden life of the world's largest vascular plant species (in prep.).

Vonlanthen, B., X. Zhang, and H. Bruehlheide. On the run for water – Root growth of two desert phreatophytes in the Taklamakan desert. *Journal of Arid Environment* (resubmitted after major revision).

Vonlanthen, B., X. Zhang, and H. Bruehlheide. Establishment and early survival of five phreatophytes of the Taklamakan desert. *Flora* (in press.).

Vonlanthen, B., X. Zhang, and H. Bruehlheide. 2010. Clonal structure and genetic diversity of three desert phreatophytes. *American Journal of Botany* 97:234–242.

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Vonlanthen, B. and H. Bruehlheide. 2006. Clonal growth in an arid environment: establishment and development of vegetation around river oases in the Taklamkan Desert, China. 8th clonal plant workshop. Generality, specificity and diversity of clonal growth. June 27th – 30st Pärnu, Estonia.

Halle (Saale), 17. Februar 2010

Erklärung über den persönlichen Anteil an den Publikationen

Da es sich hier um eine Dissertation handelt, die mehrere Publikationen mit Co-Autorenschaften umfasst, ist im Folgenden mein Eigenanteil an den Veröffentlichungen aufgelistet.

Helge Bruelheide, Beatrix Vonlanthen, Ute Jandt, Frank M. Thomas, Andrea Foetzki, Dirk Gries, Gang Wang, Ximing Zhang, Michael Runge. 2010. Life on the edge – To which degree does phreatic water sustain vegetation in the periphery of the Taklamakan Desert? *Applied Vegetation Science* 13:56–71.

Datenerhebung:

Einrichtung der Probeflächen für die Grundwassererhebung: 95%

Quantifizierung des Dünenreliefs: 95%

Messungen der Grundwassertiefe: 95%

Schriftliche Umsetzung: 10%

Beatrix Vonlanthen, Ximing Zhang, Helge Bruelheide. Establishment and early survival of five phreatophytes of the Taklamakan Desert. *Flora* (in press.).

Datenerhebung:

Experiment in China: 95%

Datenanalyse: 90%

Schriftliche Umsetzung: 90%

Beatrix Vonlanthen, Ximing Zhang, Helge Bruelheide. On the run for water – Root growth of two phreatophytes in the Taklamakan Desert. *Journal of Arid Environment* (resubmitted after major revision)

Datenerhebung:

Experiment in China: 95%

Experiment in Halle: 100%

Datenanalyse: 90%

Schriftliche Umsetzung: 90%

Beatrix Vonlanthen, Ximing Zhang, Helge Bruelheide. 2010. Clonal structure and genetic diversity of three desert phreatophytes. *American Journal of Botany* 97:234–242.

Datenerhebung:

Plots einrichten und Pflanzen messen: 95%

Sammeln der Blätter: 95%

Genetische Analyse: 95%

Datenanalyse: 90%

Schriftliche Umsetzung: 90%

Halle (Saale), 17. Februar 2010

Eigenständigkeitserklärung

Hiermit erkläre ich, dass diese Arbeit zu keinem früheren Zeitpunkt der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg oder einer anderen wissenschaftlichen Einrichtung zur Promotion vorgelegt wurde.

Darüber hinaus erkläre ich, dass ich die vorliegende Arbeit eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als in diesem Text angegebenen Quellen oder Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden als solche von mir kenntlich gemacht.

Im Übrigen erkläre ich, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), 17. Februar 2010